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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.

37 1. Introduction

38

39 Understanding how life is arranged on Earth has early occupied scientists such as Carolus
40 Linnaeus (1707-1778) and Georges-Louis Leclerc, Comte de Buffon (1707-1788) since the 18th
41 century. Partitioning the marine pelagic domain has proved to be quite difficult in comparison
42 to the terrestrial realm where demarcations are more apparent and access to the field easier
43 (Cox & Moore, 2000). Despite these difficulties, a number of partitions of the pelagic realm
44 have been proposed over the course of the 19th and 20th century. For instance, Mark Spalding
45 and colleagues listed the work of Forbes (1856), Ekman (1953), Hedgpeth (1957), Briggs (1974)
46 and Bailey (1998) (Spalding, Fox, Allen, Davidson, Ferdaña et al., 2007). Temperature
47 variability over large time scales explained well the partition of Briggs, who also considered
48 endemism (Briggs, 1974). More recently, classifications have been proposed to improve
49 ecosystem management. For instance, Large Marine Ecosystems (LMEs), implemented by
50 Sherman and colleagues, are large regions (i.e. $\geq 200,000$ km²) based on their (1) bathymetry,
51 (2) hydrography, (3) productivity and (4) trophically dependent populations (Sherman & Duda,
52 1999). Globally, a total of 66 LMEs has been proposed so far. LMEs were originally designed
53 to tackle environmental issues such as fisheries management and only concern large
54 continental shelves. Lately, Spalding and co-workers (Spalding et al., 2007) proposed an
55 expert-knowledge global system for coastal and shelf areas, termed the Marine Ecoregions of
56 the World (MEOW). This partitioning encompasses a nested system of 12 realms (i.e.
57 continent-sized areas with homogeneous geographical components and living organisms), 62
58 provinces (i.e. large ecosystems defined by the presence of distinct biocoenoses having a
59 certain level of cohesion over evolutionary time), and 232 ecoregions (i.e. areas having a
60 relatively homogeneous biocoenosis in comparison to adjacent zones). The MEOWs have
61 been implemented with the goal of directing future efforts in marine resource management
62 and biodiversity conservation (Spalding et al., 2007).

63

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

84 salinity), Reygondeau and co-workers (Reygondeau et al., 2013) applied a procedure based on
85 the Non-Parametric Probabilistic Ecological Niche model (Beaugrand, Lenoir, Ibanez & Manté,
86 2011) to propose a more dynamical partition of Longhurst's biogeochemical provinces. The
87 average demarcation of the provinces was in general in good agreement with those originally
88 proposed by Longhurst. Basing pelagic biogeography on a few biogeochemical parameters or
89 expert knowledge may lead to a too simplistic scheme because the pelagic environment and
90 composed of many species that integrate the multidimensionality of the environment.
91 Biogeographical partitions based on species distribution have also been proposed. Mary
92 Somerville (1780-1872) in her book about physical geography divided the marine ecosphere
93 into homozioc zones. Based on Mollusca, Edward Forbes (1815-1854) established nine
94 homozioc zones and related them mainly to marine isotherms. Developments of remote
95 sensing and large-scale ship-based surveys have allowed a better demarcation of the biomes
96 occupied by various taxonomic groups such as coccolithophores (Merico, Tyrrell, Brown,
97 Groom & Miller, 2003), N₂ fixers (Westberry & Siegel, 2006) and picocyanobacteria (Johnson,
98 Zinser, Coe, McNulty, Malcolm et al., 2006).

99

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

113

114

115 **2. Materials and methods**

116

117 **2.1. Physical data**

118

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

130

131 **2.2. Biological data**

132

133 The Continuous Plankton Recorder (CPR) Survey is a long-term, sub-surface marine plankton
134 monitoring programme consisting of a network of CPR transects towed monthly across the
135 major geographical regions of the North Atlantic. It has been operating in the North Sea since
136 1931 with some standard routes existing with a virtually unbroken monthly coverage back to
137 1946 (Batten, Clark, Flinkman, Hays, John et al., 2003; Reid, Colebrook, Matthews, Aiken,
138 Barnard et al., 2003). The CPR survey is recognised as the longest sustained and geographically
139 most extensive marine biological survey in the world. The dataset comprises a uniquely large
140 record of marine biodiversity covering ~1000 taxa over multi-decadal periods. The survey
141 determines the abundance and distribution of phytoplankton and zooplankton (including fish
142 larvae) in our oceans and shelf seas. Using ships of opportunity from ~30 different shipping
143 companies, it obtains samples at monthly intervals on ~50 trans-ocean routes. In this way the
144 survey autonomously collects biological and physical data from ships covering ~20,000 km of
145 the ocean per month, ranging from the Arctic to the Southern Ocean.

146

147 The CPR is a high-speed plankton recorder that is towed behind ‘ships of opportunity’ through
148 the surface layer of the ocean (~10 m depth) (Warner & Hays, 1994). Water passes through
149 the recorder and plankton are filtered by a slow-moving silk (mesh size 270 μm). A second
150 layer of silk covers the first and both are reeled into a tank containing 4% formaldehyde. Upon
151 returning to the laboratory, the silk is unwound and cut into sections corresponding to 10
152 nautical miles and approximately 3 m^3 of filtered sea water (Jonas, Walne, Beaugrand, Gregory
153 & Hays, 2004).

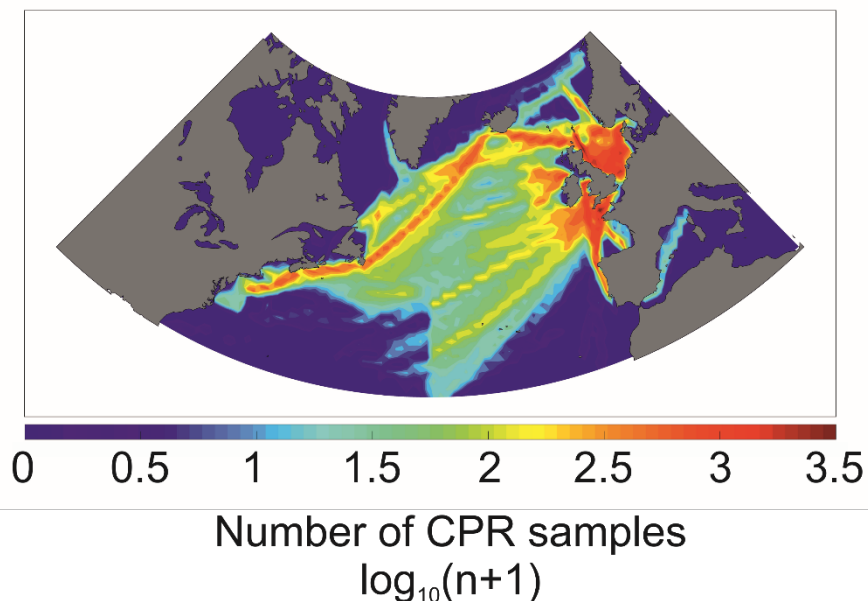
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155 There are four separate stages of analysis carried out on each CPR sample, with each focusing
156 on a different aspect of the plankton: (1) overall chlorophyll (the phytoplankton colour index;
157 PCI); (2) larger phytoplankton cells (phytoplankton); (3) smaller zooplankton (zooplankton
158 “traverse”); and (4) larger zooplankton (zooplankton “eyecount”). The phytoplankton colour
159 of each section of the CPR silk is evaluated and categorised according to four levels of
160 ‘greenness’ (green, pale green, very pale green and no colour) using a standard colour chart;
161 the numbers are given a numerical value as a measure of ‘Phytoplankton Colour Index’. Here

162 we focussed our analysis on phytoplankton cells, small and large zooplankton. Because we
163 worked at the species level, we did not use the colour index.

164
165 Phytoplankton cells are identified and recorded as either present or absent across 20
166 microscopic fields spanning each section of silk (representing $\sim 1/10,000$ of the filtering silk).
167 Due to the mesh size of CPR silks, many phytoplankton species are only semi-quantitatively
168 sampled owing to the small size of the organisms (Batten et al., 2003). There is therefore a
169 bias towards recording larger armoured flagellates and chain-forming diatoms and that
170 smaller species abundance estimates from cell counts are probably underestimated in relation
171 to other water sampling methods. However, the proportion of the population that is retained
172 by the CPR silk reflects the major changes in abundance, distribution and specific composition
173 (i.e. the percentage retention is roughly constant within each species even with very small-
174 celled species) (Edwards, Johns, Leterme, Svendsen & Richardson, 2006). Zooplankton analysis
175 is then carried out in two stages with small (< 2 mm) zooplankton identified and counted on-
176 silk (representing $\sim 1/50$ of the filtering silk) and larger (> 2 mm) zooplankton enumerated off-
177 silk (Warner & Hays, 1994). The collection and analysis of CPR samples have been carried out
178 using a consistent methodological approach, coupled with strict protocols and Quality
179 Assurance procedures since 1958, making the CPR survey the longest continuous dataset of
180 its kind in the world. Figure 1 shows the spatial distribution of the CPR samples used in this
181 study.

182



183
184

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

187

188 **2.3. Methods**

189 We performed three partitions of the North Atlantic Ocean: (1) habitat partition at a $0.08^\circ \times$
190 0.08° spatial resolution, (2) biological (CPR-based) partitions at a $2^\circ \times 2^\circ$ (areas where CPR
191 spatial coverage was lower than average) and at a $0.5 \times 0.5^\circ$ spatial resolution (regions were
192 spatial coverage was higher than average). Finally, (3) we combined the three partitions to

193 build a synthetic map to propose an ecological partition of the North Atlantic Ocean and its
 194 adjacent seas.

195

196 **2.3.1. Habitat classification**

197

198 We first partitioned the North Atlantic Ocean and its adjacent seas using an empirical
 199 (threshold-based) procedure based on SST, bathymetry, light at the seabed, salinity and
 200 current velocity at a high spatial resolution (0.08° latitude x 0.08° longitude). This partition
 201 performed at a relatively high spatial resolution was intended to complement the biological
 202 partition based on CPR data. The habitat partition was carried out hierarchically and led to 15
 203 ecoregions (Table 1). A number of thresholds were chosen based on expert knowledge.
 204 Salinity and current velocity thresholds were based either on the third quartile (Q3) or the
 205 ninth decile (D9) of all marine data. Oceanic areas were regions below 1000m, shelf-edges
 206 between 1000 and 200m and continental shelves above 200m. Light at the seabed (i.e. light
 207 at the seabed higher than 0 E.m⁻².yr⁻¹) allowed us to distinguish areas where light can or cannot
 208 reach the seabed. In oceanic areas where salinity was higher than Q3, we distinguished
 209 different pelagic habitats using the following isotherms: (1) 7-10°C, (2) 10-13°C, (3) 13-16°C,
 210 (4) 16-19°C, (5) 19-22°C, and (6) 22-25°C (Table 1). Finally, oceanic areas with current velocity
 211 above D9 enabled the identification of the average location of the Gulf Stream. Table 1
 212 summarizes the choice of the thresholds made to perform the classification and the resulting
 213 ecological characteristics of each ecoregion. This partition is shown in Figure 2.

214

215 **Table 1.** Categories of ecogeographical variables used to classify the North Atlantic Ocean and its
 216 adjacent seas into 15 ecoregions. SIC: Sea-Ice Concentration. A hyphen denotes the absence of
 217 consideration of an ecogeographical variable. An ecoregion is simply a region with similar ecological
 218 conditions with respect to the factors used to make the classification. The threshold used for salinity
 219 was the third quartile and the threshold used for current velocity was the 9th decile based on all marine
 220 areas of the world.

221

Ecozone	Higher bathymetry	lower bathymetry	SIC >0	Light the 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

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2.3.2. Biological partition

We biologically partitioned the North Atlantic Ocean and its adjacent seas using data collected from the CPR survey (Reid et al., 2003). Specifically, we applied the procedure on six taxonomic groups: diatoms (59 species or taxa; Supplementary Table 1), *Ceratium* dinoflagellates (41 species; Supplementary Table 2), small copepods (recorded in traverse; 27 species or taxa; Supplementary Table 3), small zooplankton (recorded in traverse; 15 species or taxa; Supplementary Table 4), large copepods (recorded in eyecount; 73 species; Supplementary Table 5) and large zooplankton other than copepods and including fish eggs and larvae (recorded in eyecount; 23 species or taxa; Supplementary Table 6). Therefore, a total of 238 species or taxa were considered for the period 1946-2015 (a total of 254,410 CPR samples), which represented a total of 60,549,580 data points. We partitioned the North Atlantic Ocean and its adjacent seas using two spatial resolutions: (1) a grid of 2° latitude x 2° longitude that enabled a large coverage into the North Atlantic Ocean despite the lower CPR sampling coverage and a grid of 0.5° x 0.5° from 40.5°N to 65.5°N and from 80.5°W to 9.5°E that enables a finer partition in seas around the British Isles where CPR sampling is the densest.

For the two biological partitions, we first estimated the species richness of each taxonomic group on two spatial grids: 2° latitude x 2° longitude and 0.5° latitude x 0.5° longitude. Data were analysed in the geographical area ranging from 40.5°N to 65.5°N and from 80.5°W to 9.5°E for each two-month period using CPR data from 1946 to 2015, using an approach similar to what was applied to map copepod biodiversity (Beaugrand, Ibañez & Lindley, 2001). For each geographical cell and two-month period, we calculated the species richness providing that the number of samples was higher than 15 (for the 2° x 2° partition) or 5 (for the 0.5° x 0.5° partition), thresholds (>5) that guaranty a correct estimation of the diversity of a taxonomic group from the CPR survey (Beaugrand & Edwards, 2001). In large-scale studies, indices weighted towards species richness are more useful for detecting differences between sites than indices emphasising the evenness component of biodiversity (Magurran, 1988). Even though the calculation of species richness is sensitive to sample size and leads to systematic underestimation of copepod biodiversity, it is still a satisfactory estimator that can be used for comparisons between sites with low spatial resolution (Beaugrand & Edwards, 2001). We used a first-order jackknife procedure to increase the robustness of the species or taxonomic richness. To calculate the first-order jackknife, estimator D and pseudo-values p_i that excluded samples i from each geographical cell were computed as follows (Beaugrand, Edwards & Legendre, 2010):

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

where n is the number of CPR samples in the geographical cell for a given two-month period, p^0 is the estimate of the species/taxonomic richness based on all CPR samples, and $p_i^{(-i)}$ is the value of the biodiversity index based on all samples but i . There were as many pseudo-values as samples in the geographical cell for a given two-month period. The estimated taxonomic richness (or species richness) D was the average of all pseudo-values:

267

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

268 For the first partition (2° latitude x 2° longitude), matrices of (jackknifed) taxonomic richness
 269 of 13 latitudes x 46 longitudes = 598 geographical squares x six two-month periods were built
 270 for each taxonomic group. Six matrices were therefore prepared: **Matrix A** 598 geographical
 271 cells x 6 two-month periods for diatoms, **Matrix B** 598 geographical cells x 6 two-month
 272 periods for the genus *Ceratium*, **Matrix C** 598 geographical cells x 6 two-month periods for
 273 small copepods, **Matrix D** 598 geographical cells x 6 two-month periods for small zooplankton
 274 other than copepods, **Matrix E** 598 geographical cells x 6 two-month periods for large
 275 copepods, and **Matrix F** 598 geographical cells x 6 two-month periods for large zooplankton
 276 other than copepods.

277

278 For the second partition (0.5° latitude x 0.5° longitude), matrices of (jackknifed) taxonomic
 279 richness of 51 latitudes x 181 longitudes = 9231 geographical squares x 6 two-month periods
 280 were built for each taxonomic group. Six matrices were therefore prepared: **Matrix A*** 9231
 281 geographical cells x 6 two-month periods for diatoms, **Matrix B*** 9231 geographical cells x 6
 282 two-month periods for the genus *Ceratium*, **Matrix C*** 9231 geographical cells x 6 two-month
 283 periods for small copepods, **Matrix D*** 9231 geographical cells x 6 two-month periods for
 284 small zooplankton other than copepods, **Matrix E*** 9231 geographical cells x 6 two-month
 285 periods for large copepods, and **Matrix F*** 9231 geographical cells x 6 two-month periods for
 286 large zooplankton other than copepods.

287

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

295

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

296

297

298 where q is the number of geographical cells (598 or 9231) and r is the number of two-month
 299 periods (6). An annual average of the biodiversity of the six groups was calculated (Figure 3).

300

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

308

309 We then calculated two squared matrices $K_{(598,598)}$ and $K^*_{(9231,9231)}$ using the Euclidean distance
 310 and chose an agglomerative hierarchical clustering technique using average linkage, which

311 was a good compromise between the two extreme single and complete clustering techniques
312 (Legendre & Legendre, 1998) (Figure 5). For each partition, we examined the first 8 cut-off
313 levels of the dendrogram (Figure 6). Groups composed of less than three geographical cells
314 were not considered.

315

316 We smoothed the partitions (2° x 2° and 0.5° x 0.5°) by keeping a cell group only when it was
317 composed of five adjacent geographical cells out of the nine possible (i.e. the target cell and
318 all 8 adjacent geographical cells). This procedure smoothed slightly the final partitions (Figures
319 7A and 8A).

320

321

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

327

$$328 \quad h_{i,j}=(100 (v-1))/w-1 \quad (4)$$

329

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

334

335 **2.3.3. Ecological partition**

336

337 We then built a synthetic partition by designing the numerical procedure hereafter. We
338 started our procedure using the biological partition based on a 0.5° x 0.5° spatial resolution.
339 We removed groups for which it was not possible to calculate an index of heterogeneity (i.e.
340 six groups) and merged small groups that were difficult to understand from expert knowledge
341 because they lacked spatial contiguity (i.e. three groups). A total of six groups remained
342 (Supplementary Figure 1A). Then, the biological partition at 2°x 2° spatial resolution was
343 superimposed to the 0.5° x 0.5° biological partition in areas where no group existed. At that
344 stage, we had a total of nine groups (Supplementary Figure 1B). Finally, we added some groups
345 originating from the habitat partition to divide the polar biome (*sensu* Longhurst (Longhurst,
346 1998); four more groups) into provinces and the westerly-wind biomes (*sensu* Longhurst
347 (Longhurst, 1998); one more group). The final partition had therefore a total of 14 groups
348 (Supplementary Figure 1C). The final partition is shown in Figure 9. We described each group
349 as a function of their biodiversity, seasonal patterns in species or taxonomic richness and
350 species composition using maps of each of the 238 species considered in this study. Although
351 it was not possible to show all maps in the present study, they are available in a CPR atlas
352 published in 2004 (Barnard, Batten, Beaugrand, Buckland, Conway et al., 2004; Beaugrand,
353 2004).

354

355 **2.4. Terminology**

356 In this section, we define a few key terms used in this paper:

357

358 **2.4.1. Pelagic Habitats (PHs)**

359 The Pelagic Habitats (PHs), identified here using physico-chemical variables (e.g. bathymetry,
360 light at the seabed, salinity, temperature, SIC) are merely an area where environmental
361 conditions are relatively homogeneous with respect to the variables that were used.

362

363 **2.4.2. Biome and Realm**

364 A biome is frequently defined as a primary ecological compartment in equilibrium with
365 climate. In the terrestrial ecosphere, biomes are clearly related to the climatic regime
366 (Whittaker, 1975). The word has also been frequently used in marine biogeography. For
367 example, Longhurst (Longhurst, 2007) distinguished four biomes on a global scale: (1) the
368 Polar Biome, (2) the Westerlies Biome, (3) the Trade-Winds Biome and (4) the continental
369 shelves Biome. Note however that the latter biome is fundamentally distinct from the first
370 three as it is defined by bathymetry (stable-biotope components *sensu* Van der Spoel (van der
371 Spoel, 1994)) and not climate. Therefore, it may be more appropriate to term it a realm than
372 a biome, at least in the spatial domain covered by our study. A realm is frequently defined as
373 the broadest ecological unit in either the marine or the terrestrial ecosphere. We therefore
374 expected to identify an oceanic and a neritic realm in the area covered by the CPR survey; the
375 two realms were recently identified in a recent work based on the analysis of the distribution
376 of 65,000 species of marine animals and plants (Costello, Tsai, Wong, Cheung, Basher et al.,
377 2017).

378

379 **2.4.3. Province**

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

387

388 **2.4.4. Ecoregion**

389 In this study, ecoregions are defined according to Spalding and colleagues (Spalding et al.,
390 2007): *“areas of relatively homogeneous species composition, clearly distinct from adjacent*
391 *systems. The species composition is likely to be determined by the predominance of a small*
392 *number of ecosystems and/or a distinct suite of oceanographic or topographic features”*. For
393 the authors, endemism was not a key determinant in the establishment of the Marine
394 Ecoregions of the World (MEOW).

395

396 **2.4.5. Ecological Units (EUs)**

397 Our biological classification led to Ecological Units (EUs). An EU is a unit having a relatively
398 homogeneous environmental regime or being characterised by similar levels and seasonal
399 variability in biodiversity (i.e. species richness) (Supplementary Tables 1-6). Abiotic and biotic
400 characteristics of each EU were examined in Tables 2 and 4. An EU may not be represented by
401 a single set of interconnected geographical cells, leading to several ecoregions, which can still
402 be distinguished by their species composition (Figure 9). Therefore, we also provided a
403 summary of the abiotic and biotic characteristics of each ecoregion (Figure 11, Tables 3 and
404 5).

405

406 **2.5. Statistics in the ecological units and ecoregions**

407

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

414 Average and the seasonal amplitude of the biodiversity of the 6 taxonomic groups were also
415 summarized in Table 3 for ecological units and Supplementary Table 8 for ecoregions.

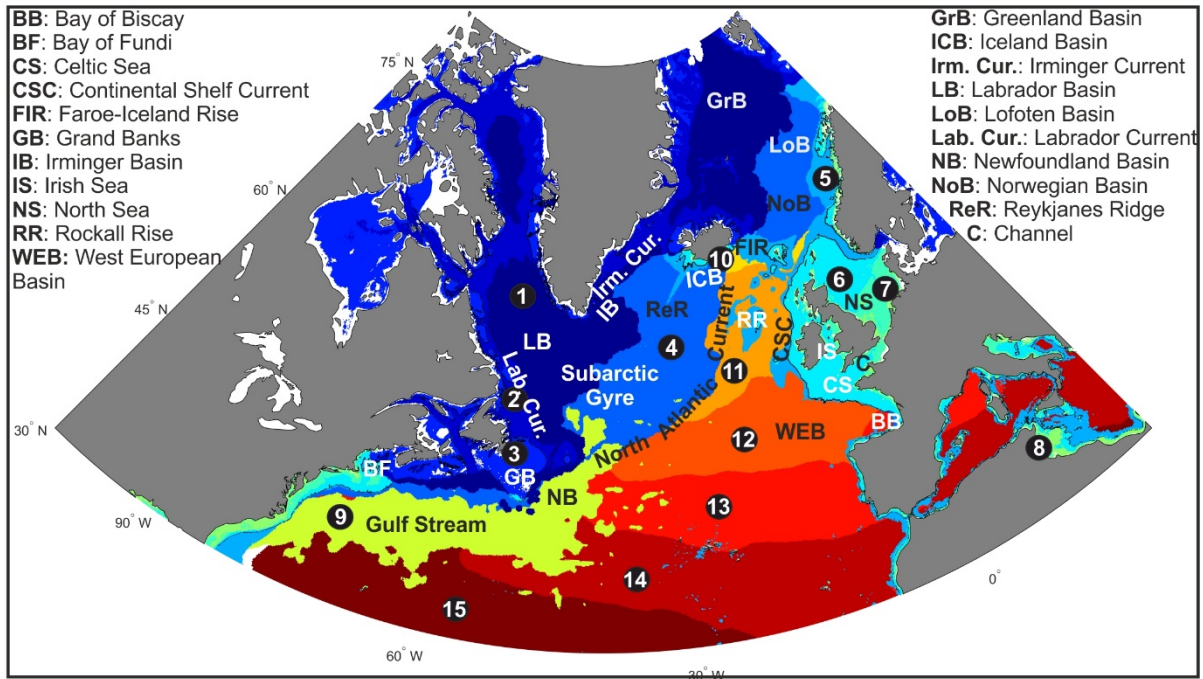
416 **3. Results**

417

418 **3.1. Habitat partition**

419

420 The first partition, resulting from a simple procedure based on expert knowledge, emphasizes
421 15 pelagic habitats (Figure 2 and Table 1). The first three Pelagic Habitats (PHs thereafter) may
422 have Sea-Ice Concentration above 0 at least a part of the year. The first PH is the oceanic ice-
423 influenced PH (>200m); it covers the Labrador Basin and part of the Irminger Basin (Figure 2).
424 The second is the shelf-edges (200-1000m) ice-influenced PH. In the Labrador Basin, it
425 channels the path of the Labrador Current that flows southwards. The third is the neritic (0-
426 200m) Continental Shelves ice-influenced PH. In particular, it covers the Newfoundland
427 Continental Shelf (e.g. Grand Banks). In the Atlantic area covered by the CPR survey, the first
428 three PHs are delimited by the Subarctic Gyre. Salinity in those three PHs is lower in
429 comparison to oceanic regions located eastwards and southwards. The fourth PH, the Oceanic
430 Subarctic PH, has no Sea-Ice Concentration (Figure 2). The fifth PH is the shelf-edges PH, which
431 is found in all regions where sea-ice is absent (e.g. western part of Norway and European Shelf-
432 edges). The sixth and seventh PHs are continental shelves where sea-ice is absent and where
433 light is limited (in particular, light does not reach the benthos). The deep (50-200m) and
434 shallow Continental Shelves pelagic habitat are well represented in the North Sea north south
435 of the Flamborough Front. The eighth PH, the continental shelves (light) pelagic habitat, is
436 marginally represented in the area under investigation. Some coastal areas of the
437 Mediterranean Sea belong to this PH. The ninth PH, the Gulf Stream PH, has current velocity
438 above $0.62 \text{ m}\cdot\text{s}^{-1}$. In oceanic areas characterized by a high salinity (higher than 35.23 PSS), we
439 distinguished 6 further PHs as function of their thermal regime: (10) oceanic subpolar PH
440 (mean SST=7-10°C), (11) oceanic cold-temperate PH (mean SST=10-13°C), (12) oceanic
441 temperate PH (mean SST=13-16°C), (13) oceanic warm-temperate PH (mean SST=16-19°C),
442 (14) oceanic subtropical (north) PH (mean SST=19-22°C), and (15) oceanic subtropical (south)
443 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 |

444
445

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

449

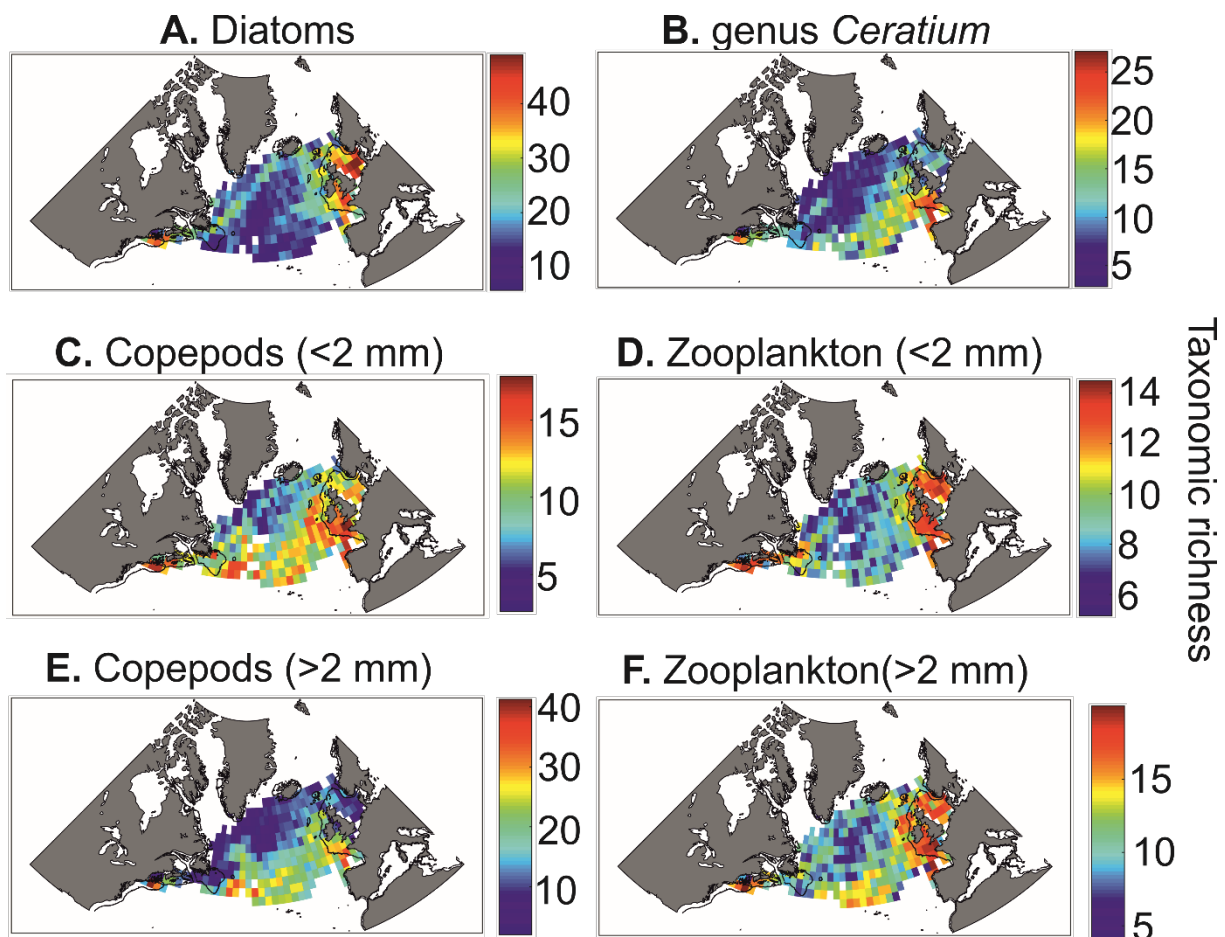
450

451 3.2. Biological partition at 2° x 2° spatial resolution

452

453 We first assessed the biodiversity of all six taxonomic groups (Figure 3). The taxonomic
454 richness of diatoms (Supplementary Table 1) was high around the British Isles and especially
455 south of the Flamborough Front, the Celtic Sea and the western part of the Channel (Figure
456 3A). On the western part of the North Atlantic, biodiversity was high over Georges Bank, the
457 Nova Scotian Shelf and to a lesser extent north of the Newfoundland Shelf. Oceanic areas had
458 in general low diatom taxonomic richness, with the exception of the oceanic cold-temperate
459 and the temperate PHs along the Faroe-Iceland Rise, the European shelf-edge and the
460 northern part of oceanic subarctic pelagic habitat, especially over the Reykjanes Ridge (Figures
461 2 and 3).

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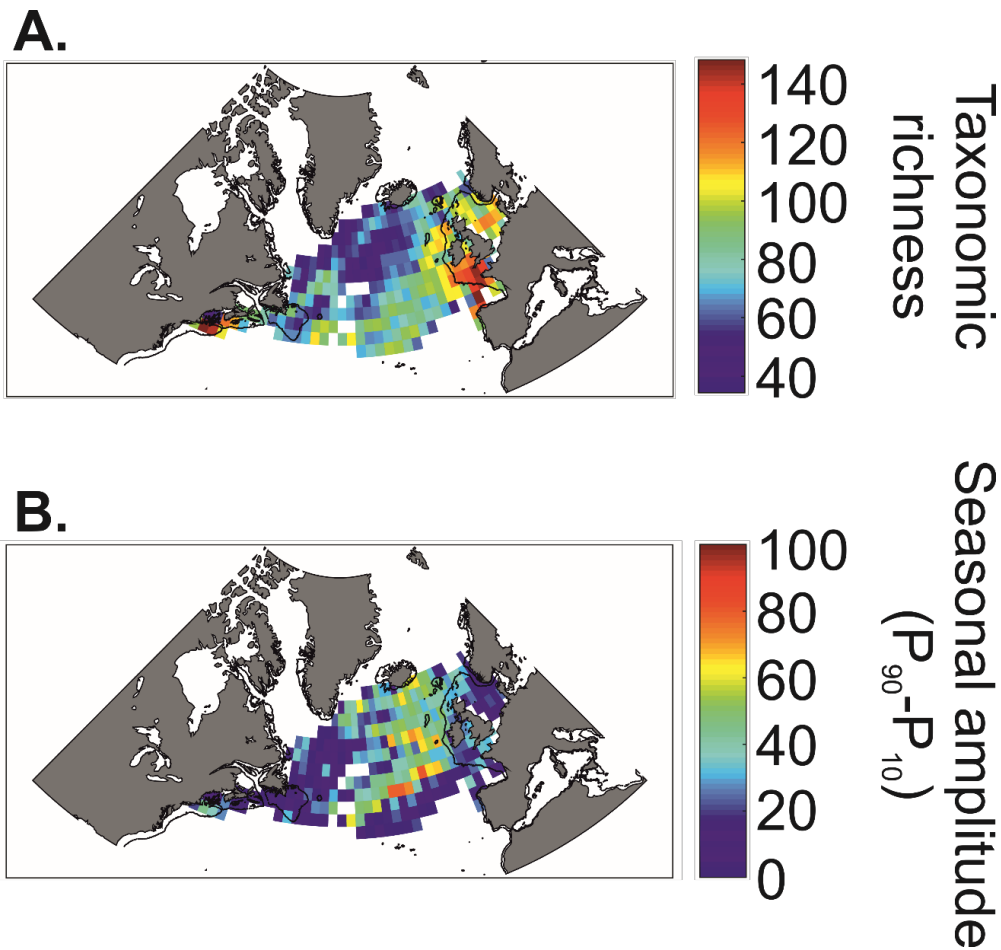
Figure 3. Mean taxonomic richness of six taxonomic groups sampled by the CPR survey calculated on a $2^\circ \times 2^\circ$ spatial resolution. The taxonomic richness was assessed using a first-order Jackknife coefficient for each 2-month period. **A.** Diatom taxonomic richness. **B.** Dinoflagellates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

471

472 The species richness of the genus *Ceratium* (Supplementary Table 2) was high in oceanic areas
473 south of the Oceanic Polar Front (Dietrich, 1964) and especially over the Bay of Biscay. Species
474 richness was also high in some neritic regions such as the Celtic Sea and Georges Bank (Figure
475 3B). Copepods (Supplementary Tables 3 and 5) also exhibited a similar pattern, although the
476 biodiversity difference between the polar and the westerlies biomes was less acute for small
477 copepods (Figures 3C and 3E). The taxonomic richness of small copepods was higher along the
478 European Shelf-edge in both oceanic and neritic regions, south of the Flamborough Front in
479 the North Sea and in Georges Bank and part of the Nova Scotian Shelf (Figure 3C). Taxonomic
480 richness was higher in the northern part of the Gulf Stream PH for all copepods. Large
481 copepods did not show a high taxonomic richness south of the Flamborough Front in the North
482 Sea and the biodiversity was less elevated and more restricted along the European Shelf-edge.
483 The taxonomic richness of small zooplankton (Supplementary Table 4) was similar to diatoms
484 (Figure 3A *versus* Figure 3D), although it was substantially higher in the Newfoundland Shelf
485 for zooplankton (Figure 3D). Large zooplankton (Supplementary Table 6) exhibited a pattern
486 closer to small zooplankton because both groups are composed of meroplanktonic species
487 (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.

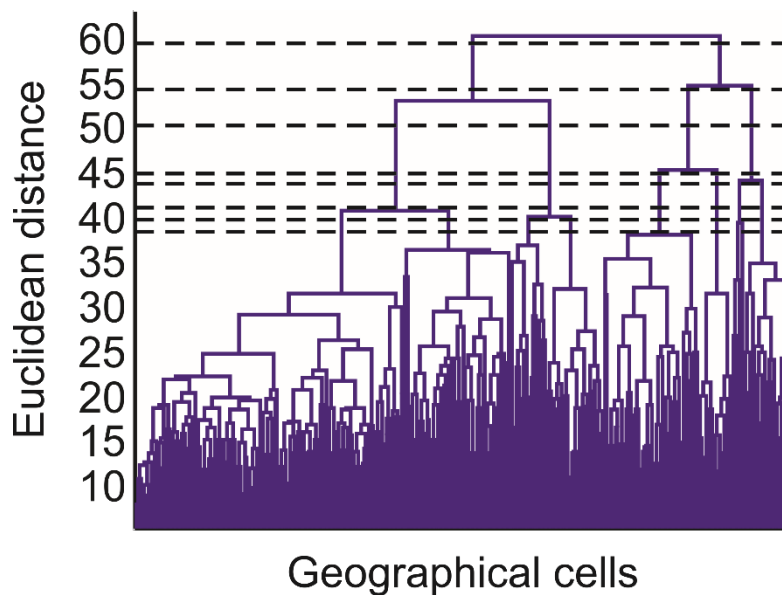


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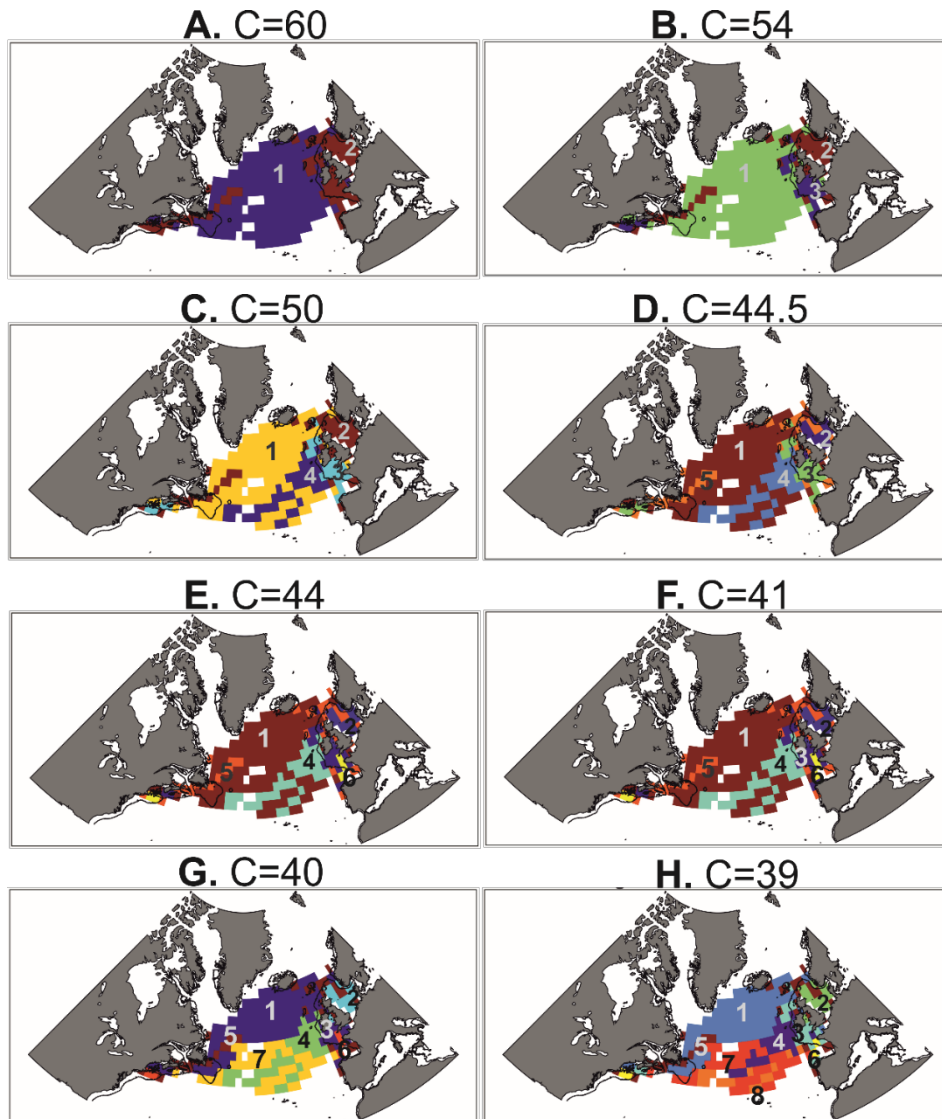
Figure 4. A. Mean total taxonomic richness of all combined taxonomic groups and **B.** seasonal amplitude of total species richness assessed here by using the interdecile ($P_{90}-P_{10}$) range. The taxonomic richness was assessed using a first-order Jackknife coefficient for each two-month period.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

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 European Continental Shelves, including the Bay of Biscay (Figure 6B). The third cut-off level

513 enable the separation of an oceanic region southwest to the Irish Sea, which is characterized
 514 by a pronounced seasonality in biodiversity and high phytoplankton and small copepod
 515 biodiversity (Figure 6C, see also Figure 4B). The fourth cut-off enabled the separation of small
 516 groups that enable the identification of an area north of the North Sea and along the Faroe-
 517 Iceland ridge (Figure 6D). Some cells were also identified over Georges Bank and the Bay of
 518 Biscay but the biological group lacked spatial contiguity. The fifth cut-off level allowed the
 519 identification of a group gathering together the Georges Bank and the Bay of Biscay (Figure
 520 6E). Although the sixth cut-off level did not allow the clear identification of a relevant
 521 biological group (Figure 6F), the next cut-off level identified an area belonging to oceanic
 522 subtropical and warm-temperate PHs and regions influenced by the Atlantic Meridional
 523 Overturning Circulation (AMOC) (Figure 6G). This cut-off level emphasized the role of the
 524 Oceanic Polar Front, which delineates the polar from the Westerlies biome. The last cut-off
 525 level (Figure 6H), as well as others (not represented here) did not provide any further relevant
 526 information.



527
 528 **Figure 5.** Dendrogram originating from the application of an agglomerative hierarchical average linkage
 529 algorithm performed on an Euclidean distance matrix (Matrix K; see Methods). The different cut-off
 530 levels are indicated by a dashed black line (see **Figure 6**).
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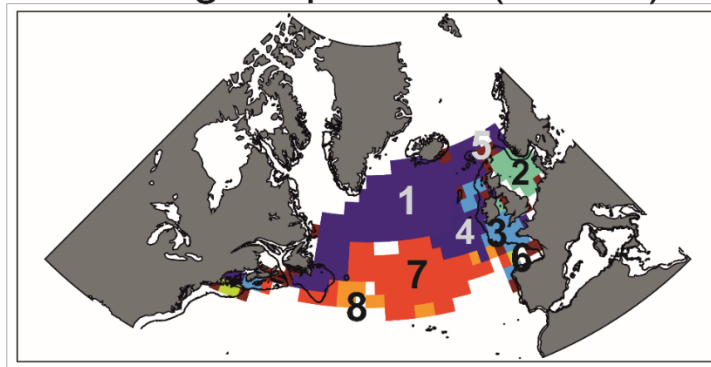
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535 **Figure 6.** Hierarchical biological partition of the North Atlantic Ocean and its adjacent seas at 2°x2°
536 spatial resolution for different cut-off levels of the dendrogram (see **Figure 5**). **A.** C=60, **B.** C=54, **C.**
537 C=50, **D.** C=44.5, **E.** C=44, **F.** C=41, **G.** C=40, and **H.** C=39.

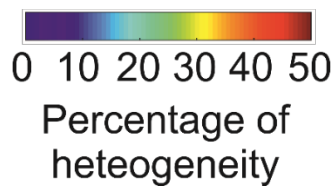
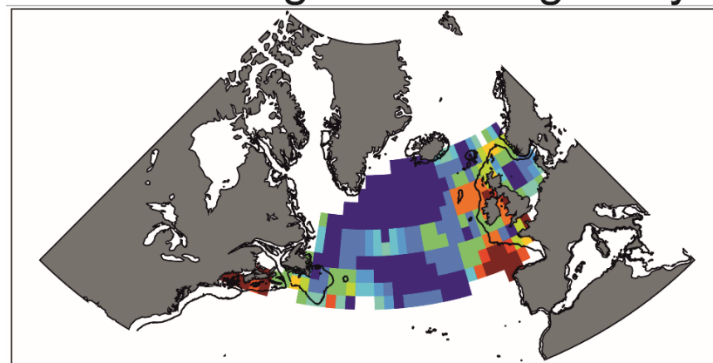
538

539 After smoothing and elimination of small groups (see Methods), the final biological partition
540 included eight biological groups, two (group 5 in the northern part of the North Sea and 6 in
541 the Bay of Biscay) of which being restricted spatially (Figure 7A). Group 1 represented in large
542 part the polar biome and their ice-influenced, subarctic and cold-temperate PHs; Group 2
543 characterized the North Sea, Group 3 denoted the Celtic Sea and some areas over the
544 European Shelf-edge, and a negligible part of the Nova Scotian Shelf; Group 4 represented an
545 oceanic area characterized by a high biodiversity south and west of the Irish Sea; Group 7 the
546 oceanic temperate and warm-temperate PHs and Group 8 the northern edge of the Gulf
547 Stream PH (Figure 7A). We calculated an index to reveal the presence of pronounced spatial
548 heterogeneity or ecotones (Figure 7B). The index was highest over the Bay of Biscay and the
549 Bay of Fundi, Georges Bank, Nova Scotian Shelf and to a lesser extent an area located to the
550 north-west of Ireland. The index was also higher between the polar and westerlies biomes
551 along the Oceanic Polar Front, the Gulf Stream PH and areas north of the North Sea and along
552 the Faroe-Iceland Rise (Figure 7B).

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



B. Percentage of heterogeneity



553

554

555 **Figure 7.** Biological partition of the North Atlantic Ocean and its adjacent seas at $2^\circ \times 2^\circ$ spatial
556 resolution. **A.** Partition. **B.** Index of spatial heterogeneity of the partition. This index indicates the
557 percentage of different groups around a given node. Each percentage value integrates 9 geographical
558 cells (see Methods).

559

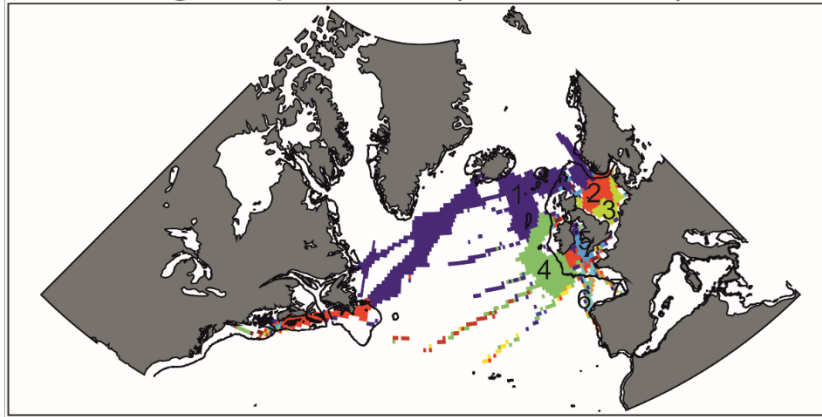
560 3.3. Biological partition at $0.5^\circ \times 0.5^\circ$ spatial resolution

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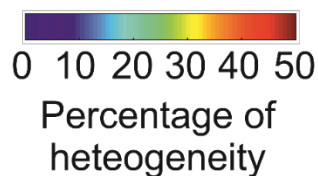
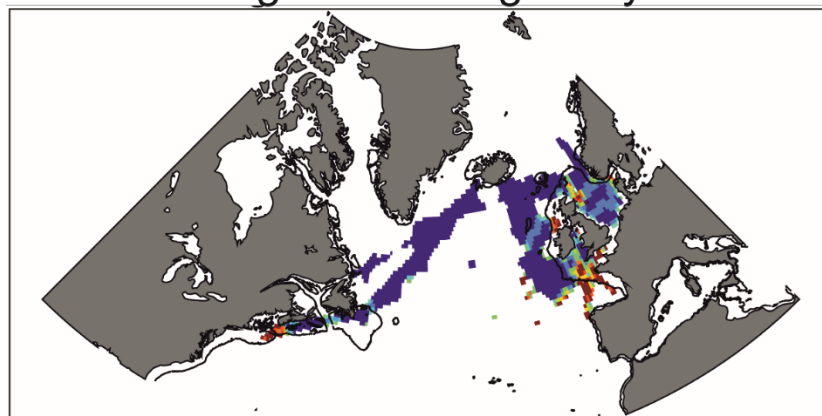
562 The same procedure was applied to identify biological groups at a $0.5^\circ \times 0.5^\circ$ spatial resolution.
563 We only show the final partition here as the procedure was similar to the $2^\circ \times 2^\circ$ division
564 (Figure 8). Fifteen biological groups were detected. Here also, some groups were only
565 composed of a few geographical cells, which exhibited low spatial contiguity (Figure 8A). After
566 smoothing and elimination of under-represented groups (see Methods), we retained 8
567 biological groups. Group 1 characterised the polar biome and the associated ice-influenced,
568 subarctic and cold-temperate PHs (see Figure 2). Some geographical cells penetrated to the
569 northern part of the North Sea. Although the previous partition at $2^\circ \times 2^\circ$ spatial resolution
570 identified only one biological group in the North Sea, the finer-scale partition revealed three
571 ecoregions: the central part of the North Sea (group 2) and an area south of the Flamborough
572 Front (group 3). The second group also occurred in the northwestern part of the Celtic Sea and
573 along the Nova Scotian Shelf, the shallow area of Newfoundland Shelf, stopping sharply at the
574 shelf-edge (Figure 8A). A fourth group was detected to the west of the British Isles; this group

575 was similar to the group identified at 2° x 2° spatial resolution (group 4; see Figure 7A). The
576 fifth group identified the north-eastern part of the Celtic Sea (Figure 7A). Some isolated
577 geographical cells also occurred in different places. The sixth and seventh groups were located
578 mainly in the western and eastern part of the Bay of Biscay, respectively (Figure 8A).
579

A. Biological partition (0.5° x 0.5°)



B. Percentage of heterogeneity

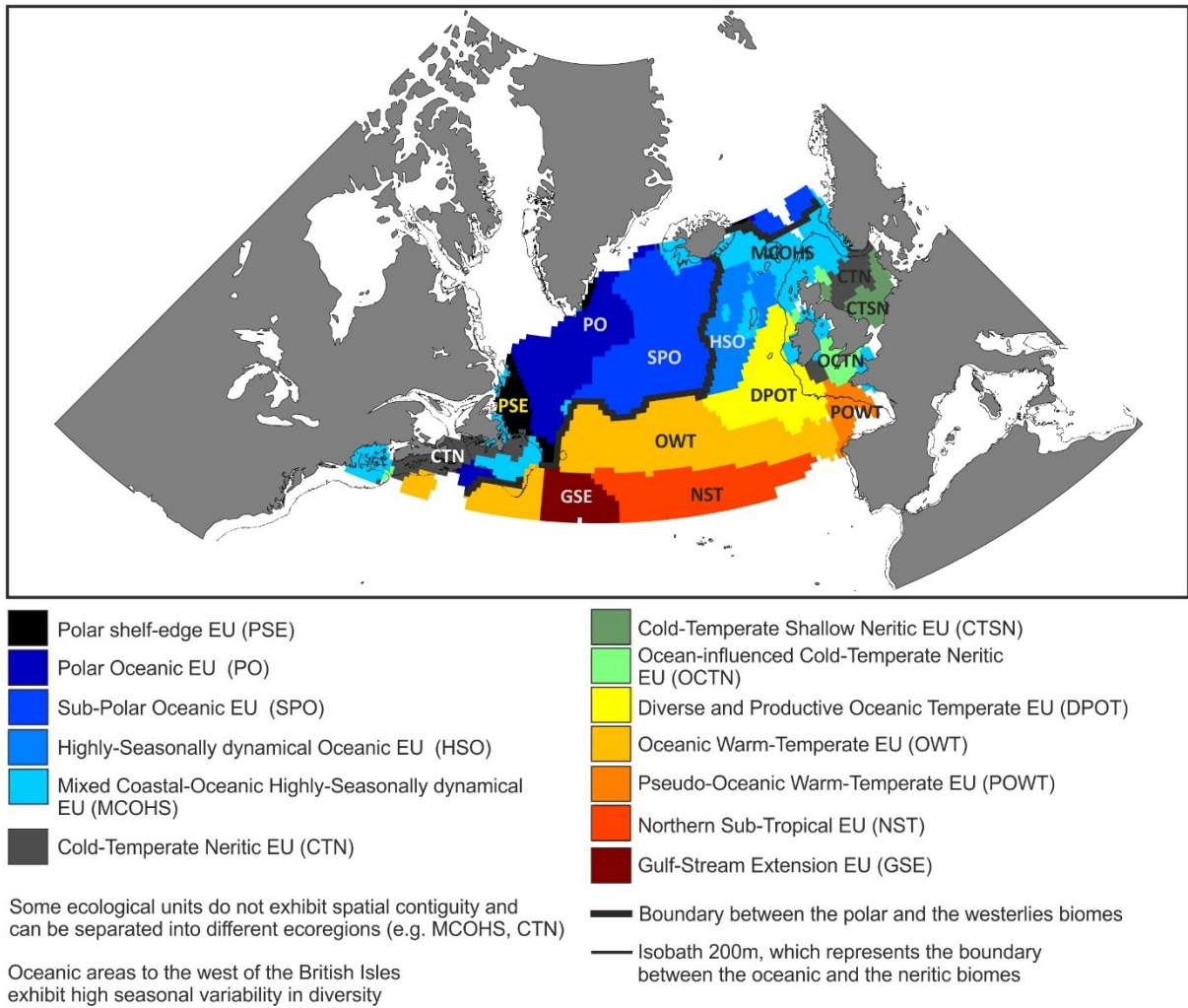


580
581 **Figure 8.** Biological partition of the North Atlantic Ocean and its adjacent seas at 0.5° x 0.5° spatial
582 resolution. **A.** Partition. **B.** Index of spatial heterogeneity of the partition. This index indicates the
583 percentage of different groups around a given node. Each percentage value integrates 9 geographical
584 cells (i.e. the target and its 8 adjacent cells). All intermediate results include figures similar to **Figures**
585 **3-7** (see Methods).
586

587 588 **3.4. Ecological partition**

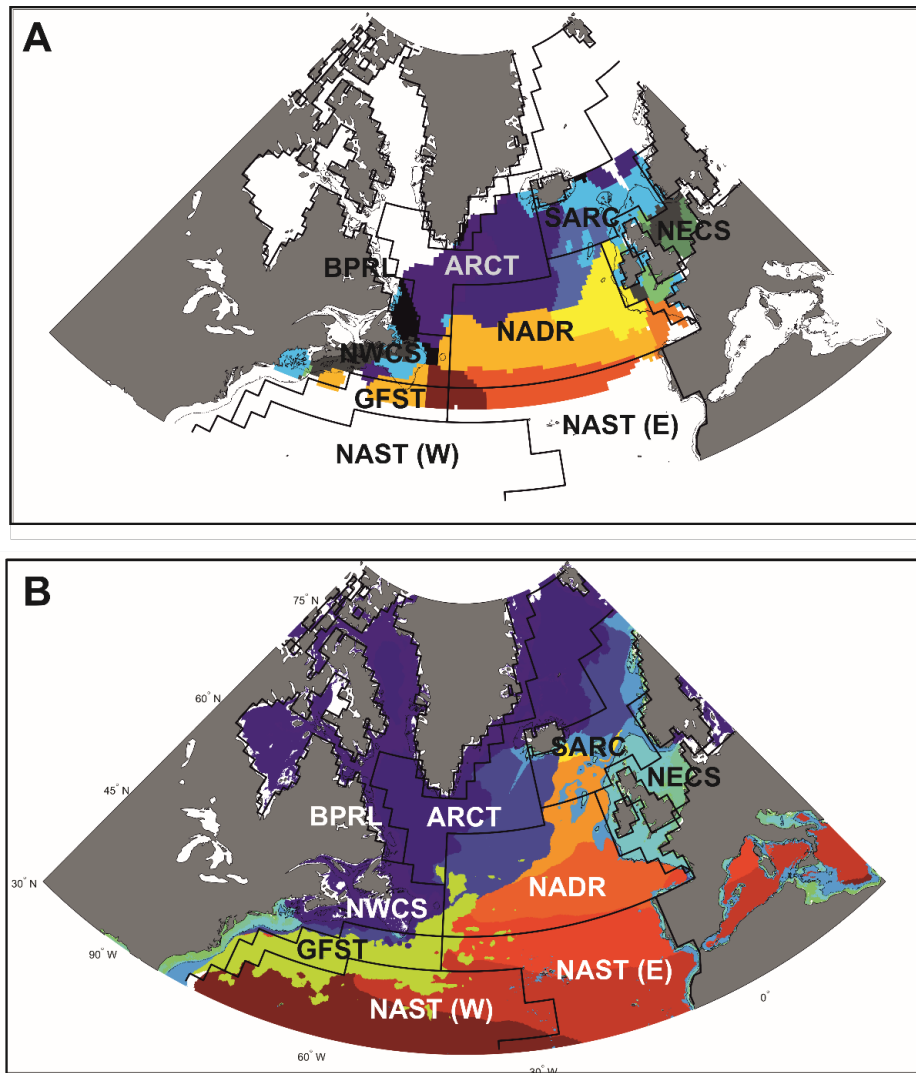
589
590 The final ecological partition was mainly based on the biological partition performed at the
591 0.5° x 0.5° spatial resolution for neritic regions (Figure 8) and mostly on the biological partition
592 made at 2° x 2° for oceanic regions (Figure 7). We further divided some ecological units by
593 using the PHs identified using some key ecogeographic variables (see Figure 2). We used the

594 term Ecological Unit (EU) because the same unit may be represented in different regions; we
 595 then divide a given EU into ecoregions when it is relevant (see the section terminology in
 596 Methods). As in the PH partition, we frequently refer to the Longhurst's classification of
 597 biomes and provinces (Longhurst, 1998; Longhurst, 2007).
 598



599 EU: Ecological Unit
 600
 601 **Figure 9.** Ecological partition of the North Atlantic Ocean and its adjacent seas. The partition results
 602 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°
 603 spatial resolutions. Abiotic and biotic properties are shown in Tables 2 and 4.
 604

605 The final ecological partition we propose is made of 13 EUs (Figure 9). Each EU has its own
 606 biodiversity (Figures 3-4), seasonal biodiversity patterns (Figure 4B) and environmental
 607 conditions (Figure 2). Widespread EUs could be further divided and some are composed of
 608 different ecoregions (Figure 9; e.g. MCOHS and CTN). Although their location did not match
 609 with our partition, the three Longhurst's biomes were identified: (1) the Westerlies, (2) the
 610 Polar biomes and the Continental Shelves biomes (Note that Longhurst termed originally this
 611 last biome a coastal biome (Longhurst, 1998)). Our EUs or HPs did not correspond to
 612 Longhurst's provinces (Figure 10), with the exception of the Gulf Stream PH and EU (Figures
 613 2, 9 and 10).
 614



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617 **Figure 10.** Final ecological partition (A) and habitat partition (B) with the boundaries of the Longhurst's
618 provinces (Longhurst, 1998) (black lines). **Coastal biomes.** NWCS: North West Atlantic Shelves
619 province, NECS: North East Atlantic Shelves province. **Westerlies biomes.** NAST (W): North Atlantic
620 Subtropical Gyral Province (West), NAST (E): North Atlantic Subtropical Gyral Province (East), GFST:
621 Gulf Stream Province, NADR: North Atlantic Drift Province. **Polar biomes.** SARC: Atlantic Subarctic
622 Province, ARCT: Atlantic Arctic Province, BPRL: Boreal Polar Province.

623

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

625

626 **Table 2. Main abiotic properties of the ecological units.** EU: Ecological Unit. SST: mean Sea Surface
627 Temperature ($^{\circ}\text{C}$). S: mean salinity (PSS). Cur: mean surface current ($\text{m}\cdot\text{s}^{-1}$). N: mean nitrate
628 concentration ($\text{mol}\cdot\text{m}^{-3}$). P: mean phosphate concentration ($\text{mol}\cdot\text{m}^{-3}$). Sil: mean silicate concentration
629 ($\text{mol}\cdot\text{m}^{-3}$). PAR: mean photosynthetically active radiation ($\text{E}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$). C: mean chlorophyll
630 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
631 (m). P5: the 5th percentile. P50: the median. P95: the 95th percentile. See text for the meaning of the
632 ecological unit acronyms. See Figure 9 for the spatial distribution of EUs and Figure 11 for the
633 ecoregions (1-40).

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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)

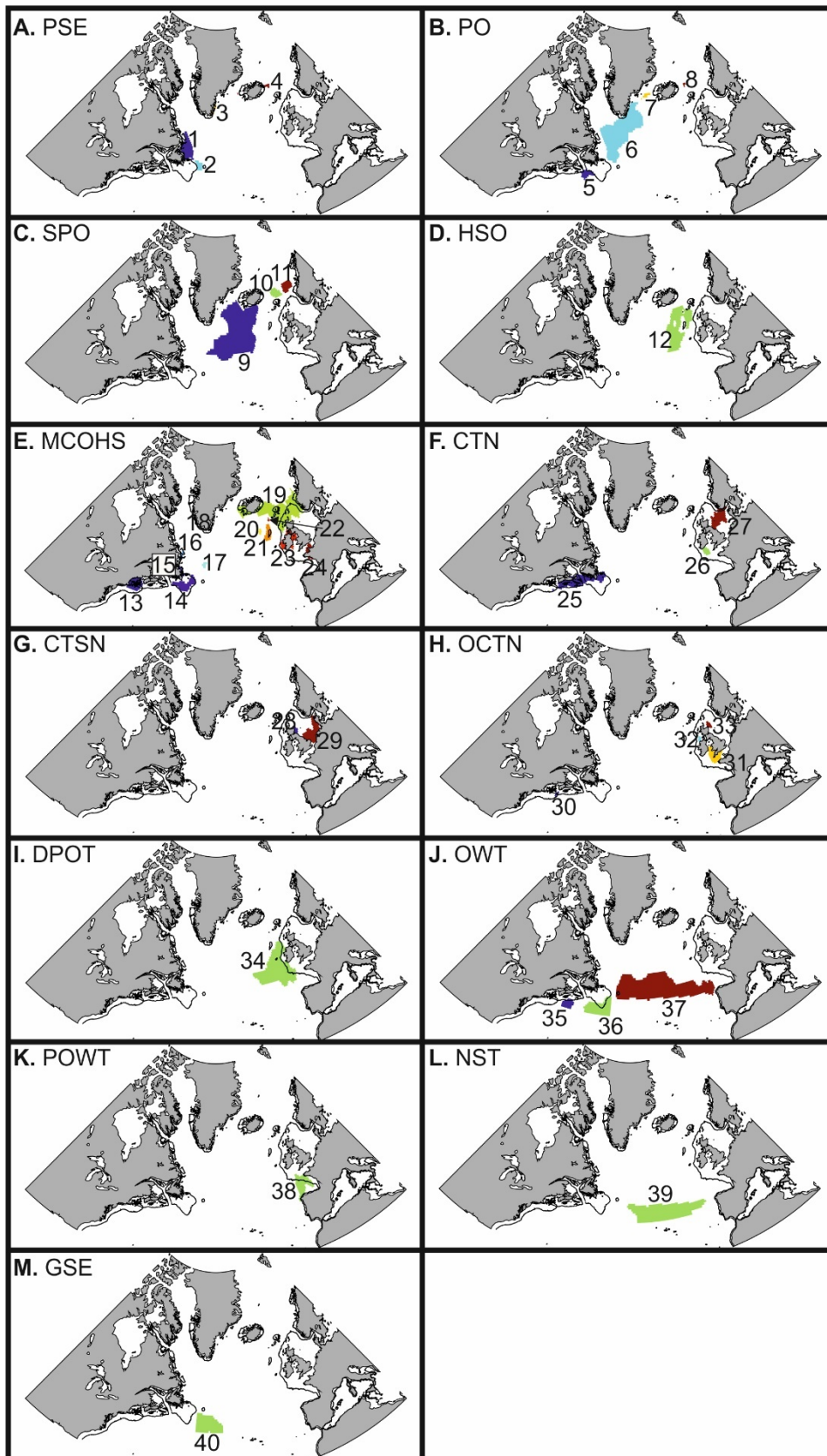
637 **Table 3. Average and seasonal amplitude of the biodiversity of the 6 taxonomic groups in each**
638 **ecological unit.** EU: Ecological Unit. Diat: diatoms. Dino: dinoflagellates. Cop: copepods. See text for
639 the meaning of the ecological unit acronyms. See Figure 9 for the spatial distribution 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	12.62	7.14	4.48	4.85	5.41	4.77	6.02	5.88	5.75	3.23	6.38	4.82
2 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
3 SPO	10.69	12.03	5.03	7.24	4.30	4.69	5.60	5.57	5.24	4.31	6.03	7.16
4 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 MCOHS	12.61	15.02	6.09	7.29	6.39	4.38	7.21	7.95	5.81	4.68	7.25	6.34
6 CTN	15.68	12.10	7.60	4.30	7.98	3.31	9.46	5.51	5.46	3.57	8.51	5.00
7 CTSN	28.47	12.43	7.56	2.95	9.11	2.97	10.79	5.58	4.77	2.62	11.31	4.41
8 OCTN	21.01	18.22	8.16	8.81	9.84	3.55	10.50	6.42	8.40	5.56	11.15	6.04
9 DPOT	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 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 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 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

640 **3.4.1. Polar Shelf-Edge EU (PSE)**

641

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



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

654 **3.4.2. Polar Oceanic EU (PO)**

655

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

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664 **3.4.3. Sub-Polar Oceanic EU (SPO)**

665

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

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682 **3.4.4. Highly-Seasonally dynamical Oceanic EU (HSO)**

683

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

695

696 **3.4.5. Mixed Coastal-Oceanic Highly-Seasonally Dynamical EU (MCOHS)**

697

698 The fifth group is the Mixed Coastal-Oceanic Highly-Seasonally Dynamical EU (MCOHS, Figure
699 9, Tables 2 and 3). Complex to interpret (ecoregions 13-24 in Figure 11E, Supplementary
700 Tables 7 and 8), this EU encompasses a main ecoregion (ecoregion 19) at the north-eastern

701 edge of the area covered by the CPR survey where polar water masses interact with more
702 temperate ones along the Faroe-Iceland Rise. It also corresponds to an area where neritic and
703 oceanic water masses interact along the European Shelf-edge and in the northern part of the
704 North Sea. The EU is also composed of many small ecoregions: (i) the offshore region of the
705 Newfoundland Shelf, (ii) Rockall Rise, (iii) the Irish Sea, (iv) south-west of Ireland, and (v) the
706 Channel where many ecosystems and ecotones co-occur (Figures 7 and 8). This area is
707 characterised by a relatively low seasonal amplitude in taxonomic richness in comparison to
708 HSO (Figure 4B). Biodiversity is low in the main ecoregion and over the Newfoundland Shelf,
709 although being substantially higher in the smaller ecoregions. Some species, mainly neritic,
710 are highly abundant in MCOHS, although being not indicative of the EU, e.g. the diatoms
711 *Asterionellopsis glacialis*, *Dactyliosolen antarcticus*, *Cylindrotheca closterium*, *Rhizosolenia*
712 *acuminata*, the dinoflagellates *Ceratium horridum*, *Dinophysis* spp. and the copepods *Aetideus*
713 *armatus* and *Temora longicornis* (Barnard et al., 2004). The ecoregion offshore the
714 Newfoundland Shelf differs substantially from the other ecoregions, probably because of its
715 thermal regime associated to the presence of sea-ice concentration during some parts of the
716 year. As a result, some cold-water species (e.g. *Ceratium arcticum*, *Calanus glacialis*) are highly
717 abundant in this ecoregion while less represented in the other MCOHS ecoregions.

718

719 **3.4.6. Cold-Temperate Neritic EU (CTN)**

720

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

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734 **3.4.7. Cold-Temperate Shallow Neritic EU (CTSN)**

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736 The seventh group is the Cold-Temperate Shallow Neritic EU (CTSN, Figure 9, Tables 2 and 3).
737 This EU is represented by only one ecoregion (ecoregion 29 in Figure 11G, Supplementary
738 Tables 7 and 8), in the North Sea south of the Flamborough Front. Biodiversity is high for
739 diatoms, zooplankton and to a lesser extent, small copepods (Figure 3 and 4). Seasonal
740 amplitude in biodiversity is low in this area (Figure 4B). Many species occur in this area, e.g.
741 the diatoms *Biddulphia alternans*, *Bellerochea malleus*, *Coscinodiscus wailesii*, *Eucampia*
742 *zodiacus*, *Guinardia flaccidia*, *Odontella regia*, *Rhaphoneis amphiceros*, the copepods
743 *Labidocera wollastoni* and *Isias clavipes*.

744

745 **3.4.8. Ocean-Influenced Cold-Temperate EU (OCTN)**

746

747 The eighth group is the Ocean-Influenced Cold-Temperate EU (OCTN, Figure 9, Tables 2 and
748 3). This EU, composed of only four small ecoregions (ecoregions 30-33 in Figure 11H,
749 Supplementary Tables 7 and 8), are located in (i) Georges Bank, (ii) North Channel, (iii) the
750 North Sea and (iv) the Celtic Sea. The last (main) ecoregion is highly diverse (Figure 3) and all
751 taxonomic groups exhibit their highest richness level (Figure 4A). The seasonal amplitude of
752 the biodiversity is low (Figure 4B). As shown by Figure 8, many ecosystems and ecotones occur
753 in this region and the Celtic Sea appears to be a biogeographic crossroad. Neritic (e.g. the
754 diatoms *Bacillaria paxillifera*, *Corethron cryophilum*, *Dactyliosolen fragilissimus*, *Paralia*
755 *sulcata*, the dinoflagellate *Noctiluca scintillans* and the copepods *Anomalocera patersoni* and
756 *Centropages hamatus*) and oceanic (e.g. the dinoflagellates *Oxytoxum* spp. and *Scrippsiella*
757 spp.) species co-occur in this ecoregion (ecoregion 31). Pseudo-oceanic species (e.g. *Ceratium*
758 *minutum*, *Calanus helgolandicus*, *Candacia armata*) also locally reinforce the biodiversity
759 (Barnard et al., 2004). Warm-temperate (e.g. *Ceratium trichoceros*, *Clausocalanus* spp.),
760 temperate (e.g. *Ceratium hexacanthum*, *Heterorhabdus papilliger*, *Neocalanus gracilis*), cold-
761 temperate (e.g. *Proboscia alata inermis*, *Metridia lucens*) and even subarctic species (e.g. *C.*
762 *finmarchicus*) co-occurs in this ecoregion. Finally, as with other EUs mainly found in the
763 continental shelf, the meroplankton group (species or taxa included in the groups
764 zooplankton) is highly diverse in the Celtic Sea (Figure 3).

765

766 **3.4.9. Diverse and Productive Oceanic Temperate EU (DPOT)**

767

768 The ninth group is the Diverse and Productive Oceanic Temperate EU (DPOT, Figure 9, Tables
769 2 and 3). This oceanic EU, composed by only one ecoregion (ecoregion 34 in Figure 11I,
770 Supplementary Tables 7 and 8), is productive and highly diverse (Figure 3 and 4). Seasonal
771 amplitude remains elevated and the number of abundant species in this ecoregion is high
772 (Barnard et al., 2004). In particular, the richness of the genus *Ceratium* and small copepods is
773 very high (Figure 3). The dinoflagellate *Ceratium hexacanthum* is indicative of this EU in the
774 region covered by the CPR survey while *C. minutum*, *Gonyaulax* spp. and *Oxytoxum* spp. are
775 also highly abundant (Barnard et al., 2004). The high biodiversity is also reinforced by neritic
776 species that expatriate from the continental shelf (e.g. holozooplankton *Pseudocalanus* spp.
777 and meroplankton such as echinoderm larvae) and pseudo-oceanic species (i.e. species
778 occurring above the oceanic and neritic regions but higher over the shelf-edge) such as
779 *Ctenocalanus vanus*, *Candacia armata* and *Calanus finmarchicus* (Barnard et al., 2004).

780

781 **3.4.10. Oceanic Warm-Temperate EU (OWP)**

782

783 The tenth group represents the Oceanic Warm-Temperate EU (OWP, Figure 9, Tables 2 and
784 3). This oceanic EU, composed of three ecoregions occurring south of the Oceanic Polar Front
785 in the Atlantic, south of Newfoundland and the Nova Scotian Shelves (ecoregions 35-37 in
786 Figure 11J, Supplementary Tables 7 and 8), is more diverse than oceanic regions north of the
787 Oceanic Polar Front (Figures 3 and 4). In particular, the biodiversity of small and large
788 copepods, as well as the genus *Ceratium* eastwards, is high. In contrast, the other groups
789 (zooplankton and diatoms) have a low biodiversity. Seasonal amplitude is substantially lower
790 than HSO and DPOT, with the exception of the eastern side of the ecoregion. A large number
791 of oceanic species occur in this EU, e.g. the copepods *Nannocalanus minor*, *Heterorhabdus*
792 *papilliger*, *Pleuromamma borealis*, *Euchaeta acuta*, *Lucicutia* spp, and the dinoflagellates
793 *Ceratium azoricum*, *C. massiliense*, and *C. trichoceros* (Barnard et al., 2004).

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

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

3.4.12. Northern Sub-Tropical EU (NST)

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

3.4.13. Gulf Stream Extension EU (GSE)

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

835 4. Discussion

836

837 Our final partition of the North Atlantic Ocean (Figure 9) was primarily based on the
838 biodiversity and seasonal patterns in the species richness of 6 planktonic groups, therefore
839 integrating information on 238 plankton species or taxa sampled by the CPR survey between
840 1946 and 2015 (60,549,580 data points). In areas where CPR sampling was high (e.g. around
841 the British Isles), the spatial resolution of the partition was relatively high (0.5° latitude x 0.5°
842 longitude) and in more remote oceanic areas, the resolution was degraded to 2° latitude x 2°
843 longitude. At the centre of the North Atlantic where CPR sampling was limited, we also used
844 the physico-chemical partition (Figure 2) to allow the geographical division of three more
845 provinces (e.g. PO, SPO and HSO). The resulting partition identified 13 EUs, units defined by a
846 relatively homogeneous biodiversity and similar patterns in seasonal variability for the six
847 taxonomic groups: (i) diatoms, (ii) dinoflagellates, small (iii, iv) and large (v, vi) copepods (iii,
848 v) and zooplankton other than copepods (iv, vi). Some EUs, which were not represented by an
849 interconnected set of geographical cells, were subsequently divided into ecoregions (Figure
850 11). We used the CPR atlas (Barnard et al., 2004; Beaugrand, 2004) to further investigate
851 whether some species were representative of each EU or associated ecoregions (Figures 9 and
852 11); this electronic atlas is available on request.

853

854 The main difficulty in partitioning the marine plankton biosphere is related to the dynamic
855 movement of water masses and the locations of surface features, which are influenced by
856 atmospheric conditions. This difficulty led the biogeographer van der Spoel (van der Spoel,
857 1994) to separate the biotope of pelagic ecosystems into two components (i) a stable-biotope
858 component (geographically stable) in which a primary related community occurs and (2) a
859 substrate-biotope component (depending on water mass) characterised by a secondary
860 related community (mixed primary community, (Beklemishev, 1961)). An ecosystem is mainly
861 characterised by a primary related community linked to a stable-biotope component whereas
862 an ecotone is more distinguished by a secondary related-community depending on water
863 masses. It is also known that an ecotone can also be characterised by its own biological
864 composition (Beaugrand, Ibañez, Lindley & Reid, 2002; Frontier, Pichot-Viale, Leprêtre,
865 Davoult & Luczak, 2004; Ramade, 1994). The distinction van der Spoel made is fundamental
866 to correctly understand how plankton biodiversity is spatially organised in the oceans and
867 seas.

868

869 Our study identified the two realms (open-ocean oceanic and the continental shelves pelagic
870 realms) revealed in a global-scale study performed at a 5° x 5° spatial resolution and based on
871 occurrence data reported in the Ocean Biogeographic Information System (OBIS) (Costello et
872 al., 2017). In the area we considered, the boundaries were similar, considering the difference
873 in the spatial resolution of the two studies. This distinction was mainly the result of a higher
874 biodiversity of diatoms and the presence of many meroplanktonic groups (zooplankton other
875 than copepods) or groups depending on shallow waters over neritic regions (Supplementary
876 Tables 4 and 6). Benthic-pelagic coupling makes the continental shelves pelagic realm very
877 specific.

878

879 Mapping of our index of spatial heterogeneity at both 2° x 2° and 0.5° x 0.5° spatial resolutions
880 revealed the presence of a complex transition zone between the two realms where
881 ecosystems are strongly intertwined (Figures 7B and 8B). The imbrication of ecoregions (DPOT,

882 POWT,CTN,OCTN and MCOHS) and the overlapping spatial distribution of species over the
883 Celtic Sea (Barnard et al., 2004) leads to complex coenoclines (i.e. a gradient of biocoenoses
884 or communities) and associated ecosystems, ecoclines and ecotones. The region can be seen
885 as a biogeographic crossroad where not only oceanic, neritic and pseudo-oceanic species
886 cohabit but also where warm and cold-water species may regularly co-occur. As a result, total
887 biodiversity is highest in this area for all taxonomic groups (Figure 3). Our procedure reduced
888 somewhat this mosaic of ecoregions, which is visible in Figure 8. Such a complex organization
889 of marine life has been rarely reported in marine biogeography to our knowledge because our
890 study lies between large-scale studies that have relatively low spatial resolution (Longhurst,
891 2007; Sherman & Duda, 1999; Spalding et al., 2007) and regional ecological studies at higher
892 resolution that lacks spatial extent to reveal this phenomenon.

893
894 The number of oceanic ecoregions in the present study is higher than previously reported by
895 large-scale oceanic partitions, which focused at the level of a realm, biome or province
896 (Costello et al., 2017; Longhurst, 2007; Reygondeau et al., 2013). The eastern side of the North
897 Atlantic seems to be very complex spatially, with ecoregions varying rapidly in space and being
898 highly seasonal to the north (Figures 4B, 7B and 8B). The influence of hydro-dynamical
899 structures such as the Oceanic Polar Front (OPF) (Dietrich 1964), the Gulf Stream Extension
900 (both being part of the AMOC) and the Labrador Current on the ecoregions is important. For
901 example, Beaugrand and colleagues (Beaugrand et al., 2001) suggested that the OPF acts as a
902 sharp boundary for subtropical, shelf-edge and warm-temperate species, thus limiting their
903 dispersal polewards. In contrast, colder-water species seemed to less influenced by the OPF
904 and were more frequently detected southwards (Barnard et al., 2004). The OPF and the GSE
905 are also areas of plankton concentration (e.g. *Metridia lucens* for the OPF)(Barnard et al.,
906 2004).

907
908 A close comparison between our partition and Longhurst's biogeography (Longhurst, 2007)
909 revealed strong differences between the location of his provinces and our ecoregions. The
910 position of the boundary between the Polar and the Westerlies Biomes was substantially
911 different (Figure 10A). This was also the case for the position of the Gulf Stream on the Habitat
912 Partition (Figure 10B). Biogeographical or satellite-based partitioning, typically based on a few
913 parameters and no real abundance data, may only reveal major features. Although they
914 definitively have been important in partitioning the ocean on a global scale, they may be
915 limited to detect regional ecosystems at a basin scale. Especially, plankton are sensitive to
916 small hydro-climatic fluctuations because it integrates those fluctuations during its entire life
917 cycle (Reid, Edwards, Hunt & Warner, 1998; Taylor, Allen & Clark, 2002). Limiting the
918 geographical division to a restricted number of physical and chemical parameters may
919 therefore lead to an oversimplified partition into biomes, provinces or ecoregions.

920
921 We found a much higher number of ecoregions compared to Large Marine Ecosystems (LMEs)
922 (Sherman & Duda, 1999) or MEOWs (Spalding et al., 2007). We found three main ecoregions
923 in the North Sea instead of only one in the classifications of LMEs or MEOWs. These three
924 ecoregions roughly corresponded with the three major ecological subdivisions proposed by
925 some authors and based on phytoplankton (Reid, Lancelot, Gieskes, Hagmeier & Weickart,
926 1990), zooplankton (Beaugrand et al., 2001; Beaugrand et al., 2002; Fransz, Colebrook,
927 Gamble & Krause, 1991), and fish (Daan, Bromley, Hislop & Nielsen, 1990). The Flamborough
928 Frontal structure, which separates seasonally thermally stratified water to the North and

929 tidally-induced mixed water to the south (Pingree, Holligan & Mardell, 1978) probably explains
930 the boundary between CTSN (ecoregion 29 in Figure 11) and CTN (ecoregion 27). North of
931 CTN, the remaining area of the North Sea belongs to a complex EU (MCOHS), revealing the
932 complex nature of the system and the influence of the Atlantic water on this part of the North
933 Sea (ecoregion 19). Two more ecoregions were detected in the North Sea but they were
934 restricted to the northeastern coast of Great Britain (ecoregions 28 and 33).

935
936 Although the proposed partition may represent a significant improvement of existing ones in
937 the North Atlantic sector (e.g. ICES or OSPAR areas), it has also a number of drawbacks that
938 we should be aware of before using it for ecosystem management. First, the partition remains
939 static even if it integrates seasonal variability in the biodiversity of six plankton groups.
940 Providing a dynamical partition is relatively difficult when it is based on biological data because
941 of the number of samples this requires. The CPR survey collects about 5000 samples every
942 year, which is unique in the world at such spatio-temporal scales and levels of taxonomic
943 resolution. However, it remains too limited to give a dynamic picture at the same spatial
944 resolution at a year-to-year scale. Nevertheless, an examination of decadal changes in the
945 ecoregions is achievable in many areas sampled by the CPR survey (Planque & Fromentin,
946 1996; Reid et al., 1998; Richardson & Schoeman, 2004). Biological data are becoming available
947 at a global scale thanks to initiatives such as OBIS. However, even those data sets remain
948 insufficient to provide a dynamic picture of the epipelagic system at a large scale and at a
949 relatively high spatial resolution.

950
951 Second, some EUs or ecoregions were poorly sampled by the CPR survey (Figure 1, Tables 2-3
952 and Supplementary Tables 7-8), which may have affected our partition. In particular, it was
953 unexpected that seasonal variability in biodiversity was so high south of the oceanic polar
954 front in the center of the North Atlantic (Figure 4B); in particular, values were higher than
955 estimated seasonal variance in calanoid biodiversity based on principal component analysis
956 (Beaugrand et al., 2001). A higher amount of variability may be related to an insufficient
957 number of samples, although we jackknifed taxonomic richness. The biological partition gave
958 an unexpected large ecoregion north of the OPF where CPR sampling is limited. We used the
959 PHs to attempt to complete the ecoregions and showed by examination of the CPR atlas that
960 had an ecological meaning. For example, the copepod *C. glacialis* is highly abundant in PSE,
961 the diatom *Ephemera planamembranacea* is found in great concentration in PO and the
962 calanoids *C. finmarchicus* and *Paraeuchaeta norvegica* in SPO (Figure 9) (Barnard et al., 2004).

963

964 **5. Conclusions**

965

966 We provide two basin-scale partitions of the North Atlantic Ocean based on physical and
967 biological data at a relatively high spatial resolution. The final ecological partition is based on
968 238 plankton species encompassing diatoms, dinoflagellates, small and large copepods and
969 other zooplankton species, including meroplankton. This partition reveals the complexity of
970 the arrangement of life in both oceanic and neritic realms. Based on a relatively high spatial
971 resolution and taxonomic resolution, our partition represents a baseline against which we will
972 (i) better understand the effects of natural variability on marine ecosystems, (ii) better
973 evaluate the implications of the human interference on marine biological and ecological
974 systems through pollution, eutrophication, fishing and global climate change and (iii) guide
975 the development of marine protected areas to protect biodiversity.

976
977

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979

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984

985 **Author contributions**

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

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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.

List of Supplementary Tables

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

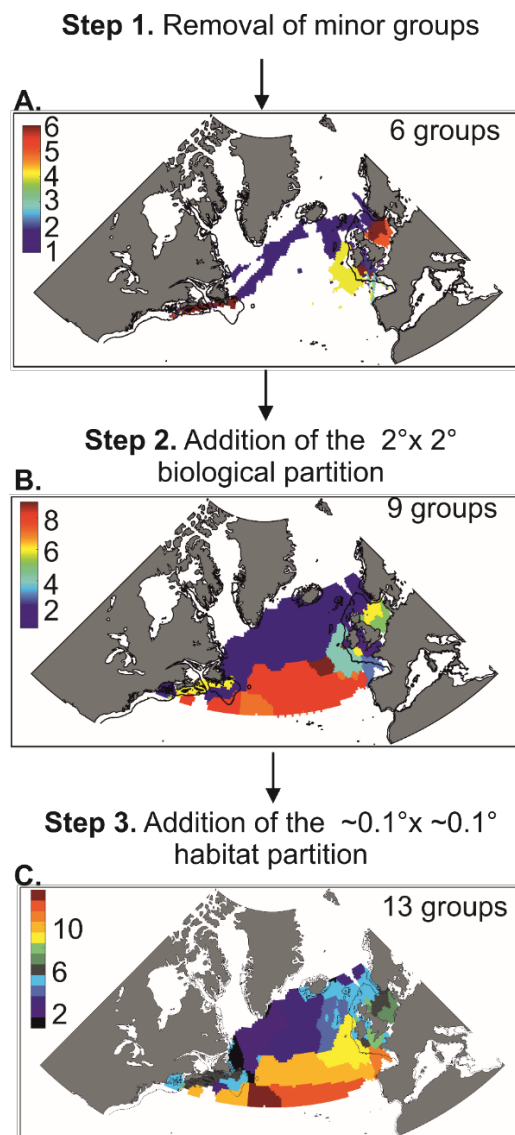
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Supplementary Table 7. Main abiotic properties of the ecoregions associated to ecological units. EU: Ecological Unit. SST: mean Sea Surface Temperature ($^\circ\text{C}$). S: mean salinity (PSS). Cur: mean surface current ($\text{m}\cdot\text{s}^{-1}$). 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: copepods. 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).

1152 **Supplementary Figure 1.**

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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>Bacteriastrum</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 amphiceros</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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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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1161 **Supplementary Table 3.** List of species used to calculate the species richness of small copepods (i.e.
 1162 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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1165 **Supplementary Table 4.** List of species used to calculate the species richness of small (i.e. recorded in
 1166 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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1170 **Supplementary Table 5.** List of species used to calculate the species richness of large copepods (i.e.
 1171 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 persecans</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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1174 **Supplementary Table 6.** List of species used to calculate the species richness of large zooplankton
 1175 other than copepods and fish (i.e. recorded in eyecount). Note that fish eggs and larvae were
 1176 considered in this analysis.

Species	Year of first record
<i>Tomopteris</i> spp.	1946
Gammaridea	1946
Hyperideida (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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1180 **Supplementary Table 7. Main abiotic properties of the ecoregions associated to ecological units.**
 1181 EU: Ecological Unit. SST: mean Sea Surface Temperature (°C). S: mean salinity (PSS). Cur: mean
 1182 surface current (m.s⁻¹). N: mean nitrate concentration (mol.m⁻³). P: mean phosphate concentration
 1183 (mol.m⁻³). Sil: mean silicate concentration (mol.m⁻³). PAR: mean photosynthetically active radiation
 1184 (E.m⁻².day⁻¹). C: mean chlorophyll concentration (mg.m⁻³). PI: mean primary production (g.m⁻³.day⁻¹).
 1185 Bathymetry is expressed in meter (m). P5: the 5th percentile. P50: the median. P95: the 95th
 1186 percentile. See text for the meaning of the ecological unit acronyms. See Figure 9 for the spatial
 1187 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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1191 **Supplementary Table 8. Average and seasonal amplitude of the biodiversity of the 6 taxonomic**
 1192 **groups in all ecoregions of each ecological unit.** Eco: Ecoregion (numbers are the identifier of an
 1193 ecoregion). EU: Ecological Unit. Diat: diatoms. Dino: dinoflagellates. '-' are missing values. Cop:
 1194 copepods. See text for the meaning of the ecological unit acronyms. See Figure 9 for the spatial
 1195 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)													
CTSN	27.29	11.99	7.21	3.03	7.92	2.68	10.68	5.13	5.50	3.98	11.12	5.20	
7 (29)													
CTSN	28.60	12.48	7.60	2.94	9.24	3.00	10.81	5.63	4.69	2.47	11.33	4.33	
8 (30)													
OCTN	18.82	9.80	9.18	4.11	9.29	3.65	10.28	4.86	7.77	6.20	9.50	5.40	
8 (31)													
OCTN	20.38	20.32	8.66	7.81	8.87	4.71	10.51	6.63	10.56	7.47	10.38	5.72	
8 (32)													
OCTN	21.10	18.11	8.17	9.50	10.20	3.57	10.50	6.76	8.42	5.32	11.22	6.10	
8 (33)													
OCTN	21.92	21.23	7.31	7.43	8.55	2.60	10.54	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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