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Modelling spatial distribution of epibenthic communities in the Gulf of St. Lawrence (Canada)

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Abstract:

Correlative habitat models using relationships between marine organisms and their surrounding environment can be used to predict species distribution, and the results can assist management of human activities sharing the marine space (e.g. fisheries, MPAs, tourism). Here, epi-benthic megafauna was sampled at 755 stations in the Lower Estuary and Northern Gulf of St. Lawrence (EGSL) each summer between 2006 and 2009. We combined various types of multivariate analyses to 1) describe the structure and spatial distribution of benthic communities, 2) analyse the relationship between these communities and environmental parameters, and subsequently 3) build a community distribution model to predict the spatial distribution of the communities, creating community distribution maps covering the entire area to be used for marine management and conservation. We identified distinct benthic communities in the study area that closely correlate with the 200 m depth contour and with major environmental variables. A redundancy analysis revealed that communities were associated with depth, oxygen saturation, temperature, bottom current, seabed uniformity, distance to coast and type of sediment. Together these environmental descriptors explained 38% of the variation in megafaunal community composition. The environmental variables were used to build a community distribution model using generalized linear models to predict high and low suitability zones of each community in the EGSL.

Highlights

► Epibenthic megafaunal communities of the Gulf of St. Lawrence were described. ► Their relationships with the environmental conditions were assessed. ► A statistical community distribution model was designed. ► Communities are strongly related to their environment. ► The different communities are predicted to live in specific habitats.

Keywords: Biodiversity ; Epibenthic Communities ; Estuary and Northern Gulf of St. Lawrence ; Generalized Linear Model ; Community Distribution Model ; Redundancy Analysis

1. INTRODUCTION

Species distribution models (SDMs) are used to provide guidance for conservation planning, for instance during the process of designing protected areas, in a context of ecosystem-based management of natural areas. These models focus on the habitat characteristics surrounding the species. According to Baretta-Bekker *et al*. (1992), a habitat is simply the distinctive space occupied by a population or a species. The set of conditions required for an individual to survive and reproduce constitutes the "ecological niche" within which a species may indefinitely maintain itself (Hutchinson, 1957), and the geographical projection of this fundamental niche corresponds to the habitat of the considered species (Chase and Leibold, 2003). Therefore, a habitat is an area with specific environmental conditions in which an organism, a population, or a community can survive (*e.g*. Eastern Channel Habitat Atlas for Marine Resource Management, Carpentier *et al*., 2009). In natural environments, most communities are associated with a recognisable suite of physical conditions, and some communities occur within a narrower physical habitat window than others (Urbanski and Szymelfenig, 2003). This relationship between physical characteristics of an area and biological composition of the associated communities can be assessed by SDMs, which was initiated in terrestrial ecosystems several decades ago and is still developing (Degraer e*t al*., 2008; Guisan and Zimmerman, 2000; Hirzel *et al*., 2006), in particular to study the possible consequences of a changing environment on species distributions (Guisan and Thuiller, 2005). In marine ecosystems more specifically, a large number of studies have demonstrated the importance of environmental factors as driving forces of the distribution of benthic and fish communities (*e.g*. Carassou *et al*., 2008; Chouinard *et al*., 2011; Glockzin and Zettler, 2008; McArthur *et al*., 2010; Rosenberg, 1995). From these analyses, full coverage spatial distribution maps of biological communities or biodiversity can be created (Degraer *et al*., 2008, Mellin *et al*., 2010).

Even though predicting species or community occurrence using modelling has become increasingly common in ecological conservation studies (Degraer *et al*., 2008; Martin *et al*., 2010, Mellin *et al*., 2012; Vaz *et al*., 2008), SDMs are often too simple scientifically speaking (they do not incorporate all ecological processes, Dormann *et al*., 2012) or too complex to be easily and safely transferred to decision makers and people responsible for natural-area management. With the higher number of management programs for marine space planning throughout the world, it is necessary to provide simple but accurate tools such as high-resolution easy-to-read present and future biodiversity distribution maps derived from SDMs to be used in environmental policies.

The Gulf of St. Lawrence (Canada) is a good candidate area in which to develop SDMs for marine ecosystem planning. Due to the variety of hydrodynamic regimes and physical processes observed, the Lower Estuary and Northern Gulf of St. Lawrence (EGSL) is often divided into distinct oceanographic sub-regions (Brunel *et al*., 1998; Koutitonsky and Bugden, 1991). This high spatial heterogeneity is combined with high faunal diversity, which make the EGSL a good area to evaluate the potential connections between environmental factors and marine communities. Notwithstanding a limited number of local or taxon-specific studies investigating diversity and distribution of benthic invertebrates (Belley et al., 2010; Bourque, 2008; Desrosiers et al., 2000; Massad and Brunel, 1979; Ouellet, 1982; Peer, 1963, Préfontaine and Brunel, 1962; Robert, 1979), benthic communities at the EGSL scale remain poorly understood. Additionally, some of the ESGL oceanographic conditions have already noticeably changed due to global climate change (modification of water layer heights and increased hypoxia: Belley *et al*., 2010; Gilbert *et al*., 2005, 2007; acidification, Mucci *et al*., 2011), which generates a strong need for tools to predict present and future biodiversity distribution and aid conservation management. Because of the presence of several diversity conservation and fishery issues (such as fishery overlap or stock management, DFO, 2006, 2010), fishery managers, governmental organisations, and research institutes are working together to gather new methods and tools to predict species distribution and community structure (*e.g*. Canadian Fisheries Research Network: http://www.cfrn-rcrp.ca), and could therefore benefit directly from this study.

Since 1990, the Department of Fisheries and Oceans Canada (DFO-Quebec region) has been conducting annual groundfish and northern shrimp bottom trawl surveys in the EGSL. The main objective was to collect biological information related to commercially important groundfish (cod, Greenland halibut, redfish) and northern shrimp stocks exploited in the EGSL. Each summer 2006 to 2009, the effort was intensified for the identification of all benthic invertebrate taxa aboard the CCGS *Teleost* research trawler. In spite of this intensive sampling effort, the relative opacity of seawaters renders species community observation on a continuous large area impossible. In this case, community distribution models (CDMs) can be implemented to give a better picture of community composition in poorly-sampled areas of the EGSL. Given that correlations between environmental conditions and species distribution are known to exist, we assume that such relationships will also be detectable at the community level. We therefore hypothesise that temperature, depth, and oxygen will be strong determinants of community structure. Sediment type and other hydrodynamic-related variables are expected to have a weaker influence on community structure. The 2006-2009 dataset was therefore used to: (1) explore the composition and distribution of the epibenthic megafaunal community using multivariate analyses; (2) correlate the communities' spatial distribution with the abiotic factors to determine which environmental parameters may drive diversity patterns; and (3) create high-resolution maps from a statistical CDM, describing megafaunal community affinities with significant environmental parameters.

2. MATERIAL AND METHODS

2.1. Study area

The EGSL has two major connections with the Atlantic Ocean, through Cabot and Belle-Isle Straits, and receives important freshwater inflows, mainly from the St. Lawrence River. Consequently, estuarine circulation occurs by water flowing seaward in the surface layer and landward in the deep layers (Saucier *et al*., 2003). The topography of the northern part of the Gulf is distinguished by three deep channels: Laurentian, Anticosti, and Esquiman (Fig. 1).

2.2. Survey method and biological data collection

Megafauna was sampled from 755 stations in total during summers 2006 to 2009 (1-31 August each year), with sampling station depth spanning from 24 to 512 m, and minimal distance between two stations being 115 m (Fig.1). The sampling strategy used consisted of a stratified random sampling following predetermined strata based on depth (Doubleday, 1981). All samples were collected with a four-sided shrimp bottom trawl (*Campelen 1800* type). The trawl was rigged with variable net mesh sizes (44 to 80 mm centre knot to centre knot) appropriate for each part of the trawl. The codend and the lengthening piece were also equipped with a 12.7 mm knotless nylon lining (McCallum and Walsh, 2002). The standard tow duration was 15 minutes on the bottom but was shorter in rare cases where the substrate was rougher. Among these cases, tows exceeding 10 minutes were retained in the analysis and tows below this threshold were removed (Archambault *et al*., 2012). The 15-minute duration was then used to calculate the biomass for all tows.

The catch from scientific surveys was sorted and identified to the lowest possible taxonomic level. Because colonial organisms such as bryozoans and hydrozoans were too abundant to be enumerated, the wet weight of each taxon was instead recorded. The sorted megafauna was photographed aboard, and images of total capture and of each identified taxon were recorded. Species not identified while at sea were preserved in 70% ethanol or frozen for later identification in the laboratory. Taxonomic names were verified using the Integrated Taxonomic Information System (www.itis.gov). Biomass estimates were standardized relative to catch per unit effort (CPUE) by dividing the mass of a taxon by the total area swept by the trawl. Biomasses in the database were therefore expressed in kg.km^{-2}.

2.3. Environmental variables and spatial distribution maps

Two sets of environmental variables characterizing the EGSL were gathered from different sources, *i.e*. at the sampling stations and throughout the EGSL.

At each sampling station, a CTD Seabird^{TM} apparatus (SBE911 Plus), combined with a SBE 43 dissolved oxygen sensor, measured the water column characteristics such as salinity (conductivity), temperature, and dissolved oxygen at predetermined depths, including the bottom. Titrations of water samples, collected with Niskin bottles fixed on a rosette, were carried out to corroborate the concentration of dissolved oxygen measured with the oxygen sensor. Geographical (*e.g*. distance to coast) and physical descriptors related to the underwater relief were also gathered for each sampling station (Dutil *et al*., 2011). Another extensive set of these water-column, geographic, and physical data, located all over the EGSL, was used (Dutil *et al*., 2011). Bottom current, included as an abiotic factor in the environmental dataset, was obtained using a three-dimensional coastal ice-ocean model with realistic tidal, atmospheric, hydrologic and oceanic forcing (Saucier *et al*., 2003). At each sampling station, the maximum mean hourly bottom current value in cm.s^{-1} was obtained for August for each corresponding year (2006 to 2009), and, for the entire EGSL, maximal values per year, averaged over 2006 to 2009, were calculated and included in the EGSL environmental dataset. A digital map of seabed sediment types, derived from Loring and Nota (1973) and validated using sediment grabs by Bourque (2008) and pictures of the seafloor from Belley *et al*. (2010), was used to determine substratum type in the entire EGSL, including at each sampling station. The original sediment classification contained 46 substratum codes identified by textual analysis, and, for simplification, 14 groups were made from these and retained for subsequent analysis (Table 1).

Continuous raster maps of the main environmental variables were produced (Fig. A.1). Interpolated values using kriging of the initial variables covering the entire EGSL were estimated on a fine regular grid of points on ArcMap (version 9.1, ESRI, Inc), and the Spatial Analyst extension was used to illustrate continuous spatial patterns of each variable.

2.4. Statistical analysis and modelling framework

A step-by-step set of analysis was used to understand the structure of epibenthic communities in the EGSL and predict their presence according to the surrounding environmental conditions: communities and the environment were first described separately using clustering and multivariate analysis, then the relationships between communities and the environment were determined using multivariate analysis. Finally, generalized linear models were used to predict habitat suitability, *i.e*. the probability of presence, of the communities in the EGSL. Data were analysed using the vegan library (Oksanen, 2011) in the statistical package R version 2.14.1 (R Development Core Team, 2011). Prior to analyses, 6 taxa (out of 221) that appeared only once were excluded from the analyses, as suggested by Clarke and Warwick (1994).

2.5. Analysis of epibenthic communities, the environment, and relationships between communities and the environment.

Bray-Curtis dissimilarity measure (Bray and Curtis, 1957) was used to build a community dissimilarity matrix, in order to define distinct communities from the co-distributions of individual species. The dissimilarity matrix was then subjected to a hierarchical cluster analysis using Ward's minimum variance agglomeration method to detect compact, spherical clusters (Ward, 1963). A number of well-defined clusters corresponding to dissimilarity between communities of less than 20% was selected. Each cluster corresponded therefore to a group of stations, and each group hosted one community. Non-metric multidimensional scaling (nMDS) ordination, based on the Euclidean distance on Hellinger-standardized biomass data (Legendre and Gallagher, 2001) was carried out to visualise the position of the clusters on the ordination diagram with minimum stress. Geographical distribution of these communities in the Gulf was then mapped using ArcGIS software (version 9.1, ESRI, Inc.).

Because many environmental variables were available (Table 1), a variable-reduction procedure was carried out to select a subset of environmental variables that minimized collinearity. A principal component analysis (PCA) was combined to an analysis of the correlation matrix to select one or two environmental variables per group of multicollinear variables. The relationship between epibenthic community composition (*i.e*. each group of station) and the selected environmental variables was then evaluated using a multivariate method of constrained linear ordination, the redundancy analysis (RDA, Legendre and Legendre, 1998). This method seeks the linear combination of explanatory (*i.e.* environmental) variables that best explain the variation of the biological community matrix. In RDA, species scores correspond to strength and direction of correlation of the species with a particular factor. RDA was performed on Hellinger-standardized data to avoid rare species and sites with many individuals to have a differential weighting (Legendre and Gallagher, 2001). To assess which environmental factors are most important to explain RDA axes, a permutation test (999 permutations) was used to test correlations between the stations and the variables on the first and second RDA axes. This allowed assessing the statistical significance of the relationship between the communities found at each station with respect to the environmental variables.

2.6. Community distribution model (CDM)

The suitability of habitat for biological communities can be evaluated from the available knowledge on the optimal range of abiotic conditions for megafaunal species. To link the presence of a given community with respect to the local environmental conditions in the EGSL, generalized linear models (GLM, McCullagh and Nedler, 1989) were applied to each community. The presence-absence of a given community at each station was used as the response variable, and the environmental variables used in the RDA were used as predictors, assuming a binomial distribution with a logit-link function.

To make predictions at the scale of the whole EGSL, only the significant variables retained for each community were included in a second set of GLMs. The resulting community-specific estimates were gathered and included in the inverse of the logit function along with the standardized environmental data covering the entire EGSL. The values obtained represent the probability of presence, or habitat suitability, of each community in the EGSL. Statistical tests using Moran's I were performed to check for spatial autocorrelation of model residuals. Continuous raster maps of presence probabilities were then drawn using the Spatial Analyst extension in ArcMap (version 9.1, ESRI, Inc).

3. RESULTS

3.1. Epibenthic community structure

Cluster analysis based on Bray-Curtis dissimilarity of biomass data highlights six groups or communities (Fig. 2a) that cluster on an MDS graph (stress = 0.16, Fig. 2b). These communities are located in distinct regions of the EGSL (Fig. 3). The 6 groups are composed of almost the same dominant species in terms of biomass (Table 2). A SIMPER analysis (results not shown) revealed that these species are also responsible for the differences between the groups, indicating that it is a specific set of several species and their respective abundance that are discriminant of community dissimilarity, rather than a single intermediate-abundance species for each community.

The largest and most diverse group (group A, Table 2) is found along the coasts, *i.e.* in the Estuary, around Anticosti Island and along most of the eastern side of the Gulf (western part of Newfoundland) up to the Strait of Belle Isle (Fig. 3A). This community is composed of sessile filter-feeder anemones (*e.g.* from order Actiniaria and phylum Cnidaria), mobile deposit-feeder Echinoderms (*e.g. Ophiura* sp., *Ctenodiscus crispatus*, *Strongylocentrotus* sp., *Gorgonocephalus* sp.), and prawns *Pandalus montagui* (adapted to cold shallow waters) and, to a lesser extent, *Pandalus borealis*. These organisms make up a large part of the total biomass of the group (Table 2). This group is also characterised by the presence of the sea star *Crossaster papposus*, frequent in coarse sediment characterising stations in this group and usually feeding on *Strongylocentrotus* urchins, and of *Rhachotropis aculeata* (from sub-order Gammaridea and order Amphipoda), which occurs only in one station of other groups.

Group B, comprising the fewest number of species among all groups (Table 2), is almost exclusively located in the upper part of the Laurentian Channel, *i.e*. in the Estuary (Fig 3B). Like in its neighbouring communities of group A, biomass is dominated by Actiniaria and the prawn species *P. montagui* (Table 2), but the compositional structure of the dominant echinoderms differs from group A (*e.g*. *Brisaster fragilis*, *Ophiura sarsi*, *Hippasteria phrygiana*). Pennatulacea and *Pasiphaea multidentata* (a caridean shrimp), adapted to great depths, are also abundant in this group.

Groups C, E and F are located in the deep channels (Laurentian, Anticosti, Esquiman) and mostly in the wider part outside of the Estuary, following a north-south gradient (group E in the north, group F in the centre, and group C in the south out to the Atlantic Ocean that begins at Cabot Strait: Fig. 3C, E, F). These groups were characterised by high occurrences of anthozoans such as Actiniaria (sea anemones) and Pennatulacea (sea pens) (Table 2), and two echinoderm species (*Ctenodiscus crispatus* and *Brisaster fragilis*).

Finally, many stations hosting group D are located on channel edges, where the community is composed of organisms adapted to depth and slope, such as Actiniaria and Porifera, and, like groups C, E and F, Pennatulacea, *Gorgonocephalus* sp, *C. crispatus* and *B. fragilis*. Group D, characterised by many stations of medium depth, also comprises high biomass of both prawn species *P. borealis* (adapted to deeper and warmer waters) and *P. montagui*. The relative importance of these two species in this group is opposite to that of group A (Table 2) due to the difference of depth and water temperature.

3.2. Relationship between communities and their environment

The RDA biplot displays the correlation of the environmental factors (depth, bottom temperature, bottom-water oxygen saturation, maximal bottom current, relief, geographic variables, and sediment types) with epibenthic communities on the first two dimensions of the ordination (Fig. 4). Among the environmental variables considered, only slope and surface of sheltered area are not significantly correlated to the communities (Table 3). Temperature, depth, distance to coast and seabed uniformity are positively correlated with the first RDA axis. Oxygen saturation and bottom current are inversely correlated with these factors and with the first RDA axis, indicating that low oxygen values and slow bottom currents correspond with deeper and warmer waters, further from the coast. Some coarse substratum types (2, 2c, 2d, 2e, 5, and, to a lesser extent, 3 and 4) are located along the first RDA axis, whereas finer substratum types (fine sand: 2a and 2b, and sandy pelite 1e), some of the main substratum compositional types found in the EGSL, are correlated with the second axis.

The RDA explains 38% of the variance in species biomass. Together, the first and second principal RDA axes account for 81% of the relationship between species and environmental parameters (first axis: 68%, and second axis: 13% of the total variation, Table 3). The arrangement of samples on the RDA biplot in relation to the environmental parameters shows two main aggregates. Stations hosting group A (Fig. 4, graph left handside) are strongly correlated with high oxygen saturation, strong bottom current, shallower cooler waters closer to the coast with coarse sediments. Conversely, stations on the right handside (Fig. 4: groups D to F and most stations of groups B and C) are more closely associated with deeper warmer waters with low oxygen saturation, weak current and fine sediments (except 5: ice-age rocks). Group B is found in the Estuary, which is characterised by medium to high depths and low oxygen saturation (Fig. 1A), and thus located on the lower part of the graph on both side of the second RDA axis. Groups D, E and F, found in the rest of the Gulf at different depths (Fig 4D, E, F), cluster on the upper part of the graph. Group C is spread along the second RDA axis, mainly on the right side of the ordination plan, indicating a high variability of the environmental conditions within this niche: stations representing this group are found at different values of depth, temperature, and on different types of sediment.

3.3. Community distribution model

The coefficients of the GLM models show that the presence of each group A to F is correlated with different significant environmental variables (Table 4). The habitat suitability maps projected by the GLMs highlight the areas of high probability of presence for each group (Fig. 5). Group A, retaining predictors of depth, oxygen saturation and coarse sediment, has high probabilities to occur along the coast, at shallow depths and on coarse-grain bottoms, especially along the north coast and around Anticosti Island (Fig. 5A). Temperature and oxygen saturation characterise groups B, D, E and F, which have comparable distribution patterns, *i.e*. mainly in deep channels (Fig. 5B, D, E, F). However, group B was previously found only in the Estuary where oxygen saturation is low (Fig. 3B), but the habitat suitability map indicates that this group can be found in other parts of the EGSL that have similar environmental characteristics. Group D is characterised by 3 different types of pelitic sediments, which explains why it occurs outside of the deep channels: species composing this group are adapted to live on different substrates (Fig. 5D). Group C, characterised by slope, is predicted to occur at moderate depth, on the edge of the deep channels (Fig. 5C). It is characterised by a complex set of environmental variables (Table 4), which indicates that several conditions have to be fulfilled for the species composing this community to live in there. Moderate to high habitat suitability for groups E and F are strongly associated with sediment (calcareous pelite for both E and F, pelitic sand for F) found in deep channels, especially in the Laurentian channel (Fig. 5E, F). Despite the fact that it was a significant variable in explaining overall EGSL community distribution (Fig. 4), bottom current was not retained as a predictor to estimate the localisation of any of the groups. No spatial autocorrelation of model residuals was found when using Moran’s I for regression residuals (not shown), except for GLM of group F which residuals display a low but slightly significant spatial autocorrelation (Moran’I = 0.06, p = 0.04). Models A to E show overall good performance (AUC ≥ 0.8, Table 4); only model F performs slightly less (AUC = 0.77).

4. DISCUSSION

4.1. Community distribution and the role of environmental variables.

The environment of the EGSL is spatially structured, which in turn affects biological community structure. Communities determined in this study are strongly correlated with their environment, which is in good agreement with preliminary studies investigating the distribution of macro- and megafaunal benthos in the Gulf of St. Lawrence (Chabot *et al*., 2007; Lévesque, 2009). We found distinct megafaunal communities that occupy different habitats, especially in the deep channels vs shallower areas, and from estuarine to more marine areas. The RDA revealed the ecological preference of species colonizing the study habitats by identifying the environmental variables strongly correlated with epibenthic community distribution. The 38% of variation explained is in the range of values for biological systems (Cottenie, 2005). No single variable appeared to be directly and exclusively controlling the distribution and richness of benthic species in the EGSL. Our results showed that the direction and magnitude of temperature and depth were rather similar, whereas oxygen saturation and bottom current were inversely correlated with these variables, in agreement with Chouinard and Dutil (2011). Coarse substratum found mainly along the coastlines can generate a range of diverse well-oxygenated habitats favouring biological organisms, which is why these areas were associated to the highest predicted suitability for the shallow-water community.

In past studies, substrate granulometry and associated biological and chemical factors operating over the long term (*e.g*. organic content and microbial biomass of the sediment: Gaston, 1987; Maurer and Leathem, 1981) were considered as important environmental factors explaining spatial patterns of benthic organisms (Labrune *et al*. 2007, 2008; Thorson, 1971). Another study carried out in the Southern North Sea showed the importance of bed shear stress on benthic community distribution (Vaz *et al*., 2007). In fact, bottom current is responsible for bed shear stress that reflects the friction pressure found on the seabed and affects sediment sorting, thus sediment particle size (Harris and Wiberg, 2002). Our CDMs showed that megafaunal community groups (except group B) were correlated with composition of pelite, sand, or gravel, rather than with bottom current, suggesting that the effects of hydrodynamics (here, bottom current influencing particle mobility and sediment stability: Newell *et al*., 1998) on community structure may be concealed behind the effects of sediment properties.

Several sub-communities from group A, B, C, and D were defined in regions where specific environmental conditions and hydrodynamic features such as upwelling and tidal-mixing are located. This explains why bottom current was one of the variables retained by the RDA to explain community structure. More specifically, the Northwest Gulf community defined by Sainte-Marie *et al*. (2005), adjacent to the Mingan Islands (north-east coast) and the Strait of Belle-Isle (corresponding to communities of group A in this study), is located in an area of the EGSL with major circulation features, such as strong tidal-mixing and wind-induced coastal upwelling and eddies (Le Fouest, 2005). Similarly, a productive zone of upwelling arises from the bottom topography and wind interaction in the western Strait of Belle-Isle (Rose and Legett, 1988). The mixing of Labrador Shelf waters that enter via the Strait of Belle-Isle into the Gulf (Houghton and Fairbanks, 2001) and waters from the rest of the Gulf could favour highly diverse benthic communities. Frontal and high bottom current areas are known to be very productive and support high species diversity because the wider range of environmental values associated to these water layers create a combination of several distinct suitable habitats (*e.g*. deep-sea, Thistle *et al*., 1985; pelagic plume front, Josefson and Conley, 1997). This high diversity may include ecosystem-engineer species (both within mega-, macro- or meiofauna) that could also increase habitat complexity and create new additional niches for epifauna (Rabaut *et al*., 2007).

The distinctiveness of the estuarine community group B may arise because of specific environmental conditions found in this part of the Estuary, compared to more marine areas of the Gulf, such as low salinity (due to arrival of freshwater), poor oxygen saturation, and turbidity (Belley *et al*., 2010). The boundaries of this community also fitted closely to the bathymetric morphology of the Laurentian Channel. However, the CDMs did predict high probabilities of occurrence of group B in all deep channels, indicating that the environment may be suitable for this community (potential ecological niche), if the species were to migrate to these habitats due to fishery or global change pressure for instance. Similar bathymetry-related community patterns, formed by some stations from groups C to F, were found in the Laurentian, Anticosti and Esquiman Channels and edges (“deep-channel community”: > 200 m).

4.2. Accuracy and usefulness of the CDM

Our approach demonstrated that modelling habitat suitability of specific communities could be done using key environmental drivers, to subsequently build large-scale predictive maps of community occurrence able to support conservation planning (*e.g.* fishery, conservation management), in marine but also terrestrial ecosystems. Because of marine space issues in the EGSL (overfishing and trawling causing the depletion of stock biomass and destruction of habitats: DFO, 2006; Messieh *et al*., 1991; climate change affecting species distribution: Swain, 1999), impacting both biological diversity and the physical environment, coupling the information about community structure and species range with habitat description and potential suitability can strengthen management decisions to ensure a long-term persistence of habitats and their associated species, including commercial (*e.g. P. borealis*) or sensitive ones (*e.g. Pennatulacea* species).

Close similarities were observed between zones of high suitability predicted by the models developed in the current work and the Ecologically and Biologically Significant Areas (EBSAs) described by Chabot *et al.* (2007), who proposed a preliminary division of the EGSL (including the southern part of it) based on data with limited taxonomic resolution. Both studies identified the same areas with particular ecological and biological characteristics that required further attention (*i.e*. Jacques-Cartier Strait, Mécatina Trough, Strait of Belle-Isle, St. Georges Bay and Honguedo Strait). The study by Chabot *et al.* (2007) had a stronger focus on commercial species, while the predictive model developed here is likely to be more informative for all benthic invertebrates. The similarities between these studies suggest that, within this area, the evaluation of commercial species, easily carried out by observers at sea, may be used as a proxy for describing variation in the ensemble of benthic megafaunal communities.

Our model provides a coherent picture of the distribution of megafaunal benthic invertebrates in the Gulf, but increasing efforts to obtain more accurate environmental and biological data throughout the years would lead to model improvement and validation. All available environmental predictors known to be influential on marine communities were considered in this study. We however acknowledge that other yet unavailable predictors could be considered (*e.g.* nutrients: Mellin *et al*., 2010; fishing effort: Mellin *et al*., 2012; sediment organic matter and porosity, Chl *a*: Pastor *et al*., 2011) in order to better understand benthic community structure, and improve elaboration and predictive power of CDMs. Biological data from other surveys using a different sampling method or in shallow near-shore locations (*i.e.* extending depth coverage to 25 m deep or above) and data gathered by the Canadian fishing industry could also be homogenised and incorporated, and used for validation and model transferability assessment to improve model accuracy and selection (Wenger and Olden, 2012). Indeed, the main database used here is updated annually by DFO through multispecies surveys and complementary efforts to monitor benthic habitat quality. In a further step, the effects of fishing activities on benthic habitats could also be investigated in the model by including information on spatial and temporal variation in fishing effort, to complete goals to be reached to evaluate the impact of fishing activities on benthic organisms in the Gulf of St. Lawrence (DFO 2006, 2010).

5. CONCLUSION

This study demonstrates the usefulness of a CDM elaborated from data (environmental observations and bottom trawl samples gathered during annual scientific surveys) to infer relationships between environmental variables and specific benthic communities. The predicted habitat suitability distribution obtained is composed of preliminary informative maps onto which additional physical and chemical parameters could be added to better delineate habitat suitability of each community. Biological organisms will react to natural and anthropogenic changes currently occurring in natural systems and may change their distributions accordingly. Distribution models may thus be used to improve predictions of the distribution change of key and indicator species and particular communities, and to identify potential diversity hot spots, by focusing on current and stable *versus* future and changing environmental conditions, with limited information on biological communities.

Within large networks of ocean and land planning gathering different actors, the aim of CDM is to help scientists and decision-makers to elaborate guidelines and priorities for adequate conservation of habitats hosting specific communities, and that take into account future biological community range changes. In the EGSL, these communities support highly valuable commercial species (e.g. prawn *P. borealis*), which stock sustainability must be secured. Informed conservation decisions will in turn ensure appropriate monitoring of the spatial and temporal quality of benthic habitats, which could help minimize or avoid impact of natural and anthropogenic disturbances.

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Table 1. EGSL environmental variables used in the analyses. Abbreviations (in alphabetical order) are given only for the variables selected after the variable-reduction procedure.

Quantitative and binary (*) environmental variables	Abbreviation	Qualitative environmental variables (sediment types)	Abbreviation
Bottom current	BC	Pelite	1
Depth	D	Sandy pelite	1a
Distance to coast	DC	Calcareous pelite	1b
Oxygen saturation	O	Gravely-sandy pelite + calcareous rocks	1c
Seabed relief uniformity	U	Very-sandy and gravely-sandy pelite	1e
Slope	S	Well-sorted and fine sand	2
Surface of protected (sheltered) area	P	Fine clayish sand	2a
Temperature	T	Poorly-sorted pelitic sand	2b
Salinity		Sand and mid-coarse grains	2c
Surface of exposed and surface of semi-exposed area		Gravely-pelitic reworked sand with poorly-sorted gravely sand	2d
Surface of: hollows; bumps		Poorly-sorted gravely sand	2e
Belongs to: channel; continental shelf; bank (*)		Calcarenite + gravel with occasional sand parcels	3
Latitude		Gravel	4
Longitude		Brown-red ice-age rocks	5

Table 2. List of benthic community groups including mean depth and number of taxa for each group. The five dominant taxa in terms of biomass and their respective frequency of occurrence within the given group are indicated.

Group	Mean depth (m)	Species richness	Dominant species	Frequency of occurrence (%)
A	116	177	Actiniaria	69
			Pandalus montagui	93
			Pandalus borealis	46
			Ophiura sarsii	24
			Porifera	67
			Ctenodiscus crispatus	46
B	273	72	Actiniaria	100
			Pandalus montagui	20
			Brisaster fragilis	98
			Ctenodiscus crispatus	100
			Ophiura sarsii	73
			Pennatulacea	91
C	303	135	*Pandalus borealis*	99
			Pennatulacea	75
			Pasiphaea multidentata	82
			Actiniaria	74
			Brisaster fragilis	63
			Ctenodiscus crispatus	67
D	239	120	*Pandalus borealis*	100
			Actiniaria	82
			Pandalus montagui	23
			Pennatulacea	62
			Pasiphaea multidentata	53
			Brisaster fragilis	52
E	268	100	*Pandalus borealis*	100
			Actiniaria	78
			Pennatulacea	69
			Brisaster fragilis	66
			Porifera	56
			Pasiphaea multidentata	67
F	288	105	*Pandalus borealis*	100
			Actiniaria	73
			Pennatulacea	71
			Porifera	54
			Pasiphaea mutlidentata	72
			Alcyonacea	29

Table 3. Results from redundancy analysis (RDA) using megafauna biomass and environmental data from 2006-2009, depicting relationships between species and environment resulting from the first two RDA axes. P-values were given from permutation tests (999 permutations, ***: <0.001). See Table 1 for environmental variable abbreviations.

	Axis 1	Axis 2		
Eigenvalues	0.14	0.03		
Variance explained	0.68	0.13		
Species-environment correlations	0.85	0.66		
Correlations with environmental variables			Conditional effects	
			P	R^2
BC	-0.978	-0.21	***	0.14
D	0.903	-0.429	***	0.67
DC	0.999	-0.021	***	0.15
O	-0.985	0.173	***	0.61
U	0.981	-0.193	***	0.08
S	0.419	-0.908		5.10^{-4}
P	-0.999	0.005		5.10^{-3}
T	0.996	-0.092	***	0.64
			***	0.26
1	0.113	0.021	***	
1a	0.067	-0.034	***	
1b	0.136	-0.021	***	
1c	-0.19	0.094	***	
1e	-0.035	0.149	***	
2	0.151	-0.015	***	
2a	0.082	-0.157	***	
2b	0.027	0.228	***	
2c	-0.115	0.045	***	
2d	-0.244	0.013	***	
2e	-0.314	-0.007	***	
3	-0.286	-0.118	***	
4	-0.332	-0.107	***	
5	0.137	-0.036	***	

Table 4. Statistics (adjusted R^2, area under the ROC curve (AUC), estimates, and p-values: ***<0.001, **<0.01, *<0.5) of GLMs predicting the presence of each group according to environmental variables used in RDA (see Table 3). See Table 1 for environmental variable abbreviations.

Group	A	B	C	D	E	F
Adj. R^2	0.59	0.80	0.44	0.42	0.49	0.42
AUC	0.95	0.95	0.85	0.83	0.80	0.77
Intercept	-3.314	5.222	-9.368***	3.740*	0.377	-9.732***
BC	1.789	0.998	-1.947	-2.247	-0.079	0.871
P	0.699	-0.963	-0.392	-0.285	-7.984	-502.526
DC	$-1.89.10^{-6}$	$-4.02.10^{-5}$*	$1.98.10^{-5}$**	$-3.86.10^{-6}$	$5.64.10^{-6}$	$-1.24.10^{-6}$
D	-0.008***	0.000	0.014***	-0.010***	-0.008**	0.002
S	0.458	1.121	1.914***	-0.975	-1.973*	-0.838
U	1.953	4.302	-0.343	-1.913	-2.419	-1.175
O	0.055***	-0.140***	0.039***	-0.039***	-0.042**	0.040**
T	-0.358	-1.462**	0.105	0.636**	0.857*	1.432***
1a	0.035	0.954	1.228***	-1.513***	0.581	0.396
1b	-0.691	0.029	0.014	-1.000**	1.362***	1.197**
1c	0.655	-15.631	0.431	-0.668	-14.410	0.556
1e	0.578	-16.159	0.711	-1.211**	0.410	0.475
2	-16.342	-15.172	21.959	-20.180	-17.444	-18.767
2a	-15.406	-15.118	2.796*	-20.024	-16.496	1.408
2b	0.407	-16.282	1.154	-1.508	-0.502	1.865*
2c	-2.535*	-15.087	-13.704	1.951	-13.377	-17.248
2d	1.697**	-16.527	0.590	-18.302	-0.849	-0.182
2e	15.618	-15.774	-13.531	-18.120	-13.800	-19.146
3	1.758	-16.774	1.064	-18.283	-13.968	-17.320
4	13.244	-16.761	-11.336	-15.216	-13.003	-15.675
5	-15.993	-13.662	1.950	-1.423	-17.129	1.510

Figure 1. Estuary and Northern Gulf of St. Lawrence map showing the location of trawl stations (grey crosses) for years 2006-2009. Bathymetric lines delineate deep channels (depth > 200 m).

Figure 2. Epibenthic megafaunal communities in the EGSL in August 2006-2009: (a) Cluster tree (Ward distance) based on Bray-Curtis dissimilarity matrix using species biomass data; (b) Non-metric multidimensional scaling (nMDS) ordination based on Hellinger-standardized biomass data, using Euclidean distance. A specific symbol was attributed to each cluster identified on the tree (groups A to F).

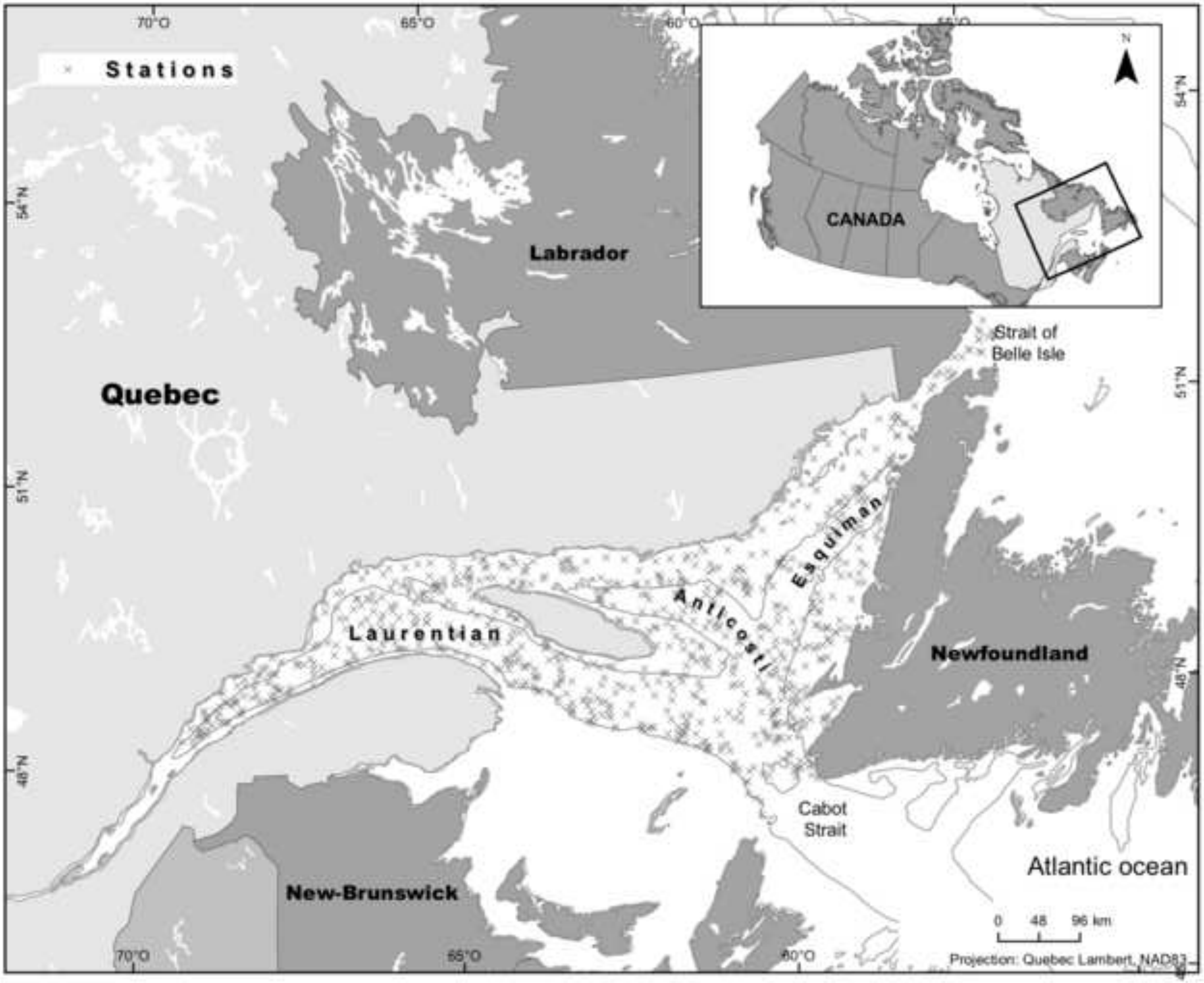
Figure 3. Location of the 6 communities in the EGSL, as determined by hierarchical cluster analysis on epibenthic fauna biomass data (graph labels correspond to group labels A to F).

Figure 4. RDA ordination diagram of 755 epibenthic fauna sampling stations for years 2006-2009, obtained using Hellinger-standardized biomass data. The quantitative environmental variables used in the RDA (shown as vectors) were selected using PCA and analysis of the correlation matrix from a bigger set of variables. Sediment types, included as factors (qualitative variable), are represented by open circles. See Table 1 for environmental variable abbreviations.

Figure 5. Habitat suitability maps (probability of presence) for epibenthic megafauna communities in the EGSL, using GLMs (graph labels correspond to group labels A to F).

Figure A.1. Maps of bottom environmental conditions for years 2006-2009: (a) depth (m), (b) oxygen (% saturation), (c) temperature (˚C), (d) maximal bottom current (cm/sec), (e) seabed relief (proportion of uniformity), (f) distance to the coast (m).

Figure(s)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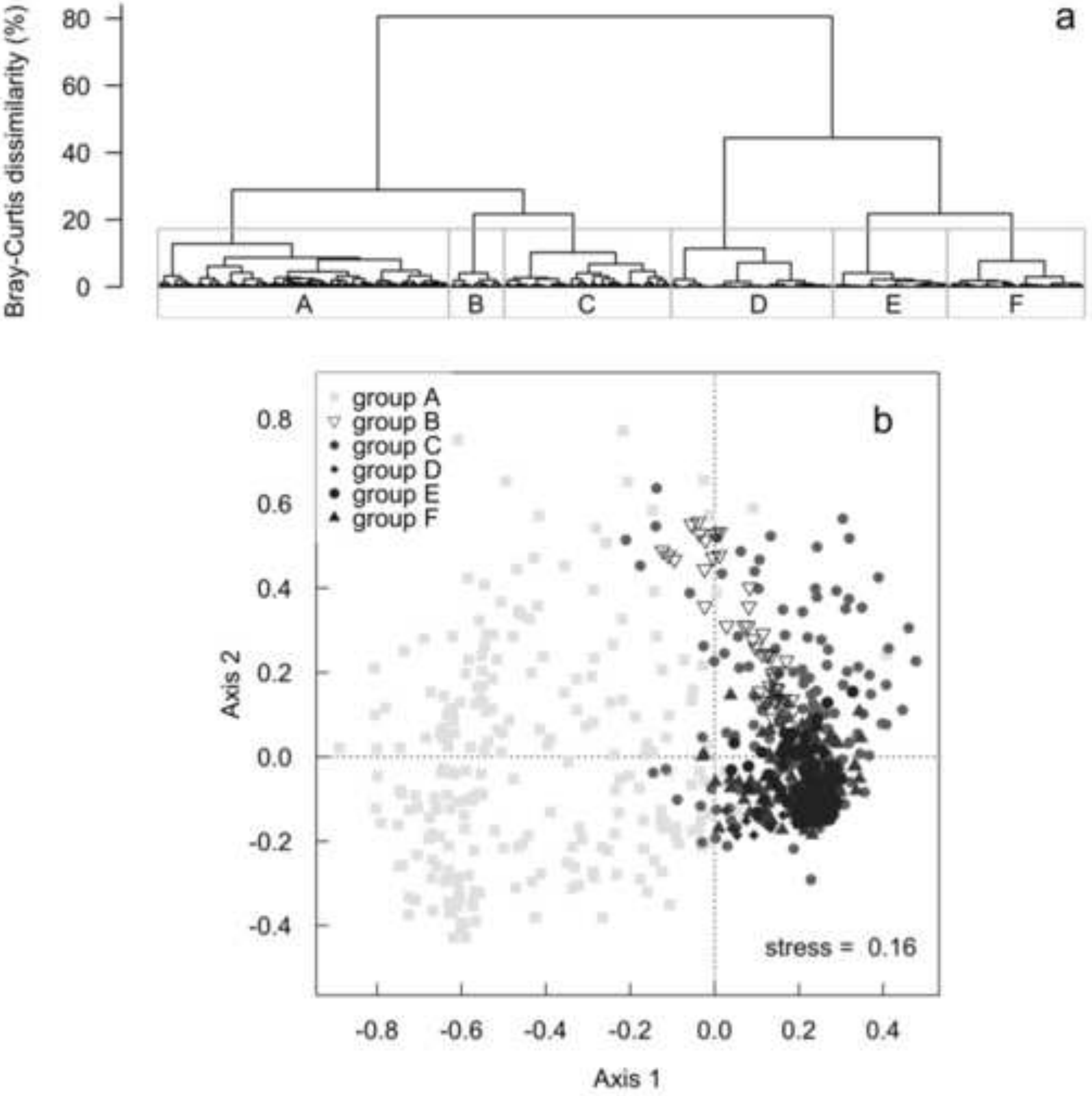
a
Bray-Curtis dissimilarity (%)
80
60
40
20
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A
B
C
D
E
F
b
group A
group B
group C
group D
group E
group F
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
Axis 2
-0.8
-0.6
-0.4
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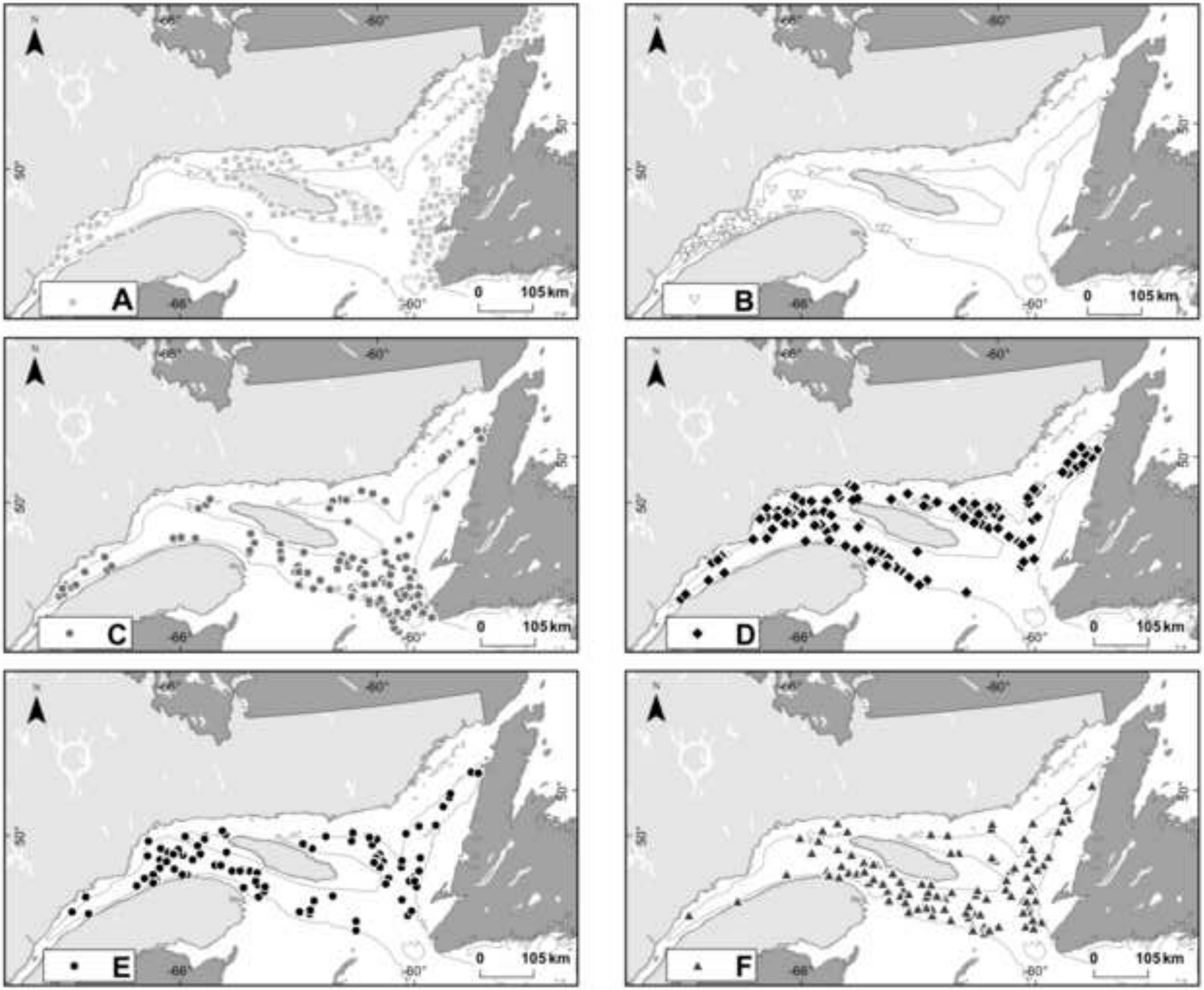
stress = 0.16

Figure(s)



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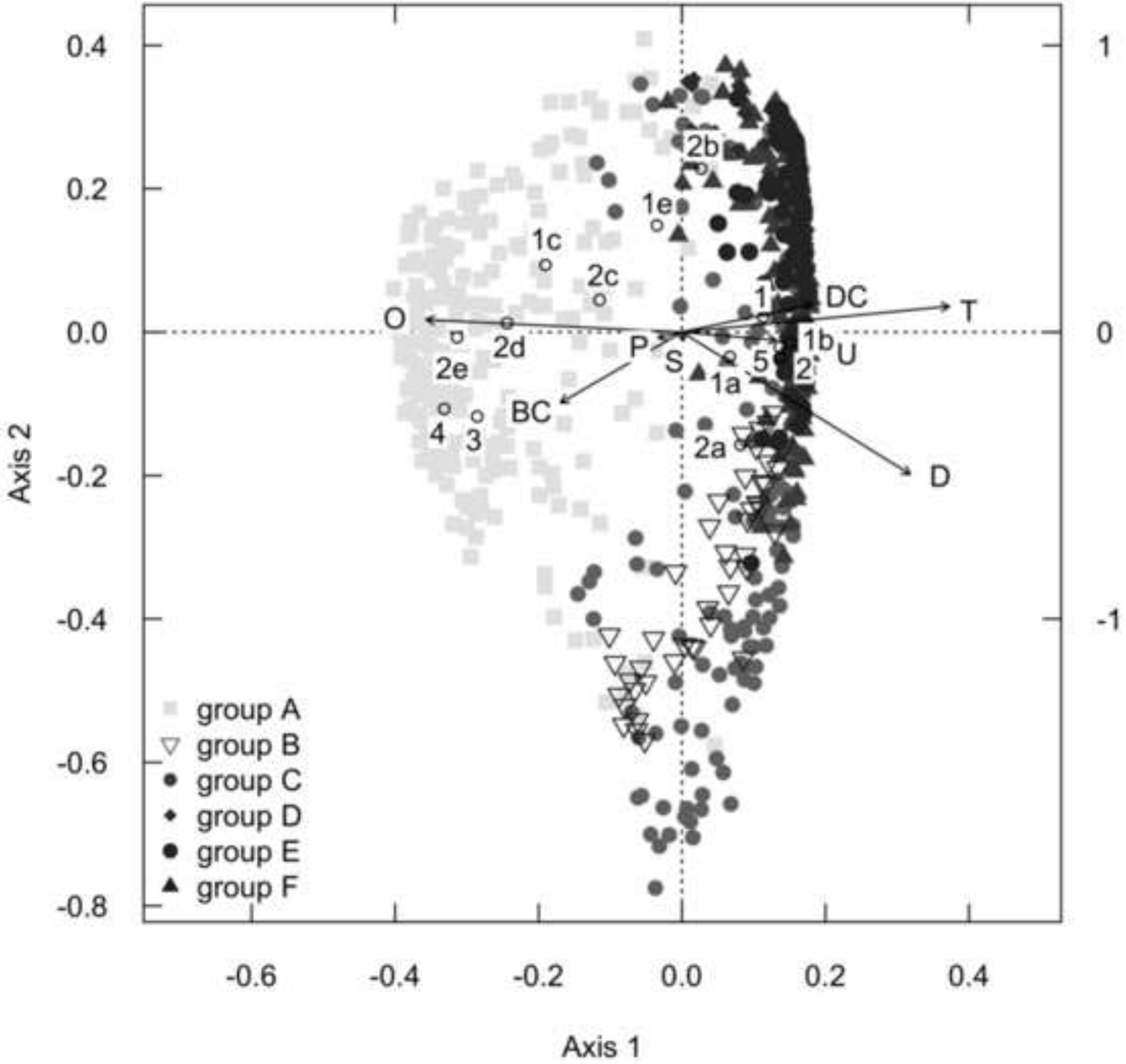

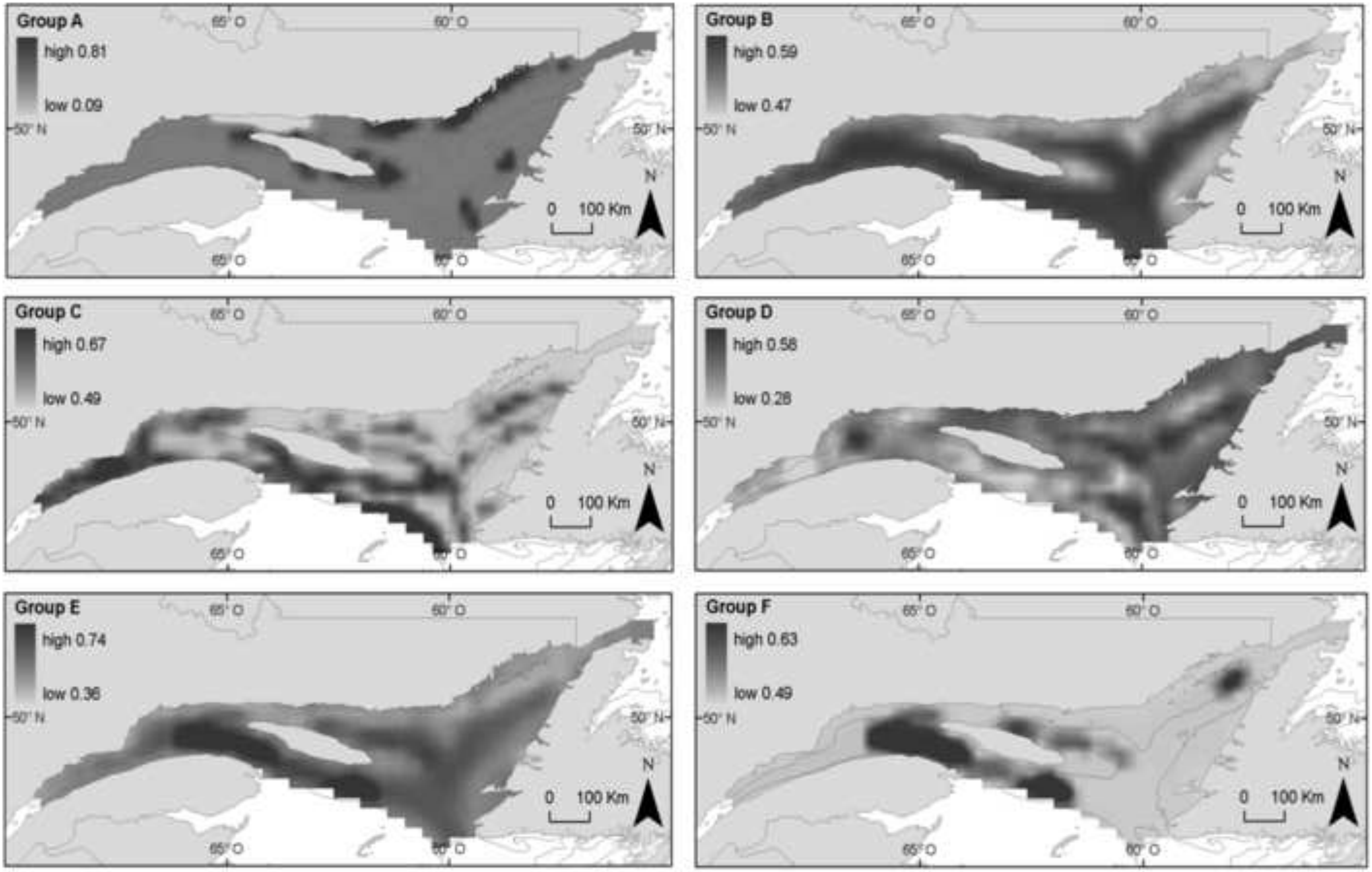
Group A
high 0.81
low 0.09
Group B
high 0.59
low 0.47
Group C
high 0.67
low 0.49
Group D
high 0.58
low 0.28
Group E
high 0.74
low 0.36
Group F
high 0.63
low 0.49
65° O
60° O
50° N
0
100 Km
N