



Epibenthic communities' structure in St. Pierre Bank revealed by underwater video

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ABSTRACT

Given the significant ecosystem services provided by benthic communities, monitoring their biodiversity enable to better understand how global changes would affect their structure in a context of biodiversity loss. Using underwater video transect, we characterize alpha and beta diversity of epibenthic communities, their structure and forcing factors in St. Pierre Bank; an area where marine benthos is still poorly documented. Video monitoring enables the detection of 74 different taxa belonging to eight phyla. Results highlighted three spatial entities of benthic assemblages distributed along a bathymetric gradient and primarily influenced by sedimentary types. In the southern and western area, rhodoliths beds substrate shelters the majority of echinoderms. The southern region was dominated by sea cucumber *Cucumaria frondosa*, whereas in the western area, brittle stars, and the green sea urchin *Strongylocentrotus droebachiensis* were dominant. Fishing activity was concentrated in the south, due to the presence of exploited sea cucumber. In contrast, the northern region featured patchy fine and soft substrates with a preponderance of giant scallop *Placopecten magellanicus* and sand dollar *Echinarachnius parma*. In addition to the contribution of environmental factors to the distribution of communities, this study highlights the complexity of several biotic interactions at the origin of these assemblages.

1. Introduction

Continental shelves provide crucial ecosystem services, making them highly valuable to human society (Costanza, 1999). However, they are subject to a wide variety of pressures exacerbated by the impacts of global change (Costanza, 1999; Worm and Lotze, 2021). As these changes accelerate the loss of biodiversity, understanding species assemblages and their spatial structure is becoming essential for establishing baseline assessments of biodiversity and managing future changes, especially in the Arctic and sub-Arctic latitudes, where sea warming is 2 to 3 times higher than the global average (AMAP, 2017; Bridier et al., 2024).

Although commercial benthic species are well-studied, global benthic communities despite their rich taxonomic and functional diversity, remain less documented (Snelgrove, 1999; Weigel et al., 2016). These communities provides key ecosystem services including water filtration or food energy transfer into benthic-pelagic coupling (Griffiths et al., 2017; Solan et al., 2020). Due to the importance of these ecosystem services, benthic community structure has gained increasing attention in recent decades (Lam-Gordillo et al., 2020; Prather et al.,

2013; Snelgrove, 1999), but still remain poorly studied in some areas.

The spatial structure of marine benthos is shaped by the effect of physico-chemical conditions, anthropogenic activities as well as biotic interactions. Similar environments may also host different species assemblages due to random processes such as ecological drift or local extinctions (Chase and Myers, 2011; Ovaskainen et al., 2017). These factors act simultaneously and vary widely across the continental shelf (Feder et al., 1994; Hargrave, 1978). On a broad scale, benthic community may vary along depth or latitudinal gradients (Piacenza et al., 2015; Rex and Etter, 2011). Nevertheless, the major global patterns of community structure can be more contrasted when looking at the dynamics on a finer scale (Piepenburg, 2005). Environmental factors like temperature, salinity, ice cover, and hydro-geomorphology significantly drive the spatial heterogeneity of benthic distributions (Feder et al., 1994; Gutt, 2001; Hargrave, 1978; Levin and Sibuet, 2012; Sisson et al., 2002). In addition to these environmental influences, the multiplicity of anthropogenic pressures and their cumulative effects may also be responsible for the patterns of community structure observed (Kenny et al., 2018). As examples, human pressures such as offshore marine mining or gas exploration impact benthic community structures by

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generating pollution and degrading habitats (Olsgard and Gray, 1995; Savage et al., 2001), leading to a reduction of species as well as a shift of species towards less sensitive species able to establish themselves in contaminated sediments (Olsgard and Gray, 1995). Fishing activity, particularly bottom trawling, has well-documented impacts on fish communities (Collie et al., 2017; Jennings and Kaiser, 1998; Smith et al., 2006; Thrush et al., 1998; van Denderen et al., 2013), and research is gradually extending to include benthic invertebrates of commercial importance (Hinz et al., 2009; Jennings et al., 2001; Kaiser, 1998a; Tillin et al., 2006), such as sea cucumbers. Initially confined to a few species in the Indo-Pacific, sea cucumber fisheries have expanded to include more species and regions globally (Therkildsen and Petersen, 2006). Nevertheless, the disparity in terms of species response to fishing pressure as well as the absence of a reference state can make the assessment of temporal changes more complex (Mérillet et al., 2017), highlighting the need for comprehensive biodiversity overviews. As environmental and anthropogenic forcing tend to co-vary, it can be particularly difficult to determine the main mechanisms behind the distribution of community (Bolam et al., 2017; Ellis et al., 2006).

In addition to being influenced by their environment, benthic species can actively modify their habitats at small-scale, particularly through the activities of ecosystem engineers (Meadows et al., 2012). Marine benthos exhibit a large range of functional traits which exert critical role in the functioning of marine ecosystem from a physical and chemical point of view (Gautreau et al., 2020; Pearson, 2001; Welsh, 2003). Activities such as bioturbation, bottom or suspension feeding induces the distribution and remineralisation of organic matter as well as the formation of specific sedimentary structures (Welsh, 2003). For example, coralline algae such as rhodoliths forms algal bioconstructions and a three-dimensional substrates that support a rich diversity of fauna and flora (Foster, 2001; Nelson, 2009; Schubert et al., 2020). Beyond the role of ecosystem engineers, marine benthos have the capacity to shape the organisation of marine systems by forming complex and interdependent assemblages of species through inter-specific interactions (Ellis et al., 2006; Meadows et al., 2012). Thus, biotic interactions, such as predation, commensalism or competition, play a key role in structuring benthic ecosystems (Uwadiae, 2014). For instance, the predation pressure exerted on mussels *Mytilus edulis* by both common seastars *Leptasterias polaris* and *Asterias vulgaris*, limits the spread of mussel beds, an epibenthic habitat (Gaymer and Himmelman, 2002). Although this enumeration is not intended to be exhaustive, it does show that benthic communities are decisive compartments in the overall organisation of ecosystems.

To assess the spatial structure of marine benthic assemblages, non-extractive sampling methods are increasingly being used (Mcgeady et al., 2023). Underwater video sampling, in particular, has become more widespread over the past decades (Jac et al., 2021; Mérillet et al., 2018; Sheehan et al., 2016). This method offers the advantage of observing the totality of habitat (Jac et al., 2021; Mérillet et al., 2018). However, it is not always possible to obtain sufficient taxonomic resolution, although high definition allows a better level of determination than what was possible few years ago (Pelletier et al., 2011). Often used for stock monitoring purposes (Coupeau et al., 2023; Simon et al., 2021), video sampling provides valuable information that can multiple purposes. In this study, we used videos initially produced for stock assessment of exploited sea cucumber *Curcumaria frondosa* stocks (Simon et al., 2021) to describe the epibenthic communities at meso-scale.

In Canadian marine ecoregions, Newfoundland-Labrador shelves inhabited a substantial diversity of species, including 255 species of fish and invertebrates (Cheung et al., 2011). However, this region is particularly vulnerable to biodiversity loss and shifts as a result of climate change (Cheung et al., 2011). While the global marine communities of Newfoundland and Grand banks continental shelves are increasingly being studied (Lacharité et al., 2020; Murillo et al., 2016; Schneider et al., 1987; Thouzeau et al., 1991), the epibenthos of St. Pierre bank remain poorly documented. It is therefore essential to

characterize existing species assemblages, as well as the factors responsible for their structure to effectively monitor and predict biodiversity dynamics in a context of global changes. This study aims to build an initial knowledge on epibenthic communities of St Pierre Bank, by (1) describing the communities through alpha and beta diversity, (2) characterizing community structure, and (3) determining the main environmental and anthropogenic drivers of community structure.

2. Materials and methods

2.1. Sampling area

Saint-Pierre-et-Miquelon (SPM) is a small archipelago of 242 km² located in the south of the Canadian province of Newfoundland and Labrador. The Exclusive Economic Zone of SPM has a total area of 12,400 km² mainly configured as corridor. The study area is concentrated in the narrow corridor of French waters, on Saint-Pierre bank (Fig. 1A). The study region covers approximately 467 km² in shallow water (comprised between 30 and 60 m) (Fig. 1B). St Pierre bank is bounded to the east by the deep glacial excavations of the Laurentian Channel (Bonifay and Piper, 1988), and is subject to the influence of three main currents (the Gulf-Stream, the Labrador, and the plume originating from the Gulf of St. Lawrence) (Sutcliffe Jr. et al., 1976). This interconnected estuarine-shelf system (Koutitonsky and Bugden, 1991; Urrego-Blanco and Sheng, 2014), generates the encounter between the cold water from the Labrador current and the fresh, nutrient-laden water from the Gulf of St. Lawrence. Concerning sedimentary structures, the study area includes a diversity of substrates ranging from soft to hard substrates dominated by rhodolith bed, a coralline seaweed (Rhodophyta, Corallinaceae) (Gagnon et al., 2012).

2.2. Data collection

The videos were acquired from May 15 to May 21, 2021 on board the F/V Marcel Angie III, a traditional sea-cucumber dredger. 50 linear video transects of 10 min were sampled using a GoPro Hero 7 Black camera attached to the dredge. Transects were carried out at a speed of 1 knot over a distance of 500 m. With a horizontal field of view of 1 m, the area sampled was estimated at 500 m². The camera was set to a resolution of 1080p, recording at 30 frames per second with a large field of view. The shutter speed is 1/300 s, and the ISO range is from 200 to 3200, allowing for adaptability in various lighting conditions. The camera exposure was set to 1/500 s (2.5 ms), and two white LEDs each with 2000 lm of power were placed on each side of the camera to fully illuminate the camera's field of view. An automatic stabilizer was employed to minimize camera shake, ensuring smooth and stable footage.

2.2.1. Faunistic data

Individuals were identified and annotated manually to the lowest possible taxonomic level. The videos transects were analysed using a VLC player at half speed (x0.5) and were regularly paused in view of the high density of taxa present. Individuals were counted manually except for two taxa *Cucumaria frondosa* and Ophiuroidea. Concerning *Cucumaria frondosa*, the annotation had previously been carried out during the HOLOTVSPM21 campaign which aims to estimate sea cucumber stocks by automating the analysis of underwater videos using deep neural networks (Simon et al., 2021). For this species, videos were first analysed on board at a half speed of 0.5 using hand-held counters. On the 50 videos analysed, 9 videos were sub-sampled (e.g. 2 min analysed instead of 10), while checking that the sub-sampled density was representative of the full videos by visual observation of the whole video. More information about the methodology is available in Simon et al. (2021). In the case of Ophiuroidea, the high density of species and their position under the rocks made counting particularly difficult. Thus, their density was estimated with the number of visible arms according to 6

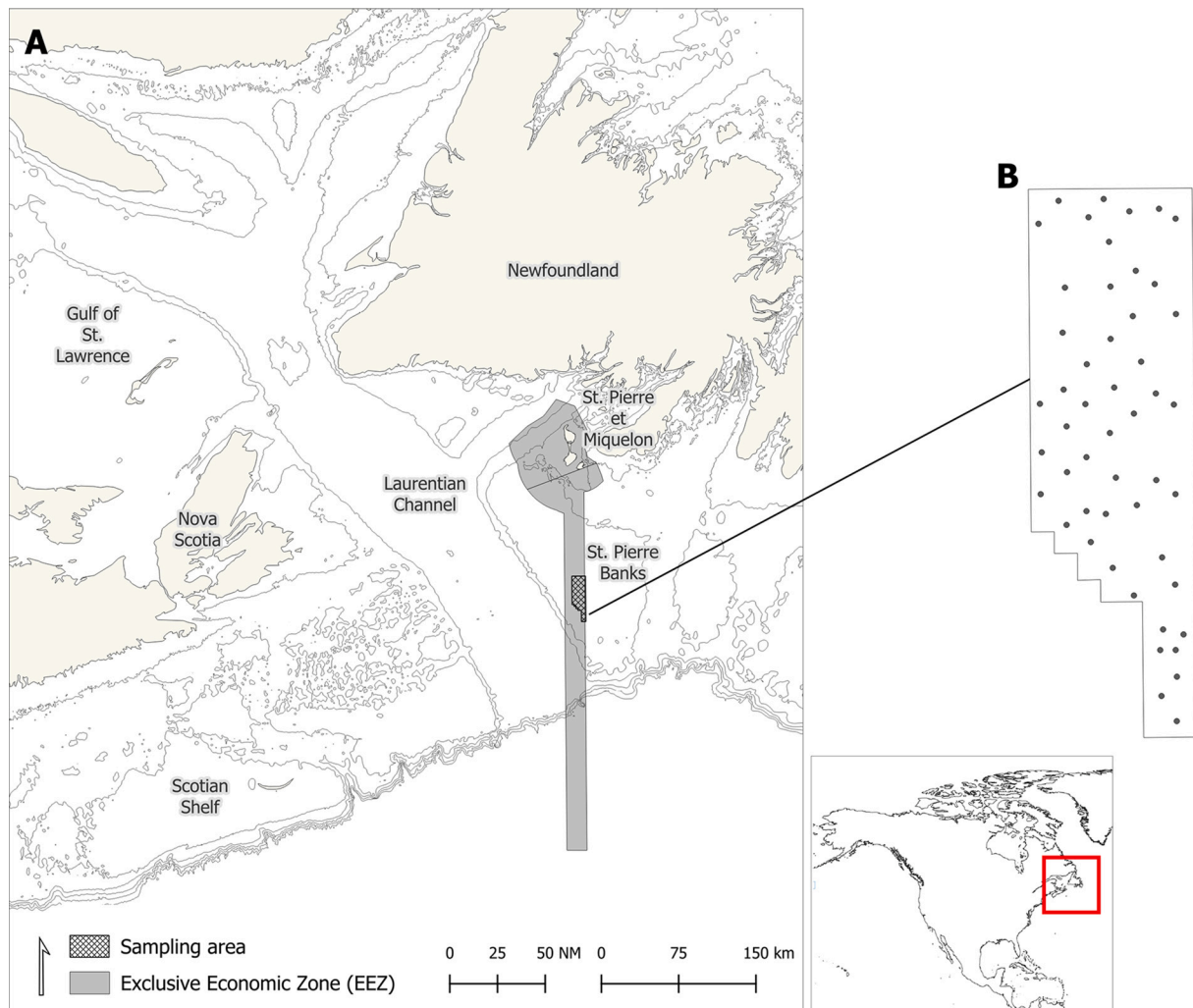


Fig. 1. Map of the study area (A) and location of the sampled stations (B) where dots represent the mean location of the videos transects. Isobaths has been extracted from GEBCO's gridded bathymetric data sets (GEBCO Compilation Group, 2023), the intersect of the Exclusive Economic Zones has been extracted from Flanders Marine Institute (2020), and terrestrial delimitation has been extracted from Natural earth (Free vector and raster map data on naturalearthdata.com).

classes of arm abundance for each 10 s of videos transects: 0, 1–50, 51–200, 201–500, 501–1000, >1000 arms. These abundance classes were initially established by manually counting the number of visible arms on sub-sampled videos (i.e. 1 min analysed instead of 10). The abundance classes of visible arms were then transformed into specific abundance values as follows: 0, 25, 125, 350, 750, and 1000 arms. To estimate the number of individuals from visible arms, the probable number of individuals was first counted in several random 10-s video slices. Hence, it was estimated that around 2.5 arms were visible per individual. Finally, the abundance of individual was obtained by dividing the number of visible arms by 2.5 and summing up the results over the entire video.

Other taxa were identified to the lowest possible taxonomic level. Although visibility was sufficient for all the videos (Fig. 2), this method can introduce biases in the identification of taxa (Jac et al., 2021). Consequently, the lowest taxonomic resolution used was reduced to the genus, considered as sufficient for providing ecological information in benthic surveys (Brind'amour et al., 2014). For taxa that could not be identified to genus level, higher taxonomic levels were used, such as family or class. Finally, abundances were divided by the sampled area (i.e. 500 m²) to obtain a density per m². For the sake of reproducibility, a photo-catalogue of the species identified in the videos is available upon request. This file includes 72 photos extracted from the videos and a metadata file indicating the species observed in each photo. It should be

noted that the screenshots of species are not always representative of our observations since the movement of certain species was a key indicator for determination.

2.2.2. Environmental data

Bathymetric information was acquired from the ETOPO Raster (ETOPO Global Relief Model, 2020). Bottom temperature (°C), bottom salinity (PSU), Eastern and Northern components of the bottom current (m.s⁻¹), sea ice concentration (%), and sea ice thickness (m) have been extracted from Global Ocean Physics Reanalysis products E.U. Copernicus Marine Service Information (CMEMS) (2023). These data were extracted for the Spring period (March, April and May 2021) and values were assigned to video transects location using the nearest neighbour method. As well, mean tidal current speed (m.s⁻¹), total current speed (m.s⁻¹), seabed disturbance index (SDI) and disturbance type classification (i.e. 1: wave dominant; 2: tide dominant; 3: circulation dominant; 4: mixed; 5: unaffected) were extracted from a modeling approach from a 3-year period which combined sediment transport by flow to simulate seabed shear stress and sediment mobilization observed on the Canadian Atlantic continental shelf (Li et al., 2024). Concerning sedimentary structure, it was obtained from visual observation and classified into six categories; (1) Sand / Gravel / Cobble banks, (2) Coarse cobble, (3) Coarse cobble / Gravel, (4) Boulder fields, (5) Boulder fields / Coarse cobble, and (6) Sandy mud area. We manually annotated the sediment

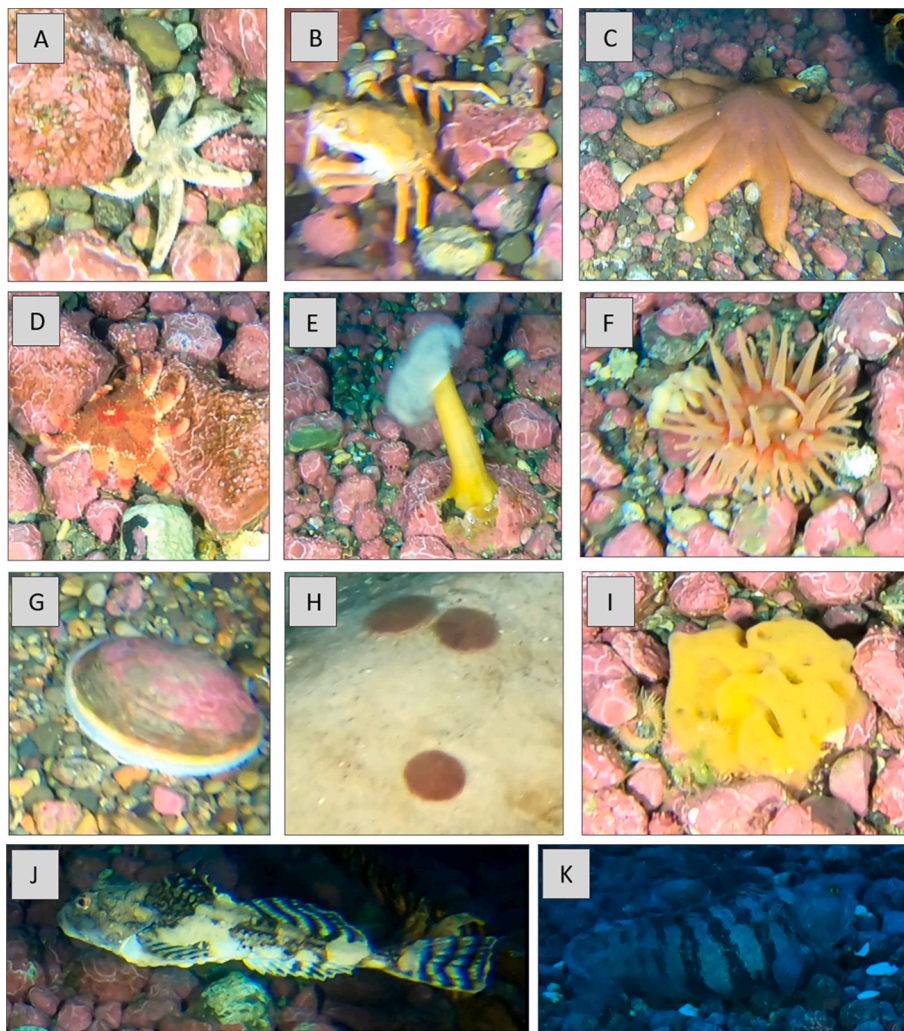


Fig. 2. Examples of organisms observed in video. (A) *Leptasterias*, (B) *Hyas*, (C) *Solaster*, (D) *Crossaster*, (E) *Metridium*, (F) *Bolocera*, (G) *Placopecten*, (H) *Echinarachnius*, (I) *Porifera*, (J) *Myoxocephalus*, (K) *Anarhichas*.

observed for each minute of video and retained the predominant sediment types for each video. Boulder fields is the predominant sediment type in the area (30 %), followed by Boulder fields / Coarse cobble (26 %), Coarse cobble / Gravel (24 %), Coarse cobble (12 %) and Sand / Gravel / Cobble banks (6 %), while Sandy mud area are poorly represented (2 %). Pictures of the described sedimentary structures are provided in Supplementary material Fig. S1.

2.2.3. Fishing data

Fishing intensity information was collected using surveys in the form of a questionnaire. The questionnaire was distributed to professionals who use dredges because of its documented effects on the diversity and composition of benthic communities (Smith et al., 2006). These surveys mainly consisted of a grid map of the area to be completed according to three levels of fishing intensity; (1) unfrequented area, (2) occasionally frequented area, (3) very frequented area. Fishing effort intensity was recorded twice for the years 2020 and 2021. For each cell of the grid map and each year, the fishing intensity was transformed into score as follows: 0: area not frequented, 1: occasionally frequented area and 2: very frequented area. Hence, these scores were summed together for areas frequented by several professionals and for both years, resulting in a single score of fishing intensity.

2.3. Data analysis

Taxonomic diversity indices were calculated for each video transect using the *vegan* package (Oksanen et al., 2022). Taxonomic richness (Stirling and Wilsey, 2001), Shannon-Weaver (Shannon, 1948), and Pielou's indices (Pielou, 1966) were calculated in R (R Core Team, 2023) and interpolated using the Inverse Distance Weighting (IDW) interpolation method under QGIS version 3.36.1-Maidenhead (QGIS Development Team, 2023). These diversity indices were then graphically represented in the form of a map for visualisation purposes only. IDW method estimates unknown value points using the spatial distance of values at the known points. Interpolations were conducted with a 100 m spatial resolution and using a distance coefficient equal to 2 to ensure that closer points have a greater influence than distant points. IDW only allow broad estimation (Setianto and Triandini, 2015), but in contrast with other methods, IDW does not estimate values that are higher than the observed input data and offer a smoother lineament (Setianto and Triandini, 2015).

To study spatial structure and define the factors influencing species distribution, a Redundancy Analysis (RDA) was carried out on Hellinger-standardized data. Analysis was carried out using the following variables: latitude, longitude, bathymetry, bottom temperature, bottom salinity, eastern and northern components of the bottom current, total current speed, mean tidal current speed, seabed disturbance index (SDI) disturbance type classification, sea ice concentration, sea ice thickness,

as well as fishing intensity (summed for 2020 and 2021) and sediment type. To avoid collinearity among the explanatory variables, collinear variables were identified using the variance inflation factor (VIF) considering a threshold of >5 (Kyriazos and Poga, 2023). Thus, latitude, longitude, bottom temperature, bottom salinity, both components of the current, sea ice concentration and thickness, mean tidal current speed, total current speed, seabed disturbance index and disturbance type classification were excluded from the RDA model. A correlation plot of all the variables is provided in Supplementary material Fig. S2. As these values vary little across the study area (Bottom temperature: 2.2 ± 0.3 °C; Bottom salinity: 31.8 ± 0.1 PSU; Northern current: 0.009 ± 0.01 m.s⁻¹; Eastern current: -0.01 ± 0.02 m.s⁻¹; Ice concentration: 0.0004 ± 0.0004 %; Ice thickness: 0.0003 ± 0.0004 m; Mean tidal current speed: 0.13 ± 0.007 ; Total current speed: 0.15 ± 0.007 ; Seabed disturbance index: 0.16 ± 0.04 ; Disturbance type classification; 92 % of station classified as wave dominant and 8 % as unaffected), it is likely that their influence on the distribution of communities at this scale is relatively small. Finally, the function *ordistep* in the *vegan* package (Oksanen et al., 2022) was used for stepwise selection of the RDA model with a *p*-value threshold <0.1 in order to include marginally significant variables. To delimitate pattern of spatial structure, transects were grouped using K-means clustering algorithm according to their RDA scores following a silhouette routine to determine the optimal number of clusters (Rousseeuw, 1987). Then, extracted clusters were characterized according to explanatory variables retained in the RDA model with the function *catdes* from the *FactorMineR* package. This allow to create a typology of conditions for each cluster derived from the K-mean partitioning (Husson et al., 2024). Furthermore, indicator taxa were determined using the Species Indicator Values (*IndVal*) in each cluster (Dufrene and Legendre, 1997) from the package *labdsv* (Laliberté and Legendre, 2010). This allows us to detect which taxa were indicative of the observed clusters. The Monte Carlo permutation tests were performed to assess the statistical significance of the association between species and site groups. Since the normality of the data was not met, A non-parametric mean comparison test (Kruskal-Wallis test) was used to test the average density and taxonomic richness differences between the

identified clusters. A non-parametric post-hoc test (Pairwise-Wilcoxon with holm correction) was then used to investigate potential differences between these delimited clusters.

3. Results

3.1. Diversity patterns

In the 50 video transects, 299,810 individuals from 74 different taxa belonging to eight phyla were observed. These included 21 chordates, 16 cnidarians, 12 echinoderms, 10 mollusks, 7 arthropods, 5 porifera, 2 annelids and 1 bryozoan. Taxa consistently present in all 50 video transects are Actinaria, *Asterias*, *Cucumaria* and Hydrozoa while 12 taxa were encountered in only one video transects (Supplementary material; Fig. S3). Across all video transects, taxa that represent the higher densities were Ophiuroidea (214 ind.m^{-2}), *Strongylocentrotus* (129 ind.m^{-2}), *Cucumaria* (125 ind.m^{-2}), *Echinarachnius* (29 ind.m^{-2}), and Hydrozoa (23 ind.m^{-2}), while 10 taxa were found at a very low density of 0.002 ind.m^{-2} (Supplementary material; Table S1).

Across the different videos transect, density ranged from 1.65 to 41.37 individuals per m². The highest density was found at the south of the sampling area (Fig. 3A), which is dominated by the sea cucumber *Cucumaria frondosa* (38 ind.m^{-2}). In contrast, the eastern part of the study area presented the lowest densities, ranging from 1.65 to 6.9 ind.m⁻². Taxonomic richness varied between 17 and 36 different taxa, displaying a gradient from west to east, with higher values in the western and southern regions of the study area (Fig. 3B). The Shannon diversity index ranged between 0.26 and 2.49, and Pielou diversity index ranged between 0.09 and 0.74. Both indices exhibited similar geographical trends, with higher values in the east and lower values in the west and south areas (Fig. 3C & D). These diversity patterns are distinct to those of taxonomic richness, primarily due to a non-uniform distribution of species density with the dominance of species such as *C. frondosa* in the south and Ophiuroidea in the eastern part of the study area.

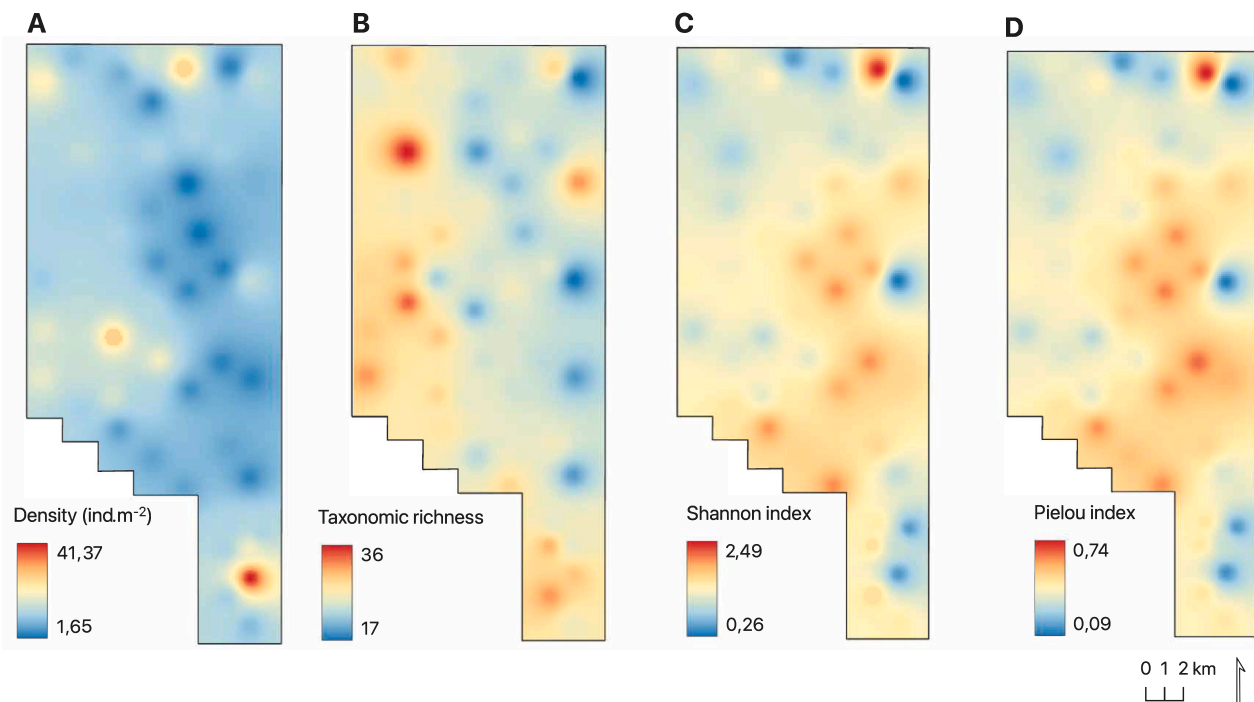


Fig. 3. Map of the Inverse Distance Weighting (IDW) interpolation method realized on alpha diversity under QGIS (Version 3.36.1-Maidenhead). Each video transect were interpolated for representation purposes only. From left to right, the maps represent density (ind.m^{-2}) (A), taxonomic richness (B), Shannon (C) and Pielou (D) diversity indices.

3.2. Spatial structure

The best RDA model selected sediment type, bathymetry, and fishing intensity as explanatory variables, and explain 62 % of the total variance (Fig. 4). The first two RDA axis accounted for 32.7 % and 12 % of the explained variability, respectively. First axis was correlated to boulder fields (0.608), coarse cobble with gravel (−0.575), coarse cobble (−0.509), boulder fields with coarse cobble (0.459), as well as fishing intensity (−0.576). Second axis was correlated to sandy mud (0.396) and bathymetry (−0.543).

The clustering highlighted a clear delineation of three groups. These clusters globally corresponded to geographic entities (Fig. 5). Cluster 1 (C1) is located in the south of the sampling area and presents *Cucumaria*, *Solaster*, *Corymorpha*, *Leptasterias*, *Asterias*, *Gymnocanthus* and *Chlamys* as indicative taxa (Indval, Table 1). This cluster is characterized by a hard substrate mostly composed of coarse cobble and gravel. It gathers the deepest transects where fishing intensity is high. Cluster 2 (C2) encompasses video transects primarily located in the northern part of the area in sand, gravel and cobble banks substrate, with *Placopecten*, Paguridae, Hydrozoa, Cerianthidae, Sabellidae, *Alcyonium*, *Haliclona* and *Echinarachnius* as indicator species. The main drivers of this cluster according *catdes* is the lower bathymetry (Table 1). As well as C1,

Cluster 3 (C3) is characterized by a hard but coarser substrate (Boulder fields). This cluster has no influence of fishing activity. Indicator taxa of C3 are Ophiuroidea, Porifera, *Bolocera*, *Metridium*, *Strongylocentrotus*, *Psolus*, Ascidiacea and *Halichondria* (Table 1). Geographically, a clear segregation appears between C1 and C2 on a latitudinal gradient, as well as between C1 and C3 on a longitudinal gradient (Fig. 5).

The three clusters identified differ in density (Fig. 6) (Kruskal-Wallis $\chi^2 = 8.47$, $df = 2$, $p = 0.0145$). The Pairwise Wilcoxon tests with Holm correction reveal that Cluster 2 and Cluster 3 are significantly different ($p = 0.03$), while the Cluster 1 and Cluster 3 ($p = 0.1$) and Cluster 1 and Cluster 2 ($p = 0.26$) are similar in terms of density. The relative density (%) of each taxa per cluster are presented in Supplementary material Table S2. In contrast, the taxonomic richness shows no statistically significant differences between the clusters (Kruskal-Wallis $\chi^2 = 3.40$, $df = 2$, $p = 0.1828$).

4. Discussion

4.1. Structure of assemblages

Underwater video method enabled to highlight well-defined spatial patterns in terms of both diversity and taxonomic composition. The

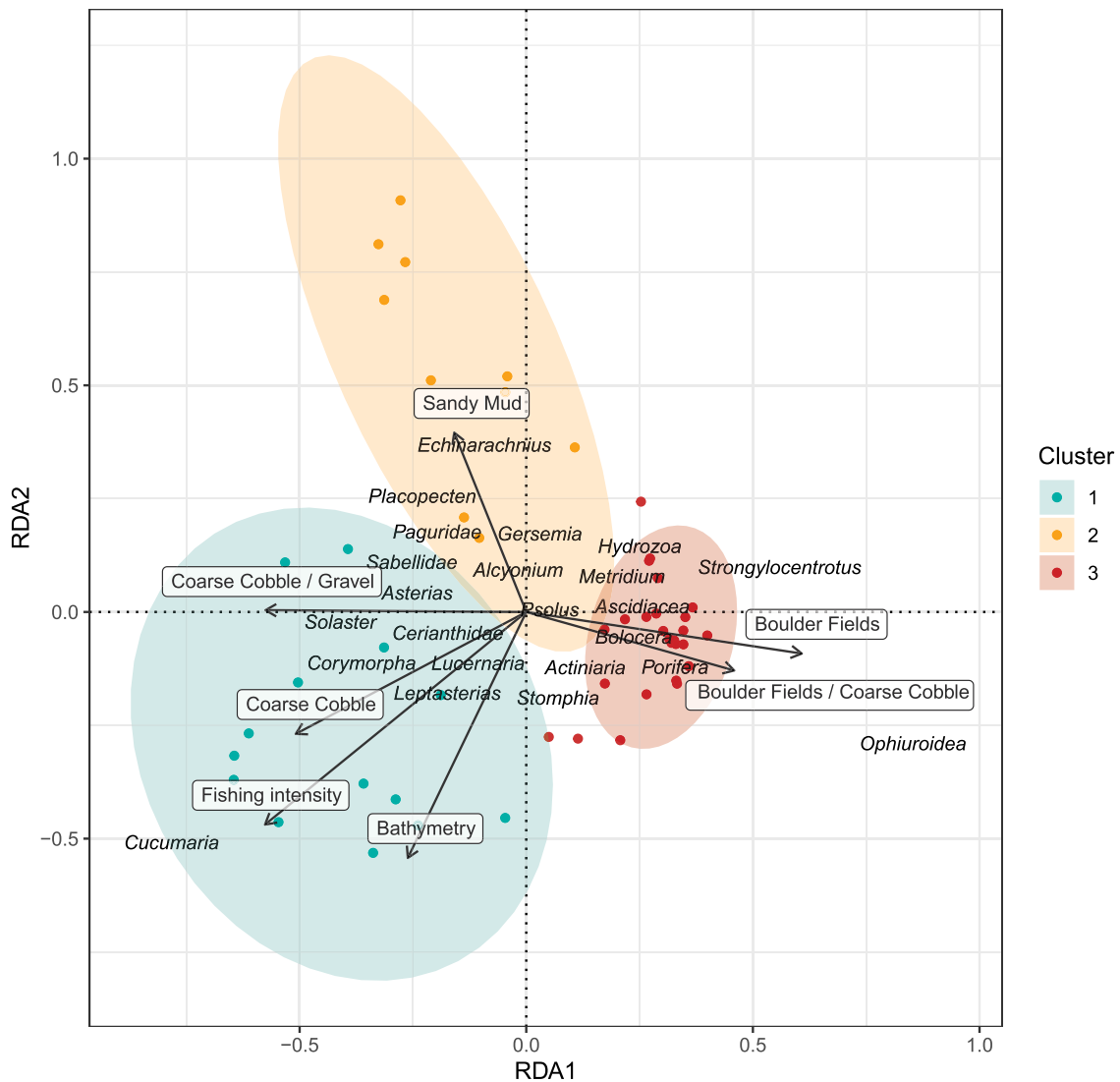


Fig. 4. Result of the Redundancy Analysis (RDA) based on Hellinger distance matrix of community. Arrows represents the significant explanatory variables, dots represent the videos transects. Colored ellipses represent the k-means clustering results based on RDA scores. For graphic purpose, only taxa having a correlation >3 % to at least one of the two first axis were represented.

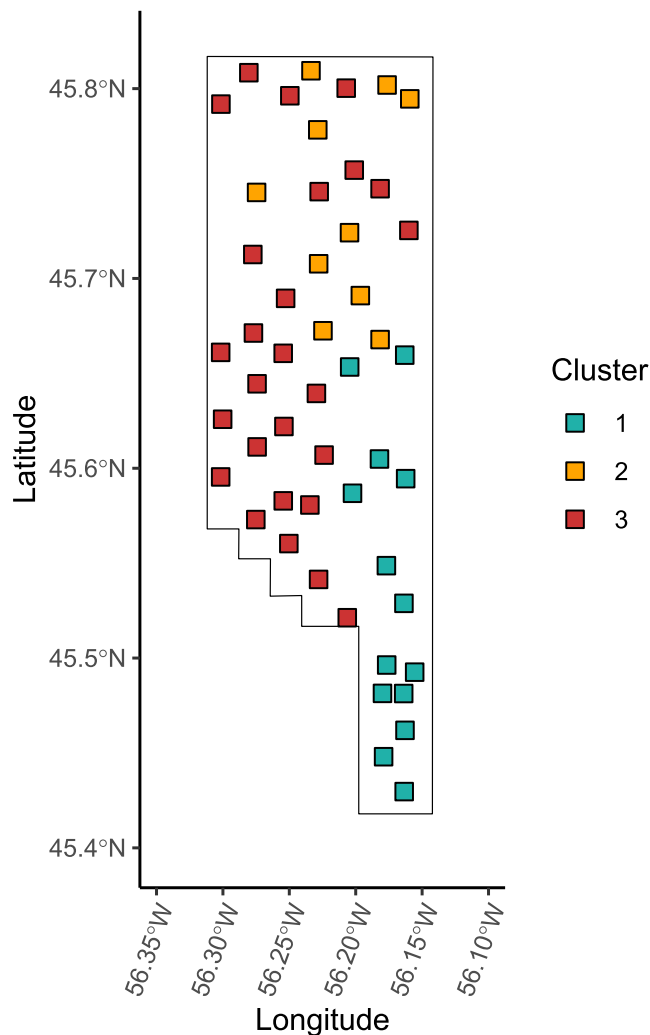


Fig. 5. Map of the k-means clustering of videos transects based on the RDA scores.

alpha diversity and clusters described are linked to geographical areas according to specific sedimentary characteristics that seem to be distributed along a longitudinal and latitudinal gradient.

Concerning alpha diversity, western and southern areas are characterized by a high taxonomic richness and density but a low level of individual evenness. This first pattern is coherent with clustering result since the western (Cluster 3) and southern (Cluster 1) areas are dominated by the high-density of few taxa, especially Ophiuroidea (C3) and *Cucumaria frondosa* (C1). The dominance of echinoderms has already been recorded at high latitudes, and particularly in the polar regions and Arctic deep-sea (MacDonald et al., 2010), where brittle stars can form beds of up to 100 ind.m⁻² (Ambrose et al., 2001; Piepenburg, 2000). Even higher densities have been reported on the continental slope of Nova Scotia (Canada), where mean abundances of brittle stars range from 390 to 1200 ind.m⁻² (Metaxas and Giffin, 2004). Within St Pierre bank, the substrate is mainly composed of rhodoliths beds, a coralline algae encrusted recorded from the tropics to the Arctic seas (Jørgensbye and Halfar, 2017). Coralline algae mainly colonize hard substrates and are only present in C1 and C3, which consist of boulder fields, boulder fields with coarse cobble, as well as coarse cobble with gravel to a lesser extent. These are stable habitats known for their great diversity and abundance given its role as a nursery for species such as mollusks, echinoderms, corals, or sponges (Bélanger and Gagnon, 2023; Gagnon et al., 2012). By creating hard stable substrate, red coralline algae forms a favourable refuge for juveniles of sea cucumbers (Hamel et al., 2023;

Table 1

Results of the *catdes* function indicating typology for each cluster derived from K-means partitioning. Selected variables were chosen from the RDA model. For each cluster, variable values in the cluster are indicated as well as the mean values for all clusters. (C1: n = 14; C2: n = 10; C3: n = 26). Results of the *IndVal* index showing indicative taxa for each cluster obtained from K-means partitioning. Only the species with *p* < 0.05 in the Monte Carlo test are listed.

Variables (mean values)	Cluster 1	Cluster 2	Cluster 3
Sedimentary structure	Coarse cobble / gravel p-value = 0.002	Sand / gravel / cobble banks p-value = 0.006	Boulder fields p-value = 0.0001
Bathymetry (48 m)	Coarse cobble p-value = 0.005 Higher bathymetry (51 m) p-value = 0.005	Lower bathymetry (45 m) p-value = 0.03	Boulder fields / Coarse cobble p-value = 0.007
Fishing intensity (0.40)	Higher fishing intensity (1.4) p-value = 0.0002		Lower fishing intensity (0) p-value = 0.02
<i>IndVal</i> (%)	<i>Cucumaria</i> (69 %) <i>Solaster</i> (61 %) <i>Corymorpha</i> (58 %) <i>Leptasterias</i> (50 %) <i>Asterias</i> (44 %) <i>Gymnocanthus</i> (37 %) <i>Chlamys</i> (30 %)	<i>Placopecten</i> (62 %) Paguridae (55 %) Hydrozoa (55 %) Cerianthidae (45 %) Sabellidae (41 %) Alcyonium (36 %) <i>Haliclona</i> (34 %) <i>Echinarachnius</i> (29 %)	Ophiuroidea (69 %) Porifera (64 %) <i>Bolocera</i> (62 %) <i>Metridium</i> (59 %) <i>Strongylocentrotus</i> (45 %) <i>Psolus</i> (40 %) Ascidiacea (37 %) <i>Halichondria</i> (35 %)

Medeiros-Bergen and Miles, 1997). Rocky area provided stable condition which optimises the stability of young individuals with a limited number of podia and tentacles (Gianasi et al., 2018; Hamel et al., 2023; Medeiros-Bergen and Miles, 1997). Furthermore, the pink to red colour of the rhodoliths beds could also be a favourable factor regarding the background colour preferences shift of juvenile cucumbers (Gianasi et al., 2018). In relation to their role as nurseries, the development and stability of rhodoliths beds as habitat is also due to the presence of grazers and their symbiotic relationship (Schoenrock et al., 2018). As associated biofilm of coralline algae feeds a large number of grazers, the high density of green sea urchin *Strongylocentrotus droebachiensis* in our study area could largely participate in the formation of suitable habitat structure by limiting the colonisation of epiphytes (Adey and Macintyre, 1973; Steneck, 1990; Teichert et al., 2014). Thus, the community structures observed in the western (within C3) and southern (within C1) parts of the study area are complex and can be associated with this specific habitat retroactively favoured by the presence of key species. Although C1 and C3 share similarities from the point of view of this habitat, we observed differences at the level of the assemblages. These can be partly explained by the diversity of biotic interactions specific to the different clusters. As explained above, C1 is dominated by the *Cucumaria frondosa*, but also constituted of starfish of the genus *Solaster* and *Leptasterias*. Since the genus *Solaster* is a major predator of sea cucumbers (Francour, 1997; So et al., 2010), the nursery area of *C. frondosa* previously identified would favour predation by *S. endeca* on juveniles (So et al., 2010). As well, *Leptasterias* and *Asterias* found next to sea cucumbers aggregation could also be a major predator of the latter. Unlike C1, Ophiuroidea and *Strongylocentrotus* mainly represent C3 assemblages in association with anemones of the *Bolocera* and *Metridium* genera and sponges.

The assemblages in Cluster 2 (C2) are mostly located in northern part of the study area associated with a soft substrate. This cluster is dominated by suspension-feeders (i.e. *Placopecten*, Hydrozoa, Cerianthidae,

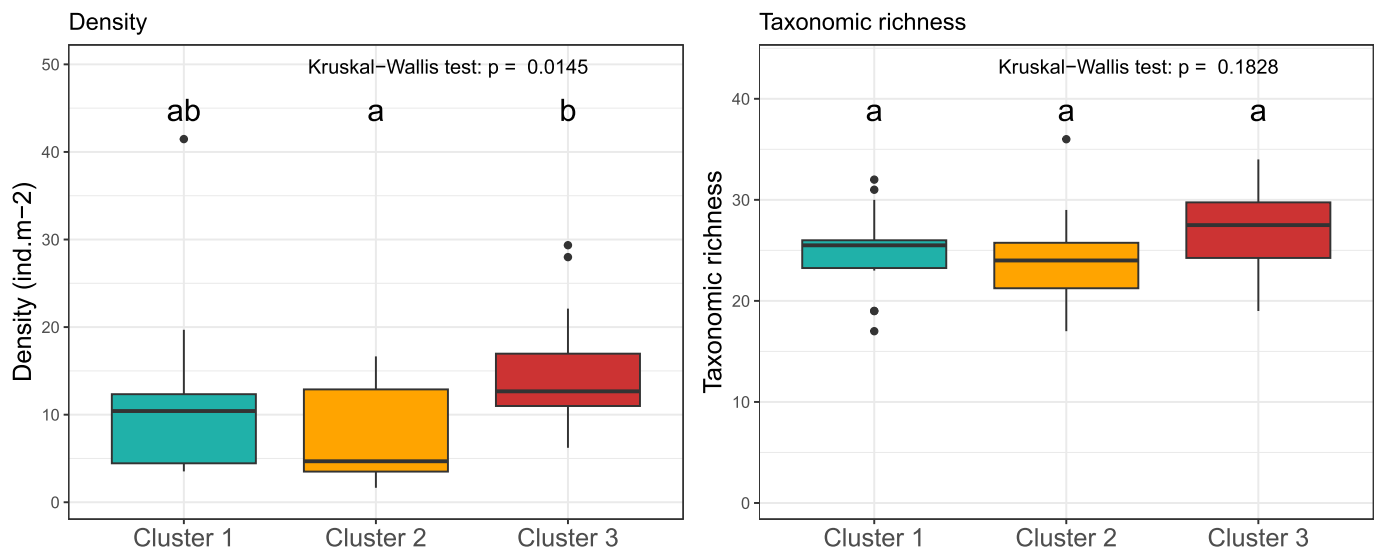


Fig. 6. Boxplot of the density (ind.m^{-2}) (left) and taxonomic richness (right) (Cluster 1: $n = 14$; Cluster 2: $n = 10$; Cluster 3: $n = 26$). The p-value of the Kruskal-Wallis test is indicated at the top of the graphic. The letters correspond to the results of the Pairwise-Wilcoxon test.

Sabellidae, *Alcyonium* and *Haliclona*) and deposit-feeders (i.e. *Echinarachnius*, Paguridae). Similar assemblages have already been recorded in the Bay of Fundy and on Georges Bank (Kennington and Full, 1994; Staniforth et al., 2023; Stokesbury and Bethoney, 2020; Thouzeau et al., 1991). Some benthic organisms are capable of profoundly modifying sediment and its transport (Gautreau et al., 2020; Jumars and Nowell, 1984; Pearson, 2001). Thus, most of the species found in this cluster that depend on a soft or at least fine substrate have the ability to rework surficial sediments (e.g. sand dollar *Echinarachnius parma* by bioturbating, or Cerianthidae and Sabellidae by creating tube-dwelling and burrowing) (Grant et al., 1998; Stanley and James, 1971). In addition to the species mentioned, we observed many tubes on this substrate, which have not been annotated because of the great uncertainty about the corresponding species. The functional traits of suspensive and deposit-feeders found in these clusters could be a decisive factor in the assemblage structures. Although a relationship of amensalism is considered between suspensive and deposit feeders (Cacabelos et al., 2009), by favouring the oxygenation of interstitial waters and by resuspending the sediment (Gautreau et al., 2020; Miller et al., 1992), the activity of deposit feeders could then benefit to cnidarians or spinner organisms (Orejas et al., 2002).

The species assemblages observed in the study area appear to be coherent and well defined. They reflect both a relation with sedimentary structures and inter-specific interactions. Inferring these assemblage results with the assemblages of the meiofauna and small macrofauna compartments including endobenthic species would provide a more complete picture of the biotic mechanisms behind these structures.

4.2. Spatial structure according to environmental factors

The RDA model has selected bathymetry and substrate as significant variables and fishing intensity as a marginally significant variable. This selection is strict because of the high degree of collinearity with bathymetry variable. On the other hand, environmental variables show only little variability over the given period and area. St. Pierre Bank is characterized by a stable temperature (above 0°) with a tendency to increase in the last few years, as well as a stable salinity (around 32 PSU) (Cyr et al., 2022). In this area, dominant current direction are southwest (3.6 cm.s^{-1} average), with a tidal component in the southwest/eastward directions (Fowler, 2014). Although ice can affect benthic community (Gutt, 2001), the absence of ice concentration and thickness signals is mainly due to the fact that the Labrador Current could lose its arctic

characteristics as it approaches the St Pierre Bank (Sutcliffe Jr. et al., 1976). Additionally, despite significant variations on the scale of the Canadian Atlantic Shelf (Li et al., 2024), seabed shear stress and sediment mobilization are relatively stable within the boundaries of our study area. Nevertheless, although the signal is weak, environmental parameters are probably still involved in the spatial structure of communities.

As benthic habitat are controlled by the stability of the seabed (Li et al., 2021; Sebens, 1991), the assemblage patterns observed greatly correspond to sedimentary type. Sediment types are partly determined by the circulation of bottom current as well as the topography, which can contribute to allocate resources or even encourages the dispersion of larvae (Bradbury and Snelgrove, 2001; Ramey-Balci and Snelgrove, 2003). The southern Newfoundland shelf is characterized by an important gulf-shelf connection, with the interaction of continental waters into the Gulf and Labrador Current with the continental slope (Han et al., 1999). It is therefore subjected to the presence of oceanic front between the Laurentian Channel and Grand Banks water (Cyr and Larouche, 2015). The presence of a very high density of *Cucumaria frondosa* (including juveniles) in the south of the area raises the hypothesis of a located supply of nutrient water at the southern end of the St. Pierre bank. Moreover, higher density of *C. frondosa* are observed in association with strong currents (Singh et al., 1999). This organic matter supplied might originate from nutrient input to the front zone, or by an input from bottom current. Furthermore, the high density of brittle stars extending arms to feed by suspension to the west of the area reinforces our hypothesis (Piepenburg, 2000). Although there is no evidence of increased biological activity in this region (Cyr and Larouche, 2015), the physical and chemical ecosystem has mainly been studied on a large scale (Bisagni et al., 2009; Shaw et al., 2014), limiting our comprehension of small-scale biological effects (Cyr and Larouche, 2015). Compared to others, the northern area (C2) is a more shallow area of soft substrate organized in patch where the influence of tidal mixing and storm forms dune (Collie et al., 1997). The Grand Banks of Newfoundland are organized in shallow banks separated by channels or enclosed basins (Li et al., 2015). The Grand Banks area is under the influence of the Labrador Current, high waves and strong winds associated with intense winter storms (Li et al., 2015). The presence of *Placopecten magellanicus* is often associated with strong hydrodynamics and fine substrates, since *P. magellanicus* adapted to unstable environment by using byssal threads or forming depressions in the sand (Stokesbury and Harris, 2006). Thus, the presence of this species seems consistent in

areas subject to strong hydrodynamic constraints with seabed shear stresses and sediment transport processes (Li et al., 2015).

In addition to the impact of environmental forcing, bottom fishing can also affect the distribution of benthic communities (Jennings and Kaiser, 1998; Kaiser, 1998b; Thrush et al., 1998). Cluster 3, which is unaffected by the impact of fishing activity, includes species that are sensitive due to their functional characteristics. Sessile species, such as branching sponges are particularly vulnerable to the effect of direct physical impacts and indirect impacts such as the increased turbidity caused by bottom trawlers (Freese, 2001; Wassenberg et al., 2002). Thus, the presence of these species in Cluster 3 is consistent with the absence of fishing pressure in this area. Cluster 1 partly stands out because of the recorded fishing intensity, which is only concentrated in the southern part of the area due to the location of a probable nursery of exploited *Curcumaria frondosa* (Foucher, 2018; Therkildsen and Petersen, 2006). Although our questionnaires did not investigate other fishing activity, the northern part of the study area (C2) is also subject to dredge exploitation due to the presence of a *Placopecten magellanicus* (Foucher, 2018). Given the highly localized nature of these both target species and the fishery's specialization in these two species (Collie et al., 1997; Foucher, 2018), dredging activities would not occur on sites where these species are absent probably explaining why dredging activity as a physical disturbance is only marginally responsible for the distribution of species (Collie et al., 1997).

4.3. Perspectives of the method

Underwater sampling method has the advantage of being non-extractive (Mallet and Pelletier, 2014; Solan et al., 2020), which comes with a main limitation relative to species identification (Jac et al., 2021). This main limitation was largely reduced thanks to the excellent quality of the images and by the conservative approach of degrading the lowest taxonomic information used to genus level. This method only allows focusing on epi-benthic species, which may affect our understanding of the biotic mechanisms at the origin of the structure of assemblages. Given the mobility of a large proportion of epibenthic fauna, the use of towed equipment may either underestimate the abundance of some species by causing individuals to flee. Nevertheless, videos sampling could be a good option to sample specific compartment in association with other method to obtain a fully pictures of community structures (Jac et al., 2021). Concerning the effect of environmental variables on species distribution, the data obtained from Copernicus and seabed shear stress and sediment mobilization modeling covers a wide area and may be less resolute on the scale of our study, as it does not allow us to identify a clear signal. While in the deep sea, environment can be relatively homogeneous, spatial structure may vary on a millimetre scale in some areas (Meadows et al., 2012). Thus, a better understanding of the physical and chemical systems on a finer scale would help to clarify the patterns of community structures observed. At the same time, expanding the study area to the continental slope and at different timescales could reveal more marked variations given sea surface warming and water column stratification (Bridier et al., 2024).

5. Conclusion

Underwater videos offered a preliminary overview of the epibenthic communities on the St. Pierre bank. Despite the inherent limitations of this approach, we were able to identify distinct spatially structured assemblages and reveal key drivers behind their formation. The interplay of environmental factors, fishing activity, and biotic interactions underscores the complexity of the community structure, shaped by the combined effects of these elements. By providing a detailed overview of an underexplored region, this study lays crucial groundwork for ongoing biodiversity monitoring on the Saint-Pierre Bank. Given the vulnerability of Newfoundland and Labrador's marine communities to biodiversity shifts and species turnover due to climate change, our findings

provide a critical baseline for assessing future changes in species composition and developing appropriate conservation strategies.

CRediT authorship contribution statement

Pauline Boët: Writing – original draft, Methodology, Formal analysis, Data curation. **Sonia Méhault:** Writing – review & editing, Validation, Supervision. **Julien Simon:** Formal analysis, Methodology, Resources, Software, Visualization. **Marie Morfin:** Writing – review & editing, Validation, Supervision. **Dorothee Kopp:** Writing – review & editing, Validation, Supervision, Conceptualization.

Declaration of competing interest

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2025.102562>.

Data availability

Data will be made available on request.

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