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An ecological partition of the Atlantic Ocean and its adjacent seas

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Abstract

In the past, partitions of the global ocean have been commonly carried out using relatively few environmental or biological variables. Although such partitions are undoubtedly useful on a global scale, we show that, at a basin scale, the use of a large number of biological variables greatly improves the accuracy of a partition. We first determined pelagic habitats using a set of selected environmental variables such as temperature, bathymetry, light at the seabed, sea ice concentration, current velocity and salinity. We then partitioned the North Atlantic Ocean and its adjacent seas at spatial resolutions of 2° latitude x 2° longitude and 0.5° x 0.5° using biological data from the Continuous Plankton Recorder (CPR survey). We used a total of 238 plankton species or taxa sampled between 1946 and 2015 representing more than 60 million data points. Finally, we combined the three biogeographies together to propose a new ecological partition of the North Atlantic and its adjacent seas into Ecological Units (EUs) and ecoregions. The comparison of our partition with the biogeochemical biogeography proposed by Longhurst reveals substantial differences in the location and size of biomes and provinces, especially over the continental shelf. In particular, boundaries of three known biomes (i.e. westerlies, polar and continental shelves biomes) differ substantially from the global-scale classifications.

40 1. Introduction

41

42 Understanding how life is arranged on Earth has long occupied scientists such as Carolus
43 Linnaeus (1707-1778) and Georges-Louis Leclerc, Comte de Buffon (1707-1788). Partitioning
44 the marine pelagic domain has proved to be quite difficult in comparison to the terrestrial
45 realm where demarcations are more apparent and access to the field easier (Cox & Moore,
46 2000). Despite these difficulties, a number of partitions of the pelagic realm have been
47 proposed over the course of the 19th and 20th century. For instance, Mark Spalding and
48 colleagues listed the work of Forbes (1856), Ekman (1953), Hedgpeth (1957), Briggs (1974)
49 and Bailey (1998) (Spalding, Fox, Allen, Davidson, Ferdaña et al., 2007). Temperature
50 variability over large time scales explained well the partition of Briggs, who also considered
51 endemism (Briggs, 1974). More recently, classifications have been proposed to improve
52 ecosystem management. For instance, Large Marine Ecosystems (LMEs), implemented by
53 Sherman and colleagues, are large regions (i.e. $\geq 200,000$ km²) based on their (1) bathymetry,
54 (2) hydrography, (3) productivity and (4) trophically dependent populations (Sherman &
55 Duda, 1999). Globally, a total of 66 LMEs has been proposed so far. LMEs were originally
56 designed to tackle environmental issues such as fisheries management and only concern
57 large continental shelves. Lately, Spalding and co-workers (Spalding et al., 2007) proposed an
58 expert-knowledge global system for coastal and shelf areas, termed the Marine Ecoregions
59 of the World (MEOW). This partitioning encompasses a nested system of 12 realms (i.e.
60 continent-sized areas with homogeneous geographical components and living organisms), 62
61 provinces (i.e. large ecosystems defined by the presence of distinct biocoenoses having a
62 certain level of cohesion over evolutionary time), and 232 ecoregions (i.e. areas having a
63 relatively homogeneous biocoenosis in comparison to adjacent zones). The MEOWs have
64 been implemented with the goal of directing future efforts in marine resource management
65 and biodiversity conservation (Spalding et al., 2007).

66

67 Generally, biological partitioning has been rarely achievable with great precision at a large
68 scale because the spatial distribution of many species is poorly known. This is perhaps why
69 some authors have proposed partitions based on biogeochemical parameters or, more
70 recently, parameters such as chlorophyll concentration assessed from satellites (D'Ortenzio
71 & d'Alcala, 2008; Longhurst, 1998; Oliver & Irwin, 2008; Reygondeau, Longhurst, Beaugrand,
72 Martinez, Antoine et al., 2013). The development of satellite technology and the
73 globalization of environmental datasets have enabled the establishment of a global
74 biogeography. A division of the marine ecosphere into biomes (i.e. a large ecosystem
75 primarily controlled by climate) and provinces has been proposed by Alan Longhurst
76 (Longhurst, 2007). Four primary biomes (Polar, Westerlies, Trades, and Coastal) and 56
77 secondary provinces have been identified. This partition of the marine ecosphere was mainly
78 based on the characterization of the seasonal cycle of primary production (Longhurst, 2007).
79 Variables used to establish the partition were chlorophyll-a concentration, mixed layer
80 depth, nutrients, the Brunt-Vaisala frequency, the Rossby radius of internal deformation,
81 photic depth, algal biomass and primary production. These variables allowed the
82 identification of a number of ecological situations: (1) polar irradiance-limited production
83 peak, (2) nutrient-limited spring bloom, (3) winter-spring production with nutrient limitation,
84 (4) small amplitude response to trade wind seasonality, (5) large amplitude response to
85 monsoon reversal, and (6) various responses to topography and wind-stress on continental
86 shelves, including coastal upwelling (Reygondeau et al., 2013). Using four parameters

87 (bathymetry, chlorophyll-a concentration, surface temperature and salinity), Reygondeau
88 and co-workers (Reygondeau et al., 2013) applied a procedure based on the Non-Parametric
89 Probabilistic Ecological Niche model (Beaugrand, Lenoir, Ibanez & Manté, 2011) to propose a
90 more dynamical partition of Longhurst's biogeochemical provinces. The average
91 demarcation of the provinces was in general in good agreement with those originally
92 proposed by Longhurst. Basing pelagic biogeography on a few biogeochemical parameters or
93 expert knowledge may lead to a too simplistic scheme because pelagic ecosystems are
94 composed of many species that integrate the multidimensionality of the environment.
95 Biogeographical partitions based on species distribution have also been proposed. Mary
96 Somerville (1780-1872) in her book about physical geography divided the marine ecosphere
97 into homozoic zones. Based on Mollusca, Edward Forbes (1815-1854) established nine
98 homozoic zones and related them mainly to marine isotherms. Developments of remote
99 sensing and large-scale ship-based surveys have allowed a better demarcation of the biomes
100 occupied by various taxonomic groups such as coccolithophores (Merico, Tyrrell, Brown,
101 Groom & Miller, 2003), N₂ fixers (Westberry & Siegel, 2006) and picocyanobacteria
102 (Johnson, Zinser, Coe, McNulty, Malcolm et al., 2006).

103
104 Here, we use the information on 238 species or taxa (phytoplankton, holozooplankton and
105 meroplankton) for every two-month period (1946-2015), originating from the Continuous
106 Plankton Recorder (CPR) survey. Together with some key physical parameters (temperature,
107 bathymetry, sea ice concentration, light at the seabed, current velocity and salinity), we
108 propose a partition of the North Atlantic Ocean and its adjacent seas into biomes, provinces
109 and ecoregions. We first partition the area into habitats at relatively high spatial resolution
110 ($0.08^\circ \times \sim 0.08^\circ$) and then assess the biodiversity of diatoms, dinoflagellates (*Ceratium*), small
111 and large copepods and zooplankton to propose a biological partition at two spatial
112 resolutions: $2^\circ \times 2^\circ$ and $0.5^\circ \times 0.5^\circ$ where sampling is sufficiently dense. Finally, we combined
113 all partitions into a single one and compare it with others exclusively based on physico-
114 chemical parameters. The final partition leads to an identification of 13 ecological units and
115 40 ecoregions in the spatial domain covered by the CPR survey, which explains well observed
116 biological patterns from the species to the community levels.

117
118

119 **2. Materials and methods**

120

121 **2.1. Physical data**

122

123 We used physical data originating from Bio-ORACLE v2.0 (Marine data layers for ecological
124 modelling) (Assis, Tyberghein, Bosh, Verbruggen, Serrão et al., 2017; Tyberghein,
125 Verbruggen, Pauly, Troupin, Mineur et al., 2012). Bio-ORACLE is a global dataset consisting of
126 23 geophysical, biotic and climate rasters. This data package for marine species distribution
127 modelling is available for download at <http://www.bio-oracle.org>. For this purpose, we used
128 both minimum and maximum sea ice concentration (fraction), sea surface temperature (°C),
129 salinity (PSS), bathymetry (m), light at the seabed ($E.m^{-2}.yr^{-1}$), Nitrate, phosphate and silicate
130 ($mol.m^{-3}$), Photosynthetically Active Radiation (PAR; $E.m^{-2}.day^{-1}$), chlorophyll concentration
131 ($mg.m^{-3}$), primary production ($g.m^{-3}.day^{-1}$) and current velocity ($m.s^{-1}$). Those parameters,
132 averaged in the dataset for the period 2000-2014, are important ecological factors that
133 shape biodiversity at a large scale. Rasters were assembled at a resolution of 5 arcmin (i.e.
134 9.2 km).

135

136 We used another dataset to test the influence of the difference in temporal coverage on the
137 ecological partition. These annual SSTs originated from the dataset ERSST_v3 (1946-2015).
138 The dataset is derived from a reanalysis based on the most recently available International
139 Comprehensive Ocean-Atmosphere Data Set (ICOADS). Improved statistical methods have
140 been applied to produce a stable monthly reconstruction, on a $2^{\circ} \times 2^{\circ}$ spatial grid, based on
141 sparse data (Smith, Reynolds, Peterson & Lawrimore, 2008). Data were interpolated on a
142 global grid of 1° latitude x 1° longitude.

143

144 **2.2. Biological data**

145

146 The Continuous Plankton Recorder (CPR) Survey is a long-term, sub-surface marine plankton
147 monitoring programme consisting of a network of CPR transects towed monthly across the
148 major geographical regions of the North Atlantic. It has been operating in the North Sea
149 since 1931 with some standard routes existing with a virtually unbroken monthly coverage
150 back to 1946 (Batten, Clark, Flinkman, Hays, John et al., 2003; Reid, Colebrook, Matthews,
151 Aiken, Barnard et al., 2003). The CPR survey is recognised as the longest sustained and
152 geographically most extensive marine biological survey in the world. The dataset comprises
153 a uniquely large record of marine biodiversity covering ~1000 taxa over multi-decadal
154 periods. The survey determines the abundance and distribution of phytoplankton and
155 zooplankton (including fish larvae) in our oceans and shelf seas. Using ships of opportunity
156 from ~30 different shipping companies, it obtains samples at monthly intervals on ~50 trans-
157 ocean routes. In this way the survey autonomously collects biological and physical data from
158 ships covering ~20,000 km of the ocean per month, ranging from the Arctic to the Southern
159 Ocean.

160

161 The CPR is a high-speed plankton recorder that is towed behind 'ships of opportunity'
162 through the surface layer of the ocean (~10 m depth) (Warner & Hays, 1994). Water passes
163 through the recorder and plankton are filtered by a slow-moving silk (mesh size 270 μm). A
164 second layer of silk covers the first and both are reeled into a tank containing 4%
165 formaldehyde. Upon returning to the laboratory, the silk is unwound and cut into sections

166 corresponding to 10 nautical miles and approximately 3 m³ of filtered sea water (Jonas,
167 Walne, Beaugrand, Gregory & Hays, 2004).

168

169 There are four separate stages of analysis carried out on each CPR sample, with each
170 focusing on a different aspect of the plankton: (1) overall chlorophyll (the phytoplankton
171 colour index; PCI); (2) larger phytoplankton cells (phytoplankton); (3) smaller zooplankton
172 (zooplankton “traverse”); and (4) larger zooplankton (zooplankton “eyecount”). The
173 phytoplankton colour of each section of the CPR silk is evaluated and categorised according
174 to four levels of ‘greenness’ (green, pale green, very pale green and no colour) using a
175 standard colour chart; the numbers are given a numerical value as a measure of
176 ‘Phytoplankton Colour Index’. Here we focussed our analysis on phytoplankton cells, small
177 and large zooplankton. Because we worked at the species level, we did not use the colour
178 index.

179

180 Phytoplankton cells are identified and recorded as either present or absent across 20
181 microscopic fields spanning each section of silk (representing ~1/10,000 of the filtering silk).
182 Due to the mesh size of CPR silks, many phytoplankton species are only semi-quantitatively
183 sampled owing to the small size of the organisms (Batten et al., 2003). There is therefore a
184 bias towards recording larger armoured flagellates and chain-forming diatoms and that
185 smaller species abundance estimates from cell counts are probably underestimated in
186 relation to other water sampling methods. However, the proportion of the population that is
187 retained by the CPR silk reflects the major changes in abundance, distribution and specific
188 composition (i.e. the percentage retention is roughly constant within each species even with
189 very small-celled species) (Edwards, Johns, Leterme, Svendsen & Richardson, 2006).
190 Zooplankton analysis is then carried out in two stages with small (<2 mm) zooplankton
191 identified and counted on-silk (representing ~1/50 of the filtering silk) and larger (>2 mm)
192 zooplankton enumerated off-silk (Warner & Hays, 1994). The collection and analysis of CPR
193 samples have been carried out using a consistent methodological approach, coupled with
194 strict protocols and Quality Assurance procedures since 1958, making the CPR survey the
195 longest continuous dataset of its kind in the world. Figure 1 shows the spatial distribution of
196 the CPR samples used in this study.

197

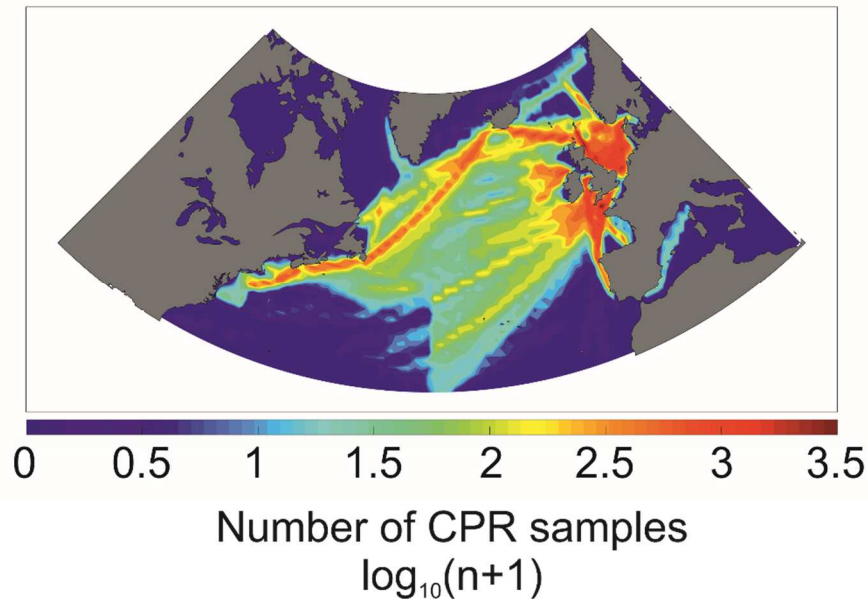


Figure 1. CPR sampling intensity (in decimal logarithm) in the North Atlantic and its adjacent seas for the period 1946-2015.

2.3. Methods

We performed three partitions of the North Atlantic Ocean: (1) habitat partition at a $0.08^\circ \times 0.08^\circ$ spatial resolution, and (2) biological (CPR-based) partitions at a $2^\circ \times 2^\circ$ (areas where CPR spatial coverage was lower than average) and at a $0.5 \times 0.5^\circ$ spatial resolution (regions where spatial coverage was higher than average). Finally, (3) we combined the three partitions to build a synthetic map to propose an ecological partition of the North Atlantic Ocean and its adjacent seas.

The different types of partition, as well as the technical terms such as ecological units and ecoregions are explained briefly or summarized in section 2.4.

2.3.1. Habitat classification

We first partitioned the North Atlantic Ocean and its adjacent seas using an empirical (threshold-based) procedure based on SST, bathymetry, light at the seabed, salinity and current velocity at a high spatial resolution (0.08° latitude \times 0.08° longitude). This partition was intended to complement the biological partition based on CPR data. The habitat partition was carried out hierarchically and led to 15 pelagic habitats (Table 1; see section 2.4 on terminology). A number of thresholds were chosen based on expert knowledge. Salinity and current velocity thresholds were based either on the third quartile (Q3) or the ninth decile (D9) of all marine data. *Oceanic* areas were regions with depth greater than 1000 m, *shelf-edges* with depth between 1000 and 200 m and *continental shelves* with depth less than 200 m. Light at the seabed (i.e. light at the seabed higher than $0 \text{ E.m}^{-2}.\text{yr}^{-1}$) allowed us to distinguish areas where light can or cannot reach the seabed. In oceanic areas where salinity was higher than Q3, we distinguished different pelagic habitats using the following isotherms: (1) 7-10°C, (2) 10-13°C, (3) 13-16°C, (4) 16-19°C, (5) 19-22°C, and (6) 22-25°C (Table 1). Finally, oceanic areas with current velocity above D9 enabled the identification of

230 the average location of the Gulf Stream. Here, the thresholds were based on expert
 231 knowledge and their modifications had only a moderate (Q3 or D9) or expected (e.g.
 232 temperature) effect on the partition. For example, the temperature categories allowed us to
 233 separate the subarctic gyre into distinct components: the Labrador Sea, and the central and
 234 eastern parts of the subarctic gyre. Table 1 summarizes the choice of the thresholds made to
 235 perform the classification and the resulting ecological characteristics of each ecoregion. This
 236 partition is shown in Figure 2.

237

238 **Table 1.** Categories of ecogeographical variables used to classify the North Atlantic Ocean and its
 239 adjacent seas into 15 pelagic habitats. SIC: Sea-Ice Concentration (average of minimum and
 240 maximum sea ice fraction). A hyphen denotes the absence of consideration of an ecogeographical
 241 variable. Indeed in some regions, the consideration of some environmental variables was not useful
 242 either because their values were relatively stable or because they did not provide any additional
 243 information. An ecoregion is simply a region with similar ecological conditions with respect to the
 244 factors used to make the classification. The threshold used for salinity was the third quartile and the
 245 threshold used for current velocity was the 9th decile based on all marine areas of the world.
 246

Pelagic habitats	Higher bathymetry	lower bathymetry	SIC >0	Light the seabed >0	Currents (m.s ⁻¹)	Salinity	SST (°C)
1	11000	1000	Yes	No	-	-	-
2	1000	200	Yes	No	-	-	-
3	200	50	Yes	No	-	-	-
4	11000	1000	No	No	<0.62 (D9)	<35.23 (Q3)	-
5	1000	200	No	No	-	-	-
6	200	50	No	No	-	-	-
7	50	0	No	No	-	-	-
8	200	0	No	Yes	-	-	-
9	11000	1000	No	No	>0.62	-	-
10	11000	1000	No	No	<0.62	>35.23	7-10
11	11000	1000	No	No	<0.62	>35.23	10-13
12	11000	1000	No	No	<0.62	>35.23	13-16
13	11000	1000	No	No	<0.62	>35.23	16-19
14	11000	1000	No	No	<0.62	>35.23	19-22
15	11000	1000	No	No	<0.62	>35.23	22-25

247

248

249 2.3.2. Biological partition

250

251 We partitioned the North Atlantic Ocean and its adjacent seas using data collected from the
 252 CPR survey (Reid et al., 2003) and define this partition as “biological partition” hereafter (see
 253 section 2.4. on terminology). Specifically, we based our partition on six taxonomic groups:
 254 diatoms (59 species or taxa; Supplementary Table 1), *Ceratium* dinoflagellates (41 species;
 255 Supplementary Table 2), small copepods (recorded in traverse; 27 species or taxa;
 256 Supplementary Table 3), small zooplankton (recorded in traverse; 15 species or taxa;
 257 Supplementary Table 4), large copepods (recorded in eyecount; 73 species; Supplementary
 258 Table 5) and large zooplankton other than copepods and including fish eggs and larvae
 259 (recorded in eyecount; 23 species or taxa; Supplementary Table 6). Therefore, a total of 238

260 species or taxa were considered for the period 1946-2015 (a total of 254,410 CPR samples),
 261 which represented a total of 60,549,580 data points. We partitioned the North Atlantic
 262 Ocean and its adjacent seas using two spatial resolutions: (1) a grid of 2° latitude x 2°
 263 longitude that enabled a large coverage into the North Atlantic Ocean despite the lower CPR
 264 sampling coverage, and (2) a grid of 0.5° x 0.5° from 40.5°N to 65.5°N and from 80.5°W to
 265 9.5°E that enables a finer partition in seas around the British Isles where CPR sampling is the
 266 densest.

267
 268 For the two biological partitions, we first estimated the species richness of each taxonomic
 269 group on the two spatial grids. CPR data from 1946 to 2015 were analysed for each two-
 270 month period using an approach similar to what was applied to map copepod biodiversity
 271 (Beaugrand, Ibañez & Lindley, 2001). For each geographical cell and two-month period, we
 272 calculated the species richness providing that the number of samples was higher than 15 (for
 273 the 2° x 2° partition) or 5 (for the 0.5° x 0.5° partition), thresholds (>5) that guarantee a
 274 correct estimation of the diversity of a taxonomic group from the CPR survey (Beaugrand &
 275 Edwards, 2001). In large-scale studies, indices weighted towards species richness are more
 276 useful for detecting differences between sites than indices emphasising the evenness
 277 component of biodiversity (Magurran, 1988). Even though the calculation of species richness
 278 is sensitive to sample size and leads to systematic underestimation of copepod biodiversity,
 279 it is still a satisfactory estimator that can be used for comparisons between sites with low
 280 spatial resolution (Beaugrand & Edwards, 2001). We used a first-order jackknife procedure
 281 to increase the robustness of the species or taxonomic richness. To calculate the first-order
 282 jackknife estimator D , pseudo-values p_i that excluded samples i from each geographical cell
 283 were computed as follows (Beaugrand, Edwards & Legendre, 2010):
 284

$$p_i = np^0 - (n-1) p_i^{(-i)} \quad (1)$$

285
 286 where n is the number of CPR samples in the geographical cell for a given two-month period,
 287 p^0 is the estimate of the species/taxonomic richness based on all CPR samples, and $p_i^{(-i)}$ is the
 288 value of the species (or taxonomic) richness based on all samples but i . Each pseudo-value
 289 gives an estimation of the number of species in a given cell. There were as many pseudo-
 290 values as samples in the geographical cell for a given two-month period. The estimated
 291 taxonomic richness (or species richness) D was the average of all pseudo-values:
 292

$$D = \sum_{i=1}^n \frac{P_i}{n} \quad (2)$$

293
 294 For the first biological partition (2° latitude x 2° longitude), matrices of (jackknifed)
 295 taxonomic richness of 13 latitudes x 46 longitudes = 598 geographical squares x six two-
 296 month periods were built for each taxonomic group. Six matrices were therefore prepared:
 297 **Matrix A** 598 geographical cells x 6 two-month periods for diatoms, **Matrix B** 598
 298 geographical cells x 6 two-month periods for the genus *Ceratium*, **Matrix C** 598 geographical
 299 cells x 6 two-month periods for small copepods, **Matrix D** 598 geographical cells x 6 two-
 300 month periods for small zooplankton other than copepods, **Matrix E** 598 geographical cells
 301 x 6 two-month periods for large copepods, and **Matrix F** 598 geographical cells x 6 two-
 302 month periods for large zooplankton other than copepods.

303
 304 For the second biological partition (0.5° latitude x 0.5° longitude), matrices of (jackknifed)
 305 taxonomic richness of 51 latitudes x 181 longitudes = 9231 geographical squares x 6 two-
 306 month periods were built for each taxonomic group. Six matrices were therefore prepared:
 307 **Matrix A*** 9231 geographical cells x 6 two-month periods for diatoms, **Matrix B*** 9231
 308 geographical cells x 6 two-month periods for the genus *Ceratium*, **Matrix C*** 9231
 309 geographical cells x 6 two-month periods for small copepods, **Matrix D*** 9231 geographical
 310 cells x 6 two-month periods for small zooplankton other than copepods, **Matrix E*** 9231
 311 geographical cells x 6 two-month periods for large copepods, and **Matrix F*** 9231
 312 geographical cells x 6 two-month periods for large zooplankton other than copepods.

313
 314 To diminish the number of missing values in oceanic areas in all matrices (i.e. **A-F** and **A*-F***),
 315 we carried out iterative Principal Component Analyses (PCAs) on each matrix using 100 PCAs
 316 and the first 5 principal components and eigenvectors (Beaugrand, McQuatters-Gollop,
 317 Edwards & Goberville, 2013). We then calculated a last PCA to remove the unexplained
 318 variance (Jolliffe, 1986). For this last analysis, the major signals were extracted by
 319 considering the first two principal components $P_{(q,2)}$ and eigenvectors $U_{(r,2)}$, which enabled
 320 smoothing the original matrices $O_{(q,r)}$:

$$O_{(q,r)} = P_{(q,2)} U'_{(r,2)} \quad (3)$$

321
 322
 323 where q is the number of geographical cells (598 or 9231) and r is the number of two-month
 324 periods (6). An annual average of the biodiversity of the six groups was calculated (Figure 3).
 325
 326

327 We combined matrices $A_{(598,6)}$ - $F_{(598,6)}$ into a new matrix $G_{(598,36)}$ for partition 2° latitude x 2°
 328 longitude and matrices $A^*_{(9231,6)}$ - $F^*_{(9231,6)}$ into a new matrix $G^*_{(9231,36)}$ for partition 0.5°
 329 latitude x 0.5° longitude. We added the richness of all taxonomic groups to obtain a matrix
 330 of total taxonomic richness for each two-month period $T_{(598,6)}$ and $T^*_{(9231,6)}$. An annual
 331 average of the total biodiversity of all taxonomic groups was calculated (Figure 4A). We
 332 calculated an index of seasonal amplitude by using the inter-decile (P_{90} - P_{10}) range on the 2° x
 333 2° partition because it had the largest spatial coverage (Figure 4B).
 334

335 We then calculated two squared matrices $K_{(598,598)}$ and $K^*_{(9231,9231)}$ using the Euclidean
 336 distance and chose a hierarchical agglomerative clustering technique using average linkage,
 337 which was a good compromise between the two extreme single and complete clustering
 338 techniques (Legendre & Legendre, 1998) (Figure 5). A hierarchical agglomerative technique
 339 is frequently displayed by a dendrogram (Legendre & Legendre, 1998), which shows the
 340 successive agglomeration of objects or clusters of objects (i.e. the geographical cells) to
 341 other groups (i.e. the groups of geographical cells). Each branching of the dendrogram
 342 occurs at a given distance value. Here, we examined the first 8 cut-off (i.e. branching of the
 343 tree) levels of the dendrogram (Figure 6). Cell groups composed of less than three
 344 geographical cells were not considered and were replaced by adjacent ones when the
 345 number of adjacent cells was high (see next analysis below).
 346

347 We smoothed the partitions (2° x 2° and 0.5° x 0.5°) by keeping a given cell group (i.e. a given
 348 group of geographical cells) only when it was composed of five adjacent geographical cells of
 349 the same group out of the nine possible (i.e. the target cell and all 8 adjacent geographical

350 cells). This procedure smoothed slightly the final biological partitions by removing
351 intertwined groups composed of a few cells (Figures 7A and 8A).

352
353

354 In addition, we calculated an index of cell group heterogeneity $H=[h_{i,j}]$. For each geographical
355 cell, we calculated the percentage of cells that belonged to different groups of geographical
356 cells, which is the number of different groups $v-1$ (maximum of nine cells; here also the
357 target cell and all 8 adjacent geographical cells) divided by the number of classified cells $w-1$
358 (maximum of nine cells). The index was therefore calculated as follows:

359
360

$$h_{i,j}=(100 (v-1))/w-1 \quad (4)$$

361
362

363 For example, for nine possible cells, the index of heterogeneity is 0% when only one group is
364 present and 100% when each cell belonged to a different group. A total number of five cells
365 was needed to have an estimation of the heterogeneity of a cell. The results of this analysis
366 are in Figures 7B and 8B. All procedures were programmed in Matlab.

367
368

2.3.3. Ecological partition

369 We then built a synthetic partition (hereafter termed ecological partition, see section 2.4. on
370 terminology) by designing the numerical procedure hereafter. We started our procedure
371 using the biological partition based on a $0.5^\circ \times 0.5^\circ$ spatial resolution. We removed groups
372 for which it was not possible to calculate an index of heterogeneity (i.e. six groups) and
373 merged small groups that were difficult to understand from expert knowledge because they
374 lacked spatial contiguity (i.e. three groups of cells). A total of six cell groups remained
375 (Supplementary Figure 1A). Then, the biological partition at $2^\circ \times 2^\circ$ spatial resolution was
376 superimposed to the $0.5^\circ \times 0.5^\circ$ biological partition in areas where no group of geographical
377 cells existed. At that stage, we had a total of nine groups (Supplementary Figure 1B). Finally,
378 we added some groups originating from the habitat partition to divide the polar biome
379 (*sensu* Longhurst (Longhurst, 1998); four more groups) into provinces and the westerly-wind
380 biomes (*sensu* Longhurst (Longhurst, 1998); one more group). The final partition had
381 therefore a total of 14 groups (Supplementary Figure 1C). The final ecological partition is
382 shown in Figure 9. We described each cell group as a function of their biodiversity, seasonal
383 patterns in species or taxonomic richness and species composition using maps of each of the
384 238 species considered in this study. Although it was not possible to show all maps in the
385 present study, they are available in a CPR atlas published in 2004 (Barnard, Batten,
386 Beaugrand, Buckland, Conway et al., 2004; Beaugrand, 2004).

387
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2.4. Terminology

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In this section, we define or summarize a few key terms used in this paper.

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392

2.4.1. Partitions

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In this study, we made three different types of partition: (i) habitat, (ii) biological and (iii)
395 ecological partitions.

396

397 **Habitat Partition:** this partition was based on an empirical (threshold-based) procedure
398 based on SST, bathymetry, light at the seabed, salinity and current velocity at a high spatial
399 resolution (0.08° latitude x 0.08° longitude). Environmental data originated from Bio-ORACLE
400 v2.0(2000-2014). The resulting Pelagic Habitats (PHs) were merely areas where
401 environmental conditions are relatively homogeneous with respect to the variables that
402 were used.

403
404 **Biological partition:** this partition was based on information on biodiversity of 6 taxonomic
405 groups sampled by the CPR survey: (i) diatoms, (ii) *Ceratium* genus, (iii) copepods < 2 mm,
406 (iv) zooplankton < 2 mm, (v) copepods ≥ 2 mm, and (vi) zooplankton ≥ 2 mm. The biological
407 partition was performed at two spatial resolutions: (i) 0.5°x 0.5° and (ii) 2° x 2°. When we
408 described this partition, we used the term group to refer to cluster of geographical cells.

409
410 **Ecological partition:** synthetic partition based on both habitat and biological partitions (at
411 the two spatial resolutions). The groups of geographical cells resulting from this partition
412 were either termed Ecological Units or Ecoregions (see below).

413

414 **2.4.2. Biome and Realm**

415 A biome is frequently defined as a primary ecological compartment in equilibrium with
416 climate. In the terrestrial ecosphere, biomes are clearly related to the climatic regime
417 (Whittaker, 1975). The word has also been frequently used in marine biogeography. For
418 example, Longhurst (Longhurst, 2007) distinguished four biomes on a global scale: (1) the
419 Polar Biome, (2) the Westerlies Biome, (3) the Trade-Winds Biome and (4) the continental
420 shelves Biome. Note however that the latter biome is fundamentally distinct from the first
421 three as it is defined by bathymetry (stable-biotope components *sensu* Van der Spoel (van
422 der Spoel, 1994)) and not climate. Therefore, it may be more appropriate to term it a realm
423 than a biome, at least in the spatial domain covered by our study. A realm is frequently
424 defined as the broadest ecological unit in either the marine or the terrestrial ecosphere. We
425 therefore expected to identify an oceanic and a neritic realm in the area covered by the CPR
426 survey; the two realms were identified in a recent study based on the analysis of the
427 distribution of 65,000 species of marine animals and plants (Costello, Tsai, Wong, Cheung,
428 Basher et al., 2017).

429

430 **2.4.3. Province**

431 Although we do not divide specifically our partition into provinces, we define this term as it
432 is used in the paper, in particular when we compare our partition to the global-scale
433 partition proposed by Longhurst (Longhurst, 1998; Longhurst, 2007). A province has been
434 defined as an area characterised by some level of endemism, with species sharing a common
435 history (Watling, Guinotte, Clark & Smith, 2013). In addition, a province has also been
436 defined as an association of ecosystems that may change over time in the same way.
437 Provinces are also sometimes divided into ecoregions (Spalding et al., 2007).

438

439 **2.4.4. Ecoregion**

440 In this study, ecoregions are defined according to Spalding and colleagues (Spalding et al.,
441 2007): “*areas of relatively homogeneous species composition, clearly distinct from adjacent*
442 *systems. The species composition is likely to be determined by the predominance of a small*
443 *number of ecosystems and/or a distinct suite of oceanographic or topographic features*”. For

444 the authors, endemism was not a key determinant in the establishment of the Marine
445 Ecoregions of the World (MEOW).

446

447 **2.4.5. Groups, Ecological Units (EUs) and Ecoregions**

448

449 Our biological classification led to groups of geographical cells (e.g. 0.5° x 0.5° and 2°x2°),
450 which were subsequently termed Ecological Units or Ecoregions in the ecological partition.

451

452 • **Ecological Units (EUs).** An EU is a unit having a relatively homogeneous
453 environmental regime or being characterised by similar levels and seasonal variability
454 in biodiversity (i.e. species richness) (Supplementary Tables 1-6). Abiotic and biotic
455 characteristics of each EU were examined in Tables 2 and 4.

456

457 • **Ecoregions.** An EU may not be represented by a single set of interconnected
458 geographical cells. When it was the case, the EU was divided into ecoregions, which
459 were distinguished by their species composition (Figure 9). Therefore, we also
460 provided a summary of the abiotic and biotic characteristics of each ecoregion
461 (Figure 11, Tables 3 and 5).

462

463 • **Groups.** The term “group” was used as part of the biological partition and meant
464 groups of geographical cells.

465

466

467 **2.5. Statistics in the ecological units and ecoregions (ecological partition)**

468

469 We calculated statistics for each ecological unit (Tables 2 and 3) and embedded ecoregions
470 (Supplementary Tables 7 and 8). Table 2 (for ecological units) and Supplementary Table 7
471 (for ecoregions) summarize the environmental characteristics of each ecological unit
472 (bathymetry, SST, salinity, surface current, nitrate, phosphate, N/P ratio, silicate, chlorophyll
473 and primary production), including area (km² and percentage) as well as the number and
474 density of CPR samples.

475 Annual average and the seasonal amplitude of the biodiversity of the 6 taxonomic groups
476 were also summarized in Table 3 for ecological units and Supplementary Table 8 for
477 ecoregions.

478

479 **2.6. Potential influence of the difference in temporal coverage among biological and 480 habitat partitions**

481 We tested whether the two different time periods used for the biological (1946-2015) and
482 habitat (2000-2014) partitions had no major influence on the ecological partition. To do so,
483 we calculated the average SST for the period 2000-2014 and 1946-2015 and mapped the
484 difference in average SST between the two periods (Supplementary Fig. 2). This analysis was
485 carried out in the area 50-66°N and 55-5°W where the two biological and habitat partitions
486 were jointly used (i.e. Polar biome). The mean SST was considered to be a good proxy for

487 temperature and sea-ice concentration, parameters implicated in the identification of the
488 pelagic habitats 1, 4 and 11 in the polar biome (Table 1 and Fig. 2).

489

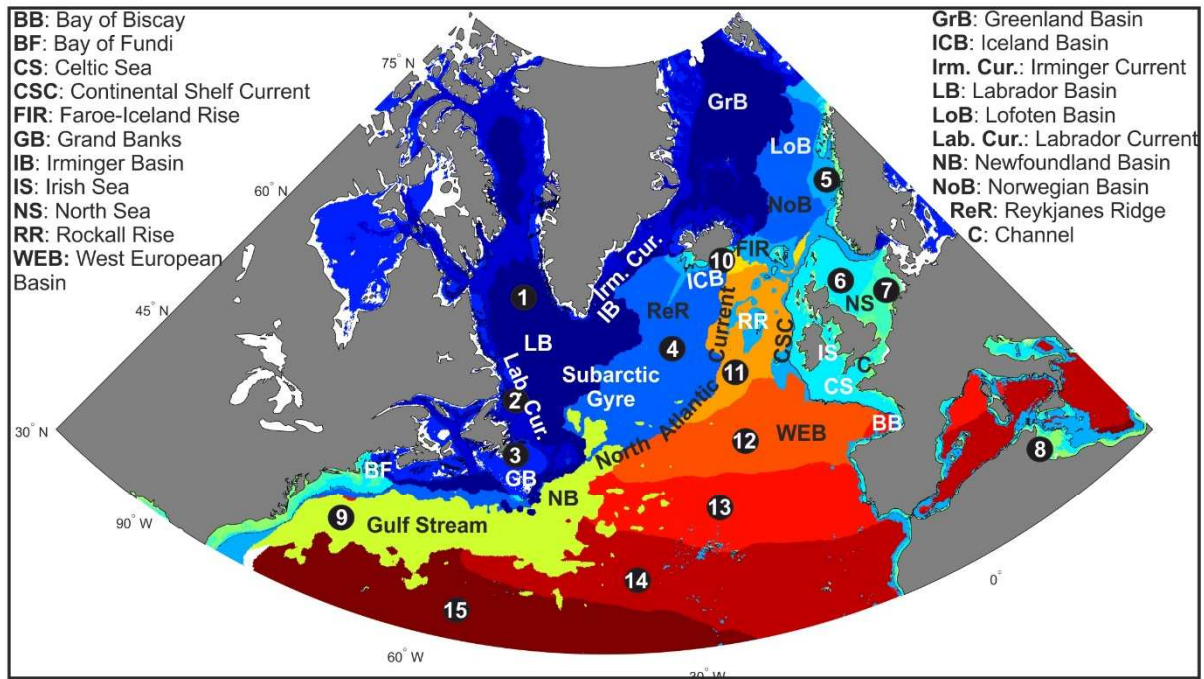
490 3. Results

491

492 3.1. Habitat partition

493

494 The habitat partition resulted in 15 pelagic habitats (Figure 2 and Table 1). The first three
495 Pelagic Habitats (PHs thereafter) may have Sea-Ice Concentration above 0 at least a part of
496 the year. The first PH is the oceanic ice-influenced PH (depth > 200m); it covers the Labrador
497 Basin and part of the Irminger Basin (Figure 2). The second is the shelf-edges (depth range of
498 200-1000m) ice-influenced PH. In the Labrador Basin, it channels the path of the Labrador
499 Current that flows southwards. The third is the neritic (depth range 0-200m) Continental
500 Shelves ice-influenced PH. In particular, it covers the Newfoundland Continental Shelf (e.g.
501 Grand Banks). In the Atlantic area covered by the CPR survey, the first three PHs are
502 delimited by the Subarctic Gyre. Salinity in those three PHs is lower in comparison to oceanic
503 regions located eastwards and southwards. The fourth PH, the Oceanic Subarctic PH, lacks
504 sea ice (Figure 2). The fifth PH is the shelf-edges PH, which is found in all shelf-edge regions
505 where sea-ice is absent (e.g. western part of Norway and European Shelf-edges). The sixth
506 and seventh PHs are continental shelves where sea-ice is absent and where light is limited
507 (in particular, light does not reach the benthos). The deep (50-200m) and shallow
508 Continental Shelves pelagic habitat are well represented in the North Sea north and south of
509 the Flamborough Front, respectively. The eighth PH, the continental shelves (light) pelagic
510 habitat, is marginally represented in the area under investigation. Some coastal areas of the
511 Mediterranean Sea belong to this PH. The ninth PH, the Gulf Stream PH, has current velocity
512 above 0.62 ms^{-1} . In oceanic areas characterized by a high salinity (higher than 35.23 PSS), we
513 distinguished 6 further PHs as function of their thermal regime: (10) oceanic subpolar PH
514 (mean SST=7-10°C), (11) oceanic cold-temperate PH (mean SST=10-13°C), (12) oceanic
515 temperate PH (mean SST=13-16°C), (13) oceanic warm-temperate PH (mean SST=16-19°C),
516 (14) oceanic subtropical (north) PH (mean SST=19-22°C), and (15) oceanic subtropical (south)
517 PH (mean SST=22-25°C).



- | | |
|--|--|
| 1 Oceanic ice-influenced pelagic habitat | 8 Continental shelves (light) pelagic habitat |
| 2 Shelf-edges ice-influenced pelagic habitat | 9 Gulf Stream pelagic habitat |
| 3 Continental shelves ice-influenced pelagic habitat | 10 Oceanic subpolar pelagic habitat |
| 4 Oceanic subarctic pelagic habitat (Salinity < 35.23) | 11 Oceanic cold-temperate pelagic habitat |
| 5 Shelf-edges pelagic habitat | 12 Oceanic temperate pelagic habitat |
| 6 Continental shelves deep (50-200m) pelagic habitat | 13 Oceanic warm-temperate pelagic habitat |
| 7 Continental shelves shallow (0-50m) pelagic habitat | 14 Oceanic subtropical (north) pelagic habitat |
| | 15 Oceanic subtropical (south) pelagic habitat |

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519

520 **Figure 2.** Habitat partition (0.08 x 0.08 spatial resolution) of the North Atlantic Ocean and its adjacent
521 seas based on Sea Surface Temperature (SST), bathymetry, sea ice concentration, light at the seabed,
522 salinity and current velocity. See Methods and Table 1.

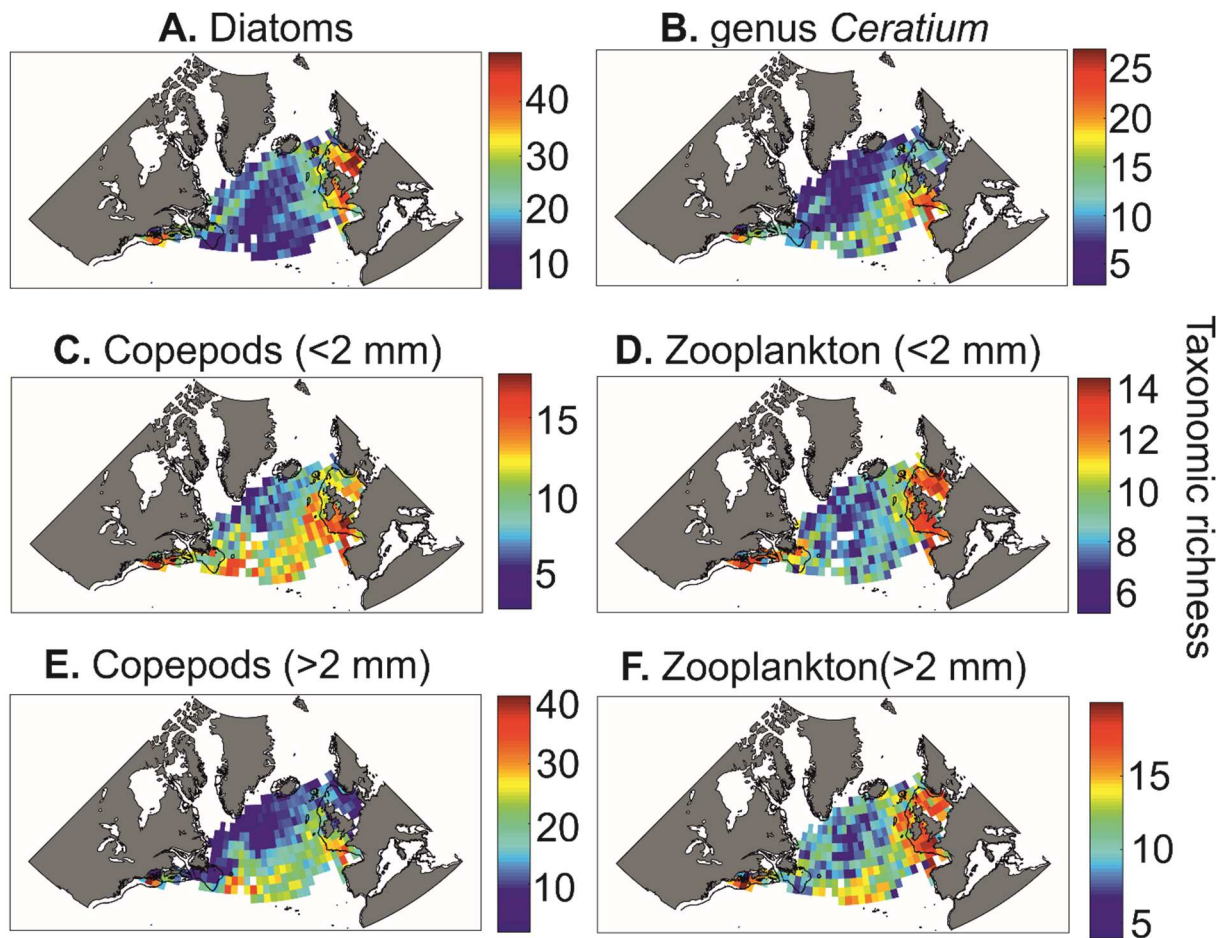
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525 3.2. Biological partition at 2° x 2° spatial resolution

526

527 We first assessed the biodiversity of all six taxonomic groups (Figure 3). The taxonomic
528 richness of diatoms (Supplementary Table 1) was high around the British Isles and especially
529 south of the Flamborough Front, the Celtic Sea and the western part of the Channel (Figure
530 3A). On the western part of the North Atlantic, biodiversity was high over Georges Bank, the
531 Nova Scotian Shelf and to a lesser extent north of the Newfoundland Shelf. Oceanic areas
532 had in general low diatom taxonomic richness, with the exception of the oceanic cold-
533 temperate and the temperate PHs along the Faroe-Iceland Rise, the European shelf-edge
534 and the northern part of oceanic subarctic pelagic habitat, especially over the Reykjanes
535 Ridge (Figures 2 and 3).

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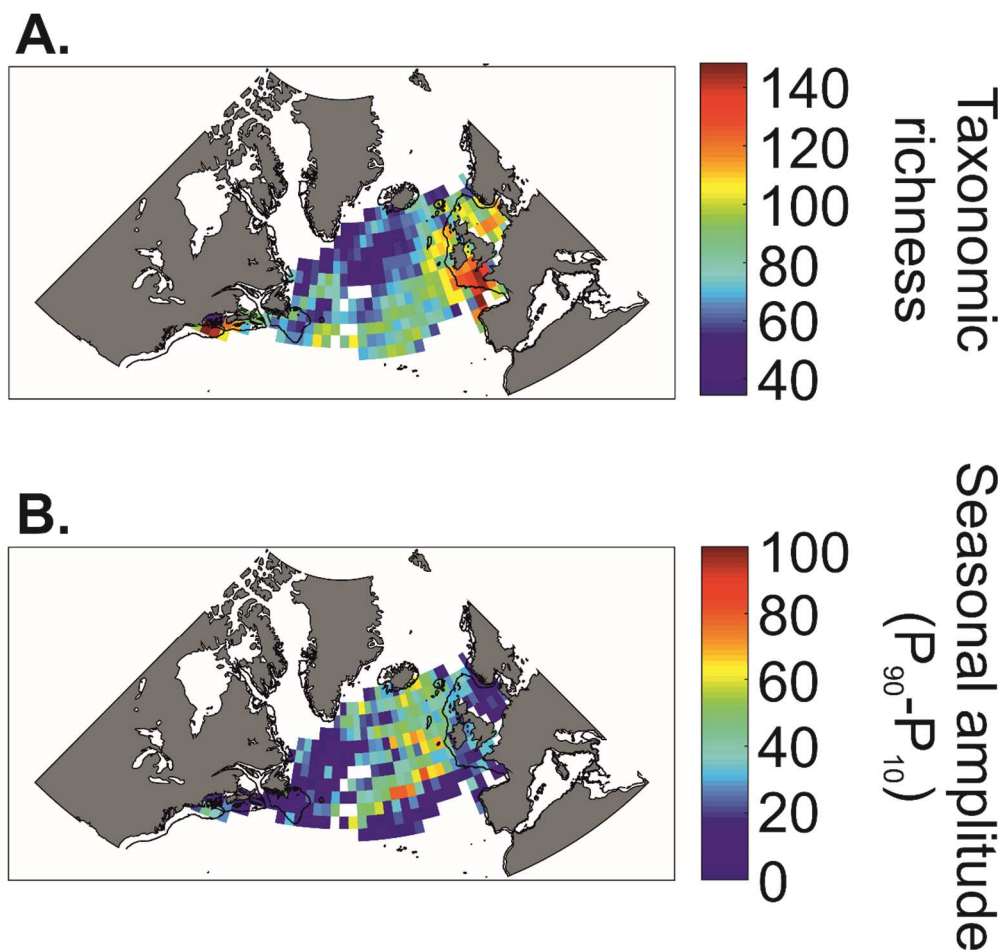
539 **Figure 3.** Mean taxonomic richness of six taxonomic groups sampled by the CPR survey calculated on
540 a $2^\circ \times 2^\circ$ spatial resolution. The taxonomic richness was assessed using a first-order Jackknife
541 coefficient for each 2-month period. **A.** Diatom taxonomic richness. **B.** Dinoflagellates (*Ceratium*)
542 species richness. **C.** Copepod (<2 mm) taxonomic richness. **D.** Zooplankton (other than copepods; < 2
543 mm) taxonomic richness. **E.** Copepod (>2 mm) taxonomic richness. **F.** Zooplankton (other than
544 copepods; >2 mm) taxonomic richness.

545

546 The species richness of the genus *Ceratium* (Supplementary Table 2) was high in oceanic
547 areas south of the Oceanic Polar Front (Dietrich, 1964) and especially over the Bay of Biscay.
548 Species richness was also high in some neritic regions such as the Celtic Sea and Georges
549 Bank (Figure 3B). Copepods (Supplementary Tables 3 and 5) also exhibited a similar pattern,
550 although the biodiversity difference between the polar and the westerlies biomes was less
551 acute for small copepods (Figures 3C and 3E). The taxonomic richness of small copepods was
552 higher along the European Shelf-edge in both oceanic and neritic regions, south of the
553 Flamborough Front in the North Sea and in Georges Bank and part of the Nova Scotian Shelf
554 (Figure 3C). Taxonomic richness was higher in the northern part of the Gulf Stream PH for all
555 copepods. Large copepods did not show a high taxonomic richness south of the
556 Flamborough Front in the North Sea and the biodiversity was less elevated and more
557 restricted along the European Shelf-edge. The taxonomic richness of small zooplankton
558 (Supplementary Table 4) was similar to diatoms (Figure 3A *versus* Figure 3D), although it was
559 substantially higher in the Newfoundland Shelf for zooplankton (Figure 3D). Large
560 zooplankton (Supplementary Table 6) exhibited a pattern closer to small zooplankton
561 because both groups are composed of meroplanktonic species (Figure 3D *versus* Figure 3F).

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When the biodiversity was combined for all groups, the mean total taxonomic richness was higher south of the Oceanic Polar Front (i.e. the Westerlies Biome *sensu* Longhurst) and showed a maximum in biodiversity over the European Shelf-edge and in both adjacent oceanic and neritic regions, as well as along the southern part of the American Shelf-edge (Figure 4A). The seasonal amplitude of the biodiversity, assessed by calculating the interdecile range of 6 2-month periods, showed a pronounced amplitude in oceanic cold-temperate and temperate PHs (Figure 4B). Unexpectedly and although less pronounced, a higher seasonal amplitude was also observed over the mid-Atlantic Ridge south of the Oceanic Polar Front.



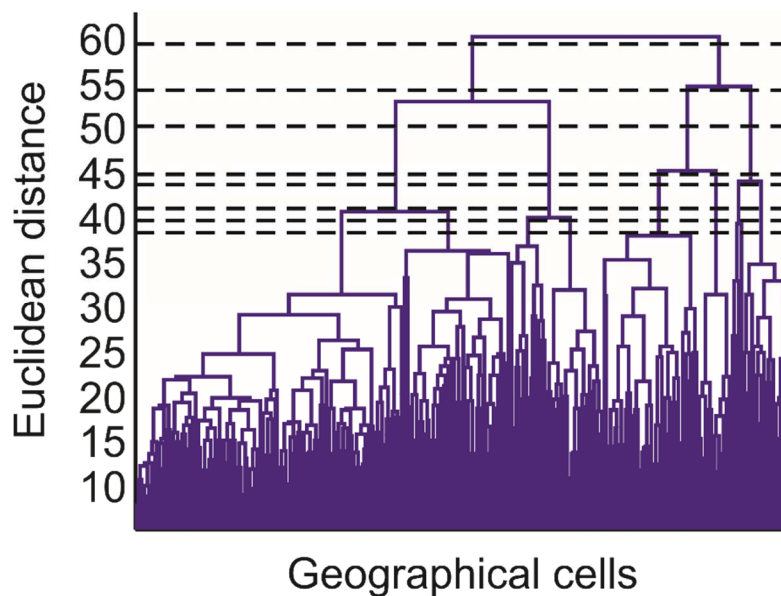
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Figure 4. A. Mean total taxonomic richness of all combined taxonomic groups and **B.** seasonal amplitude of total species richness assessed here by using the interdecile ($P_{90}-P_{10}$) range. The taxonomic richness was assessed using a first-order Jackknife coefficient for each two-month period. See Methods.

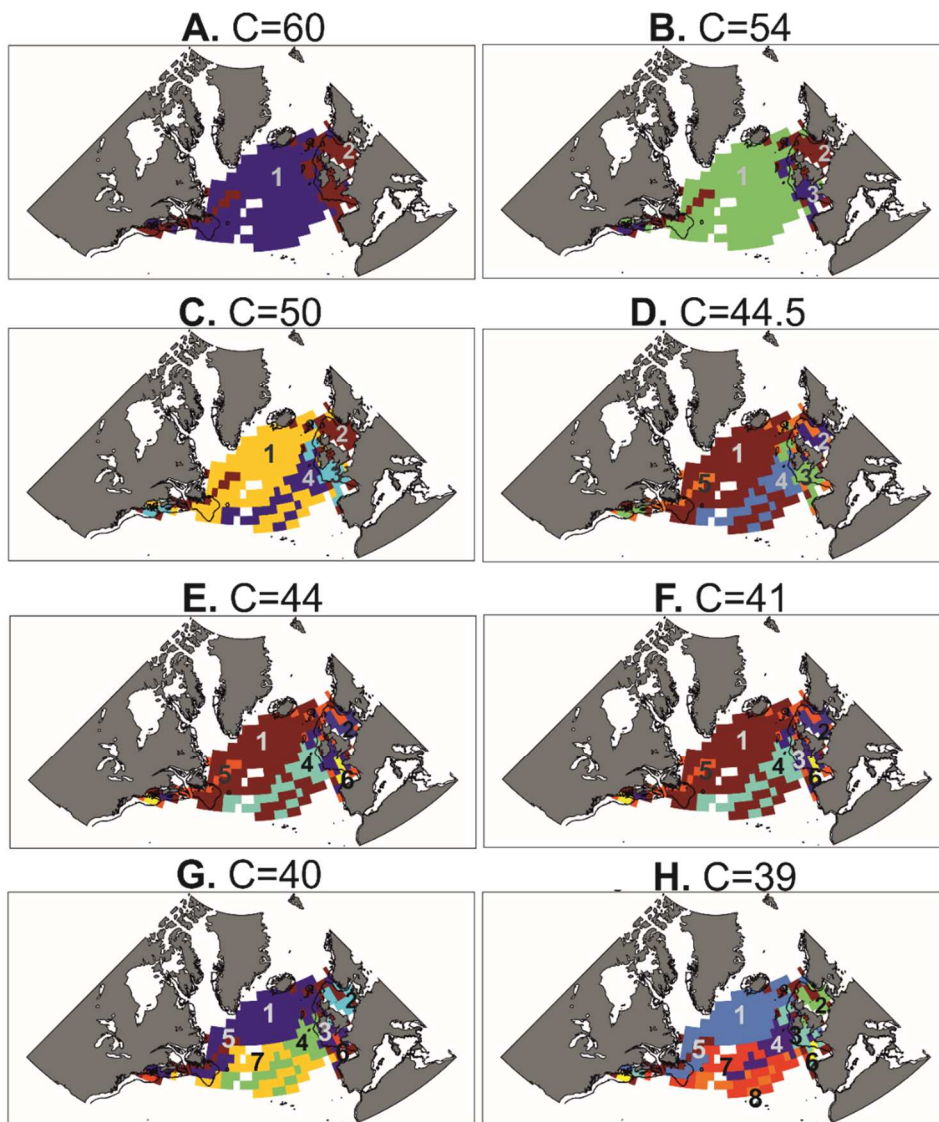
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Information on the taxonomic or species richness of all plankton groups for all two-month periods was used to partition the North Atlantic Ocean in biological systems. The resulting dendrogram was cut hierarchically using the first 8 cut-off levels (Figures 5 and 6). The first cut-off level separated neritic from oceanic areas. The European Continental Shelf was more clearly identified in contrast to the Newfoundland Shelf (Figure 6A). Some areas such as Rockall and the Faroe-Iceland Rises were also at least partially identified. The second cut-off level of the dendrogram (Figure 5) separated the southern part of both American and

587 European Continental Shelves, including the Bay of Biscay (Figure 6B). The third cut-off level
588 enable the separation of an oceanic region southwest to the Irish Sea, which is characterized
589 by a pronounced seasonality in biodiversity and high phytoplankton and small copepod
590 biodiversity (Figure 6C, see also Figure 4B). The fourth cut-off enabled the separation of
591 small groups that enable the identification of an area north of the North Sea and along the
592 Faroe-Iceland ridge (Figure 6D). Some cells were also identified over Georges Bank and the
593 Bay of Biscay but the group of geographical cells lacked spatial contiguity. The fifth cut-off
594 level allowed the identification of a cell group gathering together the Georges Bank and the
595 Bay of Biscay (Figure 6E). Although the sixth cut-off level did not allow the clear
596 identification of a relevant cell group (Figure 6F), the next cut-off level identified an area
597 belonging to oceanic subtropical and warm-temperate PHs and regions influenced by the
598 Atlantic Meridional Overturning Circulation (AMOC, i.e. the Gulf Stream and the North
599 Atlantic Current) (Figure 6G). This cut-off level emphasized the role of the Oceanic Polar
600 Front, which delineates the polar from the Westerlies biome. The last cut-off level (Figure
601 6H), as well as others (not represented here) did not provide any further relevant
602 information.



603
604 **Figure 5.** Dendrogram originating from the application of an agglomerative hierarchical average
605 linkage algorithm performed on an Euclidean distance matrix (Matrix K; see Methods). The different
606 cut-off levels are indicated by a dashed black line (see Figure 6).
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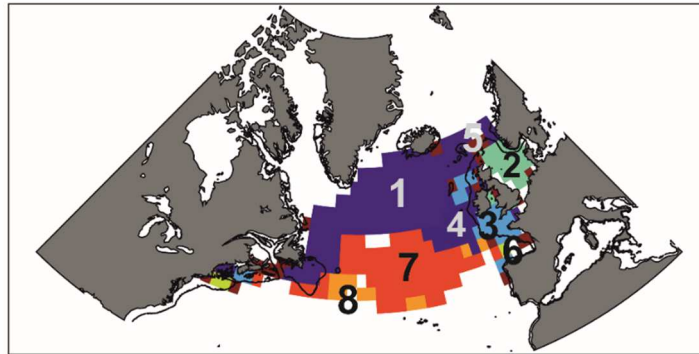
611 **Figure 6.** Hierarchical biological partition of the North Atlantic Ocean and its adjacent seas at 2°x2°
612 spatial resolution for different cut-off levels (hereafter termed C) of the dendrogram (see **Figure 5**).
613 **A.** C=60, **B.** C=54, **C.** C=50, **D.** C=44.5, **E.** C=44, **F.** C=41, **G.** C=40, and **H.** C=39.

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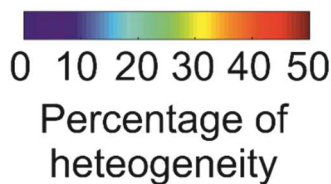
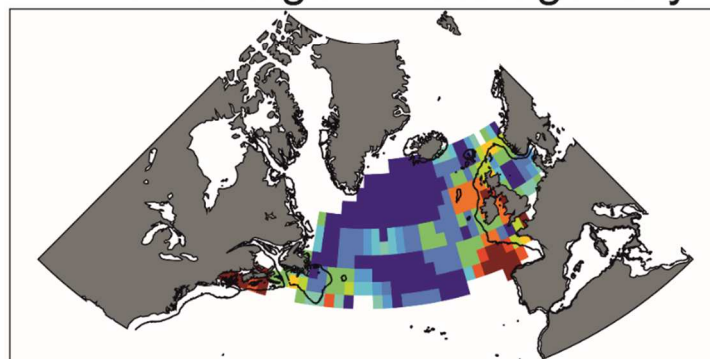
615 After smoothing and elimination of small groups of geographical cells (see Methods), the
616 final biological partition included eight groups, two (group 5 in the northern part of the
617 North Sea and 6 in the Bay of Biscay) of which being restricted spatially (Figure 7A). Group of
618 geographical cells (hereafter called group) 1 represented in large part the polar biome and
619 their ice-influenced, subarctic and cold-temperate PHs; Group 2 characterized the North Sea,
620 Group 3 denoted the Celtic Sea and some areas over the European Shelf-edge, and a
621 negligible part of the Nova Scotian Shelf; Group 4 represented an oceanic area characterized
622 by a high biodiversity south and west of the Irish Sea; Group 7 the oceanic temperate and
623 warm-temperate PHs and Group 8 the northern edge of the Gulf Stream PH (Figure 7A). We
624 calculated an index to reveal the presence of pronounced spatial heterogeneity or ecotones
625 (Figure 7B). The index was highest over the Bay of Biscay and the Bay of Fundi, Georges
626 Bank, Nova Scotian Shelf and to a lesser extent an area located to the north-west of Ireland.
627 The index was also higher between the polar and westerlies biomes along the Oceanic Polar

628 Front, the Gulf Stream PH and areas north of the North Sea and along the Faroe-Iceland Rise
629 (Figure 7B).

A. Biological partition ($2^\circ \times 2^\circ$)



B. Percentage of heterogeneity



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632 **Figure 7.** Biological partition of the North Atlantic Ocean and its adjacent seas at $2^\circ \times 2^\circ$ spatial
633 resolution. **A.** Biological partition performed at a $2^\circ \times 2^\circ$ spatial resolution. Number of the different
634 groups is indicated from 1 to 8. **B.** Index of spatial heterogeneity of the partition. This index indicates
635 the percentage of different groups around a given node. Each percentage value integrates 9
636 geographical cells (see Methods).

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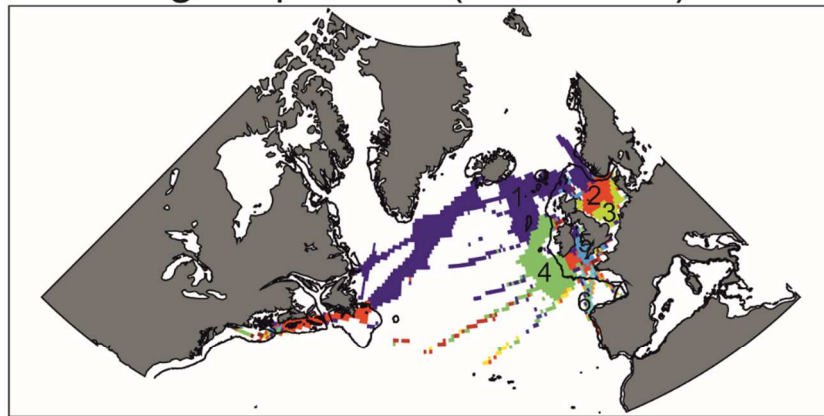
638 3.3. Biological partition at $0.5^\circ \times 0.5^\circ$ spatial resolution

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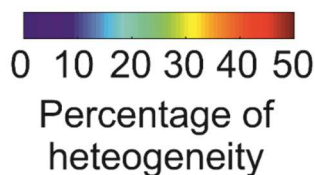
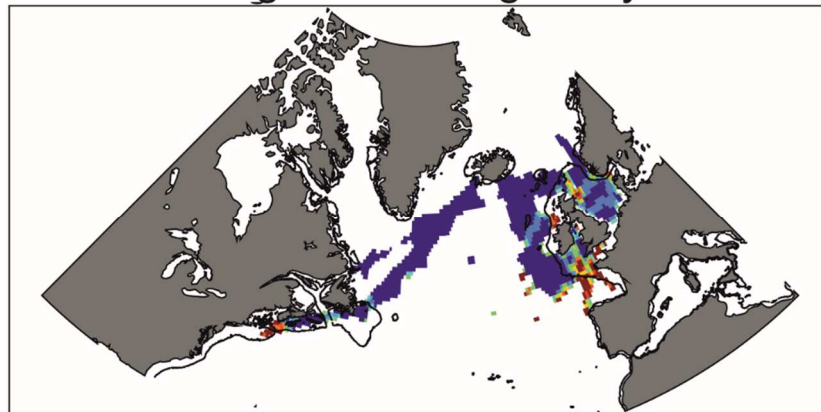
640 The same procedure was applied to identify groups of geographical cells at a $0.5^\circ \times 0.5^\circ$
641 spatial resolution. We only show the final partition here as the procedure was similar to the
642 $2^\circ \times 2^\circ$ division (Figure 8). Fifteen biological groups of geographical cells (hereafter termed
643 groups) were detected. Here also, some groups were only composed of a few geographical
644 cells, which exhibited low spatial contiguity (Figure 8A). After smoothing and elimination of
645 under-represented groups (see Methods), we retained 8 biological groups. Group 1
646 characterised the polar biome and the associated ice-influenced, subarctic and cold-
647 temperate PHs (see Figure 2). Some geographical cells penetrated to the northern part of
648 the North Sea. Although the previous partition at $2^\circ \times 2^\circ$ spatial resolution identified only
649 one biological group in the North Sea, the finer-scale partition revealed three ecoregions:

650 the central part of the North Sea (group 2) and an area south of the Flamborough Front
 651 (group 3). The second group also occurred in the northwestern part of the Celtic Sea and
 652 along the Nova Scotian Shelf, the shallow area of Newfoundland Shelf, stopping sharply at
 653 the shelf-edge (Figure 8A). A fourth group was detected to the west of the British Isles; this
 654 group was similar to the group identified at $2^\circ \times 2^\circ$ spatial resolution (group 4; see Figure
 655 7A). The fifth group identified the north-eastern part of the Celtic Sea (Figure 7A). Some
 656 isolated geographical cells also occurred in different places. The sixth and seventh groups
 657 were located mainly in the western and eastern part of the Bay of Biscay, respectively
 658 (Figure 8A).
 659

A. Biological partition ($0.5^\circ \times 0.5^\circ$)



B. Percentage of heterogeneity

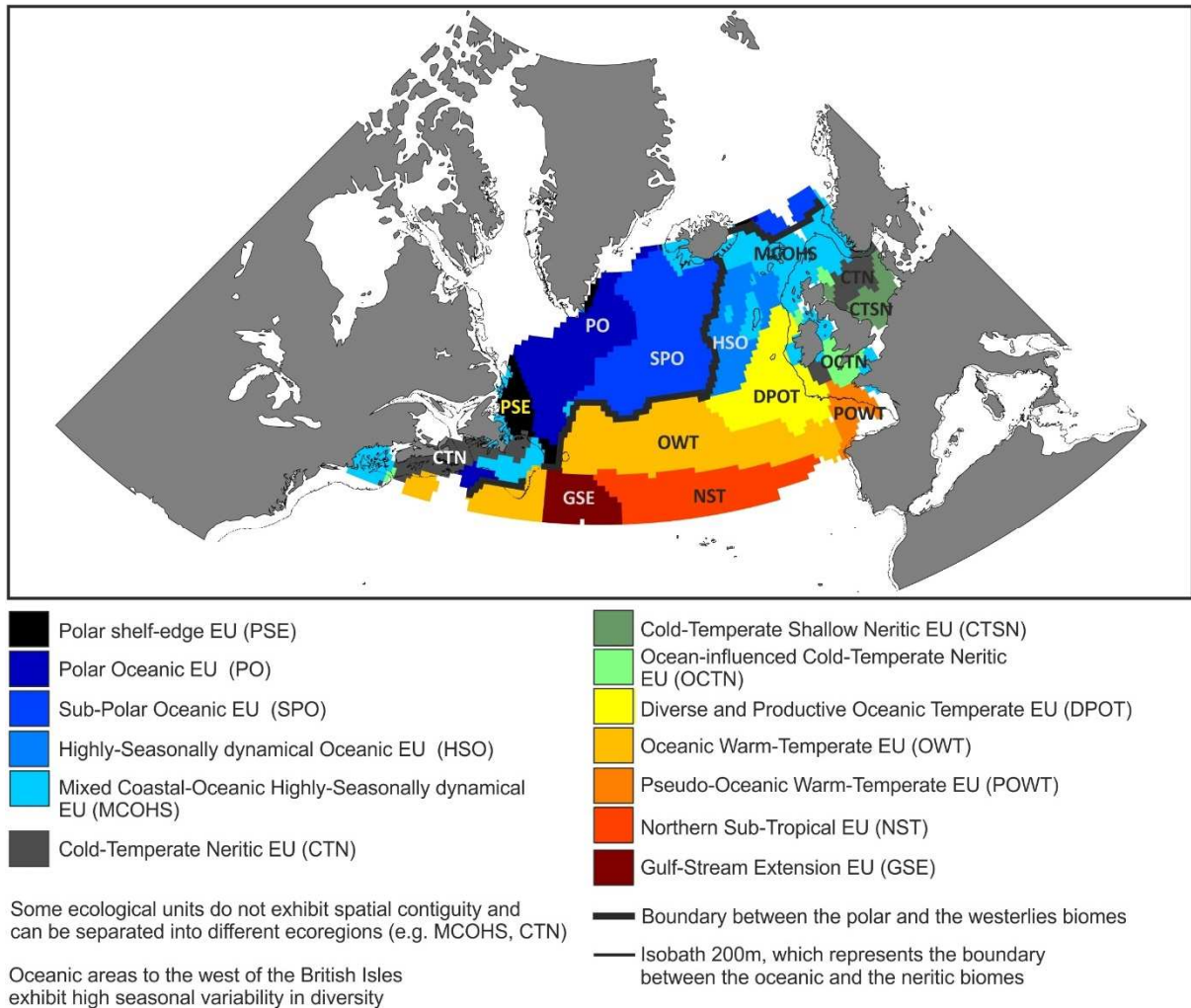


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 662 **Figure 8.** Biological partition of the North Atlantic Ocean and its adjacent seas at $0.5^\circ \times 0.5^\circ$ spatial
 663 resolution. **A.** Partition. **B.** Index of spatial heterogeneity of the partition. This index indicates the
 664 percentage of different groups of geographical cells around a given node. Each percentage value
 665 integrates 9 geographical cells (i.e. the target and its 8 adjacent cells). All intermediate results include
 666 figures similar to **Figures 3-7** (see Methods).
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668 3.4. Ecological partition

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The final ecological partition was mainly based on the biological partition performed at the 0.5° x 0.5° spatial resolution for neritic regions (Figure 8) and mostly on the biological partition made at 2° x 2° for oceanic regions (Figure 7). We further divided some ecological units by using the PHs identified using some key ecogeographic variables (see Figure 2). We used the term Ecological Unit (EU) because the same unit may be represented in different regions; we then divide a given EU into ecoregions when it is relevant (see the section terminology in Methods). As in the PH partition, we frequently refer to the Longhurst's classification of biomes and provinces (Longhurst, 1998; Longhurst, 2007).



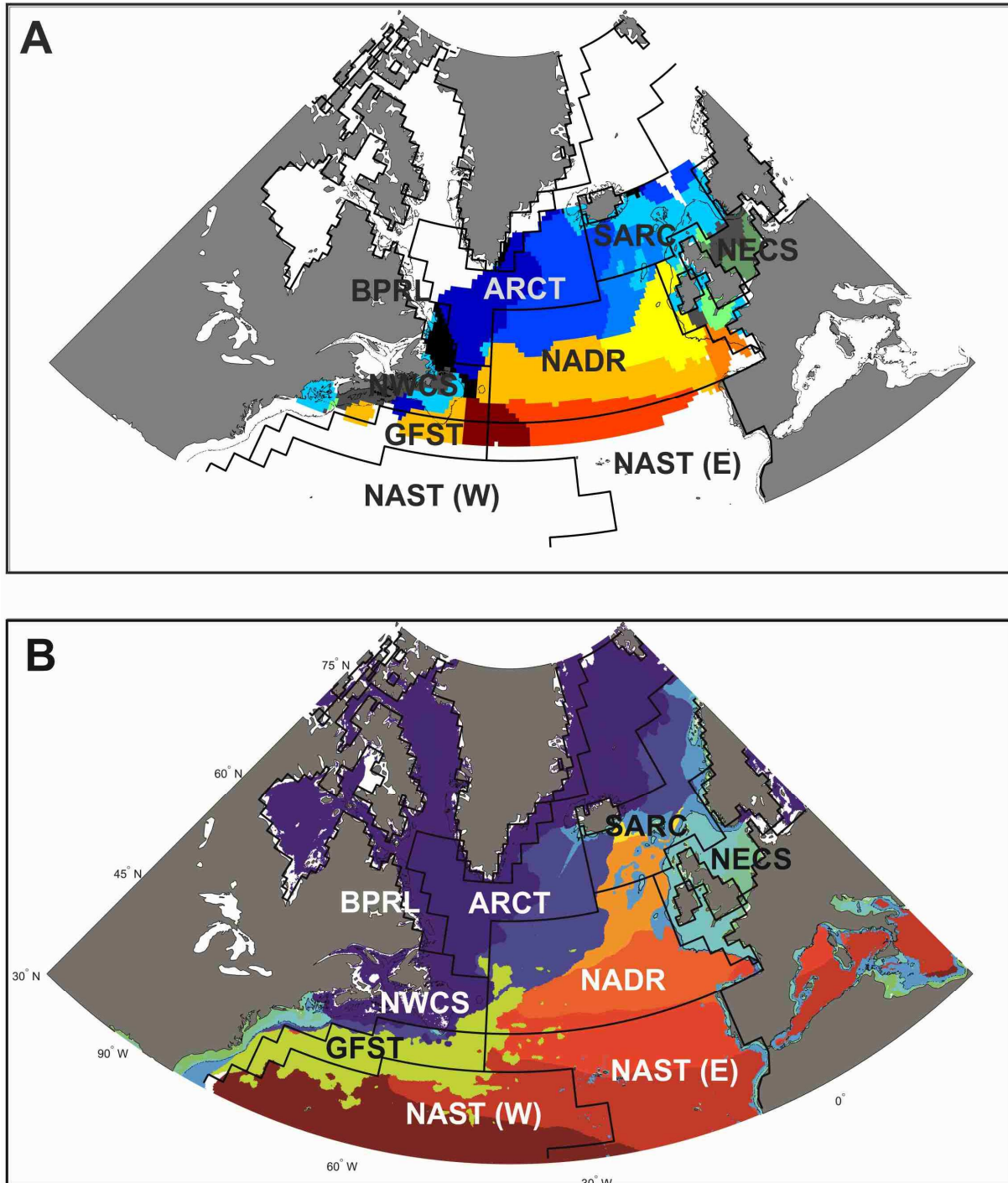
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Figure 9. Ecological partition of the North Atlantic Ocean and its adjacent seas. The partition results from the combination of the habitat (~0.1 x ~0.1) and the biological partitions at 2° x 2° and 0.5° x 0.5° spatial resolutions. Abiotic and biotic properties are shown in Tables 2 and 4.

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The final ecological partition we propose is made of 13 EUs (Figure 9). Each EU has its own biodiversity (Figures 3-4), seasonal biodiversity patterns (Figure 4B) and environmental conditions (Figure 2). Widespread EUs could be further divided and some are composed of different ecoregions (Figure 9; e.g. MCOHS and CTN). Although their location did not match with our partition, the three Longhurst's biomes were identified: (1) the Westerlies, (2) the

690 Polar biomes and the Continental Shelves biomes (Note that Longhurst termed originally this
 691 last biome a coastal biome (Longhurst, 1998)). Our EUs or HPs did not correspond to
 692 Longhurst's provinces (Figure 10), with the exception of the Gulf Stream PH and EU (Figures
 693 2, 9 and 10).
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 697 **Figure 10.** Final ecological partition (A) and habitat partition (B) with the boundaries of the
 698 Longhurst's provinces (Longhurst, 1998) (black lines). **Coastal biomes.** NWCS: North West Atlantic
 699 Shelves province, NECS: North East Atlantic Shelves province. **Westerlies biomes.** NAST (W): North
 700 Atlantic Subtropical Gyral Province (West), NAST (E): North Atlantic Subtropical Gyral Province (East),
 701 GFST: Gulf Stream Province, NADR: North Atlantic Drift Province. **Polar biomes.** SARC: Atlantic
 702 Subarctic Province, ARCT: Atlantic Arctic Province, BPRL: Boreal Polar Province.

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The Polar biome is divided into 3 EUs using information from the PH partition.

Table 2. Main abiotic properties of the ecological units. EU: Ecological Unit. SST: mean Sea Surface Temperature (°C). S: mean salinity (PSS). Cur: mean surface current (m.s⁻¹). N: mean nitrate concentration (mol.m⁻³). P: mean phosphate concentration (mol.m⁻³). Sil: mean silicate concentration (mol.m⁻³). PAR: mean photosynthetically active radiation (E.m⁻².day⁻¹). C: mean chlorophyll concentration (mg.m⁻³). PI: mean primary production (g.m⁻³.day⁻¹). Bathymetry is expressed in meter (m). P5: the 5th percentile. P50: the median. P95: the 95th percentile. See text for the meaning of the ecological unit acronyms. See Figure 9 for the spatial distribution of EUs and Figure 11 for the ecoregions (1-40).

EU	Area (km ²)	Area (%)	CPR sample	CPR sample per 100 km ²	Bathymetry P50 (P5-P95)	SST	S	Cur	N	P	N/P	Sil	PAR	C (PI)
1 PSE	245642	2.62	2526	1.03	310 (171-1170)	4.32	33.05	0.18	3.71	0.44	0.13	3.68	29.3	0.69 (0.009)
2 PO	987261	10.53	15964	1.62	3130 (1464-3912)	6.76	34.46	0.18	7.56	0.59	0.11	4.01	26.2	0.45 (0.006)
3 SPO	1517087	16.18	23947	1.58	2613 (1291-3753)	9.11	34.99	0.23	6.93	0.53	0.08	3.60	26.9	0.40 (0.005)
4 HSO	511150	5.45	9446	1.85	1890 (917-3871)	11.32	35.32	0.28	5.87	0.45	0.08	3.14	28.0	0.40 (0.006)
5 MCOHS	1597056	17.03	43450	2.72	182 (35-1457)	9.75	34.37	0.17	3.77	0.35	0.31	3.38	28.8	0.56 (0.009)
6 CTN	558408	5.95	31705	5.68	90 (35-432)	9.47	32.73	0.14	0.70	0.25	0.72	3.07	29.9	0.44 (0.005)
7 CTSN	224455	2.39	28018	12.48	31 (6-62)	11.18	33.74	0.24	1.11	0.21	1.12	3.72	31.2	0.65 (0.010)
8 OCTN	189168	2.02	22178	11.72	82 (25-127)	12.30	34.68	0.13	0.66	0.18	1.11	3.10	31.0	0.43 (0.006)
9 DPOT	761237	8.12	23072	3.03	3630 (152-4823)	13.42	35.52	0.26	3.81	0.32	0.09	2.36	29.5	0.43 (0.007)
10 OWT	1857862	19.81	12176	0.66	3974 (1452-4863)	13.99	35.07	0.46	2.42	0.26	0.14	2.29	28.2	0.39 (0.006)
11 POWT	208415	2.22	12533	6.01	3560 (119-4893)	15.11	35.59	0.14	0.90	0.14	0.20	1.72	31.3	0.34 (0.006)
12 NST	859614	9.17	5085	0.59	3620 (2196-5049)	17.00	35.90	0.36	1.07	0.14	0.14	1.62	30.4	0.27 (0.005)
13 GSE	346399	3.69	1596	0.46	4758 (3680-4941)	17.44	35.48	0.78	1.16	0.17	0.14	1.98	28.9	0.40 (0.007)

717 **Table 3. Average and seasonal amplitude of the biodiversity of the 6 taxonomic groups in each**
718 **ecological unit.** EU: Ecological Unit. Diat: diatoms. Dino: dinoflagellates. Cop: copepods. See text for
719 the meaning of the ecological unit acronyms. See Figure 9 for the spatial distribution of EUs.

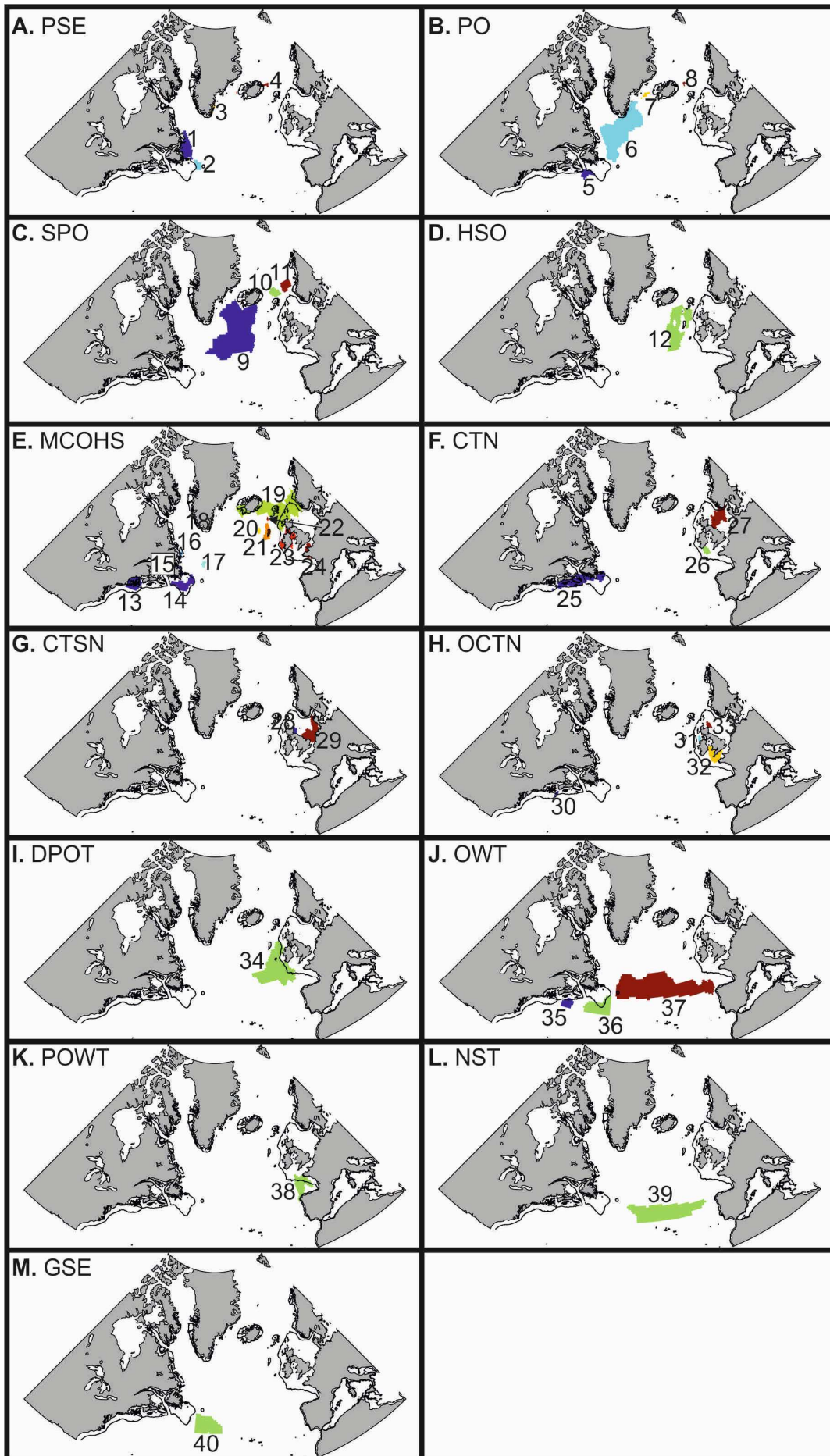
EU	Mean taxonomic richness						Seasonal amplitude in taxonomic richness						
	Diat	Dino	Small cop	Small zoo	Large cop	Large zoo	Diat	Dino	Small cop	Small zoo	Large cop	Large zoo	
1 PSE	12.6												
2 PO	2	7.14	4.48	4.85	5.41	4.77	6.02	5.88	5.75	3.23	6.38	4.82	
3 SPO	11.4	8.69	4.57	5.78	4.48	4.70	5.87	4.63	5.78	4.27	6.42	5.25	
4 HSO	10.6	12.03	5.03	7.24	4.30	4.69	5.60	5.57	5.24	4.31	6.03	7.16	
5 MCOHS	11.7	14.86	6.14	8.19	5.25	3.99	6.29	6.84	6.48	5.44	6.75	8.35	
	12.6	15.02	6.09	7.29	6.39	4.38	7.21	7.95	5.81	4.68	7.25	6.34	

MCOHS	1											
6	15.6											
CTN	8	12.10	7.60	4.30	7.98	3.31	9.46	5.51	5.46	3.57	8.51	5.00
7	28.4						10.7					
CTSN	7	12.43	7.56	2.95	9.11	2.97	9	5.58	4.77	2.62	11.31	4.41
8	21.0						10.5					
OCTN	1	18.22	8.16	8.81	9.84	3.55	0	6.42	8.40	5.56	11.15	6.04
9	12.3											
DPOT	0	12.64	8.15	10.47	7.47	5.17	7.75	6.61	11.08	8.57	8.52	7.95
10												
OWT	9.99	10.05	8.57	10.37	7.27	5.68	6.64	5.10	11.22	10.89	7.19	7.15
11	17.2											
POWT	2	12.23	12.63	13.06	10.40	3.92	9.39	5.14	15.60	6.72	10.62	5.28
12												
NST	8.48	8.28	7.47	10.33	7.79	5.18	7.01	4.47	12.66	12.83	8.31	5.83
13												
GSE	8.85	7.59	6.60	8.94	7.99	6.56	6.81	5.51	14.52	16.28	8.83	6.05

720 **3.4.1. Polar Shelf-Edge EU (PSE)**

721

722 The first group is the Polar Shelf-Edge EU (PSE, Figure 9, Tables 2 and 3). In the region
723 sampled by the CPR survey, this EU is represented by four ecoregions (Figure 11A,
724 Supplementary Tables 7 and 8); the two main ecoregions (1 and 2 in Fig. 11A) are in the path
725 of the Labrador Current, which transports cold water southwards (Han & Tang, 1999). Some
726 species such as the calanoid copepods *Calanus glacialis* and *C. hyperboeus* are highly
727 abundant in PSE (Barnard et al., 2004). Biodiversity is very low in this ice-influenced area
728 (Figure 3-4).



730

731 **Figure 11. Division of ecological units into ecoregions.** Ecoregions are labelled from 1 to 40. The
732 division of an ecological unit occurs when there is no spatial contiguity among geographical cells.
733 Abiotic and biotic properties are shown in Tables 3 and 4. See also Supplementary Tables 7 and 8 that
734 summarise the abiotic and biotic characteristics of the ecoregions.

735 **3.4.2. Polar Oceanic EU (PO)**

736

737 The second group is the Polar Oceanic EU (PO, Figure 9, Tables 2 and 3). This EU is in general
738 characterised by low biodiversity, although diatom taxonomic richness is higher, especially
739 to the south of the EU. The EU can be divided into 2 main ecoregions (ecoregions 5 and 6 in
740 Figure 11B, Supplementary Tables 7 and 8): the Labrador-Irminger Basin and a small oceanic
741 ecoregion south of the Gulf of Saint Lawrence. The first ice-influenced ecoregion is the place
742 where the diatom *Ephemera planamembranacea* is observed in high abundance (Barnard et
743 al., 2004).

744

745 **3.4.3. Sub-Polar Oceanic EU (SPO)**

746

747 The third group is the Sub-Polar Oceanic EU (SPO, Figure 9, Tables 2 and 3). This EU is not
748 influenced by sea-ice and has a salinity that remains below 35.23 in comparison to oceanic
749 regions located to the east and the south (Figure 2). Biodiversity is low for all groups but
750 seasonality can be high, especially to the eastern part of the region (Figure 4). This EU may
751 be divided into 3 ecoregions (ecoregions 9-11 in Figure 11C, Supplementary Tables 7 and 8):
752 (1) an ecoregion south of Iceland over the mid-Atlantic ridge and (2) two small ecoregions in
753 the Norwegian Sea. This area is clearly a transitional area between the Polar and the
754 Westerlies biomes (Barnard et al., 2004); for example, the diatoms *Leptocylinthus*
755 *mediterraneus* and *Proboscia alata indica* and the dinoflagellates *Ceratium furca* and *C.*
756 *lineatum* diminished substantially in this area in comparison to their eastern abundance. The
757 copepods *C. finmarchicus* and *Paraeuchaeta norvegica* also decreased with respect to their
758 western abundance (Barnard et al., 2004). Some species of Hyperiididae are well represented
759 in this region (Barnard et al., 2004), although being not indicative of the EU. Many species
760 are distributed in the first three EUs. For example, the two copepods *C. finmarchicus* and
761 *Paraeuchaeta norvegica* as well as Euphausiacea are highly abundant.

762

763 **3.4.4. Highly-Seasonally dynamical Oceanic EU (HSO)**

764

765 The next oceanic EU, the Highly-Seasonally dynamical Oceanic EU (HSO, Figure 9, Tables 2
766 and 3), is located to the eastern part of the Oceanic Polar Front (Dietrich, 1964) and
767 therefore belongs to the Westerlies biome (Longhurst, 1998). This EU, representing only one
768 ecoregion (Figure 11D, Supplementary Tables 7 and 8), is characterised by a higher
769 biodiversity for all taxonomic groups and many species exhibit high abundance in this EU,
770 although not being exclusively indicative of the region. For example, the diatom
771 *Cylindrotheca closterium*, the dinoflagellate *Oxytoxum* spp. and the copepod *Pleuromamma*
772 *robusta* are highly abundant in this region (Barnard et al., 2004). This EU exhibits a
773 pronounced seasonal amplitude in taxonomic richness and is highly influenced by the path
774 of the North Atlantic Current and associated strength and extent of the Subarctic Gyre
775 (Hatun, Payne, Beaugrand, Reid, Sando et al., 2009).

776

777 **3.4.5. Mixed Coastal-Oceanic Highly-Seasonally Dynamical EU (MCOHS)**

778

779 The fifth group is the Mixed Coastal-Oceanic Highly-Seasonally Dynamical EU (MCOHS,
780 Figure 9, Tables 2 and 3). Complex to interpret (ecoregions 13-24 in Figure 11E,
781 Supplementary Tables 7 and 8), this EU encompasses a main ecoregion (ecoregion 19) at the
782 north-eastern edge of the area covered by the CPR survey where polar water masses
783 interact with more temperate ones along the Faroe-Iceland Rise. It also corresponds to an
784 area where neritic and oceanic water masses interact along the European Shelf-edge and in
785 the northern part of the North Sea. The EU is also composed of many small ecoregions: (i)
786 the offshore region of the Newfoundland Shelf, (ii) Rockall Rise, (iii) the Irish Sea, (iv) south-
787 west of Ireland, and (v) the Channel where many ecosystems and ecotones co-occur (Figures
788 7 and 8). This area is characterised by a relatively low seasonal amplitude in taxonomic
789 richness in comparison to HSO (Figure 4B). Biodiversity is low in the main ecoregion and over
790 the Newfoundland Shelf, although being substantially higher in the smaller ecoregions. Some
791 species, mainly neritic, are highly abundant in MCOHS, although being not indicative of the
792 EU, e.g. the diatoms *Asterionellopsis glacialis*, *Dactyliosolen antarcticus*, *Cylindrotheca*
793 *closterium*, *Rhizosolenia acuminata*, the dinoflagellates *Ceratium horridum*, *Dinophysis* spp.
794 and the copepods *Aetideus armatus* and *Temora longicornis* (Barnard et al., 2004). The
795 ecoregion offshore the Newfoundland Shelf differs substantially from the other ecoregions,
796 probably because of its thermal regime associated to the presence of sea-ice concentration
797 during some parts of the year. As a result, some cold-water species (e.g. *Ceratium arcticum*,
798 *Calanus glacialis*) are highly abundant in this ecoregion while less represented in the other
799 MCOHS ecoregions.

800

801 **3.4.6. Cold-Temperate Neritic EU (CTN)**

802

803 The sixth group is the Cold-Temperate Neritic EU (CTN, Figure 9). This EU is composed of
804 three ecoregions (ecoregions 25-27 in Figure 11F, Supplementary Tables 7 and 8): (i) Central
805 North Sea, (ii) south-western part of the Celtic Sea and (iii) the Nova Scotian and coastal part
806 of the Newfoundland Shelf. Species richness is moderate in this EU, with low taxonomic
807 richness of *Ceratium* and copepods (especially large copepods) and higher taxonomic
808 richness for the other groups, especially small zooplankton (Figures 3 and 4). In the North
809 Sea, the EU is bounded by the Flamborough Front southwards and by the oceanic influence
810 northwards. In the Nova Scotian and the coastal part of the Newfoundland Shelf, the EU is
811 restricted to the coast. Species showing high abundance are the diatoms *Coscinodiscus*
812 *concinus*, *Leptocylindrus danicus*, *Skeletonema costatum*, the dinoflagellates *Ceratium*
813 *longipes*, *C. macroceros*, *C. tripos*, and the copepod *Centropages hamatus*.

814

815

816 **3.4.7. Cold-Temperate Shallow Neritic EU (CTSN)**

817

818 The seventh group is the Cold-Temperate Shallow Neritic EU (CTSN, Figure 9, Tables 2 and 3).
819 This EU is represented by only one ecoregion (ecoregion 29 in Figure 11G, Supplementary
820 Tables 7 and 8), in the North Sea south of the Flamborough Front. Biodiversity is high for
821 diatoms, zooplankton and to a lesser extent, small copepods (Figure 3 and 4). Seasonal
822 amplitude in biodiversity is low in this area (Figure 4B). Many species occur in this area, e.g.
823 the diatoms *Biddulphia alternans*, *Bellerochea malleus*, *Coscinodiscus wailesii*, *Eucampia*

824 *zodiacus*, *Guinardia flaccidia*, *Odontella regia*, *Rhaphoneis amphiceros*, the copepods
825 *Labidocera wollastoni* and *Isias clavipes*.

826

827 **3.4.8. Ocean-Influenced Cold-Temperate EU (OCTN)**

828

829 The eighth group is the Ocean-Influenced Cold-Temperate EU (OCTN, Figure 9, Tables 2 and
830 3). This EU, composed of only four small ecoregions (ecoregions 30-33 in Figure 11H,
831 Supplementary Tables 7 and 8), are located in (i) Georges Bank, (ii) North Channel, (iii) the
832 North Sea and (iv) the Celtic Sea. The last (main) ecoregion is highly diverse (Figure 3) and all
833 taxonomic groups exhibit their highest richness level (Figure 4A). The seasonal amplitude of
834 the biodiversity is low (Figure 4B). As shown by Figure 8, many ecosystems and ecotones
835 occur in this region and the Celtic Sea appears to be a biogeographic crossroad. Neritic (e.g.
836 the diatoms *Bacillaria paxillifera*, *Corethron cryophilum*, *Dactyliosolen fragilissimus*, *Paralia*
837 *sulcata*, the dinoflagellate *Noctiluca scintillans* and the copepods *Anomalocera patersoni* and
838 *Centropages hamatus*) and oceanic (e.g. the dinoflagellates *Oxytoxum* spp. and *Scrippsiella*
839 spp.) species co-occur in this ecoregion (ecoregion 32). Pseudo-oceanic species (e.g.
840 *Ceratium minutum*, *Calanus helgolandicus*, *Candacia armata*) also locally reinforce the
841 biodiversity (Barnard et al., 2004). Warm-temperate (e.g. *Ceratium trichoceros*,
842 *Clausocalanus* spp.), temperate (e.g. *Ceratium hexacanthum*, *Heterorhabdus papilliger*,
843 *Neocalanus gracilis*), cold-temperate (e.g. *Proboscia alata inermis*, *Metridia lucens*) and even
844 subarctic species (e.g. *C. finmarchicus*) co-occurs in this ecoregion. Finally, as with other EUs
845 mainly found in the continental shelf, the meroplankton group (species or taxa included in
846 the groups zooplankton) is highly diverse in the Celtic Sea (Figure 3).

847

848 **3.4.9. Diverse and Productive Oceanic Temperate EU (DPOT)**

849

850 The ninth group is the Diverse and Productive Oceanic Temperate EU (DPOT, Figure 9, Tables
851 2 and 3). This oceanic EU, composed by only one ecoregion (ecoregion 34 in Figure 11I,
852 Supplementary Tables 7 and 8), is productive and highly diverse (Figure 3 and 4). Seasonal
853 amplitude remains elevated and the number of abundant species in this ecoregion is high
854 (Barnard et al., 2004). In particular, the richness of the genus *Ceratium* and small copepods is
855 very high (Figure 3). The dinoflagellate *Ceratium hexacanthum* is indicative of this EU in the
856 region covered by the CPR survey while *C. minutum*, *Gonyaulax* spp. and *Oxytoxum* spp. are
857 also highly abundant (Barnard et al., 2004). The high biodiversity is also reinforced by neritic
858 species that expatriate from the continental shelf (e.g. holozooplankton *Pseudocalanus* spp.
859 and meroplankton such as echinoderm larvae) and pseudo-oceanic species (i.e. species
860 occurring above the oceanic and neritic regions but higher over the shelf-edge) such as
861 *Ctenocalanus vanus*, *Candacia armata* and *Calanus finmarchicus* (Barnard et al., 2004).

862

863 **3.4.10. Oceanic Warm-Temperate EU (OWP)**

864

865 The tenth group represents the Oceanic Warm-Temperate EU (OWP, Figure 9, Tables 2 and
866 3). This oceanic EU, composed of three ecoregions occurring south of the Oceanic Polar
867 Front in the Atlantic, south of Newfoundland and the Nova Scotian Shelves (ecoregions 35-
868 37 in Figure 11J, Supplementary Tables 7 and 8), is more diverse than oceanic regions north
869 of the Oceanic Polar Front (Figures 3 and 4). In particular, the biodiversity of small and large
870 copepods, as well as the genus *Ceratium* eastwards, is high. In contrast, the other groups

871 (zooplankton and diatoms) have a low biodiversity. Seasonal amplitude is substantially lower
872 than HSO and DPOT, with the exception of the eastern side of the ecoregion. A large number
873 of oceanic species occur in this EU, e.g. the copepods *Nannocalanus minor*, *Heterorhabdus*
874 *papilliger*, *Pleuromamma borealis*, *Euchaeta acuta*, *Lucicutia* spp, and the dinoflagellates
875 *Ceratium azoricum*, *C. massiliense*, and *C. trichoceros* (Barnard et al., 2004).

876

877 **3.4.11. Pseudo-Oceanic Warm-Temperate EU (POWT)**

878

879 The eleventh group is the Pseudo-Oceanic Warm-Temperate EU (POWT, Figure 9, Tables 2
880 and 3). This pseudo-oceanic EU, composed of only one ecoregion (ecoregion 38 in Figure
881 11K), Supplementary Tables 7 and 8), is characterised by a high biodiversity for all groups.
882 This is a very complex area as revealed by the index of heterogeneity, suggesting the
883 occurrence of a large imbrication of ecosystems; the area therefore may well represent an
884 ecotone (Figure 7B and 8B). The high biodiversity is explained by the high mean SST to the
885 eastern part of the Bay of Biscay (Figure 2) and the co-occurrence of oceanic, pseudo-
886 oceanic and neritic species from the distinct ecological units occurring at small spatial scales
887 (Figures 8A and 2). The biodiversity is higher in POWT than in DPOT and the seasonal
888 amplitude is remarkably reduced (Figure 4B). Examples of species occurring in this EU are
889 the diatoms *Bacteriastrum* spp., *Hemiaulus* spp., *Lauderia annulata*, the dinoflagellates
890 *Ceratium arietinum*, *C. bucephalum*, *C. candelabrum*, *C. extensum*, *C. carriense* and the
891 copepods *Calanoides carinatus* and *Ctenocalanus vanus*.

892

893 **3.4.12. Northern Sub-Tropical EU (NST)**

894

895 The twelfth group is the Northern Sub-Tropical EU (NST, Figure 9, Tables 2 and 3). Composed
896 of only one ecoregion (ecoregion 39 in Figure 11L, Supplementary Tables 7 and 8), this EU is
897 highly influenced by the northern part of the Subtropical Gyre and may correspond to the
898 north-eastern part of the North Atlantic Subtropical Gyral Province (NAST) *sensu* Longhurst
899 (Longhurst, 1998). With the exception of diatoms and small zooplankton, the biodiversity of
900 all groups is high. The seasonal amplitude of biodiversity is low in this EU. Subtropical species
901 such as the dinoflagellates *Ceratium buceros* and *C. belone*, as well as the copepod
902 *Undeuchaeta plumosa*, are typically observed (Barnard et al., 2004).

903

904 **3.4.13. Gulf Stream Extension EU (GSE)**

905

906 The thirteenth group is the Gulf Stream Extension EU (GSE, Figure 9, Tables 2 and 3). This EU,
907 composed of only one ecoregion (ecoregion 40 in Figure 11M, Supplementary Tables 7 and
908 8), corresponds to the northern extremity of the Gulf Stream Province *sensu* Longhurst
909 (Longhurst, 1998) and the Gulf Stream PH as defined in Figure 2. This is an area of high
910 biodiversity, especially for large zooplankton, copepods and, to a lesser extent, the genus
911 *Ceratium*. Many species rarely recorded by the CPR survey are located in this ecoregion.
912 Examples of species recorded in GSE are the subtropical copepods *Candacia pachydactyla*,
913 *Centropages violaceus* (also found in POWT), *Paracandacia simplex*, *Pontellina plumata* and
914 *Scolecithrix danae*, and the diatom *Cladopyxis* spp. (Barnard et al., 2004).

915

916

917

918 **3.5. Potential influence of the difference in temporal coverage between the habitat and**
919 **the biological partitions**

920
921 The biological partition was based on CPR data sampled during the period 1946-2015. The
922 habitat partition was based on the BIO-ORACLE v2 dataset, which encompassed the period
923 2000-2014. The ecological partition is similar to the biological partition but with the polar
924 biome divided into 3 EUs using information from the habitat partition; this subsequent
925 division was made because of the poor CPR sampling occurring in this area (PO, SPO and
926 HSO in Fig. 9). We merged the two (biological and habitat) partitions for a restricted region
927 corresponding to the Polar biome between ~50°N and ~66°N and ~55°W and ~5°E and
928 thereby the difference of time periods may have only affected the boundary between PO
929 and SPO and SPO and HSO (Fig. 9). Using ERSST data, we compared annual SST data based on
930 1946-2015 and 2000-2014 and no substantial differences in SST (<0.5°C) were found in the
931 areas where the PO/SPO and SPO/HSO boundaries are located (Fig. 2, Fig. 9 and
932 Supplementary Fig. 2). Because annual SST and sea ice concentration are highly correlated,
933 we conclude that the consideration of the two time periods did not affect substantially our
934 ecological partition. In addition, we assumed that the spatial changes in salinity was also
935 limited between the two time periods but no dataset was available to us for testing.

936

937 **4. Discussion**

938

939 Our final ecological partition of the North Atlantic Ocean (Figure 9) was primarily based on
940 the biodiversity and seasonal patterns in the species richness of six planktonic groups,
941 therefore integrating information on 238 plankton species or taxa sampled by the CPR
942 survey between 1946 and 2015 (60,549,580 data points). In areas where CPR sampling was
943 high (e.g. around the British Isles), the spatial resolution of the partition was relatively high
944 (0.5° latitude x 0.5° longitude) and in more remote oceanic areas, the resolution was
945 downgraded to 2° latitude x 2° longitude. At the centre of the North Atlantic, where CPR
946 sampling was limited, we also used the physico-chemical partition (Figure 2) to allow the
947 geographical division of three more provinces (e.g. PO, SPO and HSO). The resulting partition
948 identified 13 EUs, units defined by a relatively homogeneous biodiversity and similar
949 patterns in seasonal variability for the six taxonomic groups: (i) diatoms, (ii) dinoflagellates,
950 small (iii, iv) and large (v, vi) copepods (iii, v) and zooplankton other than copepods (iv, vi).
951 Some EUs, which were not represented by an interconnected set of geographical cells, were
952 subsequently divided into ecoregions (Figure 11). We used the CPR atlas (Barnard et al.,
953 2004; Beaugrand, 2004) to further investigate whether some species were representative of
954 each EU or associated ecoregions (Figures 9 and 11); this electronic atlas is available on
955 request.

956

957 The main difficulty in partitioning the marine pelagic realm is related to the dynamic
958 movement of water masses and the locations of surface features which are influenced by
959 atmospheric conditions and are highly seasonal by nature. This dynamism led the
960 biogeographer van der Spoel (van der Spoel, 1994) to attempt to separate the biotope of
961 pelagic ecosystems into two components (i) a stable-biotope component (geographically
962 stable in time) in which a primary related community occurs and (2) a substrate-biotope
963 component (depending on water mass) characterized by a secondary related community
964 (mixed primary community, (Beklemishev, 1961)). An ecosystem is mainly characterised by a

965 primary related community linked to a stable-biotope component whereas an ecotone is
966 more distinguished by a secondary related-community depending on water masses. It is also
967 known that an ecotone can further be characterised by its own biological composition
968 (Beaugrand, Ibañez, Lindley & Reid, 2002; Frontier, Pichot-Viale, Leprêtre, Davoult & Luczak,
969 2004; Ramade, 1994). The distinction van der Spoel made is fundamental in correctly
970 understanding how plankton biodiversity is spatially organised in the oceans and seas.

971

972 At the ocean-basin scale, our study identified the two realms (open oceanic and the
973 continental shelves pelagic realms), which were revealed in a global-scale study performed
974 at a 5° x 5° spatial resolution and based on occurrence data reported in the Ocean
975 Biogeographic Information System (OBIS) (Costello et al., 2017). In the area we considered,
976 the boundaries were similar considering the difference in the spatial resolution of the two
977 studies. This distinction was mainly the result of a higher biodiversity of diatoms and the
978 presence of many meroplanktonic groups (zooplankton other than copepods) or groups
979 dependent on shallow waters over neritic regions (Supplementary Tables 4 and 6). In
980 essence the benthic-pelagic coupling makes the continental shelves pelagic realm very
981 specific.

982

983 Mapping of our index of spatial heterogeneity at both 2° x 2° and 0.5° x 0.5° spatial
984 resolutions revealed the presence of a complex transition zone between the two realms
985 where the ecosystems were strongly intertwined (Figures 7B and 8B). The imbrication of
986 ecoregions (DPOT, POWT, CTN, OCTN and MCOHS) and the overlapping spatial distribution of
987 species over the Celtic Sea (Barnard et al., 2004) lead to complex coenoclines (i.e. a gradient
988 of biocoenoses or communities) and associated ecosystems, ecoclines and ecotones. The
989 region can be seen as a biogeographic crossroad where not only oceanic, neritic and pseudo-
990 oceanic species cohabit but also where warm and cold-water species regularly co-occur. As a
991 result, total biodiversity is the highest in this area for all taxonomic groups (Figure 3). Our
992 procedure reduced somewhat this mosaic of ecoregions, which is visible in Figure 8. Such a
993 complex organization of marine life has, to our knowledge, been rarely reported in marine
994 biogeography because our study lies between large-scale studies that have relatively low
995 spatial resolution (Longhurst, 2007; Sherman & Duda, 1999; Spalding et al., 2007) and
996 regional ecological studies at higher resolution that lacks spatial extent to reveal this
997 phenomenon.

998

999 The number of oceanic ecoregions in the present study is higher than previously reported by
1000 large-scale oceanic partitions, which focused at the level of a realm, biome or province
1001 (Costello et al., 2017; Longhurst, 2007; Reygondeau et al., 2013). The eastern side of the
1002 North Atlantic seems to be very complex spatially, with ecoregions varying rapidly and being
1003 highly seasonal to the north (Figures 4B, 7B and 8B). The influence of hydro-dynamical
1004 structures such as the Oceanic Polar Front (OPF) (Dietrich 1964), the Gulf Stream Extension
1005 (both being part of the AMOC) and the Labrador Current on the ecoregions is important. For
1006 example, Beaugrand and colleagues (Beaugrand et al., 2001) suggested that the OPF acts as
1007 a sharp boundary for subtropical, shelf-edge and warm-temperate species, thus limiting
1008 their dispersal polewards. In contrast, colder-water species seemed to be less influenced by
1009 the OPF and were more frequently detected southwards (Barnard et al., 2004). The OPF and
1010 the GSE are also areas of plankton concentration (e.g. *Metridia lucens* for the OPF)(Barnard
1011 et al., 2004).

1012
1013 A close comparison between our partition and Longhurst's biogeography (Longhurst, 2007)
1014 revealed substantial differences between the location of his provinces and our ecoregions.
1015 The position of the boundary between the Polar and the Westerlies Biomes was substantially
1016 different (Figure 10A). This was also the case for the position of the Gulf Stream on the
1017 Habitat Partition (Figure 10B). Biogeographical or satellite-based partitioning, typically based
1018 on a few parameters and no real abundance data, may only reveal major features. Although
1019 they definitively have been important in partitioning the ocean on a global scale, they may
1020 be limited to detect regional ecosystems at a basin scale. Especially, plankton are sensitive to
1021 small hydro-climatic fluctuations because it integrates those fluctuations during their entire
1022 life cycle (Reid, Edwards, Hunt & Warner, 1998; Taylor, Allen & Clark, 2002). Limiting the
1023 geographical division to a restricted number of physical and chemical parameters may
1024 therefore lead to an oversimplified partition into biomes, provinces or ecoregions.

1025
1026 We found a much higher number of ecoregions compared to Large Marine Ecosystems
1027 (LMEs) (Sherman & Duda, 1999) or MEOs (Spalding et al., 2007). We found three main
1028 ecoregions in the North Sea instead of only one in the classifications of LMEs or MEOs.
1029 These three ecoregions roughly corresponded with the three major ecological subdivisions
1030 proposed by some authors and based on phytoplankton (Reid, Lancelot, Gieskes, Hagmeier
1031 & Weickart, 1990), zooplankton (Beaugrand et al., 2001; Beaugrand et al., 2002; Fransz,
1032 Colebrook, Gamble & Krause, 1991), and fish (Daan, Bromley, Hislop & Nielsen, 1990). The
1033 Flamborough Frontal structure, which separates seasonally thermally stratified water to the
1034 North and tidally-induced mixed water to the south (Pingree, Holligan & Mardell, 1978)
1035 probably explains the boundary between CTSN (ecoregion 29 in Figure 11) and CTN
1036 (ecoregion 27). North of CTN, the remaining area of the North Sea belongs to a composite
1037 EU (MCOHS), revealing the complex nature of the system and the influence of the Atlantic
1038 water on this part of the North Sea (ecoregion 19). Two more ecoregions were detected in
1039 the North Sea but they were restricted to the northeastern coast of Great Britain (ecoregions
1040 28 and 33).

1041
1042 Although the proposed partition may represent a significant improvement of existing ones in
1043 the North Atlantic sector (e.g. ICES or OSPAR areas), it has also a number of drawbacks that
1044 we should be aware of before using it for ecosystem management. First, the partition
1045 remains static even if it integrates seasonal variability in the biodiversity of six plankton
1046 groups. Providing a dynamical partition is relatively difficult when it is based on biological
1047 data because of the number of samples this requires. The CPR survey collects about 5000
1048 samples every year, which is unique in the world at such spatio-temporal scales and levels of
1049 taxonomic resolution. However, it remains too limited to give a dynamic picture at the same
1050 spatial resolution at a year-to-year scale. Nevertheless, an examination of decadal changes in
1051 the ecoregions is achievable in many areas sampled by the CPR survey (Planque &
1052 Fromentin, 1996; Reid et al., 1998; Richardson & Schoeman, 2004). Biological data are
1053 becoming available at a global scale thanks to initiatives such as OBIS. However, even those
1054 datasets remain insufficient to provide a dynamic picture of the epipelagic system at a large
1055 scale and at a relatively high spatial resolution.

1056
1057 Second, some EUs or ecoregions were poorly sampled by the CPR survey (Figure 1, Tables 2-
1058 3 and Supplementary Tables 7-8), which may have affected our partition. For instance, it was

1059 unexpected that seasonal variability in biodiversity was so high south of the oceanic polar
1060 front in the center of the North Atlantic (Figure 4B); in particular, values were higher than
1061 estimated seasonal variance in calanoid biodiversity based on principal component analysis
1062 (Beaugrand et al., 2001). A higher amount of variability may be related to an insufficient
1063 number of samples. Although we jackknifed taxonomic richness, it is possible that in some
1064 poorly sampled areas, some noise remains in our estimations of biodiversity. As shown in
1065 the Figure 3 however, this is likely to only concern a few geographical cells. The biological
1066 partition gave an unexpected large ecoregion north of the OPF where CPR sampling is
1067 limited. We used the PHs to attempt to complete the ecoregions and showed by
1068 examination of the CPR atlas that the division had an ecological meaning. For example, the
1069 copepod *C. glacialis* is highly abundant in PSE, the diatom *Ephemera planamembranacea* is
1070 found in great concentration in PO and the calanoids *C. finmarchicus* and *Paraeuchaeta*
1071 *norvegica* in SPO (Figure 9) (Barnard et al., 2004).

1072
1073 Third, our partition was based on the period 1946-2015 for biological data and on the period
1074 2000-2014 for environmental data (Assis et al., 2017; Tyberghein et al., 2012). In addition,
1075 the distribution of CPR routes has changed through time and some areas have only been
1076 sampled during the first decades of the time series (e.g. southern and central regions of the
1077 North Atlantic) (Batten et al., 2003). We have shown that differences in time periods have
1078 not substantially affected our results, however (Supplementary Figure 2). This result can also
1079 be explained by the spatial variance in both biological and environmental data that is higher
1080 than the temporal variance (Beaugrand, Ibañez & Lindley, 2003).

1081

1082

1083 **5. Conclusions**

1084

1085 We provide two basin-scale partitions of the North Atlantic Ocean based on physical and
1086 biological data at a relatively high spatial resolution. The final ecological partition is based on
1087 238 plankton species encompassing diatoms, dinoflagellates, small and large copepods and
1088 other zooplankton species, including meroplankton. This partition reveals the complexity of
1089 the arrangement of life in both oceanic and neritic realms. Based on a relatively high spatial
1090 resolution and taxonomic resolution, our partition represents a baseline against which we
1091 will (i) better understand the effects of natural variability on marine ecosystems, (ii) better
1092 evaluate the implications of the human interference on marine biological and ecological
1093 systems through pollution, eutrophication, fishing and global climate change and (iii) guide
1094 the development of marine protected areas to protect biodiversity.

1095

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1097

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1102

1103 **7. Author contributions**

1104 G.B., M.E. and P.H. conceived the study; G.B. and P.H. prepared and analysed the data. G.B. wrote
1105 the initial draft. G.B., P.H. and M.E. discussed the results and contributed to the paper writing.

1106

1107 **8. References**

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Supplementary Information

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List of Supplementary Figures

Supplementary Figure 1. Creation of the ecological partition from the habitat partition ($\sim 0.1 \times \sim 0.1$) and the two biological partitions at $2^\circ \times 2^\circ$ and $0.5^\circ \times 0.5^\circ$ spatial resolutions. **Step 1:** removal of minor groups in the high-resolution biological partition (6 groups). **Step 2:** addition of the information from the $2^\circ \times 2^\circ$ biological partition in areas where there is no information (9 groups). **Step 3:** further division using information from the habitat partition. The final ecological partition is composed of 13 groups. See Methods.

Supplementary Figure 2. Effect of the consideration of the two time periods on the PO/SPO and SPO/HSO boundaries using sea surface temperature (SST) as a proxy for sea-ice concentration and temperature. **A.** Mean location of the isotherms $2\text{-}12^\circ\text{C}$ during 2000-2014. **B.** Mean location of the isotherms $2\text{-}12^\circ\text{C}$ during 1946-2015. **C.** Differences in average SST between 2000-2014 and 1946-2015. Differences $<0.5^\circ\text{C}$ are observed in the areas where the PO/SPO and SPO/HSO boundaries were located (see Fig. 2 and 9).

List of Supplementary Tables

Supplementary Table 1. List of species used to calculate the species richness of diatoms.

Supplementary Table 2. List of species used to calculate the species richness of the genus *Ceratium*.

Supplementary Table 3. List of species used to calculate the species richness of small copepods (i.e. recorded in traverse).

Supplementary Table 4. List of species used to calculate the species richness of small (i.e. recorded in traverse) zooplankton other than copepods.

Supplementary Table 5. List of species used to calculate the species richness of large copepods (i.e. recorded in eyecount).

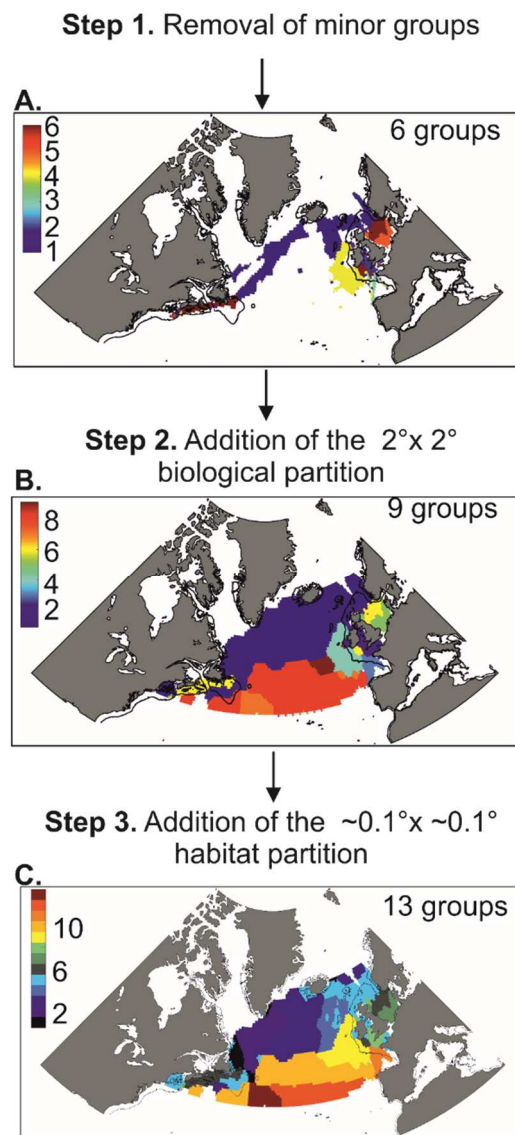
Supplementary Table 6. List of species used to calculate the species richness of large zooplankton other than copepods and fish (i.e. recorded in eyecount). Note that fish eggs and larvae were considered in this analysis.

Supplementary Table 7. Main abiotic properties of the ecoregions associated to ecological units. EU: Ecological Unit. SST: mean Sea Surface Temperature ($^\circ\text{C}$). S: mean salinity (PSS). Cur: mean surface current ($\text{m}\cdot\text{s}^{-1}$). N: mean nitrate concentration ($\text{mol}\cdot\text{m}^{-3}$). P: mean phosphate concentration ($\text{mol}\cdot\text{m}^{-3}$). Sil: mean silicate concentration ($\text{mol}\cdot\text{m}^{-3}$). PAR: mean photosynthetically active radiation ($\text{E}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$). C: mean chlorophyll concentration ($\text{mg}\cdot\text{m}^{-3}$). PI: mean primary production ($\text{g}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$). Bathymetry is expressed in meter (m). P5: the 5th percentile. P50: the median. P95: the 95th percentile. See text for the meaning of the ecological unit acronyms. See Figure 9 for the spatial distribution of EUs and Figure 11 for the ecoregions (1-40).

Supplementary Table 8. Average and seasonal amplitude of the biodiversity of the 6 taxonomic groups in all ecoregions of each ecological unit. Eco: Ecoregion (numbers are the identifier of an ecoregion). EU: Ecological Unit. Diat: diatoms. Dino: dinoflagellates. '-' are missing values. Cop:

1276 copepods. See text for the meaning of the ecological unit acronyms. See Figure 9 for the spatial
1277 distribution of EUs and Figure 11 for the ecoregions (1-40).
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1282 **Supplementary Figure 1.**
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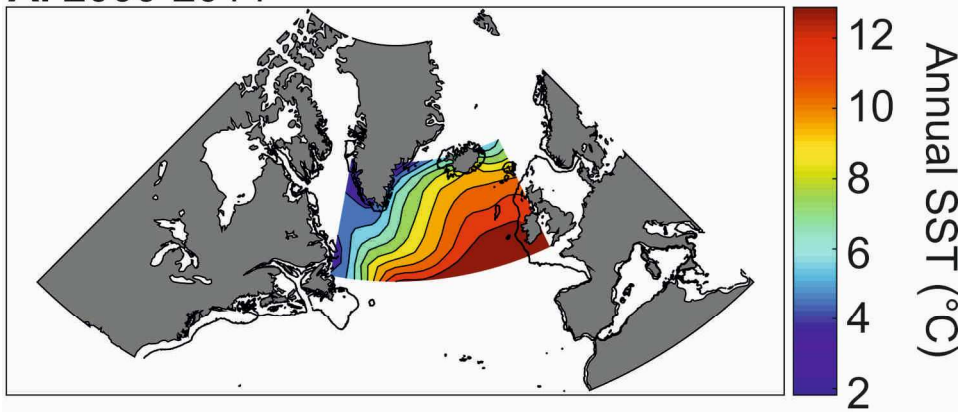
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1285 **Supplementary Figure 2.**

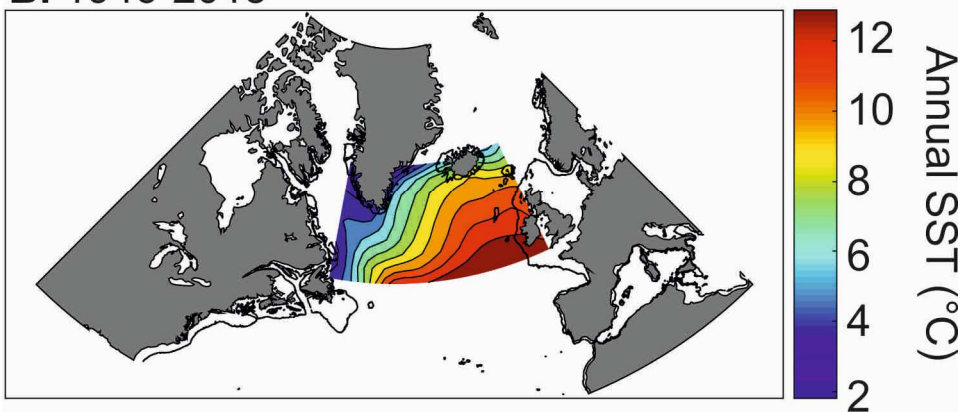
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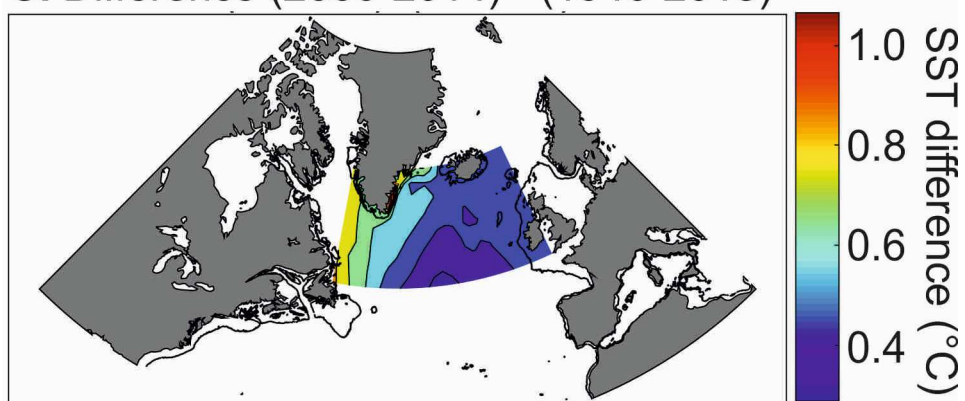
A. 2000-2014



B. 1946-2015



C. Difference (2000-2014) - (1946-2015)



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Supplementary Table 1. List of species used to calculate the species richness of diatoms.

Species	Year of first record
<i>Paralia sulcata</i>	1948
<i>Skeletonema costatum</i>	1952
<i>Thalassiosira</i> spp.	1948
<i>Dactyliosolen antarcticus</i>	1948
<i>Rhizosolenia styliformis</i>	1948
<i>Rhizosolenia hebetata semispina</i>	1948
<i>Chaetoceros</i> (<i>Hyalochaete</i>) spp.	1948
<i>Chaetoceros</i> (<i>Phaeoceros</i>) spp.	1948
<i>Odontella sinensis</i>	1948
<i>Thalassiothrix longissima</i>	1948
<i>Thalassionema nitzschioides</i>	1948
<i>Bacteriastrium</i> spp.	1951
<i>Bellerochea malleus</i>	1948
<i>Biddulphia alternans</i>	1948
<i>Odontella aurita</i>	1948
<i>Odontella granulata</i>	1948
<i>Odontella obtusa</i>	1961
<i>Odontella regia</i>	1948
<i>Odontella rhombus</i>	1948
<i>Cerataulina pelagica</i>	1958
<i>Climacodium frauenfeldianum</i>	1963
<i>Coscinodiscus concinnus</i>	1948
<i>Detonula confervacea</i>	1963
<i>Ditylum brightwellii</i>	1958
<i>Eucampia zodiacus</i>	1948
<i>Fragilaria</i> spp.	1948
<i>Guinardia flaccida</i>	1948
<i>Gyrosigma</i> spp.	1953
<i>Hemiaulus</i> spp.	1959
<i>Leptocylindrus danicus</i>	1954
<i>Navicula</i> spp.	1948
<i>Cylindrotheca closterium</i>	1958
<i>Rhaphoneis ampiceros</i>	1950
<i>Planktoniella sol</i>	1961
<i>Rhizosolenia acuminata</i>	1961
<i>Rhizosolenia bergonii</i>	1953
<i>Rhizosolenia setigera</i>	1949
<i>Stephanopyxis</i> spp.	1948
<i>Surirella</i> spp.	1960
<i>Nitzschia</i> spp. (Unidentified)	1958
<i>Odontella mobiliensis</i>	1950
<i>Pachysphaera</i> spp.	1973
<i>Hemidiscus cuneiformis</i>	1974
<i>Ephemera planamembranacea</i>	1952
<i>Pseudo-nitzschia delicatissima</i> complex	1950
<i>Pseudo-nitzschia seriata</i> complex	1948
<i>Podosira stelligera</i>	1974
<i>Pseudosolenia calcar-avis</i>	1960
<i>Guinardia cylindrus</i>	1965
<i>Guinardia delicatula</i>	1952
<i>Dactyliosolen fragilissimus</i>	1952
<i>Guinardia striata</i>	1948
<i>Detonula pumila</i>	1959
<i>Lauderia annulata</i>	1958
<i>Bacillaria paxillifera</i>	1948
<i>Corethron hystrix</i>	1953
<i>Proboscia curvirostris</i>	1952
<i>Proboscia indica</i>	1948
<i>Rhizosolenia imbricata</i>	1948

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1292 **Supplementary Table 2.** List of species used to calculate the species richness of the genus *Ceratium*.

Species	Year of first record
<i>Ceratium fusus</i>	1948
<i>Ceratium furca</i>	1948
<i>Ceratium lineatum</i>	1948
<i>Ceratium tripos</i>	1948
<i>Ceratium macroceros</i>	1948
<i>Ceratium horridum</i>	1948
<i>Ceratium longipes</i>	1948
<i>Ceratium arcticum</i>	1948
<i>Ceratium kofoidii</i>	1974
<i>Ceratium falcatum</i>	1977
<i>Ceratium breve</i>	1974
<i>Ceratium arietinum</i>	1956
<i>Ceratium azoricum</i>	1948
<i>Ceratium belone</i>	1959
<i>Ceratium bucephalum</i>	1948
<i>Ceratium buceros</i>	1949
<i>Ceratium candelabrum</i>	1956
<i>Ceratium carriense</i>	1955
<i>Ceratium compressum</i>	1963
<i>Ceratium declinatum</i>	1959
<i>Ceratium extensum</i>	1948
<i>Ceratium gibberum</i>	1958
<i>Ceratium hexacanthum</i>	1948
<i>Ceratium inflatum</i>	1965
<i>Ceratium karstenii</i>	1964
<i>Ceratium lamellicorne</i>	1965
<i>Ceratium lunula</i>	1955
<i>Ceratium massiliense</i>	1955
<i>Ceratium minutum</i>	1948
<i>Ceratium pavillardii</i>	1959
<i>Ceratium pentagonum</i>	1957
<i>Ceratium platycorne</i>	1957
<i>Ceratium pulchellum</i>	1950
<i>Ceratium setaceum</i>	1957
<i>Ceratium teres</i>	1955
<i>Ceratium trichoceros</i>	1961
<i>Ceratium vultur</i>	1965
<i>Ceratium contortum</i>	1969
<i>Ceratium falcatifforme</i>	1969
<i>Ceratium longirostrum</i>	1969
<i>Ceratium ranipes</i>	1971

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1295 **Supplementary Table 3.** List of species used to calculate the species richness of small copepods (i.e.
 1296 recorded in traverse).

Species	Year of first record
<i>Para-Pseudocalanus</i> spp.	1946
<i>Temora longicornis</i>	1946
<i>Acartia</i> spp. (unidentified)	1946
<i>Centropages typicus</i>	1946
<i>Centropages hamatus</i>	1946
<i>Isias clavipes</i>	1946
<i>Clausocalanus</i> spp.	1950
<i>Oithona</i> spp.	1946
<i>Corycaeus</i> spp.	1946
<i>Acartia danae</i>	1964
<i>Calocalanus</i> spp.	1952
<i>Ctenocalanus vanus</i>	1959
<i>Macrosetella gracilis</i>	1965
<i>Lubbockia</i> spp.	1953
<i>Lucicutia</i> spp.	1947
<i>Mecynocera clausi</i>	1948
<i>Microcalanus</i> spp.	1958
<i>Oncaea</i> spp.	1949
<i>Parapontella brevicornis</i>	1947
<i>Scolecithricella</i> spp.	1948
<i>Temora stylifera</i>	1963
<i>Temora turbinata</i>	1968
<i>Tortanus discaudatus</i>	1961
<i>Acartia longiremis</i>	1964
<i>Acartia negligens</i>	1970
<i>Diaixis hibernica</i>	1962
<i>Pseudocalanus</i> spp. Adult Atlantic	1946

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1299 **Supplementary Table 4.** List of species used to calculate the species richness of small (i.e. recorded in
 1300 traverse) zooplankton other than copepods.

Species	Year of first record
<i>Podon</i> spp.	1946
<i>Evadne</i> spp.	1946
Chaetognatha Traverse	1946
Cyphonautes	1946
Echinoderm larvae	1946
<i>Clione</i> shells	1956
<i>Penilia avirostris</i>	1977
Cirripede larvae (Total)	1946
Foraminifera (Total)	1946
<i>Radiolaria</i> Total	1946
<i>Zoothamnium pelagicum</i>	1964
Appendicularia	1946
<i>Bivalvia</i> larvae	1946
<i>Tintinnida</i> Total	1946

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1304 **Supplementary Table 5.** List of species used to calculate the species richness of large copepods (i.e.
 1305 recorded in eyecount).

Species	Year of first record
<i>Calanus finmarchicus</i>	1958
<i>Calanus helgolandicus</i>	1958
<i>Calanus glacialis</i>	1953
<i>Calanus hyperboEUs</i>	1946
<i>Neocalanus gracilis</i>	1949
<i>Nannocalanus minor</i>	1949
<i>Calanoides carinatus</i>	1953
<i>Rhincalanus nasutus</i>	1946
<i>Euchirella rostrata</i>	1951
<i>Euchaeta acuta</i>	1947
<i>Metridia lucens</i>	1946
<i>Metridia longa</i>	1949
<i>Pleuromamma robusta</i>	1946
<i>Pleuromamma abdominalis</i>	1948
<i>Pleuromamma borealis</i>	1953
<i>Pleuromamma gracilis</i>	1948
<i>Candacia armata</i>	1946
<i>Labidocera wollastoni</i>	1946
<i>Miracia efferata</i>	1965
<i>Pontellina plumata</i>	1949
<i>Scaphocalanus echinatus</i>	1965
<i>Aetideus armatus</i>	1948
<i>Anomalocera patersoni</i>	1946
<i>Candacia bipinnata</i>	1965
<i>Candacia curta</i>	1965
<i>Candacia ethiopica</i>	1957
<i>Candacia longimana</i>	1967
<i>Candacia pachydactyla</i>	1961
<i>Centropages bradyi</i>	1950
<i>Centropages chierchiae</i> eyecount	1959
<i>Centropages violaceus</i>	1962
<i>Eucalanus hyalinus</i>	1953
<i>Euchaeta marina</i>	1960
<i>Euchaeta media</i>	1963
<i>Euchaeta pubera</i>	1963
<i>Euchaeta spinosa</i>	1957
<i>Euchirella curticauda</i>	1958
<i>Euchirella messinensis</i>	1954
<i>Haloptilus longicornis</i>	1949
<i>Heterorhabdus abyssalis</i>	1953
<i>Heterorhabdus norvegicus</i>	1949
<i>Heterorhabdus papilliger</i>	1952
<i>Paracandacia bispinosa</i>	1964
<i>Phaenna spinifera</i>	1969
<i>Pleuromamma piseki</i>	1960
<i>Pleuromamma xiphias</i>	1951
<i>Rhincalanus cornutus</i>	1958
<i>Sapphirina</i> spp.	1951
<i>Scolecithrix bradyi</i>	1968
<i>Scolecithrix danae</i>	1961
<i>Scottocalanus persekans</i>	1964
<i>Undeuchaeta major</i>	1958
<i>Undeuchaeta plumosa</i>	1948
<i>Undinula vulgaris</i>	1963
<i>Neocalanus robustior</i>	1967
<i>Paracandacia simplex</i>	1958
<i>Candacia varicans</i>	1968
<i>Labidocera aestiva</i>	1976
<i>Candacia giesbrechti</i>	1998
<i>Labidocera acutifrons</i>	1991
<i>Alteutha</i> spp.	1994
<i>Corycaeus speciosus</i>	1997
<i>Mesocalanus tenuicornis</i>	1949
<i>Aetideus giesbrechti</i>	1964

<i>Subeucalanus crassus</i>	1946
<i>Subeucalanus monachus</i>	1965
<i>Subeucalanus mucronatus</i>	1964
<i>Paraeuchaeta glacialis</i>	1964
<i>Paraeuchaeta gracilis</i>	1951
<i>Paraeuchaeta hebes</i>	1949
<i>Paraeuchaeta norvegica</i>	1946
<i>Paraeuchaeta tonsa</i>	1949
<i>Parathalestris croni</i>	1958

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1308 **Supplementary Table 6.** List of species used to calculate the species richness of large zooplankton
 1309 other than copepods and fish (i.e. recorded in eyecount). Note that fish eggs and larvae were
 1310 considered in this analysis.

Species	Year of first record
<i>Tomopteris</i> spp.	1946
Gammaridea	1946
Hyperidea (Total)	1946
Decapoda larvae (Total)	1946
<i>Clione limacina</i>	1946
Euphausiacea Adult	1950
Chaetognatha eyecount	1946
Fish eggs (Total)	1946
Fish larvae	1946
Pycnogonida	1949
Siphonophora	1949
Cumacea	1946
Sergestidae	1952
Lepas nauplii	1955
Mysidacea	1946
Ostracoda	1947
Echinoderm post larvae	1946
Thaliacea	1946
Cephalopoda larvae	1947
Stomatopoda	1947
Amphipoda (Unidentified)	2009
Salpidae (Total)	1950
Doliolidae	1949

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1314 **Supplementary Table 7. Main abiotic properties of the ecoregions associated to ecological units.**
1315 EU: Ecological Unit. SST: mean Sea Surface Temperature (°C). S: mean salinity (PSS). Cur: mean
1316 surface current (m.s⁻¹). N: mean nitrate concentration (mol.m⁻³). P: mean phosphate concentration
1317 (mol.m⁻³). Sil: mean silicate concentration (mol.m⁻³). PAR: mean photosynthetically active radiation
1318 (E.m⁻².day⁻¹). C: mean chlorophyll concentration (mg.m⁻³). PI: mean primary production (g.m⁻³.day⁻¹).
1319 Bathymetry is expressed in meter (m). P5: the 5th percentile. P50: the median. P95: the 95th
1320 percentile. See text for the meaning of the ecological unit acronyms. See Figure 9 for the spatial
1321 distribution of EUs and Figure 11 for the ecoregions (1-40).
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Eco EU	Area (km ²)	Area (%)	CPR sample	CPR sample per 100 km ²	Bathymetry P50 (P5-P95)	SST	S	Cur	N	P	N/P	Sil	PAR	C (PI)
1 (1) PSE	172511	1.84	2045	1.19	298 (179-859)	3.80	32.79	0.19	3.51	0.45	0.14	3.90	30.1	0.71 (0.009)
1 (2) PSE	42179	0.45	364	0.86	534 (182-1706)	6.68	33.32	0.22	3.35	0.40	0.12	3.17	27.3	0.69 (0.011)
1 (3) PSE	17840	0.19	1	0.01	229 (80-699)	2.89	33.16	0.10	5.35	0.46	0.09	3.47	27.1	0.73 (0.009)
1 (4) PSE	13112	0.14	116	0.88	646 (218-1995)	6.03	34.74	0.18	4.29	0.40	0.10	2.94	27.4	0.51 (0.006)
2 (5) PO	64591	0.69	193	0.30	2989 (372-4223)	11.08	32.65	0.25	0.42	0.26	0.65	2.48	27.8	0.37 (0.004)
2 (6) PO	900267	9.60	15735	1.75	3165 (1593-3897)	6.50	34.55	0.17	7.96	0.60	0.08	4.10	26.0	0.46 (0.006)
2 (7) PO	17153	0.18	6	0.03	2099 (1385-2536)	7.68	35.03	0.12	8.38	0.60	0.07	4.08	26.2	0.40 (0.005)
2 (8) PO	5250	0.06	30	0.57	1875 (1114-2619)	5.35	34.70	0.12	4.99	0.44	0.09	2.84	27.5	0.46 (0.006)
3 (9) SPO	1385779	14.78	22457	1.62	2658 (1350-3772)	9.22	34.98	0.24	7.15	0.54	0.08	3.70	26.8	0.40 (0.005)
3 (10) SPO	61142	0.65	67	0.11	2515 (1072-3454)	6.98	34.92	0.20	5.12	0.44	0.09	2.84	27.4	0.50 (0.006)
3 (11) SPO	70166	0.75	1423	2.03	1803 (981-2803)	9.18	35.08	0.25	5.04	0.41	0.08	2.72	27.9	0.48 (0.007)
4 (12) HSO	511151	5.45	9446	1.85	1891 (917-3872)	11.32	35.32	0.28	5.87	0.45	0.08	3.14	27.9	0.40 (0.006)
5 (13) MCOHS	192911	2.06	1890	0.98	123 (13-243)	11.03	31.87	0.12	0.29	0.18	1.08	4.25	31.1	0.49 (0.006)
5 (14) MCOHS	142778	1.52	1095	0.77	81 (53-393)	7.78	32.34	0.11	1.09	0.32	0.38	2.51	27.2	0.50 (0.006)
5 (15) MCOHS	57747	0.62	181	0.31	126 (8-274)	6.10	31.51	0.13	1.24	0.32	0.27	4.46	30.6	0.71 (0.010)
5 (16) MCOHS	18708	0.20	229	1.22	179 (96-305)	2.72	32.02	0.11	2.87	0.45	0.16	4.65	32.1	0.75 (0.008)
5 (17) MCOHS	15541	0.17	251	1.62	4139 (4026-4228)	10.21	34.57	0.63	5.21	0.46	0.09	3.16	25.0	0.46 (0.006)
5 (18) MCOHS	3091	0.03	3	0.10	96 (2-244)	1.65	33.03	0.05	5.00	0.43	0.09	3.44	26.6	0.92 (0.013)
5 (19) MCOHS	824794	8.80	32134	3.90	272 (66-1492)	9.62	34.94	0.19	4.73	0.39	0.09	3.32	28.4	0.57 (0.009)
5 (20) MCOHS	11466	0.12	116	1.01	830 (620-1215)	11.05	35.29	0.15	6.20	0.47	0.08	3.22	27.7	0.39 (0.005)
5 (21) MCOHS	68990	0.74	2274	3.30	535 (171-1507)	11.30	35.35	0.15	6.05	0.46	0.08	3.05	28.6	0.43 (0.006)
5 (22) MCOHS	4613	0.05	136	2.95	631 (327-1214)	10.50	35.31	0.12	6.62	0.49	0.07	3.31	28.1	0.38 (0.006)
5 (23) MCOHS	165967	1.77	4546	2.74	75 (15-164)	11.77	34.66	0.14	1.38	0.20	0.23	3.70	29.8	0.71 (0.012)
5 (24) MCOHS	90450	0.96	595	0.66	39 (4-94)	13.57	34.48	0.13	0.96	0.12	4.29	3.75	31.7	0.48 (0.008)

6 (25) CTN	339203	3.62	10392	3.06	122 (34-498)	8.18	31.16	0.12	0.57	0.29	0.95	3.22	28.9	0.44 (0.004)
6 (26) CTN	39425	0.42	2534	6.43	116 (83-139)	13.05	35.19	0.11	0.76	0.19	0.28	2.17	31.2	0.42 (0.006)
6 (27) CTN	179781	1.92	18779	10.45	70 (35-271)	10.59	34.45	0.16	0.87	0.21	0.50	3.04	31.0	0.45 (0.005)
7 (28) CTSN	20517	0.22	3460	16.86	59 (22-81)	10.01	34.47	0.10	1.50	0.17	0.12	3.11	30.1	0.76 (0.012)
7 (29) CTSN	203938	2.17	24558	12.04	30 (5-50)	11.28	33.67	0.25	1.07	0.21	1.21	3.78	31.2	0.65 (0.009)
8 (30) OCTN	9188	0.10	562	6.12	91 (69-242)	10.60	32.01	0.10	0.41	0.21	0.60	3.17	30.3	0.53 (0.006)
8 (31) OCTN	12255	0.13	1843	15.04	84 (26-155)	11.56	35.19	0.21	2.13	0.22	0.10	2.67	29.6	0.78 (0.014)
8 (32) OCTN	147932	1.58	15540	10.50	79 (23-120)	12.87	34.73	0.13	0.25	0.17	1.42	3.26	31.3	0.37 (0.004)
8 (33) OCTN	19793	0.21	4233	21.39	92 (60-117)	10.14	35.06	0.12	2.27	0.24	0.11	2.39	30.3	0.59 (0.009)
9 (34) DPOT	761237	8.12	23072	3.03	3630 (152-4823)	13.42	35.52	0.26	3.81	0.32	0.09	2.36	29.5	0.43 (0.007)
10 (35) OWT	75908	0.81	82	0.11	3577 (355-4657)	14.66	33.37	0.43	0.80	0.17	0.46	2.68	29.4	0.46 (0.007)
10 (36) OWT	286595	3.06	1193	0.42	3648 (68-5071)	13.88	34.02	0.58	0.90	0.19	0.26	2.24	29.0	0.45 (0.007)
10 (37) OWT	1495360	15.95	10901	0.73	4033 (2275-4825)	13.98	35.34	0.44	2.76	0.27	0.11	2.28	27.9	0.39 (0.006)
11 (38) POWT	208415	2.22	12533	6.01	3560 (120-4894)	15.11	35.59	0.14	0.90	0.14	0.20	1.72	31.3	0.34 (0.006)
12 (39) NST	859614	9.17	5085	0.59	3621 (2196-5050)	17.00	35.90	0.36	1.07	0.14	0.14	1.62	30.3	0.28 (0.005)
13 (40) GSE	346399	3.69	1596	0.46	4758 (3680-4942)	17.44	35.48	0.78	1.16	0.17	0.14	1.98	28.8	0.40 (0.007)

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1325 **Supplementary Table 8. Average and seasonal amplitude of the biodiversity of the 6 taxonomic**
 1326 **groups in all ecoregions of each ecological unit.** Eco: Ecoregion (numbers are the identifier of an
 1327 ecoregion). EU: Ecological Unit. Diat: diatoms. Dino: dinoflagellates. '-' are missing values. Cop:
 1328 copepods. See text for the meaning of the ecological unit acronyms. See Figure 9 for the spatial
 1329 distribution of EUs and Figure 11 for the ecoregions (1-40).
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Eco EU	Mean taxonomic richness						Seasonal amplitude in taxonomic richness					
	Diat	Dino	Small cop	Small zoo	Large cop	Large zoo	Diat	Dino	Small cop	Small zoo	Large cop	Large zoo
1 (1) PSE	12.62	7.14	4.48	4.85	5.41	4.77	6.02	5.88	5.75	3.23	6.38	4.82
1 (2) PSE	--	--	--	--	--	--	--	--	--	--	--	--
1 (3) PSE	--	--	--	--	--	--	--	--	--	--	--	--
1 (4) PSE	--	--	--	--	--	--	--	--	--	--	--	--
2 (5) PO	--	--	--	--	--	--	--	--	--	--	--	--
2 (6) PO	11.40	8.69	4.57	5.78	4.48	4.70	5.87	4.63	5.78	4.27	6.42	5.25
2 (7) PO	--	--	--	--	--	--	--	--	--	--	--	--
2 (8) PO	--	--	--	--	--	--	--	--	--	--	--	--
3 (9) SPO	10.70	12.08	4.92	7.33	4.24	4.71	5.54	5.50	5.25	4.38	6.00	7.15
3 (10) SPO	--	--	--	--	--	--	--	--	--	--	--	--
3 (11) SPO	10.60	11.33	6.53	6.03	5.13	4.46	6.31	6.52	5.19	3.37	6.53	7.33
4 (12) HSO	11.72	14.86	6.14	8.19	5.25	3.99	6.29	6.84	6.48	5.44	6.75	8.35
5 (13) MCOHS	16.01	9.97	7.07	5.68	8.26	4.52	7.31	4.68	6.91	5.25	7.80	4.92
5 (14) MCOHS	11.94	10.63	6.28	4.55	7.13	2.25	7.02	4.33	5.36	6.59	6.99	7.96
5 (15) MCOHS	14.26	12.48	6.59	5.36	7.30	2.53	8.74	3.13	4.11	3.60	6.41	3.97
5 (16) MCOHS	13.87	6.90	5.59	4.50	6.23	3.10	7.17	6.93	5.27	5.17	6.49	6.29
5 (17) MCOHS	9.27	7.88	3.86	4.74	3.98	3.29	6.47	6.37	7.15	4.62	6.11	5.74
5 (18) MCOHS	--	--	--	--	--	--	--	--	--	--	--	--
5 (19) MCOHS	12.18	15.71	6.05	7.68	6.10	4.52	7.10	8.47	5.75	4.60	7.11	6.47
5 (20) MCOHS	10.09	13.86	6.27	6.87	4.66	1.57	6.04	3.09	7.54	0.88	5.58	6.84
5 (21) MCOHS	12.67	15.49	6.79	7.77	5.95	4.48	7.37	7.73	6.46	5.54	7.59	8.59
5 (22) MCOHS	12.90	17.06	6.24	8.99	5.38	5.89	5.25	4.93	6.68	4.61	8.15	3.12
5 (23) MCOHS	14.69	16.04	5.94	6.29	8.30	3.49	8.40	8.06	5.31	3.91	8.35	3.97
5 (24) MCOHS	14.39	13.51	3.33	4.82	9.44	6.75	7.25	5.99	3.38	3.14	8.22	2.25
6 (25) CTN	13.57	13.12	8.07	4.60	8.09	3.32	9.18	4.71	5.51	3.93	7.38	5.09
6 (26) CTN	13.49	12.75	7.24	8.26	8.67	5.29	9.48	8.34	7.63	4.39	9.91	5.88

6 (27)													
CTN	18.39	10.88	7.19	3.08	7.71	2.86	9.74	5.70	4.90	3.01	9.37	4.71	
7 (28)							10.6						
CTSN	27.29	11.99	7.21	3.03	7.92	2.68	8	5.13	5.50	3.98	11.12	5.20	
7 (29)							10.8						
CTSN	28.60	12.48	7.60	2.94	9.24	3.00	1	5.63	4.69	2.47	11.33	4.33	
8 (30)							10.2						
OCTN	18.82	9.80	9.18	4.11	9.29	3.65	8	4.86	7.77	6.20	9.50	5.40	
8 (31)							10.5						
OCTN	20.38	20.32	8.66	7.81	8.87	4.71	1	6.63	10.56	7.47	10.38	5.72	
8 (32)							10.5						
OCTN	21.10	18.11	8.17	9.50	10.20	3.57	0	6.76	8.42	5.32	11.22	6.10	
8 (33)							10.5						
OCTN	21.92	21.23	7.31	7.43	8.55	2.60	4	4.96	7.10	5.42	12.03	6.20	
9 (34)													
D POT	12.30	12.64	8.15	10.47	7.47	5.17	7.75	6.61	11.08	8.57	8.52	7.95	
10 (35)													
OWT	--	--	--	--	--	--	--	--	--	--	--	--	--
10 (36)													
OWT	11.21	8.21	6.92	6.88	7.38	2.51	7.35	5.88	4.33	9.30	6.02	7.97	
10 (37)													
OWT	9.97	10.09	8.60	10.43	7.27	5.73	6.63	5.09	11.34	10.92	7.21	7.14	
11 (38)													
POWT	17.22	12.23	12.63	13.06	10.40	3.92	9.39	5.14	15.60	6.72	10.62	5.28	
12 (39)													
NST	8.48	8.28	7.47	10.33	7.79	5.18	7.01	4.47	12.66	12.83	8.31	5.83	
13 (40)													
GSE	8.85	7.59	6.60	8.94	7.99	6.56	6.81	5.51	14.52	16.28	8.83	6.05	

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