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Spatio-temporal drivers of microphytoplankton community in the Bay of Biscay: do species ecological niches matter?

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Abstract :

From 2000 to 2016, substantial changes in biomass and community structure of small pelagic fish and mesozooplankton have been reported in the Bay of Biscay. Since significant relationships have been found between phytoplankton chlorophyll a and mesozooplankton as well as between phytoplankton chlorophyll a and shifts in sardine body condition, it was hypothesized that phytoplankton communities may have also been affected during this period and may have played a role in these changes. However, the available data were insufficient to validate this hypothesis and the causes of these changes remained unexplained. The present study analyzed a spatio-temporal marine microphytoplankton dataset collected during the annual PELGAS (PELagiques GAScogne) surveys from 2003 to 2014. The thorough analysis of microphytoplankton taxonomic composition, with an approach integrating the relative role of environmental conditions as well as biotic interactions and applying the concept of ecological niche, confirmed that significant modifications in microphytoplankton community structure occurred during this period. Temporal changes were stronger than spatial differences at these sampling scales. Three main periods, 2003-2005, 2006 and 2007-2014, showing different community structure, diversity and dominant taxonomic units were highlighted. Twenty eight taxonomic units were involved in these community changes. Among them, five were identified as the protagonists (Pseudo-nitzschia spp., Gymnodinium spp. + Gyrodinium spp., Leptocylindrus danicus, Leptocylindrus minimus and Chaetoceros sp.). Variations in water temperature and equivalent freshwater depth constrained the realized ecological niches of these species and explained, at least in part, changes in community structure. This study stresses the need to improve our knowledge of phytoplankton species ecological niches and to take into account biotic interactions for a thorough understanding of the processes shaping plankton communities and the resulting diversity patterns.

Highlights

► Spring microphytoplankton community structure and diversity were studied over a decade in the Bay of Biscay. ► Three main periods, 2003-2005, 2006 and 2007-2014, showing different community structure, diversity and dominant taxonomic units were highlighted. ► Five main species were responsible for these changes (Pseudo-nitzschia spp., Gymnodinium spp. + Gyrodinium spp., Leptocylindrus danicus, Leptocylindrus minimus and Chaetoceros sp.) ► Variations in water temperature and equivalent freshwater depth constrained the realized ecological niches of these species and explained, at least in part, changes in community structure.

Keywords : ecological niche, phytoplankton, outlying mean index, WitOMI, spatial processes, zooplankton

1. Introduction

Phytoplankton plays a fundamental role in most biogeochemical cycles and contributes roughly half of the biosphere net primary production (Field et al., 1998). Through its position at the base of marine food webs, phytoplankton is at the center of interactions between climate, local hydrological conditions and higher trophic-level organisms including those of economic importance such as fish (Defriez et al., 2016; McQuatters-Gollop et al., 2015). The growing concern about global change led the scientific community to pay close attention to long-term or large scale phytoplankton data series. Regime shifts as well as significant changes in phytoplankton community structure (i.e. the number and abundance of the species constituting the phytoplankton community) and bloom phenology were then highlighted in several ecosystems including the North Pacific (Wooster and Zhang, 2004), North Atlantic (Drinkwater, 2006), Baltic Sea (Dippner et al., 2012) and North Sea (Defriez et al., 2016; Scharfe and Wiltshire, 2019). It was shown that changes in phytoplankton phenology can lead to temporal decoupling between primary producers and consumers. This results in modified feeding relationships ("match-mismatch") and can have dramatic consequences on the highest trophic levels populations and ecosystem functioning (Atkinson et al., 2015; Cushing, 1990; Scharfe and Wiltshire, 2019).

Yet, the underlying mechanisms responsible for such changes and those shaping phytoplankton communities are not completely resolved. A part of these uncertainties may arise from the fact that most research on phytoplankton dynamics focused on their bottom-up control by environmental variables (mainly effects of temperature, light and nutrients) (Padisák, 2003; Reynolds, 2006) as historically, these factors have been considered to be the most important in phytoplankton community structuring (Verity and Smetacek, 1996). This approach is generally efficient to understand the relationships between phytoplankton and its surrounding

environment but it is insufficient to thoroughly resolve the processes structuring phytoplankton communities because it completely ignores biotic interactions such as predator-prey relationships.

Verity and Smetacek (1996) stated that rather than focusing on resource acquisition (bottom-up force), a better understanding of the structure of marine pelagic ecosystems would be reached by considering that resource availability and biotic interactions (including predators-prey relationships and competition) are equally important in the selection of life histories, morphologies and behaviors of organisms. In line with this statement, recent studies examining the role of several environmental variables (e.g. Mutshinda et al., 2013) or the relative importance of environmental factors and biotic interactions (Bode et al., 2015; Lima-Mendez et al., 2015; Mutshinda et al., 2019; Yang et al., 2018a), with hierarchical Bayesian models, generalized additive models, random forest-based approaches or network analyses, highlighted that environmental factors are incomplete predictors of phytoplankton community structure. Considering biotic associations within the plankton community, rather than focusing only on the relationships between phytoplankton and the environment, better explained phytoplankton dynamics and community structure (Bode et al., 2015; Karasiewicz et al., 2018; Lima-Mendez et al., 2015; Yang et al., 2018a). Such an approach also hold clues to better understand the dynamics and structure of ocean ecosystems (Lima-Mendez et al., 2015).

Evidence is also growing that the processes responsible for climate induced changes in phytoplankton composition and/or regime shifts are not well understood because of our limited knowledge of phytoplankton species ecological niches (Barton et al., 2013). Beaugrand (2015) showed that regime shifts (or abrupt community shifts) do not always originate from the transition from one alternative stable state to another but may, instead, result from interactions between climate induced environmental changes and the species ecological niche. It was also shown that variations in the species ecological niche may explain phytoplankton blooms

intensity and successions (Alves-de-Souza et al., 2019; Karasiewicz et al., 2018). Adopting an approach taking into account the effects of environmental conditions as well as biotic interactions and integrating the concept of ecological niche seems to be the key to a better understanding of food webs structure, regime shifts and ecosystems functioning. However, understanding the mechanisms shaping phytoplankton species ecological niches and the consequences of their variations in phytoplankton geographic repartition as well as seasonal community successions is an important task but also a complex one (Brun et al., 2015).

In the Bay of Biscay (Northeast Atlantic Ocean from Cap Ortegal in Spain to Penmarch Point in Brittany in France, IHO), substantial changes in biomass and community structure of small pelagic fish and mesozooplankton have been reported between the years 2000 and 2016 (Dessier et al., 2018; Doray et al., 2018a; Doray et al., 2018b; Véron et al., 2020). Significant relationships were found between phytoplankton chlorophyll *a* and mesozooplankton (Dessier et al., 2018) as well as between phytoplankton chlorophyll *a* and shifts in sardine body condition (Véron et al., 2020). Even though the question of a potential regime shift has been raised, available data are currently insufficient to conclude there has been a shift in the Bay of Biscay ecosystem functioning (e.g. Irigoien et al., 2008). The causes of these changes are therefore not completely resolved and the understanding of the respective role of bottom-up and top-down controls on food web functioning and fish recruitment remains a challenge in the Bay of Biscay (e.g. Irigoien et al., 2008). Since ecopath modeling (Lassalle et al., 2011) and an analysis of a 10-year (1992-2002) data series of phytoplankton and zooplankton biomass (Stenseth et al., 2006) have indicated that the Bay of Biscay is most likely a bottom-up controlled system, it can be hypothesized that phytoplankton may also have been impacted between 2000 and 2015. However, few studies have presented phytoplankton data collected during that period.

By analyzing chlorophyll a concentrations measured from 1993 to 2012 at a single station in the Cantabrian Sea (a sub-area of the Bay of Biscay), González-Gil et al. (2018)

showed that winter mixing influences intensity and duration of spring phytoplankton blooms: deeper and later mixing in winter resulted in delayed and more intense phytoplankton blooms. Zarauz et al. (2009) found a clear difference in the timing, magnitude and size structure of the nano-microplankton bloom between coastal and oceanic waters along a transect in the central Cantabrian sea in February-March 2005. Zarauz et al. (2007) showed that, in the Bay of Biscay from March to June 2004, nano-microplankton biomass distribution (which included phytoplankton, zooplankton, detritus and inorganic particles) was related to surface salinity, surface temperature and stratification of the water column. By contrast, by examining separately the distributions of nano-microplankton components (diatoms, ciliates and unidentified particles) in the same area but during the springs of 2004, 2005 and 2006, Zarauz et al. (2008) reported that geographical location (i.e. latitude and longitude assumed to be related to mesoscale fronts) was more relevant than hydrographic (i.e. salinity, temperature, stratification, water column depth) or biological variables in explaining these distributions. Consequently, none of these studies has provided data corroborating a modification of phytoplankton community structure between 2000 and 2015.

Based on an approach integrating the relative role of environmental conditions and biotic interactions and applying the concept of ecological niche, the objectives of the present study were: 1) to identify the main changes in microphytoplankton community structure in terms of dominant taxa, abundance, diversity and spatio-temporal structure between 2003 and 2014, 2) to understand whether there was a link between these changes, environmental conditions, spatial processes and biotic interactions (including predator-prey interactions or competition) and, 3) to study how the ecological niches of the main phytoplankton taxa involved in these community changes were possibly modified.

2. Materials and Methods

2.1 Study area

The Bay of Biscay is an important Northeast Atlantic fisheries area. From January to June, haline stratification is strong on a large part of the eastern shelf. The eastern shelf water properties are influenced by Loire and Gironde rivers runoffs (Guillaud et al., 2008; Huret et al., 2018; Marquis et al., 2011). The South western part of the Bay of Biscay (i.e. the area close to Galicia) is considered as the most productive (annual average of 43.44 mg Chl a m^{-2} and 138.07 mg C m^{-2} day^{-1}) because it is influenced by the Galicia upwelling system which extends toward the East (Borja et al., 2019). French waters in the northern part of the Bay of Biscay, and the areas influenced by river runoffs also present higher chlorophyll levels than the rest of the Bay. Phytoplankton species composition varies seasonally and among regions within the Bay of Biscay. The main phytoplankton bloom occurs in spring. It is mainly composed of microphytoplankton (principally represented by diatoms) especially in coastal waters and estuarine plumes (Dupuy et al., 2011; Muñiz et al., 2018). This bloom reduces considerably the amount of nutrients available, in particular phosphorus. Diatoms are thus progressively replaced by dinoflagellates during the summer when the thermocline develops (Borja et al., 2019). The contribution of picophytoplankton varies seasonally. Picophytoplankton abundance shows maxima in late summer-early autumn and minimum in spring (Calvo-Díaz et al., 2008).

2.2 Sampling strategy

Data were collected in spring during the annual PELGAS (PELagiques GAScogne) sea surveys conducted by the French Research Institute for the Exploitation of the Sea (IFREMER).

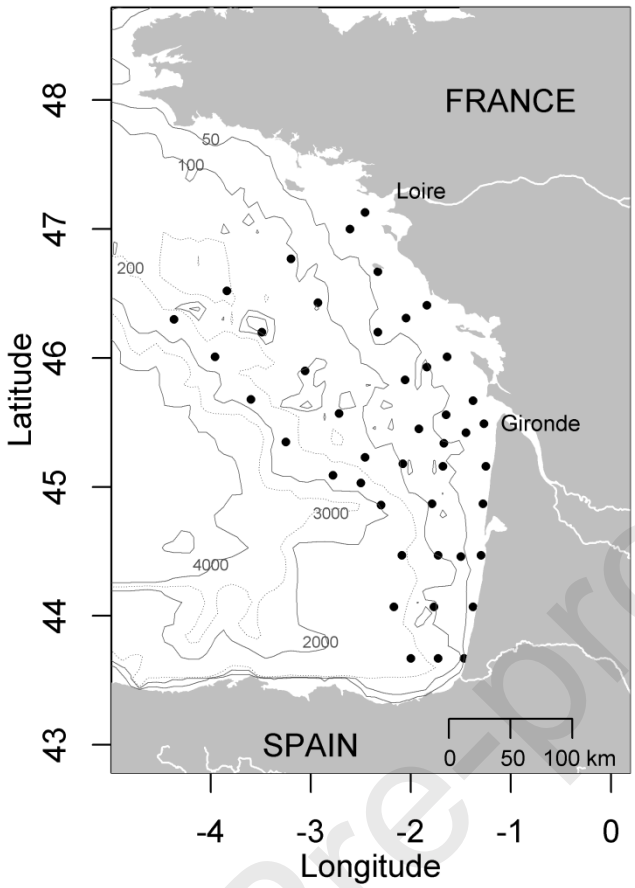

Fig. 1: Map of the eastern continental shelf of the Bay of Biscay showing the location of sampling stations (black points). Grey lines represent isobaths. The shelf zone is separated from the pelagic zone by the 200 m isobath

Phytoplankton data were collected from 2003 to 2014 with a 4 years gap between 2009 and 2012. PELGAS surveys were not carried out exactly on the same dates (especially in the beginning of the studied decade) and about 15 days separated the start and the end of the cruise due to sampling strategy and transit time (for more details see Table S1 in supplementary materials). However, all surveys were conducted from the south to the north. Additional information on PELGAS cruises can be found in Doray et al. (2018c). The sampling design was made of parallel line transects, perpendicular to the isobaths and regularly spaced 12 nautical miles apart from 43°N to 49°N and from the coast (20 m depth) to the shelf break (Doray et al., 2018c). A total of 44 stations were sampled (Fig. 1). Guided by the fluorescence profiles (see below for their measurement), water samples for laboratory analyses of nutrient concentrations

and microphytoplankton were collected with a 5-L Niskin bottle rosette system at 3 depths: subsurface (5 m), the depth of maximum fluorescence and bottom (with a maximum depth of 100 m). 120 mL microphytoplankton samples were fixed with formaldehyde (final concentration 1%) plus alkaline lugol (final concentration 1%) and stored at 4 °C until laboratory analysis. Mesozooplankton was collected with a WP2 plankton net (mesh size: 200 µm, opening area: 0.25 m^2). The WP2 was deployed at a maximum of 100 m depth (downcast and upcast at 0.5 $m.s^{-1}$) or at 5 m above the seabed when water column depth was <100 m.

2.3 Abiotic parameters

Salinity, temperature and fluorescence profiles were measured using a CTD (Conductivity-Temperature-Depth) probe (Sea-Bird SBE 19+ V2) equipped with a fluorimeter (WETStar, WET labs). From these CTD measurements, 3 water column stratification indices were calculated: the deficit of potential energy (DEP in kg m^{-1} s^{-2}), equivalent freshwater depth (Heq, in m) and pycnocline depth (Pycn in m) (see Huret et al. (2013) for equations). DEP is the energy required to homogenize the water column. It increases with the intensity of stratification and was computed from 0 to 100 m depth for the profiles where bottom depth exceeded 100 m. Heq measures the height of accumulated freshwater considering a reference seawater salinity of 35.5. This index is less sensitive to vertical mixing than surface salinity and is thought to better reflect the recent history and local effect of riverine water discharges in the Bay of Biscay (Doray et al., 2018a). Pycn was defined as the depth where the maximum vertical density gradient was higher than 0.05 kg m^{-3} m^{-1}.

Water samples used to measure dissolved nutrients (silicate (SiO_4), nitrate (NO_3^-), nitrite (NO_2^-), and phosphate (PO_4^{3-})) were filtered onto Whatman GF/F fiberglass filters and stored at -20°C (except for SiO4 at 4°C). Nutrient concentrations were measured using colorimetric

methods on an AA3 auto-analyzer (Seal) following the methodology of Strickland and Parsons (1972). Nutrients were only measured in 2004, 2008, 2013 and 2014.

Sea surface irradiance (SSI, in Watt m^{-2}) in the 0.3 - 4.0 µm band, was determined from satellite measurements. It was derived from data of the MSG (METEOSAT Second Generation) following the processing chain described in the SSI Product Manual, available on the OSI SAF web server (EUMETSAT, 2013) and validated as described in Le Borgne et al. (2006). For analysis of the realized ecological niche, sub-niches, variation partitioning and random forest models (see below), the daily SSI was averaged over five days (four previous days and day of phytoplankton sampling) (Hernandez Fariñas et al., 2015). Turbidity (in NTU) was determined from satellite reflectance-based measurements of chlorophyll a and non-algal suspended particulate matter using the methodology described in Gohin (2011).

2.4 Taxonomic determination of microphytoplankton species

50-100 mL of fixed water samples were allowed to settle for 24 h following the Utermöhl method (Utermöhl, 1958). Microphytoplankton (mainly diatoms and dinoflagellates) was identified to the lowest possible taxonomic level and enumerated using an inverse microscope (Leica, x 200 and x 400 magnification). Taxonomic determination was carried out in accordance with systematic literature (Lessard and Swift, 1986; Nezan, 1996; Ricard, 1987; Sournia, 1986). To reduce bias in the dataset due to difficulties in differentiating some species or genera using an optical microscope, taxonomic units have been used. A taxonomic unit was thus composed either by a single species (easily identifiable) or a group of several species or genera difficult to differentiate. Dinoflagellates were classified as autotrophic or heterotrophic from morphologic species recognition and relevant literature (e. g. Lessard and Swift, 1986).

2.5 Mesozooplankton biomass and abundance

To determine mesozooplankton species abundance, the samples collected with the WP2 plankton net were preserved in 4% formaldehyde (final concentration) (Dessier et al., 2018). Mesozooplanktonic organisms were then identified to the lowest possible taxonomic level and enumerated using a Leica M3Z stereo microscope (x 65 to x 100 magnification). Taxonomic determination was made by following the protocols of Rose (1993) and Trégouboff and Rose (1957). For biomass measurements, net samples were filtered onto a pre-weighed Whatman GF/C (47 mm in diameter). After filtration, each filter was rinsed twice with distilled water to remove salt. Filters were then dried at 60 °C for 12 h and weighed to estimate mesozooplankton biomass.

2.6 Statistical analyses

Spatio-temporal variations in abiotic environmental parameters

Permutational multivariate analyses of variance (PERMANOVA, Anderson, 2017) were used to test for significant differences in abiotic environmental parameters (seawater temperature, seawater salinity, deficit of potential energy, equivalent freshwater depth, pycnocline depth and sea surface irradiance) between sampling periods, sampling transects (i.e. north/south spatial position of sampling stations), coastal/offshore waters and sampling depths. PERMANOVA were based on Euclidean distance matrix and 9999 permutations were used. PERMANOVA were performed with the function "adonis" available in the R vegan package (Oksanen et al., 2018). PERMANOVA are semiparametric methods allowing, like ANOVA, to perform variance partitioning based on the calculation of F statistics but that have the advantage to retain the robust statistical properties of rank-based nonparametric methods and thus to not

require data normality while keeping the possibility to test the effects of several factors with interaction terms (Anderson, 2017).

Changes in microphytoplankton total abundance, diversity and community structure

Diversity and equitability were measured using the Shannon diversity index (H') (Shannon, 1948) and Pielou's evenness (J') (Pielou, 1966). Both indices were calculated with the "diversity" function available in the R vegan package (Oksanen et al., 2018). The Shannon diversity index (in nats) was calculated from the equation:

$H' = - \sum p_i \ln p_i$

where p_i is the proportion of individuals for the ith species. To facilitate its interpretation, the Shannon diversity index was converted into its numbers equivalent (also called equivalent number of species) using Hill (1973)'s formula: $H = \exp(H')$.

The Pielou's evenness was calculated as:

$J' = H' / \ln S$

where S is the total number of species. J' ranges from 0 to 1 with zero corresponding to no evenness and 1 meaning complete evenness.

Differences in H, J', total number of species and total microphytoplankton abundance between sampling periods, sampling transects (i.e. north/south spatial position of sampling stations), coastal/offshore waters and sampling depths were tested with PERMANOVA using the procedure described for abiotic environmental parameters. Total microphytoplankton abundances measured in 2003, 2004, 2005, 2006, 2007, 2008, 2013 and 2014 were compared to the mean decadal value using one sample t-tests (Scherrer, 2007).

Spatio-temporal changes in microphytoplankton community structure were characterized using PRIMER 6 (PRIMER-E ltd., Plymouth, UK). Phytoplankton abundances

were fourth root transformed to balance the contribution of common and rarer species and a matrix of pairwise Bray-Curtis similarity coefficients between samples was built. The fourth root transformation has the effect of down-weighting the importance of the highly abundant species, allowing not only the less common ("mid-range") species but also the rarer species to exert some influence on the calculation of the Bray-Curtis similarity (Clarke and Warwick, 2001). Based on the Bray-Curtis similarity matrix, the similarity between each sample was represented by a non-metric multidimensional scaling plot (nMDS) (Clarke, 1993; Clarke and Warwick, 2001). Significance of spatio-temporal differences in phytoplankton community structure were analyzed using an analysis of similarity (ANOSIM) (Clarke, 1993; Clarke and Warwick, 2001). The factors tested were the sampling periods, sampling transects (north/south spatial position of sampling stations), distance from the coast (coast/offshore waters) and sampling depth. A SIMPER analysis was performed to calculate the percentage of average dissimilarity between the groups of samples highlighted by the nMDS analysis and to identify taxa contributing the most to this dissimilarity. When taxa contribution was related to abundance changes, the significance of these differences was tested with a Mann-Whitney U test (Scherrer, 2007).

Relative role of environmental conditions, spatial processes and mesozooplankton in microphytoplankton communities structuring

Variation partitioning (Legendre, 2008) was used to determine the relative importance of environmental conditions, spatial processes and mesozooplankton biomass in the entire microphytoplankton community structuring. Variation partitioning was performed with the function "varpart" available in the R vegan package (Oksanen et al., 2018) using four matrices: species, environmental, spatial and zooplankton matrices. The species matrix contained

Hellinger transformed abundances per microphytoplankton taxonomic units. Before variation partitioning, it was checked there was no strong linear dependencies between the environmental variables (sea water temperature, salinity, turbidity, SSI, Heq, DEP, Pycn) and problem of multicollinearity using a correlation matrix chart based on Pearson correlation coefficient and by calculating the variance inflation factor (VIF) of each environmental variable (Borcard et al., 2018). A cut-off value of VIF > 5 was applied to identify highly collinear variables (Legendre and Legendre, 2012). A redundancy analysis (RDA) was then performed to relate these environmental variables to the species matrix using the function "rda" available in the R vegan package (Oksanen et al., 2018). The significance of the RDA was tested using the function "anova.cca" (vegan package). A forward selection model with Monte Carlo permutation tests (with 9999 permutations) was performed with the function "forward.sel" from the R adespatial package (Dray et al., 2016) to select environmental variables explaining a significant variation in microphytoplankton communities ($p<0.05$). The spatial coordinates of sampling stations were used to quantitatively describe spatial patterns of microphytoplankton community by generating Principal Coordinates of Neighbour Matrices (PCNM, Borcard and Legendre, 2002) with the function "pcnm" (vegan package). Significant PCNM vectors were selected using the procedure previously applied for environmental variables (i.e. RDA, anova.cca and forward.sel). Variation partitioning with RDA was finally performed using the species matrix, environmental matrix containing the significant environmental variables, spatial matrix containing the significant PCNM vectors and zooplankton matrix containing mesozooplankton biomass. RDA-adjusted R^2 values were obtained and the significance of each fraction was tested with a permutation test for redundancy analysis.

Random forest regression models were used to define which processes (biotic interactions with the other phytoplankton taxonomic units, environmental conditions, spatial processes or mesozooplankton) influenced abundance of the microphytoplankton species

identified by the SIMPER analysis as responsible for the changes in community structure. For each responsible taxonomic unit, five models were built to relate abundance of the responsible taxonomic unit to 1) abundance of the other responsible taxonomic units, 2) abundance of the other taxonomic units not involved in the community changes, 3) environmental conditions, 4) PCNM vectors (space) and 5) zooplankton (biomass or abundance of mesozooplankton). Random forest regressions were performed with the function "randomForest" available in the R RandomForest package (Liaw and Wiener, 2002). For each of the 5 models, a random forest of 500 trees was built. Three variables were randomly sampled as candidates at each split. The percentage of variation explained by each model was then compared to define the most influencing processes.

Realized ecological niche and sub-niches

As delineated by Hutchinson (1957), the ecological niche of a species is defined as a n-dimensional hypervolume of favorable environmental (biotic and abiotic) conditions allowing the species to survive and reproduce. These dimensions include both scenopoetic and bionomic niche axes (Hutchinson, 1978). Scenopoetic axes set the bioclimatic environmental conditions in which a species performs while bionomic axes correspond to the resources used by this species. The fundamental ecological niche is the hypervolume that permits growth and persistence. It is determined by the species physiological range of tolerance to environmental factors in the absence of biotic interactions (Soberon and Arroyo-Peña, 2017). Because of biological interactions, a species hardly ever realizes the full size of its fundamental niche. The hypervolume it actually occupies is thus called the realized niche. This is a subset of its fundamental niche restricted by biotic interactions like interspecific competition or predation. It corresponds to the conditions under which the species can be observed (Brun et al., 2015).

The Outlying Mean Index (OMI, Dolédec et al., 2000) and Within Outlying Mean Indexes (WitOMI, Karasiewicz et al., 2017) were used to define the realized ecological niche and realized sub-niches of phytoplankton taxonomic units. The OMI and WitOMI analyses were both carried out in R (R Core Team, 2016). The OMI analysis was performed using the "niche" and "rtest" functions available in the R ade4 package (Dray and Dufour, 2007) while the WitOMI analysis was performed with the R subniche package (Karasiewicz et al., 2017). The OMI and WitOMI analyses were both based on a principal component analysis (PCA) performed on environmental parameters and a data frame containing fourth root transformed phytoplankton abundances.

The OMI is a multivariate method characterizing the realized ecological niche of each taxonomic unit within an environmental space. The realized niche is characterized by three parameters: niche position, niche breadth and residual tolerance. Niche position (or marginality) is the distance between the average habitat conditions used by the taxonomic unit and the average habitat conditions of the study area. Niche position of each taxonomic unit depends on its deviation from the distribution of a theoretical ubiquitous taxonomic unit that is uniformly distributed within the study area and tolerates the most general environmental conditions. It corresponds to the niche center of gravity. Taxonomic units with a high marginality occupy a marginal niche and occur in atypical habitats within the study area. Inversely, those with a low marginality occupy a non-marginal niche and occur in the typical average habitat conditions encountered within the study area. Niche breadth (or tolerance) describes variability in the conditions used by each taxonomic unit. Taxonomic units with a high tolerance can persist under a wide range of environmental conditions. They are generalists. Inversely, those with a low tolerance are specialists and are encountered under specific environmental conditions. A residual tolerance is also provided by the analysis. It represents the niche variance that is not taken into account by the marginality and helps to determine the reliability of a set of

environmental conditions in the niche definition. The OMI analysis is accompanied by a test defining the statistical significance of the marginality. It compares the observed marginality to the distribution of 1000 random marginality values obtained by permutations under the null hypothesis that the taxonomic unit is indifferent to its environment. If the observed marginality is greater or lower than marginality values obtained by permutations, the null hypothesis can be rejected. The OMI analysis provides several graphics. The first graphic represents the projection of environmental variables on the first two first axes of the OMI. The second graphic represents the projection of the niche position of each taxonomic unit on the two first axes of the OMI. The third graphic represents with polygons the realized niche of each taxonomic unit within the environmental space (called "realized environmental space" in Karasiewicz et al., 2017) on the plane defined by the OMI axes (for more details see Fig. S1 in supplementary materials).

The WitOMI analysis uses the environmental space defined by the OMI axes as a reference and decomposes the realized ecological niche of each taxonomic unit into realized sub-niches to take into account temporal and/or spatial subsets in the sampling design. This offers the possibility to monitor realized niche variations in time and/or space. For each subset studied, two additional marginalities are provided. $WitOMI_G$ is the distance between the average habitat conditions used by the taxonomic unit within the studied subset and the average habitat conditions of the whole study area. $WitOMI_{Gk}$ is the distance between the average habitat conditions used by the taxonomic unit within the studied subset and the average habitat conditions used by the community within the same subset. Each of these marginalities is accompanied by tolerance ($Tol_{WitOMIG}$ and $Tol_{WitOMIGk}$) and residual tolerance values. Associated Monte Carlo permutation tests define the significance of $WitOMI_G$ and $WitOMI_{Gk}$ (see Karasiewicz et al., 2017 for more details). Graphically for each taxonomic unit, the WitOMI results are represented by polygons corresponding to the 1) environmental conditions

within each subset (sub-environmental space called "subset realized environmental space" in Karasiewicz et al., 2017), 2) potential sub-niche within each subset (called "existing fundamental sub-niche" in Karasiewicz et al., 2017), 3) realized sub-niche within each subset and 4) biological constraints. The potential sub-niche is the intersection between the sub-environmental space within the subset and the realized niche coming from the OMI analysis. Biological constraints due to biotic interactions correspond to size differences between the potential sub-niche and realized sub-niche (supplementary materials, Fig. S1). The goal of each multivariate analysis used in this publication is summarized in supplementary materials, Table S2.

3. Results

3.1 Abiotic environmental conditions

Seawater temperature varied significantly through time (PERMANOVA, $p<0.05$) and no persistent spatial trend was observed over the decade. There were significant interactions between the sampling year and coastal-offshore waters as well as between the sampling year and sampling depths (PERMANOVA, $p<0.05$). Seawater temperature was significantly higher in surface (mean = 14.8°C) than at depth (mean = 12.1°C) and there was a significant difference in temperature between the coastal and offshore waters and between transects (i.e. between the northern and southern parts of the Bay) (PERMANOVA, $p<0.05$). Surface seawater temperature ranged from 11.3°C to 19.8°C. The highest surface seawater temperature was observed in 2003, 2007 presented intermediate values and the other years were colder (Fig. 2A). Bottom seawater temperature ranged from 10.0°C to 14.5°C and showed lower values in 2005-2006 than during the other sampling years (Fig. 2B).

Seawater salinity ranged from 26.1 to 36.4 (Fig. 2C). Spatially, seawater salinity was influenced by the plumes of the Loire, Gironde and Adour estuaries and presented a gradient with significantly higher salinity values in offshore (mean = 35.5) than in coastal waters (mean = 34.2, PERMANOVA $p<0.05$) (supplementary materials, Fig. S2). Within the water column, salinity was significantly lower in surface (mean = 34.4) than at depth (mean = 35.3, PERMANOVA $p<0.05$). By contrast, no significant difference was observed between transects and temporal variations were not significant (PERMANOVA, $p>0.05$) (Fig. 2C).

Equivalent freshwater depth (Heq) ranged from 0 to 2.07 m. Heq was also influenced by the estuarine plumes but presented a gradient with higher values in coastal (mean = 0.79 m) than in offshore waters (mean = 0.04 m) (supplementary materials, Fig. S3). No significant difference was observed between transects (PERMANOVA, $p>0.05$). Mean Heq respectively decreased in 2006 and increased in 2014 (Fig. 2D).

Deficit of potential energy (DEP) ranged from 0.7 to 203.3 kg m^{-1} s^{-2}. DEP did not show persistent spatial trend over the decade (data not shown). There was significant interactions between the sampling year and coastal-offshore waters as well as between the

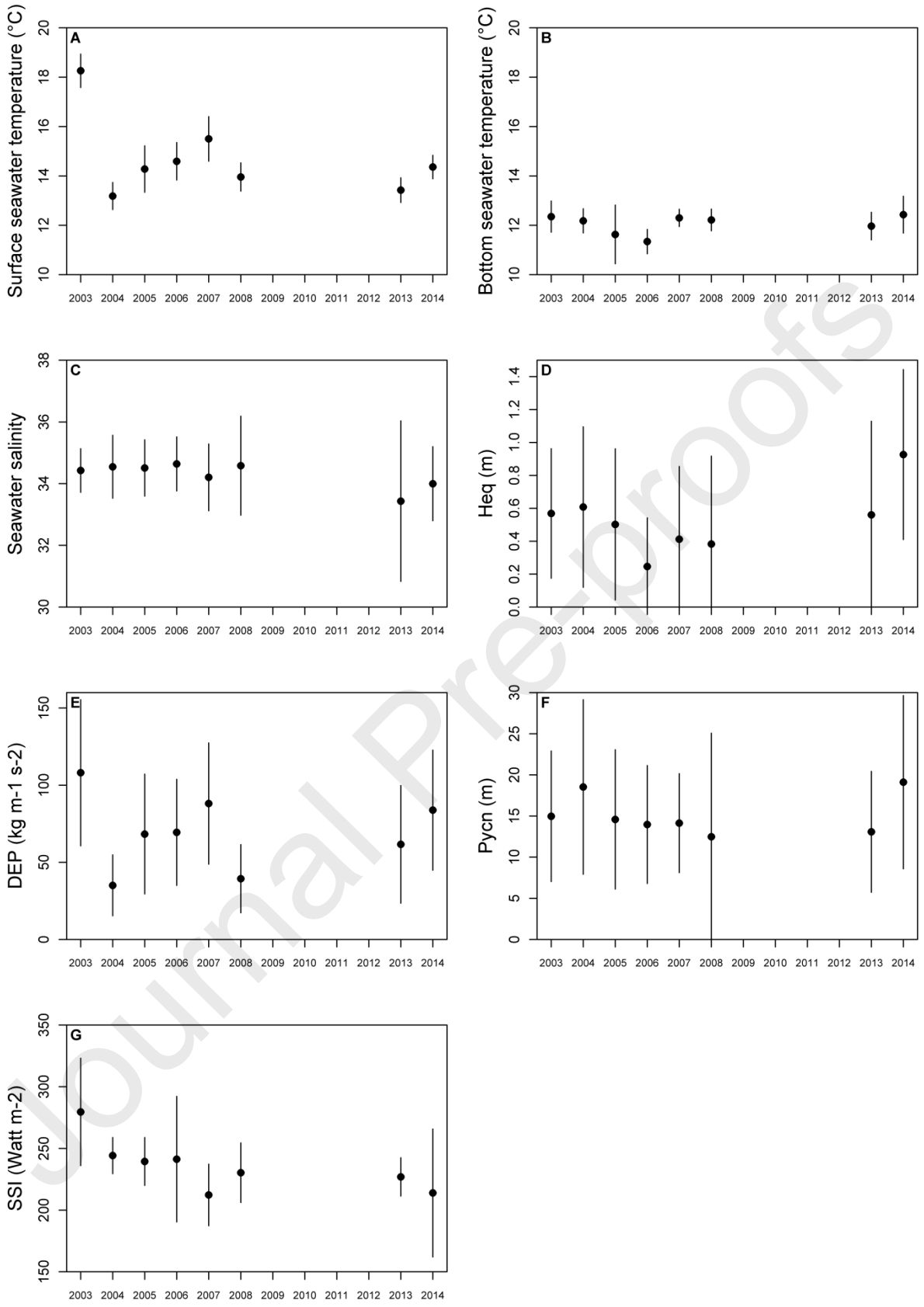

Fig. 2: Temporal variations of (A) surface seawater temperature, (B) bottom seawater temperature, (C) seawater salinity, (D) equivalent freshwater depth (Heq), (E) deficit of potential energy (DEP), (F) pycnocline depth (Pycn) and (G) sea surface irradiance (SSI). Data are mean ± standard deviation

sampling year and transects (PERMANOVA, $p<0.05$). DEP was high in 2003, low in 2004 and 2008 and intermediate in 2005-2007 and 2013-2014 (Fig. 2E).

Pycnocline depth (Pycn) ranged from 1 to 49 m. Pycn did not show persistent spatial trend but in 2004 and 2014, Pycn increased gradually from coastal (mean = 10.5 m) to offshore waters (mean =18.54 m, PERMANOVA, $p<0.05$) (supplementary materials, Fig. S4). Spatial differences between transects and temporal variations were not significant (PERMANOVA, $p>0.05$) (Fig.2F).

Sea surface irradiance (SSI) ranged from 138.5 to 336.7 Watt m^{-2} (Fig. 2G). SSI showed no persistent spatial patterns over the decade but was significantly high in 2003 and low in 2014 (PERMANOVA, $p<0.05$).

3.2 Microphytoplankton diversity and community structure

A total of 163 taxonomic units were found from 2003 to 2014. Shannon diversity index (H) ranged from 1.0 to 24.1. Pielou's evenness (J') ranged from 0.03 to 0.98. The total number of species, H and J' all varied significantly between sampling years (PERMANOVA, $p<0.05$) while spatially, they showed different patterns. The total number of species was relatively stable from 2003 to 2006, increased in 2007 and was intermediate in 2013-2014 (Fig. 3A). It decreased significantly from coastal to offshore waters (PERMANOVA, $p<0.001$) (supplementary materials, Fig. S5). The lowest H and J' were observed in 2006 and 2013-2014 (Fig. 3B). H only varied significantly within the water column (PERMANOVA, $p<0.05$) and was higher at depth (mean = 6.0) than in surface waters (mean = 4.4). J' also varied significantly within the water column (PERMANOVA, $p<0.001$) with higher values at depth (mean = 0.61) than in surface waters (mean = 0.51). However contrary to H, the interaction between the factors: sampling periods and coastal/offshore waters was significant (PERMANOVA, $p<0.05$). In

surface, in 2003 and 2013, J' decreased gradually from coastal to offshore waters (supplementary materials, Fig. S6). In 2006, the gradient was reversed: J' increased gradually from coastal to offshore waters. In 2004, 2005, 2007, 2008 and 2014, J' distribution from coastal to offshore waters differed between the parts of the Bay north and south of the Gironde estuary. In 2005 and 2014, north of the Gironde estuary, J' increased gradually from coastal to offshore waters while in the south, it decreased from coastal to offshore waters. The opposite trend was observed in 2007 and 2008. In 2004, there was not a real gradient in J'. North of the Gironde estuary, J' was higher at some coastal stations than at offshore stations while in south, it was higher at some offshore stations than at coastal stations.

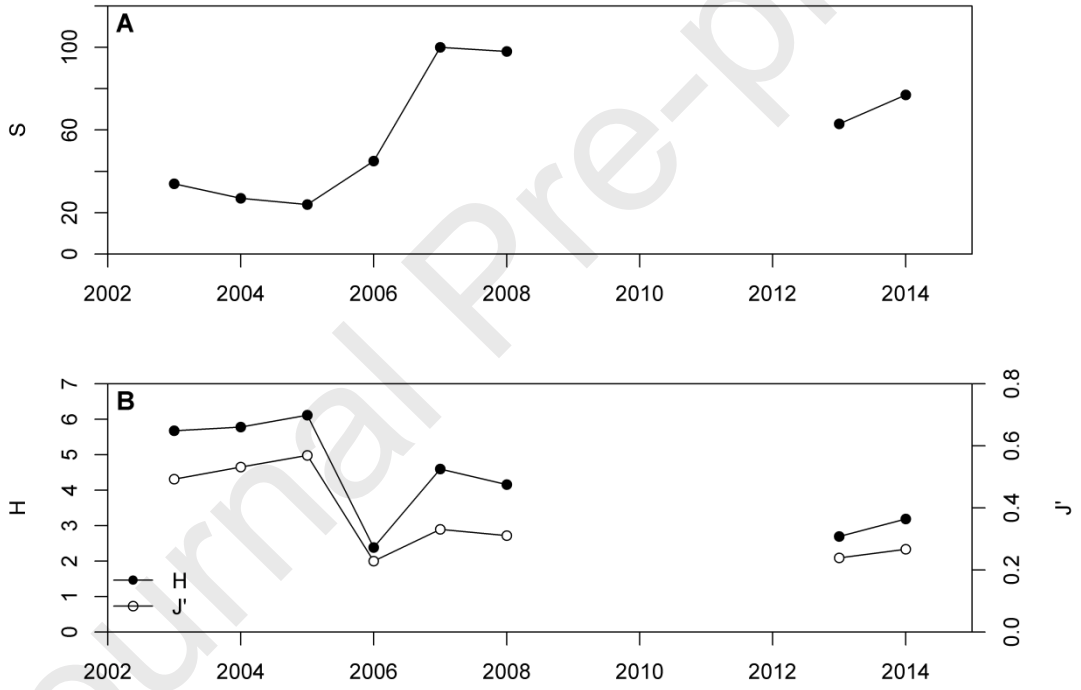

Fig. 3: Temporal variations of (A) the total number of species, (B) numbers equivalent of Shannon diversity index (H) and (C) Pielou's evenness (J')

Total microphytoplankton abundance (Fig. 4A) was significantly higher in 2004 (PERMANOVA, $p<0.005$). In comparison to the mean decadal value, it was lower in 2003 and 2005 (one sample t-test, $p<0.001$) and higher in 2004 (one sample t-test, $p=0.001$).

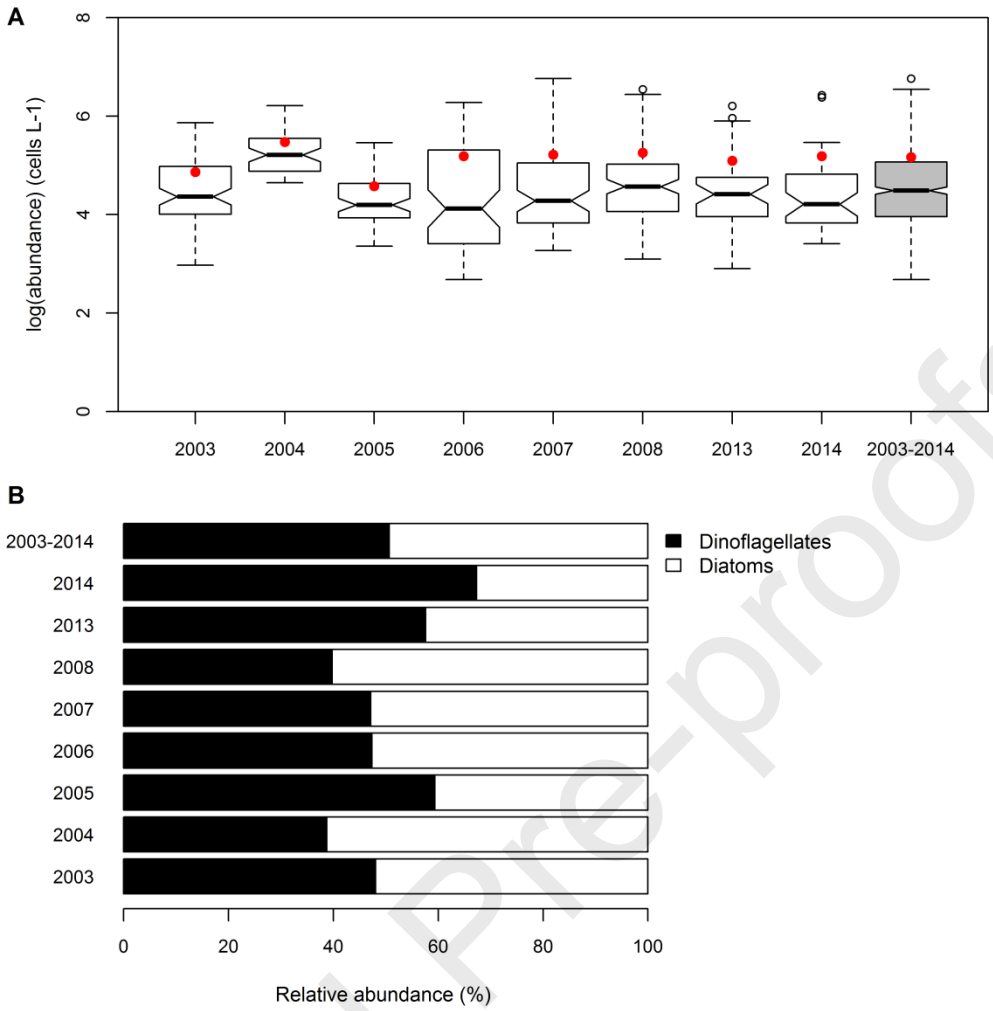

Fig. 4: Temporal variations of microphytoplankton (A) abundance and (B) community composition. Red dots in (A) represent the mean microphytoplankton abundance. Open circles are outliers. Whiskers correspond to Q1 - 1.5 x interquartile range and Q3 + 1.5 x interquartile range

From 2006 to 2014, it was close to the mean decadal value (one sample t-test, $p>0.05$). Spatial distribution of total microphytoplankton abundance showed different patterns from one year to another with significant interactions between the factors: sampling periods, coastal/offshore waters and transects (PERMANOVA, $p<0.05$). In 2003 and from 2005 to 2008, there were coastal-offshore gradients in total microphytoplankton abundance distribution (supplementary materials, Fig. S7). In 2003, 2005, 2006 and 2007, total microphytoplankton abundance increased from coastal to offshore waters while in 2008, the gradient was reversed. In 2004, only the part of the Bay south of the Gironde estuary showed a gradient in total

microphytoplankton abundance with higher values in coastal than in offshore waters. In 2013 and 2014, total microphytoplankton abundance varied with latitude and was higher in the northern part of the sampling area.

The relative proportions of diatoms and dinoflagellates varied through time (Fig. 4B). Diatoms proportions ranged from 32.66% in 2014 to 61.24% in 2004 while dinoflagellates ranged from 38.76% in 2004 to 67.34% in 2014. The highest proportions of dinoflagellates were observed in 2005, 2013 and 2014. Spatially, relative proportions of dinoflagellates and diatoms were distributed along coastal-offshore gradients with more diatoms in coastal than in offshore waters in 2003, 2005, 2006 and 2007 (supplementary materials, Fig. S8). In 2013 and 2014, they were rather distributed along a north-south axis with diatoms mainly present north of the sampling area.

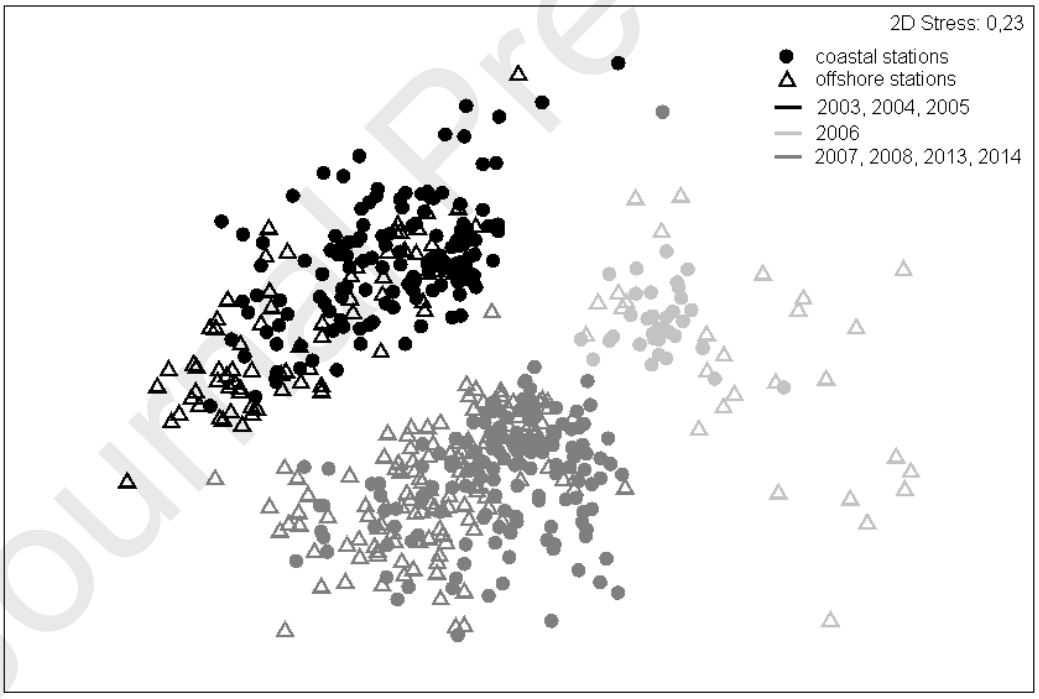

Fig. 5: Non-metric multidimensional scaling (nMDS) of microphytoplankton communities based on Bray-Curtis similarities

Non-metric multidimensional scaling analysis (Fig. 5) separated three groups in microphytoplankton community structure (group 1: 2003-2005, group 2: 2006 and group 3:

2007-2014) and highlighted that temporal changes were stronger than spatial differences. ANOSIM analysis confirmed the significance of temporal changes in community structure between groups 1, 2, 3 ($R = 0.71$, $p = 0.001$) and the low spatial differences. There were significant differences between the coastal and offshore stations ($R = 0.13$, $p = 0.001$) but not between transects (i.e. between the communities located in the northern and southern part of the Bay, $R = 0.04$) and within the water column (between surface and bottom depths, $R = 0.06$).

Dissimilarity between groups 1 and 2, 2 and 3, and 1 and 3 was respectively 97.51%, 94.17% and 86.45% (SIMPER analysis, supplementary materials Table S3). 28 taxonomic units were involved in the dissimilarity between these 3 groups (see supplementary materials Table S3 for a list of these taxonomic units and codes). Among them, 5 taxonomic units (*Pseudo-nitzschia* spp. (*Ps*), *Gymnodinium* spp. + *Gyrodinium* spp. (*Gg*), *Leptocylindrus danicus* (*Ldc*), *Leptocylindrus minimus* (*Lem*) and *Chaetoceros* sp. (*Ch*)) were the main contributors to these community changes. Indeed, they explained: 72.63% of the dissimilarity between groups 1 and 2, 61.61% of the dissimilarity between groups 2 and 3 and 69.97% of the dissimilarity between groups 1 and 3. *Ps* average abundance increased significantly from 2003-2005 to 2006 (Mann Whitney U test, $p<0.001$) (Fig. 6). From 2006 to 2007-2014, *Ps* average abundance decreased significantly (Mann Whitney U test, $p<0.001$) but remained higher in 2007-2014 than in 2003-2005. Inversely, *Gg*, *Ldc* and *Ch* average abundance decreased significantly from 2003-2005 to 2006 (Mann Whitney U test, $p<0.001$) and recovered from 2006 to 2007-2014. *Lem* was present in 2003-2005, disappeared in 2006 and came back in 2007-2014 but with a significantly lower average abundance (Mann Whitney U test, $p<0.001$) in 2007-2014 than in 2003-2005. Temporal changes were also observed in dominant taxonomic unit. The dominant taxonomic units were: *Lem* in 2003-2005, *Ps* in 2006 and *Ldc* in 2007-2014.

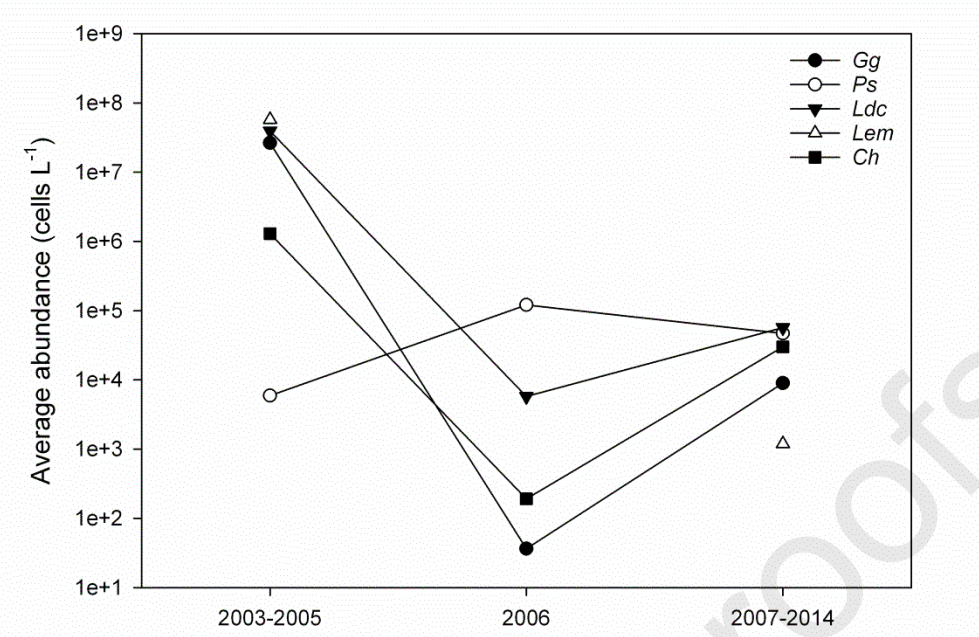

Fig. 6: Average abundance of *Gymnodinium* spp. + *Gyrodinium* spp. (*Gg*), *Pseudo-nitzschia* spp. (*Ps*), *Leptocylindrus danicus* (*Ldc*), *Leptocylindrus minimus* (*Lem*) and *Chaetoceros* sp. (*Ch*) in 2003-2005, 2006 and 2007-2014

3.3 Processes structuring microphytoplankton communities

RDA and forward selections resulted in the selection of 6 environmental variables and 5 spatial variables (out of a total of 59 PCNM vectors) explaining a significant variation in microphytoplankton communities (Table 2). Variation partitioning showed that microphytoplankton community structure (Fig. 7) was better explained by environmental conditions (8.9%) than spatial processes (4.3%) or mesozooplankton biomass (0.6%). The shared effect between environmental conditions and spatial processes was the highest (2.2%) followed by the shared effect of the 3 factors (environmental conditions, spatial processes and mesozooplankton biomass, 1.7%). Shared effects between environmental conditions and mesozooplankton biomass and between spatial processes and mesozooplankton biomass were equal (0.3%). Shared effects of environmental conditions and spatial processes operated at broad and intermediate scales as PCNM1, PCNM4, PCNM6 (corresponding to the broad scale) and PCNM14 (corresponding to the intermediate scale) were significantly related to

Table 2: Results of forward selection of environmental variables and PCNM vectors explaining a significant variation in microphytoplankton communities and variance inflation factors (VIF) for each variable included in variation partitioning

	Variables	F	Cumulative Adjusted R^2 (%)	P value	VIF
Environmental variables	Heq	9.37	4.30	0.0001	2.49
	Dep	8.60	8.08	0.0001	1.42
	Ssi	4.10	9.60	0.0005	1.08
	Temp	4.22	11.16	0.0004	1.35
	Sal	3.56	12.40	0.0013	2.99
	Pycn	2.41	13.07	0.0147	1.16
Spatial variables	PCNM4	7.78	3.52	0.0010	1.00
	PCNM58	3.36	4.73	0.0030	1.00
	PCNM1	3.32	5.92	0.0020	1.00
	PCNM14	2.88	6.88	0.0060	1.00
	PCNM6	2.47	7.62	0.0170	1.00

Heq = equivalent freshwater depth, Dep = deficit of potential energy, Ssi = sea surface irradiance, Temp = seawater temperature, Sal = salinity and Pycn = pycnocline depth. VIF were all <3 indicating there was no problem of multicollinearity in the RDA models used to perform variation partitioning. For zooplankton, mesozooplankton biomass was the only variable. Consequently, no forward selection was applied on mesozooplankton biomass and it was not possible and useful to calculate variance inflation factors.

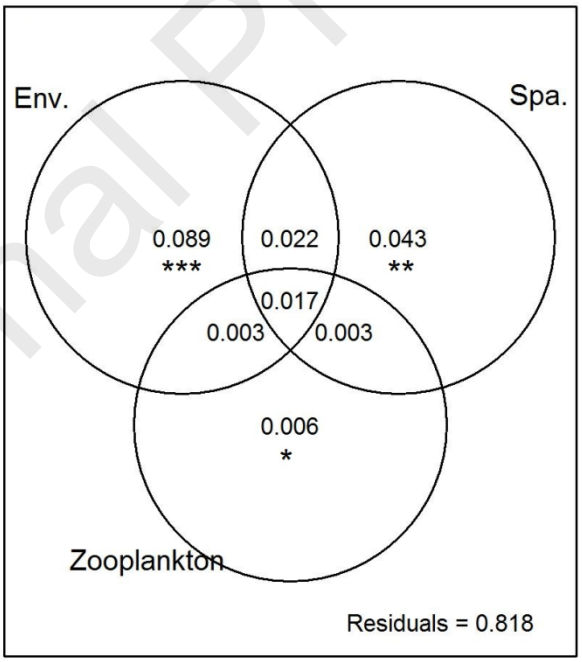

Fig. 7: Venn diagram presenting variation partitioning results. Shown are the relative contributions of environmental conditions, spatial processes and zooplankton biomass, as well as their shared effects, in explaining variation in microphytoplankton communities. Statistically significant pure fractions are indicated as: *** for $P \leq 0.001$, ** for $P \leq 0.01$ and * for $P \leq 0.05$. Env. = environmental conditions. Spa. = spatial processes. Zooplankton = zooplankton biomass environmental conditions. PCNM1 and PCNM14 were related to equivalent freshwater depth

(Heq, respectively adjusted $R^2 = 0.09$, $p = 0.001$; adjusted $R^2 = 0.06$, $p = 0.001$). PCNM4 was

related to Heq, deficit of potential energy (Dep) and sea surface irradiance (Ssi) (adjusted R^2 = 0.25, $p<0.001$). PCNM6 was related to Heq, salinity, pycnocline depth (Pycn) and seawater temperature (Temp) (adjusted R^2 = 0.10, $p<0.001$). Only the PCNM vector at fine scale (PCNM58) was not related to environmental conditions.

Table 3: Percentage of variation in abundance of each taxonomic unit involved in community structure changes explained by the different random forest-based models

TU	Responsible TU	Other TU	Zooplankton	Environment	Space
Ch	15.04	17.08	—	11.02	4.41
Gg	69.66	56.94	—	26.30	12.06
Ldc	41.99	22.91	—	25.24	—
Lem	56.65	51.16	—	16.54	—
Ps	22.90	20.83	12.90	14.47	—
Ams	59.67	41.58	1.61	28.98	—
Cep	3.55	7.10	—	6.32	—
Ces	8.63	0.35	10.43	—	—
Cfu	31.11	30.32	—	40.01	—
Cef	30.73	24.54	—	11.46	—
Clm	27.14	29.98	—	0.63	—
Cet	12.51	5.68	—	6.34	—
Cyc	10.90	32.95	—	—	—
Dd	59.06	56.07	—	8.79	—
Gs	70.14	74.99	—	23.36	—
Kag	64.65	69.04	1.48	29.79	—
Kat	48.55	53.41	—	27.25	—
Men	—	0.04	—	—	—
Nfh	—	9.44	—	4.22	—
Ns	16.18	10.27	—	7.60	—
Pa	43.60	50.57	0.36	20.62	2.86
Prs	19.58	11.74	—	—	—
Rhi	37.76	38.80	—	—	—
Rhe	19.26	3.95	—	—	—
Sc	22.44	28.32	—	11.94	—
To	33.68	32.21	—	23.79	—

TU = taxonomic unit(s), Responsible TU = abundance of the other microphytoplankton species identified by the SIMPER analysis as responsible for the changes in community structure, Other TU = abundance of the other microphytoplankton species not involved in community structure changes, — = non significant

The taxonomic units that were identified by RDA as the most strongly impacted by environmental conditions and, thus drove the changes in microphytoplankton community structure, were: *Gg*, *Ps*, *Ch*, *Lem* and *Ldc* (supplementary materials Fig. S9).

Random forest-based regression models (Table 3) revealed that 86% (24 in 28) of the taxonomic units involved in community changes were more accurately related to the others taxonomic units than environmental conditions, spatial processes or mesozooplankton. Only *Cfu* was better explained by environmental conditions. Only 2 taxonomic units (*Ps* and *Ces*) presented a high percentage of variation explained by mesozooplankton. Spatial processes influenced 3 taxonomic units (*Ch*, *Gg* and *Pa*) but the percentage of variance explained was always lower than the variance explained by the models based on interactions with the other taxonomic units.

3.4 Microphytoplankton realized ecological niche and sub-niches

OMI analysis

The first two axis of the OMI analysis explained 73.24% of total inertia (i.e. 73.24% of total variation of the dataset Fig. 8A). The first axis (OMI1) represented 57.02% of total inertia and the second (OMI2) 16.22%. OMI1 was mainly explained by salinity and Heq. OMI2 was explained by temperature and sea surface irradiance (SSI). Among the 5 taxonomic units contributing the most to the community structure changes between 2003-2005, 2006 and 2007-2014, *Gg* had the lowest marginality and *Lem* the highest (Table 4).

Tolerance was, however, the highest for *Gg* and the lowest for *Ps*. Along OMI1, *Lem*, *Ch* and *Ldc* had their realized ecological niche centered at higher Heq (and thus lower salinity) than *Ps* and *Gg* (Fig. 8B). The realized ecological niches of these taxonomic units were distributed along OMI2 according to the species temperature and light preferences. *Lem* and *Ch* had their realized ecological niche centered at higher temperature and light conditions than *Ps* while *Gg* and *Ldc* were found at intermediate light and temperature conditions.

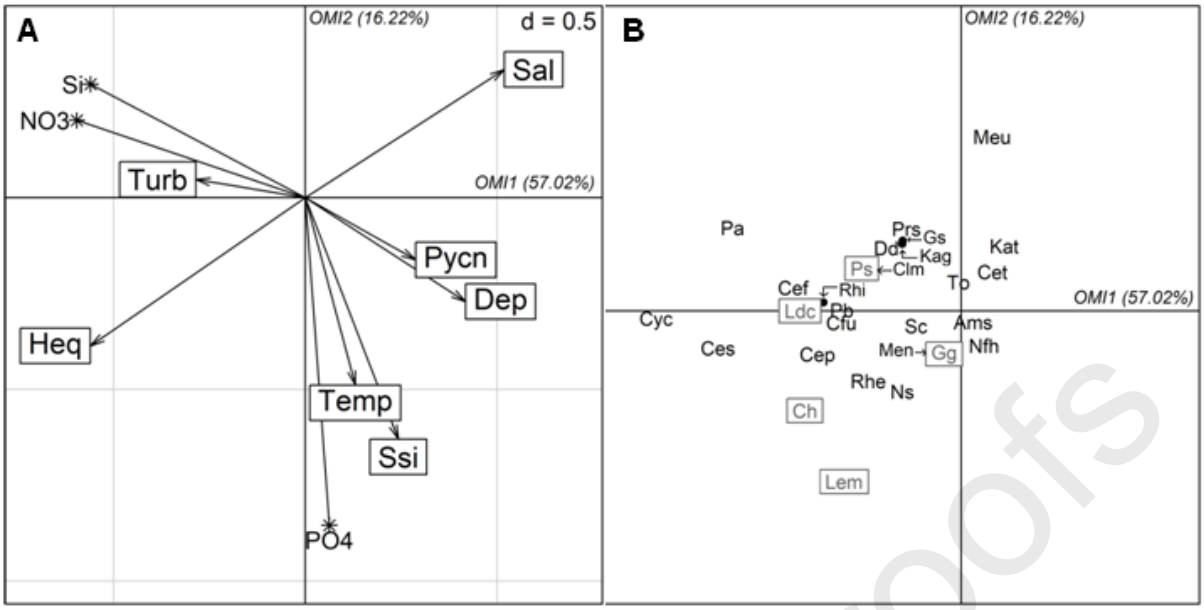

Fig. 8: OMI analysis. (A) Projection of environmental variables on the first two axes. Labels surrounded by rectangles represent active variables while labels with stars are supplementary variables. Si = silicate concentration, NO3 = nitrate concentration, Sal = salinity, Turb = turbidity, Pycn = pycnocline depth, Dep = deficit of potential energy, Heq = equivalent freshwater depth, Temp = temperature, Ssi = sea surface irradiance, PO4 = phosphate concentration. (B) Projection of species niche position on the first two axes. Only the 28 taxonomic units contributing to the dissimilarity between the three groups highlighted by the nMDS analysis (2003-2005, 2006 and 2007-2014) are represented. Codes of taxonomic units name are defined in table 1. To avoid labels overlay, the position of some taxonomic units is represented by arrows. Labels of *Gymnodinium* spp. + *Gyrodinium* spp*., Pseudo-nitzschia* spp., *Leptocylindrus danicus, Chaetoceros* sp. and *Leptocylindrus minimus* are surrounding by rectangles and written in grey to highlight their position

Table 4: OMI niche parameters

Taxonomic units	Code	Inertia	Marg.	Tol.	Rtol	P
Chaetoceros sp.	*Ch*	7.24	0.66	1.49	5.09	0.01
Gymnodinium spp. + *Gyrodinium* spp.	*Gg*	7.29	0.04	1.55	5.71	0.01
Leptocylindrus minimus	*Lem*	8.00	0.82	1.24	5.93	0.01
Leptocylindrus danicus	*Ldc*	6.80	0.50	1.00	5.30	0.01
Pseudo-nitzschia spp.	*Ps*	6.60	0.28	0.93	5.39	0.01

Marg. = marginality. Tol. = tolerance. Rtol. = residual tolerance. P = P value

WitOMI analysis

The WitOMI analysis showed that environmental conditions varied between the 3 periods (subsets) defined by nMDS analysis (2003-2005, 2006 and 2007-2014) (Fig. 9).

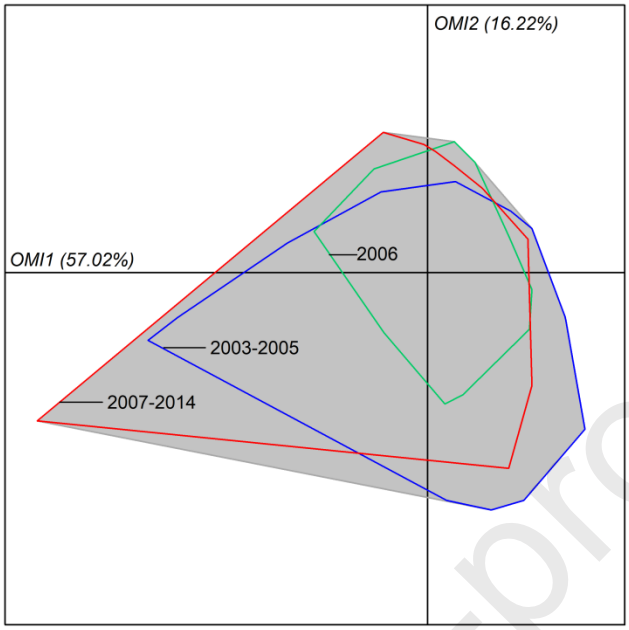

Fig. 9: WitOMI analysis showing the environmental space in grey and available environmental conditions (sub-environmental space) in 2003-2005 (blue polygon), 2006 (green polygon) and 2007-2014 (red polygon)

In 2003-2005 and 2007-2014, among the 5 taxonomic units contributing the most to the community structure changes, *Gg* had the lowest marginality ($WitOMI_g$) in 2003-2005 and 2007-2014 and the highest tolerance ($Tol_{WitOMIG}$) in 2003-2005 but not in 2007-2014 (Table 5). Its realized sub-niche was not significantly different from the niche of a theoretical ubiquitous species uniformly distributed within habitat conditions and it took up the totality of its potential sub-niche (Fig. 10A, C). By contrast, the realized sub-niches of *Ps* (Fig. 10D, F), *Ldc* (Fig. 10G, I), *Ch* (Fig. 10J, L) and *Lem* (Fig. 10M, N) differed significantly from the niche of a theoretical ubiquitous species. *Ps*, *Ldc, Ch* and *Lem* occupied only partially their potential sub-niche with a percentage of occupation higher in 2003-2005 than in 2007-2014 (Table 5).

The year 2006 was the period with the narrowest range of environmental variables. Environmental conditions were therefore potentially more restrictive for some microphytoplankton species. *Lem* was not detectable during this period. The realized sub-niches

of *Ps* (Fig. 10E) and *Ldc* (Fig. 10H) were not significantly different from the niche of a theoretical ubiquitous species. *Ps* took up the totality of its potential sub-niche while *Ldc* occupied 61.61% of its potential sub-niche. Among the 5 taxonomic units contributing the most to the community changes, it was *Ps* which had the lowest $WitOMI_g$ and highest $Tol_{WitOMIG}$ during this period. The realized sub-niche of *Gg* (Fig. 10B) and *Ch* (Fig. 10K) differed significantly from the niche of a theoretical ubiquitous species and they respectively occupied 47.61% and 28.79% of their potential sub-niche.

Niche overlaps

Among the 47 taxonomic units present in 2003-2005, *Gg* had the largest realized sub-niche and this sub-niche covered 100% of the realized sub-niche of all the other taxonomic units. In addition to *Gg* only 5 taxonomic units took up the totality of their potential sub-niche (supplementary materials, Table S4). In 2006, it was *Ps* which had the largest realized sub-niche that covered 100% of the realized sub-niche of the 48 other taxonomic units present. In addition to *Ps,* only 2 taxonomic units occupied the totality of their potential sub-niche. In 2007-2014, *Gg* was again the taxonomic unit with the largest realized sub-niche. However, contrary to 2003-2005, its realized sub-niche did not completely covered the realized sub-niche of the 119 other taxonomic units present. In addition to *Gg*, 65 taxonomic units were thus able to take up the totality of their potential sub-niche.

Table 5: WitOMI$_G$ niche parameters

	2003-2005						2006						2007-2014					
TU	Inertia	Marg.	Tol.	Rtol	P	% N.O.	Inertia	Marg.	Tol.	Rtol	P	% N.O.	Inertia	Marg.	Tol.	Rtol	P	% N.O.
Ch	6.67	0.73	0.75	5.18	0.03	94.51	4.32	1.48	0.36	2.48	0.01	28.76	8.13	0.89	2.83	4.41	0.01	71.06
Gg	7.48	0.40	1.27	5.81	0.10	100.00	5.22	0.81	0.23	4.19	0.01	47.61	7.15	0.19	0.68	6.27	0.90	100.00
Lem	7.42	1.14	0.97	5.31	0.03	92.50							10.13	0.80	2.45	6.87	0.01	72.92
Ldc	6.43	1.04	0.63	4.76	0.01	92.28	4.04	0.42	0.41	3.20	0.65	61.61	7.21	0.55	0.91	5.74	0.01	65.66
Ps	6.71	0.69	0.65	5.38	0.02	83.78	5.02	0.26	0.72	4.03	0.95	99.86	7.32	0.59	0.74	5.99	0.01	80.10

TU = taxonomic units, Marg. = marginality. Tol. = tolerance. Rtol. = residual tolerance. P = P value. % N.O. = percentage of the potential sub-niche occupied

4. Discussion

4.1 Changes in microphytoplankton community structure

In the Bay of Biscay, over the period 2003-2013, Dessier et al. (2018) reported significant temporal modifications in mesozooplankton community structure with three main periods (2003-2006, 2007-2009 and 2010-2013) and a major change in terms of both abundance and taxonomic composition in 2006. In the same area, over a similar period (2003-2016), Véron et al. (2020) observed major temporal changes in sardine growth and body condition with three main periods (2003-2006, 2007-2011 and 2012-2016) and a significant decrease in body condition-at-age for all age classes in 2007. The reasons of these changes are not completely resolved but these studies pointed out the importance of trophic links in the control of sardine and mesozooplankton communities. They found significant relationships between phytoplankton chlorophyll *a* and both mesozooplankton (Dessier et al., 2018) and shifts in sardine body condition (Véron et al., 2020). It was therefore hypothesized that changes in mesozooplankton and sardine communities may have resulted at least in part from modifications in phytoplankton phenology or community structure (Dessier et al., 2018; Véron et al., 2020). However, since there was no data available in literature and because chlorophyll *a* is not a good indicator to highlight changes in phytoplankton community structure, it was not possible to confirm these hypotheses. With a thorough analysis of microphytoplankton taxonomic composition, the present study confirmed that significant modifications in spatio-temporal microphytoplankton total abundance, community structure and diversity occurred from 2003 to 2014. Three main periods with different community structure were also highlighted for microphytoplankton: 2003-2005, 2006 and 2007-2014. There were some spatial patterns in microphytoplankton abundance, diversity and community

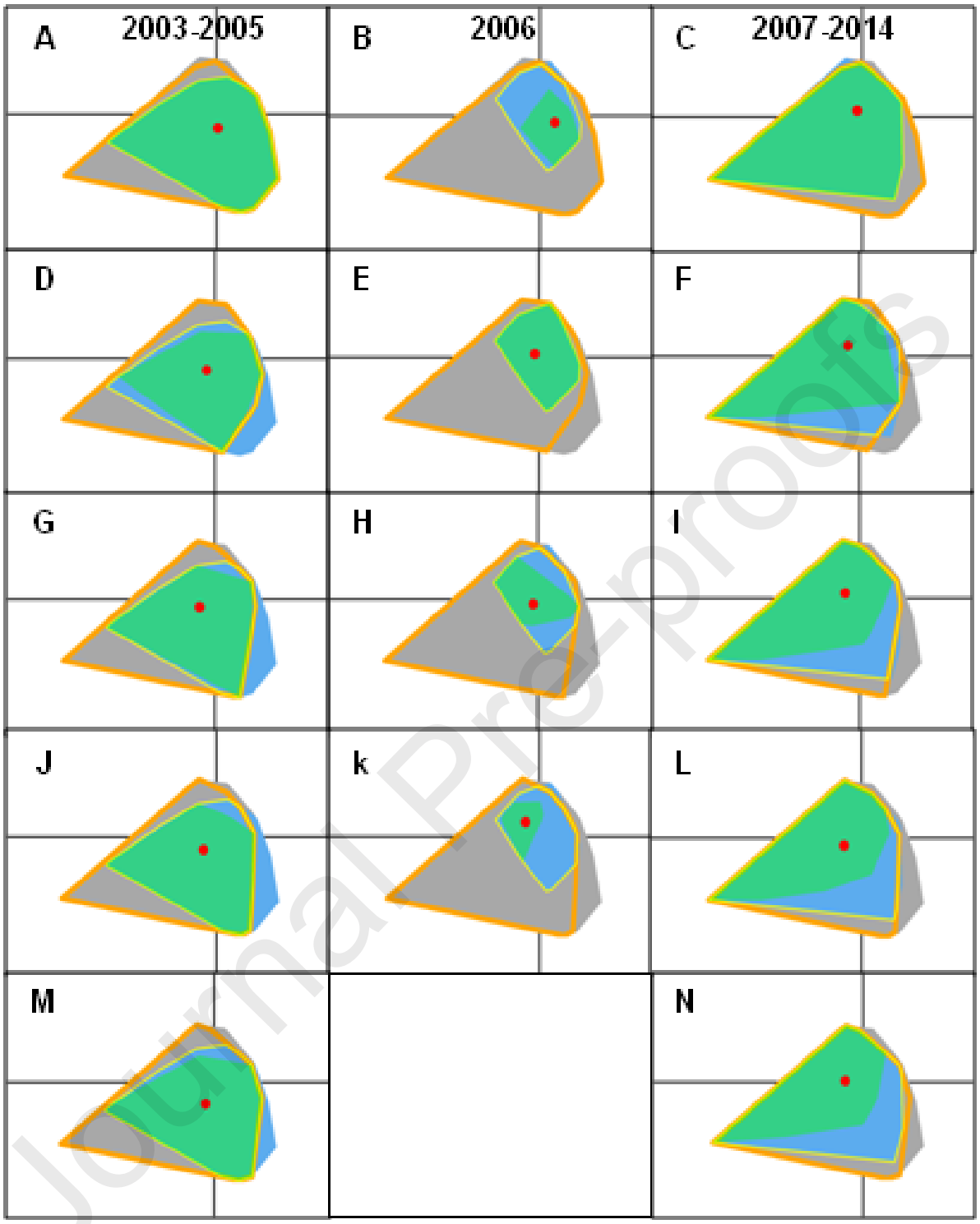

Fig. 10: WitOMI analysis. Sub-niches of *Gymnodinium* spp. + *Gyrodinium* spp. (A, B, C), *Pseudo-nitzschia* spp. (D, E, F), *Leptocylindrus danicus* (G, H, I), *Chaetoceros* sp. (J, K, L) and *Leptocylindrus minimus* (M, N) in subset 1 (2003-2005) (first column), subset 2 (2006) (second column) and subset 3 (2007-2014) (third column). Grey polygon = environmental space. Orange polygon = realized niche. Blue polygon = sub-environmental space. Yellow polygon = potential sub-niche. Green polygon = realized sub-niche. Red dot = $WitOMI_G$

structure but they were not stable through time. Temporal changes were thus more pronounced than spatial patterns at these sampling scales.

4.2 Relative role of environmental conditions, spatial processes and biotic interactions

Environmental conditions, spatial processes (through dispersal) and biotic interactions (including competition and predation) are often considered as the 3 main factors controlling phytoplankton community structure (Huszar et al., 2015; Naselli-Flores and Padisák, 2016). In the present study, environmental variables were the most influential factor followed by spatial processes. Also, spatial processes structuring microphytoplankton communities at broad and intermediate scales reflected the spatial distribution of environmental conditions mainly the riverine water discharges and physical properties of water masses (Dupuy et al., 2011). Only spatial processes at fine scale were not related to the environment. This indicates that microphytoplankton communities were not spatially structured by neutral processes that involve stochastic events and dispersal limitation of species with identical fitness (Hubbell, 2001; Huszar et al., 2015). Instead they were temporally and spatially structured by the environment. Such results correspond to communities structured by niche-based processes and support the main role of environmental filters (Leibold et al., 2004). The predominance of the environmental factors over spatial processes contrast with the findings of Zarauz et al. (2008) who reported that geographical location (latitude and longitude) was more relevant than hydrographic variables (temperature, salinity, stratification) to describe phytoplankton distribution in the Bay of Biscay. These differences can be explained by the fact that Zarauz et al. (2008) studied the relative effects of environmental and spatial variables by considering separately diatom chains (larger than 20 µm) and ciliates (larger than 50 µm) biomass. The present study analyzed these effects at the community scale based on cell counts per species or

genera of diatoms and dinoflagellates. Data set of the present study comprised samples collected at three depths (subsurface = 5 m, depth of maximum fluorescence and bottom) while the samples of Zarauz et al. (2008) were collected at a single depth (3 m). In addition, the temporal scale was not the same. Zarauz et al. (2008) studied three years (2004, 2005 and 2006) while the present study included 8 years (2003, 2004, 2005, 2006, 2007, 2008, 2013 and 2014). Finally, the environmental and spatial variables tested were not exactly the same. In addition to temperature, salinity and stratification, the present study included sea surface irradiance, pycnocline depth and equivalent freshwater depth and for spatial variables, it used PCNM i.e. it tested spatial processes at several scales.

In comparison to environmental conditions and spatial processes, impact of mesozooplankton on microphytoplankton community structure seemed to be weaker but it was significant and cannot be overlooked. Few studies investigated, at the same time, the effects of environmental conditions, spatial processes and zooplankton in variation partitioning of phytoplankton communities but, the available results were in line with the present study (Guo et al., 2019; Yang et al., 2018a). This is also in accordance with the Zarauz et al. (2008)'s results of generalized additive models (GAM) in the Bay of Biscay. A GAM based on mesozooplankton biomass explained only 7.6% of diatom biomass distribution while a GAM including latitude-longitude, water temperature and stratification explained 56.7%.

Like in other studies on phytoplankton communities (e.g. Beisner et al., 2006; Huszar et al., 2015; Soininen et al., 2007; Yang et al., 2018a; Yang et al., 2018b) a large part of variance in variation partitioning remained unexplained. This may be due to unmeasured explanatory environmental parameters. For instance, it was shown that winter mixing may influence intensity and duration of spring phytoplankton blooms in the Cantabrian Sea (a sub-area of the Bay of Biscay) (González-Gil et al., 2018). But it is also most likely due to the fact that competitive biotic interactions between phytoplankton taxonomic units were not directly

characterized in variation partitioning. Indeed, the random forest regressions made at the taxonomic unit scale showed that for 86% of the taxonomic units involved in the community changes, models based on abundance of the other phytoplankton taxonomic units explained a higher percentage of variation in their abundance than spatial, environmental and mesozooplankton models. These observations stress the need to study phytoplankton responses at the taxonomic units-specific level with a method considering biotic interactions to understand properly the underlying changes which ultimately affect phytoplankton community composition. Bode et al. (2015) also highlighted the need to study independently the responses of each phytoplankton species in the Galician upwelling and Yang et al. (2018a) pointed out the importance of considering interspecific biotic interactions within the phytoplankton community in a Chinese tropical reservoir.

4.3 Dynamics in microphytoplankton species ecological niches

Five taxonomic units (*Gymnodinium* spp. + *Gyrodinium* spp. (*Gg*), *Pseudo-nitzschia* spp. (*Ps*), *Leptocylindrus danicus* (*Ldc*), *Chaetoceros* sp. (*Ch*) and *Leptocylindrus minimus* (*Lem*)) were identified as the protagonists in community changes between 2003-2005, 2006 and 2007-2014. All of them are commonly found in the Bay of Biscay (Lampert et al., 2002; Lunven et al., 2005; Quevedo and Anadón, 2000; Smythe-Wright et al., 2014). Even though, they were present at the same period of the year (spring) and some of them (such as *Ps*) are considered as cosmopolite (Trainer et al., 2012), the present study showed they occupied different ecological niches and responded differently to environmental conditions.

The OMI and WitOMI analyses revealed that water temperature and equivalent freshwater depth (Heq) were the main factors structuring microphytoplankton ecological realized niches and explaining, at least in part, community successions between 2003-2005,

2006 and 2007-2014. Indeed, 2003-2005 was dominated in abundance by *Lem*. During this period, *Gg* occupied 100% of its potential sub-niche and had a large realized sub-niche which covered the realized sub-niche of all the other taxonomic units present. In 2006, Heq and bottom water temperature decreased likely due to the occurrence of an upwelling along the French coasts (between the Gironde and Adour estuaries) and to the fact that the Gironde estuary plume brought waters with lower temperature (Dessier et al., 2018; Zarauz et al., 2008). Environmental conditions became therefore more restrictive for some microphytoplankton species. *Lem*, which already occupied a marginal realized sub-niche in 2003-2005 and had preference for high Heq and water temperature, was not detected in 2006. *Ps*, with its ecological niche centered at lower water temperature and Heq than *Lem*, *Ch*, *Gg* and *Ldc*, took advantage of these environmental conditions and became the dominant taxonomic unit. It occupied the totality of its potential sub-niche and its realized sub-niche covered completely those of all the other taxonomic units present. Because the conditions were less favorable to *Ch*, *Gg* and *Ldc*, they occupied a reduced part of their potential sub-niche. Random forest analysis showed a relationship between mesozooplankton biomass and *Ps* abundance. This indicates that, during this period, mesozooplankton may have also played a role in phytoplankton changes or mesozooplankton communities may have been influenced by changes in phytoplankton composition. This is consistent with the results of Dessier et al. (2018) showing, in 2006, a shift from a copepod-dominated mesozooplankton community to a community with lowest proportion of copepods and increased proportion of cnidaria, siphonophora and meroplankton organisms (Bivalvia larvae and Cirripedia). In 2007-2014, the Bay of Biscay presented again high values of Heq (higher than in 2003-2005) and water temperature increased but remained lower than in 2003-2005 (especially at surface). *Ps* abundance decreased and it occupied a lower part of its potential sub-niche. *Lem* was again present but, in opposition to 2003-2005, it did not dominate the community. It was *Ldc* that was the most abundant likely because its ecological niche was

centered at lower temperature than *Lem*. *Gg* occupied again the totality of its potential sub-niche and had the largest realized sub-niche. However, contrary to 2003-2005, its realized sub-niche did not completely cover those of all the other taxonomic units present. During this period, species richness increased and the taxonomic units able to occupy the totality of their potential sub-niche were more numerous. This suggests greater niche partitioning.

Effects of Heq on inter-annual microphytoplankton composition are consistent with the suspected role of riverine water discharges in structuring phytoplankton in the Bay of Biscay (Gailhard et al., 2002). Indeed, by studying inter-annual variability in microphytoplankton composition along French coasts including the Bay of Biscay, Gailhard et al. (2002) observed, in 1994-1995, a shift from a community with high concentration of *Ps* to a community with high concentration of *Gymnodinium* spp. + *Amphidinium* sp. + *Cochlodinium* sp. + *Gyrodinium* sp. + *Katodinium* sp. + *Warnovia* sp. + *Nematodinium* sp. accompanied by an extensive development of *Karenia mikimotoi*. During this period, the Bay of Biscay experienced exceptional physical conditions: the plumes of two large estuaries (Gironde and Loire) overlapped (Labry et al., 2001). Gailhard et al. (2002) indicated that shifts in phytoplankton composition may have been driven by these exceptional discharges from Loire and Gironde that affected haline stratification. The role of Heq (and thus salinity) is also coherent with the findings that high salinities are more favorable than low salinities to *Ps* growth (Ayache et al., 2019). In the eastern English Channel and southern Bight of the North Sea, Hernandez-Fariñas et al. (2014) also observed that the highest abundance of *Ps* occurred during periods with an increased salinity. However, in opposition to the Bay of Biscay, *Gg* abundances increased during the same periods as *Ps*. The Bay of Biscay and eastern English Channel + southern Bight of the North Sea, differ in their levels of stratification and river inputs. In the eastern English Channel and southern Bight of the North Sea, water column is well-mixed all year round, tidal currents are strong and river inputs are low (Otto et al., 1990; Walters, 1987). By opposition,

the Bay of Biscay, is subjected to high river inputs, tidal currents are lower and water circulation is mainly wind-driven (Lazure and Jegou, 1998). It is known that water column mixing properties influence diatoms and dinoflagellates proliferation and their respective dominance (Alves-de-Souza et al., 2008; Margalef, 1978; Reynolds et al., 2002; Smayda and Reynolds, 2003). It is thus likely that hydrological conditions influenced differently interactions between *Ps* and *Gg* in both systems allowing them to coexist in the eastern English Channel and southern Bight of the North Sea while in the Bay of Biscay there was a negative competitive interaction.

Conclusions

Spatio-temporal changes in microphytoplankton community structure and diversity were highlighted. Three main periods (2003-2005, 2006 and 2007-2014) with different phytoplankton community structure were identified. *Pseudo-nitzschia* spp., *Gymnodinium* spp. + *Gyrodinium* spp., *Leptocylindrus danicus, Leptocylindrus minimus* and *Chaetoceros* sp. were the protagonists of these changes. Environmental conditions and interactions between phytoplankton species (through niche-based processes), rather than spatial processes and mesozooplankton biomass, were the main factors driving these changes in community structure and diversity. Variations in water temperature and equivalent freshwater depth constrained the species realized ecological niches and modified the relationships between phytoplankton species. This explained, at least in part, changes in community structure between 2003-2005, 2006 and 2007-2014. This study illustrates why it is important to improve our knowledge of phytoplankton species ecological niches and to take into account biotic interactions for a thorough understanding of the processes shaping plankton communities and the resulting diversity patterns. However, the present study only touched the surface of biotic interactions occurring in phytoplankton communities in the Bay of Biscay. With the statistical analyses

used, it was not possible to know with certainty whether interactions between phytoplankton species were positive or negative. The use of network analyses, such as the extended local similarity analysis (eLSA) (Xia et al., 2011; Yang et al., 2018a), could help to better understand the nature of these relationships. The other kinds of interactions should also be explored, for instance the impacts that parasites, viruses or planktivorous fish may have on phytoplankton species. Predation by zooplankton also requires further analyses because the present study only examined effects of mesozooplankton biomass. The present study also analyzed phytoplankton communities at only one season (spring) and considered only one size class (microphytoplankton). Extending the analysis of phytoplankton community structure to the entire year would improve the description of phytoplankton phenology. This would help to better understand the feeding relationships in food webs especially the synchrony between phytoplankton blooms and the highest trophic levels populations.

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Supplementary materials

Spatio-temporal drivers of spring microphytoplankton community over a decade in a large temperate bay (eastern continental shelf of the Bay of Biscay, North-East Atlantic): do species ecological niches matter?

Emilie Houliez, Sébastien Lefebvre, Aurélie Dessier, Martin Huret, Elise Marquis, Martine Bréret, Christine Dupuy

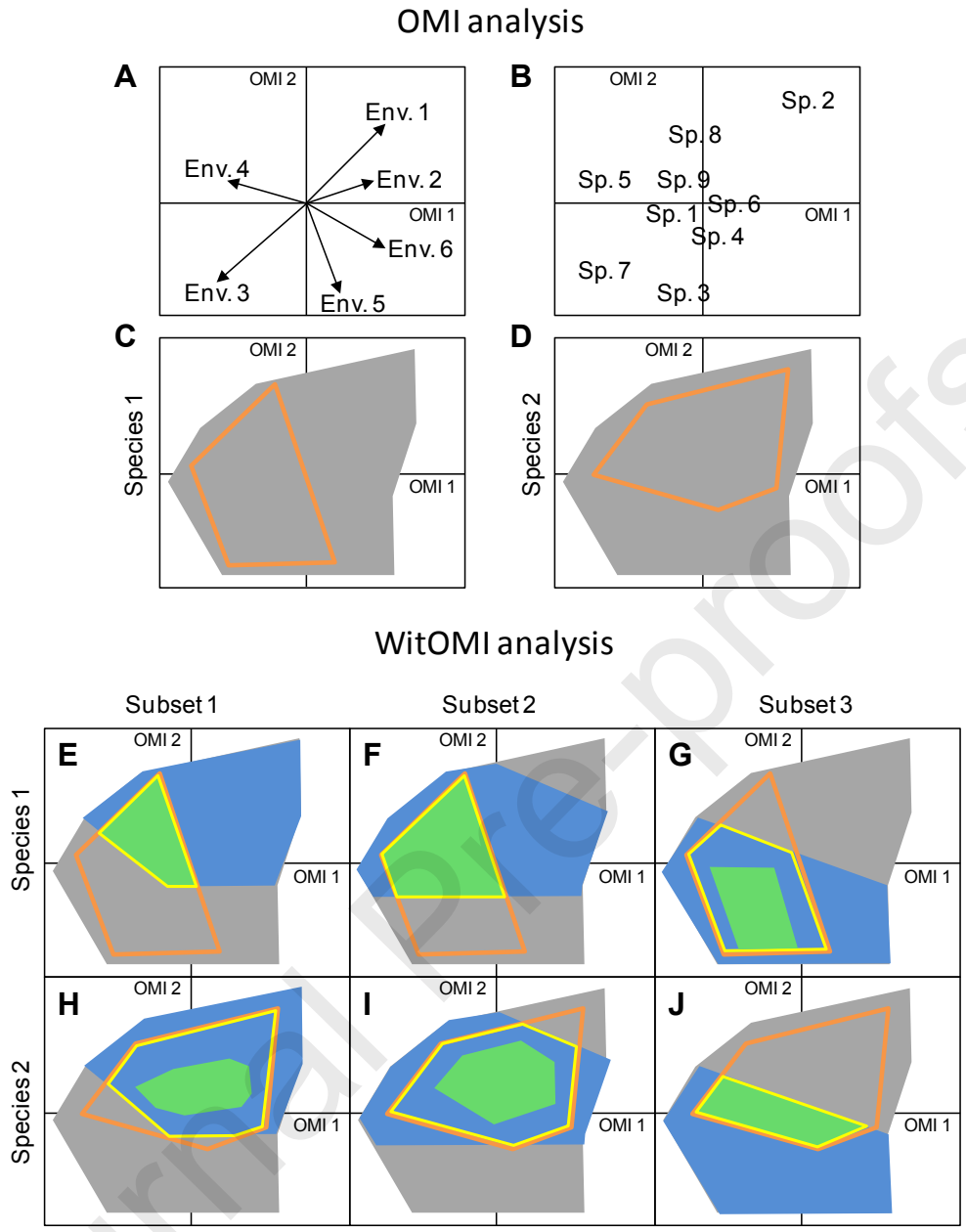

Fig. S1: Schematic representation of the OMI and WitOMI analyses results. **(**A) Projection of environmental variables on the first two axes of the OMI (OMI 1 and OMI2). Env. = environmental variable. (B) Projection of the niche position of each taxonomic unit on the first two axes of the OMI. Sp. = species. Realized niche of species 1 (C) and species 2 (D). Sub-niches of species 1 (E, F, G) and species 2 (H, I, J) in the first subset (first column), second subset (second column) and third subset (third column). Grey polygon = environmental space. Orange polygon = realized niche. Blue polygon = sub-environmental space. Yellow polygon = potential realized sub-niche. Green polygon = realized sub-niche. In G, H, I, the realized sub-niche of species 1 and 2 is smaller than their respective potential realized sub-niche due to biotic interactions. The blue area inside the yellow polygon and around the green polygon represents thus the biological constraints. In E, F, G, the size of the realized sub-niche of species 1 and species 2 is not reduced by biotic interactions and they occupy the totality of their potential sub-niche. Their realized sub-niche has thus the same size as their potential sub-niche. Figure adapted from Karasiewicz et al. (2017) and Karasiewicz et al. (2020)

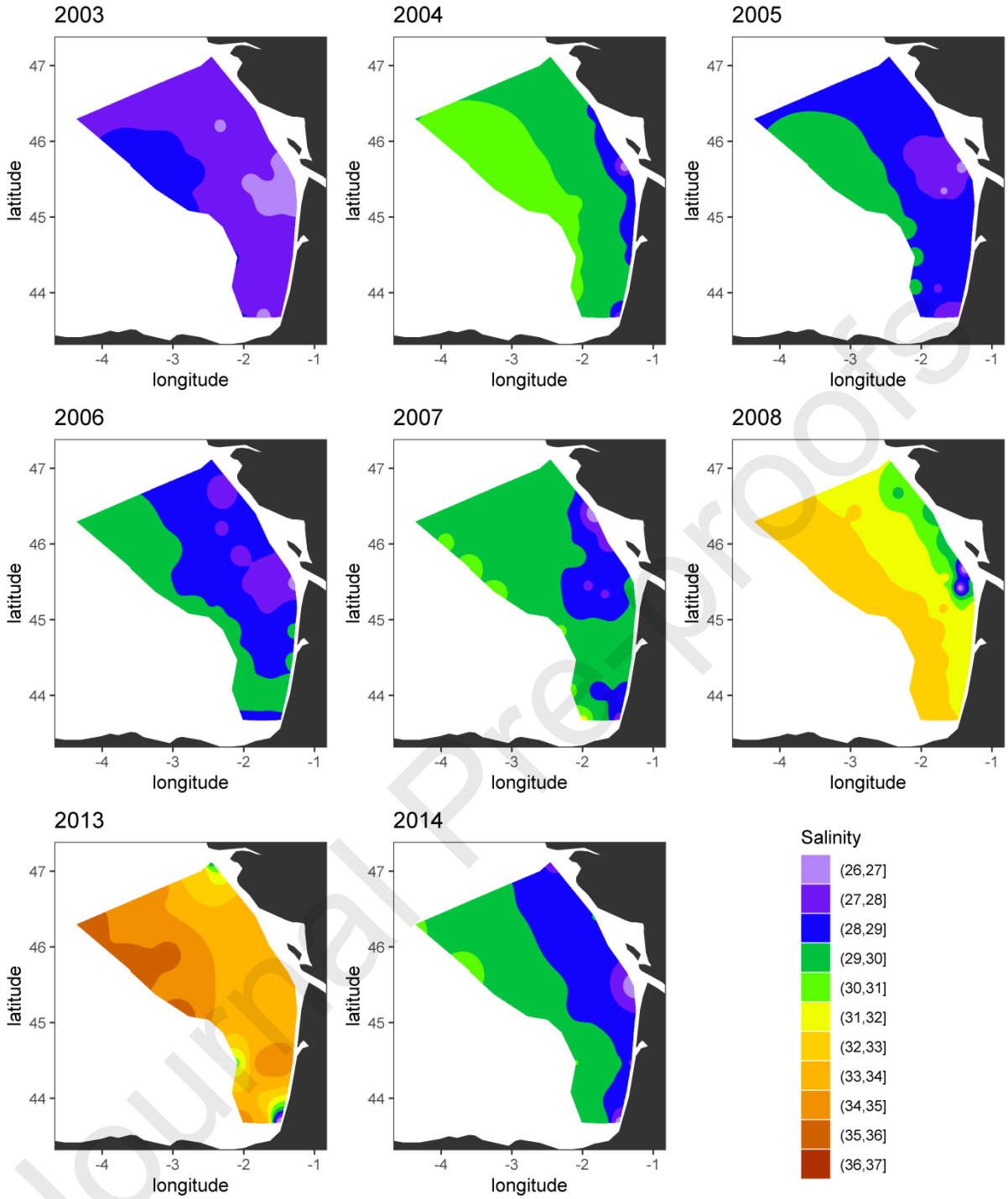

Fig. S2: Spatio-temporal variations of surface seawater salinity from 2003 to 2014 in the Bay of Biscay

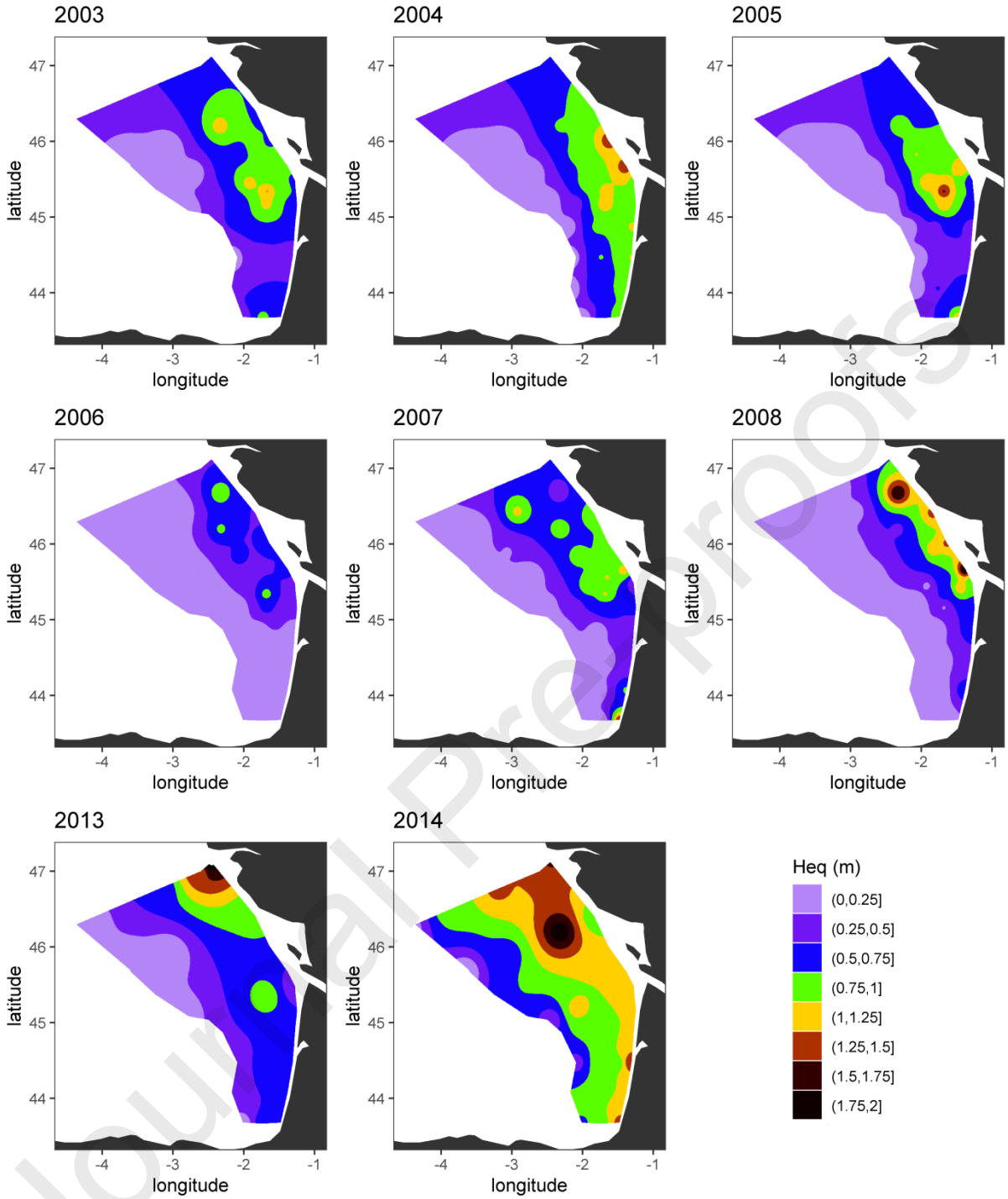

Fig. S3: Spatio-temporal variations of equivalent freshwater depth (Heq, in m) from 2003 to 2014 in the Bay of Biscay

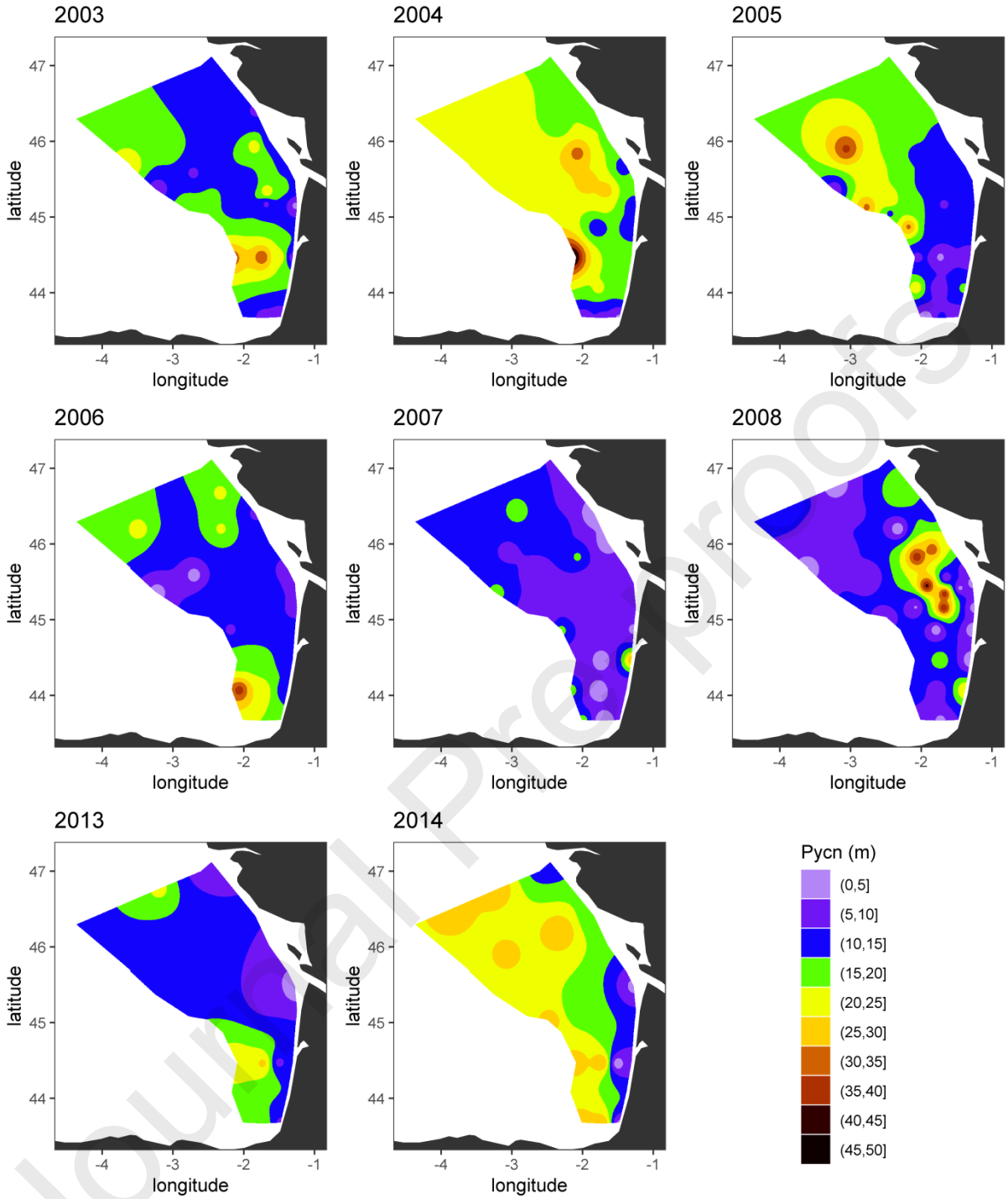

Fig. S4: Spatio-temporal variations of pycnocline depth (Pycn, in m) from 2003 to 2014 in the Bay of Biscay

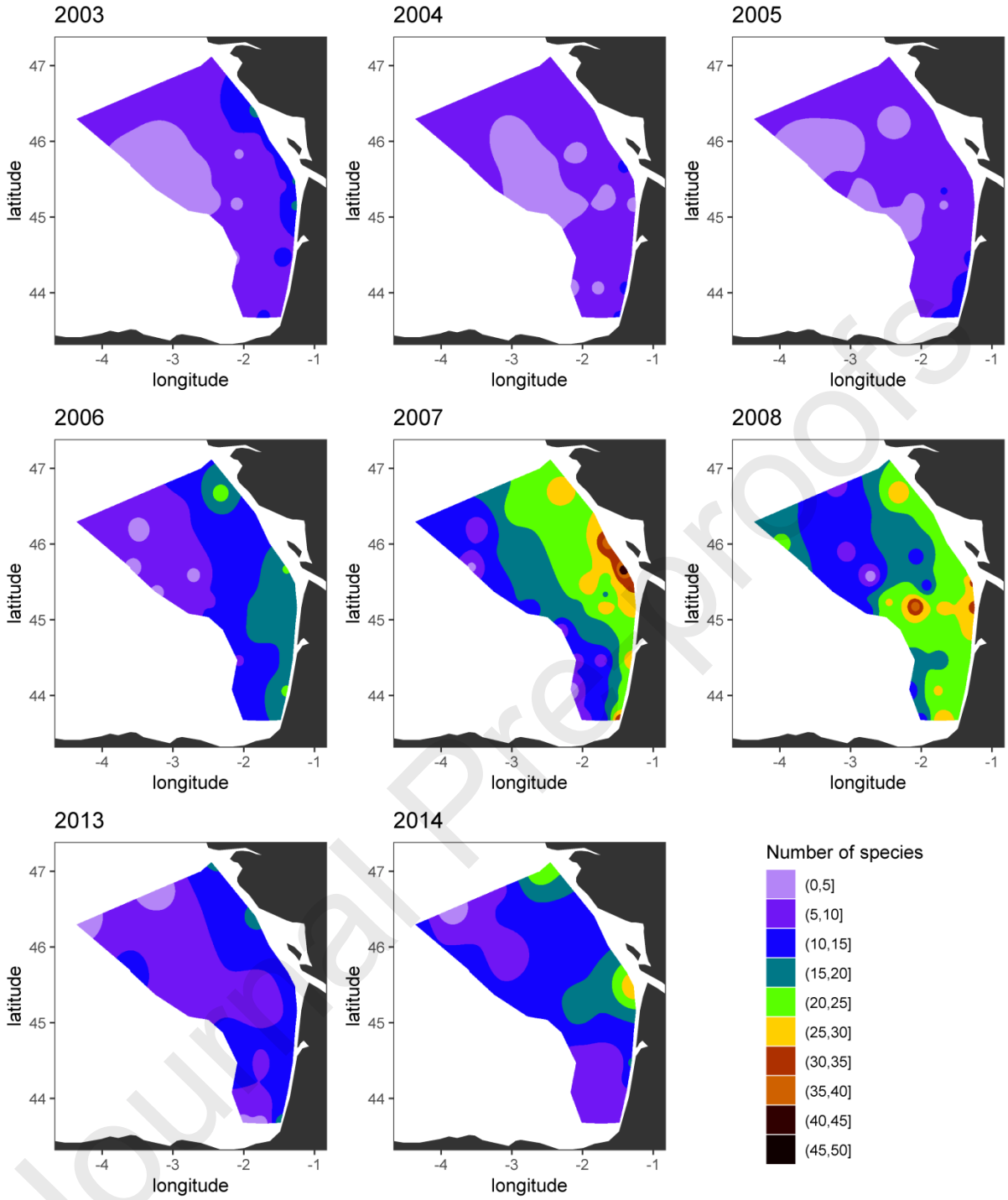

Fig. S5: Spatio-temporal variations of the number of species in surface waters from 2003 to 2014 in the Bay of Biscay

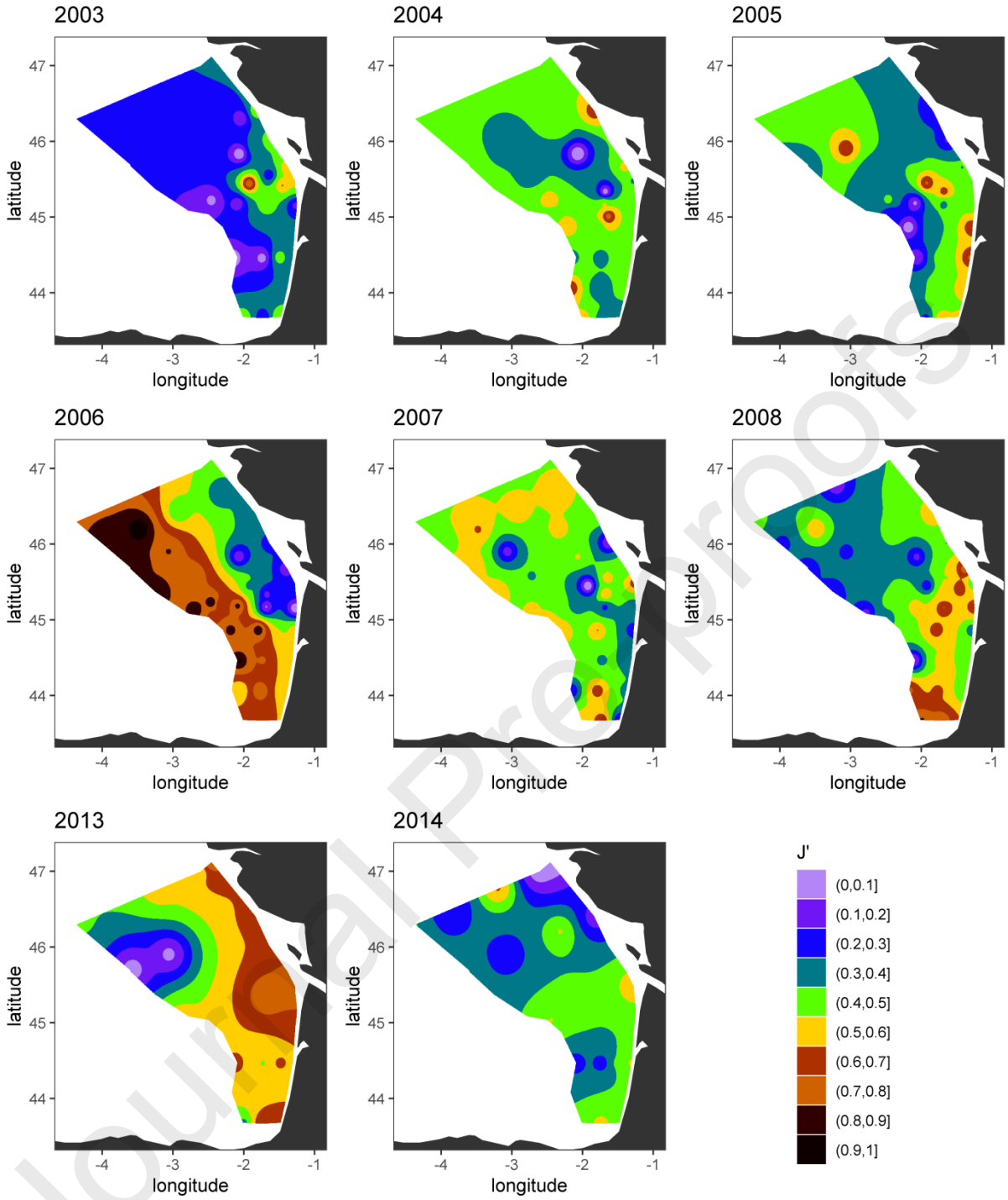

Fig. S6: Spatio-temporal variations of Pielou's evenness (J') in surface waters from 2003 to 2014 in the Bay of Biscay

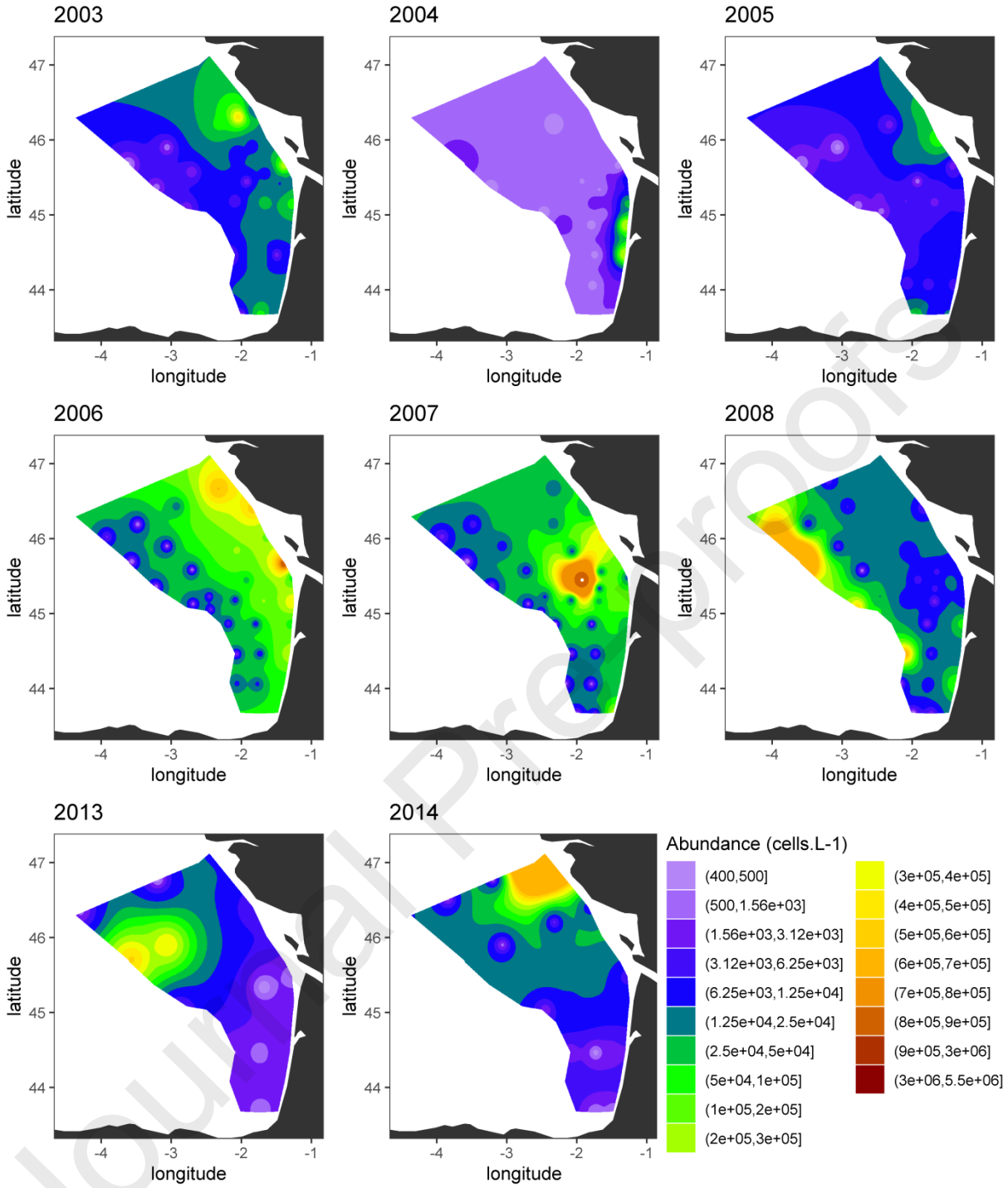

Fig. S7: Spatio-temporal variations of total microphytoplankton abundance in surface waters from 2003 to 2014 in the Bay of Biscay

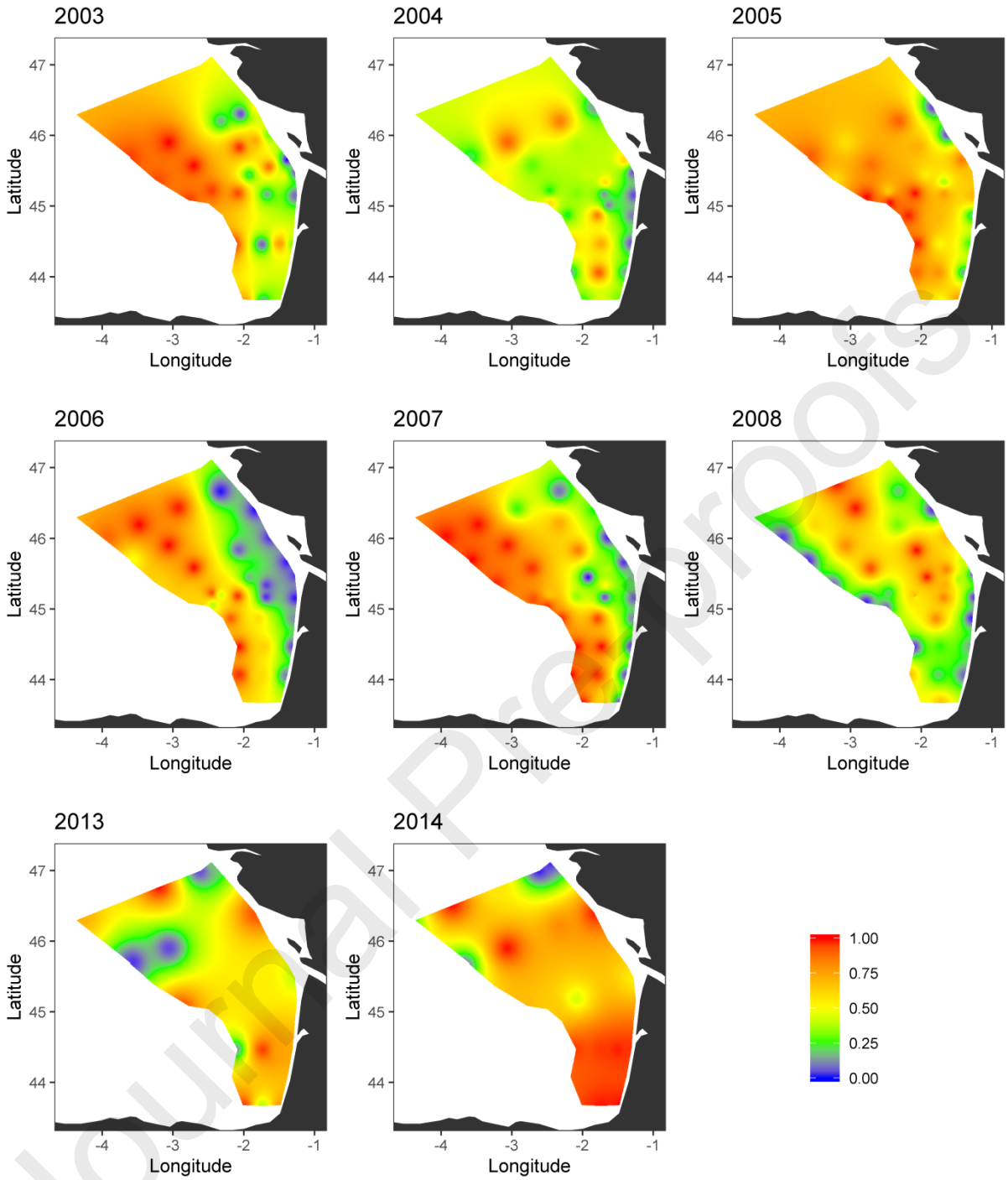

Fig. S8: Spatio-temporal variations of dinoflagellates / diatoms relative proportions in surface waters from 2003 to 2014 in the Bay of Biscay. Graphs scale ranges from 0 (= community dominated by diatoms) to 1 (= community dominated by dinoflagellates)

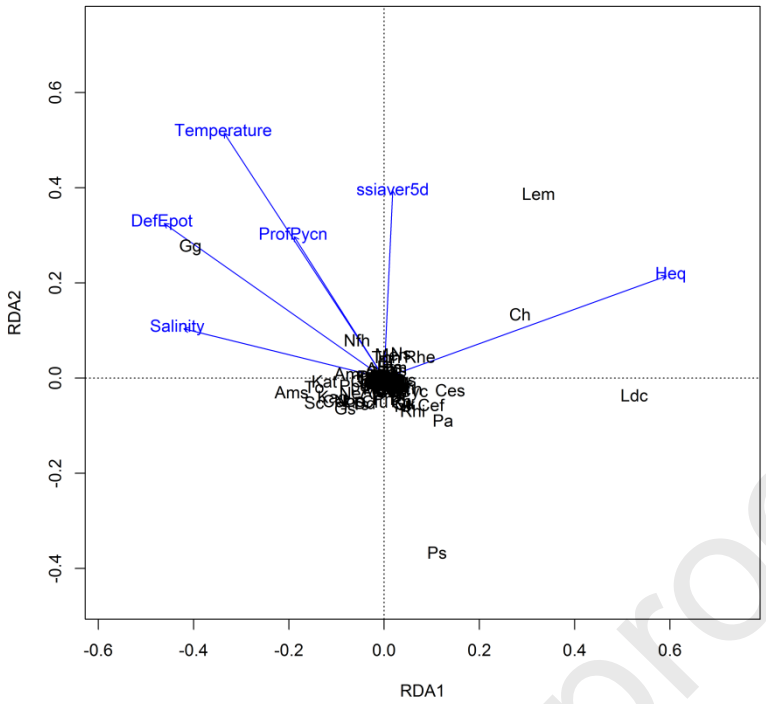

Fig. S9 : Redundancy analysis. DefEpot = deficit of potential energy (in $kg.m^{-1}.s^{-2}$), ProfPycn = pycnocline depth (in m), ssiaver5d = sea surface irradiance (in Watt m^{-2}), Heq = equivalent freshwater depth (in m)

Table S1: Sampling dates and number of microphytoplankton samples

Year	Sampling dates	Number of samples
2003	May 30th - June 10th	83
2004	April 28th - May 10th	58
2005	May 5th - May 16th	69
2006	May 2nd - May 16th	62
2007	April 27th - May 10th	79
2008	April 27th - May 12th	109
2013	April 28th - May 17th	42
2014	April 28th - May 19th	43

Table S2: Multivariate analyses. Summary of the different steps in data analysis

Steps	Analyses	Objectives
Identifying potential changes in microphytoplankton community structure	nMDS	nMDS analysis is a graphical representation of the similarity between each pair of samples in terms of abundance and number of shared species. It was used to highlight groups of samples with different microphytoplankton composition
	ANOSIM	Testing for statistical significance of differences between groups of samples in terms of taxonomic composition
	SIMPER	Quantifying the level of dissimilarity between groups of samples and identifying the taxonomic units responsible for these dissimilarities
Defining the relative role of environmental conditions, spatial processes and mesozooplankton in microphytoplankton communities structuring	Variation partitioning	Quantifying variation in the entire microphytoplankton community explained respectively by environmental variables, spatial variables and mesozooplankton biomass
	Random forest regression	For each of the taxonomic unit responsible for changes in microphytoplankton community, quantifying the percentage of variation in their abundance explained respectively by environmental variables, spatial variables, mesozooplankton and biotic interactions (including the relationships with the other taxonomic units responsible for community structure changes and relationships with the taxonomic units not involved in these changes)
Defining the role of species ecological niches in variations of microphytoplankton community structure	OMI	Characterizing the realized ecological niche of each taxonomic within the environmental space of the whole sampling period (i.e. 2003 to 2014) and quantifying their marginality and tolerance in this environmental space
	WitOMI	Characterizing the realized ecological sub-niches of each taxonomic within the environmental space of the three periods highlighted by the nMDS analysis (i.e. 2003-2005, 2006 and 2007-2014) and quantifying their marginality and tolerance in these 3 sub-environmental spaces

Table S3: SIMPER analysis identifying the main taxonomic units involved in the dissimilarity between the groups defined by nMDS analysis

Groups: 1 (2003-2005) vs. 2 (2006)
Average dissimilarity = 97.51

Taxonomic units	Class	Code	2003-2005	2006	Average dissimilarity	Contribution %
			Average abundance (cells.L^{-1})	Average abundance (cells.L^{-1})		
Pseudo-nitzschia spp.	Bacillariophyceae	*Ps*	5.92E+03	1.21E+05	24.04	24.65
Gymnodinium spp. + *Gyrodinium* spp.	Dinophyceae	*Gg*	2.64E+07	36	23.52	24.12
Leptocylindrus minimus	Bacillariophyceae	*Lem*	5.76E+07	0	9.66	9.91
Leptocylindrus danicus	Bacillariophyceae	*Ldc*	3.94E+07	5.77E+03	6.88	7.05
Chaetoceros sp.	Bacillariophyceae	*Ch*	1.30E+06	190	6.73	6.90
Rhizosolenia sp.	Bacillariophyceae	*Rhe*	1.32E+07	9.68E+03	4.01	4.11
Cerataulina sp.	Bacillariophyceae	*Ces*	5.24E+03	0	2.43	2.50
Scrippsiella spp. + *Ensiculifera* spp.	Dinophyceae	*Sc*	6.60E+06	645	1.66	1.70
Cerataulina bergonii	Bacillariophyceae	*Cep*	0	6.96E+03	1.64	1.69
Navicula sp. + *Fallacia* sp.	Bacillariophyceae	*Nfh*	2.64E+07	0	1.31	1.34

Groups: 2 (2006) vs. 3 (2007-2014)
Average dissimilarity = 94.77

Taxonomic units	Class	Code	2006	2007-2014	Average dissimilarity	Contribution %
			Average abundance (cells.L^{-1})	Average abundance (cells.L^{-1})		
Pseudo-nitzschia spp.	Bacillariophyceae	*Ps*	1.21E+05	4.68E+04	31.45	33.19
Gymnodinium spp. + *Gyrodinium* spp.	Dinophyceae	*Gg*	36	8.94E+03	13.34	14.08
Leptocylindrus danicus	Bacillariophyceae	*Ldc*	5.77E+03	5.71E+04	10.31	10.88
Rhizosolenia sp.	Bacillariophyceae	*Rhe*	9.68E+03	25	3.34	3.53
Chaetoceros sp.	Bacillariophyceae	*Ch*	190	2.99E+04	3.28	3.46
Cerataulina bergonii	Bacillariophyceae	*Cep*	6.96E+03	2.53E+03	2.79	2.95
Scrippsiella spp. + *Ensiculifera* spp.	Dinophyceae	*Sc*	645	836	2.19	2.31
Paralia marina	Bacillariophyceae	*Pa*	45	1.01E+03	1.86	1.97
Katodinium glaucum	Dinophyceae	*Kag*	0	838	1.58	1.67
Prorocentrum cordatum +	Dinophyceae	*Pb*	310	1.12E+03	1.45	1.52

Prorocentrum balticum						
Amphidinium sp.	Dinophyceae	*Ams*	838	108	1.21	1.28
Rhizosolenia imbricata	Bacillariophyceae	*Rhi*	518	1.46E+03	1.13	1.20
Prorocentrum sp.	Dinophyceae	*Prs*	68	809	0.84	0.89
Tripos fusus	Dinophyceae	*Cef*	357	702	0.78	0.83
Tripos muelleri	Dinophyceae	*Cet*	277	16	0.75	0.79
Katodinium sp.	Dinophyceae	*Kat*	0	376	0.71	0.75
Tripos furca	Dinophyceae	*Cfu*	68	278	0.67	0.70
Meuniera spp.	Bacillariophyceae	*Meu*	0	585	0.64	0.68
Torodinium spp.	Dinophyceae	*To*	70	244	0.63	0.66
Diplopsalis spp. + *Diplopelta* spp.	Dinophyceae	*Dd*	12	523	0.62	0.66
Gyrodinium spirale	Dinophyceae	*Gs*	55	401	0.59	0.63
Cylindrotheca closterium	Bacillariophyceae	*Cyc*	0	605	0.59	0.62

Groups: 1 (2003-2005) vs. 3 (2007-2014)
Average dissimilarity = 86.45

Taxonomic units	Class	Code	2003-2005	2007-2014	Average dissimilarity	Contribution %
			Average abundance (cells.L^{-1})	Average abundance (cells.L^{-1})		
Gymnodinium spp. + *Gyrodinium* spp.	Dinophyceae	*Gg*	2.64E+07	8.94E+03	19.12	22.12
Leptocylindrus danicus	Bacillariophyceae	*Ldc*	3.94E+07	5.71E+04	12.64	14.62
Pseudo-nitzschia spp.	Bacillariophyceae	*Ps*	5.92E+03	4.68E+04	10.03	11.61
Leptocylindrus minimus	Bacillariophyceae	*Lem*	5.76E+07	1.18E+03	9.93	11.48
Chaetoceros sp.	Bacillariophyceae	*Ch*	1.30E+06	2.99E+04	8.76	10.14
Cerataulina sp.	Bacillariophyceae	*Ces*	5.24E+03	658	2.41	2.79
Rhizosolenia sp.	Bacillariophyceae	*Rhe*	1.32E+07	25	1.30	1.50
Paralia marina	Bacillariophyceae	*Pa*	0	1.01E+03	1.20	1.39
Navicula sp. + *Fallacia* sp.	Bacillariophyceae	*Nfh*	2.64E+07	74	1.16	1.34
Scrippsiella spp. + *Ensiculifera* spp.	Dinophyceae	*Sc*	6.60E+07	836	1.04	1.20
Prorocentrum cordatum + *Prorocentrum balticum*	Dinophyceae	*Pb*	0	1.12E+03	0.98	1.13
Katodinium glaucum	Dinophyceae	*Kag*	0	838	0.96	1.11
Tripos fusus	Dinophyceae	*Cef*	633	702	0.94	1.09
Cerataulina bergonii	Bacillariophyceae	*Cep*	0	2.53E+03	0.91	1.05

Rhizosolenia imbricata	Bacillariophyceae	*Rhi*	0	1.46E+03	0.73	0.85
Nitzschia sp.	Bacillariophyceae	*Ns*	724	21	0.73	0.85
Melosira nummuloides	Bacillariophyceae	*Men*	2.51E+07	16	0.62	0.72
Prorocentrum sp.	Dinophyceae	*Prs*	4	809	0.49	0.57
Meuniera spp.	Bacillariophyceae	*Meu*	0	585	0.48	0.56
Tripos lineatus + *Tripos minutus*	Dinophyceae	*Clm*	236	290	0.47	0.54
Katodinium sp.	Dinophyceae	*Kat*	0	376	0.46	0.53
Cylindrotheca closterium	Bacillariophyceae	*Cyc*	0	605	0.45	0.52

Table S4: Taxonomic units that occupied the totality of their potential sub-niche

2003-2005	2006	2007-2014
Gymnodinium spp. + *Gyrodinium* spp. *Trieres chinensis* *Cerataulina* sp. *Coscinodiscus* sp. *Pyrocystis lunula* *Rhabdonema* spp.	*Pseudo-nitzschia* spp. *Guinardia* sp. *Karenia mikimotoi*	*Gymnodinium* spp. + *Gyrodinium* spp. *Achnanthes* spp. *Actinocyclus* spp. *Amphora* spp. *Asteromphalus* spp. *Vibrio paxillifer* *Bacteriastrum* spp. *Plagiogramma brockmanni* *Caloneis* spp. *Chaetoceros decipiens* + *Chaetoceros lorenzianus* *Chaetoceros teres* *Corethron* spp. *Coscinodiscus* sp. + *Stellarima* sp. *Cyclotella* spp. *Cylindrotheca closterium* *Cylindrotheca gracilis* *Dactyliosolen* spp. *Ditylum brightwellii* *Entomoneis* spp. *Grammatophora* spp. *Rhizosolenia delicatula* *Rhizosolenia flaccida* *Hemidiscus* spp. *Licmophora* spp. *Lithodesmium* spp. *Aulacoseira granulata* *Meuniera* spp. *Navicula pennata*

		Nitzschia longissima *Navicula transitans* *Trieres mobiliensis* *Paralia marina* *Pinnularia* spp. *Plagiogrammopsis* spp. *Pleurosigma angulatum* *Proboscia indica* *Rhizosolenia setigera* + *Rhizosolenia pungens* *Rhizosolenia robusta* *Rhaphoneis* spp. *Skeletonema costatum* *Surirella* spp. *Synedra* spp. + *Toxarium* spp. *Thalassionema* sp. *Triceratium favus* *Cochlodinium* spp. *Tripos horridum* *Tripos macroceros* *Diplopsalis* spp. + *Diplopelta* spp. + *Diplopsalopsis* spp. *Dinophysis acuminata* *Dinophysis tripos* *Dinophysis sacculus* *Gymnodinium aureolum* *Gonyaulax spinifera* *Akashiwo sanguinea* *Karenia mikimotoi* *Katodinium glaucum* *Kofoidinium* spp. *Nematodinium* spp. + *Warnowia* spp. *Ostreopsis* spp. *Phalocroma* spp. + *Oxyrrhis* spp.

		Polykrikos spp. *Protoperidinium stenii* + *Protoperidinium pyriforme* *Protoperidinium leonis* *Protoperidinium pyriforme* *Protoceratium reticulatum* *Pyrophacus* spp.

Highlights

- Spring microphytoplankton community structure and diversity were studied over a decade in the Bay of Biscay
- Three main periods, 2003-2005, 2006 and 2007-2014, showing different community structure, diversity and dominant taxonomic units were highlighted
- Five main species were responsible for these changes (*Pseudo-nitzschia* spp., *Gymnodinium* spp. + *Gyrodinium* spp., *Leptocylindrus danicus, Leptocylindrus minimus* and *Chaetoceros* sp.)
- Variations in water temperature and equivalent freshwater depth constrained the realized ecological niches of these species and explained, at least in part, changes in community structure