Predictive benthic habitat suitability model for the Estuary and northern Gulf of St. Lawrence (2006)

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by

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ABSTRACT

Lévesque, M., P. Archambault, C. W. McKindsey, S. Vaz, and D. Archambault. 2010. Predictive benthic habitat suitability model for the Estuary and the northern Gulf of St. Lawrence (2006) Can. Tech. Rep. Fish. Aquat. Sci. 2893: viii + 27 pp.

This study used geostatistical techniques and a generalized linear model (GLM) approach to describe the affinity of macrofaunal communities to environmental parameters in the Estuary and the northern Gulf of St. Lawrence using bycatch and environmental data from 2006. The habitat suitability model (HS) derived from those data explained nearly 40% of the variation in macrofaunal communities, with the significant predictive environmental variables being depth, oxygen saturation, temperature, and bottom current. Results from the prediction model therefore allowed the identification of zones of greater and lesser suitability for specific species community types, higlighted by canonical analysis. This study also assembled a primary database of benthic habitats and physical parameters for the St. Lawrence system. An annual update of this database will thus be possible following the multispecific surveys.

RÉSUMÉ

Lévesque, M., P. Archambault, C. W. McKindsey, S. Vaz, and D. Archambault. 2010. Predictive benthic habitat suitability model for the Estuary and the northern Gulf of St. Lawrence (2006). Can. Tech. Rep. Fish. Aquat. Sci. 2893: viii + 27 pp.

Les analyses de cette étude se basent essentiellement sur l’utilisation des techniques de géostatistiques et des modèles linéaires généralisés (GLM). L’objectif principal est ainsi de prédire les habitats potentiels des communautés de la macrofaune benthique de l’Estuaire et du nord du Golfe du Saint-Laurent, en fonction des paramètres environnementaux étudiés, pour l’année 2006. L’équation résultante de la modélisation a ainsi retenue l’oxygène dissous, la profondeur, la température et le courant de fond afin d’expliquer près de 40 % de la variation des communautés benthiques présentes. L’analyse de l’équation de prédiction résultante, permet ainsi de mettre en évidence les zones à fort et faible potentiel de la présence de communautés benthique spécifique, mis en évidence par l’application d’analyse canonique. Cette étude a ainsi permis de mettre sur pied une base de données primaire d’informations relatives aux habitats benthiques ainsi que sur les paramètres physiques qui s’y retrouvent. Une mise à jour annuelle de cette base de données pourra donc être effectuée suite aux missions multispécifiques.

PREFACE

This report is a part of Mélanie Lévesque's M.Sc. thesis:

Lévesque, M. Caractérisation de la macrofaune epibenthique de l'Estuaire et du nord du Golfe du Saint-Laurent (Québec-Canada), en relation avec les paramètres environnementaux : analyses multivariées et approche de géostatistique. M.Sc. Thesis, ISMER, Université du Québec à Rimouski, Rimouski, QC, Canada.

INTRODUCTION

The St. Lawrence system is a productive area with a large range of oceanographic conditions (Roy and Sundby 2000). With the variety of hydrodynamic regimes and physical parameters observed, the Gulf of St. Lawrence is often divided into distinct oceanographic subregions. Koutitonsky and Bugden (1991) proposed eight subregions, based mainly on a number of physical parameters, and Brunel et al. (1998) proposed 20 marine zones classified on the basis of coastal contour, oceanographic, biogeographic, and bathymetric criteria. Because of the heterogeneity of the system, it is a good area to evaluate potential links between environmental factors and benthic communities.

Many studies have described the diversity and distribution of benthic invertebrate communities in the Estuary and the northern Gulf of St. Lawrence (EGSL). Most have focussed on specific taxa, such as molluscs (Robert 1979) and polychaetes (Massad and Brunel 1979). A few studies have investigated the resident infauna using quantitative approaches (Préfontaine and Brunel 1962; Peer 1963; Ouellet 1982; Bourque 2008). Recently, relationships between infaunal assemblages and bioturbation by epibenthic fauna, as measured by biologically produced traces (*lebensspuren*) on benthic sediments (Belley et al. 2008), and environmental factors were examined in the EGSL (Desrosiers et al. 2000; Bourque 2008). Notwithstanding this work, the benthic invertebrates of the St. Lawrence system remain poorly known.

Chabot et al. (2007) proposed a preliminary division of 17 Ecologically and Biologically Significant Areas (EBSAs) in the EGSL (including the southern part) based on the distribution and relative abundance of benthic invertebrates collected during surveys done in the study area between 1990 and 2006 by Fisheries and Oceans Canada (DFO) (Fig. 14 in Chabot et al. 2007). However, the data on invertebrates used to delimit the EBSAs were only accurate for shrimp species and snow crabs; other non-commercial invertebrates were not well identified during past cruises.

In August 2006, monitoring of epibenthic macrofauna invertebrates with a high level of taxonomic identification was initiated during the annual DFO summer groundfish survey for the northern Gulf of St. Lawrence. This was the first study of its kind to quantitatively characterize the benthic habitat over the whole EGSL system and included collecting data on both the abundance of benthic invertebrate species (commercial and non-commercial) and environmental parameters.

The term “habitat” may be defined in a number of ways. According to Baretta-Bekker et al. (1992), habitat is simply the characteristic space occupied by a population or a species. Using a methodological approach similar to that used in the present study, CHARM (Eastern Channel Habitat Atlas for Marine Resource Management) defined habitat as an area with specific environmental conditions in which an organism, a population, or a community can survive (Carpentier et al. 2005). Most communities in the environment appear to occur within a recognizable suite of physical conditions, and some occur within a narrower physical habitat window than others (Urbanski and Szymelfenig 2003). This close relationship between the physical environment of an area and the biological composition of the associated community is highlighted by habitat suitability (HS) models (Guisan and Zimmerman 2000; Hirzel and Arlettaz 2003; Hirzel et al. 2006; Degraer et al. 2008).

One strategy to describe habitats is to create a full coverage mapping tool rather than a map with punctual data restricted to observation points. The resulting HS model predicts the presence of benthic invertebrate communities based on the suitability of the physical habitat for a given habitat measure (Degraer et al. 2008). Degraer et al. (2008) suggest that full coverage spatial distribution maps of macrobenthos may be created if full coverage maps of environmental variables are available. While very few ecological studies consider the dynamic state of community species in response to environmental changes, the HS model uses a dynamic approach to study the possible consequences of a changing environment on species distributions (Woodward and Cramer 1996). Predicting species or community occurrence using this modelling approach has become increasingly common in ecological conservation studies, including entomology (Hein et al. 2007), mammalogy (Catullo et al. 2008), and oceanography (Vaz et al. 2006; Martin et al. 2005; Degraer et al. 2008).

The main purpose of this work is to help scientists and decision-makers define guidelines and priorities for the adequate conservation of benthic habitats. To achieve this goal, many objectives were completed within the framework of providing tools and information to evaluate the impact of fishing activities in the northern Gulf of St. Lawrence, including:

- The collection of data and assembly of a database on all available physical, chemical, and geophysical parameters related to the seabed environment of the EGSL, including temperature, bathymetry, salinity, chlorophyll *a* concentration, oxygen saturation, maximal bottom current velocity, and sediment type;
- The collection of all available biological data relating to benthic organisms in the EGSL;
- The determination of which environmental parameters best explain species distribution patterns;
- The development of a predictive habitat suitability model to describe the ecological preference of macrofaunal species and communities; and
- The identification of areas with the greatest suitability for benthic organisms.

MATERIALS AND METHODS

Multidisciplinary bottom trawl survey

DFO (Quebec region) has done an annual groundfish and northern shrimp survey in the EGSL since 1990. The main objectives of this bottom trawl survey have been to collect biological information related to the main fish stocks exploited in the EGSL (cod, Greenland halibut, redfish, and northern shrimp). In August 2006, greater effort was made for the identification of all benthic invertebrate taxa was done aboard the CCGS *Teleost* research trawler.

Study area

The sampling area covered by the EGSL bottom trawl survey includes all of the Northwest Atlantic Fisheries Organization (NAFO) division 4RS and part of 4T (for strata deeper than 100 fathoms) (Appendix 1). As for previous annual summer surveys, the sampling strategy used consisted of a stratified random sampling following predetermined strata based on depth (Doubleday 1981). Macrofauna were thus sampled from 193 stations in 2006 (1-31 Aug) (Fig. 1).

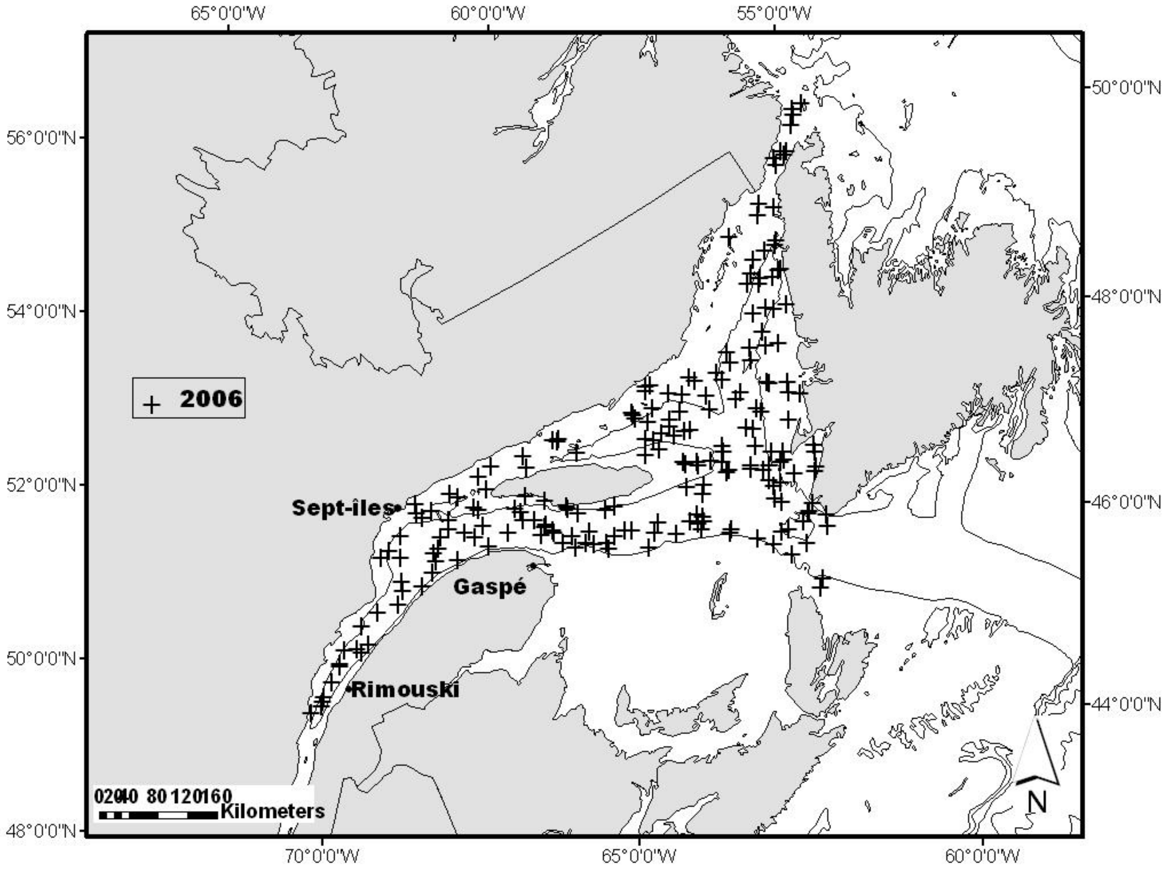

Figure 1. Map of the estuary and the northern Gulf of St. Lawrence showing the 2006 multispecific survey stations.

All samples were collected with a four sided shrimp bottom trawl (*Campelen 1800*). The trawl was rigged with variable net mesh sizes appropriate for each part of the trawl: 80 mm ("centre knot" to "centre knot") for the wings, 60 mm for the first belly and square, and 44 mm for the second and third bellies. The codend and the lengthening piece were also of 44 mm stretched mesh and equipped with a 12.7 mm knotless nylon lining. The trawl is fitted with Rockhopper foot gear (McCallum and Walsh 2002). The standard tow duration was 15 minutes on the bottom but was shorter when the substrate was rougher. Trawl configuration (e.g., distance between doors and wings, vertical net opening and bottom depth) was monitored using Scanmar™ hydroacoustic sensors. More than 80% of the biomass caught using the *URI 81'/114'* shrimp trawl, which was used until 2003, was composed of shrimp species (C. Savenkoff, Institut Maurice Lamontagne, DFO; pers comm.). In contrast, 72% of the total invertebrate biomass caught with the *Campelen 1800* bottom trawl was non-shrimp species, thus indicating the efficacy of the newer sampling method to characterize EGSL macrofauna.

The catch from the scientific survey was sorted and identified to the lowest taxonomic level possible, counted, and the biomass recorded. The sorted macrofauna was photographed aboard, and images of the total macrofauna captures and of each identified taxa were recorded at most sampling stations. Distinctive physical characteristics such as colour and form were thus recorded to improve taxonomic identification. Invertebrate species that were not easily identified 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). Abundance and biomass estimates were standardized relative to catch per unit effort (CPUE), thus allowing comparisons to be made between invertebrate and fish species. Macrofauna density estimates were obtained by dividing the number or mass of a taxon by the total area swept by the trawl. Density of invertebrate taxa were generally expressed as km^{-2}, but biomass indices (expressed as $kg \cdot km^{-2}$) were used for many taxa that were too abundant to be counted. Colonial organisms such as bryozoans and hydrozoans could not be enumerated and were expressed as biomass in the database. The phyla Cnidaria and Echinodermata are predominantly composed of *Brisaster fragilis*, *Ctenodiscus crispatus*, *Gorgonocephalus* sp., and *Strongylocentrotus* sp., and were also included in this database. Subsamples were taken when the catch was too big to be sorted and thus only a few organisms were retained after weighing the total.

Database

A relational database (RDB) was created to meet the requirements of the annual research survey, including data recording and updates, with the ability to directly record the biological and physical data on-board during the surveys. Information included in the RDB correspond to the specific needs of the on-board survey work, providing survey station metadata (e.g., latitude, longitude, trawl start and end times) as well as the total weight of catches and samples by species. Each species/taxon was classified with a unique code. Biological characteristics of organisms, including weight, length, sex, and sexual maturity, could also be recorded in the RDB but are not considered in the current work.

The RDB was originally created for targeted commercial species (e.g., Atlantic cod, Greenland halibut, northern shrimp), thus explaining why the code system used for non-commercial species had to be adapted and updated. As the macrobenthic fauna was first considered only in 2006, numerous species were therefore newly listed under a higher taxon level (i.e., often the genus or the family) in the on-board computerized database. When no code existed for any taxonomic levels for a particular species, the “unknown” code 999 was given to that species. The information that could not be included in the database during the sea mission was recorded on survey sheets that were used to update the database post-survey.

Environmental parameters

Water column depth and characteristics including conductivity, oxygen, temperature, and chlorophyll *a* concentration (fluorescence) were measured near the sampling stations using a Sea-Bird model SBE911*Plus* CTD. Vertical profiles were measured at stations over the whole territory. Dissolved oxygen levels recorded by the CTD were validated using Winkler titrations (Carrit and Carpenter 1966) of water samples taken at predetermined depths. Sediment types at each sampling station were estimated from a digital map of seabed sediment types in the general area as outlined by Loring and Nota (1973). Sediment types such as relict pelite and residual sand yield insight into the dominant depositional processes in a location. The original sediment classification was kept, with 46 substrata codes identified by textural analysis. For example, pelite, sandy-pelite, and gravel-shell were three of the principal substrata compositions observed in the St. Lawrence. A further environmental parameter, maximal bottom current ($m \cdot sec^{-2}$), was estimated at each sampling station using a hydrodynamic simulation model of the St. Lawrence (Saucier et al. 2003) that uses riverine, oceanic, and atmospheric forcings. At each sampling station, bottom current values were estimated for 31 days in August and the maximal value at each station included in subsequent analyses. Chlorophyll *a* data for 2006 were calculated in the laboratory using a specific standard curve for each Gulf subregion (S. Plourde, Institut Maurice Lamontagne, DFO; pers comm.).

Geostatistics and GIS mapping

Continuous raster maps of the spatial distribution of environmental parameters and community patterns were produced using kriging (Appendix 2a).Variogram model fit estimates and kriging interpolation were performed using GENSTAT (7th edition) (GENSTAT Committee, 2003). The interpolated values were estimated on a fine regular grid of points (mesh size: 0.02) that was then imported into Arcmap (version 9.1) (ESRI). Continuous raster maps were created using the spatial analyst extension and have a final resolution of 0.02 decimal degrees and illustrate the spatial pattern of each variable.

Predictive ecological model of community habitat

Prior to modelling, macrobenthic datasets ($ind \cdot km^{-2}$ and $kg \cdot km^{-2}$) were combined and square-root transformed. This intermediate transformation provides a balance between a “narrow view” of community structure based on the abundance of few dominant taxa when data are untransformed and a “wide view” of community structure whereby rare taxa have inordinate weight, when presence–absence data are used (Clarke and Warwick 1994). As suggested by Clarke and Warwick (1994), taxa that appeared once or were associated with only one station were excluded from the analyses.

Habitat suitability model (HS)

The approach to quantifying habitat was similar to that used by Channel Habitat Atlas for marine Resource Management, CHARM (Carpentier et al. 2005), which consists in evaluating the habitat based on the available knowledge on the optimal range of abiotic conditions for macrofaunal species. In the environment, most communities are associated with a recognizable suite of physical conditions, with some occurring within a more tightly defined physical habitat than others (Urbanski & Szymelfenig 2003). The HS model (Guisan and Zimmerman 2000; Hirzel and Arlettaz 2003; Hirzel et al. 2006; Degraer et al. 2008) highlights this close relationship between the physical environment of a study area and the biological composition of its associated community.

Preliminary correspondance analysis (CA) and canonical correspondance analysis (CCA) were performed using the database with the combined square-root transformed abundance and biomass data (Legendre and Legendre 1998). The first analysis described the main gradients present in the structure of the observed communities and the second allowed to explore which available explanatory variables better match these gradients using Monte-Carlo permutation tests (CANOCO 4.5 software, ter Braak and Smilauer 2002). The relationship between the community structure and environmental parameters recorded at each trawl station was then modelled using a generalized linear model (GLM), which may be used for data that are not normally distributed (McCullagh and Nedler 1989). The resulting model was then used to construct a predictive map of potential macrobenthic habitat types. Each sample was scored in the CA using taxonomic abundance data, and their score on the first two axes were used as response variables and the significant environmental variables identified with CCA were used as predictors in the GLM model. Second order polynomials of the retained predictors were tested in the model to better illustrate the potential unimodal relationship between communities and environmental parameters. Stepwise selection of significant predictors was done using Akaike's Information Criterion (AIC) (Akaike 1974). Model fitting and selection was done using the R free software (R Development Core Team 2005). The resulting equation describes how benthic assemblages varied according to variations in each environmental factor. Model equations thus obtained were applied to the interpolated maps of the relevant environmental variables in the Raster calculator option in ArcMap® to produce a predictive map for benthic organisms.

RESULTS

The observed benthic species components and assemblages were significantly but variably correlated to the diverse interacting physical gradients. The preliminary CCA of the 2006 data shows how the various physical factors evaluated (depth, temperature, bottom-water oxygen saturation, maximal bottom current, and the presence of various pelites and gravel in the sediment composition) explain the variation in invertebrate communities (Fig. 2). Together, the first and second principal CCA axes accounted for 39.1% of the relationship between species and environmental parameters, with the first axis accounting for 22.3% of the total variation explained. The presence of a gravel–shell substratum was strongly positively correlated with the first CCA axis (0.50), whereas temperature, oxygen saturation, and depth were strongly negatively correlated, with -0.46, -0.44, and -0.42 respectively (Table 1a). The physical variable with the greatest correlation with the second CCA axis was the presence of a sandy-pelite substrate (0.78). As indicated on the ordination plan (Fig. 2), the direction and the magnitude of temperature and depth were very similar whereas oxygen saturation was inversely correlated, with low oxygen values when depth and temperature were high. The arrangement of samples in relation to the ten environmental parameters illustrated two distinct spatial plans (Fig. 2). Samples to the right of the ordination were strongly correlated to oxygen and substratum composition of gravel (gravel–shell [GSh] and gravelly pelite–sand [GPS]). Conversely, samples to the left were more associated with depth, temperature, current, and substratum composition of pelite (VSP, P, SP, CP) The largest group, IV (▲), found on the left side of the ordination plan, indicated a large variety of ecological niches. Stations representing this group were found at different depths, temperatures, and bottom currents. Group III (▼) and group I (○) were principally found on the right side or the ordination plan. Samples from groups I, II, and III were spread out along the axis 1 in the CCA analysis (Fig. 2), which underscores the influence of these groups by the presence of gravel–shell, depth, and oxygen. These groups were composed of more species and characterized by the presence of many free-living (*Strongylocentrotus* sp., *Henricia* sp., *Crossaster papposus*, *Gorgonocephalus* sp., and *Rhachotropis aculeate*) and sessile (*Boltenia ovifera* and *Gersemia rubiformis*) species; this is different from group IV, which is found in deep channels and with fewer species (Lévesque 2009).

The HS model highlighted the importance of the physical environment parameters in the determination and characterization of seabed macrofauna habitats of the St. Lawrence.The final 2006 ecological model of axis 1 (Eq. 1) sample scores retained four significant environmental variables: depth, bottom current, mean temperature, and oxygen saturation (Fig. 3). Second-order polynomials for depth, temperature, and bottom current were included in the model to improve its fit. Regression coefficients for the model are given in Appendix 3a. Only depth, temperature, and bottom current explained significant ($p < 0.05$) amounts of the variation in community structure. The habitat model was not able to distinguish the community structure corresponding to the second axis (Eq. 2), and thus the substratum variables (presence of pelite and gravel) identified by canonical analysis were removed from the final model. Only the model predicted by CCA axis 1 was retained for further analysis (Eq. 1).

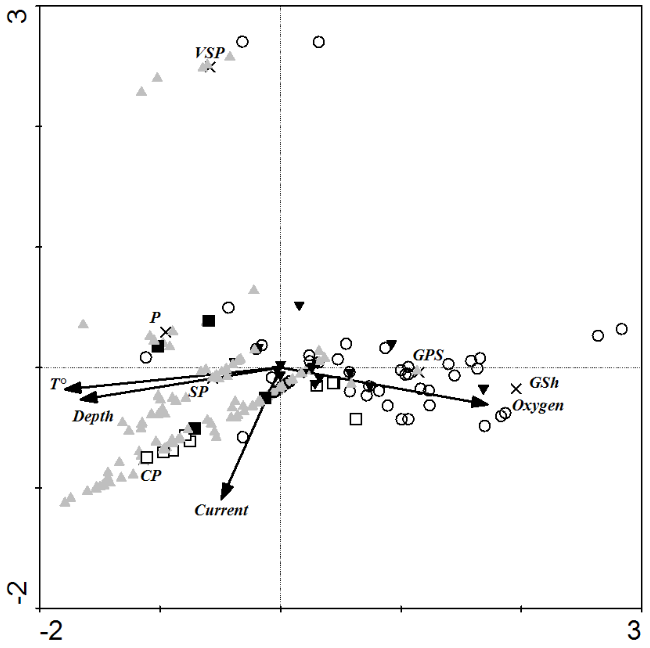

Figure 2. Canonical correspondence analyse (CCA) of epibenthic macrofauna sampling stations and corresponding environmental factors. CCA was calculated using square-root √ transformed data (abundance and biomass), and a matrix of ten significant environmental variables was tested. The arrows and X marks indicate significant explanatory variables, with the arrowheads indicating the increase in gradient. Group legend: empty circles = group I, black squares = group II, black triangles = group III, grey triangles = group IV, empty squares = group V. Substrata legend: CP = calcareous pelite, SP = sandy pelite, P = pelite, VSP = very sandy pelite, GPS = gravel–pelite–sand, GSh: gravel–shell.

Table 1. Results from canonical correspondence analyses (CCA) using data from 2006.

Axes	Axis 1	Axis 2
Eigenvalues	0.49	0.37
Species–environment correlations	0.85	0.86
Cumulative percentage variance		
of species data	3	5.3
of species–environment correlations	22.3	39.1

Environmental variable correlations	Inter-set		Conditional effects	
	Axis 1	Axis 2	P	F
Bottom current	-0.12	-0.29	0.002	2.97
Depth	-0.42	-0.07	0.002	2.06
Temp	-0.46	-0.05	0.002	1.90
Oxygen	-0.44	-0.08	0.002	2.28
Pelite	-0.23	0.09	0.002	2.63
Calcareous pelite	-0.38	-0.33	0.002	1.64
Sandy pelite	-0.24	-0.05	0.004	1.53
Very sandy pelite	-0.14	0.78	0.002	4.22
Gravelly pelite sand	0.30	-0.01	0.002	2.37
Gravel–shell	0.50	-0.06	0.002	3.75

(Eq. 1) Axis 1 ~ oxygen saturation^2 + depth + depth^2 + temperature + temperature^2 + bottomcurrent^2

(Eq. 2) Axis 2 ~ chlorophyll + chlorophyll^2 + oxygen saturation + oxygen saturation^2 + depth + depth^2 + temperature + temperature^2 + bottom current + bottom current^2 + substrata

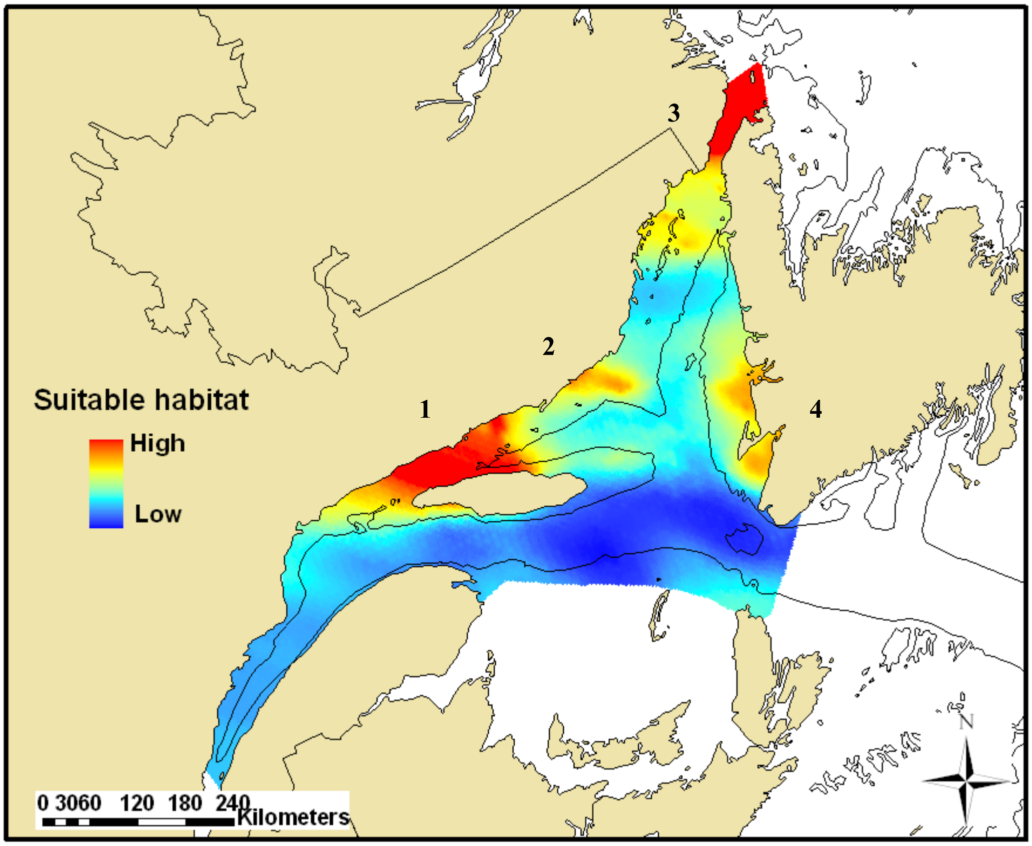

Figure 3. Modelled habitat suitability (GLM) for the epibenthic macrofauna community of the Estuary and the northern Gulf of St. Lawrence resulted from the first CA axis (1 to 4 are the high suitability benthic habitat).

DISCUSSION

The analyses of the biological and physical data from 2006 indicated that depth, oxygen saturation, and maximal bottom currents explained significant proportions of the variance in the distribution of benthic communities. The HS models suggest that depth was one of the most important driving factors affecting benthic community distribution. Moreover, grouping methods produced in the same study (Lévesque 2009) revealed distinctive differences between deep channel macrofauna assemblages and those from shallower areas. Cluster analysis showed a division of the Estuary and northern Gulf of St. Lawrence into biogeographic regions previously identified by Brunel et al. (1998) and that corresponds to production units for snow crabs (Fig. 5 in Sainte-Marie et al. 2005). This characterization was mainly based on the natural boundaries of the seabed topography of the St. Lawrence ecosystem and corresponded to the results obtained by the HS model. The HS model equation derived from the 2006 data also indicated that temperature might influence the distribution of macrofaunal communities. In fact, the relationship between temperature and depth in the present study is likely to be causal as the two parameters covary to a great degree. As suggested by Ardisson et al. (1990), the inclusion of depth as an explanatory variable may limit the ability of detecting the importance of other variables that potentially influence the geographical variation in the distribution of benthic organisms.

The resulting benthic habitat suitability map illustrated in Figure 3 shows areas with high suitability values (warm colours) at (1) the Mingan Islands and the northwestern end of Anticosti Island, (2) on Quebec’s Lower North Shore near Beaugé Bank, (3) from the head of Esquiman Channel to the Strait of Belle Isle, and finally (4) at two locations on the southwestern coast of Newfoundland. Conversely, the Laurentian and Esquiman channels had lower values. Because this HS model was based only on the first axis, it means that these high and low suitability zones mainly represent group I, II, and III. Interestingly, these favourable and unfavourable zones showed good agreement with the map of species richness (Fig. 2 in Lévesque 2009). Moreover, 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 Estuary and Gulf of St. Lawrence (including the southern part) based on data with limited taxonomic resolution. Both studies identified the same areas with particular ecological and biological characteristics that required further attention, specifically, Jacques Cartier Strait, Mécatina Trough, the Strait of Belle Isle, St. Georges Bay, and Honguedo Strait (southwestern Anticosti) (see Fig. 4) . The Chabot et al. (2007) study was more representative for commercial species while the prediction model developed in the current study may be more informative for non-commercial benthic invertebrate species. This also suggested that, for the area currently under study, the evaluation of commercial species may be used as a proxy for describing variation for the ensemble of the benthic macrofaunal assemblages.

The Mingan area and the Strait of Belle Isle are known for their intense circulation patterns that may have an important influence on benthic community structure. The Mingan area is characterized by strong tidal mixing and wind-induced coastal upwellings and eddies (Le Fouest 2005), whereas topography and wind stress interact to create a productive upwelling zone in the southern Strait of Belle Isle (Rose and Leggett 1988). Moreover, the mixing of St.

Lawrence and Labrador Shelf Waters, the latter of which enters via the Strait of Belle Isle (Houghton and Fairbanks 2001), could also favour benthic organisms. The presence of these dynamic conditions may thus partly explain why high benthic habitat suitability spots were predicted in these two areas. On the other hand, the area with the lowest predicted suitability was that from the lower Estuary to the Gulf. This observation may be partly explained by specific conditions within this zone, such as the lowest available food supply to support populations of many species (Desrosiers et al. 2000).

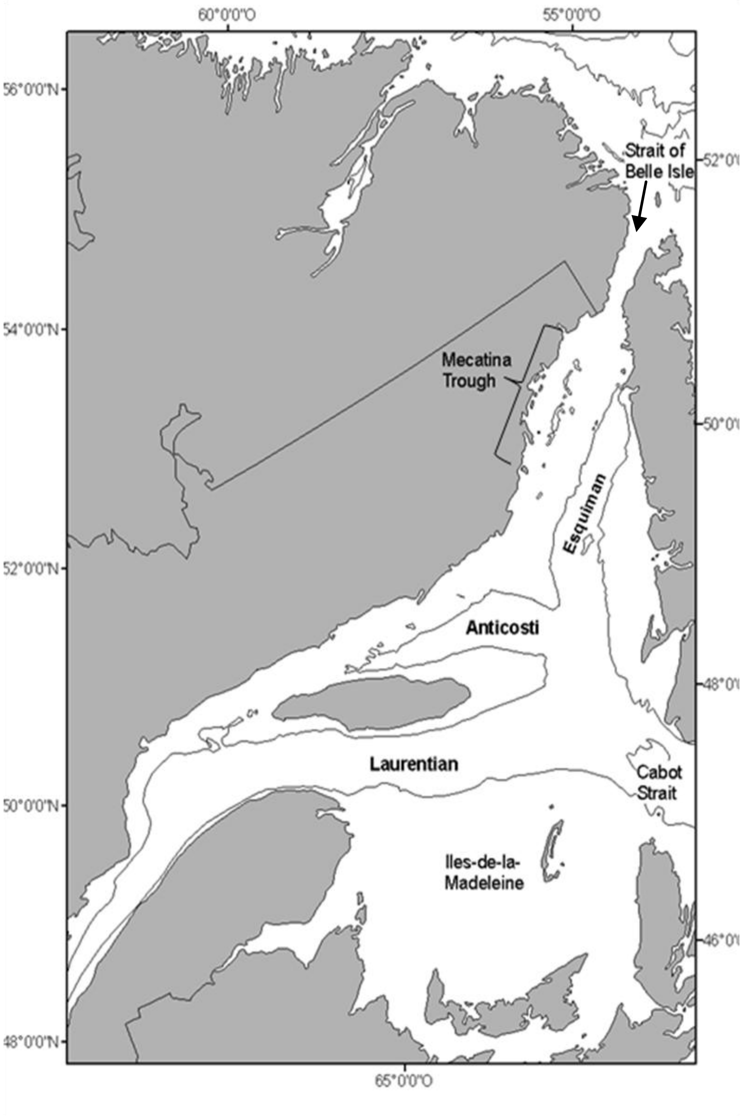

Figure 4 The estuary and the northern Gulf of St. Lawrence showing the location of the different channels, straits, and the Mecatina trough.

The 2006 prediction model highlights the importance of maximum bottom currents in predicting benthic communities. In fact, bed stress appears to be very important in structuring patterns in the major biological habitats of the seabed (Pitcher 2001). The maximal bottom current recorded at sampling stations is directly correlated with the seabed current stress, which also influences sediment type. Bed shear stress reflects the friction pressure on the seabed and is often directly correlated with sediment particle size (Vaz et al. 2006). However, the predictive models derived in the present study excluded the variable “substrate” from the environmental parameters selected by the canonical analyses, suggesting that this variable does not significantly influence benthic invertebrate communities. However, as pointed out by Newell et al. (1998), benthic community composition is not only controlled by the granulometric properties of sediments and bathymetric features. For example, particle mobility and the association of biological and chemical factors operating over the long term must also be taken into account (Newell et al. 1998). Moreover, the trophic composition of soft-bottom communities can be significantly influenced by factors such as sediment stability, water and organic content, and the microbial biomass in sediments (Maurer and Leathem 1981; Gaston 1987).

CONCLUSION

This study demonstrates the usefulness of bottom trawl observations obtained during fisheries surveys to infer relationships between benthic macrofauna community structure and environmental variables. This predicted habitat suitability distribution is simply a preliminary information layer to which further physical and chemical parameters should be added to better describe the habitat. It is difficult to predict how benthic fauna will react to natural and anthropogenic changes, and better information is needed to improve our understanding. The database of benthic communities in the St. Lawrence can be updated annually or at other intervals via the DFO multispecific survey. This information could be used with data obtained through complementary efforts to monitor the spatial and temporal quality of these benthic habitats. However, additional information is needed to improve the present HS model. Seabed heterogeneity, topography, and sediment structure have been recognized as major factors regulating species distribution within a community (Newell et al. 1998) and should be better evaluated. The effect of fishing activities on benthic habitats should also be investigated by including and evaluating information on the spatial variation in fishing effort within the model.

The HS model and methods developed and described here may be used in the future to improve our understanding of the distribution of key and indicator species and to identify potential hot spots for benthic organisms. The model may be used to monitor the spatial and temporal quality of benthic habitat types and to help elaborate conservation and protection strategies to reduce impacts from natural and anthropogenic disturbances.

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REFERENCES

Akaike, H. 1974. A new look at the statistical model identification. IEEE Trans. Automat. Contr. AC-19: 716–723.

Ardisson, P.-L., Bourget, E., and P. Legendre. 1990. Multivariate approach to study species assemblages at large spatiotemporal scales: the community structure of the epibenthic fauna of the Estuary and Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 47: 1364–1377.

Barette-Bekker, J. G., Dunnrsma, E. K., and B. R. Kuipers. 1992. Encyclopedia of marine sciences. Berlin: Spinger. 309 pp.

Belley, R., Archambault, P., Sundby, B., and F. Gilbert. 2008. Environmental factors influencing macrobenthic biodiversity and bioturbation in the Estuary and Gulf of St. Lawrence, Canada. Working document, ICES CM 2008/J: 05.

Bourdages, H., Archambault, D., Bernier, B., Fréchet, A., Gauthier, J., Grégoire, F., Lambert, J., and L. Savard. 2010. Preliminary results in the groundfish and shrimp multidisciplinary survey from August 2009 in the northern Gulf of St. Lawrence. Can. Data Rep. Fish. Aquat. Sci. 1226: xii + 72 p.

Bourque, M. 2008. Variabilité spatio-temporelle de la macrofaune endobenthique profonde du Saint-Laurent (Québec, Canada) au cours d'un évênement hypoxique. Master's thesis, Université du Québec à Rimouski, Rimouski (Québec). ii + 188 pp.

Brunel, P., Bossé, L., and G. Lamarche. 1998. Catalogue des invertébrés marins de l'estuaire et du golfe du Saint-Laurent. Publication Spéciale Canadienne des Sciences Halieutiques et Aquatiques. 126. 405 pp.

Carrit, D. E., and J. H. Carpenter. 1966. Comparisons and evaluation of currently employed modification of the Winkler method for determining dissolved oxygen in sea-water; a NASCO report. J. Mar. Res. 24: 286–288.

Carpentier, A., Vaz, S., Martin, C. S., Coppin, F., Dauvin, J.-C., Desroy, N., Dewarumez, J.-M., Eastwood, P. D., Ernande, B., Harrop, S., Kemp, Z., Koubbi, P., Leader-Williams, N., Lefèbvre, A., Lemoine, M., Meaden, G. J., Ryan, N., and M. Walkey. 2005. Eastern Channel Habitat Atlas for Marine Resource Management (CHARM). Atlas des Habitats des Ressources Marines de la Manche Orientale, INTERREG IIIA. 225 pp.

Catullo, G., Masi, M., Falcucci, A., Moiorano, L., Rondinini, C., and L. Boitani. 2008. A gap analysis of Southeast Asian mammals based on habitat suitability models. Biol. Conserv. 141: 2730–2744.

Chabot, D., Rondeau, A., Sainte-Marie, B., Savard, L., Surette, T., and P. Archambault. 2007. Distribution des invertébrés benthiques dans l’estuaire et le golfe du Saint-Laurent. Secrétariat canadien de consultation scientifique du MPO. Document de Recherche. 2007/018: iii + 108 pp.

Clarke, K.R., and R. M. Warwick. 1994. Similarity-based testing for community pattern: the two-way layout with no replication. Mar. Biol.118: 167–176.

Degraer, S., Verfaillie, E., Willems, W., Adriaens, E., Vincx, M., and V. V. Lancker. 2008. Habitat suitability modelling as a mapping tool for macrobenthic communities: An example from the Belgian part of the North Sea. Cont. Shelf Res. 28: 369–379.

Desrosiers, G., Savenkoff, C., Olivier, M., Stora, G., Juniper, K., Caron, A., Gagné, J.-P., Legendre, L., Mulsow, S., Grant, J., Roy, S., Grehan, A., Scaps, P., Silverberg, N., Klein, B., Tremblay, J.-E., and J.-C. Therriault. 2000. Trophic structure of macrobenthos in the Gulf of St. Lawrence and on the Scotian Shelf. Deep-Sea Res. Part II. 47: 663–697.

Doubleday, W. G. 1981. Manual on groundfish surveys in the NAFO area (Revised). NAFO Scientific Council Studies. 81/VI/7: 78 pp.

Gaston, G. R. 1987. Benthic polychaeta of the Middle Atlantic Bight: Feeding and distribution. Mar. Ecol. Progr. Ser. 36: 251–262.

GenStat Committee. 2003. GenStat Release 7.1. IACRP-Rothamsted, Harpenden. Herfordsshire, UK.

Guisan, A., and E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecol. Modell. 135: 147–186.

Hein, S., Binzenhöfer, B., Poethke, H.-J., Biedermann, R., Settele, J., and B. Schröder. 2007. The generality of habitat suitability models: A practical test with two insect groups. Basic Appl. Ecol. 8: 310–320.

Hirzel, A. H., and R. Arlettaz. 2003. Modeling habitat suitability for complex species distributions by environmental-distance geometric mean. Environ. Manag. 32 (5): 614–623.

Hirzel, A. H., Le Lay, G., Helfer, V., Randin, C., and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecol. Modell. 199: 142–152.

Houghton, R. W., and R. G. Fairbanks. 2001. Water sources for Georges Bank. Deep-Sea Res. Part II*:* 48 (1–3): 95–114.

Koutitonsky, V. G., and G. L. Bugden. 1991. The physical oceanography of the Gulf of St. Lawrence: a review with emphasis on the synoptic variability of the motion. In J.-C. Therriault (Editor), The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aqua. Sci. 113: 57–90.

Le Fouest, V. 2005. Étude couplage circulation-production planctonique à méso-échelle dans le Golfe du Saint-Laurent (Canada) via une approche par modélisation tridimensionnelle. Thèse de Doctorat. Rimouski : Université du Québec à Rimouski. Département de biologie. xiii + 212 pp.

Legendre, P., and L. Legendre. 1998. Numerical Ecology, Elsevier. Amsterdam.

Lévesque, M. 2009. Caractérisation de la macrofaune epibenhique de l’estuaire et du nord du Golfe du Saint-Laurent (Québec-Canada) en relation avec les paramètres environnementaux : analyses multivariées et approche de géostatistique. Master’s thesis Université du Québec à Rimouski, Rimouski (Québec). ii + 103 pp.

Loring, D. H., and D. J. G. Nota. 1973. Morphology and sediment of the Gulf of St.Lawrence. J. Fish. Res. Board Can. 182: 147 pp.

Martin, C. S., Vaz, S., Ernande, B., Ellis, J. R., Eastwood, P. D., Coppin, F., Harrop, S., Meaden, G. J., and A. Carpentier. 2005. Spatial distribution (1989–2004) and preferential habitats of thornback ray and lesser-spotted dogfish in the Eastern English Channel. Working document, ICES CM. 2005/N: 23.

Massad, R., and P. Brunel 1979. Associations par stations, densités et diversité des polychètes du benthos circalittoral et bathyal de l'estuaire maritime du Saint-Laurent. Nat. Can.: 229–253.

Maurer, D., and W. Leathem. 1981. Polychaete feeding guilds from Georges Bank, USA. Mar. Biol. 62: 161–171.

McCallum, B. R., and S. J. Walsh. 2002. An update on the performance of the Campelen 1800 during the bottom trawl survey in NAFO subareas 2 and 3 in 2001 NAFO SCR Doc., No. 32, Serial No. N4643. 16 pp.

McCullagh, P.. and J. A. Nedler. 1989. Generalized Linear Models, second ed. Chapman and Hall, London.

Newell, R. C., Seiderer, L. J., and D. R. Hitchcock. 1998. The impact of dredging works in coastal waters: a review of the sensitivity to disturbance and subsequent recovery of biological resources on the sea bed. Oceanogr. Mar. Biol. 36: 127–178.

Ouellet, G. 1982. Étude de l'interaction des animaux benthiques avec les sédiments du Chenal Laurentien. Master’s thesis Université du Québec à Rimouski, Rimouski (Québec). xiii + 188 pp.

Peer, D. L. 1963. A preliminary study of the composition of benthic communities in the Gulf of St. Lawrence. Manuscript Report Series (Oceanogr. and Limnological). Atlantic Oceanographic Group. 145: 1–24.

Pitcher, T. J. 2001. Fisheries managed to rebuild ecosystems? Reconstructing the past to salvage the future. Ecol. Appl. 11: 601–617.

Préfontaine, G., and P. Brunel 1962. Liste d’invertébrés marins recueillis dans l’estuaire du Saint-Laurent de 1929 à 1934. Nat. Can. 89: 237–263.

R Development Core Team, 2008, Vienna, Austria.

Robert, G. 1979. Benthic molluscan fauna of the St. Lawrence estuary and its ecology as assessed by numerical methods. Nat. Can. 106: 211–227.

Rose, G. A., and W. C. Leggett. 1988. Hydroacoustic signal classification of fish schools by species. Can. J. Fish. Aquat. Sci. 45 (4): 597–604.

Roy, S., Sundby, B., Vézina, A. F., and L. Legendre. 2000. A Canadian JGOFS process study in the Gulf of St. Lawrence (Canada): Introduction. Deep-Sea Res. Part II. 47 (3–4): 377–384

Sainte-Marie, B., Dufour, R., Bourassa, L., Chabot, D., Dionne, M., Gilbert, D., Rondeau, A., and J.-M. Sévigny. 2005. Criteria and proposition for the definition of snow crab (*Chionoecetes opilio*) production units in the estuary and northern Gulf of St. Lawrence. Secrétariat canadien de consultation scientifique du MPO. Document de Recherche. 2005/059. iii + 20 pp.

Saucier, J-.F., Roy, F., Gilbert, D., Pellerin, P., and H. Ritchie. 2003. Modelling the formation and circulation processes of water masses and sea ice in the Gulf of St. Lawrence, Canada. J. Geophys. Res. 108 (C8): 3269.

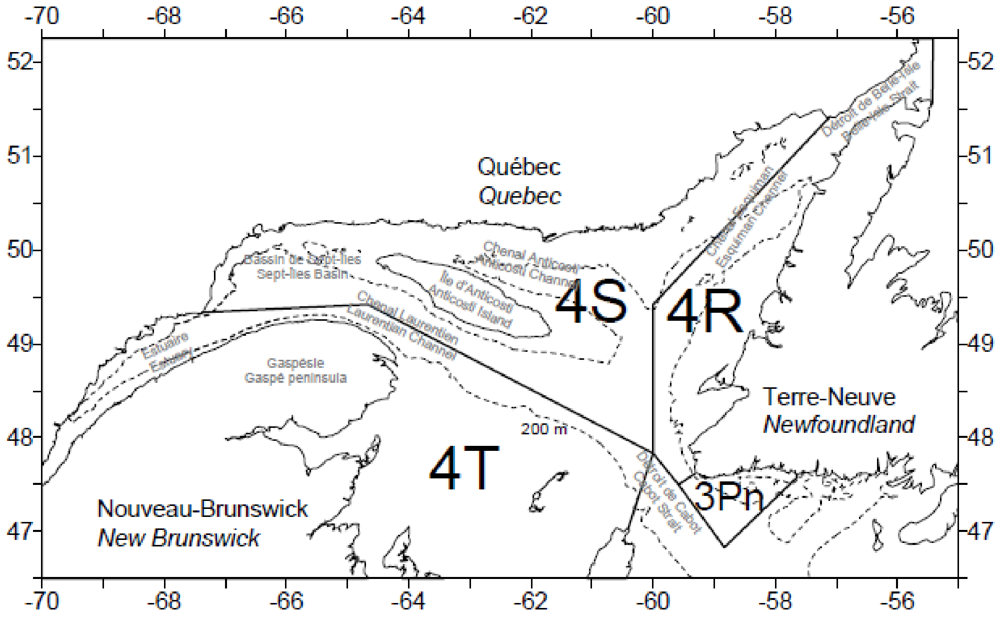
Ter Braak, C. J. F., and P. Simlauer. 2002. CANOCO reference manual and CanoDraw for windows User's guide: software for canocical community ordination (Version 4.5). Microcomputer Power, Ithaca, New-York, 500 pp.

Urbanski, J. A., and M. Szymelfenig. 2003. GIS-based mapping of benthic habitats. Estuar. Coast. Shelf Sci. 56: 99–109.

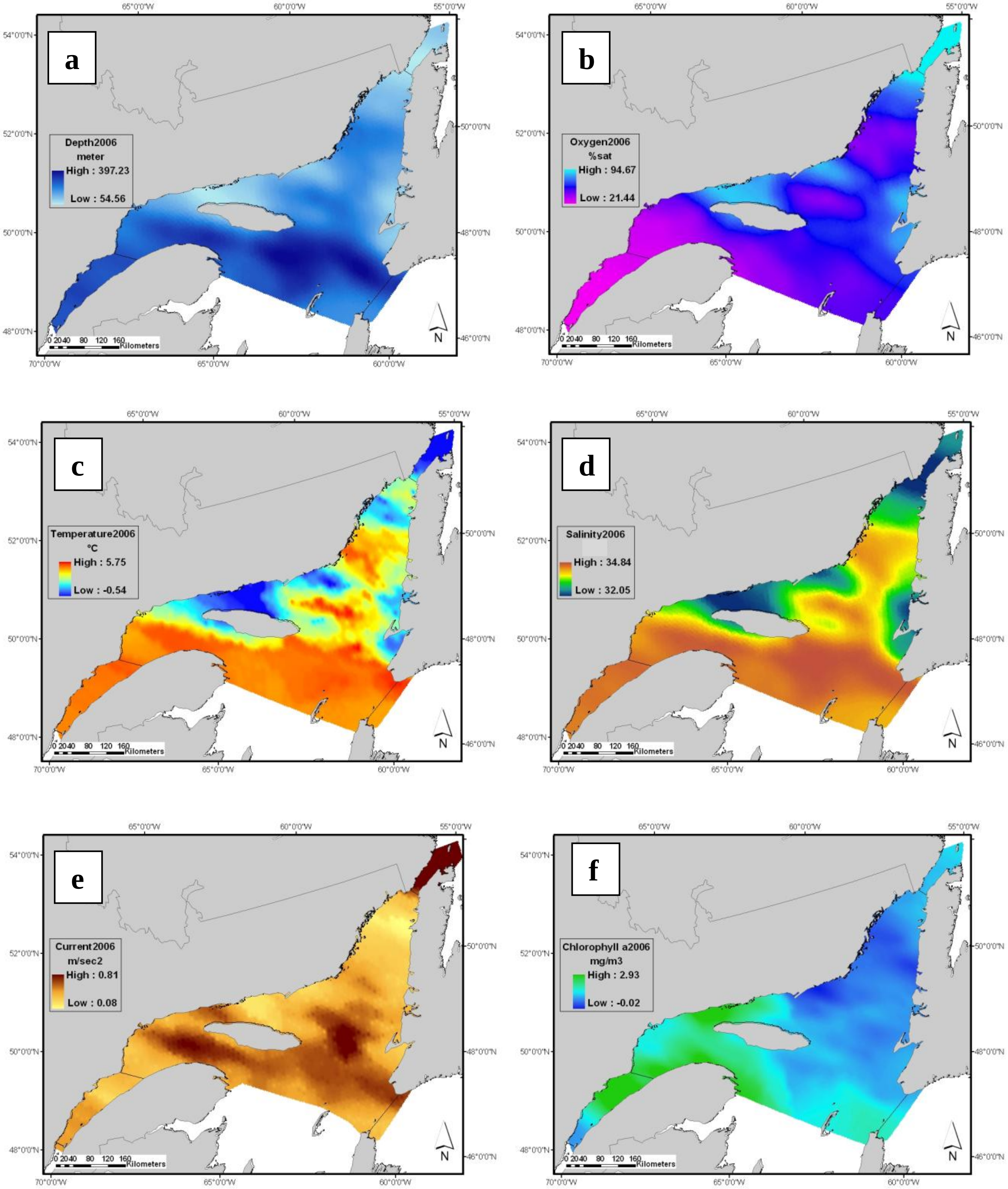
Vaz, S., Martin, J. S., Verin, Y., and D. LeRoy. 2006. Mapping benthic invertebrate assemblages from bottom trawl haul observations. Working document, ICES CM, 2006/D: 15.

Woodward, F. I., and W. Cramer. 1996. Plant functional type and climatic change: introduction. J. Veg. Sci.7: 306–308.

Appendix 1. NAFO divisions of the Gulf of St. Lawrence cited in the text (from Bourdage et al. 2010).



Appendix 2. Continuous maps of bottom environmental parameters in 2006: (a) depth, (b) oxygen, (c) temperature, (d) salinity, (e) maximal bottom current, (f) chlorophyll *a*.



Appendix 3. Summary of generalized linear model results for the 2006 environmental parameters (R software). Data presented are regression coefficients and p values (in parentheses). Superscripts indicate significance of correlations: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; †, $p < 0.1$.

Parameter	Axis 1	Axis 2
intercept	4.73 (0.00)***	-5.38 (0.00613)**
oxygen saturation		0.14 (0.00089)***
oxygen saturation2	0.00 (0.03)*	0.00 (0.05263)†
depth	-0.02 (0.00)***	0.01 (0.18351)
depth2	0.00 (0.01)**	0.00 (0.21479)
temperature	-0.85 (0.00)***	0.63 (0.05284)†
temperature2	0.09 (0.00)**	-0.05 (0.23131)
bottom current		-6.05 (0.09974)†
bottom current2	1.42 (0.02)*	9.38 (0.05582)†
chlorophyll		-0.16 (0.05573)†
chlorophyll2		0.01 (0.12842)
Gdc sediment		-2.12 (0.14777)
Ggs sediment		-1.04 (0.32065)
Pp sediment¤		-1.63 (0.06467)†
Ppc sediment¤		-1.02 (0.25265)
Ppgs sediment¤		-1.03 (0.23821)
Pps sediment¤		-0.59 (0.47359)
Ppts sediment¤		-1.19 (0.18279)
Pptspgs sediment¤		-1.13 (0.21784)
SGcc sediment¤		-0.09 (0.9178)
Ssfa sediment¤		0.13 (0.89329)
Ssgmt sediment¤		-0.56 (0.59885)
Ssgppr sediment¤		-0.24 (0.7668)
Sspmt sediment¤		-2.22 (0.09372)†

¤ : legend for these non significant parameters are explained in Lévesque (2009)