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Abstract

Mesozooplankton can be considered the most important secondary producers in marine food webs because they hold an intermediate position between the phytoplankton assemblage and the upper trophic levels. They also are a robust indicator of climatic and hydrological conditions. We conducted an analysis of the interannual variability of the spring mesozooplankton assemblage, as sampled by the PELGAS fisheries survey in the southern part of the Bay of Biscay (Northeast Atlantic Ocean) between 2003 and 2013. We examined hydrology and trophic drivers to explain the variability. Our results revealed that the subsurface temperature, the subsurface salinity, the biomasses of subsurface pico-, nano-, and microphytoplankton, and the copepod assemblage exhibited a recurrent spatial pattern that was driven mainly by freshwater and nutrient inputs from the main rivers. The mesozooplankton assemblage was dominated by copepods (82%), composed of coastal, neritic, and oceanic copepod genera that paralleled the various hydrological fronts converging in the southern Bay of Biscay. The copepod community displayed high temporal-variability; there were three periods of abundant adult copepods throughout the southern Bay of Biscay. The copepod community was structured primarily around the drive for resource control, especially by the microphytoplankton biomass (24.3% of the total variability), and to a lesser extent by hydrological features (13.7% of the total variability).

Introduction

Mesozooplankton (200–2,000 µm) play a pivotal role in marine ecosystems by transferring energy from primary producers to the upper trophic levels. They are very sensitive to hydroclimatic features, so climate-mediated changes in zooplankton abundance and composition may affect upper trophic levels and fisheries (Beaugrand, 2003). Zooplankton monitoring therefore represents a powerful tool to detect, understand, and anticipate how global changes induce modifications in pelagic ecosystems (Beaugrand et al., 2003; Beaugrand, 2004; Perry et al., 2004; Richardson, 2008; Hinder et al., 2014). Although extensive and long-term zooplankton surveys have been undertaken (ICES Working Group on Zooplankton Ecology Zooplankton Status Report: http://wgze.net/zooplankton-status-report; O'Brien et al., 2013), they still are in relatively short supply compared to fish time-series from commercial catches (Batchelder et al., 2012).

In this study, we investigated the assemblage structure of mesozooplankton (at the level of the species, genus, or family) in the Bay of Biscay, an important Northeast Atlantic fisheries area and a relatively stable ecosystem that primarily is structured around bottom-up forces (e.g., Lassalle et al., 2014). Our investigation covers a large spatio-temporal scale: from the Spanish coast at 46°N to the French coast at 3°35'W, from the spring of 2003 through the spring of 2013. Previous mesozooplankton studies in the Bay of Biscay have been conducted in the spring as well because it is the key period for plankton blooms and the reproductive period for anchovies and sardines (Huret et al., this issue). Although some of these studies considered large spatial and/or temporal scales, they had more limited scopes; some relied on the LOPC (Laser Optical Plankton Counter) technique and were limited to size-structure analyses (Sourisseau and Carlotti, 2006), while others used the CPR (Continuous Plankton Recorder) method and were restricted to the "ultra subsurface" (0–7 m) (Beaugrand et al. 2000a, 2000b). Studies with high taxonomic resolution focused on a single field survey

(Albaina and Irigoien, 2007; Irigoien et al., 2011) or were conducted on limited spatial scales despite their large temporal scales (Albaina and Irigoien, 2007; Stenseth et al., 2006; Valdés and Moral, 1998; Valdés et al., 2007; Gonzalez-Gil et al., 2015; Cabal et al., 2008; Bode et al., 2012 and 2013). Other studies focused on one or two species on a high spatio-temporal scale, such as Bonnet et al. (2005) on *Calanus helgolandicus* and Lindley and Daykin (2005) on *Temora stylifera* and *Centropages chierchiae*. Finally, only two studies were quite similar to ours, conducting large spatio-temporal surveys of the Bay of Biscay, albeit with a lower taxonomic resolution (groups were defined by image analysis) (Irigoien et al. 2009; Vandromme et al. 2014). Irigoien et al. (2009) identified permanent features in the spatial distribution of spring zooplankton between 1998 and 2006, with a higher abundance of large organisms over the shelf break and offshore areas. Vandromme et al. (2014) used a combination of LOPC data and WP2 sampling processed with the Zooscan and employed it over the same network of stations used in our study between 2005 and 2012. They found a negative relationship between the zooplankton biomass and normalized biomass size spectra slopes, thus suggesting a clear association between zooplankton size distribution, productivity, and transfer efficiency.

The novelty of the present study lies in the temporal and spatial coverage of the mesozooplankton community structure, with a focus on the main mesozooplankton groups and the key genera or species of copepods. These aspects have not been investigated previously in the Bay of Biscay. From a large data set of annual spring PELGAS ('PELagique GAScogne') surveys (Doray et al., this issue), our study aimed to elucidate which drivers control the spring mesozooplankton community and whether any spatial and/or temporal changes in this community occurred between 2003 and 2013. We had three objectives: 1) to summarize the habitat variabilities in terms of temperature, salinity, and chlorophyll *a* data; 2) to analyze the temporal patterns of the mesozooplankton and copepod spring communities

over the studied decade; and 3) to elucidate which local hydrological and trophic variables may account for the variability of mesozooplankton communities over space and time.

Materials and Methods

Sampling area

The Bay of Biscay is characterized by a morphostructural dissymmetry opposing the large northeastern edge of a narrow meridional shelf (Fig. 1). Our study focused on the southern part of the Armorican shelves, which are largely under the influence of the Gironde and the Adour river plumes.

Data collection

Samples were collected during the annual PELGAS surveys (Doray et al., this volume-b), which have been conducted every spring since 2000 over the whole continental shelf of the Bay of Biscay. In this study, we selected a subset of data with a homogenous mesozooplankton sampling protocol, i.e. data related to the southern part of the Bay of Biscay from 2000–2013 (Fig. 1). PELGAS surveys routinely collect several parameters for all system components, including hydrobiology, pelagic fish abundance and distribution, marine mammals, and seabird observations. We used data that had been collected at night from a total of 118 visited stations (Table 1). Each station was separated from the next by approximately 44 km in the along-shore direction and 10–25 km in the cross-shelf direction. PELGAS surveys were not carried out on exactly the same calendar dates over the series (especially at the beginning of the studied decade), although they always did take place during springtime over the course of about 15 days (Table 1).

Hydrology and phytoplankton biomass

Our station network for hydrology data consisted of 26 to 34 stations per year (Table 1, Fig. 1). At each station, the salinity and temperature were measured over the water column with a CTD (Seabird 19+v2) probe. Two water column integrated indices were calculated: the equivalent freshwater depth (m) and the deficit of potential energy or DEP ($kg.m^{-1}.s^{-2}$). As detailed in Huret et al. (2013), the equivalent freshwater depth represents the local depth of freshwater in the absence of mixing. As such, equivalent freshwater depth is a good indicator of the plume influence in a given year and location. The DEP is an index of stratification that is calculated from the vertical distribution of density values.

Chlorophyll *a*-based biomass (chl*a*, see Introduction of Boyer et al. 2009) was used as a proxy of autotrophic biomass (mostly phytoplankton). Water samples (200–500 mL) were collected with Niskin bottles at the subsurface. Once on board, the samples were passed through successive filtrations on three membranes with different porosities (Whatman GF/F with pore sizes of 0.7, 3, and 20 µm and a diameter of 25 mm) to fractionate the samples into three size classes: pico- (< 3 µm), nano- (3–20 µm), and microphytoplankton (>20 µm) including large taxa such as diatoms. Each sample was stored at -20°C for subsequent analysis. Laboratory extraction was performed with a Turner TD-700 fluorometer according to the protocols of Aminot and Kérouel (2005) and of Lorenzen (1967). The chl*a*-based biomass was expressed in $\mu g.L^{-1}$. An index of water-column integrated chl*a* biomass ($\mu g.m^{-2}$) was calculated using the fluorescence data from the vertical profiles (WETStar fluorometer, WET Labs, USA) and corrected by chl*a*-based biomass data.

Mesozooplankton

The mesozooplankton samples were collected by vertical trawls using WP2 nets (0.25 m^2 opening, 200 µm mesh size), from a depth of 100 m (or the bottom depth for inshore stations). For each annual survey, ten or 12 stations were selected from four transects; this

sampling included coastal, continental shelf, and slope stations (Fig. 1B). After collection, the net samples were preserved in 4% formaldehyde. The organisms were identified by species, genus, family, or more general categories/forms (Table 2; identification protocol of Rose (1933) and Tregoubof and Rose (1957)), and were enumerated using a Leica M3Z stereo microscope (65× to 100× magnification). The abundance was expressed in individuals m^{-3} ($ind.m^{-3}$).

Data analysis

Ordinary kriging

To describe the spatio-temporal patterns of the different studied compartments, an ordinary kriging procedure (ArcMap 10.2 using the Geostatistical Analyst toolbox) was applied to the data for the subsurface temperature, salinity, and size-fractionated chl*a*-based biomass. For each parameter, annual data were compiled from 2003–2013 and interpolated to provide an overview of the spring spatial patterns over the time series. For each parameter, annual kriged maps are presented in Supplemental Figures 1–4. To identify significant temporal variations (i.e., across years) for each parameter (temperature, salinity, and pico-, nano-, and microphytoplankton biomasses), a non-parametric multiple pairwise comparison (Statistica®, Tulsa, OK, USA) of mean ranks was applied to all years from 2003–2013; p-values < 0.05 were considered significant. All other statistical analyses were performed with the R-Cran project free software (R Core Team, 2014). Furthermore, to consider these five water mass variables together throughout the decade, confidence ellipses (surrounding the barycentre of coordinate stations) were determined on a station factor map produced by a principal component analysis (PCA, 'FactoMineR' package (Husson et al., 2012)).

Mesozooplankton community analysis

The time-variability of the mesozooplankton community was analyzed by considering the mean yearly relative abundance of classical characteristic groups of mesozooplankton (meroplankton, gelatinous plankton, copepods, and other holoplankton). The abundance and taxonomic composition of the dominant group (copepods) was analyzed according to the variability in space and over time. As done in previous studies, a temporal analysis was conducted via a multiple comparison of the mean ranks for all years based on copepod abundance. The spatio-temporal variation in the composition of the adult copepod community was also described with a non-metric multi-dimensional scaling (NMDS), performed using Primer 6 (Plymouth Routines In Multivariate Ecological Research) software. A matrix of sampling points (n=118 samples; see Table 1) was created for the abundance data of copepods species or genera (n= 23). In this matrix, the columns corresponded to the copepod taxa abundances, and the lines to the sampling points. The data were transformed with log x + 1 before the Bray-Curtis metric was applied to estimate the similarity between stations. The similarity matrix was then ordinated by NMDS. A SIMPER (SIMilarity PERcentage) analysis was performed to identify the genera or species contributing most to similarity (or dissimilarity) within (or between) three groups of sampling years defined from the time series analysis.

Finally, to quantify the relative influences of the food-resource (chl*a*) and abiotic parameters (temperature, salinity) that underlie the patterns observed in the copepod community structure, a variation partitioning analysis (using “vegan” and “ade4” packages in the R-Cran project free software) was applied (Volis et al., 2011). .We considered biotic variables (subsurface and integrated water column values of chl*a* for pico-, nano-, and microphytoplankton fractions) and abiotic variables (subsurface values of temperature and salinity, and three water column integrated indices; the DEP, the equivalent fresh water, and the mixed-layer depth). First the variables to include in the analysis (ie variables that

191 influenced the most the copepod distribution) were selected through forward selection (pack
192 for package). After the forward selection, two matrices (H matrix for abiotic parameter and C
193 matrix for biotic parameters) were buit using only the most influential variables. Finally,
194 using these two matrices, the variation partitioning was performed aiming at identifying the
195 part of technology copepod distribution variation explained by each variable. By this way, our
196 aim is to evaluate if copepod distribution is better explained by hydrological parameters than
197 by food resources. Indeed, in ecological matrices each variable has a pure variation and a part
198 of variation linked to the other variables. This covariation between variables can be evaluated
199 through the variation partitioning.

200 Variation partitioning evaluates diverse components of variation: 1) the pure effect of
201 each individual matrix, 2) the redundancy of the two explicative matrices, and 3) the residual
202 effects that are unexplained by the chosen variables. Redundancy analysis (RDA), partial
203 redundancy analysis (pRDA), and Monte Carlo permutation (999 permutations) tests were
204 used to test the significance of the canonical axis.

205

206 **Results**

207 **Subsurface salinity and temperature**

208 The absence of a spatial pattern in the decadal average map (Fig. 2) means that no
209 spring-time mesoscale process had a strong recurrent impact on the surface temperature in the
210 southern Bay of Biscay. However, a coast-to-offshore positive gradient can be observed in
211 certain years (e.g., in 2006, 2010, and 2013; see Fig. S1), revealing the intermittent
212 occurrence of an upwelling process along the southern French coast. The Gironde plume
213 brought characteristically lower temperatures in 2005 and 2006, and a latitudinal gradient also
214 appeared in some years (e.g., in 2010, 2012, and 2013), albeit without any consistent pattern
215 across years. These anomalies may be explained by the changing meteorological conditions

(e.g., wind, irradiance) during the 15-day survey conduction. During the studied decade (2003–2013), the subsurface temperature varied from 10.8°C to 19.8°C, highlighting the large interannual variability in the surface warming and the stratification process during this rapidly changing season. The non-parametric multiple pairwise comparison allowed for a separation of the years into three groups: 2003 was the warmest, 2007 and 2011 had intermediate temperatures, and the remaining years were the coldest (see Fig. S1).

The spatial pattern of salinity was driven by the plumes of the Gironde and the Adour rivers (Fig.2). Despite some interannual variability in the extension of the plumes (maxima in 2007, 2009, and 2013; minima in 2011 and 2012), the interannual variability of the subsurface salinity was not significantly different between years (multiple pairwise comparison, p=0.05) (see Fig. S2). Subsurface salinities varied from 26.07 psu to 36.4 psu (see Fig. S2).

Chlorophyll *a*-based biomasses

The average picture of the chl*a* biomasses (Fig.2) revealed a homogeneous concentration over the shelf, with lower values off-shelf, for the two smallest size classes (< 3 µm and 3–20 µm). For the largest size class (> 20 µm), the highest values were found over a coastal strip only. Generally, biomasses were higher in the area influenced by the Gironde plume as compared to the most other southern locations.

Substantial differences appeared when analyzing the annual maps of chl*a* biomasses (see Figs. S3, S4, and S5). For the smallest size class (Fig. S3), significant interannual differences allowed the years to be divided into five groups: 2003 exhibited the lowest values (0.20 ± 0.38 µg.L^{-1}) and 2009–2010 exhibited the highest (0.66 ± 0.41 µg.L^{-1}). For the 3–20 µm size class, the interannual variability revealed four groups of years, with mean biomasses ranging from 0.17 ± 0.26 µg.L^{-1} to 0.45 ± 0.37 µg.L^{-1}. For the > 20 µm size class, no significant interannual differences were found between years.

The non-parametric multiple pairwise comparison of the five environmental variables (subsurface salinity and temperature, subsurface pico-, nano-, and microphytoplankton biomasses) over the decade could not extract significant differences between years.

The average contribution of each size class over the studied decade (Fig. 3) was 44% for picophytoplankton (< 3 µm), 23% for nanophytoplankton (3–20 µm), and 33% for microphytoplankton (> 20 µm) (Fig. 3). The relative contributions varied from 23% (2003) to 67% (2009) for the picophytoplankton, from 19% (2008) to 42% (2003) for the nanophytoplankton, and from 10% (2007) to 42% (2008) for the microphytoplankton (including larger taxa such as diatoms).

Mesozooplankton

Total abundance and the contribution of the main groups

The mean spring abundance of mesozooplanktonic organisms over the study period varied from 1,321 ± 391 ind.m^{-3} (2008) to 4,986 ± 355 ind.m^{-3} (2005) (Fig. 4A). Between 2003 and 2006, abundances were higher (4,454, 3,233, 4,985, and 4,191 ind.m^{-3} for each year, respectively) than the mean decadal value (2,995 ± 1,195 ind.m^{-3}), while the mean abundances were lower than the mean decadal value between 2007 and 2013, with the exceptions of 2010 and 2012 (with 3,349 and 3,061 ind.m^{-3}, respectively). The spring abundance of mesozooplanktonic organisms revealed three temporal phases: from 2003–2006 (higher than the mean decadal value), from 2007–2009 (lower than the mean decadal value), and from 2010–2013 (close to the mean decadal value, except 2011, which was below the mean decadal value). The lowest contribution of copepods was registered in 2006 (Fig. 4B). The gelatinous organisms encountered in 2006 were mainly cnidaria and siphonophora as well as major meroplankton organisms (Bivalvia larvae and Cirripedia). On average, more than 80% of the spring mesozooplankton community comprised copepods, 8% meroplankton,

8% gelatinous plankton, and 4% other holoplanktonic organisms (Fig. 4B). Depending on the year, the relative abundance of copepods varied from 42% (2006) to 87% (both 2011 and 2009), those of meroplankton from 1% (2009) to 22% (2006), those of gelatinous organisms from 3% (2011) to 24% (2006), and those of the other holoplanktonic organisms from 2% (2009) to 11% (2010). Meroplanktonic organisms were found mostly along the coast, gelatinous organisms were scattered, and the other holoplanktonic organisms were widespread among the sampling stations (data not shown). Based on these observations, the following results focus on the main group: the copepods.

Copepod patterns

Over the 11 springtime surveys, copepodites (16% of the total copepod abundance) and nauplii (1.4%) of miscellaneous copepod species were recorded.

Twenty-five adult copepod taxa (at the family, genus, or species level) were recorded; orders included Harpacticoida, Poecilostomatoida, Cyclopoida, and Calanoida, as well as copepodites and copepod nauplii (Table 2). The spatial distribution of these 25 taxa is shown in Fig. 5. Irrespective of the year, the copepod abundance followed a longitudinal gradient: coastal waters had the highest values (2,848 ± 2,507 ind.m^{-3}), shelf waters had intermediate values (2,335 ± 3,787 ind.m^{-3}), and the continental slope had the lowest values (1,304 ± 1,546 ind.m^{-3}), except for in 2010 (1,467 ind.m^{-3}). One outlier of copepod abundance (21,127 ind.m^{-3}) was recorded in 2005 at a single station on the northern coast. From a temporal viewpoint and based on the annual abundances at each station, only 2009 could be distinguished from the other years (Fig. S6). Moreover, eight of these 25 adult taxa (*Oithona* spp., *Acartia* spp., *Temora longicornis*, *Oncaea* spp., Calanidae, *Calanus helgolandicus*, Paracalanidae, and *Euterpina acutifrons*) alone represented more than 1.5% of the copepod abundance (Table 2). Their spring spatial abundances in the Bay of Biscay are plotted in Fig. 5. *Oithona* spp. was

present preferentially from the continental shelf to the slope; *Acartia* spp., *Oncaea* spp., and *Temora longicornis* were most common at the coastal stations; and the genera *Acartia*, *Oithona*, *Temora*, and *Oncaea* were the most abundant within the copepod community (66% between 2003 and 2013; see details in Table 2).

Spatio-temporal variations of adult copepods

The NMDS ordination of the adult copepod abundance data (stress value of 0.23, indicating a good ordination) discriminated the temporal variations better than the spatial variations. The plots of the three time-sampling groups previously discerned by the temporal analysis of abundance (see above) showed that the adult copepod community in the 2003–2006 period was clearly distinct from the 2007–2009 period (Fig. 6). The last period (2010–2013) was intermediate, suggesting a return toward the initial situation (2003–2006) (Fig. 6). The SIMPER analysis (Tables 3 and 4) confirmed this trend, with the same four taxa (*Oithona* spp., *Oncaea* spp., *Acartia* spp., and *Temora longicornis*) explaining > 65% of the similarity within the 2003–2006 and 2010–2013 periods, whereas in 2007–2009, Paracalanidae (15% contribution for this group) replaced *Temora longicornis* (7.8%) in these top-four taxa. Overall, the within-group similarity was higher for the 2003–2006 (67.0%) and the 2010–2013 (59.9%) periods than for the 2007–2009 period (52.3%). The level of dissimilarity between the groups was highest between 2003–2006 and 2007–2009 (52.0%), and lowest between 2003–2006 and 2010–2013 (45.5%).

Hydrological versus trophic control on the spring copepod community

The forward selection identified four significant variables that significantly drive the copepod distribution:: microphytoplankton (> 20 µm) biomass at the subsurface, equivalent freshwater height, DEP, and subsurface temperature (Table 5). The variation partitioning highlighted that

316 49.2% of the variation was explained by both matrices H and C with the most variance
317 (24.3%) attributable to chl*a*-based microphytoplankton biomass and the next-most variance
318 (13.7%) attributable to hydrological parameters (Figure 7, Supplemental table 1). The part of
319 the variation due by the interaction between the 2 matrices (ie. between hydrological
320 parameters and subsurface microphytoplankton) was 11.2 %. Partial RDA (without
321 interaction between variables) concurred that the distribution of the copepod community was
322 influenced significantly by the microphytoplankton subsurface biomass, equivalent freshwater
323 height, and DEP (Supplemental table 1). The contribution of the subsurface temperature was
324 not significant in the variation partitioning analysis.
325
326 **Discussion**
327 *Hydrological and biological features of the mesozooplankton habitat*
328 Throughout the 2003–2013 decade, surface water warming occurred continually in the
329 Bay of Biscay, from the south to the north and from the coast to the open sea. The water mass
330 circulation in the Bay of Biscay is drived by a combination of large-scale and local forces (Le
331 Boyer et al., 2013); the warming of water masses in spring is modulated by slope currents,
332 shelf residual circulation, and the Iberian Poleward Current from Galicia to the Bay of Biscay
333 on a larger scale, and wind and irradiance conditions on a local scale (Koutsikopoulos and Le
334 Cann, 1996; Puillat et al., 2004; Rubio et al., 2013). From our study, the spatial pattern of
335 variability in the south of the Bay appeared to be independent of the interannual variability of
336 the hydrobiological parameters (e.g., the subsurface temperature). From 2003–2013, the
337 survey observed a mix of warm (in 2003, 2007, and 2011), intermediate, and cold years. This
338 variation in temperature regimes is consistent with results previously reported in this area
339 (e.g., Huret et al., 2013).

The size structure of the phytoplankton community contribute to the structure of pelagic food webs, so our study considered three size classes (pico-, nano-, and microphytoplankton). Indeed, mesozooplanktonic organisms are major grazers of nano- and microphytoplankton (Marquis et al., 2007). Calvo-Díaz et al. (2008) recorded the monthly contributions (in Iberian Peninsula waters from 2003–2006) of each size fraction of phytoplankton, and showed that the spring (i.e., April) contribution of picophytoplankton was about 20%, corresponding to the minimum recorded over an annual cycle. By contrast, the contributions of nanophytoplankton and microphytoplankton were around 50% and 30%, respectively. In our study, the mean balance between pico- and nanophytoplankton varied widely, most likely because our spatial coverage involved more oceanic features beyond 200 m of bathymetry. It is important to note that the survey dates were not exactly the same throughout the decade and hence added further variability. For example, compared to the later surveys, the 2003 survey captured significantly different hydrology, plankton concentration, and size structure.

To summarize, taking into account both the hydrological and the phytoplanktonic components of the mesozooplankton habitat, the Bay of Biscay appeared to support a consistent spatial structure across years, due mainly to the continental supply of freshwater and nutrients, although a degree of interannual variability occurred in the range of the observed values.

The spring mesozooplankton community

Among the prominent groups of the mesozooplankton community, meroplanktonic organisms were restricted to the coastal area in our study, as previously reported by Ayata et al. (2011). By contrast, gelatinous organisms were dispersed throughout the Bay of Biscay. No clear spatio-temporal development of gelatinous plankton was observed, although this

group (mainly cnidaria and siphonophora) was particularly abundant in 2006. Their proliferation may be linked to climate change, eutrophication, and/or habitat modifications (e.g., Lo et al., 2008). However, the WP2 net used in the study probably was not the most suitable device for monitoring gelatinous plankton.

In the present study, copepods represented the most dominant holoplankton taxa of the mesozooplankton community, as highlighted by various studies in the same area (e.g., Albaina and Irigoien, 2007; Irigoien et al., 2009; Valdés et al., 2007; Villate et al., 2014, 1997). Previous observations of the spatial distribution of the spring size structure of mesozooplankton have reported a negative coastal-to-offshore gradient (e.g., Vandromme et al., 2014), as also observed in the present study for copepod taxa. Here, the sample represented three dominant genera and one dominant species (> 10% of the copepod abundance) *Acartia* spp., *Oncaea* spp., *Oithona* spp., and *Temora longicornis*—consistent with previous investigations (e.g., Albaina and Irigoien, 2007; Irigoien et al., 2011). According to the literature regarding the copepod community in the Bay of Biscay, *Temora longicornis* and *Pseudocalanus elongatus* are dominant neritic species that occur preferentially on the continental shelf, whereas *Acartia* spp. dominates stations under coastal influence, and *Calanus helgolandicus* and *Eucalanidae* dominate under oceanic influence. More specifically, *C. helgolandicus* is found in the southern part of the Bay of Biscay and in the surface layers in the north during the spring (Bonnet et al. 2005).

Temporal trends in the mesozooplankton and copepod communities

Climatic indicators increasingly are being explored to identify major changes affecting plankton (e.g.,Wouters et al., 2015) and fish communities (Guénette and Gascuel, 2012). On a similar spatial scale as in the present study, previous research detected oscillations mainly in the vicinity of the Gironde river plume, which represents a major source of nutrient inputs

into the Bay of Biscay for both plankton (David et al., 2005) and fish (Pasquaud et al., 2012). Overall temperatures in the Gironde estuary increased significantly around 1987 and again around 2001 (Chaalali et al., 2013).

During the decade studied here, the year 2005 brought additional abrupt changes in mesozooplankton abundance and diversity in the Gironde estuary—a relatively closed system—and in the Arcachon basin (Chaalali, personal communication). It is possible that this abrupt change also occurred in the Bay of Biscay, albeit with a time lag that is linked to the Bay's resilience properties. As described above, three temporal phases of adult copepod dominance were observed in the present study: 2003–2006, 2007–2009, and 2010–2013, with abundance values that were higher, lower, and higher, respectively, than the spring mean decadal abundance (including 2003–2013). This temporal oscillation also correlated with taxonomic composition changes (see Tables 3 and 4). However, we observed that 2010–2013 witnessed a reversal to the initial situation (2003–2006) with regard to both the abundance and taxonomic composition of the adult copepod community. The only anomaly detected was the high percentage of gelatinous organisms in the spring of 2006, which correlated with the low percentage of copepods observed that year. These gelatinous organisms comprised cnidaria and siphonophora primarily. It is reasonable to consider predation as a possible cause, as this would result in top-down control on copepods and spatial occupation of a very close ecological niche between carnivorous copepods, cnidarian, and siphonophora organisms.

Factors controlling the spring copepod community

The structure and functioning of planktonic food webs depend largely on the hydrodynamics of the water column. Our study found that four variables of the pelagic habitat (subsurface temperature, stratification with the deficit of potential energy, equivalent

freshwater height, and subsurface microphytoplankton biomass) accounted for more than 49% of the variability in the main mesozooplanktonic community. Zarauz et al. (2008) suggested that the mesozooplankton biomass is driven mainly by hydrogeographic data (e.g., latitude, longitude, surface temperature, salinity, stratification index, and water depth), and to a lesser extent by potential trophic resources (e.g., the nano-microplankton biomass). By contrast, the present study showed that for the same study site (same scale and season), the spring copepod community (described taxonomically) was influenced more by trophic variables (e.g., microphytoplankton biomass; 24.3% of the total variability) than by hydrographic variables (13.7% of the total variability) over the 11-year time period. These differences can be explained by the fact that Zarauz et al. (2008) studied mesozooplankton at the biomass level only, whereas our study took into account the abundance of taxa (species, gender, or family) to describe the community. These methods do not provide the same ecological information. Moreover, the temporal dataset was not exactly the same: Zarauz et al. (2008) studied three spring seasons (2004–2006) while the present study included eleven spring seasons (2003–2013). Finally, the two studies used different trophic variables for the statistical analysis: nano-microplankton biomass in Zarauz et al. (2008) vs. phytoplankton biomasses by size classes in the present study.

At the scale and with the spring timing of our study, the trophic link (i.e., the subsurface microphytoplankton biomass) appeared to be the major driver of the copepod community, while hydrographic variables appeared to play less important roles. There are two potential reasons for this: i) the trophic dimension probably represents a time integration of hydrological conditions (i.e., more integrated than the temperature and salinity variables in the present context), and ii) the planktonic food web probably has an ecological succession of physical and geographical parameters that control the initial phytoplanktonic blooms in late winter. Nutrients then become limited in spring, ultimately influencing the production and life

cycle of mesozooplankton, which thus are maintained by trophic control during the PELGAS spring surveys. However, copepods have other potential trophic sources, such as ciliates and heterotrophic flagellates, that can influence the mesozooplankton distribution but were not considered in our study.

According to the present observations, both the thermal stratification and equivalent freshwater height significantly affected the copepod community, whereas subsurface salinity did not. This probably is because thermal stratification and equivalent freshwater height are more integrated spatially and temporally. However, it is surprising the water column integrated chl*a* index did not have a prominent effect in the non-parametric multiple pairwise comparison of mean ranks. Thus, an approach using functional traits appears to be more efficient for understanding the springtime copepod community, as copepods are major predators of microphytoplankton (Marquis et al., 2007). Moreover, although fewer stations were sampled in our study than in Irigoien et al. (2011), we explained a greater percentage of the community's variability, probably because our data set spanned a longer period of time and therefore captured more variability. However, half of the variation in the copepod community over the studied decade remained unexplained. We concur with Irigoien et al. (2011) that other biological functional traits of the present community—including the effect of copepod density on feeding activities—merit consideration.

Concluding remarks

This study of annual springtime PELGAS survey data is the only analysis of the southern Bay of Biscay's mesozooplankton community between 2003 and 2013. We claim the following contributions:

- We demonstrated that the spatial structure found in the Bay of Biscay is attributable to continental outflow, although some interannual variability occurred in the range of the values observed.
- We generated interpolation maps that represent a valuable foundation for future studies in the Bay of Biscay.
- We identified three time-oscillation phases (in terms of both abundance and taxonomic composition) in the mesozooplankton community, with a major change recorded in 2006.
- We demonstrated, for the first time in this area, the influence of trophic variables (i.e., microphytoplankton biomass) from 2003–2013.

Acknowledgments

We thank the entire PELGAS team – researchers, technicians, students, captains and crews of R/V "Thalassa" – who have contributed to the collection of the PELGAS samples since 2003. We would like to express our thanks to two teams' laboratory, LIENSs and EMH and especially, M. Jacques, P. Petitgas, M. Doray, and P. Bourriau. We are grateful to Proof-reading and Dr. Sophie Domingues-Montanari for English corrections. We also grateful to Céline Lavergne for its statistical advices. The IUF (Institut Universitaire de France) is acknowledged for its support to PB as a Senior Member. This research was supported through a PhD grant for A. Dessier from the Conseil Régional de Poitou-Charentes and by the European project REPRODUCE (EraNet-Marifish, FP7). This work was supported by the "Plateau Microscopie" of the LIENSs laboratory.

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654

655 **List of Figures**

656 **Figure 1:** Map of the Bay of Biscay showing the location of the sampling stations of A) sub-
657 surface water environmental parameters (temperature, salinity, size-fractionated biomass of
658 chlorophyll *a*), and B) the mesozooplankton community. Isobaths100 m (dotted line), 200 m
659 (solid line) and 500 m (dashed line) are drawn.

660 **Figure 2:** Results of the annual (2003-2013) spatial interpolation of sub-surface temperature
661 (°C), salinity (psu), picophytoplankton (chl*a*< 3µm) biomass, nanophytoplankton (3 µm
662 <chl*a*< 20 µm), and microphytoplankton (chl*a*> 20µm) biomass ($\mu g.L^{-1}$) in the southern Bay
663 of Biscay.

664 **Figure 3:** Interannual variation of the mean relative biomass of surface size-fractionated
665 chlorophyll *a* between 2003 and 2013 in the southern Bay of Biscay; in black for the
666 picophytoplankton biomass (<3µm), in light grey for the nanophytoplankton biomass (3-
667 20µm) and in dark grey (>20µm) for the microphytoplankton biomass.

668 **Figure 4:** Interannual variation of the mesozooplankton abundance between 2003 and 2013:
669 A) mean decadal and annual abundances ($ind.m^{-3}$ ±SD) of the entire mesozooplankton
670 community and, B) stacked bar charts presenting the relative abundance of identified
671 organisms belonging to copepods, gelatinous, other holoplankton and meroplankton groups
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673 **Figure 5:** Annual spatial distribution of abundance ($ind.m^{-3}$) for major families, genera or
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677 **Figure 6:** Non-metric Multi-Dimensional Scaling (NMDS) on adult's copepods dataset in two
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679 keeping the ones having correlation coefficient >0.25). Spatial location of each station was

680 reported by their situation in the Bay of Biscay: coastal (C), continental shelf (Sh) and
681 continental slope (Sl). The choice of the three temporal groups was based on observations
682 following Fig. 4A.
683
684 Figure 7: Venn diagram based on a variation partitioning presenting the explained variability
685 of copepods community with two matrices, H and C. *H* was built with subsurface
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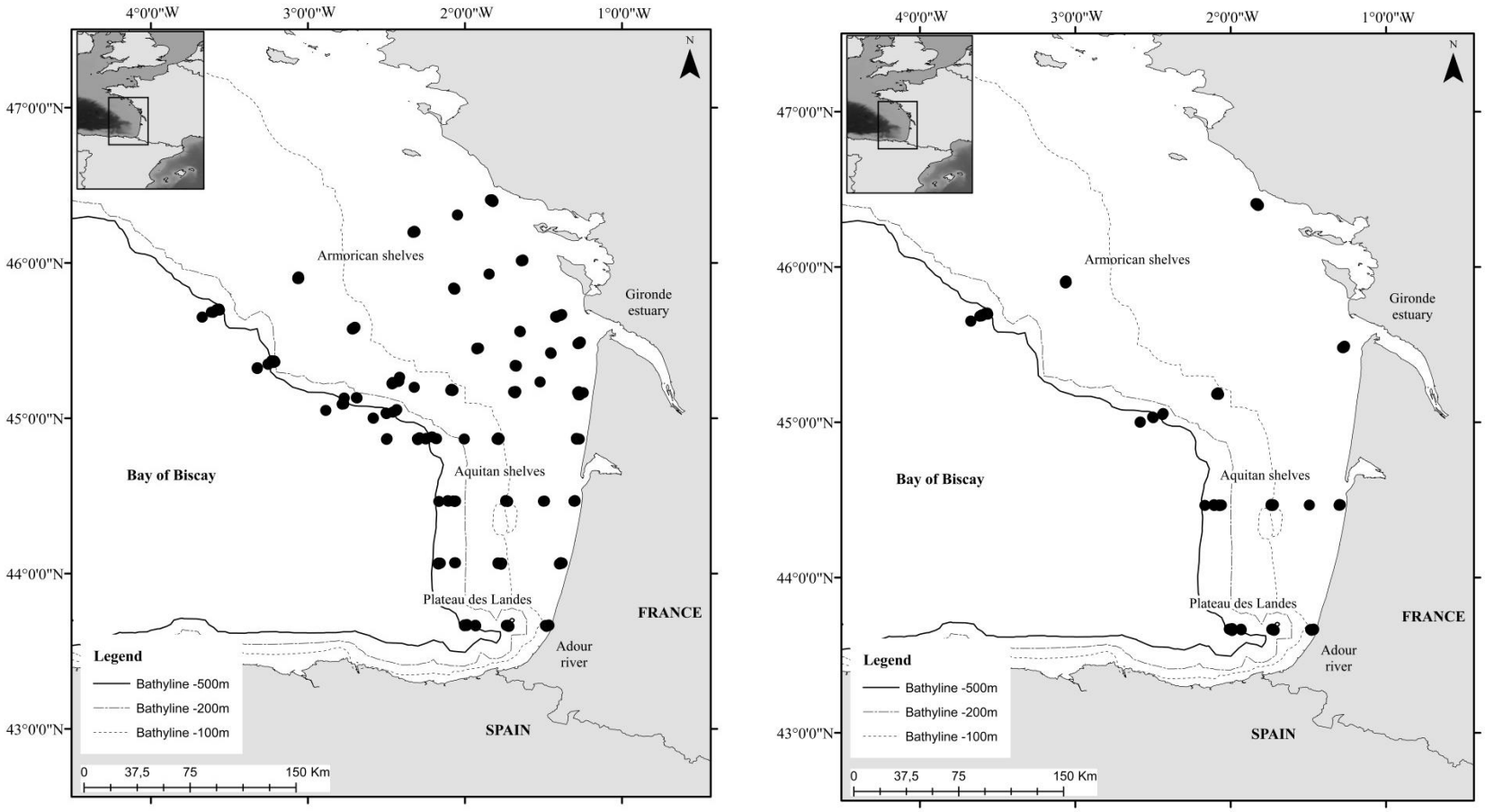
687 microphytoplankton (> 20 µm) biomass at the subsurface (the chl*a* based-biomass > 20 µm).
688 The external square represents the whole variation of the copepod community. Each circle
689 represents the explanatory tables and values are the part of the variation explained by each
690 explanatory table. The fraction "Int" is the intersection of the amount of variation explained
691 by both types of explanatory variables. Statistically significant pure fraction of variation of
692 copepod community is given in supplemental table 1.

693 **Figure 1**



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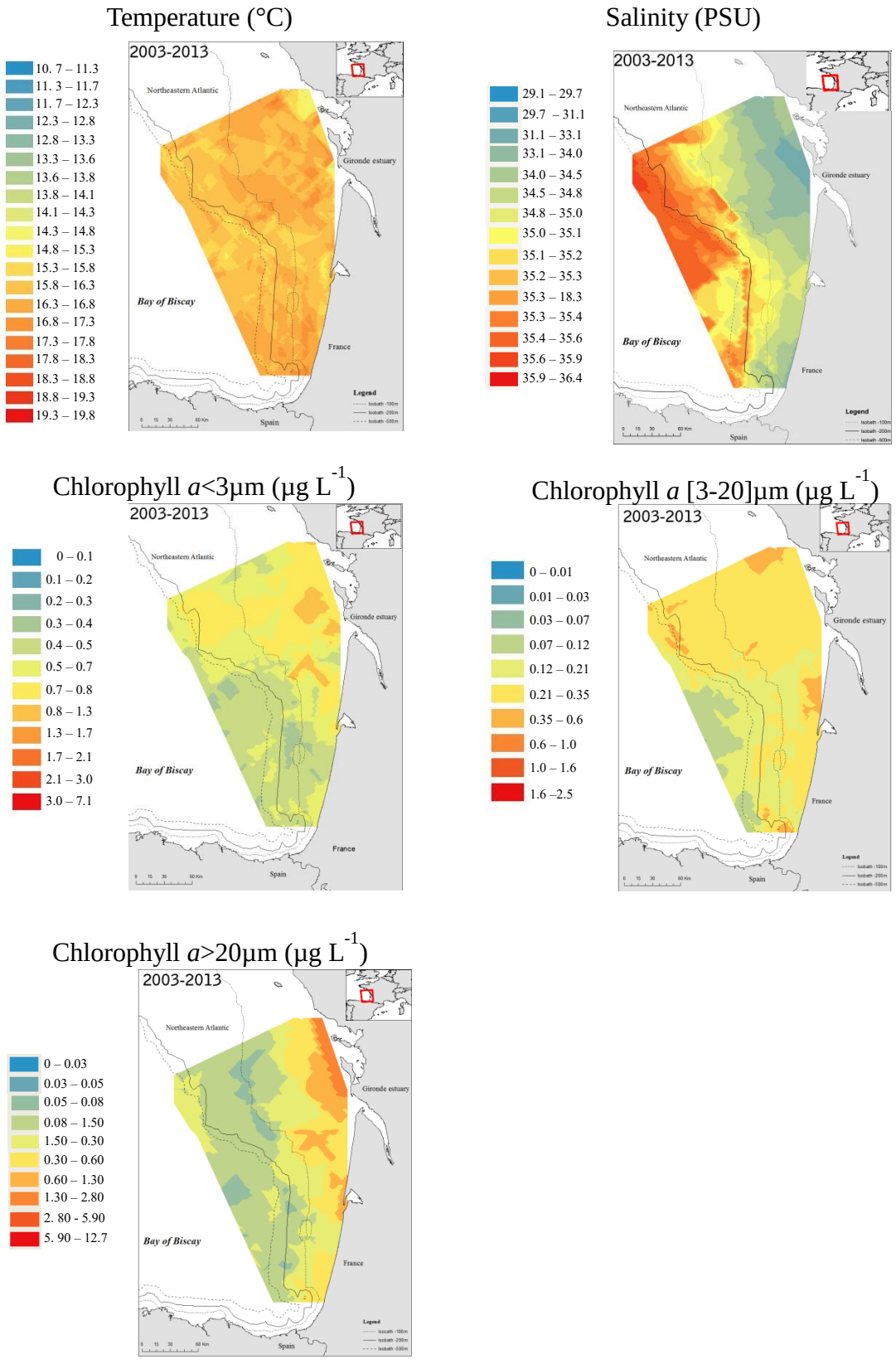
697 **Figure 2**



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700 **Figure 3**

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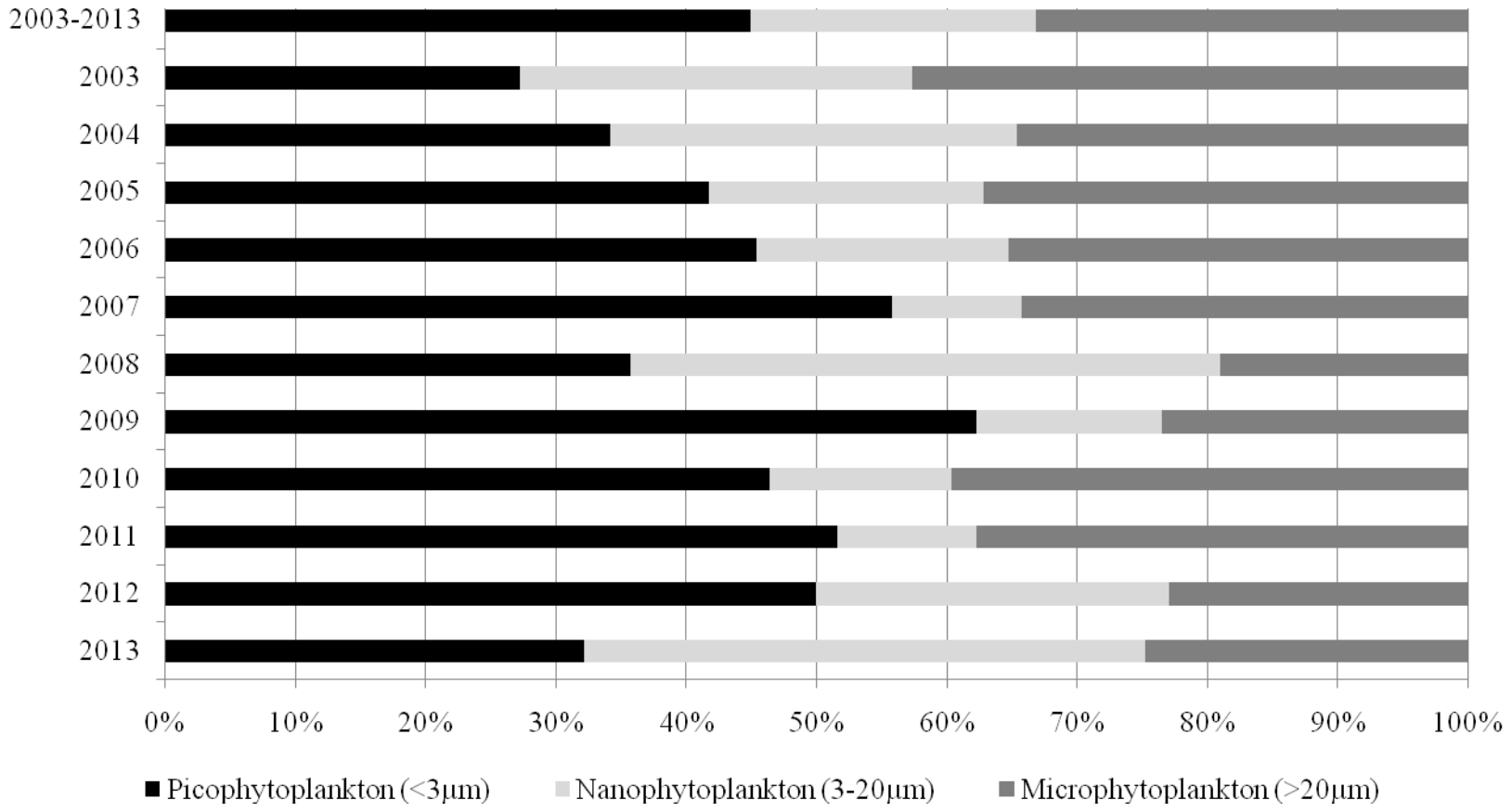

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703 **Figure 4**

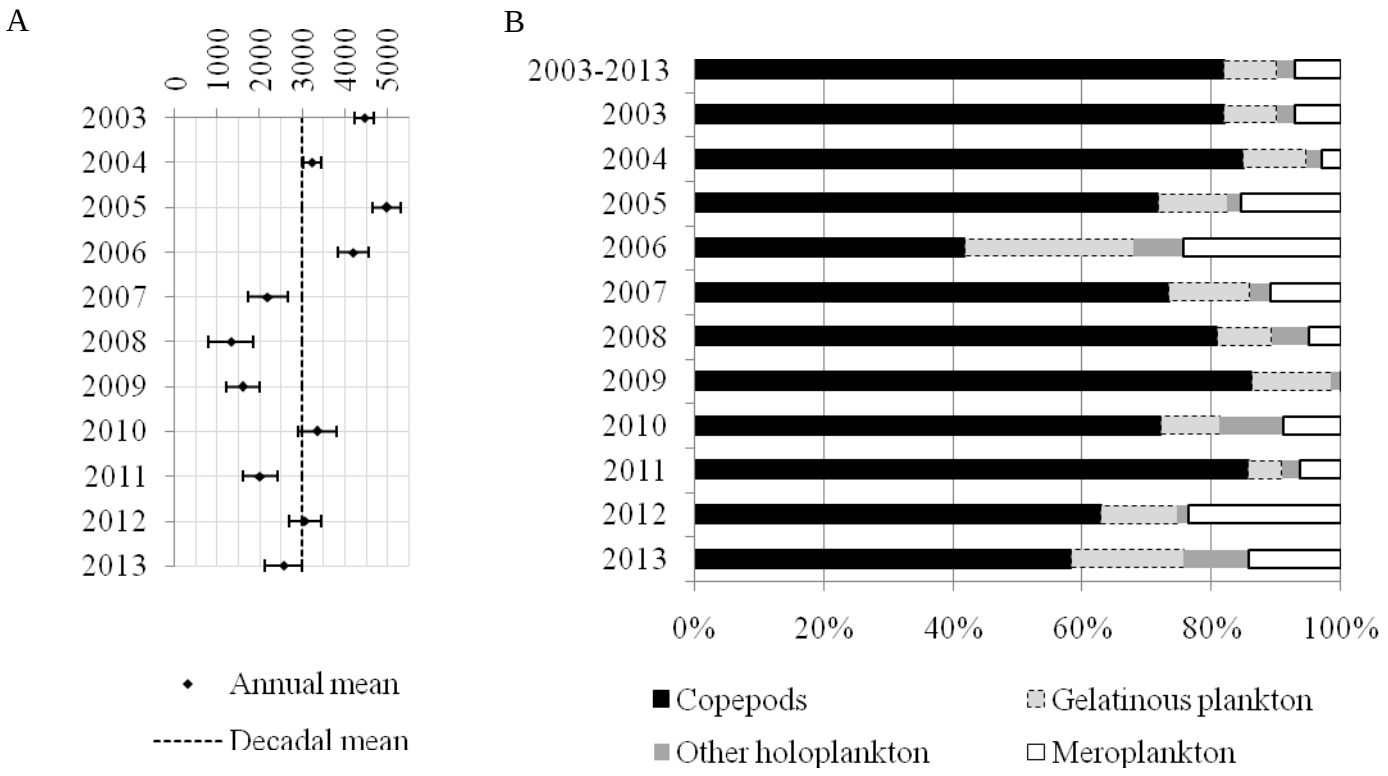

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Figure 5

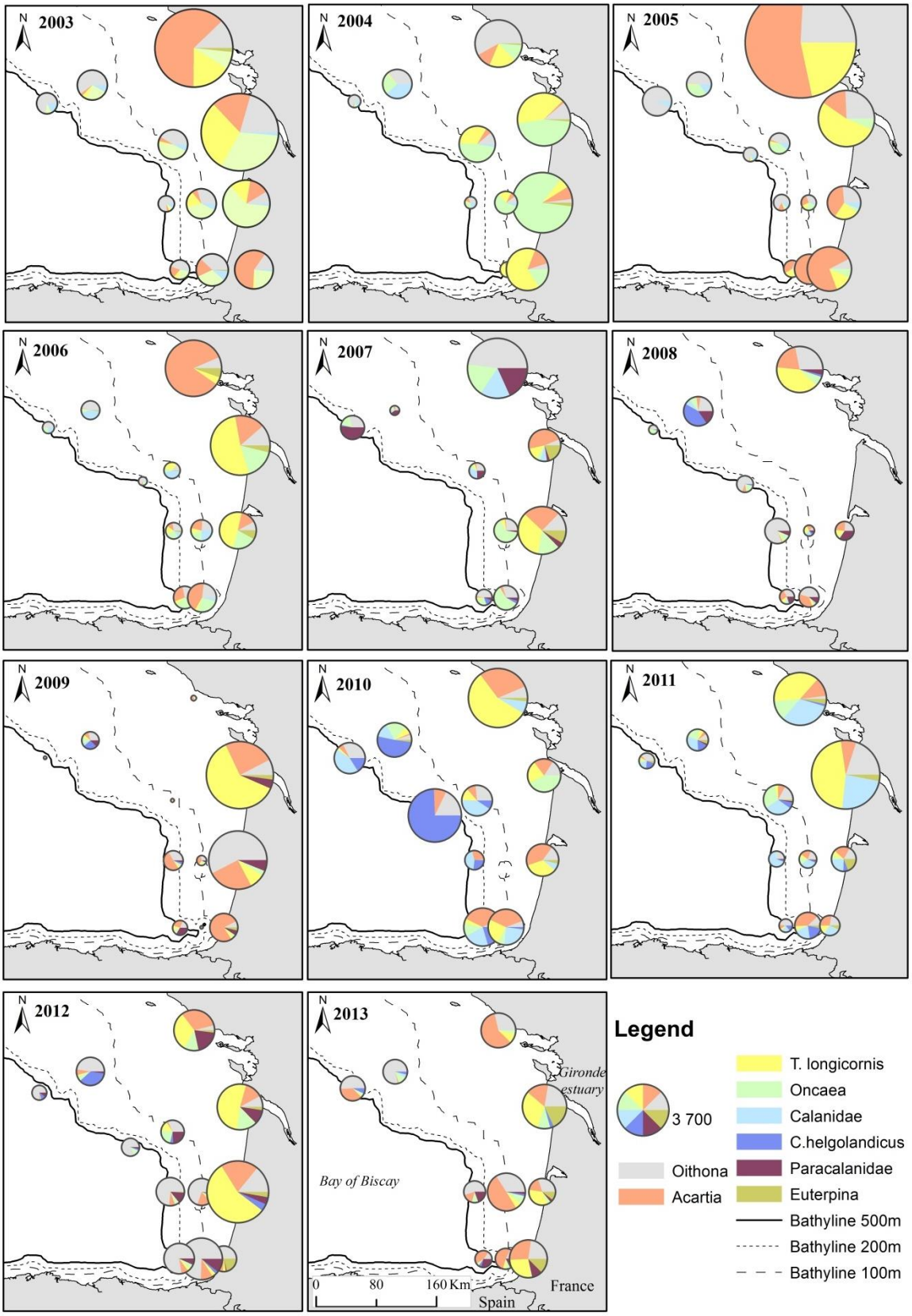
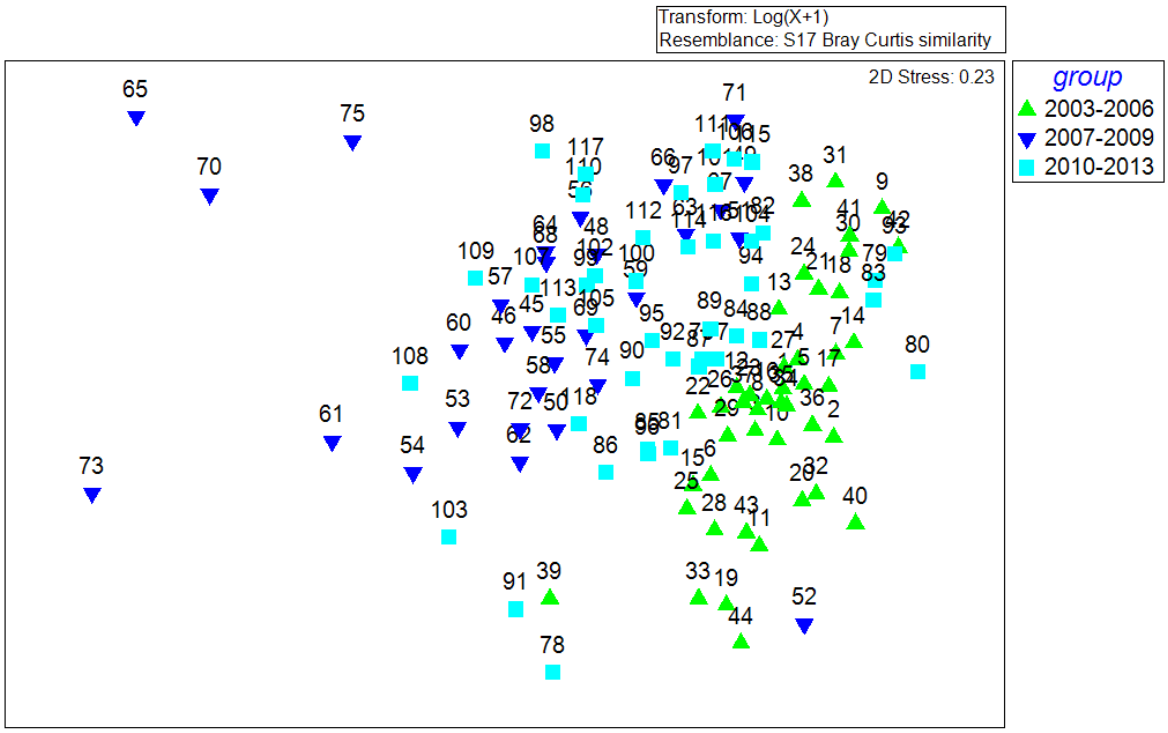

2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
Gironde estuary
Bay of Biscay
0
80
160 Km
France
Spain
Legend
3 700
Oithona
Acartia
T. longicornis
Oncaea
Calanidae
C.helgolandicus
Paracalanidae
Euterpina
Bathyline 500m
Bathyline 200m
Bathyline 100m

Figure 6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group
2003-2006
2007-2009
2010-2013

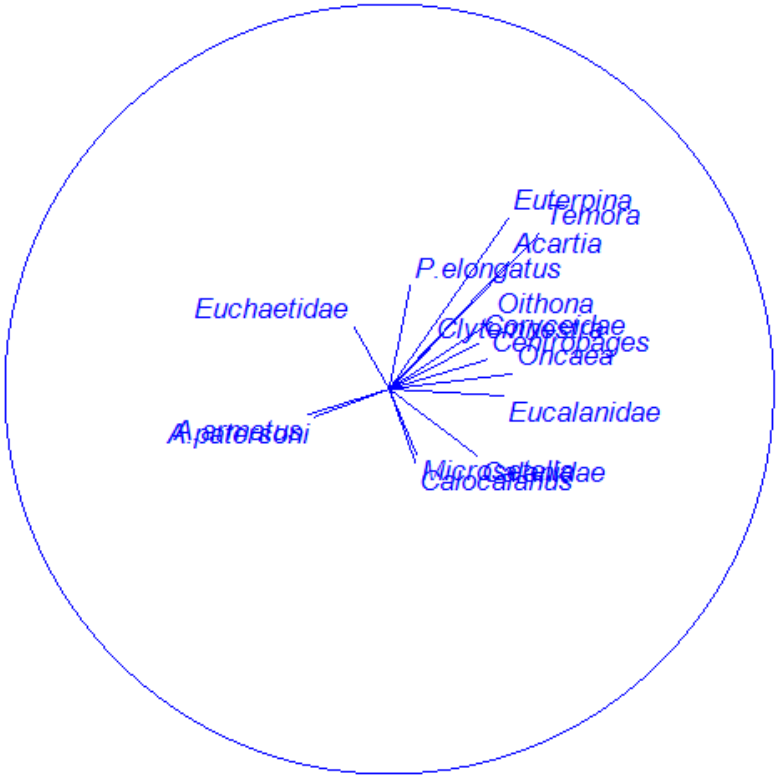
Euterpina
Temora
Acartia
P.elongatus
Euchaetidae
Oithona
Clytemnestra
Corycaeidae
Centropages
Oncaea
Eucalanidae
A.amoenus
A.tonsa
A.clausi
Microsetella
Calocalanus

Figure 7

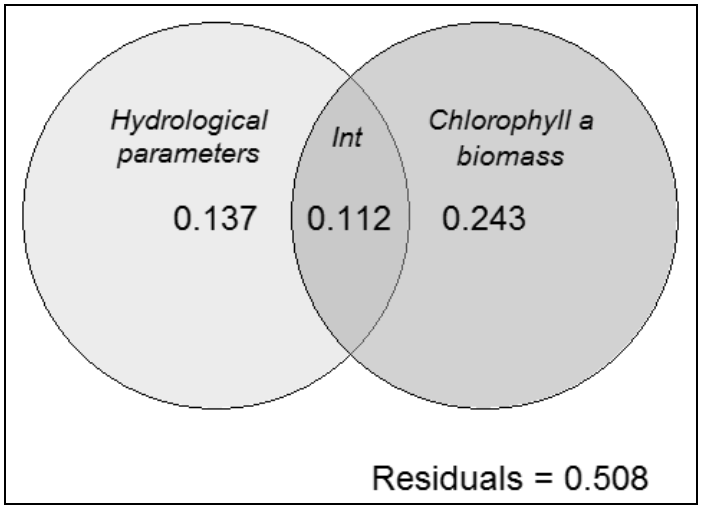
Hydrological parameters
Int
Chlorophyll a biomass
0.137
0.112
0.243
Residuals = 0.508

Table 1: Number of stations used in kriging (N.Station.Kriging) and multivariate (N.Station.VarPart) analysis per year start and the end dates of the surveys.

Year	First Station	Last Station	N.Station.Kriging	N.Station.VarPart
2003	30 May	09 June	34	11
2004	29 April	10 May	26	10
2005	05 May	16 May	30	12
2006	02 May	13 May	30	11
2007	27 April	08 May	31	10
2008	27 April	09 May	31	9
2009	26 April	09 May	29	12
2010	26 April	09 May	29	10
2011	26 April	09 May	28	11
2012	27 April	13 May	31	12
2013	28 April	16 May	30	10

Table 2: Representative list of taxa and species of mesozooplankton found in the Bay of Biscay with distinction between major groups: copepods, gelatinous organisms (G), other holoplankton (H) and meroplankton (M) organisms. For adult copepods, order affiliation is represented by Calanoida (Ca), Poecilostomatoida (P), Cyclopoida (Cy) and Harpaticoida (Ha) following by their relative percentage of abundance between 2003 and 2013 on copepods community.

Copepods	**Taxonomic level**	**Order(%)**	**Other taxonomic groups**	**Taxonomic level**	**Group**
Acartia spp.	Genus	Ca (19.3)	Appendicularia	Class	G
Oithona spp.	Genus	Cy (18.5)	Siphonophorae	Order	G
Temora longicornis	Species	Ca (17.4)	Indetermined Cnidaria	Phylum	G
Copepodites	Development stage	-(16)	Chaetognata	Phylum	G
Oncaea spp.	Genus	P (10.8)	Salpida	Order	G
Calanidae	Family	Ca (4.5)	Doliolida	Order	G
Calanus helgolandicus	Species	Ca (2.8)	Annelida larvae	Phylum	M
Paracalanidae	Family	Ca (2.2)	Cirripedia	Infra-class	M
Euterpina acutifrons	Genus	H (1.6)	Decapoda	Order	M
Centropages spp.	Genus	Ca (1.5)	Scaphopoda	Class	M
Copepods nauplii	Development stage	-(1.4)	Gastropoda larvae	Class	M

742 **Table 2:** continued

Copepods	Taxonomic level	Order(%)	Other taxonomic groups	Taxonomic level	Group
Coryceidae	Family	P (1.3)	Bivalvia larvae	Class	M
Eucalanidae	Family	Ca (1.3)	Enteropneusta	Class	M
Metridia spp.	Genus	Ca (0.4)	Anthozoa larva	Class	M
Pseudocalanus elongatus	Species	Ca (0.5)	Ectoprota	Phylum	M
Microsetella spp.	Genus	H (0.1)	Cyphonauta larvae	Development stage	M
Candacia spp.	Genus	Ca (0.1)	Bryozoa	Phylum	M
Pleuromamma spp.	Genus	Ca (0.1)	Echinodermata larvae	Phylum	M
Calocalanus spp.	Genus	Ca (0.1)	Hydrozoa	Class	M
Clytemnestra spp.	Genus	H (<0.05)	Scyphozoa	Class	M
Aegistus spp.	Genus	H (<0.05)	Ostracoda	Class	H
Aetideus armatus	Species	Ca (<0.05)	Isopoda	Order	H
Euchaetidae	Family	Ca (<0.01)	Mysida	Order	H
Rhincalanidae	Family	Ca (<0.01)	Amphipoda	Order	H
Anomalocera patersoni	Species	Ca (<0.01)	Euphausiacea	Order	H
			Cladocera	Infraorder	H
			Chordata	Phylum	H
			Cumacea	Order	H
			Foraminifera	Phylum	H

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744 **Table 3:** Results of the similarity percentage (SIMPER) analysis based on spring adult copepods matrix in the Bay of Biscay between 2003 and
745 2013.
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Group [2003-2006]		**Group [2007-2009]**		**Group [2010-2013]**	
Average similarity: 66.83		Average similarity: 52.32		Average similarity: 59.89	
Genus/Species/Family	Contrib%	Genus/Species/Family	Contrib%	Genus/Species/Family	Contrib%
Oithona spp.	22.4	*Oithona* spp.	24.37	*Oithona* spp.	24.02
Oncaea spp.	17.8	*Acartia* spp.	17.96	*Acartia* spp.	19.21
Acartia spp.	13.04	*Oncaea* spp.	17.1	*Temora longicornis*	13.24
Temora longicornis	12.2	Paracalanidae	15.16	*Oncaea* spp.	10.96
Eucalanidae	11.94	*Temora longicornis*	7.77	*Calanus helgolandicus*	7.95
Calanidae	10.54	Coryceidae	3.76	Calanidae	6.97
Centropages spp.	5.31	*Calanus helgolandicus*	3.04	Paracalanidae	4.84
		Calanidae	2.9	*Euterpina acutifrons*	4.11

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749 **Table 4:** Results of the dissimilarity percentage (SIMPER) analysis based on spring adult copepods matrix in in the Bay of Biscay between 2003
750 and 2013.
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Groups [2003-2006] and [2007-2009]		**Groups [2003-2006] and [2010-2013]**		**Groups [2007-2009]and [2010-2013]**	
Average dissimilarity: 52.01		Average dissimilarity: 45.51		Average dissimilarity: 46.88	
Genus/Species/Family	Contrib%	Genus/Species/Family	Contrib%	Genus/Species/Family	Contrib%
Eucalanidae	11.04	Eucalanidae	11.29	*Temora longicornis*	10.09
Paracalanidae	10.49	*Calanus helgolandicus*	9.44	Calanidae	9.78
Temora longicornis	9.62	Calanidae	8.55	*Calanus helgolandicus*	9.05
Calanidae	8.59	*Temora longicornis*	8.46	Paracalanidae	8.79
Acartia spp.	8.2	*Acartia* spp.	7.85	*Acartia* spp.	8.39
Oncaea spp.	7.2	*Oncaea* spp.	7.67	*Euterpina acutifrons*	7.48
Centropages spp.	6.87	Paracalanidae	7.15	*Oncaea* spp.	7.38
Coryceidae	6.29	*Euterpina acutifrons*	7.1	*Oithon a*spp.	6.31
Oithona spp.	5.77	*Centropages* spp.	6.92	*Centropages* spp.	5.99
Euterpina acutifrons	4.98	Coryceidae	6.49	Coryceidae	5.97
Metridia spp.	4.54	*Metridia* spp.	4.79	*Metridia* spp.	4.71
Calanus helgolandicus	4.4	*Oithona* spp.	3.74	*Pseudocalanus elongatus*	3.46
Candacia armata	2.65	*Microsetella* spp.	3.06	*Candacia armata*	3.04

754 **Table 5:** Selection of the most influential variables explaining the most the patterns of copepod community using a forward selection. The eigen
755 values sums (a measure of explained variance, R^2), "*F"* statistic and p-values were reported.
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Variables order	Eigenvalues sums	*F*	
Sub-Surface Chl*a*>20µm (Microphytoplankton) Based biomass	0.35	65.28	**
Equivalent fresh water height	0.42	15.47	**
Deficit of potential energy	0.45	7.50	*
Sub-surface temperature	0.49	8.84	**

Codes:0 '***';0.001 '**';0.01 '*'

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List of supplemental figures

Supplemental figure S1: Annual interpolated maps of results of the annual spatial interpolation of sub-surface temperature measures (°C), performed for each year between 2003 and 2013 in the southern Bay of Biscay. Thanks to a non-parametric multiple pairwise comparison of mean ranks applied for all years, significant differences of sub-surface temperature according to year are indicated by letters.

Supplemental figure S2: Annual interpolated maps of results of the spatial interpolation of sub-surface salinity (PSUpsu) performed for each year between 2003 and 2013, in the southern Bay of Biscay.

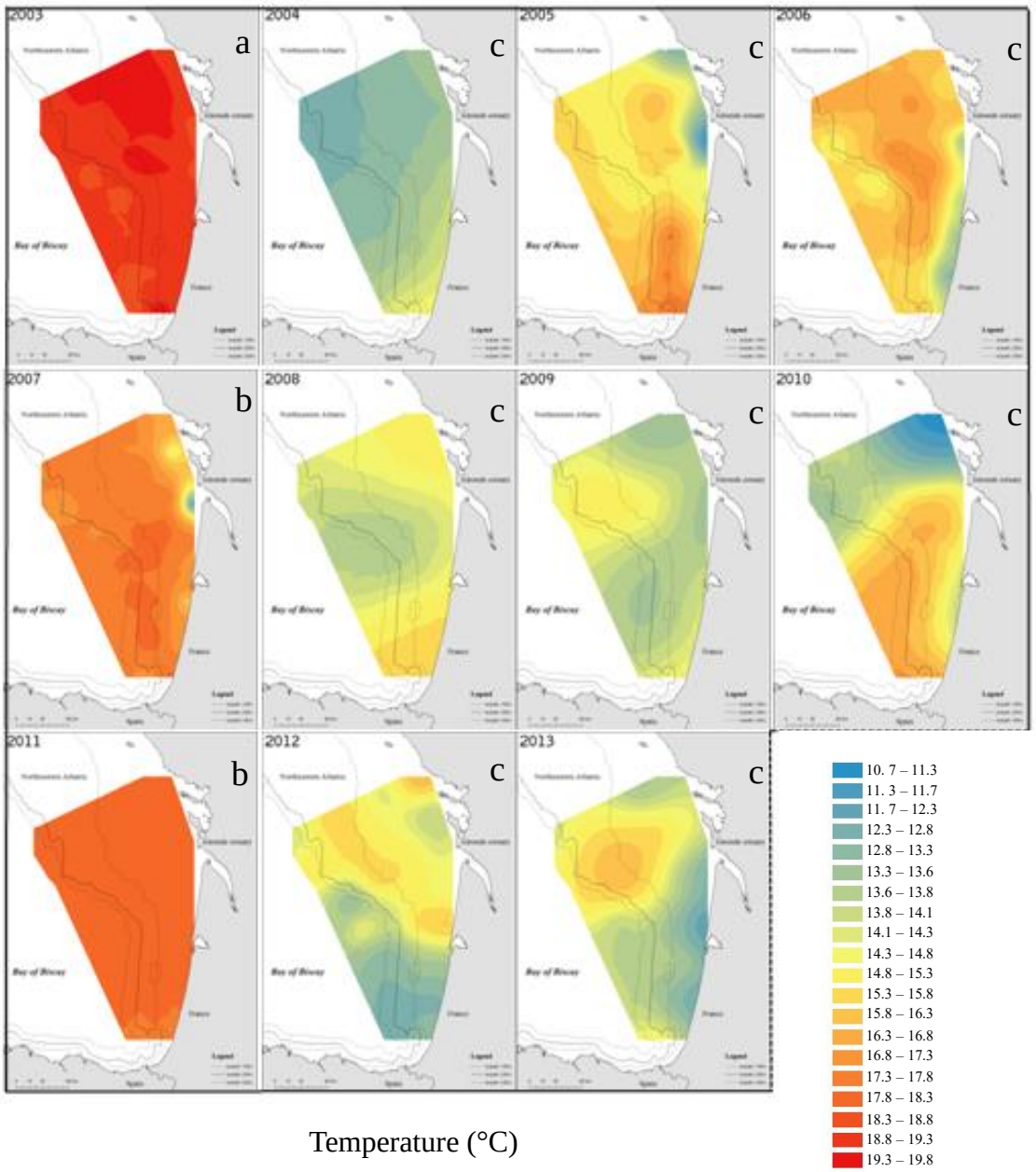
Supplemental figure S3: Annual interpolated maps of results of the spatial interpolation of sub-surface picophytoplankton (chl*a*< 3µm) biomass ($\mu g.L^{-1}$) performed for each year between 2003 and 2013, in the southern Bay of Biscay. Thanks to a non-parametric multiple pairwise comparison of mean ranks applied for all years, significant differences of sub-surface picophytoplankton biomass according to year are indicated by letters.

Supplemental figure S4: Annual interpolated maps of results of the spatial interpolation of sub-surface nanophytoplankton ([3-20] µm) biomass ($\mu g.L^{-1}$) performed for each year between 2003 and 2013, in the southern Bay of Biscay. Thanks to a non-parametric multiple pairwise comparison of mean ranks applied for all years, significant differences of sub-surface nanophytoplankton biomass according to year are indicated by letters.

Supplemental figure S5: Annual interpolated maps of Results of the spatial interpolation of sub-surface microphytoplankton (chl*a*> 20 µm) biomass ($\mu g.L^{-1}$) performed for each year between 2003 and 2013, in the southern Bay of Biscay. Thanks to a non-parametric multiple pairwise comparison of mean ranks applied for all years, significant differences of sub-surface microphytoplankton biomass according to year are indicated by letters.

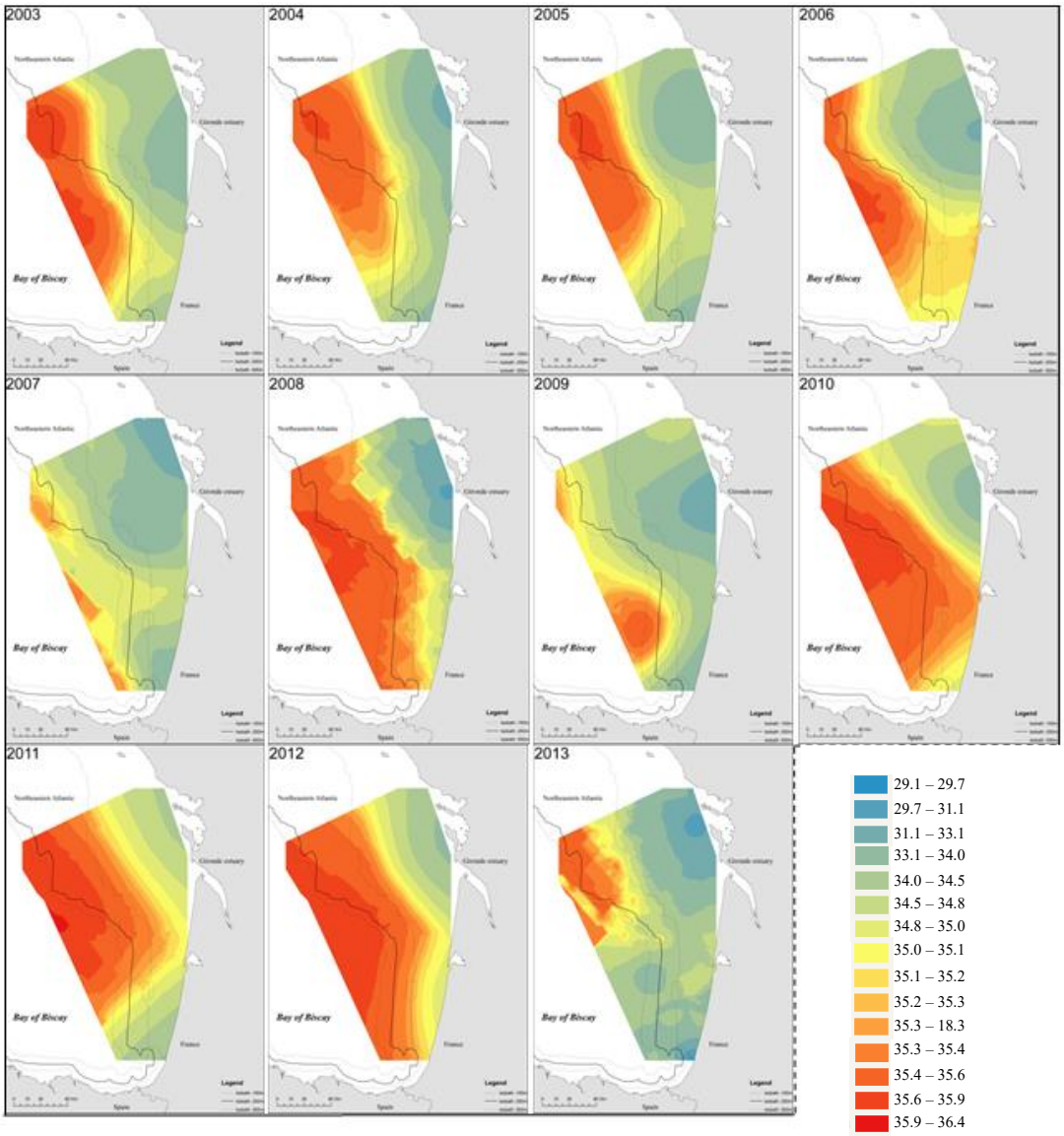
Supplemental figure S6: Spatial distribution of abundance (ind.m^{-3}) of copepods nauplii, copepodites and Harpacticoida, Poecilostomatoida, Cyclopoida, Calanoida (orders) between 2003 and 2013 in the southern Bay of Biscay. The size of the pies is proportional to the total abundance of from each station throughout the decade. Significant differences in abundance according to year are indicated by letters.

Supplemental figure 1:



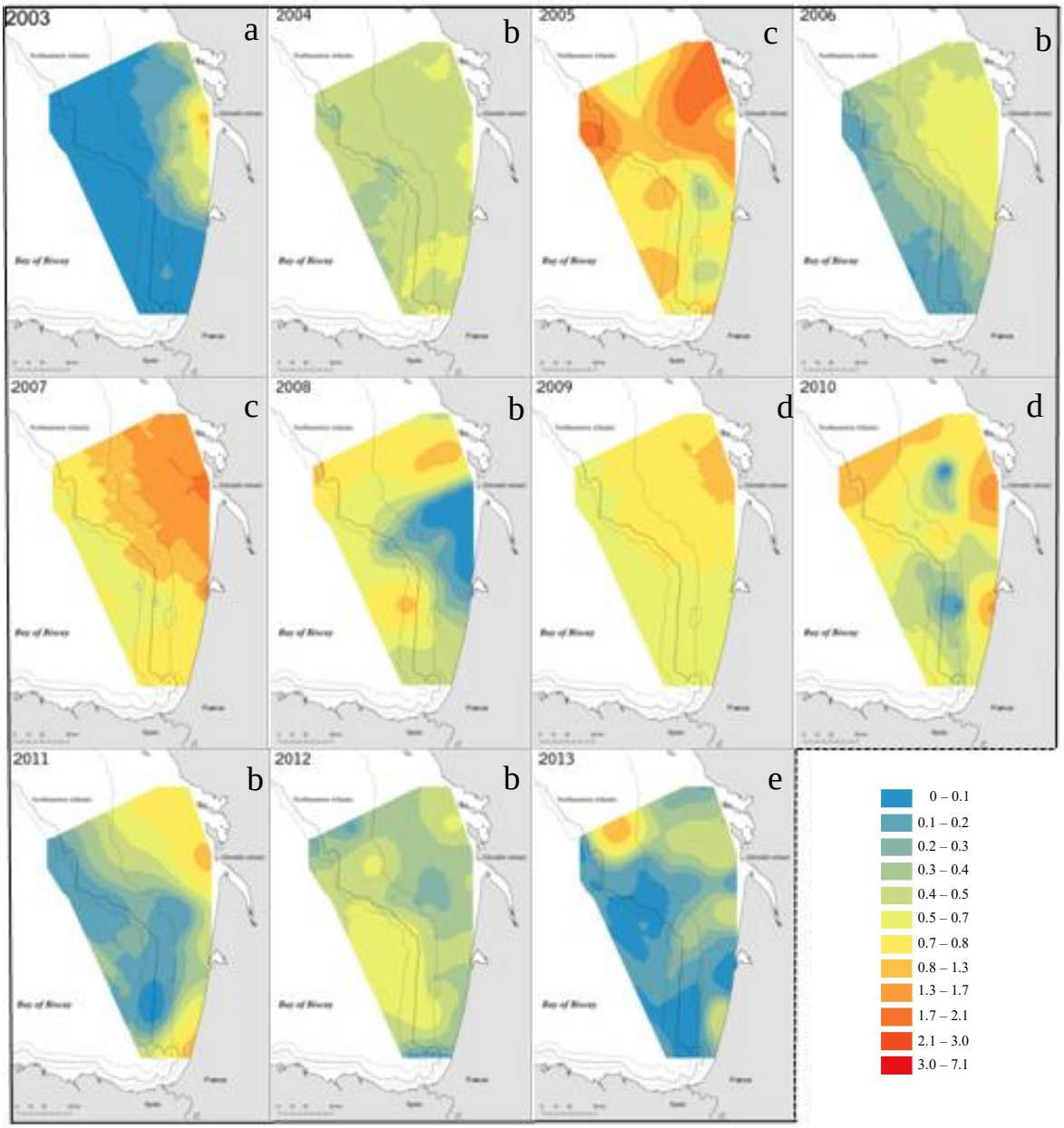
Temperature (°C)

Supplemental figure 2:



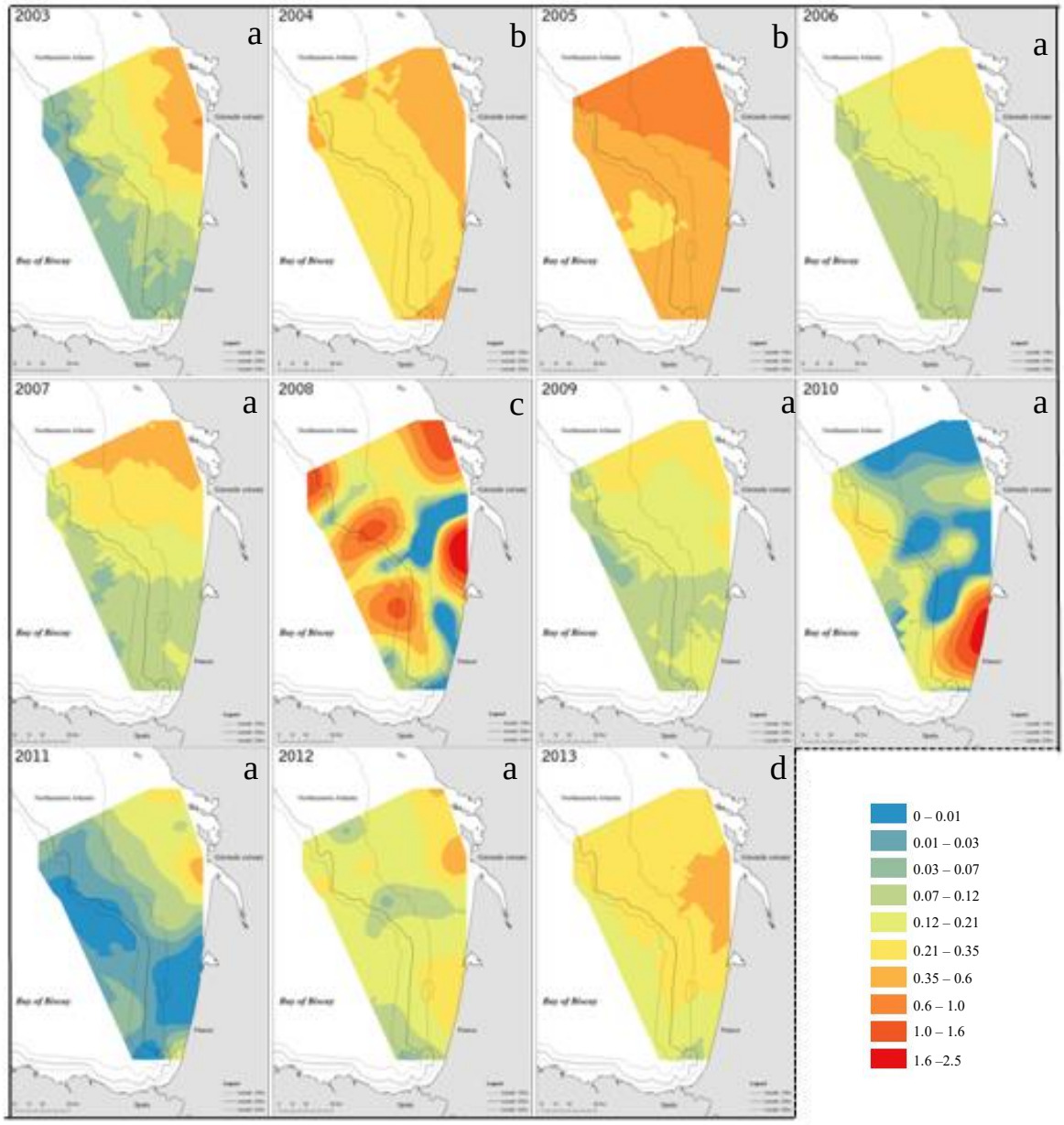
Salinity (PSU)

Supplemental figure 3:



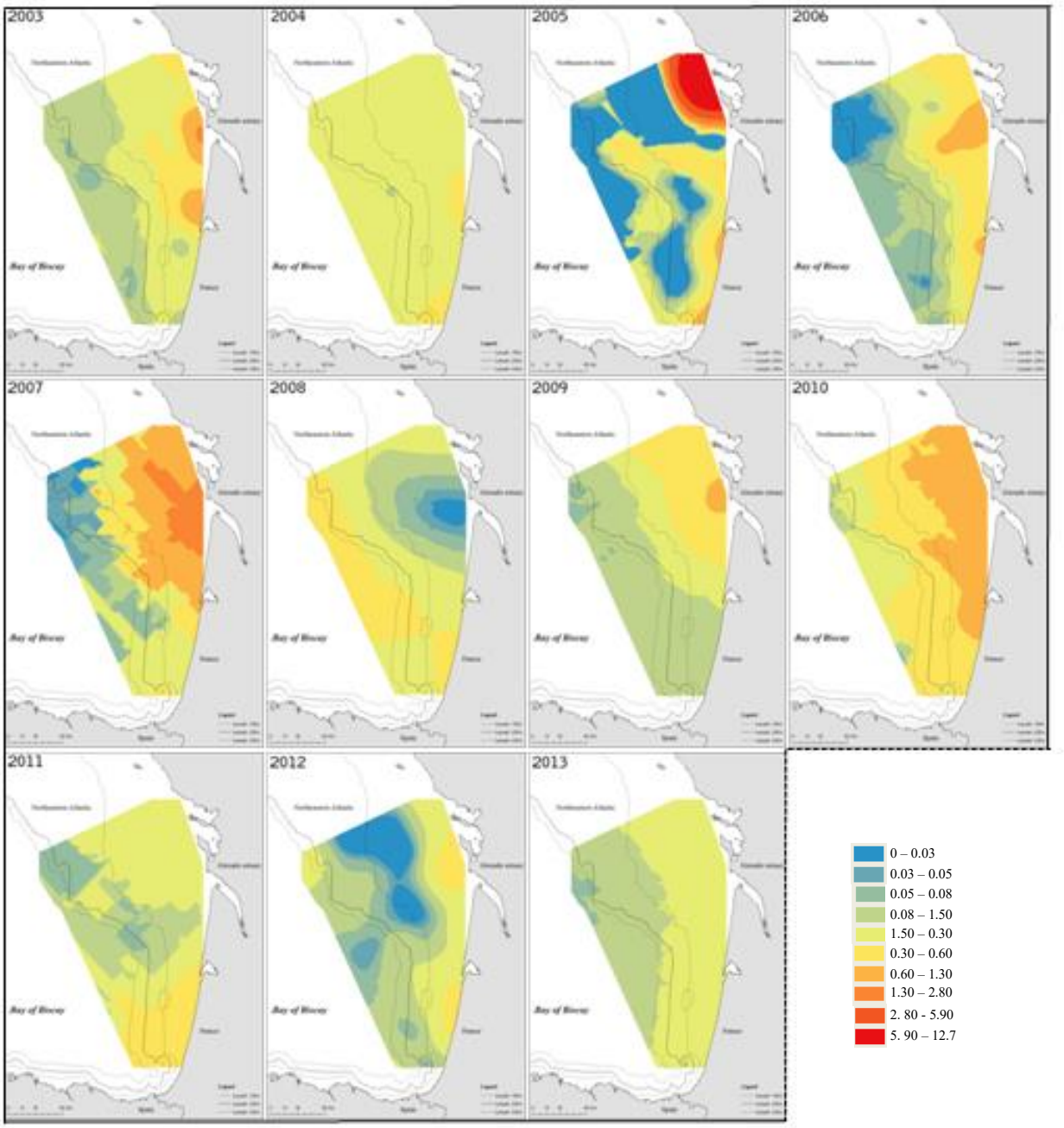
Chlorophyll *a*< 3µm (µg L^{-1})

Supplemental figure 4:



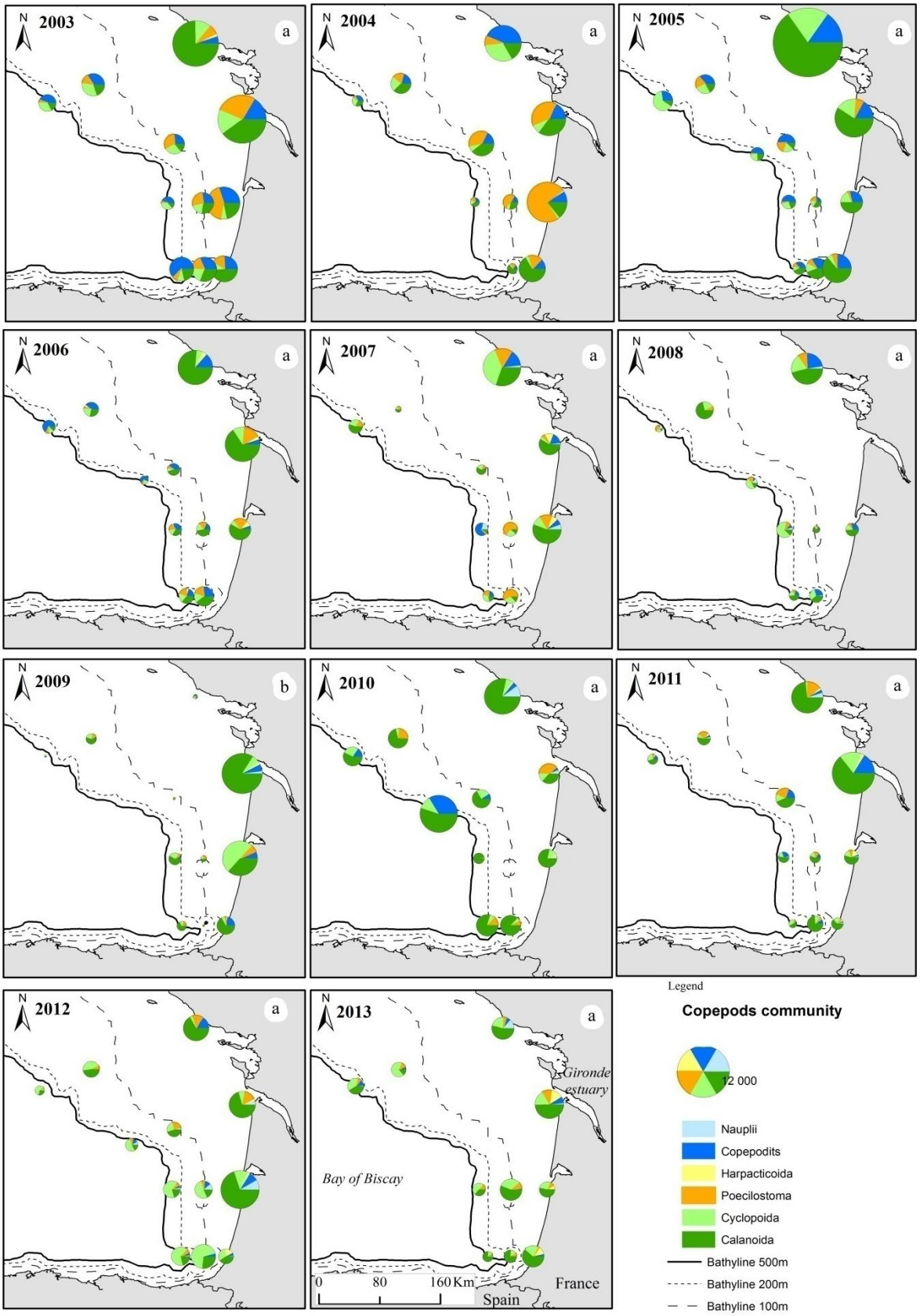
Chlorophyll *a* [3-20]µm (µg L^{-1})

Supplemental figure 5:



Chlorophyll *a*>20µm (µg L^{-1})

Supplemental figure 6:



List of supplemental figure :

Supplemental table 1: Identification of copepod community drivers by variation partitioning analysis based on ordination analyses. Matrix H contained environmental variables (sub-surface temperature values, deficit of potential energy and equivalent freshwater height), matrix C contained the chlorophyll *a* >20 µm biomass (microphytoplankton biomass). Multivariate analysis, covariables, component of variation, eigenvalues and statistical p-values are reported. Explanatory matrix / component of variation; H/h – hydrological parameters, C/c – chlorophyll *a* based biomass.

Analysis	**Constraining variable**	**Covariate**	**Component of the variation**	**Eigenvalues sums**	***p-value***
ACP	-	-	-		
RDA	H		h + hc	0.24	***
RDA	C		c + hc	0.35	***
RDA	H+C		h + c + hc	0.49	***
RDAp	H	C	h	0.13	***
RDAp	C	H	c	0.24	**

Codes for p-values: 0 '***';0.001 '**';0.01 '*'