

## Spatial and long-term changes in the functional and structural phytoplankton communities along the French Atlantic coast

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### Abstract:

Spatial and interannual variations of phytoplankton diversity were characterized along the French Atlantic Coast in relation to physical factors and large-scale climatic indices using phytoplankton surveys conducted from 1993 to 2010 in four geographical areas. This study relates phytoplankton diversity to oyster recruitment success by comparing a 'specific' *versus* a 'functional' diversity approach. Functional diversity was represented by functional groups of different phytoplanktonic functional traits (size, shape, toxicity), relevant for oyster feeding during growth, reproduction and larval development. Phytoplankton diversity patterns along the French Atlantic coast corresponded to a geographical distribution mainly driven by a latitudinal gradient and hydrodynamic features as confirmed by the functional characteristics of the indicator species recorded for each geographical area (C-S-R strategies of Reynolds, specific habitat). This geographical typology was less clear for functional diversity. Only few functional groups were explained by physical factors: the non-toxic small and solitary cells were in particular related to temperature, with high densities observed in the southern areas. Even if temporal variation was less important in explaining the phytoplankton diversity patterns, the main drivers explaining the interannual pattern were the large-scale climatic indices, mainly the Atlantic Multidecadal Oscillation. Functional groups were readily explained by climatic indices than species even if the relationships cannot be applied generally because of the non-linearity of the correlations (local and temporal variations). However, the potentially toxic, small and linear phytoplankton were anticorrelated to NAO. The functional approach thus brings constructive elements concerning the relationships between the prey assemblage of oysters and their physical drivers. Redundancy and co-inertia analyses appeared as complementary analyses in investigating phytoplankton pattern of variation, being particularly useful in analyzing geographical and temporal diversity fluctuation, respectively.

**Keywords:** phytoplankton ; long-term variation ; spatial variation ; climate ; Atlantic coast

## 45 1. Introduction

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3 46 Plankton plays a key role in the trophodynamics of aquatic ecosystems. Several  
4 47 planktonic taxa are important food source for pelagic or benthic species (fishes, mollusks) of  
5 48 economical interest (Baldwin and Newell, 1995; Beaugrand et al., 2003; Pasquaud et al., 2010).  
6 49 The trophic link is direct and generally „specific“ of a size, a form or a taxa. This specificity  
7 50 varies according to the presence and abundance of predator species. For example, larval  
8 51 oysters feed preferentially on smaller phytoplankton cells instead of bacteria, protozoa or  
9 52 dissolved particulate organic matter (Olson and Olson, 1989) whereas larval cods prefer one  
10 53 particular species of copepods due to its size and phenology (Munk, 1997). This narrow prey-  
11 54 predator link is often restricted to a short period in the life stages of these species. It thus  
12 55 necessitates a perfect matching between prey and predator to allow the survival of predators  
13 56 (Beaugrand et al., 2003).

14 57 Plankton is also used as indicators of climatic changes since its quick response to  
15 58 hydroclimatic forcing in the pelagic trophic web (Beaugrand, 2005). Such responses are due to  
16 59 its short life span and its ability to produce resting stages (Guerrero and Rodriguez, 1998;  
17 60 McQuoid et al., 2002). Moreover, long-term changes had been recorded for different plankton  
18 61 compartments at different spatial scales and attributed to hydroclimatic variability at local,  
19 62 regional and global scale (Boyce et al., 2010), and meso- or macrozooplankton at local or  
20 63 regional scale (Beaugrand et al., 2002; Roemmich and McGowan, 1995). For both phyto- or  
21 64 zooplankton, such changes concern not only their respective biomass (Roemmich and  
22 65 McGowan, 1995) but also their biogeography (Beaugrand et al., 2002; Leterme et al., 2008),  
23 66 their phenology (Edwards et al., 2001) or some physiological features such as size or fecundity  
24 67 rate (David et al., 2007). Even if the decline of exploited fish or mollusks had classically been  
25 68 attributed to human activities (e.g. overfishing, climatic changes could thus have drastic  
26 69 consequences in the trophodynamics of aquatic food webs through bottom up or wasp-waist  
27 70 control (Griffiths et al., 2010; Richardson and Schoeman, 2004). They could alter the  
28 71 functioning of ecosystems, their resilience and the services they provide in synergism with  
29 72 other anthropogenic pressures (Goberville et al., 2010; Llope et al., 2011). Recent works have  
30 73 actually shown that climatic change may lead to large-scale redistribution of global catch  
31 74 potential for some exploited marine fishes and invertebrates (Cheung et al., 2010) and could  
32 75 cause the destruction of such species assemblages because of the alteration in habitat quality  
33 76 (Wilson et al., 2008) . However, the indirect link between climate change and exploited  
34 77 macrofauna through planktonic forms remains tenuous in the management of exploited marine

78 species. A functional diversity approach, i.e. considering the species according specific  
1 79 functional traits in the ecosystem, could be particularly relevant to understand the relationship  
2 80 between prey and predator. Functional diversity is actually important for the understanding of  
3 81 ecosystem functioning as the number of functional groups are a more powerful determinant of  
4 82 processes than species richness (Downing and Leibold, 2002; Tilman et al., 1997). Such a  
5 83 functional approach has been criticized when used for planktonic models. Anderson (2005)  
6 84 underlined that the danger of trying to „run before walk“ because of the lack of ecological  
7 85 knowledge and thus the difficulties of aggregating diverse organisms into functional groups.  
8 86 However, this approach has been particularly useful to clearly understand the mechanisms in  
9 87 prey-predator relationships (Azemar et al. 2007; Pasquaud et al 2010) and thus highlight the  
10 88 consequences of the variability of prey assemblages on predator survival (Beaugrand et al.,  
11 89 2003). Azemar et al. (2007) and Pasquaud et al. (2010) used population characteristics of prey  
12 90 (growth rate, individual weight, and population biomass) to understand the feeding strategy of  
13 91 predators (generalist, specialist or opportunistic). Functional traits such as prey size or  
14 92 phenology have also been used to build an index for long-term monitoring of larval cod  
15 93 survival in the North Sea (Beaugrand et al., 2003).

94 Phytoplankton is the main food source for benthic filter-feeders such as oysters, mussels  
95 or cockles, which are of commercial interest (Robert, 2003). Growth and reproduction of the  
96 Pacific oyster, *Crassostrea gigas*, are clearly related to phytoplankton densities (Bourlès et al.,  
97 2009). Several economical problems related to decline of the oyster livestock have risen  
98 recently throughout the world and notably along the French Atlantic coast, For example (i)  
99 „abnormal“ mortalities (>30% of the population) of one-and two-year-old oyster during spring-  
100 summer (Soletchnik et al., 2007) which seemed to be, at least partly, attributed to  
101 phytoplankton biomass (chl *a* concentrations), and (ii) weak settlement of oyster larvae  
102 particularly in 2002, 2005 and 2009 in Arcachon Bay and Marennes-Oléron Bay, the two main  
103 center of spat production in France. Oyster larval settlement depends on both (i) larval survival  
104 as meroplankton during their development and (ii) larval densities resulting from the  
105 reproductive effort of the adults. The latter could be related to phytoplankton availability for  
106 adults before the summer spawning (i.e. between February and June).

107 Global warming could induce noticeable taxonomic changes with a global shift from a  
108 diatom-based system to a more flagellate-based one (Leterme et al., 2008). It also contribute to  
109 the development of non-endemic species, including toxic species involve in harmful algal  
110 blooms (Penna et al., 2005).<sup>4</sup> Such changes in phytoplankton species composition can induce  
111 changes in functional attributes of the communities (Beaugrand, 2005)). Actually, some

112 features of phytoplankton, such as size and nutritional quality (Baldwin and Newell, 1995;  
113 Barillé et al., 1993), are especially important for the development and recruitment success of  
114 oyster larvae (Robert and Trintingnac, 1997). The long-term variability of phytoplankton  
115 diversity, both specific and functional, might thus be interesting in understanding the  
116 recruitment success of oyster larvae.

117 Phytoplankton communities have been described along the French Atlantic coast and  
118 two large areas have been distinguished based on specific diversity, according to the temporal  
119 variability patterns of microphytoplankton populations between 1992 and 2000 (English  
120 Channel and Bay of Biscay) and have been related to hydrodynamic features (Gailhard et al.,  
121 2003). However, spatial variability was considered so important in explaining the specific  
122 diversity patterns that it curtailed analysis of temporal variability. Finally, Beliaeff et al. (2001)  
123 highlighted the difficulty to distinguish site-specific seasonal variations of phytoplankton  
124 species from high between-year variations and attributed the latter to climate change.

125 The aim of the present study was to characterize the spatial and interannual variations  
126 of phytoplankton diversity along the French Atlantic coast in relation with physical factors and  
127 large-scale climate indices. Both specific and functional diversities were considered. The  
128 functional groups were assessed using phytoplankton functional traits based on their  
129 availability to oyster feeding.

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## 132 2. Material and methods

### 133 2.1. Study area

134 Phytoplankton communities were studied in 4 geographical zones along the French  
135 Coast, namely North of Brittany (NB), South of Brittany (SB), the Pertuis Charentais area (PC)  
136 and the Arcachon Bay (AB) (see Figure 1). The data collected belong to the REPHY program  
137 and were extracted from the Ifremer Quadrigé database. The REPHY aims are 1) to describe  
138 the spatio-temporal distribution of the different phytoplankton species along the French Coast  
139 and 2) to detect the occurrence of toxins-producing species, a public health hazard for shellfish  
140 consumption. Only 8 stations were selected of the 29 stations available in the REPHY database  
141 because of the lack of temporal synchronicity between station sampling over a long-term  
142 period.

143 All geographical areas have a temperate climate under oceanic influence characterized  
144 by mild winters (about 10°C) and summers (< 23°C). Precipitation is high (about 700-  
145 800mm/year) with higher rainfall between October and January. All sites were also  
146 characterized by dominant West wind and semi diurnal tides.

147 The Arcachon Bay (AB) is a macrotidal coastal lagoon of 174 km<sup>2</sup> connected to the  
148 Bay of Biscay by a narrow channel (2-3 km wide). In the inner lagoon, tidal channels (41 km<sup>2</sup>)  
149 penetrate between large intertidal areas (115 km<sup>2</sup>). Sixty percent of these tidal flats are covered  
150 by *Zostera noltii* meadows. Semi-diurnal tides enable important water exchanges with the  
151 adjacent oceanic waters. The input of fresh water is mainly by the Leyre River with an average  
152 annual river-flow of 19 m<sup>3</sup> s<sup>-1</sup>. The sampling station, localized near the connecting channel  
153 with the Bay of Biscay, is slightly influenced by the river input. The Arcachon Bay is the  
154 greatest European spat production site for the Pacific oyster, *Crassostrea gigas* and a major  
155 center for oyster farming.

156 The Pertuis Charentais is a semi-diurnal macrotidal area located northward on the  
157 French Atlantic coast, largely characterized by a marine water influence and with a total  
158 surface area of 1300 km<sup>2</sup> comprising 340 km<sup>2</sup> of shallow (0–5 m depth) soft bottom areas  
159 located in the inner bays. It consists of two main straits; the Pertuis Breton on the North and the  
160 Pertuis d'Antioche - Marennes-Oléron Bay on the South. Only small rivers flow into each  
161 strait: (i) in the Pertuis Breton, an average annual river-flow of 20 m<sup>3</sup> s<sup>-1</sup> from the Lay River,  
162 25 m<sup>3</sup> s<sup>-1</sup> from the Sèvre-Niortaise River, (ii) in the Marennes-Oléron Bay 50 m<sup>3</sup> s<sup>-1</sup> from the  
163 Charente River, 1-2 m<sup>3</sup> s<sup>-1</sup> from the Seudre River (Durieux et al., 2010). The tidal range and  
164 currents allow the rapid renewal of marine water and a well-mixed environment, particularly in

165 the shallower areas. However, water masses presented different residence time in both straits:  
 166 about 30 days in the Pertuis Breton and 10 days in the Marennes-Oleron Bay. The Pertuis  
 167 Charentais is the Europe's largest production area for the Pacific oyster: with a standing stock  
 168 of 125,000 tonnes and an annual production of 38,000 tonnes in 2001 (Gouilletquer and Le  
 169 Moine, 2002). Four stations were sampled in this bay: Eperon located in the Pertuis Breton, Le  
 170 Cornard, Boyard and Auger in the Marennes-Oleron Bay. The two southern stations can also be  
 171 influenced by Gironde estuary outputs.

172 The North and South of Brittany areas are also located near oyster farming areas  
 173 (Soletchnik et al., 2007) even if production is low compared to Pertuis Charentais and  
 174 Arcachon Bay. The Bay of Le Croisic is the main production site of the cockle, *Cerastoderma*  
 175 *edule* in France of about 1200 tons a year (Rollo and Robin, 2010). It is located on the Atlantic  
 176 Coast of France in the South of Brittany (SB). The main freshwater output is coming from the  
 177 Loire River presenting an average annual river-flow of about  $931 \text{ m}^3 \cdot \text{s}^{-1}$ .

178 The two Northern stations are located in the western part of the English Channel, in the  
 179 western part of the North of Brittany (NB). The main river inputs are provided by small coastal  
 180 rivers (the Arguenon River at the Saint-Cast station and the Le Trieux River at the Paimpol  
 181 station). The average annual river-flow of both is  $<5 \text{ m}^3 \text{ s}^{-1}$ .

## 182 **2.2. Presentation of the raw database**

183 Both environmental and biological data were available for stations over different time  
 184 periods: (1) the NB stations (Saint-Cast and Paimpol) from April 1993 to march 2004, (2) the  
 185 SB station (Le Croisic) and the 3 northern PC stations (Eperon, Le cornard and Boyard) from  
 186 April 1993 to January 2010, (3) the southern PC station (Auger) and the AB station (Arcachon)  
 187 from February 2003 to January 2010.

188 Sampling was conducted approximately every fortnight at each station. The phytoplankton  
 189 was identified to the lowest taxonomic level possible and counted with an inverted microscope  
 190 using the Utermöhl method (Utermohl, 1958): 358 taxa were identified over the eight stations. :  
 191 The water temperature ( $^{\circ}\text{C}$ ), salinity (PSU) and turbidity (NTU) were also measured during  
 192 each sampling session at each station. Both phytoplankton and physical databases were  
 193 recorded on 349 dates for both the NB stations, on 595 dates for the SB station and the 3 PC  
 194 stations and on 214 dates for the southern PC station and the AB station.

195 Two large-scale hydro-climatic indices were considered during this sampling period (1993  
 196 to 2010) because of their importance in the studied area (Beaugrand, 2009; Goberville et al.,  
 197 2010). The winter North Atlantic Oscillation (NAO) index (Hurrell, 1995) is a basin-scale

198 alternation of atmospheric masses between the subtropical and the Arctic Atlantic (Dickson and  
 199 Turrell, 2000). The Atlantic Multidecadal Oscillation (AMO) index is a large-scale oceanic  
 200 phenomenon, the source of natural variability in the range of 0.4°C in many oceanic regions  
 201 (Enfield et al., 2001). This index was downloaded from <http://climexp.knmi.nl/> and was  
 202 constructed from Extended Reconstruction SST (ERSST) data and averaged in the area of 25 to  
 203 60°N and 7 to 75°W, minus regression (i.e. detrending is intended to remove the North Atlantic  
 204 SST anomaly data from the analysis) on global mean temperature (National Climate Data  
 205 Center, USA: NCDC).

### 2.3. Data analysis

207 All tests were performed with R software routines (R Development Core Team, 2008)

208 In the phytoplankton database, rare species were excluded using the abundance sorting  
 209 method (Figure 2). This method, adapted from Ibanez et al. (1993), uses an index mixing  
 210 species abundances and frequencies, retaining only the frequent and locally abundant taxa at  
 211 least at one station (Roussel et al., 2010): 106 taxa were kept, i.e. 30% of the total taxa richness,  
 212 representing between 90 and 96% of the total abundances at each station.

213 Each series of taxa abundances, physical parameters and climatic indices were regularized  
 214 for each station using a SPLINE function (package PASTECS for R) (Grosjean and Ibanez,  
 215 2002) in order to obtain regulated series with 24 dates per year, synchronized between stations  
 216 (Figure 2). Consequently, the long-term series presented a similar number of values per year  
 217 and could be subjected to numerical analyses (David et al., 2005). Both phytoplankton,  
 218 physical factors and climatic indices represented by 268 dates for NB stations, 409 dates for  
 219 the SB station and 3 for the PC stations and 168 dates for the southern PC station and the AB  
 220 station.

221 Phytoplankton taxa were classified according to functional traits based upon their  
 222 availability to oyster feeding. The factors conditioning the phytoplankton availability for oyster  
 223 feeding include their availability for ingestion – size, shape and availability in the water  
 224 column-, and for digestibility –cell wall structures and biochemical composition (Brown et al.,  
 225 1998). The functional traits that have been used in this study were thus: (i) the size of an  
 226 individual cell, (ii) the individual or colonial shape, (iii) the potential toxicity.

227 • the size of an individual cell: only particles measuring between 5 and 100µm are efficiently  
 228 retained by pacific oysters (Barillé et al., 1993). Moreover, larvae preferentially feed on  
 229 phytoplankton cells smaller than 20µm (Baldwin and Newell, 1995; Raby et al., 1997).  
 230 Consequently, phytoplankton taxa were classified according to 3 size-classes: small size (T1,



231 equivalent spherical diameter (ESD) between 5 and 20 $\mu$ m) consumed preferentially by oyster  
 232 larvae, juveniles and adults; median size ESD (T2, between 20 and 100 $\mu$ m) used at least by  
 233 adults, whereas large size ESD (>20 $\mu$ m, T3) are consumed to a lesser extent by oysters.

234 • the shape: this trait can influence the size perception by the oyster. Colonial taxa (*versus*  
 235 solitary taxa) would be seen as larger than their individual ESD size, while a “linear” colony  
 236 would be more easily consumed than an ovoid colony. Phytoplankton taxa were thus classified  
 237 according to 3 shapes: (1) solitary cells (s) and (2) a linear colony of cells (ln); both assumed to  
 238 be consumed by oysters, and (3) other shapes.

239 The microphytoplankton data was thus separated into two databases: (1) a „specific  
 240 database“ including the abundances of the 106 species for each station/date and (2) a  
 241 „functional database“ presenting the abundances of the 10 functional groups for each  
 242 station/date. For each database, different diversity indices were calculated, namely species  
 243 richness (number of taxa or functional groups), the Pielou evenness and the Shannon diversity  
 244 indices (Gosselin, 2006; Washington, 1984).

245 Interannual variability of each variable (specific and functional diversity, physical factors  
 246 and climatic indices) were extracted using moving averages with a step of 24 (24 data a year)  
 247 for each station. The new series included trends and pluriannual cycles, seasonal variability  
 248 being removed from the previous regularized series (David et al., 2005). Both diversity  
 249 database were log-transformed, i.e.  $\log(x+1)$ , to attain homogeneity of the variances and  
 250 environmental factors (climatic indices and physical factors) were normalized.

251 The relationship between environmental parameters (physical factors and climate indices)  
 252 and specific/ functional diversity were then analyzed on a database constituted of different two-  
 253 way tables (i.e., diversity *vs* environmental factors parameters) with spatial (eight stations) and  
 254 temporal variations (from 1993 to 2010). Two types of two-table coupling methods, i.e. one  
 255 derived from canonical analysis, redundancy analysis (RDA) (Wollenberg, 1977) and one co-  
 256 inertia analysis, partial triadic analysis (PTA) (Kroonenberg, 1989; Thioulouse et al., 2004)  
 257 were used to elucidate patterns in both specific and functional diversity in relation with  
 258 physical factors and climatic indices for all stations and time periods (package ade4 for R;  
 259 Figure 2). The principle of both analyses is similar except that it is the covariance between the  
 260 row coordinates of the two tables that are maximized in PTA, instead of the correlation in RDA  
 261 (as other canonical analysis). An additional regression step is also added for RDA, ensuring  
 262 that sampling scores are linear combinations of environmental variables. The use of these two  
 263 complementary methods allowed to analyze a three-way table (diversity  $\times$  environment  $\times$   
 264 stations) over time



- 265 (i) as a sequence of two-way tables (diversity *vs* environment for each station), that  
 266 is to say to search for interannual pattern that are stables among the stations  
 267 using the PTA.
- 268 (ii) without considering stations independently and thus allowing to estimate the  
 269 greater source of variability (spatial or temporal) in phytoplankton patterns.

### 270 **Step 1. Spatial versus temporal pattern in phytoplankton diversity.**

271 The redundancy analysis (RDA) was used on both specific and functional diversity to  
 272 elucidate phytoplankton patterns in relation with physical factors and climatic indices for all  
 273 stations and time periods (package ade4 for R; Figure 2). The significance of the eigenvalues  
 274 and species–environment correlations of the five axes were determined by Monte Carlo tests  
 275 (499 permutations; package vegan for R).

276 The various measures between geographical areas (NB, SB, PC and AB, „space“), time  
 277 period (interannual variability, „time“) and interaction space  $\times$  time were tested with a Two-way  
 278 ANOVA for (1) physical factors, (2) total phytoplankton abundances, abundances of some  
 279 characteristic groups of taxa or functional groups and (3) other diversity indices as richness, the  
 280 Shannon-Weaver or the Simpson evenness indices for both taxonomic and functional diversity.  
 281 Post-hoc comparison were inferred when  $p < 0.05$  (Figure 2). Time was separated in four periods  
 282 corresponding to various large scale climate indices (from 1993 to 1995, from 1996 to 1998,  
 283 from 2002 to 2007 and 1999, 2000-2001, 2008-2010).

284 The most characteristic taxa and functional groups of the different geographical areas were  
 285 identified using the IndVal method developed by (Dufrêne and Legendre, 1997). This method  
 286 consists in computing an indicator value (IndVal index) by taking into account both measures  
 287 of fidelity and specificity. The indicator species assemblages can be obtained from any kind of  
 288 cluster. The index for a given taxa is independent of the relative abundance of any other taxa  
 289 and it is maximal when all individuals of a taxa are found in a single geographical area or when  
 290 the taxa occurs in all geographical areas for that group.

### 292 **Step 2. Temporal variation of the phytoplankton related to physical factors and climatic** 293 **indices.**

294 The partial triadic analysis (PTA) was used on both specific and functional diversity to  
 295 elucidate phytoplankton patterns in relation with physical factors and climatic indices for all  
 296 stations and time periods (package ade4 for R; Figure 2). Three PTA routines were used  
 297 because all stations were not sampled over the same temporal periods: The first one on the

298 whole period (from 1993 to 2010 ) was only available for the SB station, Eperon, Cornard and  
299 Boyard for the PC area, the second one on the period 1993 to 2004 available for the 6 northern  
300 stations (NB and SB stations, Eperon, Le Cornard and Boyard for PC area) and the third PTA  
301 routine on the period from 2003 to 2010 available for the 6 southern stations (SB, PC and AB  
302 stations).

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### 304 3. Results

#### 305 **3.2. Spatial versus temporal pattern in phytoplankton diversity**

306 The redundancy analysis explained significantly 47.2% of the total variance of the  
 307 specific diversity (Monte Carlo permutation test,  $p=0.002$ ), with 42.5% of the total variance  
 308 explained by the first 3 axes (22.0% by the first axis, 13.4% by the second axis and 7.1% by the  
 309 third axis). All these canonical axes and the explaining variables were significant (Monte Carlo  
 310 permutation tests,  $p<0.01$ ). The coefficients between the environmental variables and the  
 311 ordination axes showed that temperature (0.869) was the best explanatory variable on the first  
 312 canonical axis (Figure 3A and 3D), followed by salinity (-0.723) and turbidity (0.651). Salinity  
 313 was also well-represented on the second canonical axis (-0.636) and turbidity on the third  
 314 canonical axis (0.626).

315 The RDA analysis explained significantly 34.3% of the total variance of the functional  
 316 diversity (Monte Carlo permutation test,  $p=0.002$ ), with 30.6% of the total variance explained  
 317 by the first 2 axes (22.4% by the first axis and 8.2% by the second axis). All these canonical  
 318 axes and the explaining variables were significant (Monte Carlo permutation tests,  $p<0.01$ ).  
 319 The coefficients between the environmental variables and the ordination axes showed that  
 320 salinity (-0.800) and temperature (0.772) (Figure 4A) were the best explanatory variables on  
 321 the first canonical axis. AMO (-0.620) and turbidity (-0.565) were moderately represented on  
 322 the second canonical axis. The coefficients between the functional groups and the ordination  
 323 axes showed that T1s (0.833) and T1 (0.77) were highly correlated to the first axis, followed by  
 324 T3 (0.687) and T2sTx (0.624; Figure 4C). All this functional groups were favored by high  
 325 temperature and low salinity. Moreover, T2 seemed to be inversely correlated to turbidity on  
 326 the second axis.

327 Consequently, the RDA showed a spatial discrimination of phytoplankton specific and  
 328 functional diversity highly related to physical factors (temperature, salinity and turbidity) rather  
 329 than a temporal pattern. The four geographical areas were well-distinguished on the third 3  
 330 axes of the taxonomic Redundancy Analysis. *Biddulphia* spp. and *Dactyliosolen fragilissimus*  
 331 can be considered as opportunistic taxa and T2s and T2ln as opportunistic functional groups for  
 332 all the geographical areas since they share high and comparable IndVal values at the highest  
 333 hierarchical level (Figure 5A and 5B).

334 The North of Brittany zone (NB) was significantly characterized by the lowest  
 335 temperature and turbidity compared to others zones (Two-way ANOVA, factor „space“,

336 p<0.001). This area contained the lowest phytoplankton densities (Two-way ANOVA, factor  
 337 „space“, p<0.05). This zone is also significantly characterized by the lowest abundances of T1s,  
 338 T1ln, T1lnSpTx, T1, T2s and T2sTx (Two-way ANOVA, factor „space“ ; p<0.001). The lowest  
 339 specific and functional richness (Two-way ANOVA, factor „space“ ; p<0.001). It is also  
 340 characterized by the lowest abundances of freshwater and neritic species (Two-way ANOVA,  
 341 factor „space“ ; p<0.001). Five taxa reaching their highest IndVal values were considered as  
 342 specialists of the NB: *Guinardia striata*, *G. delicatula*, *Rhizosolenia styliformis* and *Pseudo-*  
 343 *Nitzschia delicatissima* (Figure 5A).

344 Twenty-one taxa and six functional groups are reported as generalist of the Atlantic  
 345 coast, the functional groups being T3, T2sTx, T1s, T1, T1lnSpTx and T1ln.

346 The South Brittany zone (SB) is significantly characterized by the lowest salinity (Two-  
 347 way ANOVA, factor „space“; p<0.001). It presented the highest phytoplankton densities (Two-  
 348 way ANOVA, factor „space“ ; p<0.05). Seven taxa can be considered as specialist of this  
 349 geographical area – *Heterocapsa triquetra*, *Leptocylindricus* spp., *Pediastrum* spp., *Cocconeis*  
 350 spp., *Katodinium* spp., *Cerataulina* spp., and *Melosira* spp.,. SB presented the highest  
 351 abundances of T1s, T1ln, T2s, T2sTx, and T2 and T3, T1sTx and T2 being specialist functional  
 352 groups of this area. SB presented the highest Shannon indices for functional groups (Two-way  
 353 ANOVA, factor „space“ ; p<0.001).

354 The Pertuis Charentais zone (PC) is significantly characterized by the highest  
 355 temperature and turbidity (Two-way ANOVA, factor „space“; p<0.001). The lowest  
 356 abundances of T2ln, evenness and Shannon indices for taxonomic and functional diversity and  
 357 the highest abundances of T1ln, benthic species and specific richness were observed in this area  
 358 (Two-way ANOVA, factor „space“ ; p<0.001). A warm and high-turbidity taxon *Actinoptychus*  
 359 spp. only reported in this area (IndVal=100) and two high-turbidity taxa *Biddulphia paxilifer*  
 360 and *Prorocentrum triestinum* are specialist of this area.

361 The Arcachon bay zone (AB) is significantly characterized by the highest salinity and  
 362 temperature (Two-way ANOVA, factor „space“ ; p<0.001). The lowest densities of T2, benthic  
 363 species, functional evenness and Shannon indices and the highest densities of T1lnSpTx, T2sTx  
 364 and T1, far neritic species, taxonomic richness and Shannon diversity were observed in this  
 365 zone (Two-way ANOVA, factor „space“ ; p<0.05). Eleven taxa are specialist of the Arcachon  
 366 bay with 2 taxa only reported in this area (*Palaeophalacroma* spp. and *Prorocentrum*  
 367 *compressum*).

### 368 **3.2.3. Relation between climate and local phytoplankton communities**

1  
2 369 Salinity, temperature and turbidity showed significant variations according to the period  
3  
4 370 of time characterized by different values of NAO and AMO (Two-way ANOVA, factor „time“;  
5  
6 371  $p < 0.001$ ). Globally, salinity and temperature were high when NAO and AMO were low.  
7  
8 372 Moreover, this fluctuations over time were significantly different according to the geographical  
9  
10 373 area for temperature and turbidity (Two-way ANOVA, factor „space“  $\times$  „time“ ;  $p < 0.01$ ). Total  
11  
12 374 abundances of phytoplankton were not significant different according to time (Two-way  
13  
14 375 ANOVA, factor „space“ ;  $p > 0.05$ ).

#### 15 376 **Specific diversity**

17 377 Over the period 1993 to 2010 for the SB and the three northern stations of PC, the two  
18  
19 378 first axes of the partial triadic analysis explained 89.7% of the total inertia, with the main  
20  
21 379 information brought by the first axis (66.6 %). The first factorial plan of the compromise for  
22  
23 380 the environmental variables showed that the large-scale climatic indices AMO was the best  
24  
25 381 explanatory variable on this first axis (0.716) and the NAO on the second axis (0.956; Figure  
26  
27 382 6A). Temperature was also inversely correlated to AMO on the first axis (-0.560). The Fam.  
28  
29 383 Naviculaceae was correlated to AMO (0.310 on the first axis) and *Leptocylindricus danicus* to  
30  
31 384 NAO (0.379 on the second axis) on the first factorial plan for species (Figure 6C). Over the  
32  
33 385 period 1993 to 2004 for the six northern stations, the two first axes of the PTA explained 96.9%  
34  
35 386 of the total inertia, the main information was brought by the first axis (86.9 %). The first  
36  
37 387 factorial plan of the compromise for the environmental variables showed that the large-scale  
38  
39 388 climatic indices AMO was the best explanatory variable on this first axis and the NAO on the  
40  
41 389 second axis. In contrast, over the period 2003-2010, the first two axes explained 97.5% of the  
42  
43 390 total inertia (88.2% and 9.3%, respectively) but both AMO and NAO were explained by the  
44  
45 391 two axis. The same species, Naviculaceae and *Leptocylindricus danicus* were respectively  
46  
47 392 correlated to AMO and NAO respectively on the first factorial plan for species for both  
48  
49 393 analyses. Moreover, *Pseudo-Nitzschia* spp seemed also to be correlated to AMO for both  
50  
51 394 analysis while *Guinardia striata* was negatively correlated to NAO for the second analysis.

52 395 Considering the first factorial plan of the compromise for the date points for the three  
53  
54 396 PTA, all stations showed the same interannual evolution, namely (1) from negative values to  
55  
56 397 positive values on the first axis corresponding to an increase of the AMO index and strong  
57  
58 398 fluctuations over the second axis (associated to variations of the NAO index) from 1993 to  
59  
60 399 2001, and (2) low fluctuations over both axes from 2001 to 2006 and increasing values over  
61  
62 400 the second axis (NAO) from 2006 to 2010 corresponding to an increase of the NAO index

401 whereas AMO was high and stable. The same results were observed on the both other PTA  
 402 (periods 1993-2001 and 2003-2010).

403         Dinoflagellate abundances were significantly higher for high AMO and NAO values  
 404 (Two-way ANOVA, factor „time“;  $p < 0.001$ ) and species richness was greater for high AMO  
 405 (Two-way ANOVA, factor „time“;  $p < 0.001$ ). These schemes were different between the  
 406 geographical areas (Two-way ANOVA, factor „space“  $\times$  „time“;  $p < 0.01$ ). Marine species were  
 407 also less abundant for high NAO and this was observed for all geographical areas (Two-way  
 408 ANOVA, factor „time“;  $p > 0.05$ )

### 409 **Functional diversity**

410         Over the period 1993 to 2010 for the SB and the three northern stations of PC, the two  
 411 first axes of the partial triadic analysis explained 90.4% of the total inertia, with the main  
 412 information brought by the first axis (64.0 %). The first factorial plan of the environmental  
 413 variables was highly comparable to specific diversity, showing that the large-scale climatic  
 414 indices AMO (0.785) was the best explanatory variable on this first axis and the NAO on the  
 415 second axis (-0.903; Figure 6D). Temperature was also inversely correlated to AMO on the first  
 416 axis (-0.545). T2 (-0.600), T1sTx (-0.411), T1lnTx (-0.420) and T3 (-0.446) were anticorrelated  
 417 to the first axis (and thus to AMO) and T1lnTx to the second axis (to NAO) on the first  
 418 factorial plan for species (Figure 6F). Over the period 1993 to 2004 for the six northern  
 419 stations, the two first axes of the PTA explained 97.1% of the total inertia, with the main  
 420 information brought by the first axis (83.0 %). The first factorial plan of the environmental  
 421 variables was highly comparable to specific diversity, showing that the large-scale climatic  
 422 indices AMO was the best explanatory variable on this first axis and the NAO on the second  
 423 axis. In contrast, from 2003 to 2010, the two first axes of the second PTA explained 98.9% of  
 424 the total inertia (59.2 and 49.7%, for axis 1 and 2 respectively) but both AMO and NAO are  
 425 well explained by the two axes as for specific diversity and opposed along the first axis. T1sTx  
 426 were highly anticorrelated to AMO for both analysis whereas T1lnTx was only correlated to  
 427 NAO for the second analysis (Figure 6F).

428         Considering the first factorial plan of the compromise for the date points for both PTA,  
 429 all stations showed the same interannual evolution, the same as for specific diversity. The  
 430 interstructure tables showed globally the same differences inter-stations than for specific  
 431 diversity.

432         T1S, T1lnTx, T1ln, T2sTx were significantly higher for high NAO values and T2 were  
 433 significantly higher for high AMO (Two-way ANOVA, factor „time“;  $p < 0.001$ ). Only T1lnTx

434 presented the same variations whatever the geographical area considered (Two-way ANOVA,  
1 factor „space“ × „time“;  $p > 0.05$ )  
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#### 4. Discussion

Among the functional groups defined according to the functional diversity approach, at least 2 can be highly exploited by oyster and thus influenced their growth, reproduction and recruitment. Food availability is actually a key factor for oyster recruitment even if previous works have shown that temperature highly influences larval growth and settling of the Pacific oyster during *in vitro* experiments (His et al., 1989; Scholtz et al., 1984). Moreover, previous works had shown food quality is much more important than food quantity for the recruitment success and that the factors conditioning the phytoplankton characteristics conducive for consumption by oyster adults and juveniles include their availability for ingestion (size, shape and quantity), and for digestibility (cell wall structures and biochemical composition (Barillé et al., 2003; Barillé et al., 1997; Brown et al., 1998). Oyster larvae are also able to actively select their prey according to their size and biochemical composition (Baldwin and Newell, 1995; Raby et al., 1997; Rico-Villa et al., 2006). Larvae prefer smaller phytoplankton cells to other prey in such as bacteria, and dissolved organic matter (Baldwin et al., 1989; Olson and Olson, 1989)).

Moreover, small but potentially toxic cell (T1sTx) might be highly damaging for oyster recruitment. This functional group is mainly represented by the abundances of two dinoflagellates, *Karlodinium* spp. and *Karenia mikimotoi* (about 55% and 31% of the abundances of the functional group, respectively). The first one, *Karlodinium* spp., is usually found in highly nutrient-enriched eutrophic conditions, and clearly benefit from a combination of abiotic factors (excessive nutrients and low turbulence) and biotic factors (low grazing pressure and good prey availability (Hall et al., 2008): the presence of nano-planktonic cryptophytes is indeed a key factor driving the formation of toxic *Karlodinium* blooms, which are able of mixotrophic nutrition (Adolf et al., 2008). Even if cryptophytes were not recorded in this study because they were not counted for at all eight stations, this factor could explain that *Karlodinium* spp are extremely localized on only 2 stations of the Pertuis Charentais area and sporadically observed in Arcachon Bay. The second species, *Karenia mikimotoi* is a cosmopolitan species. Toxic blooms of *K. mikimotoi* is frequently recorded worldwide (eastern North Atlantic, Japan, Europe, Australia, South America, North Africa and China) (Zhang et al., 2009) suggesting less environmental requirements than *Karlodinium* spp.. Blooms of both species are commonly associated with shellfish mortality through toxin production inducing growth inhibition and the disruption of critical larval processes (Leverone et al., 2006; Zhang et

470 al., 2009). Both dinoflagellates are marine species typical of the continental shelf region and  
 471 benefiting from low turbulence. Blooms are observed during summer and fall when a thermal  
 472 stratification appeared (Smayda and Reynolds, 2001).

473 The functional group T1sTx did not show any significant variation in abundances  
 474 between the four geographical areas even though its species diversity is highly variable.  
 475 *Karenia mikimotoi* is the common species in the four geographical areas, constituting at least  
 476 22% of the functional groups in terms of numbers. This species is the sole component of  
 477 T1sTx for the northern area (the North of Brittany) and its abundance was low at the PC  
 478 stations. However, the dominant species was *Karlodinium spp.* at 2 stations of the Pertuis  
 479 Charentais and *Prorocentrum spp.*, particularly *P. minimum* in the Arcachon Bay. The latter is  
 480 a common, neritic, bloom-forming dinoflagellate, widely distributed geographically in  
 481 temperate and subtropical estuarine and coastal environments (Heil et al., 2005; Wikfors,  
 482 2005). *Prorocentrum* effects on oysters include poor larval development, tissue pathologies and  
 483 systemic immune responses (Wikfors, 2005). Its blooms generally occur under conditions of  
 484 high temperatures and incident irradiances and low to moderate salinities in eutrophic coastal  
 485 and estuarine environments even if they have been found under widely varying salinities and  
 486 temperatures (Heil et al., 2005). Moreover, *Karlodinium spp.* and *Prorocentrum spp.* appeared  
 487 as specialist indicator species for the Pertuis Charentais and the Arcachon Bay areas  
 488 respectively. *Heterosigma akashiwo* is another species constituting the toxic functional groups  
 489 but with weak abundances, appearing in contrast as a generalist species of the French Atlantic  
 490 coast (the three southern areas). The specific composition of small toxic phytoplankton is thus  
 491 different between the 2 geographical areas presenting a spat production (Pertuis Charentais and  
 492 Arcachon Bay) even if their mean abundances were not significantly different.

#### 4.1. How to analyze spatial *versus* temporal variation of phytoplankton communities?

495 The RDA analyzed a three-way table (diversity  $\times$  environment  $\times$  stations) over time  
 496 without introducing a spatial discrimination in the analysis: temporal (through „date“) and  
 497 spatial (through „stations“) fluctuations were thus considered equally before calculations.  
 498 Results clearly showed a spatial discrimination of phytoplankton diversity highly related to  
 499 physical factors (temperature, salinity and turbidity) rather than a temporal pattern. This means  
 500 that more differences are observed in phytoplankton communities between geographical areas  
 501 than over the 17 years sampling (1993 to 2010) at each station. Consequently, diversity pattern

502 of phytoplankton along the French Atlantic coast was mainly driven by geographical features at  
 503 the mesoscale dimension.

504 However, the use of partial triadic analysis (PTA) enabled to elucidate the  
 505 temporal fluctuations of phytoplankton communities over the 17-years period. The factors  
 506 explaining this temporal pattern were different from those explaining spatial variation, i.e.  
 507 climate indices *versus* physical factors. The intention of such an analysis is actually to  
 508 consider a three-way table (diversity  $\times$  environment  $\times$  stations) over time as a sequence of two-  
 509 way tables (diversity  $\times$  environment for each station). It thus established an intra-station pattern  
 510 of variation, proposing a compromise for all stations and stating how much each station is  
 511 closer than this compromise.

512 Consequently, RDA and PTA might be complementary analysis in investigating  
 513 phytoplankton pattern of variation. PTA has been particularly useful in this work in analyzing  
 514 interannual fluctuations since RDA highlighted the geographical pattern of variation. However,  
 515 the use of both RDA and PTA would have been useless if the pattern analyzed by the RDA  
 516 would be the same as the PTA, that is to say the intra-station one. Moreover, the main  
 517 drawback that could limit the use of a PTA is that this statistical method needs the same  
 518 number of observations by sequence (i.e. the same number of date for each station in our  
 519 study), making the RDA more accessible.

## 520 **4.2. Geographical typology of phytoplankton diversity**

521 The pattern of specific diversity corresponded to the geographical distribution of  
 522 phytoplankton communities. Temperature correlated the best on the first axis of the redundancy  
 523 analysis, showing a latitudinal decreasing gradient between North and South areas. Salinity was  
 524 also important in discriminating the four areas according to the relative importance of marine  
 525 *versus* continental influences. Three zones were identified:

- 526 • The North of Brittany zone (NB), localized in the Southern East part of the English Channel,  
 527 and was characterized by low temperatures and turbidities.
- 528 • The South Brittany (SB) and the Pertuis Charentais (PC) zones, localized in the coastal zone  
 529 of the Bay of Biscay, were systems with low salinities and high turbidities; the PC zone a little  
 530 more warmer, salty and turbid than the SB zone.
- 531 • The Arcachon Bay (AB) occupied an intermediate position between these two areas (SB and  
 532 PC), because of its high salinity and low turbidity.

533 The geographical typology of microphytoplankton in the English Channel and Bay of  
1 534 Biscay was previously recorded by (Gailhard et al., 2003), but without any consideration of  
2  
3 535 physical factors. This biogeographical typology was established on 17 stations (REPHY  
4  
5 536 network) distributed along the French coast (English Channel, Bay of Biscay and  
6  
7 537 Mediterranean coast) using a co-inertia analysis (STATIS method). Her typology did not  
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9 538 highlight the distinctiveness of the Arcachon Bay even if this station seemed to be isolated  
10  
11 539 from the Northern stations of the Bay-of-Biscay on the interstructure analysis (Gailhard et al.,  
12  
13 540 2003)).

14 541 Even if such geographical typology was mainly explained by temperature, only few  
15  
16 542 species showed a clear gradient between the Northern (and colder) area and the southern (and  
17  
18 543 warmer) area. Only seven species were present in the four geographical areas with a decreasing  
19  
20 544 Indval from South to North for four of them (*Dictyocha* spp., *Nitzschia longissima*, *Odontella*  
21  
22 545 *regia* and *Thalassionema nitzchioides*) and inversely for *Guinardia delicatula*, *Lauderia* spp.,  
23  
24 546 and *Licmophora* spp. Such latitudinal increasing or decreasing gradient of species densities  
25  
26 547 would clearly suggest a biogeographical distribution subject to temperature. *Thalassionema*  
27  
28 548 *nitzchioides* preferred warm temperature which explain its decreasing northward gradient  
29  
30 549 (optimum at 20°C; (Karentz and Smayda, 1984). Moreover, some species are specialist for the  
31  
32 550 intermediate areas such as *Actinoptychus* for PC or *Heterocapsa triquetra* for SB. Latitude thus  
33  
34 551 appear not to play a role in phytoplankton distribution.

35 552 Gaillard et al. (2003) attributed the geographical typology concerning phytoplankton  
36  
37 553 diversity to the hydrodynamic characteristics of each area and were of the opinion that local  
38  
39 554 influences such as differences in nutrient input were of secondary importance. For example,  
40  
41 555 Gaillard et al. (2003) argued that the phytoplankton community of the English channel was  
42  
43 556 dominated by diatoms whereas dinoflagellates were more prevalent in the Bay of Biscay. The  
44  
45 557 diatoms/dinoflagellates dominance had historically been related to the physical properties of  
46  
47 558 the water column (Estrada et al., 1999; Kaneta et al., 1985), according to the „Margalef  
48  
49 559 Mandala“ model. The latter described a species succession in phytoplankton assemblages in  
50  
51 560 which diatoms dominate periods of mixing and high nutrient concentrations (r-strategists) and  
52  
53 561 dinoflagellates prevail under oligotrophic and stratified conditions as K-strategists (Margalef,  
54  
55 562 1978). High mixing rates would inhibit dinoflagellate growth through physiological damaging  
56  
57 563 and behavioral changes, whereas diatoms would be less sensitive to mixing (Thomas and  
58  
59 564 Gibson, 1990).

60 565 However, recent works considered that the „Margalef Mandala“ model was over  
61  
62 566 restrictive because of the probable independence between mixing and nutrient availability.

567 Reynolds et al. (2002) proposed a more complex phytoplankton classification system based on  
 1 568 the species tolerances to different degrees of mixing and nutrient availability. The  
 2 569 surface/volume (S/V) ratio and maximum linear dimension were used to group the species in  
 3 570 three strategies (C–S–R) rather than the previous two (r–K) proposed in the „Margalef  
 4 571 Mandala“ model. The C-strategists are small and fast-growing species dominating in stratified  
 5 572 waters with high nutrient levels. The R-strategists are characterized by high a S/V ratio that  
 6 573 would allow them to survive under high mixing conditions, but at high nutrient concentrations,  
 7 574 while the S-strategists would be large and slow-growing species, dominating in oligotrophic  
 8 575 waters and developing mixotrophy or vertical migration to obtain nutrients. This Reynolds  
 9 576 scheme has been applied to marine dinoflagellates (Smayda and Reynolds, 2001; Smayda and  
 10 577 Reynolds, 2003) and diatoms ((Alves-de-Souza et al., 2008). Dinoflagellate species were  
 11 578 distributed among the three strategies but diatoms were recognized as R-strategists (except for  
 12 579 *Coscinodiscus* spp.). In spite of their R-strategy, diatoms are not a homogeneous group in their  
 13 580 ecological responses and they can be classified in different functional groups, reminiscent of  
 14 581 the r-K strategies of Margalef (1978), correlated mainly to a gradient of N:Si ratio (Alves-de-  
 15 582 Souza et al., 2008)..

29 583 We thus tried to relate the geographical typology of microphytoplankton observed along  
 30 584 the Atlantic coast to different functional traits of the species: (i) C-S-R and r-K strategies to the  
 31 585 species behavior to mixing and nutrient availability; (ii) their preferred habitat (marine *versus*  
 32 586 estuarine *versus* freshwater); (iii) their planktonic *versus* benthic features.

36 587 ► The North of Brittany, and more generally the English Channel coasts is characterized by a  
 37 588 very high marine (*versus* continental) influence compared to the southern areas. This is due to  
 38 589 low river inputs and very strong tidal currents. The latter are important physical forcing  
 39 590 vectors leading to a high vertical mixing all year round (Gailhard et al., 2003; Ryckaert et al.,  
 40 591 1983). The specific diversity of phytoplankton corroborated such an assumption since (i) NB  
 41 592 had the lowest densities of dinoflagellates and (ii) the specialist species recorded for NB were  
 42 593 only R-strategist diatoms adapted to mixing: Among the diatoms, one r-strategist (*Pseudo-*  
 43 594 *nitzchia delicatissima*), which favor high mixing, was also recorded as a specialist species in  
 44 595 NB (Alves-de-Souza et al., 2008). However, none of these species was typical specialist of this  
 45 596 area since they have also been recorded in the southern areas. Moreover, this diatom dominance  
 46 597 was not associated with a high species-rich pool in contrast with a dinoflagellate dominance  
 47 598 that more likely develop monospecific blooms as suggested by (Smayda and Reynolds, 2003).

58 599 ► The two northern areas localized on the coast of the Bay of Biscay (SB and PC) are  
 59 600 characterized by a high continental influence since they are submitted to high river inputs

601 (Loire, Gironde, Charente) and lower tidal currents than in the English Channel. The  
602 hydrodynamic circulation is thus mainly controlled by winds, favoring the freshwater  
603 dispersion offshore. This haline stratification combined with an increase in luminosity caused a  
604 vertical stratification during summer (Lazure and Jegou, 1998) enhancing phytoplankton  
605 blooms (Labry et al., 2001). As for the North of Brittany, this hydrodynamic feature is also  
606 associated with the specific diversity of microphytoplankton. The highest mean density of  
607 dinoflagellate was actually recorded for both areas and generalist species of the Bay of Biscay  
608 were predominantly constituted by dinoflagellates in contrast with the specialist species of the  
609 English Channel. Moreover, the dinoflagellates *Heterocapsa triquetra*, *Katodinium* spp. (SB)  
610 and *Karlodinium* spp. (PC). *Heterocapsa triquetra*, *Katodinium* spp. (SB) and *Karlodinium*  
611 spp. (PC). were recorded as specialist species in both areas as C-strategists according to  
612 (Smayda and Reynolds, 2001). Both areas are also characterized by (i) freshwater specialist  
613 species (Olenina et al., 2006): *Pediastrum* spp., *Melosira* spp. (SB) and *Bacillaria Paxillifer*  
614 (PC), and (ii) specialist benthic and tychopelagic species (Jouenne et al., 2007; Olenina et al.,  
615 2006), namely *Synedra* spp. as generalist species of the Bay of Biscay and Fragilariaceae,  
616 Naviculaceae, *Actinoptychus*, *Bacillaria paxillifer*, *Rhaphoneis* as specialist species for PC,  
617 pointing to benthic resuspension through turbulence induced by the high river discharge and  
618 the wind-induced hydrodynamic features (Alpine and Cloern, 1992). The main difference  
619 observed between the two areas is the relative importance of freshwater and benthic organisms.  
620 The low saline SB area contained more freshwater specialist species and abundances whereas  
621 the highly turbid PC area contained a high number of benthic specialist species and high  
622 abundances. In this system, microphytobenthos is a great source of primary production through  
623 resuspension of algae due to the relative importance of the mudflat areas (Guarini et al., 2008).

624 The great connectivity with both marine, freshwater and benthic habitat can explain the  
625 high specific richness of the Pertuis Charentais. The oceanic interface is known to be an  
626 important source of diversity for phytoplankton due to species dispersion and immigration  
627 caused by hydrodynamic processes (Cloern and Dufford, 2005). On the other hand, the  
628 sporadic contribution of freshwater and benthic species compared to marine species could  
629 explain the low Pielou equitability and Shannon indices for this area.

630 ► The low continental inputs by the Leyre River and the important water exchanges with the  
631 adjacent oceanic waters in Arcachon Bay provide hydrodynamic conditions similar to the  
632 English Channel (Glé et al., 2008) in spite of their southern localization on the Bay of Biscay.  
633 The vertical mixing prevents the summer stratification and thus limits dinoflagellate  
634 proliferation. North of Brittany specialist species are mostly constituted by R-strategist favored

635 by high mixing: diatoms (*Proboscia alata*, *Cerataulina pelagica*), notably r-strategist  
636 (*Chaetoceros* spp. and *Cylindrotheca closterium*) and dinoflagellates (*Gonyaulax* spp.).  
637 However, two dinoflagellate species (*Gyrodinium spirale* and *Prorocentrum* spp.) recognized  
638 as C-strategists according to (Smayda and Reynolds, 2001) and thus favored by a stratification  
639 were also recorded among the specialist species of this area in the two northern areas of the  
640 Bay of Biscay. *Guinardia* spp, are also recorded among the specialist species illustrating that  
641 silicate can be limited during summer in the Northern station (Jouenne et al., 2007; Raymont,  
642 1980; Reid et al., 1990). All these observations agree with an intermediate hydrodynamic  
643 feature between NB and SB-PC.

644 Consequently, the specific diversity of microphytoplankton highlights a geographical  
645 pattern of distribution ((Boström et al., 2006; Kruk et al., 2002). This geographical typology is  
646 highly related to the physical parameters temperature, salinity and turbidity and mainly driven  
647 by the hydrodynamic features of each area such as mixing and nutrient availability, and not by  
648 a latitudinal gradient of temperature. The combination of tools as the IndVal method (Dufrêne  
649 and Legendre, 1997) associated to the functional traits of the indicator species based on CSR  
650 strategies identified by (Smayda and Reynolds, 2001) and (Alves-de-Souza et al., 2008) for  
651 marine diatoms and dinoflagellates, the preferential habitat and specific indices of diversity  
652 allowed an understanding of the phytoplankton communities observed in each area.

653 Contrary to specific diversity, the geographical typology was not so clear for the  
654 functional diversity based on the oyster requirement for food. The small, solitary and non toxic  
655 cells are among the functional group might be important to the recruitment success of oysters.  
656 The high positive correlation with temperature and negative with salinity could explain why the  
657 2 southern areas are the sole site of oyster spat production in France.

658 Concerning the potential toxic species, only the large forms of *Dinophysis* spp (*D.*  
659 *caudata* and *D. acuminata*) (*D. caudata* and *D. acuminata*). seemed to be related to  
660 temperature. These species occurred as generalist species in the Bay of Biscay occurring in  
661 low-nutrient and highly stratified habitats with toxic effects occurring at very low population  
662 levels ((Smayda and Reynolds, 2001; Smayda and Reynolds, 2003). In the Pertuis Charentais,  
663 *Dinophysis* blooms are actually favored inside the bay during summer and fall when a thermal  
664 stratification appeared and nutrient are highly limiting (Delmas et al., 1992). Such conditions  
665 seemed be favored during warmer years.

#### 666 4.3. Interannual variability of phytoplanktonic communities



667 Climatic indices (*versus* local physical factors) were the main drivers explaining the  
1 668 interannual pattern of phytoplankton communities along the French Atlantic coast. These  
2 669 results suggest that, locally, phytoplankton communities were affected by large-scale climate  
3 670 variability between 1993 and 2010. Changes in phytoplankton biomass at local, regional and  
4 671 global scales had previously been linked to climate forcing: interannual to decadal variations  
5 672 were strongly correlated with basin-scale climate indices, whereas long-term declining trend  
6 673 was related to increasing sea surface temperatures (Boyce et al., 2010). The climate effect on  
7 674 phytoplankton is indirect and caused by changes in hydrological conditions. For example, the  
8 675 interannual change of the phytoplankton biomass over the whole Northeast Atlantic had been  
9 676 attributed to increasing phytoplankton metabolic rates due to higher temperatures in cooler  
10 677 regions and to a decrease in nutrient supply leading to a biomass decrease in warmer regions  
11 678 (Doney, 2006; Richardson and Schoeman, 2004). Along the French Atlantic Coast, regional  
12 679 climate also influences European coastal systems modifying hydrological (physical and  
13 680 chemical) parameters (Goberville et al., 2010): This effect has been attributed to temperature,  
14 681 local atmospheric and ocean circulation changes. Such climatic effect had also being detected  
15 682 in chl *a* used as an index of the phytoplankton biomass (Goberville et al., 2010).

683 Along the French Atlantic coast, both regional hydro-climatic and coastal changes were  
684 influenced by NHT (Northern Hemisphere Temperature anomalies), a large-scale  
685 climatological index, but the correlation was also significant with the Atlantic Multidecennial  
686 Oscillation (AMO (Goberville et al., 2010)). In our study, phytoplankton communities seemed  
687 to be related mostly to AMO than to NAO (first axis of the PTA). This suggests a high impact  
688 of climate through temperature instead of local atmospheric or circulation changes on  
689 phytoplankton communities. Previous works had actually established positive correlations  
690 between NHT and SST (Sea surface temperatures anomalies) stronger than with NAO in the  
691 eastern part of the North Atlantic, around the British Isles and the North Sea (Beaugrand and  
692 Reid, 2003). Moreover, AMO is an index constructed from Extended Reconstruction SST  
693 (ERSST), with temperature as the NHT index. SST appears as the master parameter governing  
694 the changes in the coastal environment (Beaugrand, 2009). On the contrary, the NAO measures  
695 a basin-scale alternation of atmospheric masses between the subtropical and the Arctic Atlantic  
696 (Dickson and Turrell, 2000). The low influence of the NAO compared with AMO could be  
697 attributed to a modest influence of atmospheric change on the local climatological parameters  
698 (Beaugrand and Reid, 2003).

699 However, the NAO seemed to drive interannual variation of phytoplankton  
700 communities from 2006 to 2010. This corresponded to a time period during which AMO

701 variations were very weak. Such anomalies in the relationship between large scale climatic  
1 702 indices and biological compartments had yet been observed. (Fromentin and Planque (1996)  
2 703 reported a breaking down after 1996 in the strong negative correlation between NAO and the  
3 704 abundance of the copepod *Calanus finmarchicus* in the North Sea. The effect of climate  
4 705 depended upon the intensity of the climate anomalies. Only substantial negative or positive  
5 706 forcings were related to changes in the state of the coastal systems, while moderate forcing had  
6 707 no effect (Carpenter and Brock, 2006; Goberville et al., 2010). Consequently, the strength of  
7 708 the correlation between climate and hydrological or biological factors may vary locally and  
8 709 temporally (e.g. non-linearity of the correlation).

16 710 Besides the temporally change in the strength of correlation between AMO and  
17 711 phytoplankton communities, spatial variations have been pointed out. First, the strength and  
18 712 even the direction of the relationships between taxa or functional groups and AMO or NAO  
19 713 varied according the geographical areas. Moreover, the interannual variation of phytoplankton  
20 714 was clearly explained by AMO for both the South Brittany area and the Pertuis Charentais,  
21 715 butd was not for the North of Brittany and the Arcachon Bay. The effect of SST in the water  
22 716 column could increase the vertical stratification in the coastal regions, except for areas where  
23 717 mixing by tidal currents is intense and limits stratification (Goberville et al., 2010). The AMO  
24 718 effect was thus masked in the the North of Brittany and the Arcachon Bay zones. This  
25 719 assumption seemed to be confirmed by the positive correlation between AMO and *Pseudo-*  
26 720 *nitzchia* spp. which are flourish under stratified conditions (Alves-de-Souza et al., 2008). High  
27 721 AMO also favored benthic species (Jouenne et al., 2007) as Naviculaceae, a specialist taxa of  
28 722 *Pertuis charentais*. This confirmed that resuspension is induced by high river discharge,  
29 723 causing stratification in the dilution plume of rivers. Highly significant correlations had also  
30 724 been established between AMO and turbidity at most of the PC stations.

43 725 Toxic functional groups seemed to be particularly related to large-scale climatic indices  
44 726 because (1) small and solitary cells (T1sTx) were anticorrelated to AMO when the effect of this  
45 727 index is high (from 1993 to 2004) and highly anticorrelated to NAO after 2005, and (2) small  
46 728 linear cells (T1lnTx) were anticorrelated to NAO. Thus, functional groups are better explained  
47 729 by climatic indices than physical factors even if this relation is complex. These observations are  
48 730 particularly interesting considering that detecting the occurrence of toxins-producing species is  
49 731 a public health preoccupation for shellfish consumption and thus economical activities of  
50 732 coastal ecosystems. This revealed that climate might strongly influence the presence of toxic  
51 733 species and thus act in synergism with other anthropogenic pressures to alter the state and  
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734 functioning of biological and ecological systems and the services they provide (Goberville et  
1 735 al., 2010).  
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#### 5 736 **4.4. Specific *versus* functional diversity: what can we expect from such** 6 7 737 **approach?** 8

9 738 Even if warmer years would favor oyster recruitment through favoring the development  
10 of small and solitary cells, no direct physical factor seemed to explain the proliferation of small  
11 739 and potentially toxic cells that also impact significantly on oyster recruitment. This functional  
12 and potentially toxic cells that also impact significantly on oyster recruitment. This functional  
13 740 group had nevertheless been correlated with climatic indices even if these correlations evolved  
14 and potentially toxic cells that also impact significantly on oyster recruitment. This functional  
15 741 group had nevertheless been correlated with climatic indices even if these correlations evolved  
16 over time (high correlation with either AMO or NAO according to the temporal period  
17 742 considered). The harmful algae recorded in the functional group T1sTx are dependent on  
18 different environmental factors: *Karenia mikimotoi* and *Karlodinium* are typically marine  
19 743 species blooming during summer (Hall et al., 2008; Zhang et al., 2009) whereas *Prorocentrum*  
20 744 *spp.* is an estuarine species developing during spring-summer (Heil et al., 2005). This remark  
21 can be extended to all the other functional groups, explaining why none of them appears as  
22 745 specialist in one geographical area. Indicator species provide information about the  
23 characteristics of the different geographical areas thanks to their own functional traits (habitat,  
24 746 sensitivity to nutrients, turbulence, etc.) whereas functional groups defined on the basis of  
25 oyster requirement for feeding can allow understanding the relationships between prey  
26 747 assemblages and predator. The functional approach based on the morphological and  
27 physiological trait proposed by (Smayda and Reynolds, 2001) -S/V ratio and maximum linear  
28 748 dimension would allow to divide the species according to the C-,S-,R- strategies in relation to  
29 nutrient availability and turbulence, and would provide more similar results concerning the  
30 749 geographical typology of phytoplankton than specific diversity. Both functional approaches  
31 bring very interesting and informative elements for the understanding of the system; the first  
32 750 one concerning the relationships between oyster recruitment, prey assemblage and the  
33 complexity of their relation with the environment and the second one on the physical factors  
34 751 driving the phytoplankton community.  
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51 761 Consequently, the choice of functional trait in a functional approach is really important  
52 in these kind of studies. Unfortunately, the first criteria in the choice of functional traits implied  
53 762 in the building of functional groups are often the knowledge availability instead of the real  
54 adequacy to the objectives of the study or the considered system even if different authors have  
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765 proposed some reviews on the different possible and available functional traits of  
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2 766 phytoplankton (Reynolds et al., 2002).

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## FIGURES CAPTIONS

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3 1029 **Figure 1:** Geographical distribution of the 8 stations along the Atlantic Coast. These stations are  
4 1030 localized on 4 geographical zones from North to South: North Brittany (Saint Cast, Paimpol),  
5 1031 South Brittany (Le Croisic), Pertuis Charentais (Eperon, Cornard, Boyard, Auger) and  
6 1032 Arcachon Bay (Arcachon).  
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10 1033 **Figure 2:** Diagram of the analysis steps  
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12 1034  
13 1035 **Figure 3:** Redundancy analysis of interannual variability of the eight stations along the Atlantic  
14 1036 Coast based on species abundances for axis 2 vs axis 1 (A-C) and Axis 3 vs Axis 1(D-F).  
15 1037 Environmental variables (physical factors and climate indices, A and D), observations (B and  
16 1038 E) and species abundances (C and F).  
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21 1039 **Figure 4:** Redundancy analysis of interannual variability of the eight stations along the Atlantic  
22 1040 Coast based on functional groups abundances for axis 2 vs axis 1. Environmental variables (A),  
23 1041 observations (B) and functional group abundances (C).  
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28 1042 **Figure 5:** Indicator taxa (A) or functional groups (B) for each hierarchical level of cluster  
29 1043 established according the similarity between geographical areas. IndVal values are shown in  
30 1044 brackets. Only the highest IndVal values for each taxon were reported at each hierarchical level  
31 1045 (IndVal bold values indicate the highest IndVal values).  
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36 1046 **Figure 6:** Partial triadic analysis on interannual variability of the four stations sampled between  
37 1047 1993 and 2010 based on species abundances („specific diversity“, left) and functional-groups  
38 1048 abundances („functional diversity“, right). First factorial plan of the compromise for the  
39 1049 environmental variables (A and D, respectively); First factorial plan of the compromise for the  
40 1050 date points (grey continuous lines for the SB station -Le Croisic-, black continuous line for  
41 1051 Eperon, large dotted line for Le Cornard and thin dotted line for Boyard) (B and E,  
42 1052 respectively, years were reported on the figure); First factorial plan of the compromise (C and  
43 1053 F, respectively).  
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51 1054 **Table 1:** Phytoplanktonic functional groups defined according to important functional traits for  
52 1055 oyster feeding.  
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Figure 1

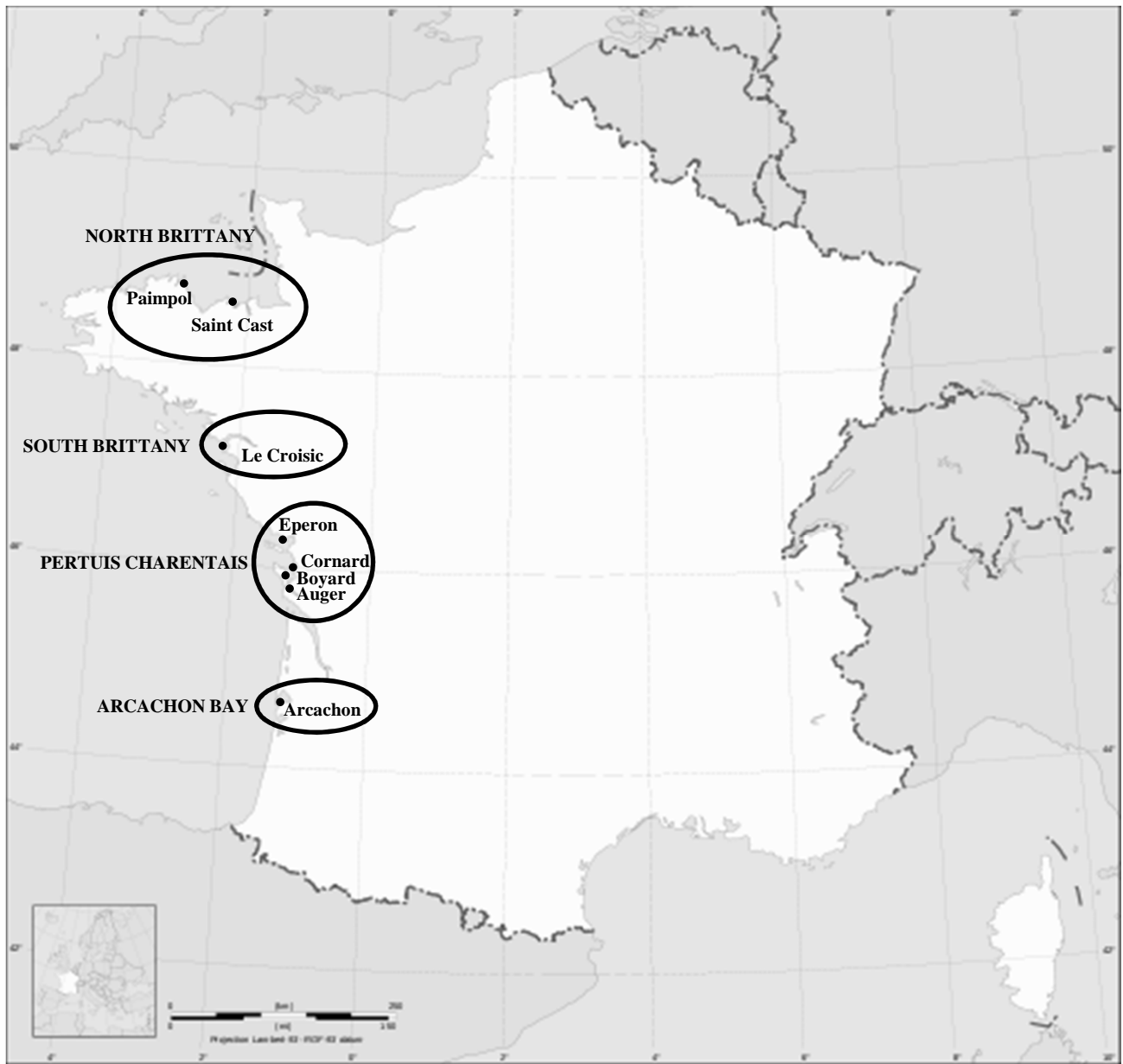




Figure 2

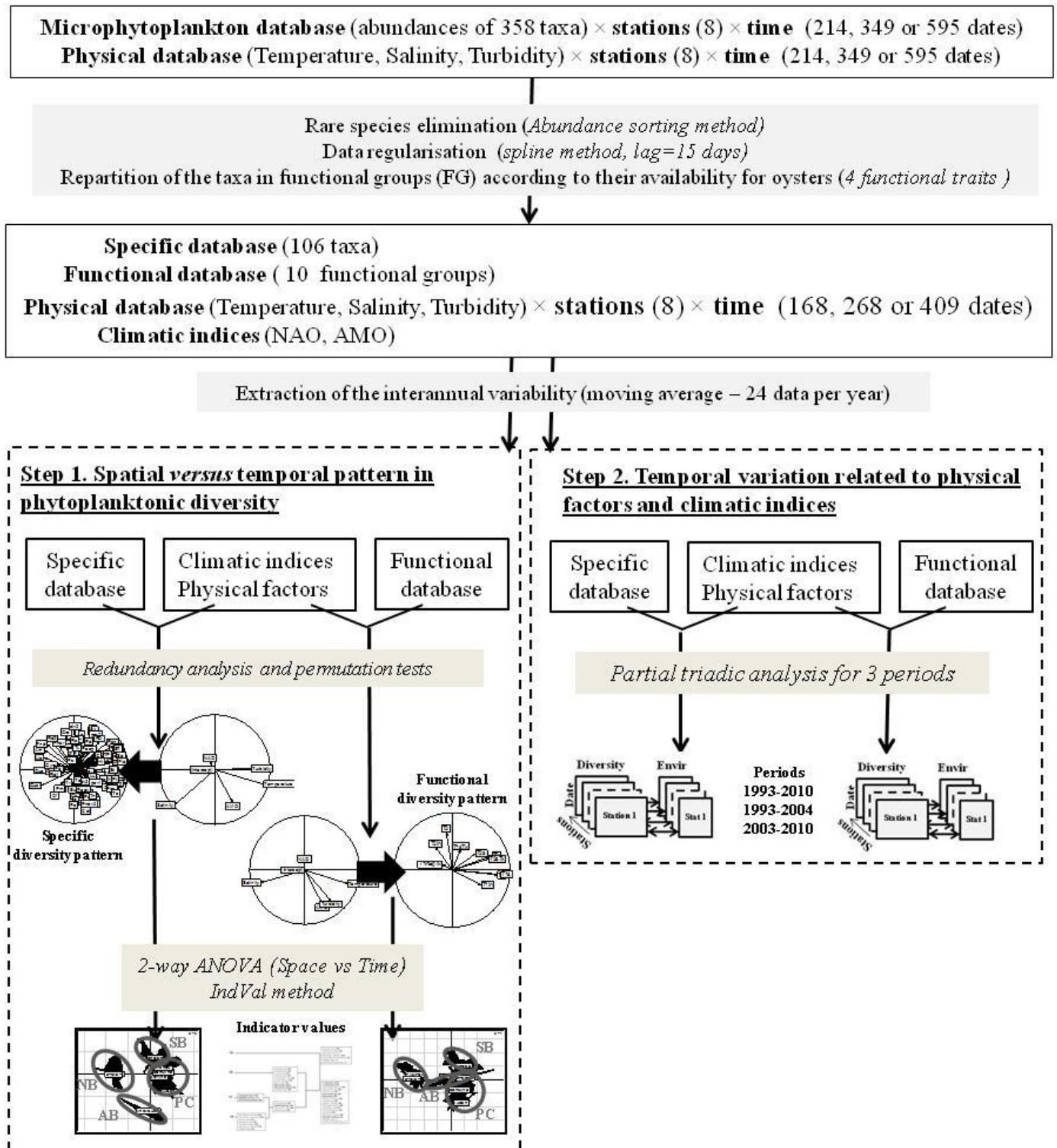


Figure 3

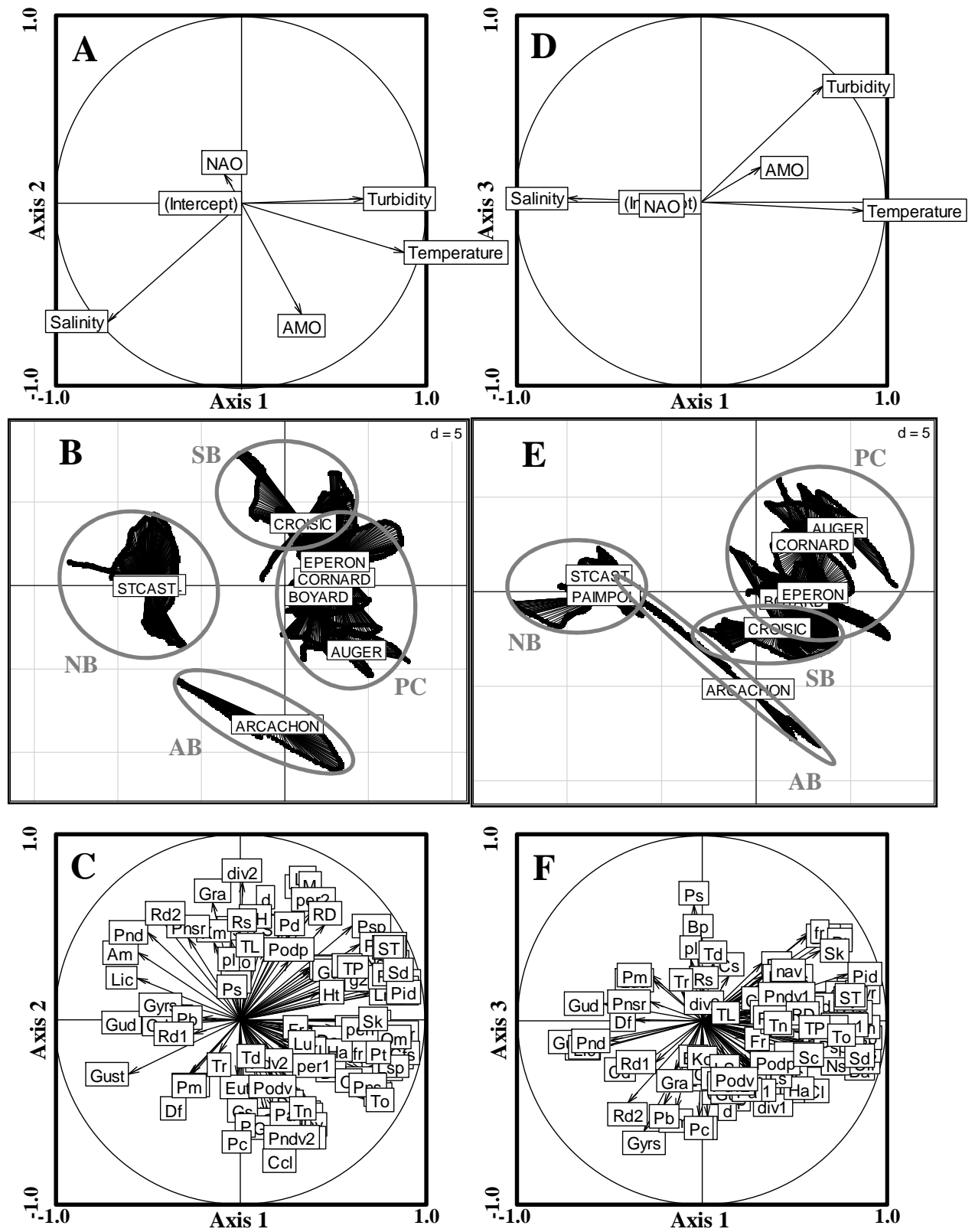


Figure 4

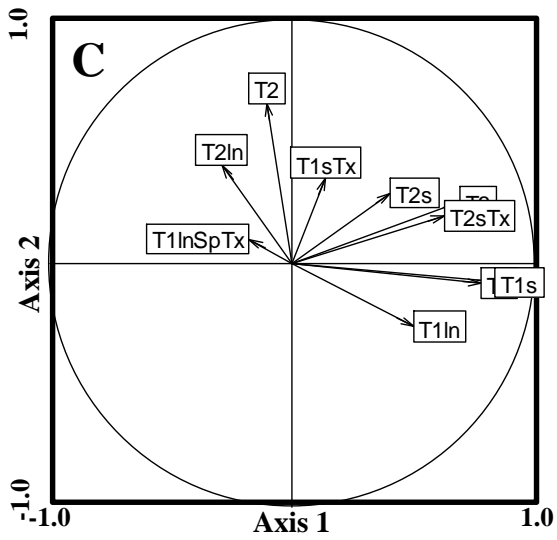
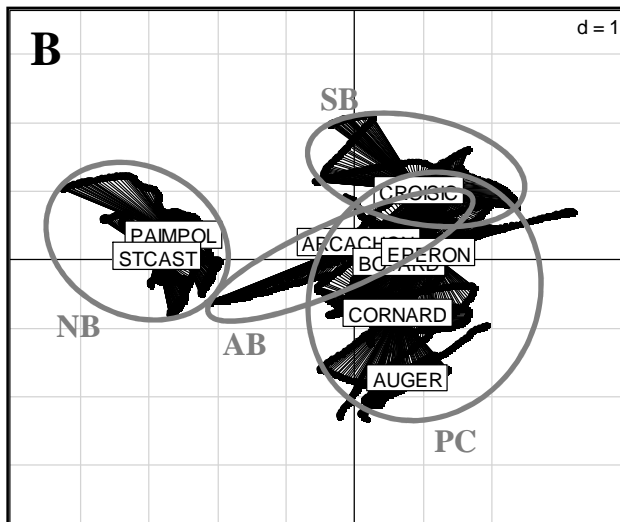
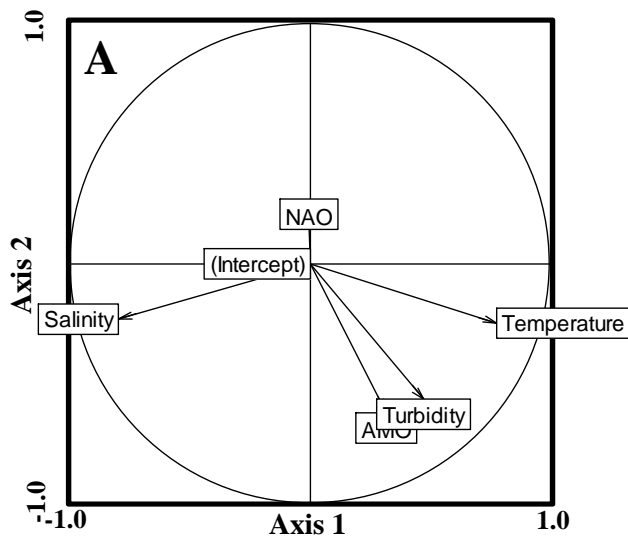


Figure 5

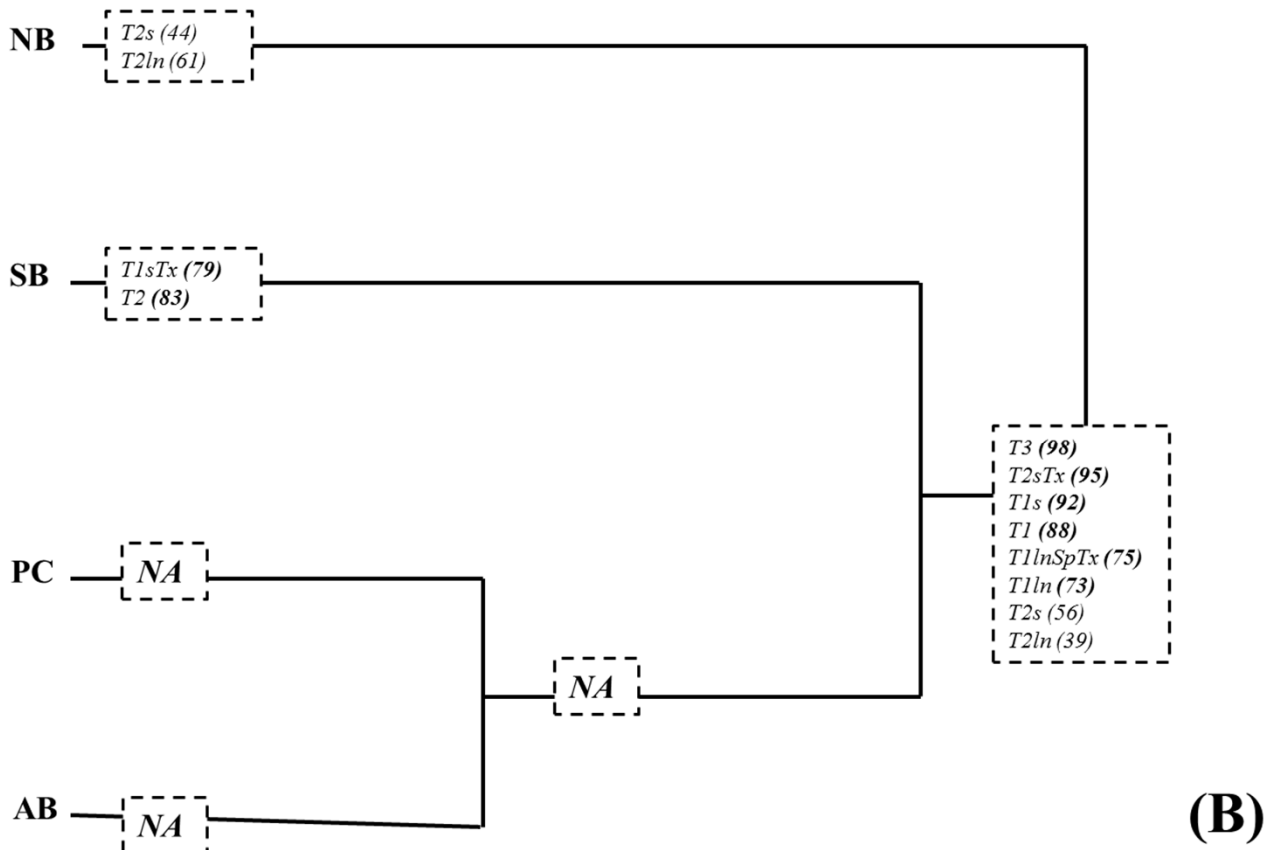
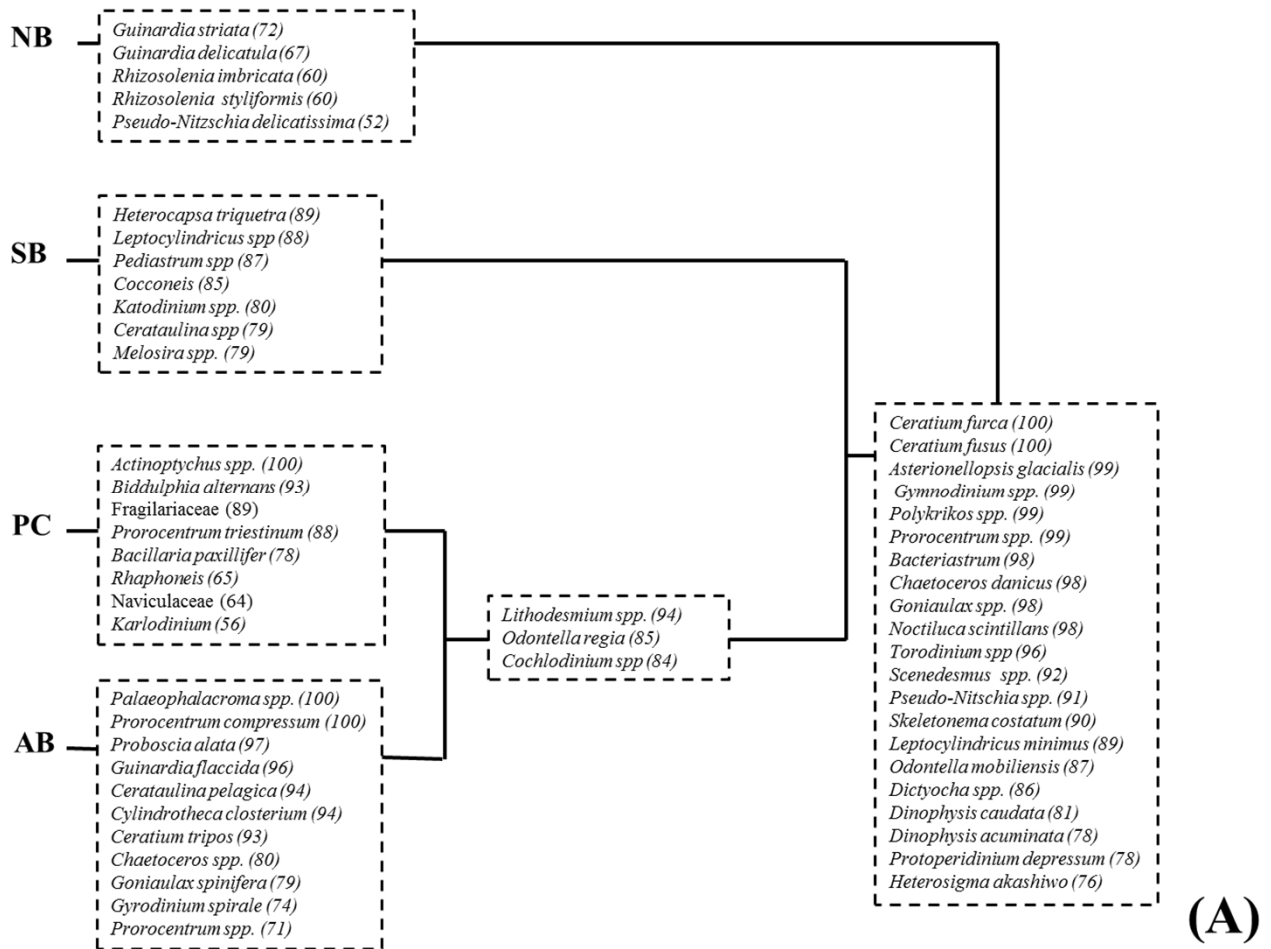
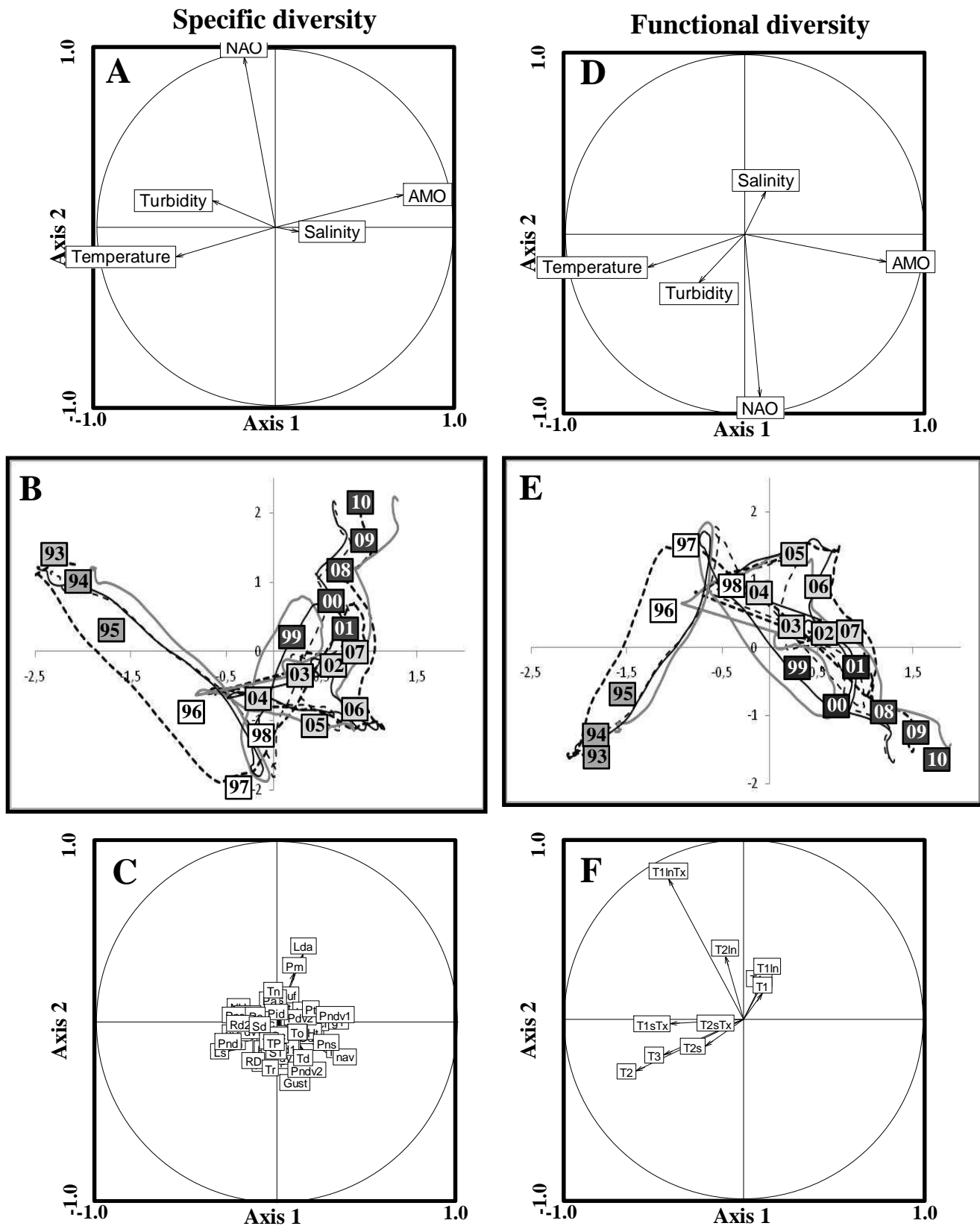


Figure 6



**TABLE 1**

<b>Codes</b>	<b>Functional traits</b>	<b>Examples</b>
<b>T1s</b>	Small size / solitary / no spines /non toxic	<i>Scenedesmus</i> <i>Naviculaceae</i>
<b>T1sTx</b>	Small size / solitary / no spines / potentially toxic	<i>Karlodinium</i> spp., <i>Karenia mikimotoi</i>
<b>T1ln</b>	Small size / linear colony / no spines non toxic	<i>Thalassionema</i> <i>nitzschioides</i>
<b>T1lnSpTx</b>	Small size / linear colony with spines or pointed tips / potentially toxic	<i>Pseudo-nitzschia</i>
<b>T1</b>	Small size / others	<i>Cylindrotheca closterium</i>
<b>T2s</b>	Median size / solitary / no spines /non toxic	<i>Rhizosolenia styliformis</i> <i>Katodinium</i> spp.
<b>T2sTx</b>	Median size / solitary / no spines / potentially toxic	<i>Dinophysis caudata</i>
<b>T2ln</b>	Median size / linear colony / no spines non toxic	<i>Guinardia striata</i>
<b>T2</b>	Median size / others	<i>Rhizosolenia</i>
<b>T3</b>	Large size	<i>Noctiluca scintillans</i>