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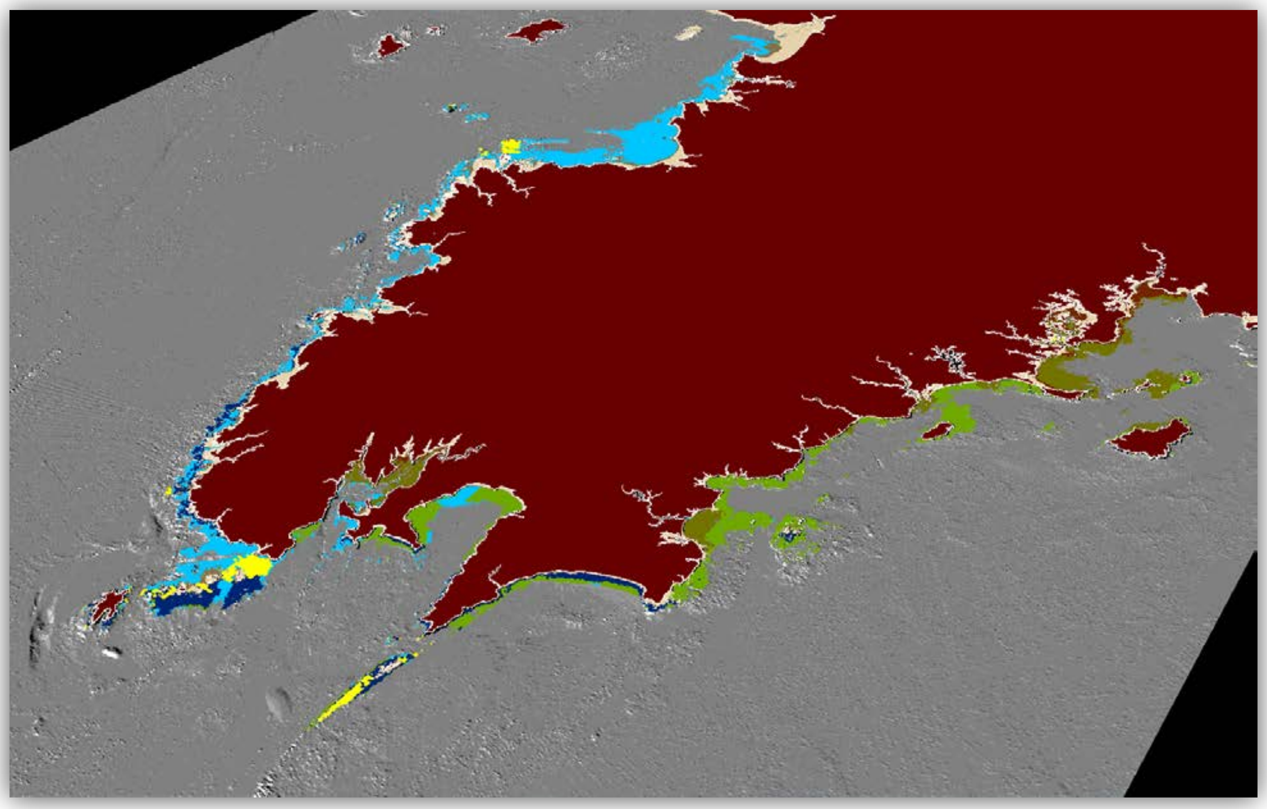
BRITTANY'S INFRALITTORAL SEABED: An objective partitioning into marine ecological units



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Résumé :

Les patrons de distribution des espèces et communautés marines sont largement régulés par les propriétés physico-chimiques des eaux environnantes. La mise à disposition de nouvelles couches environnementales à résolution sub-kilométrique s'avère, par conséquent, d'une grande utilité pour cartographier de façon objective les paysages écologiques marins en vue d'interpréter des patrons biogéographiques, optimiser les campagnes à la mer ou planifier de manière adéquate les expérimentations *in situ*.

Le présent rapport a pour objet la segmentation à haute résolution des fonds marins infralittoraux de la Bretagne en zones aux conditions environnementales analogues. Six facteurs abiotiques majeurs régissant la distribution spatiale des communautés biologiques infralittorales sont utilisés pour composer l'espace environnemental, à savoir : la température, la salinité, l'oxygène, la lumière, l'énergie cinétique due aux vagues et l'énergie cinétique induite par les courants. Chaque facteur se présente dans l'analyse sous la forme d'un raster climatologique caractérisant les conditions moyennes au fond calculées à partir de séries pluriannuelles issues des modèles océanographiques ou de l'imagerie satellitaire de dernière génération.

Un partitionnement non-supervisé par la méthode des k-médoïdes, assistée par une estimation du nombre optimal de clusters, est utilisé pour regrouper statistiquement les points représentant l'espace environnemental, décrits uniquement par leurs attributs environnementaux. Le résultat met en évidence une série de zones benthiques écologiquement similaires qui sont en accord avec les patrons écologiques connus en Bretagne par les experts, mais dont les contours étaient flous. La démarcation Nord/Sud en Bretagne est ainsi bien capturée, de même que d'autres unités écologiques particulières telles que (i) les baies, (ii) les zones à influence estuarienne, (iii) les zones côtières exposées aux vagues, et (iv) les secteurs exposés aux courant. L'analyse met aussi en évidence des petites enclaves écologiques isolées géographiquement de leurs analogues plus étendus.

Grâce à une bonne représentation des conditions aux abords des fonds marins, le résultat permet de meilleures interprétations du compartiment benthique que les résultats issus des analyses précédentes qui utilisaient des conditions de surface ou moyennées

verticalement sur la colonne d'eau. Le succès de l'approche démontre la capacité à analyser et à valoriser une grande quantité de données environnementales originales produites à l'Ifremer pour cartographier avec plus de détail les paysages écologiques marins.

Abstract

Marine biological distribution patterns are largely regulated by the physico-chemical properties of the overlying waters. The availability of new environmental layers with sub-kilometric resolution is therefore of great use to map marine in objective ways and therefrom interpret biogeographic patterns, optimize region-wide field surveys or plan *in situ* experiments.

This report presents a data-driven high-resolution partitioning of Brittany's infralittoral seabed environment areas with comparable environmental conditions. Six major abiotic drivers of shallow-water biological communities are used to compose its environmental space, notably: temperature, salinity, oxygen, light, wave-induced kinetic energy and baroclinic currents kinetic energy. Each parameter is represented in the analysis by a climatologic raster corresponding to average conditions at seabed computed from multiannual series extracted from latest generation oceanographic models and satellite imagery.

A k-means unsupervised partitioning, assisted by an optimal cluster number estimation, is used to statistically partition the points representing the environmental space, which are exclusively described by their environmental attributes. Mapping of the clustered data depicts spatially-coherent areas that match ecological divisions traditionally-recognised in Brittany by experts but which previously lacked a fine and objective spatial delimitation. The divide between northern and southern Brittany is successfully demarcated as well as specific ecological conditions associated to (i) bays, (ii) areas influenced by freshwater outflows, (iii) swell-exposed coastal stretches and (iv) current-exposed sectors. The analysis further highlights small ecological enclaves geographically isolated from their larger analogues.

By representing conditions at seabed in great detail, the result permits a better understanding of the benthic compartment than previous analyses based on surface and/or vertically-integrated conditions. The approaches success demonstrates the capacity to analyse and exploit Ifremer wealth of novel environmental datasets to objectively map marine ecological units.

Mots-clés/ Key words :

écorégionalisation, paysages écologiques benthiques, partitionnement statistique, Bretagne, infralittoral

ecoregionalisation, benthic ecological units, statistical partitioning, Brittany, infralittoral

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1. Introduction

The distribution patterns of benthic marine biota are largely regulated by the physico-chemical properties of the overlying waters. Exploiting objective data and methods to map areas showing comparable conditions at regional scales (ecoregions) is key for macroecological research as well as for planning and implementing ecosystem-based management measures.

Over the last few decades, full-coverage environmental layers derived from satellite imagery of the ocean and oceanographic models have become increasingly available. This has allowed marine ecoregionalisation studies to become more quantitative and objective (*e.g.*, Commonwealth of Australia, 2006; Douglass et al., 2014; Reygondeau et al., 2017; Sayre et al., 2017). In France, similar analyses were made in the scope of the implementation of the Water Framework Directive (WFD) and the Marine Strategy Framework Directive (MSFD) covering the mainland seaboards (ex. : Huret et al., 2012a,b,c; Gailhard-Rocher et al., 2012) as well as overseas ones (Lazure, 2004).

By using vertically-integrated information derived from oceanographic models and ocean surface satellite imagery, the resulting segmentations concentrated on environmental drivers and patterns of the water column (pelagic domain). Seabed environments were not addressed specifically, despite differences relative to the overlying water mass growing as we move away from shallow well-mixed settings.

For that reason, a delimitation of benthic ecological unit suitably based upon temperature, light, salinity and hydrodynamics conditions at seabed is still due.

Over the last few decades, Ifremer has successfully implemented validated oceanographic models such as WAVEWATCH III, MARS3D or ECOMARS3D that continually generate geospatial information on an abundance of bio-physico-chemical parameters known to regulate benthic communities. Depending on the model, outputs may attain hourly time steps, sub-kilometric spatial resolutions, tens of depth levels and represent multi-annual time series (for more detail see Boudière et al., 2013; Lazure & Dumas, 2008; Ménesguen et al., 2019). Resolving environmental conditions down to the seabed in such spatio-temporal detail opens the door to extract robust environmental climatologies as well as envisages very fine partitioning of the marine environment, ultimately in 3 dimensions.

The present work demonstrates this opportunity by exploiting sub-kilometric multi-annual climatological rasters to perform a non-supervised multivariate partitioning of Brittany’s infralittoral domain (France, NE Atlantic). Areas with similar environmental conditions (ecoregions) are thereby delimited throughout the intricate mosaic of distinct environmental gradients that overlap along Brittany’s 2860-km length coastline. The result provides a stratification basis for optimizing sample distribution in the scope of projects IDEALG and MARHA but is of further use to investigate and manage Brittany’s infralittoral domain.

2. Methodology

2.1. Study area

Brittany is the northwest-most region of mainland France. Its 2.860km-length coastline encompasses a major biogeographical transition zone between cold-temperate and warm-temperate waters in the northeast Atlantic (Spalding et al., 2007). The northern shores (Manche) are characterised by well-mixed waters produced by a macrotidal regime that intensifies eastwards. Contrastingly, the waters to the south are seasonally to permanently stratified and therefore show larger temperature fluctuations throughout the year (*e.g.*, Blauw et al., 2019). Brittany's western-most sector is subject to the macrotidal regime as well as the full impact of Atlantic storms, which jointly produce well-mixed waters with colder and more stable temperatures. Ushant's thermo-haline front, which forms in the Iroise Sea during summer months (Le Fèvre, 1986), is the prime expression of Brittany's ecotone, with the English Channel's tidally-mixed waters encountering the Celtic Sea's thermally-stratified open waters.

Owing to the confluence of cold and warm-affinity species, Brittany is considered a biodiversity hotspot (Kerswell, 2006; Santelices et al., 2009; Gallon et al, 2017). The cold-water enclave of western-most Brittany constitutes a climate warming refuge for biota benefiting from a buffered oceanographic regime (Provan, 2013) but pole-ward shifts and/or range constrictions have nonetheless been observed around Brittany during the last few decades (Gallon et al., 2014).

2.2. Environmental space

A way of characterizing the marine environment around Brittany objectively and systematically is to resort to full-coverage rasters extracted from validated oceanographic modelling outputs and satellite imagery archives. For this study, a series of climatological rasters were derived from datasets held by Ifremer, namely in its LOPS and DYNECO units. The rasters represent multiannual average conditions at seabed level for six major drivers of shallow-water biological communities: Temperature, Salinity, Light, Wave-induced kinetic energy, Current-induced kinetic energy and Oxygen (**Figure 1**). Further specifications on the source models, averaged periods or native resolutions are presented in **Table** 1.

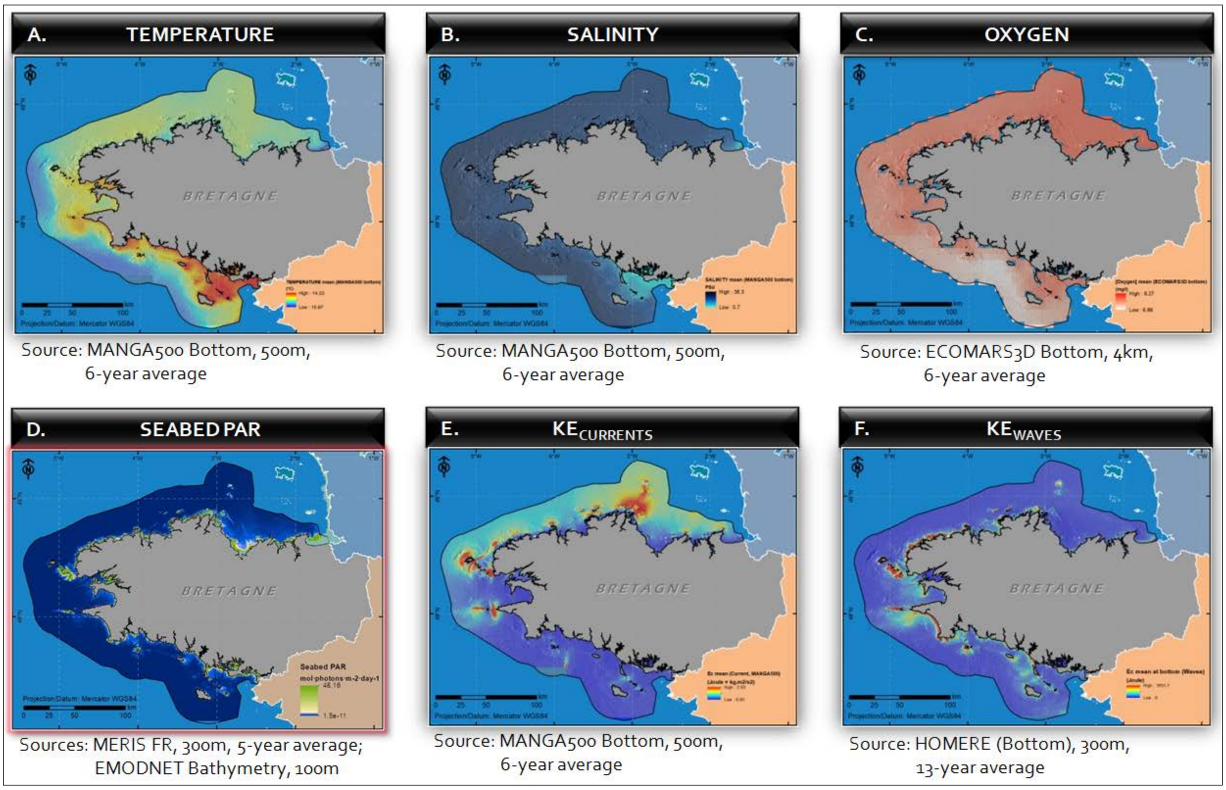


Figure 1: Maps of the environmental variables (multiannual averages) used to compound Brittany's benthic environmental space: A. Temperature; B. Salinity; C. Oxygen; D. Seabed PAR; E. Current-induced kinetic energy; F. Wave-induced kinetic energy.

Table 1: Specifications about the environmental rasters used in the analysis.

Description	Statistic	Units	Period	Source	Resolution
Temperature at seabed level	multiannual average	°C	2010-2015	MANGA500-MARS3D model*	~500 m
Salinity at seabed level	multiannual average	PSU	2010-2015	MANGA500-MARS3D model*	~500 m
Oxygen concentration at seabed level	multiannual average	mg/l	2012-2017	ECOMARS3D-MANGA4000 model	~4 km
Kd_{PAR} light attenuation coefficient	multiannual average	m^{-1}	2005-2009	MERIS FR satellite imagery	~300 m
Bathymetry	multi-survey compilation	m	2018	EMODNET Bathymetry	~100
Kinetic energy of wave-induced currents at the seabed level	multiannual average	J	1994-2016	IOWAGA-WAVEWATCH III model	Irregular grid rasterized to 300m-resol.
Kinetic energy of baroclinic currents at seabed level	multiannual average	J	2010-2015	MANGA500-MARS3D model*	~500 m

* Base layers published by Caillaud et al (2016).

All rasters were clipped to the extent of Brittany's infralittoral biological zone, which represented our study area. As suggested by Populus et al. (2017), the infralittoral zone was delimited from the chart datum down to the 0.7 mol photons·m^{-2}·day^{-1} seabed PAR limit. The chart datum polyline was sourced from a "zero hydrographique" shapefile derived from SHOM bathymetry at Ifremer in 2002. The data to derive the PAR limit was sourced in January 2019 from the EMODNET Seabed Habitats portal (PAR and Kd_{PAR} rasters at ~300 m resolution) and the EMODNET Bathymetry portal (100m-resolution bathymetry raster). The resulting study area is represented in **Figure 2**.

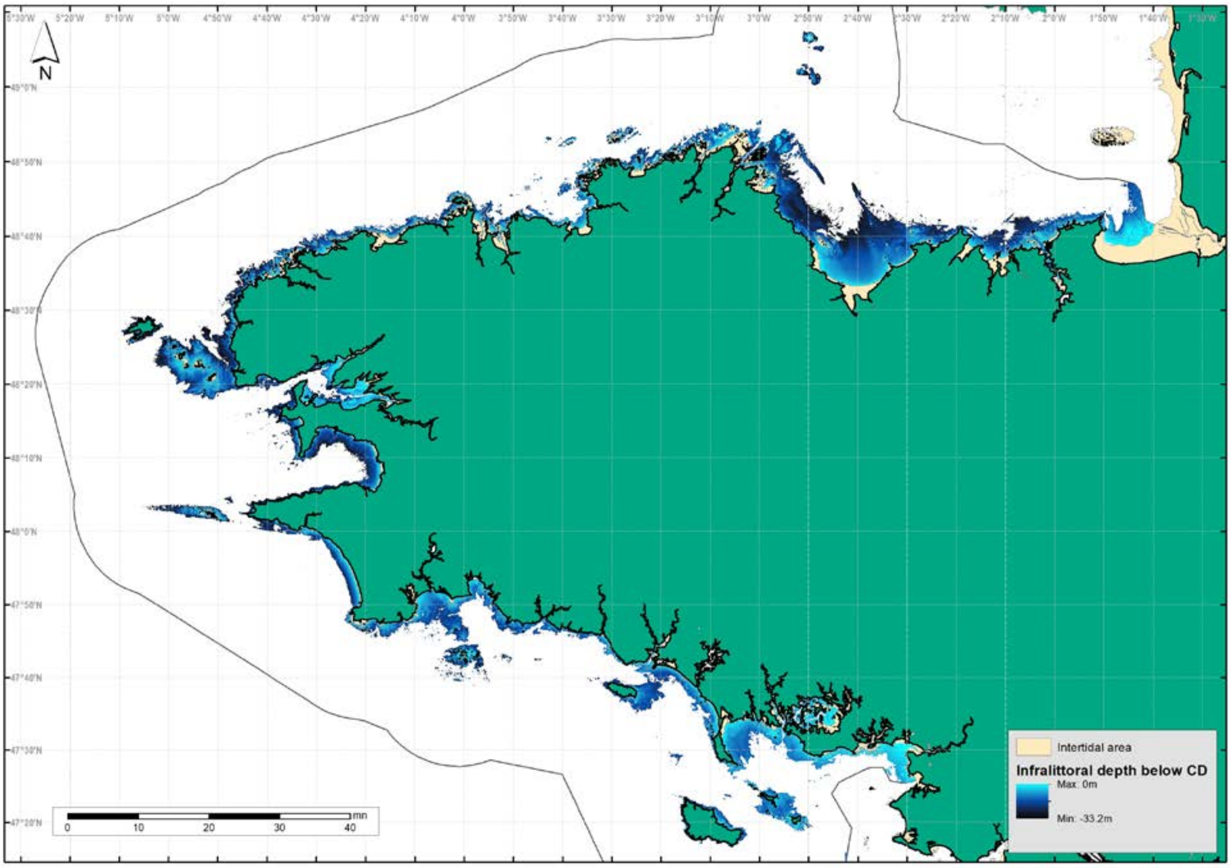


Figure 2: Brittany's infralittoral extent as delimited between the chart datum and the 0.7 mol photons·m^{-2}·day^{-1} seabed PAR level.

2.3. Data preparation

Using the centres of the infralittoral bathymetry grid cells, a 100m-resolution point dataset was created to sample the environmental rasters and represent the environmental space to be partitioned. The chosen spatial frequency matched that of the environmental layer with the highest spatial resolution (percentage of surface light at seabed level). The resulting dataset comprised 269,829 points after excluding points with missing values. Its attribute table was the basis for the partitioning analysis described below.

In order to mitigate the fact that variables had disparate units and value ranges, variables were standardized (i.e., centred to a mean=0 and reduced to a SD=1) prior to the analysis. This treatment gave variables equal relative weightings when computing dissimilarity between points (Euclidean distances).
Since collinearity among variables may disproportionally reinforce the influence of some environmental gradients during cluster formation, the condition was investigated by computing Pearson correlations between the six input variables.

2.5. Partitioning algorithm

K-means (Hartigan & Wong, 1979) is a well-known non-supervised clustering method that can handle large datasets like ours. The method was used to partition the point dataset representing the environmental space into groups of ecologically-similar points. Euclidean distances computed from the standardised environmental attributes were used as a measure of the dissimilarity between the points. By iteratively minimizing within-cluster variance the k-means algorithm gradually converges into categorizing the unlabeled observations into a number of groups.
The stats::kmeans R function was used to perform the analysis.
Since the approach can be sensitive to the random configuration of cluster centroids used to initiate the iterative convergence process, 36 initial configurations were trialled (*nstart*=36). For each initial configuration, a default 10 iterations of the centroids positions (*iter.max*=10) was then allowed before the “optimal” cluster membership was chosen.

2.5.1. Number of clusters

Clustering methods like k-means require setting the number of clusters (k) to which the observations will be assigned to. The choice of this essential parameter was jointly guided by data-driven numerical indexes (more than twenty provided by the NbClust::NbClust R function), analysis of Elbow, Sillouette and D index graphs (produced using factoextra::fviz_nbclust R function) and an expert analysis of the resulting maps.

3. Results

Pairwise Pearson correlations between the six input variables did not exceed 0.64 (**Figure 3**). This suggested no excessive correlation (P>0.70) was present allowing the analysis to proceed with all 6 variables.
Graphical methods and numerical indices suggested that the optimal number of clusters was between 2 and 7. A critical, ecologically-based interpretation of the resulting maps made the choice clearer. A two-class split corresponded to separating the most prominent ecological types of the study area: the permanently-

mixed waters of northern Brittany on one hand, and the seasonally to permanently stratified waters of southern Brittany on the other.

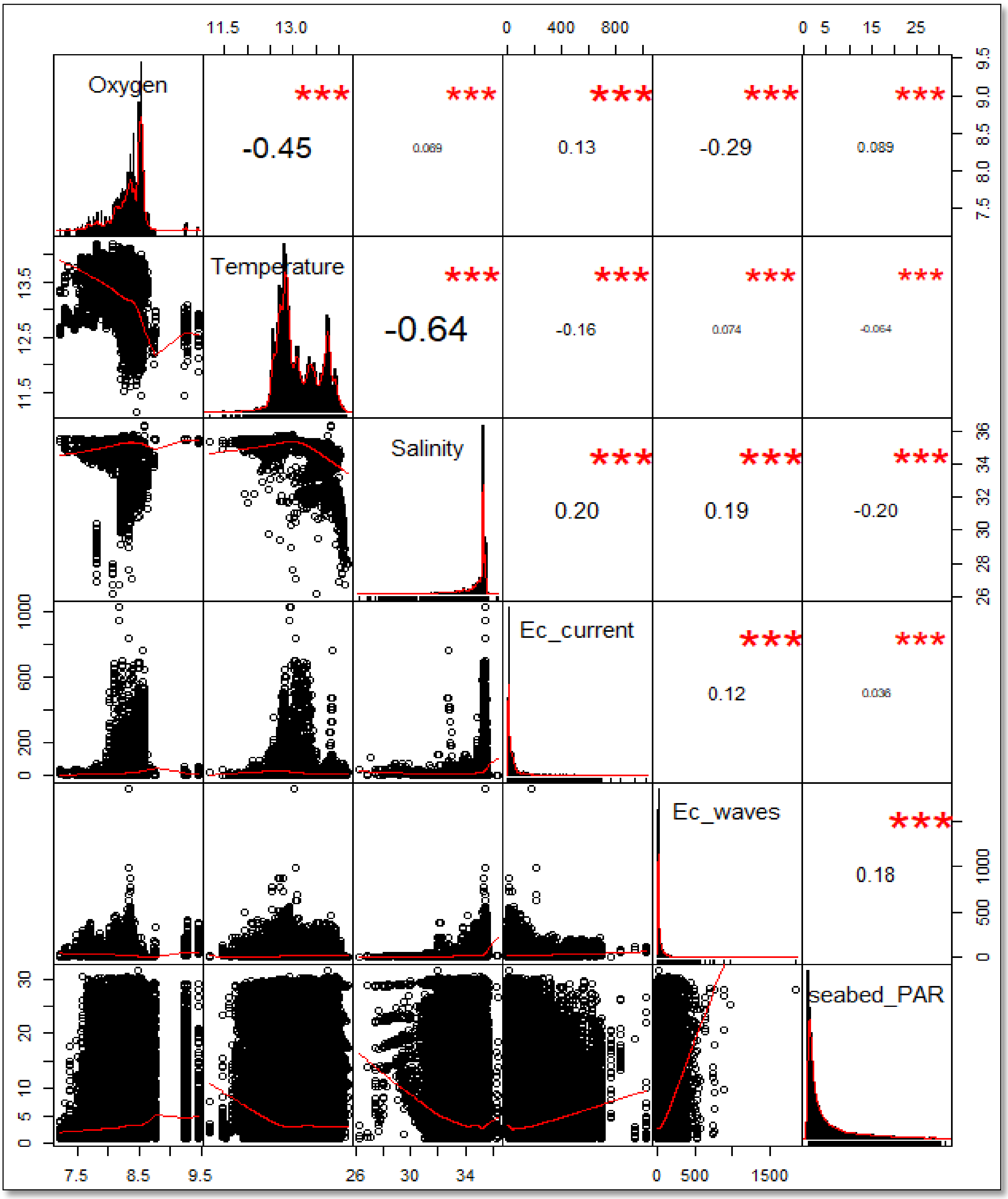


Figure 3: Pairwise scatterplots and Pearson correlations between the 6 variables used to compound the environmental space.

However, since we aimed at partitioning the ecological diversity of Brittany produced in greater detail for sampling across different environmental gradients, a 7-class partitioning was chosen instead. The ecological profiles of the resulting clusters are shown in **Figure 4** using average z-scores that highlight distinguishing environmental characteristics. Names given to the clusters were based either on their geographical position or on their mostly distinguish environmental characteristics.

Average values for the six environmental variables in their original measuring units are also shown in **Table 2**. Post-hoc Dunn tests for multiple comparisons with *p*-values adjusted by using the Holm method attest that all clusters show statistically-significant differences among themselves for all environmental variables with two minor exceptions indicated in the table.

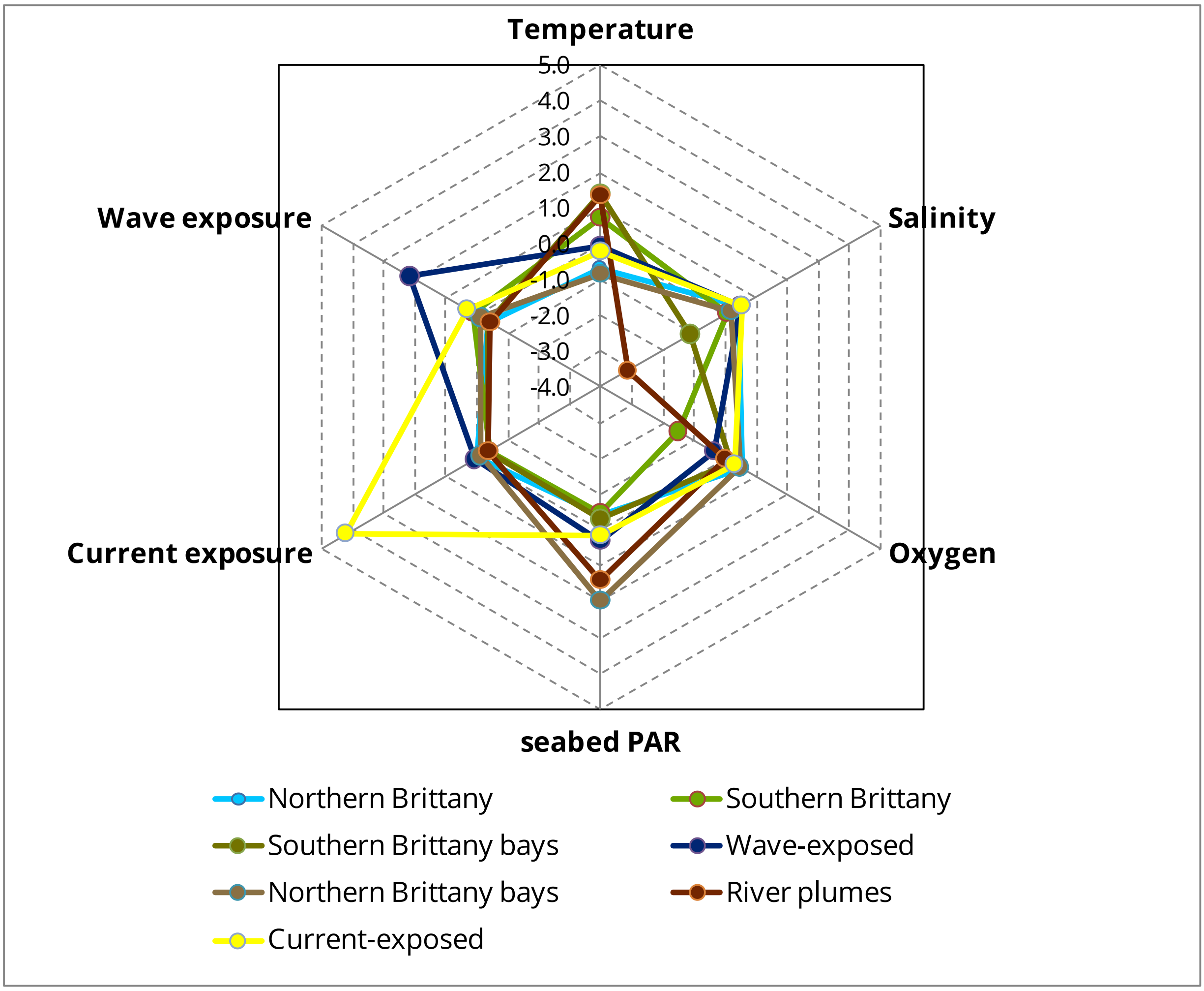


Figure 4: Z-score-based ecological profiles highlighting the environmental characteristics that distinguish each ecoregion.

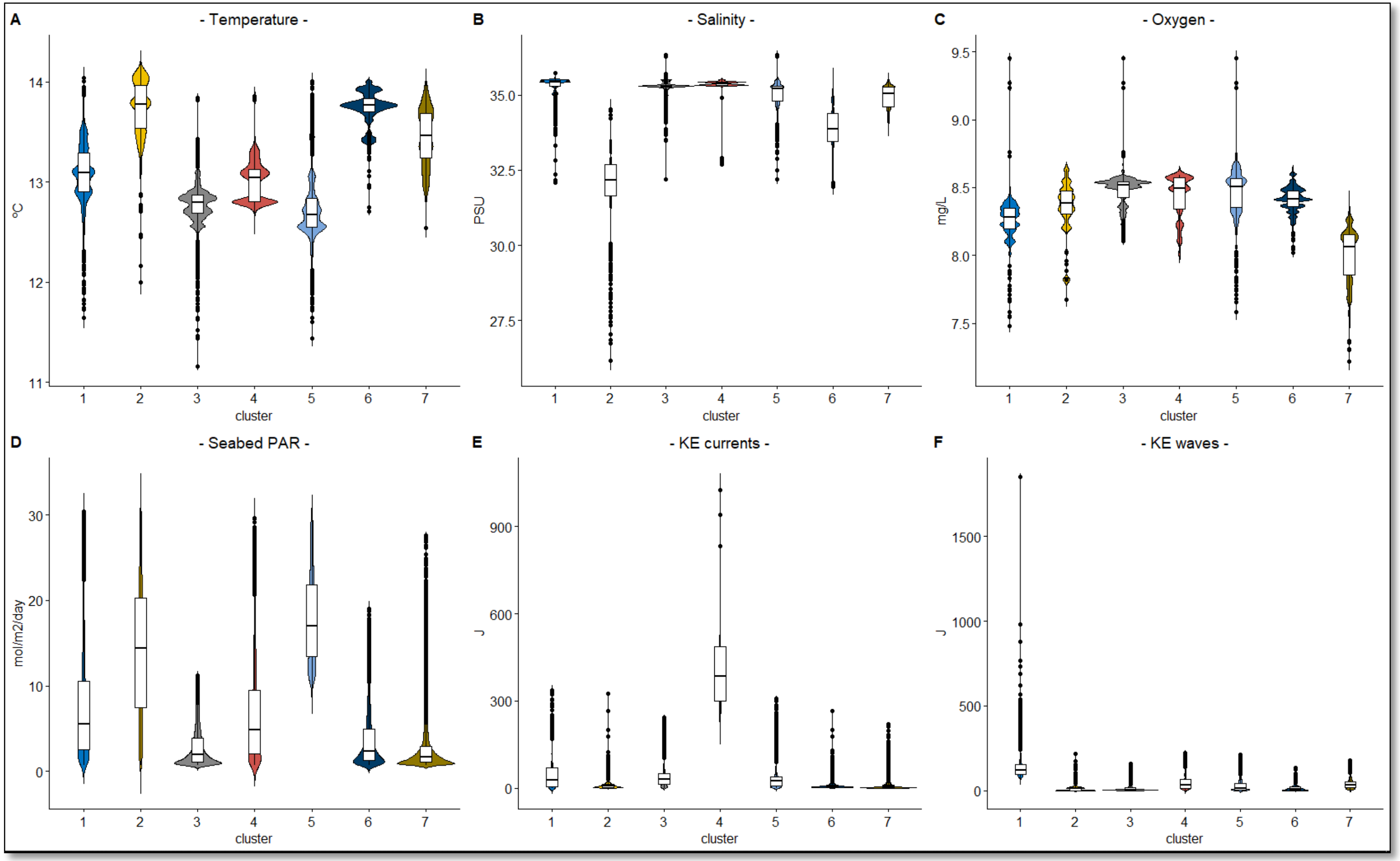
The distribution of each environmental variable per cluster is shown in **Figure 5**. Variables are represented in their original scales for ease of interpretation of the environmental ranges at issue.

Table 2. Ecoregions ecological profiles: average value of each environmental variable.[a]

	Temperature (ºC)	Salinity (PSU)	Oxygen (mg/l)	Light at Seabed (seabed PAR in mol photons$_{PAR}$/ m^2/day)	Current exposure (KE in J)	Wave exposure (KE in J)	Main characteristics	Area
Northern Brittany	12.8	35.3	8.5	2.8	42.6	13.9	reduced temperature; enhanced oxygen; reduced light levels	1019 km^2
Southern Brittany	13.4	34.9	8.0	2.7	9.6	37.6[c]	reduced oxygen; weak currents; reduced light	457 km^2
Southern Brittany bays	13.7	33.9	8.4	3.7	11.0	14.5	enhanced temperature; reduced salinity; sheltered from currents and waves	333 km^2
Exposed to waves	13.1	35.3	8.3	7.5	51.0	136.1	high exposure to waves	210 km^2
Northern Brittany bays	12.7	35.1	8.5	17.9	33.9[b]	26.2	reduced temperature; enhanced oxygen; light above average (=shallow)	196 km^2
River plumes	13.7	32.0	8.4	14.4	11.1[b]	11.6	enhanced temperature; reduced salinity; sheltered from waves and currents; light above average (=shallow)	109 km^2
Exposed to currents	13.0	35.4	8.4	6.5	405.2	48.2[c]	high exposure to currents	91 km^2
Brittany infralittoral	*13.1*	*34.9*	*8.4*	*5.2*	*44.4*	*31.2*		*2415 km^2*

[a] - list is ordered by descending area; each parameter is coloured from high to low using a red-to-yellow-to-blue gradient applied to the column range of values; [b,c] – clusters failing to show statistically-significant differences for the parameters in question in a Dunn test.

Figure 5. Distribution of each environmental variable per cluster.*



* centreline represents the median; hinges represent percentiles 25 and 75; data lying beyond 1.5*IQR (i.e., distance between the 1st and 3rd quartiles) from the hinges are plotted individually as outliers; Clusters: 1 - "Wave-exposed", 2 - "River plumes", 3 - "Northern Brittany", 4 - "Current-exposed", 5 - "Northern Brittany bays", 6 - "Southern Brittany bays", 7 - "Southern Brittany"

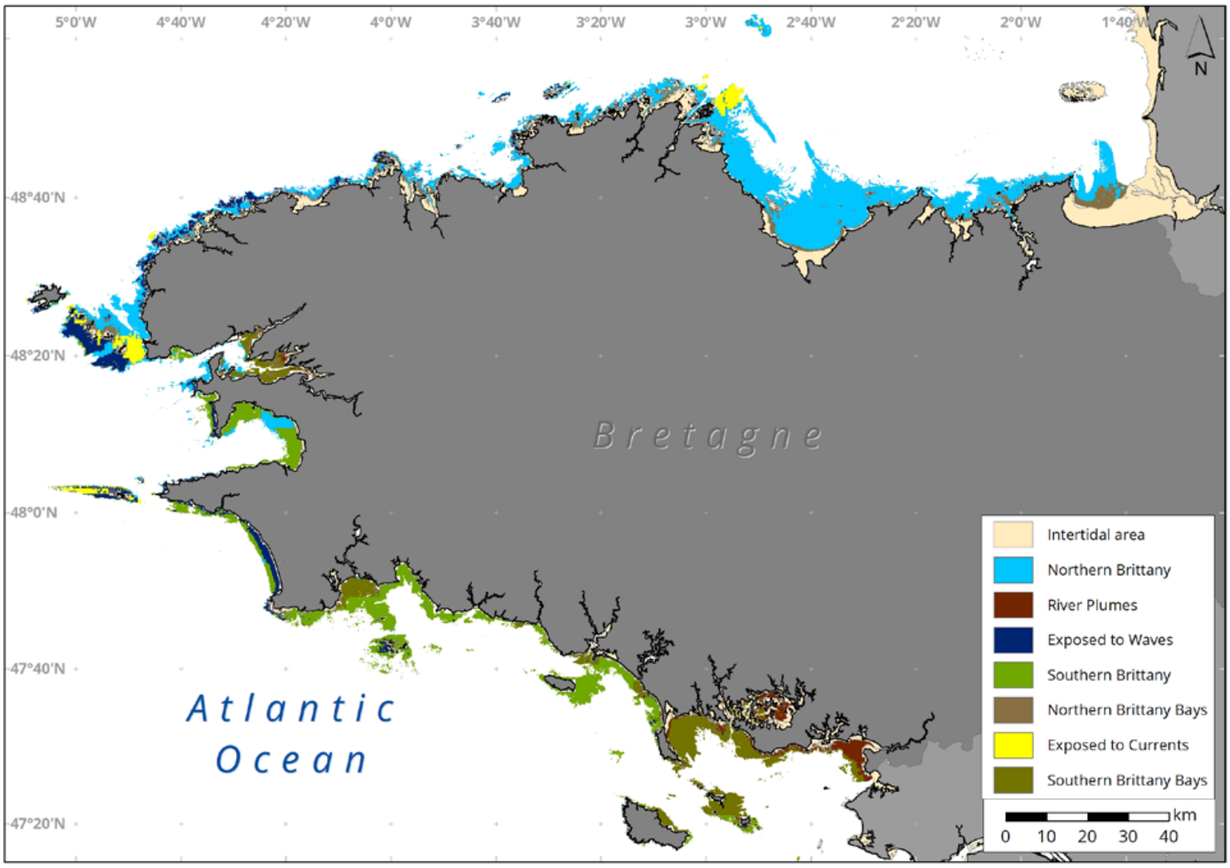


Figure 6: Segmentation of Brittany's infralittoral environmental space by k-means partitioning.

The geographical distribution of the 7 clusters is shown in **Figure 6**. The coherence they show attests the success of the statistical approach in bringing out spatially-explicit ecological patterns independently of any conventional spatial attributes.
As in the two cluster partitioning, the split between northern and southern Brittany still dominates the general pattern of identifiable ecoregions, with some blending occurring along the western-most shores. However, the partitioning highlights also particular conditions brought about by specific environmental conditions.
Most of northern and northwestern Brittany was assigned to a cluster covering 1,019 km^2 and extending from the Pen Hir headland to the outer parts of the Mont Saint Michel bay. Its environment is characterised by fully saline waters showing slightly lower than average temperature, enhanced oxygen and reduced light levels. Shoreward from this unit, the inner parts of most bays were assigned to a distinct cluster covering a total area of 196 km^2. This unit, here named "northern Brittany bays", is characterised by colder and more oxygenated conditions, as well as higher than average light levels (which is justified by the shallow depths of the bays). The parts of the western and north-western coast that are highly exposed to swells form an additional cluster occupying 210km^2.

A cluster that we identify as “Southern Brittany” dominates the coast between the Pen Hir headland and the western shore of the Quiberon peninsula, occupying a total area of 457 km^2. Its character deviates from Brittany’s infralittoral global averages by presenting a slightly higher temperature, reduced oxygen levels, slightly lower salinity and reduced current exposure. Within it, a few discontinuous areas are separated by their minor freshwater influence and enhanced temperature. They form a cluster here named “Southern Brittany bays”, which occupies an overall area of 333 km^2. This unit encompasses the Bénodet bay (on the west), the Quiberon bay (on the east), as well as small stretches of open coast in between the two which pick up the riverine output from small “rias”.

Seabed areas experiencing stronger freshwater influence are separated in a cluster here named “River Plumes”. This unit, typified by the Vilaine bay (southernmost Brittany), recurs in the neighbouring Golfe du Morbihan and in the inner sectors of the Rade de Brest (western Brittany). In what appears counterintuitive, these areas exhibit light levels above average, yet a consequence of their comparatively shallow depths.

Finally, a discontinuous cluster occupying a mere 91km^2 isolates seabed areas characterised by an exceptionally-high exposure to currents. This character is mostly expressed in the megatidal shores of western and north-western Brittany, including the Chaussée de Sein, the Saint Mathieu headland, some sectors of the Ushant and Molène archipelago, the rocky outcrops off the Bréhat-Paimpol sector and a few small prominences of the coast. A part of the Golfe du Morbihan, in south-eastern Brittany, is also assigned to this class as a result of the current funnelling that occurs at the entrance to its inner part.

Overall, it is worth noting the transitional character of the western coast, where northern and southern Brittany units overlap and exclaves from other units re-emerge. For instance, southern Brittany’s character recurs on the southern facing stretch of coast between Plougonvelin and the Pointe de Saint Mathieu while the northern Brittany character recurs in the middle of the Douarnenez Bay, which is hit more directly by incoming swells. Inside the Rade de Brest, a mosaic of conditions resembling either the “Southern Brittany bays” or the “northern Brittany bays” occurs.

4. Discussion

The present work demonstrates the capacity to use existing sub-kilometric multi-annual climatological datasets to perform a non-supervised multivariate partitioning of Brittany’s infralittoral domain (France, NE Atlantic).The result is an objective fine-scale delimitation of areas with similar environmental conditions (ecoregions).

The fact that the analyses exploits new climatological information for the seafloor, instead of surface or vertically averaged conditions, makes it particularly valuable for works targeting benthic environments. Foreseeable uses in macroecological research include (i) the interpretation of biogeographic patterns, (ii) the optimization of region-wide field surveys and (iii) the planning of *in situ* experiments. In addition, the information is also instrumental to plan and implement ecosystem-based management actions including (i) planning balanced and representative networks of marine protected areas, (ii) optimising monitoring networks, or (iii) designing balanced environmental status indicators.

4.1. Expert feedback

As a summary of diverse and intricate gradients that overlap along Brittany's 2860-km length coastline, the segmentation represents an objective basis to interpret Brittany's benthic biogeography. Consultation of experts at Ifremer and at the MNHN attested that the segmentation seizes Brittany's dominant biogeographic patterns and provides an objective delimitation for ecological zones that were previously uncharted at such fine scale.

The north-south divide substantiates Brittany's character as a transition area between the fully-exposed Atlantic seaboard and the broad well-mixed continental shelf domain of the English Channel (Manche). In addition, other ecological boundaries mapped by the 7-class partitioning were also endorsed, including (i) the freshwater influence in the Quiberon and Vilaine bays, (ii) the transition along the Penmarc'h headland, (iii) the particularly fully-open character of the western and northwestern shores of the Finistère, (iv) the re-emergence of a southern Brittany character outside the Rade de Brest with a transition at the Saint Mathieu headland.

4.2. Future studies

This climatology-based analysis may be seen as the environmental component of a set of spatially-explicit analyses converging into a fine-scale understanding of Brittany's marine biogeography. Its validation depends on at least three other complementary analyses:

i. a connectivity analysis exploiting models of coastal circulation to map potential links (dispersal pathways), or lack thereof (barriers), among the identified ecological units at multiple spatio-temporal scales;
ii. an analysis testing the specificity of the biodiversity found within each suggested ecoregion (bioregionalisation patterns);
iii. an analysis exploiting the ecological functions characterising each ecoregion and their interdependence (or lack thereof) on functions performed in neighbouring ecological units (functional regionalisation).

Other analyses that should further take advantage of the wealth of environmental information being generated by Ifremer oceanographic models include:

i. extending the ecoregionalisation approach to the entire seaboards where high resolution environmental layers are available (notably the Atlantic, English Channel and Mediterranean ones);
ii. moving beyond basing the analysis on single multiannual averaged values for each environmental variable and exploit more exhaustive statistics of yearly variation (*e.g.*, Fourrier transforms or cyclic spline generalisations adjusted to multiannual series of daily averages);
iii. studying the variation of the benthic ecoregion partitioning in time (*e.g.*, annual dynamics based on monthly averages);
iv. projecting the spatial evolution of the ecoregionalisation expected in view of climate change (dependent on projections for the different parameters being available);
v. conducting volumetric segmentations of the marine environment as a whole using the original 3D data meshes output by oceanographic models.

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