When bioregionalisation emphasises the presence of Vulnerable Marine Ecosystem indicator species in *Nephrops* fishing grounds: evidence in the Bay of Biscay/Irish Sea continuum

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Abstract :

Under the apparent homogeneity of soft-bottom ecosystems hides an heterogeneity of habitats driven by variations in sediment composition and environmental conditions.

Using an extensive underwater video survey dataset, we explored the taxonomic diversity of soft-bottom Nephrops fishing grounds and their environmental drivers on a large latitudinal scale from the Bay of Biscay to the Irish Sea (Northeast Atlantic). Biogeographical network clustering highlighted indicator species of the different communities and a Between-Class Analysis characterised the abiotic factors influencing each community.

Our analyses confirmed a biogeographical limit between the Bay of Biscay and the northern areas driven by a latitudinal temperature gradient and highlighting the distribution of Lusitanian and Boreal species. Mobile fish and crustaceans, and sessile filter-feeder assemblages differed along a depth, bottom current and fishing gradient. Some species assemblages covered the whole latitudinal range, implying a greater influence of optimal environmental surroundings rather than their geographical position. Vulnerable Marine Ecosystem indicator taxa such as Virgularia mirabilis and Pennatula phosphorea are potential indicator species of some clusters, while harvested species such as Nephrops norvegicus or mobile fish characterized other bioregions.

Spatial knowledge produced in this study could be integrated as biodiversity layers together with fisheries activities layers in decision support tools such as Marine Spatial Planning in order to define compromise between conservational and fishing objectives. Outcomes of management scenarios would then consider the whole species stock (e.g. Nephrops) rather that local populations independently.

Highlights

► Underwater videos were used to explore taxonomic diversity in 4 *Nephrops* grounds. ► Biogeographical analysis highlighted indicator species of the different communities. ► Species differed along a depth, bottom current and fishing gradient. ► Even in fished areas, Vulnerable Marine Ecosystem indicator species are present.

Keywords : bentho-demersal communities, environmental drivers, Northeast Atlantic, underwater video, fishing

1. Introduction

Subtidal soft sediment are one of the most widespread types of seabeds in our oceans (Snelgrove, 1998; Hüneke and Mulder, 2010). These substrates provide important resources and ecosystem services, such as food provision (Costanza *et al.*, 1997; Snelgrove, 1998), and also host remarkable biodiversity.

Soft-bottom habitats are spatially heterogeneous due to the influence of hydrodynamic variables, such as current and wind or seasonal storms, on seabed topography and sediment composition (McConnaughey and Syrjala, 2014; Mestdagh *et al.*, 2020). This habitat heterogeneity benefits bentho-demersal assemblages (Snelgrove, 1998), the distribution of which is also influenced by other abiotic factors, such as temperature, salinity, and current, and biotic factors, such as predation or food availability (Boero, 1984; Rosenberg, 2001; Williams, 2011; Puerta *et al.*, 2020; Punzón *et al.*, 2021).

Additionally, soft sediment ecosystems are also affected by external large scale processes, such as climate change, which leads to geographic shifts in species distribution (Schiel *et al.*, 2004), and fishing that is likely the main external driver impacting species distribution (Hall, 2002; Sköld *et al.*, 2018; McConnaughey *et al.*, 2019; Mazor *et al.*, 2020; Pitcher *et al.*, 2022). Thus, fishing has led to sediment and communities homogenisation in heavily fished areas, leading to an increase of fine-mud sedimentation and reduced species richness in disturbed areas (Hily *et al.*, 2008; Handley *et al.*, 2014). Fishing may also drive community composition based on its vulnerability to anthropogenic pressure, where areas fished for a long time exhibit more mobile species that can recover rapidly, while less disturbed areas harbour sensitive species such as fixed or filter-feeding organisms (de Juan and Demestre, 2012; Dupaix *et al.*, 2021).

In the Northeast Atlantic, subtidal soft sediments can be found in large patches on coastal, continental shelf and slope areas. *Nephrops norvegicus* (*Nephrops* hereafter), also known as the Norway lobster, is one of the principal commercial species of soft sediment communities in the Bay of Biscay, Celtic Sea and Irish Sea. Other commercially important fish species are also widely distributed in these areas, such as cod (*Gadus morhua*), hake (*Merluccius merluccius*), whiting (*Merlangius merlangus*) or common sole (*Solea solea*). Furthermore, *Nephrops* fishing grounds also shelter sensitive biocenosis, such as species that, due to their specific life-history traits and importance as potential biogenic habitats (e.g., sea pens), are listed as indicators of Vulnerable Marine Ecosystems (VME) (FAO, 2009; Miatta and Snelgrove, 2022).

Traditionally, benthic communities have been studied on local scales such as the Grande Vasière in the northern Bay of Biscay (Le Loc'h *et al.*, 2008; Mérillet *et al.*, 2018), the Celtic Sea (Dupaix *et al.*, 2021), the Irish Sea (Ball, 2000; Ellis *et al.*, 2000), but are rarely described at large latitudinal scales. To understand the structure and distribution of species at large geographical scale, a relevant approach is bioregionalisation (Spalding *et al.*, 2007; Costello *et al.*, 2017). Bioregionalisation consists in partitioning the geographic space, based on the spatial distribution of multiple species, into distinct bioregions of

homogeneous composition. To identify bioregions, the classical approach in biogeography consists in calculating distances between sites based on the composition of sampled assemblages, such as beta-diversity indices, and then apply a clustering algorithm such as hierarchical clustering (Kreft and Jetz, 2010; Costello *et al.*, 2017). More recently, biogeographical networks have been proposed as an alternative approach to distance-based clustering (Vilhena and Antonelli, 2015; Costello *et al.*, 2017). Network approaches consist in building a bipartite site-species network from the sampled assemblages, and applying upon them community detection algorithm, which identify homogenous clusters in terms of species composition (Leroy *et al.*, 2019). A thorough comparison between distance-based and network-based bioregionalisation approaches is missing in the literature, hence the relative performances of both approaches is currently unresolved, although some studies comparing both approaches have shown that network-based approaches produced more biologically meaningful results (Bloomfield *et al.*, 2018; Leroy *et al.*, 2019). Notwithstanding, network-based methods have several features which make them particularly interesting for bioregionalisation. First, they are relatively insensitive to differences in sampling intensities, most likely because they retain species identity throughout the whole process, whereas distance-based approaches abstract species identities into numbers (Leroy *et al.*, 2019). Second, network-based clustering requires less subjective decisions than distance-based clustering (e.g., the number of clusters or the height of cut of dendrograms), which improves the standardisation and comparability among studies. Third, because networks keep track of species identities, the algorithm assigns each species to a specific bioregion, which facilitates describing and understanding the biological significance of clusters.

In view of decades of trawling in *Nephrops* fishing grounds that could have led to a homogenisation of the bentho-demersal communities, studying the distribution of bentho-demersal communities on a large scale should help understand the processes underlying species distribution. This study aims to answer several questions. How similar or different in terms of bentho-demersal communities are the different *Nephrops* fishing grounds in the North-western part of the European seas? Can these community patterns be explained by environmental and anthropogenic variables? To explore these

questions, we compared biodiversity patterns in bentho-demersal assemblages between four *Nephrops* fishing grounds located on a north-south latitudinal gradient going from the Irish Sea to the northern Bay of Biscay. Firstly, we explored the taxonomic diversity of each area. Secondly, we performed network-based clustering methods over all areas. Thirdly, each cluster was characterised by its indicator species and driving factors among environmental and anthropogenic variables.

2. Methods

2.1 Sampling area

The study took place in the Bay of Biscay, Celtic Sea and Irish Sea, that are part of two provinces from the Temperate Northern Atlantic marine ecoregion (Spalding *et al.*, 2007) and where important soft-bottom *Nephrops* fishing grounds occurred. *Nephrops* stocks are assessed by the International Council for Exploration of the Sea (ICES) at the Functional Unit level (FU) – where each FU is an aggregation of ICES statistical rectangles. In the Celtic Sea, there are three *Nephrops* FUs defined by ICES which are FU 19, FU22 and FU 2021 and in the Bay of Biscay, one FU that is FU2324 (ICES, 2022). This four FUs were considered in this study. The most southern FU is the Grande Vasière *Nephrops* fishing grounds (FU2324). It is part of the Lusitanian/South European Atlantic shelf and covers around 18,360 km^2 in the northern part of the Bay of Biscay. The Labadie, Cockburn and Jones Banks (FU2021), the Smalls (FU22) and the Irish Sea West (FU15) *Nephrops* grounds are all part of the Northern European Seas Ecoregion. FU2021 and FU22 cover around 10,014 and 2,439 km^2 respectively and are both located in the Celtic Sea, on the south coast of Ireland. FU15 covers approximately 5700 km^2 in the western Irish Sea.

2.2. Data collection

2.2.1 Survey operations

Data on benthic communities was collected during the dedicated UnderWater TV surveys (UWTV) on national research vessels in spring and summer 2018 (Table 1). In total, 448 stations were sampled in the four areas. The sampling effort varied from 42 stations in FU22 to 215 in FU 2324 (Table 1). In each

area, stations were selected randomly using a fixed isometric grid with intervals of 4.5-6 nmi (nautical mile). Following the same recommended international survey protocols (Leocádio *et al.*, 2018; Dobby *et al.*, 2021), at each station an underwater sledge equipped with a standard definition camera was deployed on the seabed (see Dobby *et al.*, 2021 for an extensive description of the sledge), and once stable was towed behind the vessel at an average speed of 0.85 knots. The sledge was the same for all the 448 stations. Each UWTV transect lasted for 10 minutes and time referenced video was recorded. On the sledge, two spot lasers 0.74-0.75 meters apart were used to calibrate a constant field of view (FOV) to calculate the area. The sledge was also equipped with GPS/USBL (Global Positioning System/Ultra-Short Baseline) system and a CTD (Conductivity, Temperature and Depth) device providing sledge position, depth, bottom temperature and salinity for each UWTV transect. Overall, operational depth ranged between 17 and 159 m. On average UWTV transects covered an area of 144 (± 27) m^2 and measured 193 (± 36) m long.

Table 1. Characteristics of each Functional Unit (FU) in the Bay of Biscay, Celtic and Irish Seas. GPS coordinates correspond to the centre of each area. Mean ± standard deviation is expressed for bottom temperature, salinity, current and depth. Nmi = nautical mile; m = meter; s = second; °C = degree Celsius; PSU = Practical Salinity Unit.

FU number	FU2324	FU2021	FU22	FU15
FU name	Grande Vasière	Labadie - Jones	Smalls	Irish Sea West
GPS coordinates	46°43'58.2"N 3°24'20.8"W	50°14'08.1"N 8°11'36.5"W	51°17'07.8"N 6°09'57.4"W	53°59'42.6"N 5°29'55.8"W
Operational country	France	Ireland	Ireland	Northern Ireland
Number of stations	215	91	42	100
Isometric grid intervals	4.5-4.7 (nmi)	6 (nmi)	4.5-4.7 (nmi)	4.5-4.7 (nmi)
Video field of view (m)	0.75	0.75	0.75	0.74
Bottom temperature (°C)	12.11 ± 0.26	10.77 ± 0.28	10.37 ± 0.30	10.59 ± 0.30
Bottom salinity (PSU)	35.48 ± 0.11	35.65 ± 0.01	35.61 ± 0.00	35.06 ± 0.23
Bottom current (m/s)	0.106 ± 0.017	0.134 ± 0.022	0.160 ± 0.029	0.148 ± 0.050
Depth (m)	103 ± 17	114 ± 12	98 ± 9	78 ± 32

2.2.2. Video Analysis

Each video was read twice by the same scientist so that no intercalibration was needed. Benthic megafauna individuals were counted and identified up to the lowest taxonomic level possible. If it was

not possible to identify to species level, then higher taxonomic levels were used such as genus, family or class. Taxa that could be identified only at the phylum/subphylum level (i.e. unidentified Actinopterygii, Annelida and Crustacea) were removed from the dataset as little informative and not discriminant in the analyses.

During video review if the visibility deteriorated hampering detailed observation, for example due to sediment clouds obscuring the view, then the time-stamp and associated distance was removed from the distance over ground calculation. The first seven complete minutes with sufficient visibility for taxonomic identification were used to count individuals (Leocádio *et al.*, 2018).

2.3. Explanatory variables

2.3.1. Fishing effort

Fishing effort was measured in hours from VMS data (Vessel Monitoring System) and used as a proxy of fishing intensity. Access to the French VMS data was provided by the French Department of Maritime Fisheries and Aquaculture (DPMA – Direction des pêches maritimes et de l'aquaculture). The French VMS data was processed with the SACROIS algorithm which filters data to select records assumed to correspond to fishing activity, based on vessel speed and distance to the nearest port (Demaneche *et al.*, 2010). Access to an aggregated, anonymised analysis of the Irish VMS data was provided via the Marine Institute, Ireland; and appended to the data provided by France and Northern Ireland. The Irish and Northern Irish VMS data was processed by classifying fishing activity using vessel speed, the details can be found at Gerritsen and Lordan (2011) and Gerritsen and Kelly (2019). Fishing intensity was used at a 3'x3' spatial aggregation level as to be closest to the isometric grids used for the biological data.

The effort per gear type aggregated from the three countries was classified into three categories according to their level of impact on the seafloor – High, Medium or Low (Supplementary material S1) (Eigaard *et al.*, 2016; Savina *et al.*, 2018; Kopp *et al.*, 2020). High impact gear included *métiers* using active gears that have physical consequences on the surface and subsurface of the seafloor, such as trawls, dredges and seines. Medium impact gear, for example gillnets and trammel nets, included

passive gear with a sweeping motion on the seabed. Finally, low impact gear comprised passive gears such as pots, traps and longline, which could have punctual impact because of weights or because they lay resting on the seafloor. Effort from pelagic gear was removed from the analysis as it has zero impact on the seafloor and because this study focuses on the bentho-demersal compartment.

The annual fishing effort was then calculated for each category at each station, for the year preceding the surveys – July 2017 to June 2018. Data for the other UK (Scottish, Welsh and English) vessels were unavailable at the time our study. According to experts' knowledge the missing effort represented around 20% of effort in FU2021 and 3% in FU22 of the high impact gear.

2.3.2. Environmental variables

Sediment characteristics in each area were made available by the EMODnet Geology project (European Marine Observation and Data Network - http://www.emodnet-geology.eu/) at a scale of 1:1,000,000 using Folk's sediment triangle with seven substrate classes. These seven modalities were recoded into a numeric variable, from 1 to 7 with smaller values corresponding to smaller particles and larger values corresponding to larger ones – 1 = Mud; 2 = Muddy Sand; 3 = Sandy Mud; 4 = Sand; 5 = Mixed sediment; 6 = Coarse sediment; 7 = Rock & Boulders (Supplementary material S2).

Mean annual bottom temperature, salinity and current data for each station were calculated from the monthly extracted values of the MARS3D model simulations (Lazure and Dumas, 2008) for the year preceding the surveys. Bottom salinity variations between the four areas were marginal (Table 1). Therefore, salinity was not accounted for in the analyses.

2.4. Data analysis

2.4.1. Species richness and density

Species richness (SR) and density (D) were mapped for each zone using the Inverse Distance Weighting interpolation (IDW) in QGIS (3.16 – Hannover version). Densities of each taxonomic level (individuals.m^{-2}) were calculated by dividing the abundance by the sampled area (calculated as the distance over

ground multiplied by the FOV). D was log-transformed in the representation to reduce skewedness and improve visualisation. To assess the link between these two metrics and environmental variables, Spearman's rank correlations were calculated.

2.4.2. Network biogeographical clustering

The distribution of benthic density data was transformed into a bipartite network, with two types of nodes, species and stations, using the "biogeonetworks" R package (Leroy, 2019; Leroy *et al.*, 2019). In this type of network, nodes are connected by links that are weighted with density (Vilhena and Antonelli, 2015). Links exist only between species and stations, therefore there are no station-station or species-species links. The hierarchical community clustering algorithm Map Equation (ME) (Rosvall and Bergstrom, 2008; Rosvall *et al.*, 2009), was then implemented, with 1000 runs, in Infomap, to detect clusters. This algorithm looks for communities by maximising the number of intra-group links while minimising the number of inter-group links, and assigns each node (species and stations) to a cluster. There are various benefits to using the network method: i) Species identity is preserved where each species is assigned to a region/cluster which allows species level description; ii) Links between samples are mapped using species. Clusters are composed of stations and species, which allow us to describe which taxa drives which station; iii) ME considers link weight, which includes species abundance in clustering analysis. Clusters are driven by abundant species and not rare ones. iv) ME is relatively robust to differences in sampling intensities, compared to more classical methods such as hierarchical clustering based on beta diversity (see, e.g., Appendix S2 in Leroy et al. 2019). Additionally, ME also has the characteristic of identifying separately "transition clusters", i.e. areas which contains overlapping distributions of species from distinct clusters (Vilhena & Antonelli 2015).

Clusters with more than 20 nodes were considered as major clusters. The others (less than 20 nodes) were regarded as minor clusters. This arbitrary limit was decided after looking at the range of number of stations per cluster (Supplementary material S3). They were then mapped in R and generated on a network, using the ForceAtlas2 algorithm (LinLog mode; gravity = 0; edge weight influence = 0.65) in

Gephi v0.9.2 (Bastian *et al.*, 2009). Gephi is a network visualisation software used for network drawing, with subtle control over visual variables.

2.4.3. Species characterisation of clusters

The indicator value (Indval) method is a statistical method for the identification of indicator species (Dufrêne and Legendre, 1997; Legendre, 2013). It combines a species mean abundance (or occurrence) and its frequency of occurrences in the clusters. A high Indval corresponds to a combination of a large mean abundance (or occurrence) within a group compared to other groups, and a presence in most stations of that group. The Dilution value (Dilval) helps to identify ubiquitous species widely distributed in all areas and overlapping in other clusters (Bernardo-Madrid *et al.*, 2019).

Firstly, occurrence-based Indval and Dilval indices (occ-Indval and occ-Dilval) were used to assess the correct allocation of species to each biogeographical cluster, and the coherence of a cluster's existence. These two metrics are used to distinguish real clusters from transition clusters identified by the ME algorithm. Clusters with species with low occ-Indval (< 0.15) and high occ-Dilval (> 0.85) are considered here as transition clusters. The clusterMetrics function from "biogeonetworks" R package was used to calculate occurrence-based Indval and Dilval.

Secondly, abundance-based Indval (ab-Indval), from the "labdsv" R package (Roberts, 2019), was used to characterise indicator species for each cluster. An arbitrary threshold of 0.25 was kept for the ab-Indval index, which corresponds to species that are present in at least 50% of the stations in the cluster and whose relative abundance in that cluster is at least 50%. If either its presence or relative abundance reaches 100% then the other is always greater or equal to 25% (Dufrêne and Legendre, 1997). The statistical significance of the index is assessed a-posteriori with a Monte-Carlo permutation test.

2.4.4. Abiotic characterisation of clusters

To evaluate the relative influence of the environmental variables on each cluster, a between-class analysis (BCA) on the standardised environmental data was performed (Dolédec and Chessel, 1987). Considering a partition of the data (clusters), the BCA investigates the differences between clusters by

maximising the variance between clusters without accounting for the variance within clusters (Dray and Jombart, 2011). A BCA is performed in two steps. First, a PCA is run on the standardised environmental data (station x environmental variables). The environmental variables are standardised as they have different units. Secondly, information on cluster classification for each station is added to the table, the barycentre of each cluster is calculated on the first PCA and a second PCA (=BCA) is performed on the barycentre's coordinates to maximise between cluster (i.e. class) variance. A Monte-Carlo test on the between-groups inertia percentage was done a-posteriori to test the significance of the between group variability, using 999 permutations. BCA and Monte-Carlo test were performed with the "ade4" R package (Thioulouse *et al.*, 1997; Chessel *et al.*, 2004).

3. Results

3.1. Diversity structure

In the four study areas, a total of 26,355 individuals corresponding to 44 taxa were identified (see species list in Supplementary material S4).

Species richness (SR) varies between 0 and 15 taxa across stations (Figure 1a). SR hotspots (stations > 11 taxa) are found in each area, often on the external margins (Figure 1a). In FU2324, SR is high on the north-western margin and in the centre of the area. In the Celtic and the Irish Seas, hotspots are located around the edges of each FU.

Density (D) per station ranges between 0 and 12.2 individuals.m^{-2} (Figure 1b). The highest densities are found on the north-western margin of FU2324, due to large colonies of Crinoids with up to 12 individual/m^2. Other high-density areas can be noticed in some stations of FU15 and FU2021 (Figure 1b). The external margins of FU15 show higher densities, related to high numbers of brittle stars Ophiuroidea (2 ind.m^{-2}), and Hydrozoa (up to 3.9 ind.m^{-2}). The density hotspots (stations with density > 0.58; Figure 1b) in FU2021 are mostly linked to high concentrations of *Virgularia mirabilis* (up to 1.8 ind.m^{-2}) and unidentified Actiniaria (1.4 ind.m^{-2}).
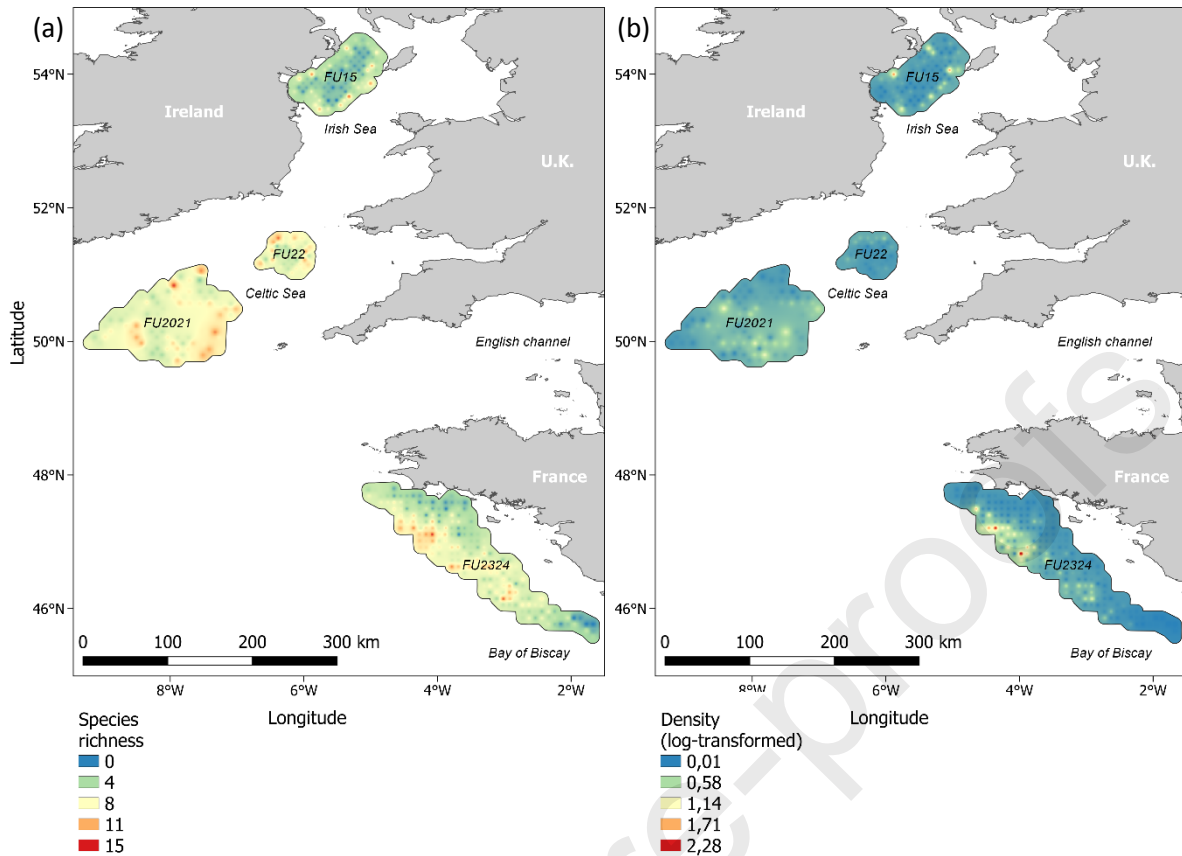
Figure 1. (a) Bentho-demersal species richness (number of taxa) in the four Functional Units (FU) of the Bay of Biscay, Celtic and Irish Seas. (b) Bentho-demersal density (abundance per m^2). For better visualisation of the density and to reduce skewedness, data was log-transformed. Inverse distance weighting was applied to interpolate values inside each FU.

Species relative abundance and occurrence varies in the different FUs (Figure 2). In FU15, Hydrozoa and *Nephrops norvegicus* are the two most abundant species (Figure 2a). *Nephrops norvegicus* also is the most observed taxa in FU15, present in more than 60 stations (corresponding to more than 50% of the stations of the area; Figure 2b). In FU2021, six taxa are encountered in more than 50% of the stations, Hydrozoa, *Virgularia mirabilis*, Sabellidae, unidentified Actiniaria, Pleuronectiformes and Asteroidea. In terms of relative and total abundance, *Virgularia* mirabilis is by far the most abundant in that area (Figure 2A; Supplementary material S4). Eight taxa are found to be more occurrent than the others in FU22, Hydrozoa, *Virgularia mirabilis*, *Nephrops norvegicus*, Sabellidae, unidentified Actiniaria, Pleuronectiformes, Asteroidea and Gadiformes. Finally, in FU2324, four taxa are present in more than

100 stations, Hydrozoa, Sabellidae, *Pennatula phosphorea* and Ceriantharia. Crinoidea and Hydrozoa are the most abundant species in these grounds.
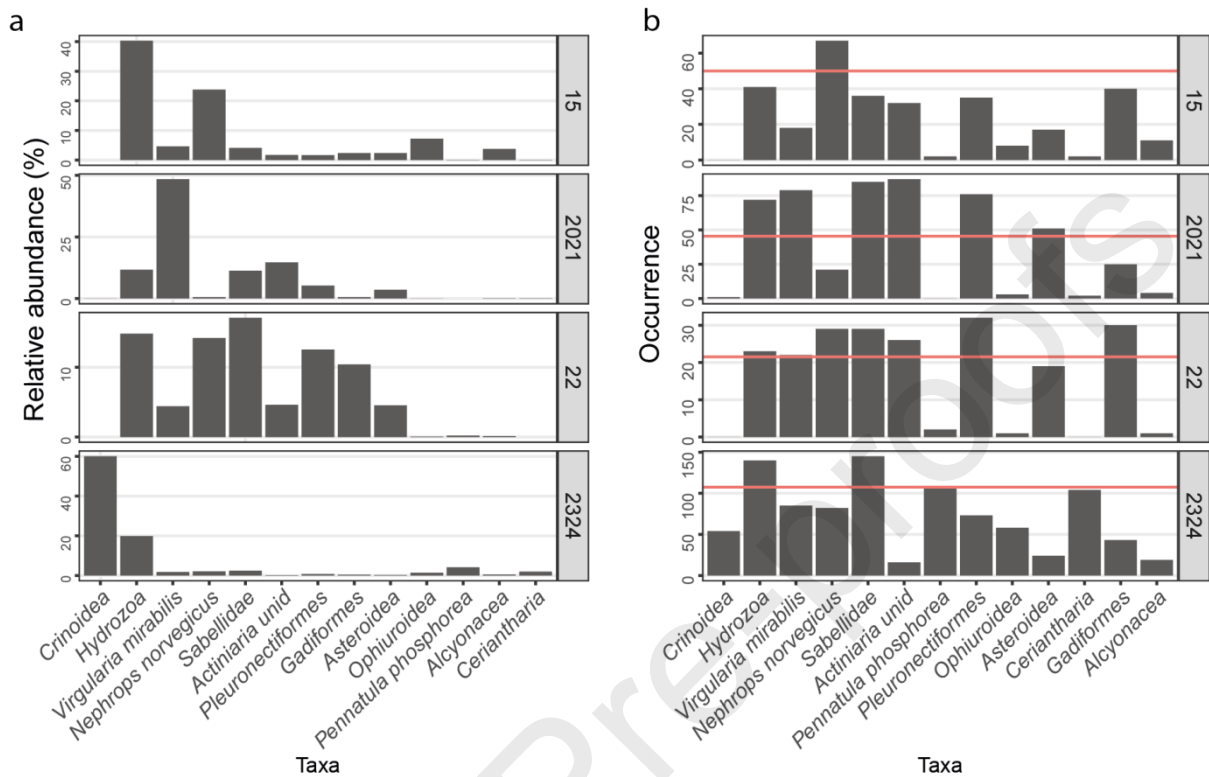

Figure 2. (a) Relative abundance (in %) per taxa in each Functional Unit (FU) of the Bay of Biscay, Celtic and Irish Seas. (b) Total occurrence of taxa per FU. The scale varies because the number of sampled stations varies in each FU. The thirteen most abundant species across all areas are represented. The red line corresponds to 50% of the stations in each FU.

SR and D are both positively correlated with depth (0.29 and 0.31 respectively; Supplementary material S5) and bottom current (0.25 and 0.33 respectively). There is a negative correlation between both metrics and high impact gear fishing intensity (-0.31 for both) as well as Longitude (Supplementary material S5; -0.14 and -0.28 respectively, p-value < 0.05). Latitude is correlated negatively with species richness (-0.18), and density is negatively correlated with bottom temperature (-0.13) and medium gear impact (-0.20). No correlation was found between the metrics (SR and D) and low impact gear intensity.

3.2. Bioregionalisation

3.2.1. Cluster description

Eight major clusters emerged in the four study areas from the Map Equation Algorithm of the biogeographical analysis (Figure 3a).

Indval and Dilval values based on occurrence reveal that among the eight clusters issued from the biogeographical analysis, two clusters (i.e. clusters 5 and 8 on Figure 3a) are spread out in the different zones and present a ubiquitous composition (Supplementary material S6). These clusters are characterised by low occ-Indval values (i.e. no indicator species in the cluster) and high occ-Dilval values (i.e. the species contribute to numerous clusters besides its main cluster). Hence, they were classified as transitional clusters between communities or areas. Hereafter, all the clusters except these two were analysed.

Clusters 1, 2 and 7 are predominantly located in FU2324 (Figure 3a). Cluster 1 is located exclusively on the north-western margin of FU2324. It is composed of 22 stations and associated to a single and very abundant taxon, the suspension-feeder Crinoidea (ab-Indval = 0.99; p-value < 0.001; table 2). Cluster 2 contains 74 stations and is largely dominated by Hydrozoa (ab-Indval = 0.63; p-value < 0.001) but also associated with five other taxa, Buccinidae, Soleidae, Holothuroidea, *Capros aper* and *Trachurus trachurus* (table 2). It is located mainly in the south-western margin of the FU2324 with some stations in the southern margin of FU15. Cluster 7 is composed of 48 stations scattered in FU2324 and associated with ten taxa, Cerantharia (indicator species of the cluster; ab-Indval = 0.39; p-value < 0.001) as well as *Pennatula phosphorea*, *Microchirus variegatus*, *Funiculina quadrangularis*, *Munida* sp., *Conger conger*, *Cepola* sp., *Mustelus* sp., Sepiidae and *Lophius* sp (Table 2).
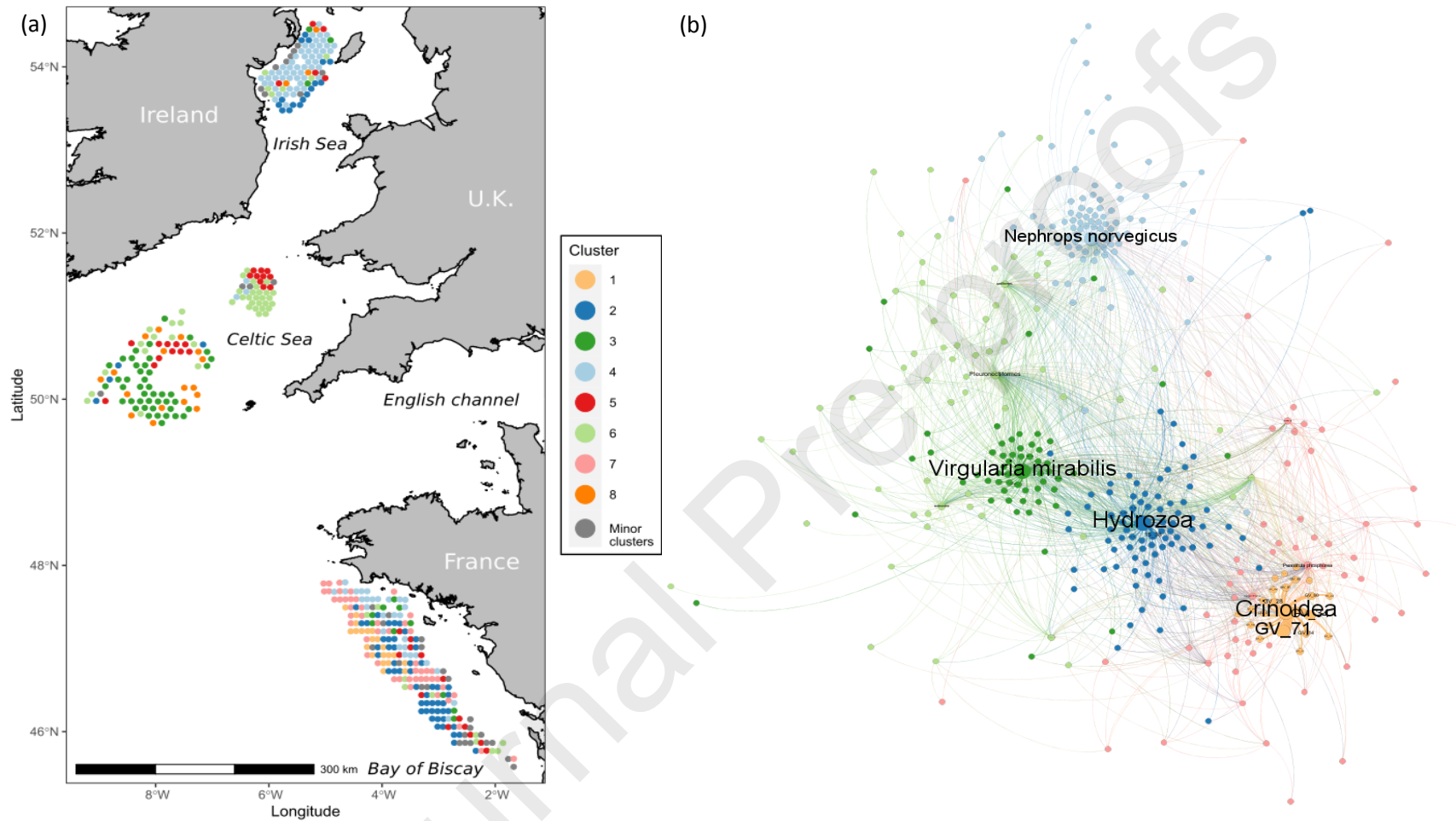
Figure 3. (a) The eight major biogeographical clusters identified in the four Functional Units (FU). Each major cluster is coloured differently with arbitrary colours, while the minor clusters are in grey.

(b) Biogeographical network of the 6 major community clusters. Colours are the same as for the map. Label and node size represent the number of links weighted by density, the larger the node, the more connections it will have. GV_71 is a station present in FU2324.

Table 2. Abundance based-Indicator value taxa (INDVAL) and taxa associated (ME) to the six major biogeographical clusters in the four Functional Units of the Bay of Biscay, Celtic and Irish Seas. Examples of indicators species are given in Supplementary material S7.

CLUSTER	Number of stations	INDVAL *Taxa with an ab-indval > 0.25 and p-value < 0.001*	BIOGEO *Taxa associated to each cluster*
1	22	Crinoidea, *Pennatula phosphorea*	Crinoidea
2	74	Hydrozoa	Hydrozoa, Buccinidae, Soleidae, Holothuroidea, *Capros aper, Trachurus trachurus*
3	57	*Virgularia mirabilis*	*Virgularia mirabilis*
4	86	*Nephrops norvegicus*	*Nephrops norvegicus, Cancer pagurus*
6	57	Pleuronectiformes, Gadiformes	Asteroidea, Pleuronectiformes, Gadiformes, *Scyliorhinus* sp., *Lepidorhombus* sp., *Glyptocephalus cynoglossus, Hippoglossoides platessoides*
7	48	Ceriantharia	Ceriantharia, *Pennatula phosphorea, Microchirus variegatus, Funiculina quadrangularis, Munida* sp., *Conger conger, Cepola* sp., *Mustelus* sp., Sepiidae, *Lophius* sp.

Clusters 3 and 6 are mainly located in FUs 2021 and 22 respectively (Figure 3a). Cluster 3 includes 57 stations scattered in FU2021 which are associated with a single indicator taxon, the sea pen *Virgularia mirabilis* (ab-Indval = 0.72; p-value < 0.001). Cluster 6 also has 57 stations and is located mainly in FU22, with a few stations scattered in the other three study areas. It is associated with seven taxa, the first two being indicator species of the cluster: Pleuronectiformes, Gadiformes (both with an ab-Indval = 0.29; p-value < 0.001), Asteroidea, *Scyliorhinus* sp., *Lepidorhombus* sp., *Glyptocephalus cynoglossus* and *Hippoglossoides platessoides* (Table 2).

FU15 is mostly composed of stations from Cluster 4 (Figure 3a). This cluster has 86 stations covering most of FU15 as well as the north-eastern margin of FU2324. It is associated with the commercially important species *Nephrops norvegicus* (ab-Indval = 0.71; p-value < 0.001) and *Cancer pagurus* (Table 2).

Overall, FU2324 is the most heterogeneous zone, with the presence of all six clusters in varying degrees of abundance. The other three FUs, 15, 2021 and 22 have respectively four, three and two clusters present.

3.2.2. Cluster connections

The network spatialisation with the six biogeographical clusters described above provides information on the drivers of our communities where a high density of nodes indicates clustering (Figure 3b). The most connected nodes in our network are species nodes corresponding to Crinoidea, Hydrozoa, *Virgularia mirabilis* and *Nephrops norvegicus*. These nodes correspond to species that are present in many stations and/or very abundant. The only station to appear clearly on the biogeographical network is GV_71, a station present in FU2324, with very high abundance of Crinoids, over 1730 individuals.

3.3. Abiotic characterisation of biogeographical clusters

The first two axes of the BCA, represented in Figure 4, explain 89.3% of the between-cluster variance (66.6% and 22.7% respectively), confirmed by the Monte-Carlo test (Observation = 0.1897; p-value = 0.001). The first axis opposes latitude to bottom temperature, sediment and medium and low impact gear fishing intensity. The second axis contrasted depth and bottom current to high impact gear fishing intensity and longitude.

The first axis presents a latitudinal gradient and clearly separates stations of FU2324 (left side of the BCA, Figure 4) from stations of FU 2021, FU 15 and FU 22 (right side of the BCA). Mean bottom temperature is a structuring variable on this axis with warmer waters in the Bay of Biscay and colder waters above the western tip of Brittany in France.

Cluster 1, 2 and 7 (left side of the BCA, Figure 4) all have higher bottom temperatures, linked to the more southern and warmer waters of the Bay of Biscay, as opposed to the Celtic and Irish Seas. These clusters include the deepest stations. They also differ from clusters 3, 4, and 6 in terms of fishing conditions, with a higher fishing time than average for medium impact gear in cluster 7, and for low impact gear in cluster 2 (right side of the BCA, Figure 4).

The second axis reveals another, more local, North-South latitudinal gradient structure by depth, bottom current and high impact fishing intensity (Figure 4). It separates stations of each of the three FUs in the Celtic and Irish Seas, with at the bottom stations from FU2021 with higher bottom current and depth, in the middle stations from FU22, and at the top stations from FU15 with shallower stations characterised by high impact gear fishing activity.
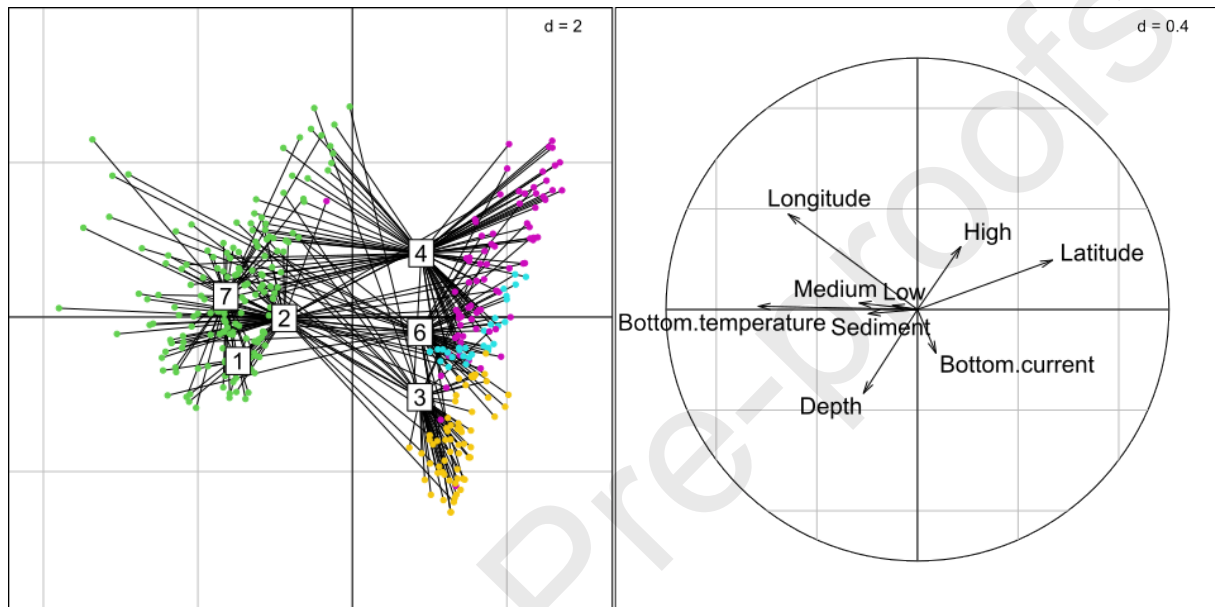

Figure 4. Between-class analysis plot. The left panel of this figure represents the ordination plot of the stations on the BCA and the right panel the circle of correlation of environmental variables. The first two axes of the BCA explain 89.3% of the between-cluster variance (66.6% and 22.7% respectively). At the top right of each graph d = grid size. The centroid of each biogeographical clusters are represented by the numbered squares, and correspond to the clusters visible on the biogeographical map and network – figure 3. Points represent the stations and are coloured according to their FU: Green = FU2324; Orange = FU2021; Turquoise = FU22; Pink = FU15. Fishing intensity is represented here by the vectors "High", "Medium" and "Low" corresponding to their gears level of impact on the seafloor.

4. Discussion

The study of bentho-demersal communities in four *Nephrops* fishing grounds using biogeography has shed light on the biological and environmental parameters driving these assemblages. We highlighted six different clusters between and within the four FU. Our findings suggest that *Nephrops* fishing

grounds on a regional scale harbour different types of species assemblages, influenced by the local scale combinations of environmental conditions and fishing pressure.

4.1. Diversity patterns in soft-bottom habitats

Taxonomic diversity patterns in the studied *Nephrops* grounds reveal that species richness and density are negatively correlated with high impact gear (i.e. trawls and dredges) fishing intensity (McConnaughey *et al.*, 2019; Mazor *et al.*, 2020; Pitcher *et al.*, 2022). At the same time, species richness and density are positively correlated with depth. This relationship was expected as fishing intensity decreases with depth (Eigaard *et al.*, 2017).

The areas of low species richness coincide with areas with high abundances and density of *Nephrops*, located in the Irish Sea West grounds (FU15) and in the north and south of the Grande Vasière (FU2324). Such a finding is difficult to disentangle, especially because fishing intensity may lead to a diminution in species richness but also because fishing occurs in areas that happen to be less diverse and dominated by the target species, or both reasons at the same time. These grounds have been heavily fished for more than a century making it difficult to compare our findings with reference or baseline studies. Comparing unfished grounds around shipwrecks with fishing grounds in the Irish Sea, Ball (2000) showed that a decreased species richness was a consequence of long-term fishing intensity, especially for vulnerable species. Moreover, trawling fisheries is often linked with a diminution in species richness and an increase in homogeneity, particularly in areas with finer sediment grain size (Jennings and Kaiser, 1998; Hiddink *et al.*, 2006; van Denderen *et al.*, 2014). Having less destructive fishing would allow the presence of more long-lived and vulnerable species, therefore increasing species richness.

Furthermore, higher species richness and densities are linked to the margins of each area, potentially due to a positive 'edge effect' (Ries *et al.*, 2004). A higher species richness around the margins of each area could be the result of a lower fishing intensity towards the edges of the Functional Units. In particular, species richness is higher on the external margin of the Grande Vasière, as well as stations in the Labadie, Jones, Cockburn (FU2021) and the Smalls (FU22) grounds. These stations are the deepest

stations of the study. It has been shown that species richness increases with depth, from coastal areas up to 2000 m deep where it starts to decline (Sanders, 1968; Gray, 2002; Escaravage *et al.*, 2009). The positive correlation between depth and density could also be explained by aggregations and high densities of some taxa. Crinoids were aggregated in some stations with up to 12 individuals/m^2 on the northern external margin of the Grande Vasière (also seen in Mérillet *et al.*, 2018).

4.2. Environmental drivers influencing bentho-demersal communities

4.2.1. Lusitanian and boreal biogeographical limit

Bottom temperature, bottom current, depth and fishing intensity are the main environmental drivers of our clusters, with clear environmental differences between the Grande Vasière in the Bay of Biscay, and the three other FUs in the Celtic and Irish Seas. Temperature drives these differences, with a strong gradient going from the warmer waters of the Bay of Biscay to the colder waters of the Irish and Celtic Seas. Sea temperatures in the Bay of Biscay are warmer, especially during the summer months, and continue to endure an increase due to climate change since the nineteenth century, confirming the latitudinal trend found in this study (Koutsikopoulos *et al.*, 1998; Planque *et al.*, 2003). The western tip of Brittany (France) might represent a temperature biogeographical limit (Dinter, 2001; Spalding *et al.*, 2007). As a consequence, Poulard and Blanchard (2005) have shown that many fish species are either at their most southern (Boreal) or northern (Lusitanian) distribution limit in the Bay of Biscay. Consequently, we observe a transition between Boreal and Lusitanian species within our study (Supplementary material S4). Some boreal species such as *Hippoglossoides platessoides* and *Glyptocephalus cynoglossus* for example, are found in and above the Celtic and Irish Seas (Froese and Pauly, 2022). In the same way, the subtropical boarfish *Capros aper*, although present in the Celtic Sea, was essentially found in the Bay of Biscay, where it has shown an exponential increase in its abundance in the last 50 years alongside the increase in bottom temperature, turning from a rare species in the 1970s to a dominant one currently (Blanchard and Vandermeirsch, 2005; Coad *et al.*, 2014).

Future studies should include the study of the biogeographical distribution of species on a temporal scale, across seasons to fully describe the dynamics and changes across these areas, but also annually. This would be particularly relevant with respect to potential changes due to climate change, where many studies show a poleward shift in the distribution and abundance of species (Poulard and Blanchard, 2005; Simpson *et al.*, 2011). This knowledge could help understand species distribution and poleward shifts, and feed models such as habitat suitability models for predicting species occurrences in VME (Anderson *et* al., 2016) but also in harvested grounds for that the fishing fleets can adapt in the face of these changes (Simpson *et al.*, 2011). The commercially important *Nephrops* fishery could potentially be affected, especially in the most southern areas of the Northeast Atlantic, by a shift towards colder waters and a decrease in abundance in warmer waters.

4.2.2. Mobile communities – *Nephrops* and fish

The two clusters that sheltered *Nephrops* and fish (i.e. Pleuronectiformes and Gadiformes), clusters 4 and 6 respectively, were deeply influenced by high impact fishing gear (Supplementary material S8). The occurrence of these taxa in highly trawled areas indicated that they are probably less sensitive to trawling due to their high mobility, burrowing behaviour, exoskeleton or feeding strategy – scavengers or deposit feeders (de Juan *et al.*, 2009; de Juan and Demestre, 2012; Dupaix *et al.*, 2021). Fishing intensity, especially bottom trawling, contributes to sediment resuspension (Mengual *et al.*, 2016; Oberle *et al.*, 2016). It may also increase the proportion of fine-silt mud and clay when mud content is high (Oberle *et al.,* 2016 but see Mengual *et al.,* 2016 for another point of view when a higher resistance to penetration is observed), which could in turn profit to *Nephrops* burrowing behaviour (Johnson *et al.*, 2013). Bottom trawl fisheries discards has become an important and easy catch food resource, and benefit opportunistic and scavenger species (Olaso *et al.*, 2002). In the North Sea, an increase in abundance of benthic prey for plaice and sole was observed simultaneously with the increase of beam trawling improving feeding conditions for these two flatfish species (Rijnsdorp and Vingerhoed, 2001).

The same was observed in the southern Bay of Biscay, where lesser spotted dogfish benefited from blue whiting discards (Olaso *et al.*, 1998). In the present study, scavenger species such as *Nephrops* or dogfish as well as flatfish, are associated species of the clusters seen just above (4 and 6) that could benefit from damaged species, highlighting that ~~all~~ these species are well adapted to fishing consequences.

4.2.3. Sessile communities – Sea pens, crinoids, hydrozoans, ceriantharians

On the contrary, the four remaining clusters sheltered a majority of sensitive species such as sea pens, crinoids, hydrozoans and ceriantharians. The life-history traits of these taxa such as fragile shells, slow growth, sessile or sedentary species and filter-feeding strategy makes them more vulnerable to trawling disturbances (de Juan *et al.*, 2009). These clusters were located in areas with less high impact gear fishing intensity and showed to be more dependent of environmental variables such as bottom current velocity and depth. For instance, *Virgularia mirabilis* and *Pennatula phosphorea*, are associated with the highest current velocity and depths. These VME indicator species are highly vulnerable to active fishing methods, such as trawling (Curd, 2010) probably explaining their affinity for areas where passive fishing gear are more used than active ones. As filter-feeder species their filtering organs get easily clogged due to the increased resuspension caused by trawls (de Juan *et al.*, 2007; Mengual *et al.*, 2016). Furthermore, these colonies need a specific current velocity to feed. Bottom current speed has been proved to be an important factor in the distribution patterns of sea pens (Burgos *et al.*, 2020).

The same patterns may explain the same distribution for other sessile predatory, suspension-feeders and colonial organisms (i.e. hydrozoans, ceriantharians and Crinoids). These indicator species still rely on current velocity for feeding such as shown by Conan *et al.* (1981) for another species crinoids with highly aggregated populations in the Bay of Biscay.

4.3. The importance and contribution of biogeography

Bioregions are a key feature for management because they simplify complex species assemblages into units that are understandable and describe the complexity of sampled biological characteristics (Woolley et al. 2020). For *Nephrops* fishing grounds, biogeography has the potential to contribute to

marine conservation planning. It can for example, provide an overview of the ecosystem, identify target species (the commercially important *Nephrops* or the vulnerable *Pennatula phosphorea* for example), understand the distribution of Lusitanian and Boreal species depending on the environmental conditions as well as the connectivity between distant areas (Lourie and Vincent, 2004). Our study of the biogeographical clustering of bentho-demersal communities in *Nephrops* fishing grounds provides insight on the structure of the communities and their distribution. The real benefit of biogeography is that it provides information on the patterns of species distribution and the species driving these patterns, by assigning the different taxa to a cluster and showing the ones that are links between and within communities. The communities highlighted by this bioregionalisation method are clustered in groups of stations with similar compositions and abundances. Thus, even though some stations were geographically/spatially very close, their communities were different. The Grande Vasière, for instance, had the most heterogeneous composition, including all six clusters within its boundaries, as already observed by Mérillet et al. (2018). Cluster 4, whose indicator species is *Nephrops*, in turn, showed that it was not restricted to a specific geographical area, but rather present in areas where the environmental conditions were favourable, that is the shallowest and more coastal stations of the most southern and northern FUs of this study.

Using biogeographic approaches rather than local studies can help gain time and resources by providing meaningful information that is useful on a regional scale. Our study considering large spatial scale. provides information on species spatial distribution along the Bay of Biscay/Celtic Sea continuum but also on the species that are specific to certain areas. This approach is fully updatable and in light of fishing changes that will probably occur in a near future due to the implementation of fishing restrictions, marine protected areas or offshore wind farms, our approach will give stakeholders ammunition to take management decisions. Decision-support tools for marine spatial planning (Pınarbaşı et al., 2017) are widely used by science and conservation communities for prioritization and optimization of space. Spatial knowledge produced in this study could be integrated as biodiversity layers together with fisheries activities layers in order to define compromise between conservational

and fishing objectives, as done by Boussarie et al. (2023) in the FU2324 area, but at a larger regional

scale. Outcomes of management scenarios would then consider the whole species stock (e.g. *Nephrops*)

rather that local populations independently.

Acknowledgments

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- Underwater videos were used to explore taxonomic diversity in 4 *Nephrops* grounds.
- Biogeographical analysis highlighted indicator species of the different communities.
- Species differed along a depth, bottom current and fishing gradient.
- Even in fished areas, Vulnerable Marine Ecosystem indicator species are present.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: