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Stakeholder engagement relating to this task*

WHO are your most important stakeholders?	<input type="checkbox"/> Private company If yes, is it an SME <input type="checkbox"/> or a large company <input type="checkbox"/> ? <input type="checkbox"/> National governmental body <input type="checkbox"/> International organization <input type="checkbox"/> NGO <input type="checkbox"/> others Please give the name(s) of the stakeholder(s): ...International organisations such as GOOS and GEOBON as well as European organisations such as OSPAR and MSFD directive
WHERE is/are the company(ies) or organization(s) from?	<input type="checkbox"/> Your own country <input type="checkbox"/> Another country in the EU <input type="checkbox"/> Another country outside the EU Please name the country(ies): International and European
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NOTE: This information is being collected for the following purposes:

1. To make a list of all companies/organizations with which AtlantOS partners have had contact. This is important to demonstrate the extent of industry and public-sector collaboration in the obs community. Please note that we will only publish one aggregated list of companies and not mention specific partnerships.
2. To better report success stories from the AtlantOS community on how observing delivers concrete value to society.

*For ideas about relations with stakeholders you are invited to consult [D10.5](#) Best Practices in Stakeholder Engagement, Data Dissemination and Exploitation.

Pelagic Habitats of the North Atlantic

Based on observations from the Continuous Plankton Recorder survey

Sir Alister Hardy Foundation for Ocean Science 2018

AtlantOS



254,410 analysed CPR samples

representing a total of 60,549,580 data points used

Pelagic Habitats of the North Atlantic

From biomes to ecoregions

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Introduction

The Continuous Plankton Recorder (CPR) survey is one of the most well established autonomous observing systems covering the North Atlantic basin-scale over multiple decades. It has 80 years of experience with working with the commercial shipping industry and is an established platform providing a global network of Ships of Opportunity for scientific research.

As part of the European project AtlantOS that aims to build a more integrated Atlantic wide observation system, the CPR survey aims to optimize and enhance its current CPR survey network and provide important biological data in the form of Essential Ocean Variables (EOV). The CPR is an autonomous instrument mainly towed from ships of opportunity that has been in use for over 80 years. Currently, samples are collected monthly covering 20,000 km in the major ecosystems of the North Atlantic. Recently the network has expanded to sample in the South Atlantic and other regions globally. It has been observing over 1000 biological variables over a eighty year period as well as a number of physical variables.

Using CPR's rich biodiversity data, the project aims to delineate the North Atlantic Ocean into specific habitats from the provincial scale to the ecoregional scale. This will entail defining regions by their physical structure but more importantly in this case ecologically defined regions. These regional areas will constitute an adequate unit to accurately monitor ecological changes across large spatio-temporal scales using EOVs. These newly defined ecoregions of the Atlantic will help the community target observations to measure regional variation in the Atlantic. Processed EOVs will target



specific areas relevant to observing change and will directly deliver key information of significant societal relevance such as human health climate change impacts on ecosystems, ocean acidification, biodiversity and fisheries.

Currently CPR data is extracted using standard CPR regions which were loosely based on ICES fishery boundaries and physical regions in the past. These regions are, however, not perfect in delineating and defining the actual ecosystems found in the North Atlantic. The purpose of our current study is to create new ecoregions for the North Atlantic based on biodiversity and communities found there ranging from the provincial scale (e.g. warm temperate oceanic systems) down to the ecoregional scale (e.g. Celtic Sea). These new ecoregions will be the geographical areas we extract the biological EOVs used in the AtlantOS programme.

Continuous Plankton Recorder observations in the North Atlantic

The Continuous Plankton Recorder Survey is a long-term, sub-surface marine plankton monitoring programme consisting of a network of CPR transects towed monthly across the major geographical regions of the North Atlantic (Fig. 1). It has been operating in the North Sea since 1931 with some standard routes existing with a virtually unbroken monthly coverage back to 1946. The CPR survey is recognised as the longest sustained and geographically most extensive marine biological survey in the world. The dataset comprises a uniquely large record of marine biodiversity covering ~1000 taxa over multi-decadal periods. The survey determines the abundance and distribution of microscopic plants (phytoplankton) and animals (zooplankton including fish larvae) in our oceans and shelf seas. Using ships of opportunity from ~30 different shipping companies, it obtains samples at monthly intervals on ~50 trans-ocean routes. In this way the survey autonomously collects biological and physical data from ships covering ~20,000 km of the ocean per month, ranging from the Arctic to the Southern Ocean. The survey is an internationally funded charity (with operational funding from UK, USA, Canada and Norway) with a wide consortium of stakeholders.

The CPR is a high-speed plankton recorder that is towed behind 'ships of opportunity' through the surface layer of the ocean (~10 m depth). Water passes through the recorder and plankton are filtered by a slow moving silk (mesh size 270 μm). A second layer of silk covers the first and both are reeled into a tank containing 4% formaldehyde. Upon returning to the laboratory, the silk is unwound and cut into sections corresponding to 10 nautical miles and approximately 3 m³ of filtered sea water. There are four separate stages of analysis carried out on each CPR sample, with each focusing on a different aspect of the plankton: viz. (1) overall chlorophyll (the phytoplankton colour index; PCI); (2) larger phytoplankton cells (phytoplankton); (3) smaller zooplankton (zooplankton traverse); and (4) larger zooplankton (zooplankton eyecount) The phytoplankton colour of each section of the CPR silk is evaluated and categorised according to four levels of 'greenness' (green, pale green, very pale green and no colour) using a standard colour chart; the numbers are given a numerical value as a measure of 'Phytoplankton Colour Index'. Direct comparisons between the phytoplankton colour index and other chlorophyll a estimates including SeaWiFS satellite estimates indicate strong positive correlations (Batten et al. 2003; Raitsos et al. 2005). This is a semiquantitative measure of phytoplankton biomass; the silk gets its green colour from the chloroplasts of the filtered phytoplankton.

Phytoplankton cells are identified and recorded as either present or absent across 20 microscopic fields spanning each section of silk (representing ~1/10,000 of the filtering silk). Due to the mesh size of CPR silks, many phytoplankton species are only semi-quantitatively sampled owing to the small size of the organisms. There is thus a bias towards recording larger armoured flagellates and chain-forming diatoms and that smaller species abundance estimates from cell counts will probably be underestimated in relation to other water sampling methods. However, the proportion of the population that is retained by the CPR silk reflects the major changes in abundance, distribution and specific composition (i.e. the percentage retention is roughly constant within each species even with very small-celled species) (Edwards, et al. 2006). Zooplankton analysis is then carried out in two stages with small (<2 mm) zooplankton identified and counted on-silk (representing ~1/50 of the filtering silk) and larger (>2 mm) zooplankton enumerated off-silk. The collection and analysis of CPR samples have been carried out using a consistent methodological approach, coupled with strict protocols and Quality Assurance procedures since 1958, making the CPR survey the longest continuous dataset of its kind in the world.

The addition of a water sampler onboard certain CPRs can provide information on the whole size-spectrum of plankton using molecular techniques from bacteria and viruses to flagellates and other taxa not normally identified using standard CPR analysis. In addition to this many CPRs currently have near-real-time sensors for variables such as conductivity, temperature and chlorophyll-a fluorescence from bespoke sensors that are being operated on CPR transects across some coastal to open ocean waters (see Fig.2 for additional sensors on the CPR).

For the purpose of this report, the North Atlantic Basin will be geographically subdivided into different ecoregions based on biodiversity data. As part of the AtlantOS project the standard CPR regions will become redefined based on the biological communities there and become new ecoregional areas for the North Atlantic.



Current and historic CPR sampling in the North Atlantic



Fig. 1. Historic sampling in the North Atlantic by the CPR survey (red samples) and current CPR routes (lines). Letters refer to CPR route identification. Targeted AtlantOS instrumented routes are in yellow and targeted molecular route in green.



Enhancing the CPR platform: Monitoring marine biodiversity from genes to ecosystems

In addition to the traditional biological sampling undertaken by the CPR the towed body can be equipped with a range of sensing capabilities to extend its utility for integrated observing.

SAHFOS Planktag : Conductivity, Temperature, Chlorophyll-a, Fluorescence and ambient Light. Data telemetry enables observations to be streamed back to SAHFOS within minutes of the CPR surfacing

SAHFOS WaMS : Water and Molecular Sampler

Vemco Minilog : Temperature sensor

Star Oddi CTD : Conductivity, Temperature and Pressure (Depth)

Seawater enters via the aperture. Plankton is captured on a filter silk band then covered by a further silk band. The continuously moving band is wound through the CPR on rollers turned by gears, which are powered by a propeller allowing for long distances to be towed

SAHFOS CPR Internal : Phytoplankton, Zooplankton, Planktonic Bacteria and Viruses

UFE Multispectral Fluorometers : Rapid optical detection of Phytoplankton forms, Pressure (Depth) and Temperature

RBR CTD : Conductivity, Temperature, Pressure (Depth) and Fluorescence

Key Statistics

Length x width x height : 100 x 36 x 42 cm
Weight : 85kg
Tow depth : 5 - 10 metres
Tow speed : 8 - 25 knots
Aperture size : 1.27 cm²

Collects: Phyto- and Zooplankton, planktonic bacteria and viruses.

Instruments record: Conductivity, Temperature, Depth, Chlorophyll-a, Fluorescence, ambient Light, and three-axis accelerations.

Fig.2. The CPR continues to collect over 1000 taxonomic entities using traditional methods but now employs a number of modern methods from flow cytometry to molecular probes to capture the whole size range and biodiversity of the planktonic system. Biological data is further complimented with the additional measurement of physical variables using instrumented CPRs.

Defining pelagic habitats of the North Atlantic

Physical and geographical classification of the North Atlantic Ocean

We first partitioned the North Atlantic Ocean and its adjacent seas using an empirical procedure based on the physics and geography of the North Atlantic using SST, bathymetry, light at bottom, salinity and current velocity at a high spatial resolution ($<0.1^\circ$ latitude \times 0.1° longitude). This partition at a relatively high spatial resolution was intended to complement the biological partition based on CPR data. The habitat partition was carried out hierarchically using 15 ecoregions determined empirically (Fig 3.). Figure 3 summarizes the ecological characteristics of each resulting ecoregions. We used physical data originating from Bio-ORACLE v2.0 (Marine data layers for ecological modelling) (Tyberghein et al. 2012). Bio-ORACLE is a global dataset consisting of 23 geophysical, biotic and climate rasters. This data package for marine species distribution modelling is available for download at <http://www.bio-oracle.ugent.be>. For this purpose, we used both minimum and maximum sea ice concentration (as fraction), sea surface temperature ($^\circ\text{C}$), salinity, bathymetry (m) and light at bottom. Those parameters are important ecological factors that shape biodiversity at large scale. Rasters were assembled at a resolution of 5 arcmin (i.e. 9.2 km).

Biological and community classification of the North Atlantic Ocean

We partitioned biologically the North Atlantic Ocean and its adjacent seas by using data collected from the Continuous Plankton Recorder (CPR) survey (Reid et al. 2003). Specifically, we applied the procedure on six taxonomic groups: diatoms (59 species or taxa; Ceratium dinoflagellates (41 species), small copepods (i.e. recorded in traverse) (27 species or taxa), small zooplankton (i.e. recorded in traverse) (15 species or taxa), large copepods (i.e. recorded in eyecount) (73 species), and large zooplankton (i.e. recorded in eyecount) other than copepods and including fish eggs and larvae (23 species or taxa). Therefore, a total of 238 species or taxa were considered for the period 1948-2015 (a total of 254,410 analysed 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 \times 2° longitude that enables a large coverage into the North Atlantic Ocean despite the lower

CPR sampling coverage and a grid of $0.5^\circ \times 0.5^\circ$ from 40.5°N to 65.5°N and from 80.5°W to 9.5°E that enabled a finer partition in seas around the NE Atlantic where CPR sampling is denser.

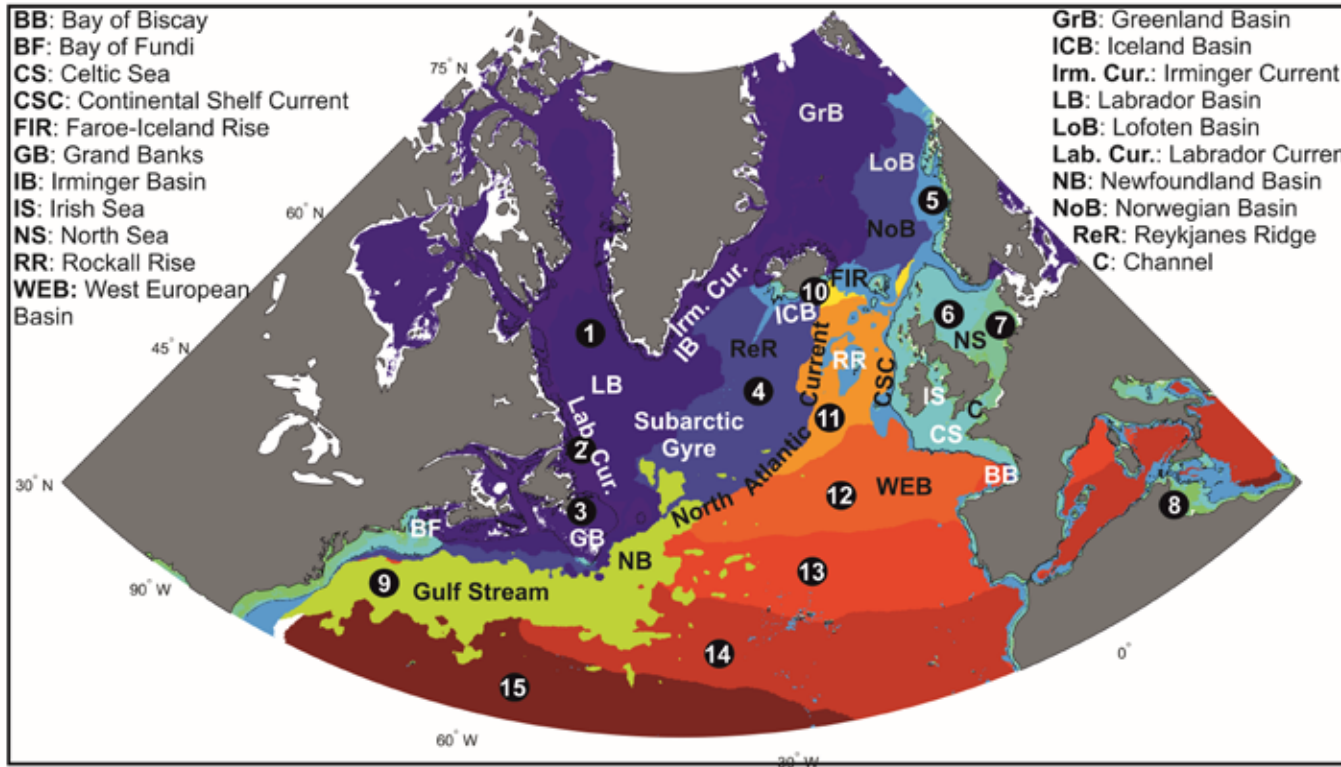
For the two biological partitions, we first estimated the species richness of each taxonomic group on the corresponding grid (2° latitude \times 2° longitude and 0.5° latitude \times 0.5° longitude) from 40.5°N to 65.5°N and from 80.5°W to 9.5°E for each 2-month period using CPR data from 1946 to 2015. For each geographical cell and 2-month period, we calculated the species richness providing that the number of samples was higher than 15 (for the $2^\circ \times 2^\circ$ partition) or 5 (for the $0.5^\circ \times 0.5^\circ$ 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 the indices that emphasise the evenness component of biodiversity. Indeed, 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. We used a first-order jackknife procedure to increase the robustness of the species or taxonomic richness.

For the first partition (2° latitude \times 2° longitude), matrices of (jackknifed) taxonomic richness of 13 latitudes \times 46 longitudes = 598 geographical squares \times 6 2-month periods were built for each taxonomic group. Six matrices were therefore prepared: Matrix A 598 geographical cells \times 6 2-month periods for diatoms, Matrix B 598 geographical cells \times 6 2-month periods for the genus Ceratium, Matrix C 598 geographical cells \times 6 2-month periods for small copepods, Matrix D 598 geographical cells \times 6 2-month periods for small zooplankton other than copepods, Matrix E 598 geographical cells \times 6 2-month periods for large copepods, and Matrix F 598 geographical cells \times 6 2-month periods for large zooplankton other than copepods (see Figures 4-9).

For the second partition (0.5° latitude \times 0.5° longitude), matrices of (jackknifed) taxonomic richness of 51 latitudes \times 181 longitudes = 9231 geographical squares \times 6 2-month periods were built for each taxonomic group. Six matrices were therefore prepared: Matrix A* 9231 geographical cells \times 6 2-month periods for diatoms, Matrix B* 9231 geographical cells \times 6 2-month periods for the genus Ceratium, Matrix C* 9231 geographical cells \times 6 2-month periods for small copepods, Matrix D* 9231 geographical cells \times 6 2-month periods for



Physical and geographical classification of the North Atlantic Ocean



Ecoregion	Higher bathymetry	lower bathymetry	SIC >0	Light bottom >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	<35.23	-
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

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

Fig.3. The physical and geographical partition of the North Atlantic based on using SST, bathymetry, light at bottom, salinity and current velocity at a high spatial resolution (<0.1° latitude x 0.1° longitude). The habitat partition was carried out hierarchically using 15 ecoregions determined empirically. SIC: Sea-Ice Concentration. A hyphen denotes the absence of consideration of an ecoregion. An ecoregion is simply a region with similar ecological conditions with respect to the factors used to make the classification.

small zooplankton other than copepods, Matrix E* 9231 geographical cells x 6 2-month periods for large copepods, and Matrix F* 9231 geographical cells x 6 2-month periods for large zooplankton other than copepods.

To diminish the number of missing values in oceanic areas in all matrices A-F and A*-F*, we carried out iterative Principal Component Analyses (PCAs) on each matrix using 100 PCAs and the first 5 principal components and eigenvectors. We then calculated a last PCA to remove the unexplained variance.

For both biological partitions, we combined matrices A(598,6)-F(598,6) into a new matrix G(598,36) for partition 2° latitude x 2° longitude and matrices A*(9231,6)-F*(9231,6) into a new matrix G*(9231,36) for partition 0.5° latitude x 0.5° longitude. We then calculated two squared matrices K(598,598) and K*(9231,9231) using the Euclidean distance and chose an Agglomerative hierarchical clustering technique using average linkage, which is a good compromise between the two extreme single and complete clustering techniques. For each partition, we examined the first 8 cut-off levels of the dendrogram. Groups composed of less than 3 geographical cells were not considered (Figure 10).

We smoothed the partition by keeping a cell group only when it was composed of five adjacent geographical cells out of the nine possible (i.e. the target cell and all 8 adjacent geographical cells). This procedure smoothed slightly the final partitions. In addition, we calculated an index of group heterogeneity $H=[h_i, j]$. For each geographical cell, we calculated the percentage of cells that belonged to different groups, which is the number of different groups $v-1$ (maximum of nine cells; here also the target cell and all 8 adjacent geographical cells) on the number of classified cells $w-1$ (maximum of nine cells).

We then built an ecological partition by designing the numerical procedure hereafter. We started our procedure using the biological partition based on a 0.5° x 0.5° spatial resolution. We removed groups for which it was not possible to calculate an index of heterogeneity (i.e. 6 groups) and merged small groups that were difficult to understand from expert knowledge because they lacked spatial contiguity (i.e. 3 groups). A total of six groups remained. Then, the biological partition at 2° x 2° spatial resolution was superimposed to the 0.5° x 0.5° biological partition in areas where no group existed. At that stage, we had a total of 9 groups. Finally, we added some groups originating from the habitat partition to divide the polar biome (sensu Longhurst 1998; 4 more groups) into provinces and the westerly-wind biomes (sensu Longhurst 1998; one more group). The final partition had therefore a total of 14 groups but split into 16 provinces and ecoregions.



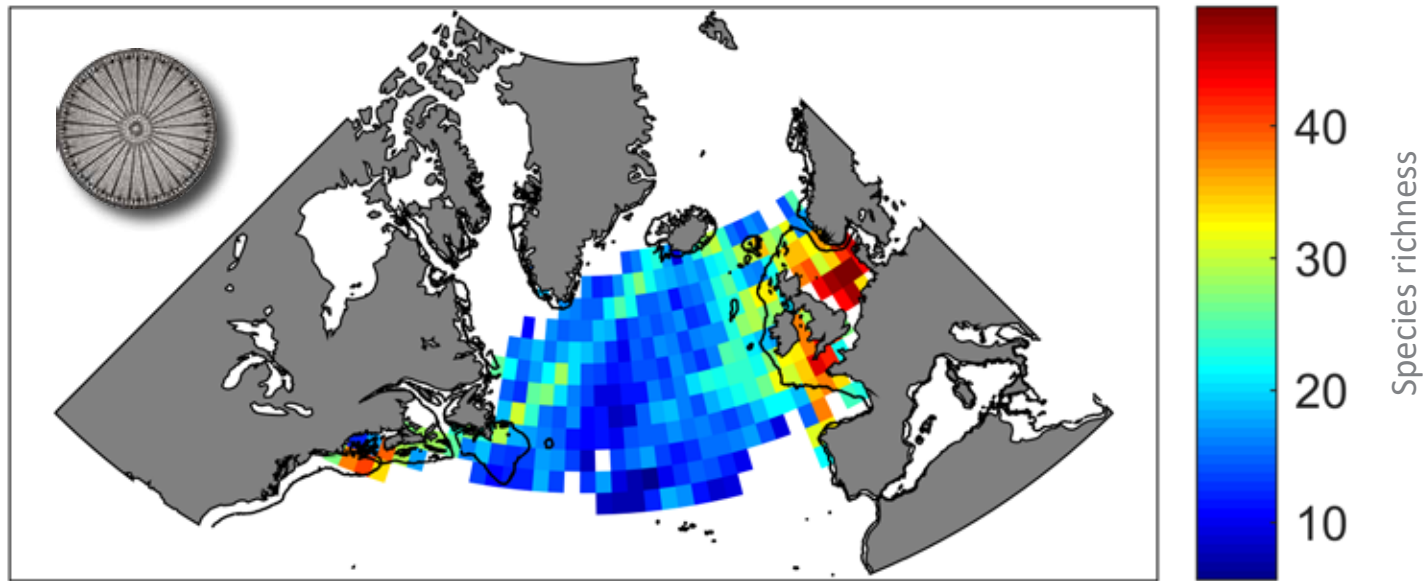


Fig.4. Diversity of diatoms in the North Atlantic based on the species richness of each taxonomic group on the corresponding grid (2° latitude x 2° longitude).

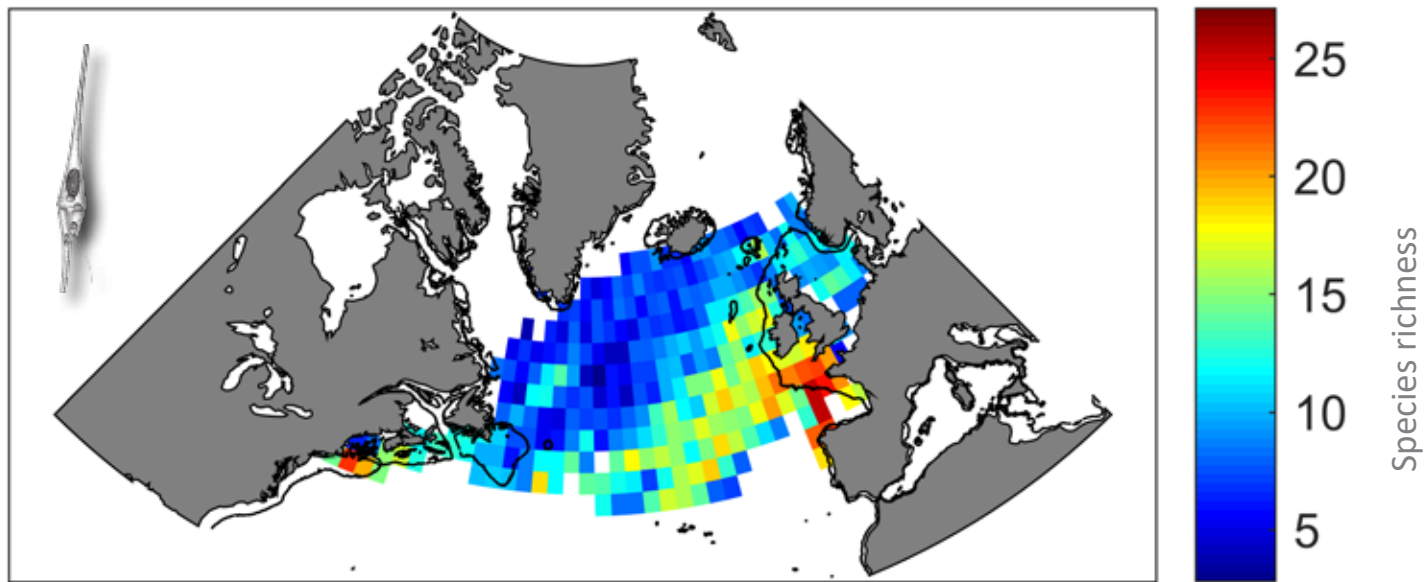


Fig.5. Diversity of dinoflagellates in the North Atlantic based on the species richness of each taxonomic group on the corresponding grid (2° latitude x 2° longitude).

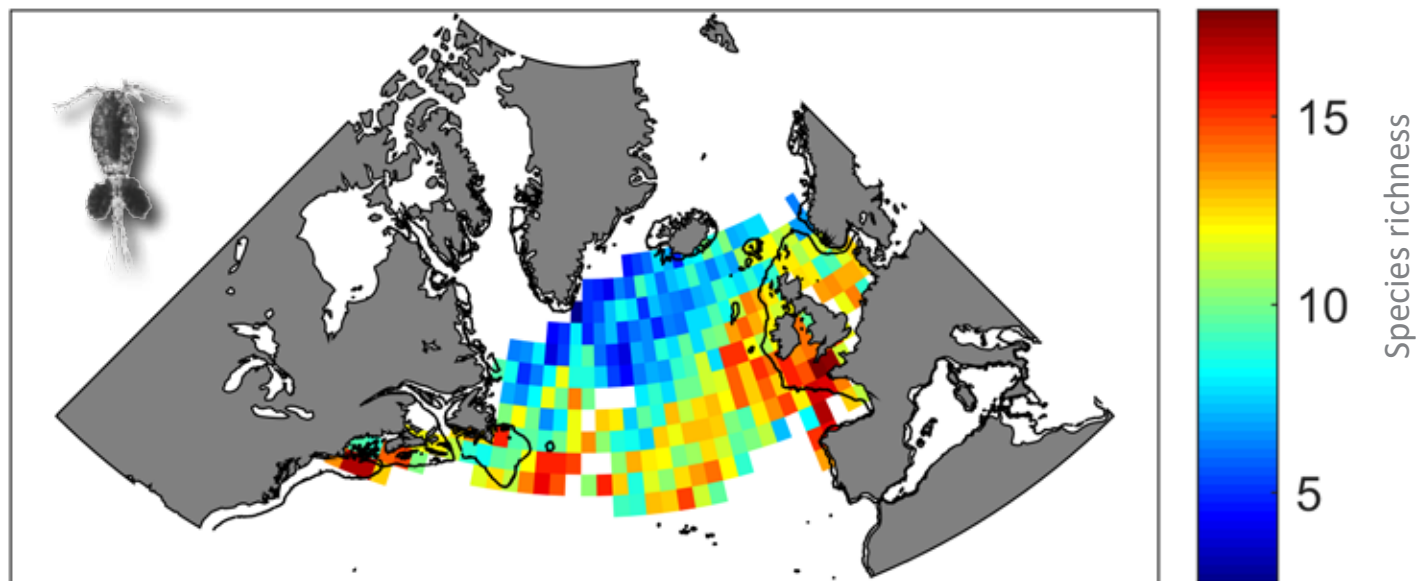


Fig.6. Diversity of small copepods (traverse) in the North Atlantic based on the species richness of each taxonomic group on the corresponding grid (2° latitude x 2°longitude).

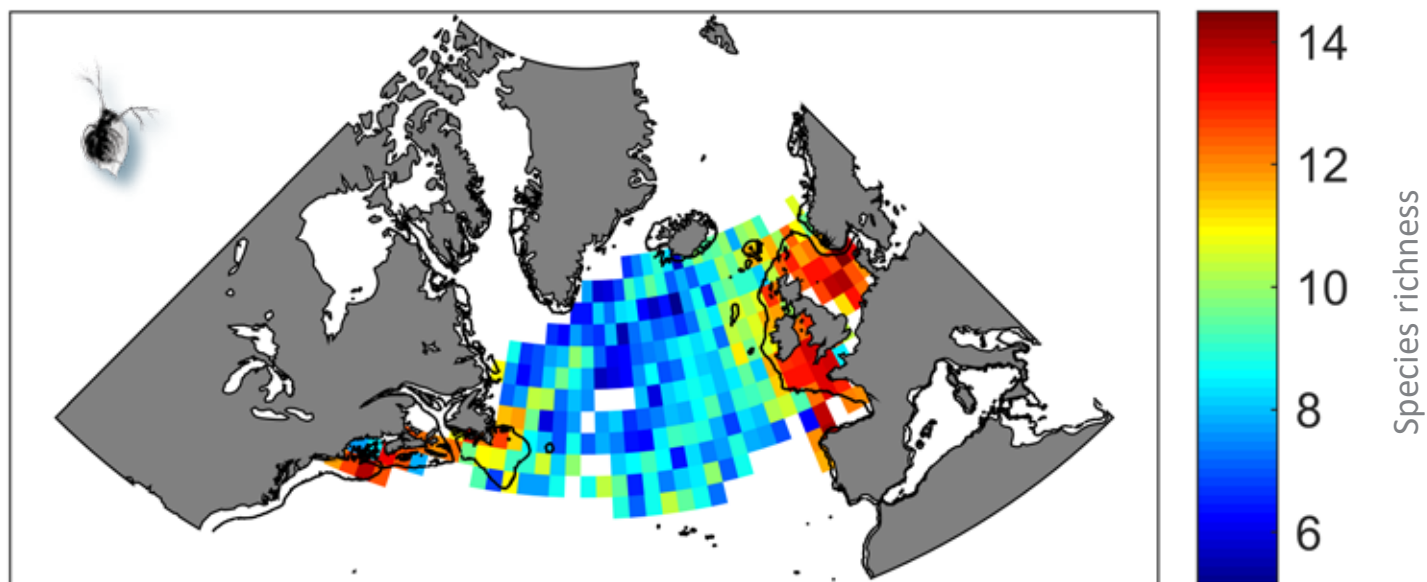


Fig.7. Diversity of small zooplankton (traverse and excluding copepods) in the North Atlantic based on the species richness of each taxonomic group on the corresponding grid (2° latitude x 2°longitude).

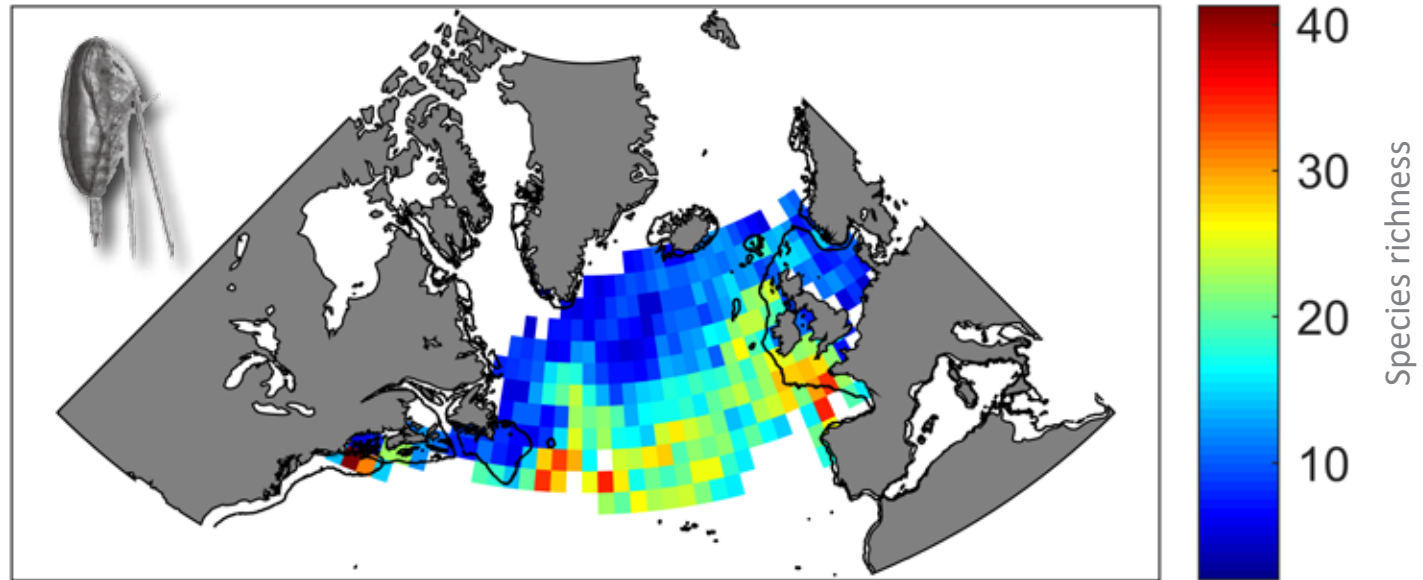


Fig.8. Diversity of large copepods (eyecount) in the North Atlantic based on the species richness of each taxonomic group on the corresponding grid (2° latitude x 2° longitude).

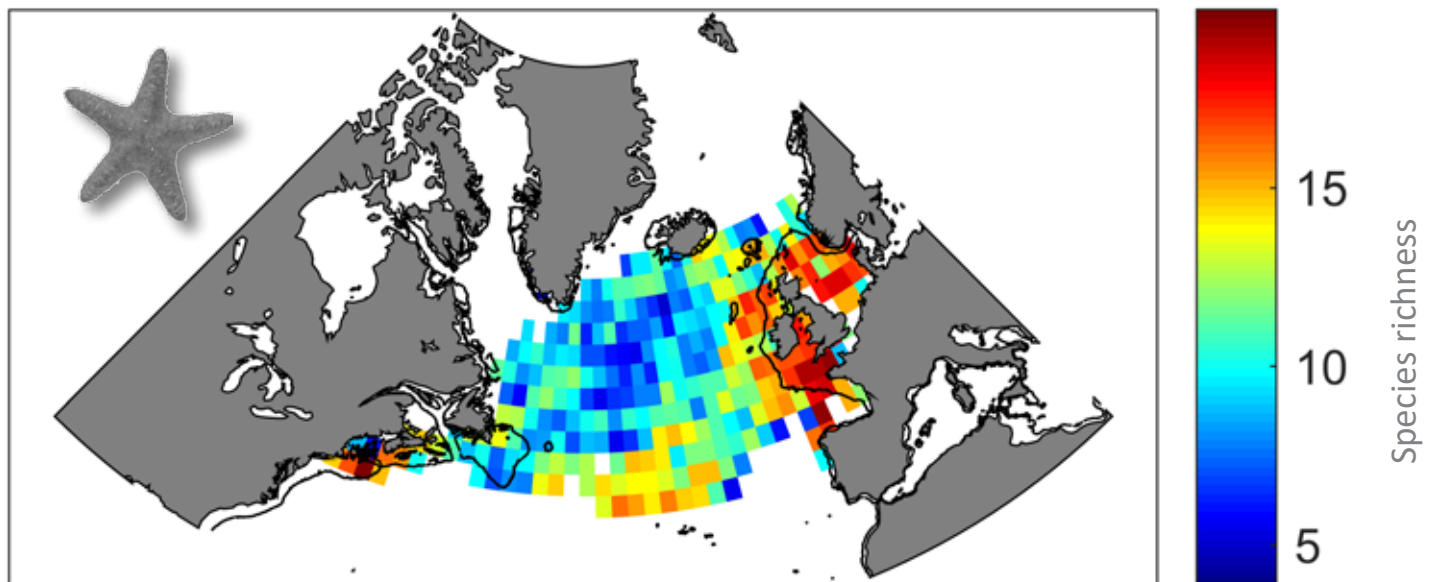


Fig.9. Diversity of large zooplankton (eyecount and excluding copepods) in the North Atlantic based on the species richness of each taxonomic group on the corresponding grid (2° latitude x 2° longitude).

Pelagic habitats and biodiversity of the North Atlantic

The first partition, resulting from a simple procedure based on expert knowledge, emphasizes 15 pelagic habitats (Fig. 3). The first three Pelagic Habitats (PHs hereafter) may have sea-ice concentration above 0 at least a part of the year. The first PH is the oceanic ice-influenced PH (200-11000m); it covers the Labrador Basin and part of the Irminger Basin. The second is the shelf-edges (200-1000m) ice-influenced PH. In the Labrador Basin, it channels the path of the Labrador Current that flows southwards. The third is the neritic (0-200m) Continental Shelves ice-influenced PH. In particular, it covers the Newfoundland Continental Shelf (e.g. Grand Banks). The fourth PH, the Oceanic Subarctic PH, has no sea-ice concentration. In the Atlantic area covered by the CPR survey, the first three PHs are delimited by the Subarctic Gyre. Salinity in those three PHs is lower in comparison to oceanic regions located eastwards and southwards. The fifth PH is the shelf-edges PH, which is found in all regions where sea-ice is absent (e.g. western part of Norway and European Shelf-edges). The sixth and seventh PHs are continental shelves where sea-ice is absent and where light is limited (in particular, light does not reach the benthos). The deep (50-200m) and shallow Continental Shelves pelagic habitat are well represented in the North Sea north and south of the Flamborough Front. The eighth PH, the continental shelves (light) pelagic habitat is marginally represented in the area under investigation. Some coastal areas of the Mediterranean Sea belong to this PH. The ninth PH, the Gulf Stream PH, has current velocity above the ninth decile (i.e. $D_9=0.62 \text{ m.s}^{-1}$). In oceanic areas characterized by a high salinity (higher than $Q_3=35.23 \text{ PSS}$), we distinguished 6 further PHs as function of their thermal regime: (10) oceanic subpolar PH (mean SST= $7-10^\circ\text{C}$), (11) oceanic cold-temperate PH (mean SST= $10-13^\circ\text{C}$), (12) oceanic temperate PH (mean SST= $13-16^\circ\text{C}$), (13) oceanic warm-temperate PH (mean SST= $16-19^\circ\text{C}$), (14) oceanic subtropical (north) PH (mean SST= $19-22^\circ\text{C}$), and (15) oceanic subtropical (south) PH (mean SST= $22-25^\circ\text{C}$).

We first assessed the biodiversity of all six taxonomic groups (Fig. 4-9). The taxonomic richness of diatoms was high around the British Isles and especially south of the Flamborough Front and the Celtic Sea (Fig. 4). On western part of the North Atlantic, biodiversity was high in Georges Bank, and the Nova Scotian Shelf and to a lesser extent north of the Newfoundland Shelf. Oceanic areas had in general low diatom taxonomic richness, with the exception of the oceanic cold-temperate and the temperate pelagic habitats along the Faroe-Iceland Rise and the European shelf-edge and in the northern part of oceanic subarctic pelagic habitat, especially over the Reykjanes Ridge.

The species richness of the genus *Ceratium* was high in oceanic areas south of the Oceanic Polar Front and especially over the Bay of Biscay and in neritic regions such as the

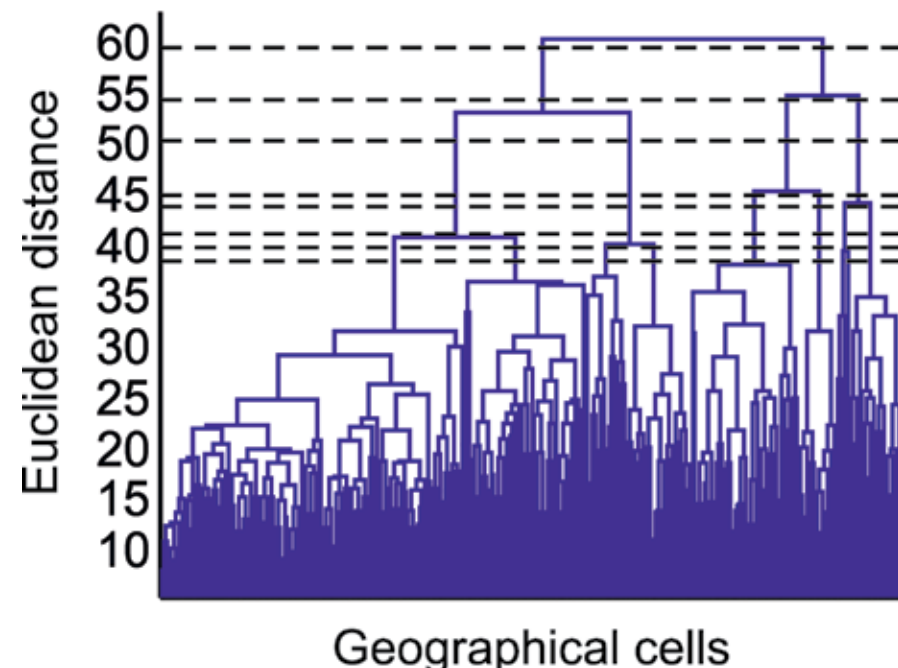
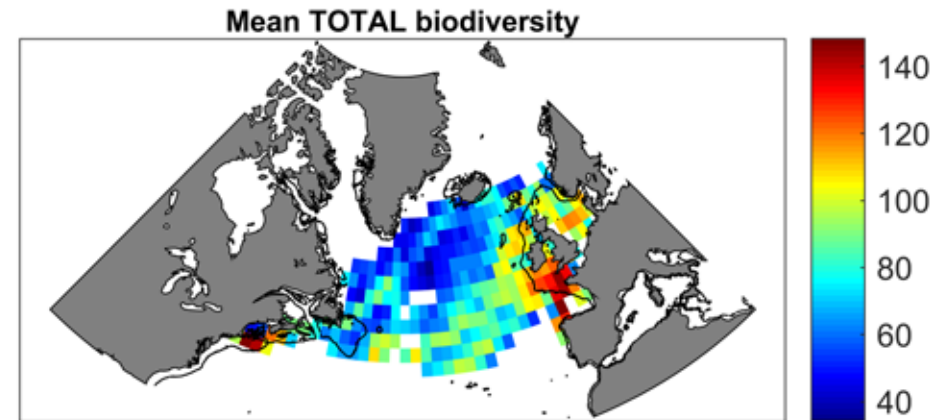


Fig.10. Mean total biodiversity of all groups combined. Agglomerative hierarchical clustering technique using average linkage for the all the geographical cells. For each partition, we examined the first 8 cut-off levels of the dendrogram.

Celtic Sea and Georges Bank (Fig. 5). Copepods also exhibited a similar pattern, although the biodiversity difference between the polar and the westerlies biomes was less acute for small copepods (Fig. 6). The taxonomic richness of small copepods was higher along the European Shelf-edge in both oceanic and neritic regions, south of the Flamborough Front in the North Sea and in Georges Bank and part of the Nova Scotian Shelf. Taxonomic richness was higher in the northern part of the Gulf Stream PH for all copepods. Large copepods did not show a high taxonomic richness south of the Flamborough Front in the North Sea and the biodiversity was less elevated along the European Shelf-edge and adjacent regions. The taxonomic richness of small zooplankton was similar to diatoms, although it was substantially higher in the Newfoundland Shelf for zooplankton. Large zooplankton exhibited a pattern closer to the species richness of dinoflagellate *Ceratium* (Fig. 5 versus Fig. 8), although biodiversity remained high in all neritic regions of the European Continental Shelf.

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) 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 (Fig 10.). 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. Unexpectedly and although less pronounced, a higher seasonal amplitude was also observed over the mid-Atlantic Ridge south of the Oceanic Polar Front.

Information of the taxonomic or species richness of all plankton groups for all 2-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 (Fig. 10). The first cut-off level separated neritic from oceanic areas. The European Continental Shelf was more clearly identified in contrast to the Newfoundland Shelf (Fig. 11). Some areas such as Rockall and the Faroe-Iceland Rises were also at least partially identified. The second cut-off level of the dendrogram separated the southern part of both American and European Continental Shelves, including the Bay of Biscay (Fig. 11). The third cut-off level enabled the separation of an oceanic region southwest to the Irish Sea, which is characterized by a pronounced seasonality in biodiversity and high phytoplankton and small copepod biodiversity. The fourth cut-off enabled the separation of small group that enable the identification of an area north of the North Sea and along the Faroe-Iceland ridge. Some cells were also identified over Georges Bank and the Bay of Biscay but the biological group lacked spatial contiguity. The fifth cut-off level allowed the identification of a group gathering together the Georges Bank and the Bay of Biscay. Although the sixth cut-off level did not allow the clear identification of a relevant biological group (Fig. 12), the next cut-off level identified an area belonging to oceanic subtropical and warm-temperate PHs and regions influenced by the Atlantic Meridional Overturning Circulation (AMOC) (Fig. 12). This cut-off level revealed the Oceanic Polar Front, which delineates the polar and the Westerlies biomes. The last cut-off level, as

well as others (not represented here) did not allow to better partition the area in a relevant way.

The final biological partition included only 8 biological groups, two (group 5 in the northern part of the North Sea and 6 in the Bay of Biscay) of which being poorly represented (Fig. 12). Group 1 represented in large part the polar biome and their ice-influenced, subarctic and cold-temperate PHs; Group 2 characterized the North Sea, Group 3 denoted the Celtic Sea and some areas over the European Shelf-edge, and a minor part of the Nova Scotian Shelf; Group 4 represented an oceanic area characterized by a high biodiversity south and west of the Irish Sea; Group 7 the oceanic temperate and warm-temperate PHs and Group 8 the northern edge of the Gulf Stream PH. We calculated an index to reveal the presence of pronounced spatial heterogeneity or ecotones. The index was highest over the Bay of Biscay and the Bay of Fundi, Georges Bank, Nova Scotian Shelf and to a lesser extent an area located to the north-west of Ireland. The index was also higher between the polar and westerlies biomes along the Oceanic Polar Front, the Gulf Stream PH and areas north of the North Sea and along the Faroe-Iceland Rise.

The same procedure was applied to identify biological groups at 0.5° x 0.5° spatial resolution. Fifteen biological groups were detected. Here also, some groups were only composed of a few geographical cells, which exhibited low spatial contiguity. We retained here 8 biological groups. Biological group 1 characterised the polar biome and the associated ice-influenced, subarctic and cold-temperate PHs. Some geographical cells penetrated to the North Sea. Although the previous partition at 2° x 2° spatial resolution identified only one biological group in the North Sea, the finer scale partition revealed three ecoregions: the central part of the North Sea (biological group 2) and an area south of the Flamborough Front (biological group 3). The second biological group also occurred in the northwestern part of the Celtic Sea and along the Nova Scotian Shelf, the shallow area of Newfoundland Shelf, stopping sharply at the shelf-edge. A fourth biological group was detected to the west of the British Isles; this group was similar to the group identified at 2° x 2° spatial resolution (biological group 4). The fifth biological group identified the north-eastern part of the Celtic Sea. Some isolated geographical cells also occurred in different places. The sixth and seventh groups were located mainly in the western and eastern part of the Bay of Biscay, respectively. ecoregions.



Biological classification of the North Atlantic Ocean

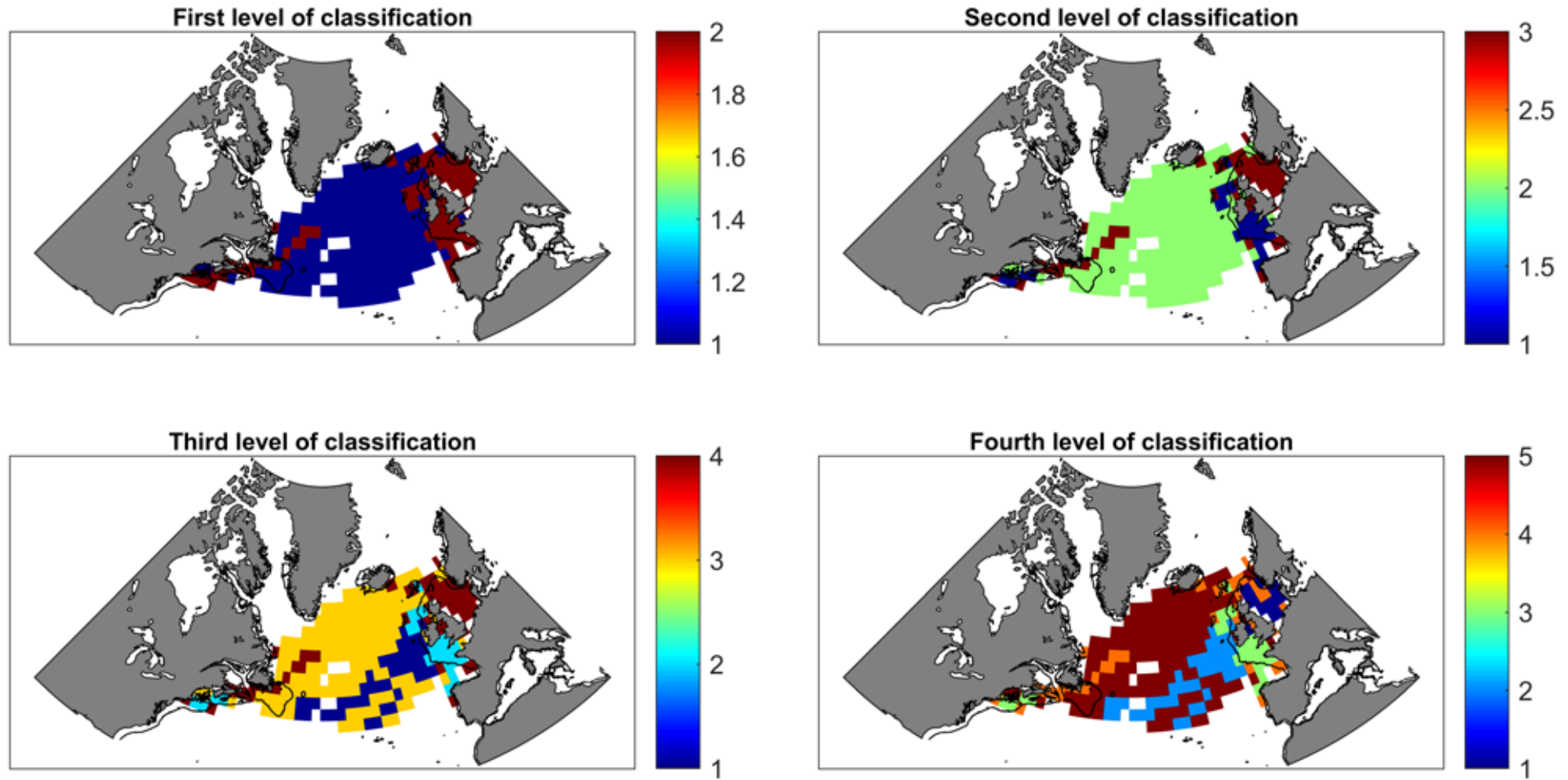


Fig.11. The first 4 levels of biological classification (1-4) in the North Atlantic based on the clustering of species richness of all taxonomic groups from a Principal Component Analysis on the corresponding grid (2° latitude x 2° longitude).



Biological classification of the North Atlantic Ocean

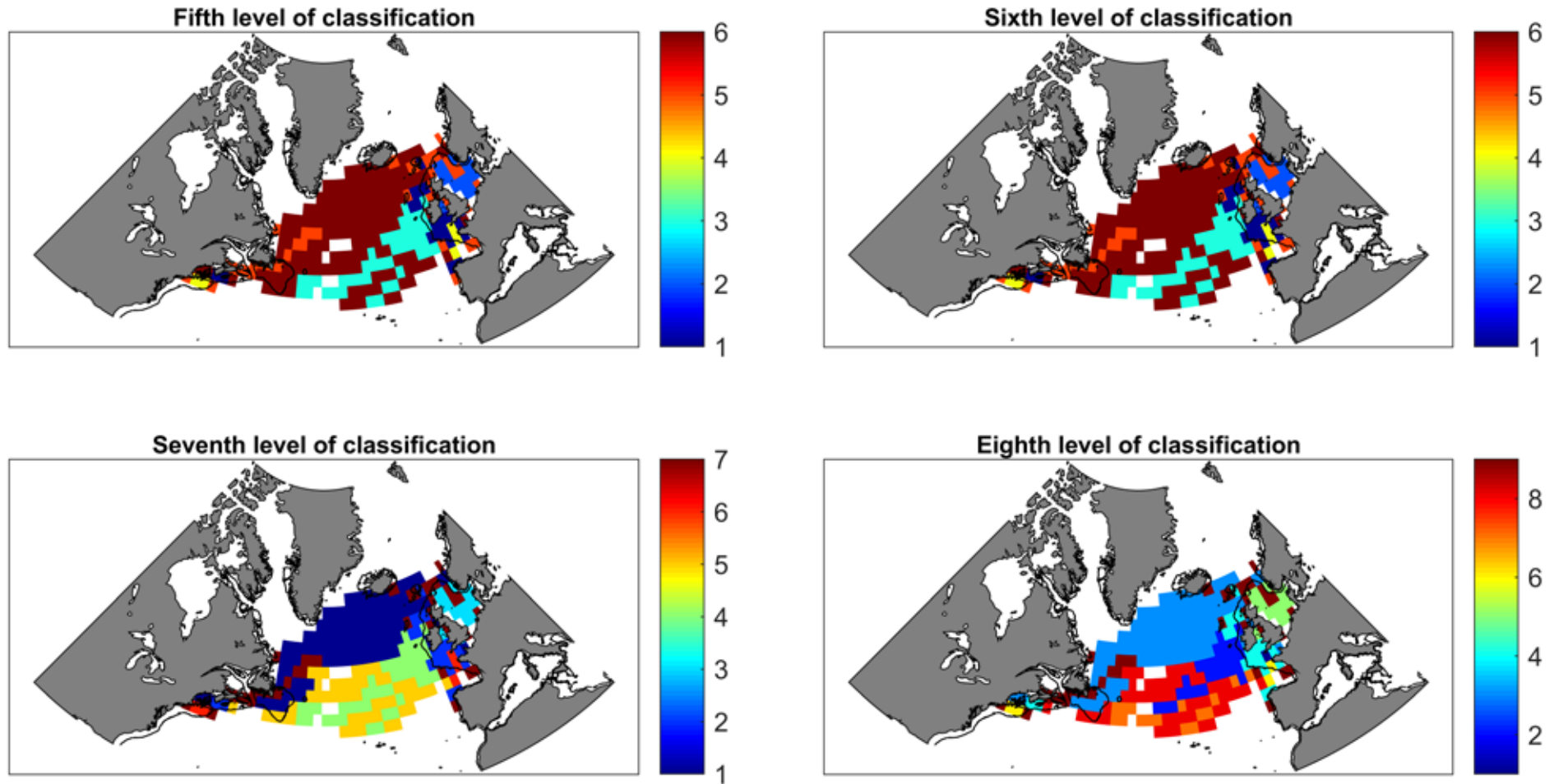


Fig.12. The second 4 levels of biological classification (5-8) in the North Atlantic based on the clustering of species richness of all taxonomic groups from a Principal Component Analysis on the corresponding grid (2° latitude x 2° longitude).

Final ecological partition of the North Atlantic

The final ecological partition was mainly based on the biological partition performed at the 0.5° x 0.5° spatial resolution for neritic regions, and the biological partition made at 2° x 2° for oceanic regions. We further divided some ecological units by using the PHs identified using some key ecogeographic variables (see Fig. 3). We used the term ecological unit because the same unit may be represented in different regions. As in the PH partition, we refer to the Longhurst's classification of biomes (Longhurst, 1998).

The final ecological partition we propose is made of 16 provinces and ecoregions or Regional Ecological Units, hereafter termed REUs (Fig. 13). Each REU has its own biodiversity (Fig. 4-9), seasonal biodiversity patterns and environmental conditions (Fig. 3). Widespread REUs could be further divided and some are composed of different ecoregions. Although their location did not match with our partition, the three Longhurst's biomes were clearly identified: (1) the Westerlies, (2) the Polar biomes and the Continental Shelves biomes. (Note that Longhurst termed originally this last biome a coastal biome (Longhurst, 1998). Our REUs or HPs did not correspond to Longhurst's provinces, with the exception of the Gulf Stream PH. Therefore, although we refer to some of his provinces, we did not consider the Longhurst's partition of the North Atlantic Ocean into provinces.

The Polar biome was divided into 3 REUs using information from the PH partition which included the Irminger Basin, Labrador Basin and Newfoundland shelf edge group. This latter REU is influenced by the Labrador Current, which transports cold water southwards. Some species such as the calanoid copepods *Calanus glacialis* and *C. hyperboreus* are highly abundant in this ecoregion. The biodiversity is very low in this ice-influenced area. In the region sampled by the CPR survey, this REU can be considered as representing a unique ecoregion. The second group was the Labrador Basin REU (15). This REU is in general characterized by low biodiversity, although diatom taxonomic richness is higher, especially to the south of the REU. The REU can be divided into 2 distinct regions: the Labrador Basin and a small oceanic ecoregion south of the Gulf of Saint Lawrence. The first ice-influenced ecoregion is the place where the diatom *Ephemera planamembranacea* is observed in high abundance. The third group in this area is the Irminger Basin area REU. This REU is not influenced by sea-ice and

has a salinity that remains below 35.23 in comparison to oceanic regions located to the east and the south. Biodiversity is low for all groups but seasonality can be higher, especially to the east. This REU may be divided into 2 ecoregions: (1) an ecoregion south of Iceland over the mid-Atlantic ridge and (2) a small ecoregion in the Norwegian Sea. This area is clearly a transitional area between arctic/subarctic temperate and cold-temperate species; for example, the diatoms *Leptocylindrus mediterraneus* and *Proboscia alata indica* and the dinoflagellates *Ceratium furca* and *C. lineatum* diminished substantially in this area in comparison to their eastern abundance. The copepods *C. finmarchicus* and *Paraeuchaeta norvegica* also decreased with respect to their western abundance. Some species of Hyperiididae are well represented in this region, although being not indicative of the REU. Many species are distributed in the first three REUs. For example, the copepods *C. finmarchicus*, *Paraeuchaeta norvegica* and *Euphausiacea* are highly abundant.

The next oceanic REUs were located to the eastern part of the Oceanic Polar Front and therefore belonged to the Westerlies biomes. This REU, representing only one ecoregion, was characterized by a higher biodiversity for all taxonomic groups and many species exhibit high abundance in this REU, although being not exclusively indicative of the region. For example, the diatom *Cylindrotheca closterium*, the dinoflagellate *Oxytoxum spp.* and the copepod *Pleuromma robusta* were highly abundant in this region. This REU exhibited a pronounced seasonal amplitude in taxonomic richness and is highly influenced by the path of the North Atlantic Current and associated strength and extent of the Subarctic Gyre.

The warm oceanic region and Porcupine Bight region and the Bay of Biscay ecoregion can be characterised by being quite productive and highly diverse. Seasonal amplitude remained elevated. The number of species abundant in this ecoregion was great, although here also no endemic species was identified. In particular, the richness of the genus *Ceratium* and small copepods was very high. The dinoflagellate *Ceratium hexacanthum* was indicative of this REU in the region covered by the CPR survey and *C. minutum* as well as *Gonyaulax spp.* and *Oxytoxum spp.* were also highly abundant. The high biodiversity was also reinforced by neritic species that expatriate from the



Combined biophysical ecological partition of the North Atlantic Ocean

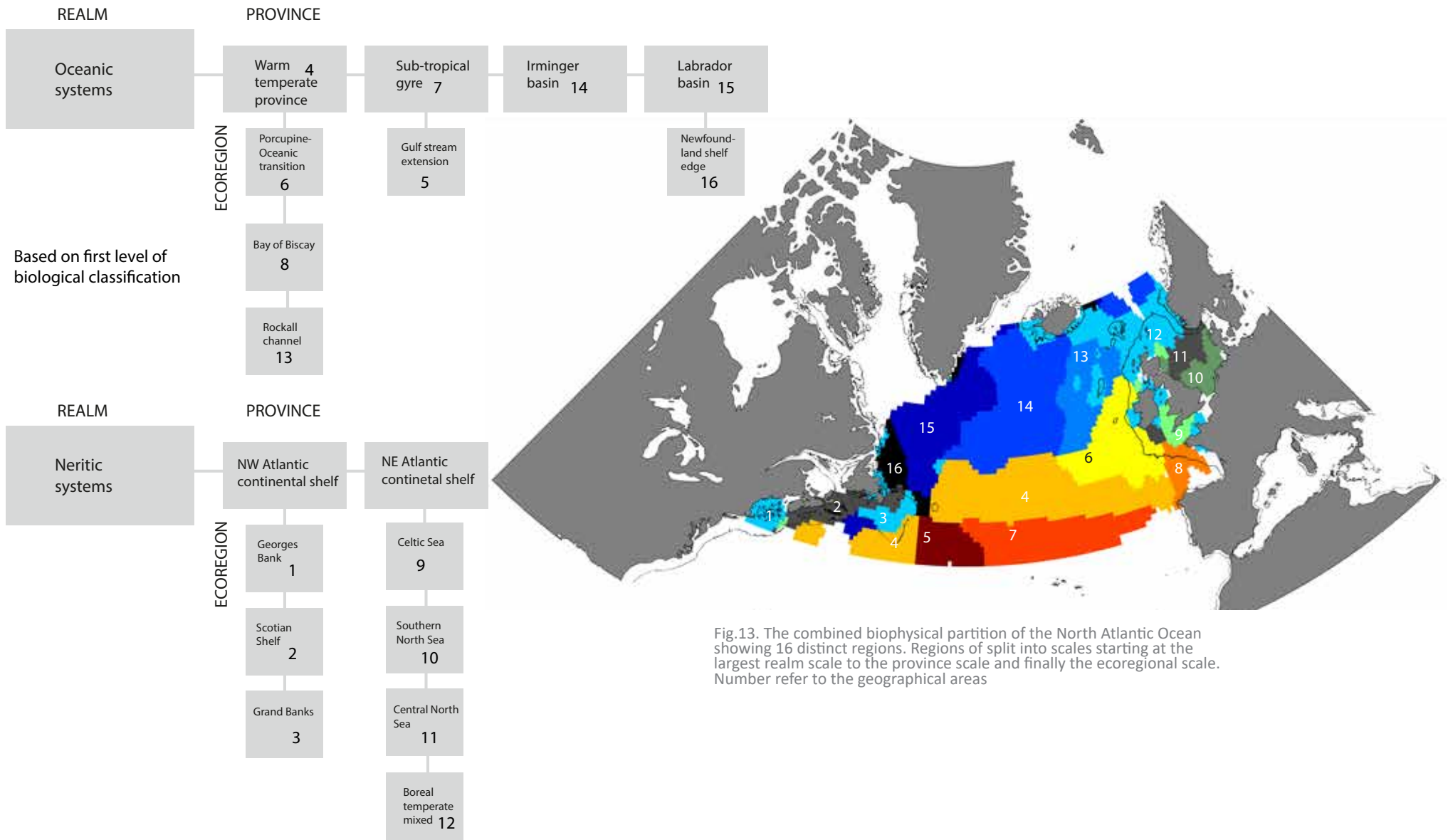


Fig.13. The combined biophysical partition of the North Atlantic Ocean showing 16 distinct regions. Regions of split into scales starting at the largest realm scale to the province scale and finally the ecoregional scale. Number refer to the geographical areas

continental shelf (e.g. holozooplankton *Pseudocalanus* spp. and meroplankton such as echinoderm larvae) and pseudo-oceanic species (species occurring above the oceanic and neritic regions but higher over the shelf-edge; e.g. *Ctenocalanus vanus*, *Candacia armata* and *Calanus finmarchicus*).

On the NW Atlantic continental shelf a further two regions can be found including the Georges Bank ecoregion and the Scotian shelf ecoregion. In particular, the biodiversity of small and large copepods, as well as the genus *Ceratium* in the eastern part of the main ecoregion, was high. In contrast, the other groups (zooplankton and diatoms) have a low biodiversity. Seasonal amplitude was substantially lower than most other regions, with the exception of the eastern side of the main ecoregion. Off the shelf in warmer oceanic waters a large number of oceanic species occurred in the main ecoregion of this REU, e.g. the copepods *Nannocalanus minor*, *Heterorhabdus papilliger*, *Euchaeta acuta*, *Lucicutia* spp, and the dinoflagellates *Ceratium azoricum*, *C. massiliense*, and *C. trichoceros*.

The Bay of Biscay ecoregion in particular is a very complex area as revealed by the index of heterogeneity, suggesting the occurrence of a large imbrication of ecosystems and ecotones. The high biodiversity in this region was explained by the high mean SST to the eastern part of the Bay of Biscay, and the co-occurrence of oceanic, pseudo-oceanic and neritic species from the distinct ecological units occurring at small spatial scales. The biodiversity was higher in compared to other oceanic regions and the seasonal amplitude was considerably reduced. Examples of species occurring in this REU were 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*.



Plankton Essential Ocean Variables

The global network of CPR surveys now routinely monitors the North Sea, North Atlantic, Arctic, North Pacific and Southern Ocean. Recent surveys are underway in the eastern Mediterranean, Australian, New Zealand, Japanese and South African waters while Brazilian and Indian Ocean survey activities began in 2016. This global network also brings together the expertise of approximately 70 plankton specialists, scientists and technicians from 14 laboratories around the world and has established links or formal affiliations with a number of key stakeholders including, Global Ocean Observing System (GOOS), GEO-BON, the International Oceanographic Commission (IOC), the Scientific Commission on Oceanic Research (SCOR), the International Council for the Exploration of the Sea (ICES), the Partnership for Observation of the Global Oceans (POGO) and the North Pacific Marine Science Organization (PICES).

It is recognised that there is an increasing need to monitor the marine environment as part of global initiatives like the development of 'Essential Ocean Variables (EOVs) for the Global Ocean Observing System (GOOS). Of particular relevance to the CPR survey and AtlantOS at an Atlantic wide and global perspective are some of the recent recommendations given by G7 Ministers of Science to 'the future of the seas and oceans' and include:

- Continuing critical regional observing in the tropics and maintaining and enhancing our observing capacity in the marine cryosphere (Arctic and Antarctic)
- Enhancing the effective use and international coordination of research ships and satellites to leverage their unique capabilities in the ocean observing strategy
- Fostering increased collaboration with the shipping industry on ocean observations to explore increasing use of commercial fleets for observing of the ocean and seas.
- Supporting and accelerating the development and implementation of ecosystem/biodiversity Essential Ocean Variables (EOVs) for routine implementation
- ensure sustainable science-based ocean management and provide clarity on resource-management
- promote observing and data sharing and development of products and models that provide integrated ocean state knowledge
- promote co-ordination with relevant activities of the Intergovernmental Panel on Climate Change/ Intergovernmental Platform on Biodiversity and Ecosystem Services

SAHFOS scientists have already been taking an active lead in developing ecosystem EOVs (identified in the G7 statement) through its involvement with the GOOS panel on Biology and Ecosystems (Grimes, 2014) and with the GEO-BON Working group 5 (marine ecosystem change). As part of its involvement with these organisations, SAHFOS is helping to develop biological and ecosystem Essential Ocean Variables (EOVs) through its involvement with the AtlantOS framework programme which aims to build a North Atlantic wide integrated observing system.

A key component for the success of EOVs is the need for the variable to have a high impact in responding to scientific and societal needs and crucially to have a high feasibility of sustained observation. Ocean observations are the 'bread and butter' of ocean and climate change science (Cai et al., 2014) and the network of CPR surveys operating around the world were seen as a critical ongoing network for a sustained and internationally coordinated effort for biological observation at the global scale (Constable et al., 2016).

An important goal of the global CPR programme is to develop indicators for scientists and policy makers to monitor and understand global plankton changes as well as providing the global community with useful products such as EOVs that can be used to monitor and assess marine biodiversity and ecosystem health. Once there has been international agreement on what ecosystem EOVs are required SAHFOS will primarily disseminate them through SAHFOS's Ecological Status Report and through international programmes such as GOOS, GEO-BON and the EU AtlantOS programme. Although at this stage of development the biological and ecosystem EOVs have not been formalised they will come under the general heading of phytoplankton biomass and diversity; zooplankton biomass and diversity; fish abundance and distribution; marine turtles, birds and mammals abundance and distribution; live coral; seagrass cover; mangrove cover and macroalgal canopy. In the context of the CPR survey and AtlantOS we are particularly concerned with the phytoplankton and zooplankton variables that will aim to address the biological phenomena shown in figure 14.



Developing phytoplankton and zooplankton Essential Ocean Variables for monitoring biology and ecosystems

1. Societal drivers

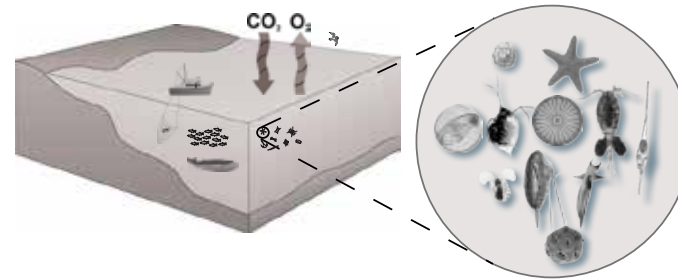
- Sustainable economic growth/development
- Conservation/ biodiversity
- Improved management/ ecosystem approach
- Capacity building and technology transfer
- Food security - fishing/aquaculture
- Environmental quality and health
- Energy production

2. Societal pressures

- Climate change
- Ocean acidification
- Extreme weather events
- Loss of resources/habitats
- Overfishing
- Seabed mining
- Solid wastes/ marine litter
- Pollution/eutrophication
- Invasive species
- Coastal development

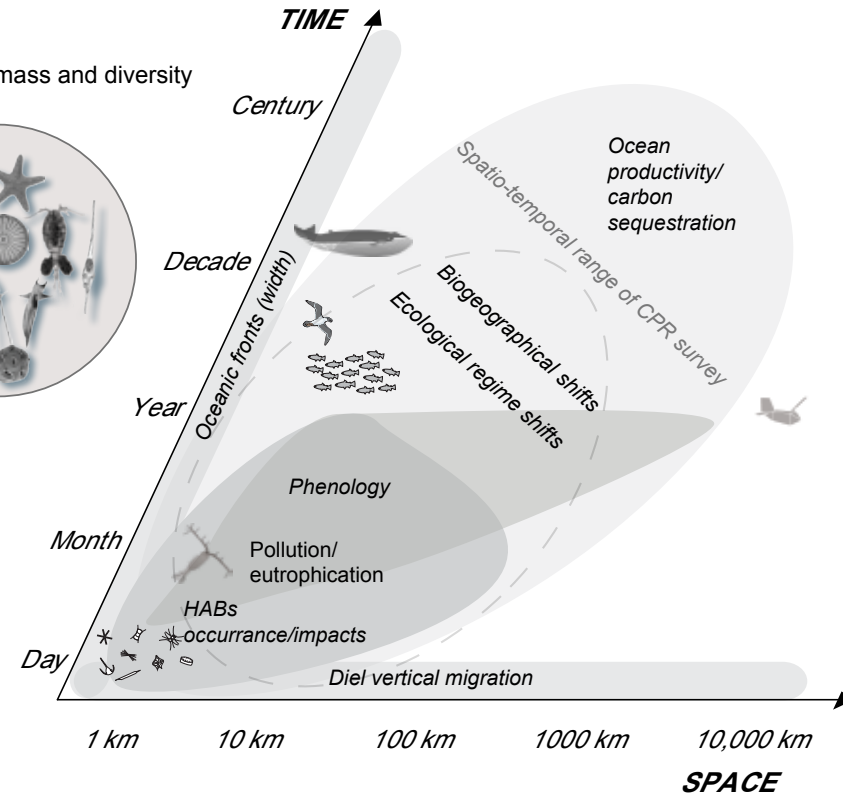


Biological EOVs: phytoplankton and zooplankton biomass and diversity



3. Scientific questions

- What is the current status of life and biodiversity in the oceans?
- How is life in the oceans changing?
- What are the natural and anthropogenic drivers of change?
- Are HAB events increasing in frequency or spatial location?
- Are invasive species increasing?
- How does the changing life in the oceans affect ecosystem function (health and services)?



4. Biological phenomena to capture (plus spatio/temporal scales)

- Phenology
- Occurrence of Harmful Algal Blooms (HABs)
- Biogeographical shifts
- Biodiversity/invasive species
- Impact on calcareous organisms
- Ecological regime shifts
- Ocean productivity
- Carbon sequestration

Fig.14. A schematic representing the main societal drivers and pressures and the biological phenomena used to capture these changes in our oceans. From a plankton and monitoring perspective many of the processes to be addressed occur on a number of spatial and temporal scales which equally needs a monitoring system operating on similar scales such as the CPR Survey network.



North Atlantic biological EOVs

As part of the AtlantOS project new habitats have become redefined based on the biological communities there and become new ecoregional areas for the North Atlantic. From the new habitats and ecoregions defined by the ecological partition of the North Atlantic, we calculated monthly means from 1958 to 2016 for all 16 new ecoregions. The preliminary and basic biological EOVs for each region at this stage included the Phytoplankton Colour Index, Total Diatom abundance, Total Dinoflagellate abundance and Total Copepod abundance. The Figures 15-18 show regional trends in standard areas generated using standard statistical methods for calculating annual means.

To summarise the long-term trends in plankton in the North Atlantic Basin we used preliminary EOVs of plankton that included the CPR Phytoplankton Colour Index (PCI) and the sum of the abundance of all counted diatoms and all counted dinoflagellates and total copepod numbers and mean copepod size. Using basic and bulk indices like this are less sensitive to environmental change and will quite often mask the subtleties that individual species will give you; however, it is thought that these bulk indices represent the general functional response of plankton to the changing environment. In the North Atlantic, at the ocean basin scale and over multidecadal periods, changes in plankton species and communities have been associated with Northern Hemisphere Temperature (NHT) trends, the Atlantic Multidecadal Oscillation (AMO), the East Atlantic Pattern (EAP) and variations in the North Atlantic Oscillation (NAO) index. These have included changes in species distributions and abundance, the occurrence of sub-tropical species in temperate waters, changes in overall plankton biomass and seasonal length, changes in the ecosystem functioning and productivity of the North Atlantic (Beaugrand, et al. 2003; Edwards, et al. 2002; Edwards & Richardson, 2004)

It must be noted, however, that climate variability has a spatially heterogeneous impact on plankton in the North Atlantic and not all regional areas are correlated to the same climatic index. For example, trends in the AMO are particularly prevalent in the oceanic regions and in the sub-polar gyre of the North Atlantic and the NAO has a higher impact in the southern North Sea where the atmosphere-ocean interface is most pronounced (Harris et al. 2013). This is also apparent with respect to the Northern Hemisphere Temperature where the response is also spatially heterogeneous with areas of the North East Atlantic and shelf areas of the North West Atlantic warming faster than the North Atlantic average and some areas like the sub-polar gyre actually cooling. Similarly, regime shifts or abrupt ecosystem shifts do not always occur in the same region or at the same time. The major regime shift that

occurred in plankton in the late 1980s was particularly prevalent in the North Sea and was not seen in oceanic regions of the North Atlantic. However, a similar regime shift occurred in the plankton colour index 10 years later in the Icelandic Basin and in oceanic regions west of the British Isles. The different timing and differing regional responses to regime shifts have been associated with the movement of the 10°C thermal boundary as it moves northwards in the North Atlantic (Edwards et al. 2013).

In examining the long-term trends in the plankton indices, the general pattern is an increase in PCI for most ecoregions in the North Atlantic with differing timings for the main step-wise increase being later in oceanic regions compared to the North Sea. For the dinoflagellates there has been a general increase in abundance in the North West Atlantic and a decline in the North East Atlantic over a multi-decadal period (see Fig. 16). In particular, some regions of the North Sea have experienced a sharp decline over the last decade. This decline has been mainly caused by the dramatically reduced abundance of the *Neoceratium* genus in the North Sea. However, *Neoceratium* abundance has recovered in the North Sea over the last 5 years. For the diatoms there is not really a predominant trend for the North Atlantic Basin as a whole but some regions show a strong cyclic behaviour over the multidecadal period. The time signal resembles an oscillation of about 50-60 years and a minimum around 1980 reflecting changes in the AMO signal. Trends in copepod abundances have been more stable in offshore regions but have shown a decrease in abundance, particularly in the southern North Sea ecoregion (10) (Fig.18). In summary, while climate warming is a major driver for the overall biomass of phytoplankton, diatoms are less influenced by temperature and show a strong correlation with the AMO signal and wind intensity in many regions (Harris et al. 2013). The increase in diatoms associated with the positive phase of the AMO and the decline in dinoflagellate abundance over the last 10 years in the NE Atlantic can be reflected in the diatom/dinoflagellates ratio favouring diatoms.

Phytoplankton abundance (PCI)

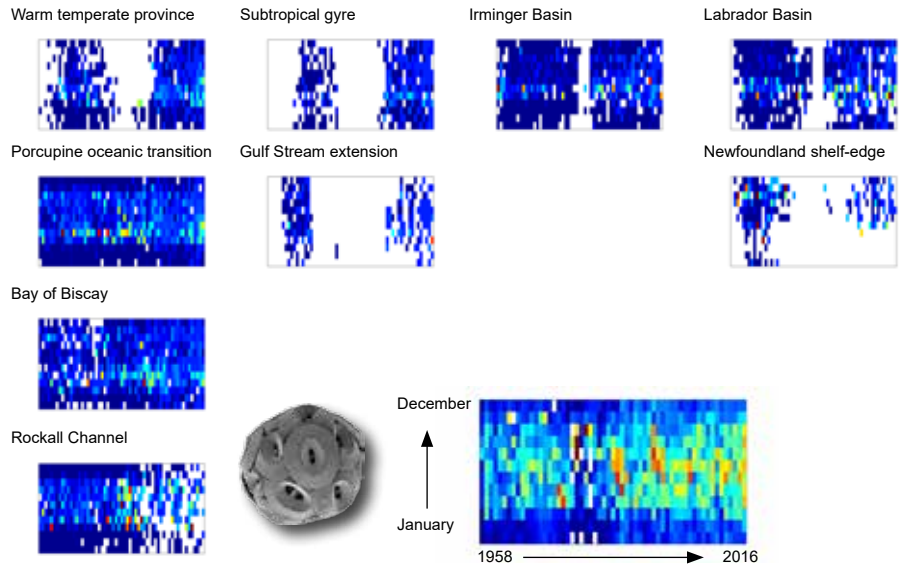
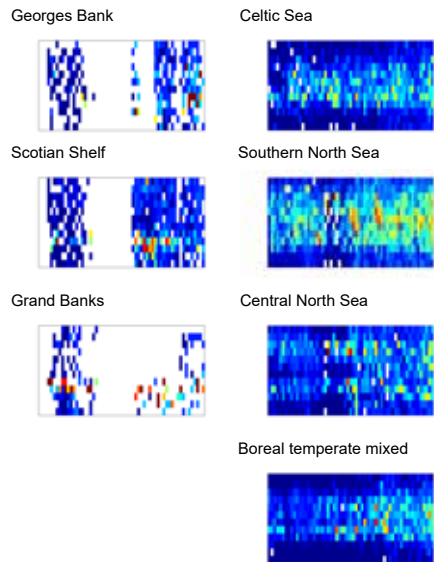


Fig.15. Phytoplankton Colour Index (PCI) for the 16 habitats and ecoregions of the North Atlantic. Data is monthly means from 1958 to 2016.



Diatom abundance

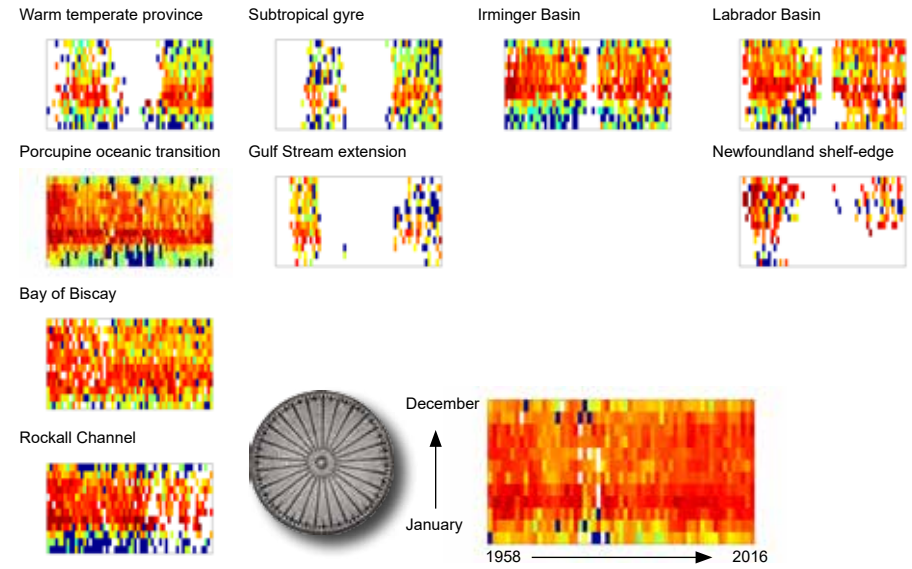
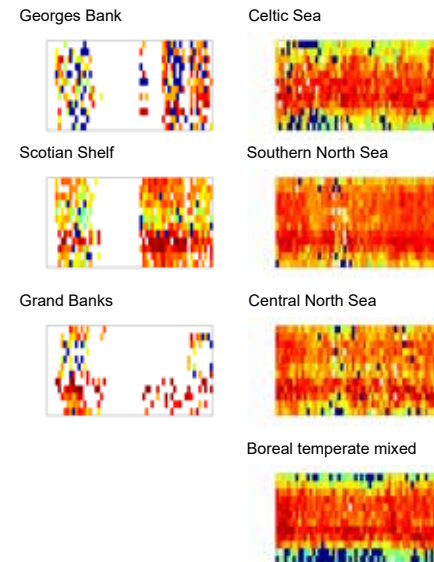


Fig.16. Total diatom abundance for the 16 habitats and ecoregions of the North Atlantic. Data is monthly means from 1958 to 2016.



Dinoflagellate abundance

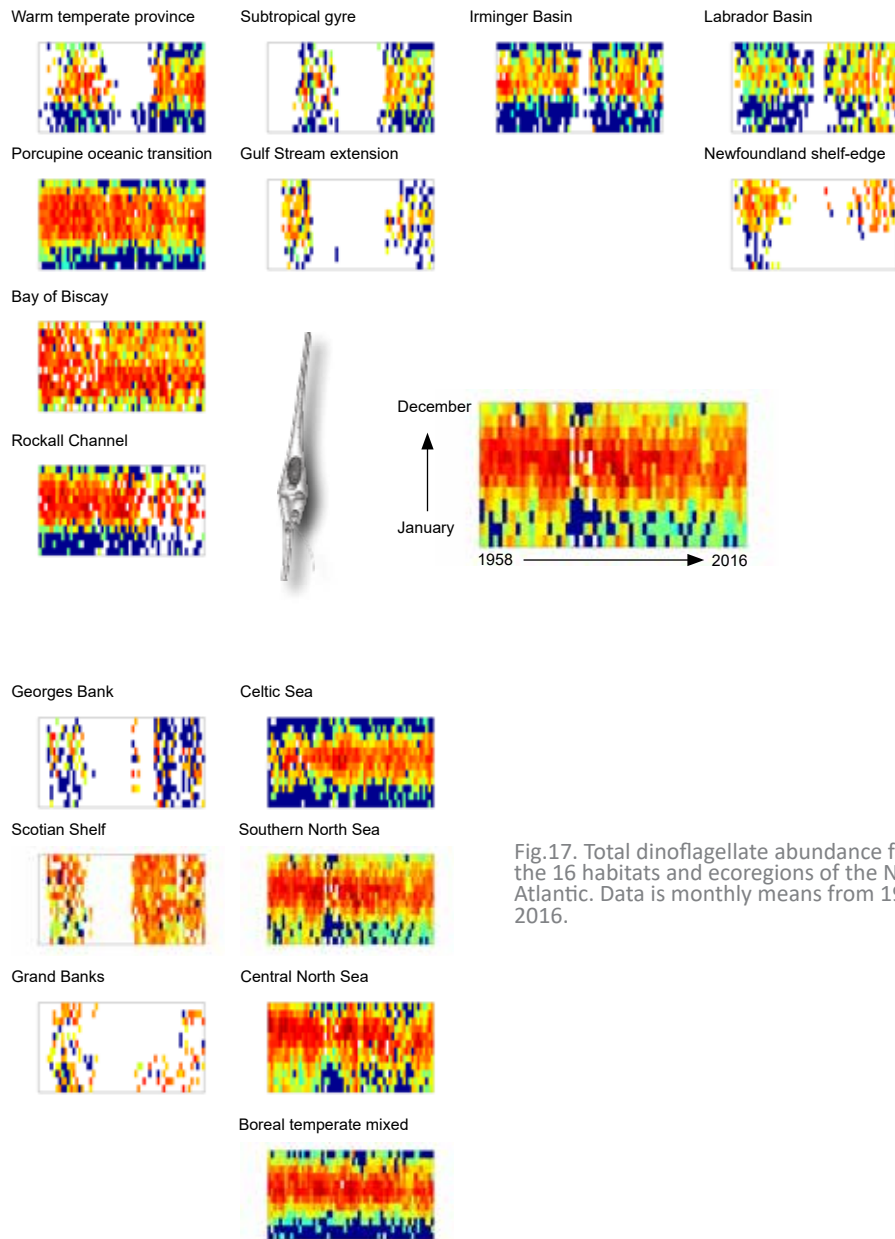


Fig.17. Total dinoflagellate abundance for the 16 habitats and ecoregions of the North Atlantic. Data is monthly means from 1958 to 2016.

Copepod abundance

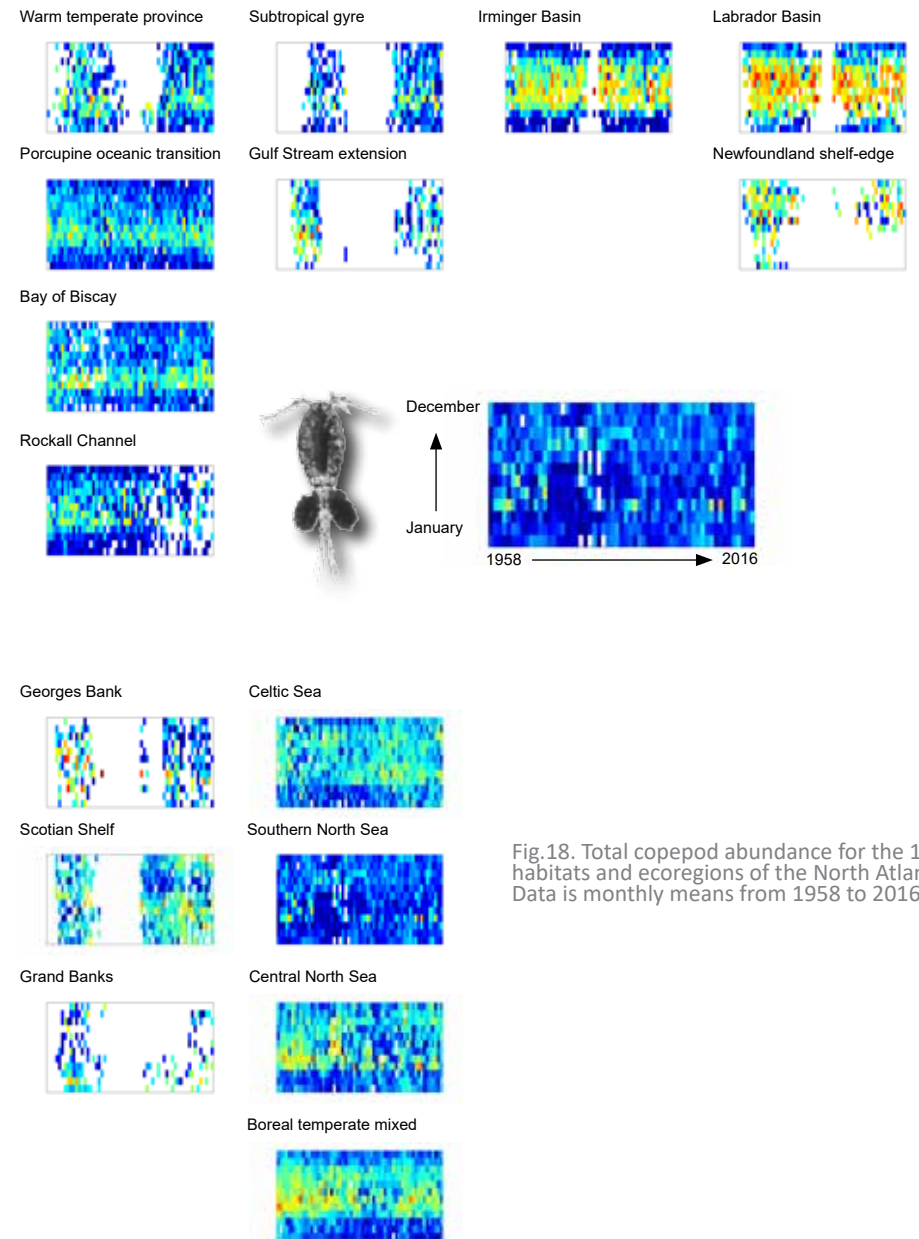


Fig.18. Total copepod abundance for the 16 habitats and ecoregions of the North Atlantic. Data is monthly means from 1958 to 2016.

The Sir Alister Hardy Foundation for Ocean Science (SAHFOS) is an internationally funded independent research organisation (Canada, Norway, UK and the USA) that operates the Continuous Plankton Recorder (CPR) survey. The Foundation has been collecting data from the North Atlantic and the North Sea on biogeography and ecology of plankton since 1931. More recently, work has been expanded to include other regions and organisations around the globe to create a global cooperative. The results of the survey are used by marine biologists, scientific institutes and in environmental change studies across the world. The international SAHFOS team is based in Plymouth, England and consists of analysts, technicians, researchers from around the world.

AtlantOS is an EU research and innovation project that proposes the integration of ocean observing activities across all disciplines for the Atlantic. The vision of AtlantOS is to improve and innovate Atlantic observing by using the Framework of Ocean Observing to obtain an international, more sustainable, more efficient, more integrated, and fit-for-purpose system. The overarching target of the AtlantOS initiative is to deliver an advanced framework for the development of an integrated Atlantic Ocean Observing System that goes beyond the state-of-the-art, and leaves a legacy of sustainability after the life of the project. The project consists of 62 (research institutes, universities, marine service providers, international partners, private sector) from 18 countries (13 EU & 5 non-EU) plus supporters.



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