

Environmental mediation of Atlantic cod on fish community composition: an application of multivariate regression tree analysis to exploited marine ecosystems

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ABSTRACT: Changes in species abundances caused by climatic variability have long been linked to alterations in community composition, species interactions and maintenance of biodiversity in marine ecosystems. Here we use multivariate regression tree (MRT) analyses to quantify how changes in species abundances and environmental variability contributed to observed patterns of community composition in the Gulf of St. Lawrence during 2 contrasting periods (the cooler and less saline period 1991 to 1995 and the warmer and more saline period 1997 to 2003). Broad-scale patterns of community composition in both periods were consistently explained by the depth and salinity of the benthic environment, but biological factors differed. In the cold period, the previous year's catches of snow crab *Chionoecetes opilio* and northern shrimp (mainly *Pandalus borealis*) were most important, while in the warm period the previous year's catch of Atlantic cod *Gadus morhua* dominated. MRT models further identified spatially discrete areas where communities are characterized by relatively high abundances of these species. These results indicate that environmental variability leads to dynamic and spatially explicit responses not only of single species, but of marine communities. Applications of ecosystem management in the face of climate change must take this into account.

KEY WORDS: Environmental variability · Community dynamics · Community composition · Atlantic cod · Spatio-temporal analysis · Multivariate analysis · Multivariate regression trees

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INTRODUCTION

Changes in species abundances, whether induced by environmental conditions or anthropogenic activities, have been linked to changes in community composition and interactions between species within many marine ecosystems (Myers & Worm 2003, Scheffer et al. 2005, Heithaus et al. 2008). These changes have the potential to disrupt ecosystem function and maintenance of biodiversity by influencing distributions, abundances, behaviour and population dynamics of species at multiple trophic levels (Frid et al. 2008,

Sandin et al. 2008). Despite the importance of community dynamics to marine ecosystems, most studies have focused on single populations with few studies emphasizing the effects of population changes at the community level (Benoît & Swain 2008, Sandin et al. 2008). On the one hand, the common approach in fisheries science has been to conduct single-species management at the population level, with emphasis on managing the anthropogenic influences on abundance. In doing this, much of the information with regards to interactions among species may be lost, and, as a result, community level processes are not recognized (Beare et al.

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2005). On the other hand, a historical approach in community ecology was to evaluate the impact of single ecological processes on community composition separately (Agrawal et al. 2007), despite ecology having transitioned to incorporating multiple processes that include competition, mutualism, predation, parasitism and the environment (Bronstein 1994, Wootton 1994, Stachowicz 2001). For example, predator declines may be occurring concurrently with changes in environmental conditions, with both influencing interactions between lower trophic level species and potentially altering community composition.

Substantial changes in the structure of fish communities have been documented throughout the north-western Atlantic for many shelf ecosystems (Benoit & Swain 2008). This boreal subarctic region experiences both 'top-down' structuring of community dynamics (e.g. Savenkoff et al. 2007b), where a predominant predator is Atlantic cod *Gadus morhua*, and 'bottom-up' forcing, which is more tightly linked to environmental change (e.g. Greene et al. 2008). Cod stocks in this region were once among the most abundant worldwide and have been studied extensively, but due to overexploitation during a period of low productivity, declines were widespread in the late 1980s and early 1990s (Rose 2007, Halliday & Pinhorn 2009). In the Gulf of St. Lawrence during the last decade, a moratorium on cod fisheries reduced exploitation, and, with the poor environmental conditions of the early 1990s also abating, stock rebuilding has been slower than anticipated and biomass remains well below historic levels (DFO 2009, 2010a). Mechanisms contributing to low productivity in cod may be complex and accompanied by many other changes within the ecosystem and biological community. For example, cod declines occurred almost concurrently with increases in snow crab *Chionoecetes opilio* and shrimp (mainly *Pandalus borealis*) (Savenkoff et al. 2007a) during the 1990s. Catch rates in 2008 and 2009 indicate major changes in the community, suggesting that crab and shrimp stocks in the Gulf are in decline (DFO 2010b,c) and cod stocks are showing modest increases in the northern Gulf, but modest declines in the southern Gulf (DFO 2009, 2010a). Such dynamics suggest not only a strong environmental influence (Lilly et al. 2008), but second-order cascading effects, such as predation on lower trophic levels, with resultant community structural change.

Investigating spatio-temporal relationships between community structure and environmental variability can help to determine whether environmental influence and cascading effects on lower trophic levels are contributing to dramatic shifts in community composition throughout the Gulf. Environmental variability observed at smaller scales within the northern Gulf

throughout the 1990s and early 2000s was associated with a shift in site fidelity of cod, such that greater site fidelity to summer feeding grounds was demonstrated for warmer years compared to colder years (Ruppert et al. 2009). Although cod dynamics are clearly influenced by environmental variability, whether the change in environmental conditions throughout the Gulf (at a regional level) impacts the broader community is poorly understood. Further, if second-order cascading effects influence patterns of community composition, changes in cod site fidelity (as demonstrated at a smaller scale in the northern Gulf) may be inferred to have an effect on community composition patterns throughout the Gulf.

The relationship between community dynamics and the environment can also be scale dependent, such that environmental characteristics influence community dynamics at either regional and/or local spatial scales. Previous studies at broad continental scales have suggested that trophic dynamics and community composition within traditionally cod-dominated ecosystems in the Atlantic have a strong association with temperature and biodiversity gradients (Worm & Myers 2003, Frank et al. 2007). At finer scales Benoit & Swain (2008) have identified significant effects of fisheries and climate on the composition of the community within the southern Gulf of St. Lawrence. Further, the relationship between densities of species has also shown scale dependence between cod and capelin (predator and prey, respectively) within the northern Gulf of St. Lawrence (Rose & Leggett 1990). Hence, it is likely that the effects of environmental variability on community dynamics in the Gulf of St. Lawrence are scale dependent, and a multi-scale approach would be well suited for investigating community–environment relationships at a regional scale.

In the present paper we used a predictive community approach to investigate the dynamics in a portion of the community for which data were available (capelin presence/absence along with cod, shrimp and snow crab catch weight). This paper expands upon a single-species and local-scale study published by Ruppert et al. (2009) by investigating community dynamics at both broad and fine spatial scales in the Gulf of St. Lawrence, in relation to environmental variability and the abundances of those species. The goal of the present paper was to ascertain how environmental conditions and species abundances can influence community composition distribution during periods of differing ocean climate. We used a multi-scale, multivariate technique within a temporal framework, multivariate regression tree (MRT) analyses, to assess differences in the relationship between environmental variability and patterns of community composition.

MATERIALS AND METHODS

Study area. The Gulf of St. Lawrence is a semi-enclosed sea, forming the Northwest Atlantic Fisheries Organization (NAFO) management zones 4SRT and 3Pn (Fig. 1). Some commercial species within the Gulf, such as cod, are managed as 2 separate units (northern and southern regions), but often the northern and southern units are viewed as subregions of a single, semi-enclosed Gulf ecosystem (DFO 2005). The Gulf is characterized by highly variable bathymetry, to a maximum depth of about 500 m, and is dominated by shallow coastal shelves with deep trenches that bisect both the eastern and northern extensions. The present study is concerned mainly with environmental conditions and community composition in the benthic environment, meaning that the variability in depth is likely to be a strong contributor to patterns in abiotic and biotic conditions throughout the region. Further, as a boreal marine ecosystem and semi-enclosed sea, the gulf experiences strong interannual variability in water and ice properties (Smith et al. 2006).

Data. Atlantic cod *Gadus morhua*, snow crab *Chionoecetes opilio* and northern shrimp *Pandalus borealis* abundance data were obtained from Department of Fisheries and Oceans (DFO) Québec and Gulf Region annual bottom trawl surveys (BTS) spanning the years from 1991 to 1995 and from 1997 to 2003. The BTS for northern and southern Gulf regions follow a depth-stratified random survey design and were conducted during August and September of each year (Double-day 1981, Gagnon 1991). Factors that could differ between the north and south regional BTS include: duration of tow, length of tow, the vessel and the type of gear used. All survey catches for the entire study region were standardized individually by tow duration to a 15 min tow. Vessel and gear types were similar between regions, and changes between years have been subjected to standardization procedures (Fréchet et al. 2005, Benoît 2006).

BTS data also include information about the location (latitude and longitude), bottom temperature and bottom salinity (no salinity data were available for the northern area in 1996; hence, this year was not included). The BTS data also contain capelin *Mallotus*

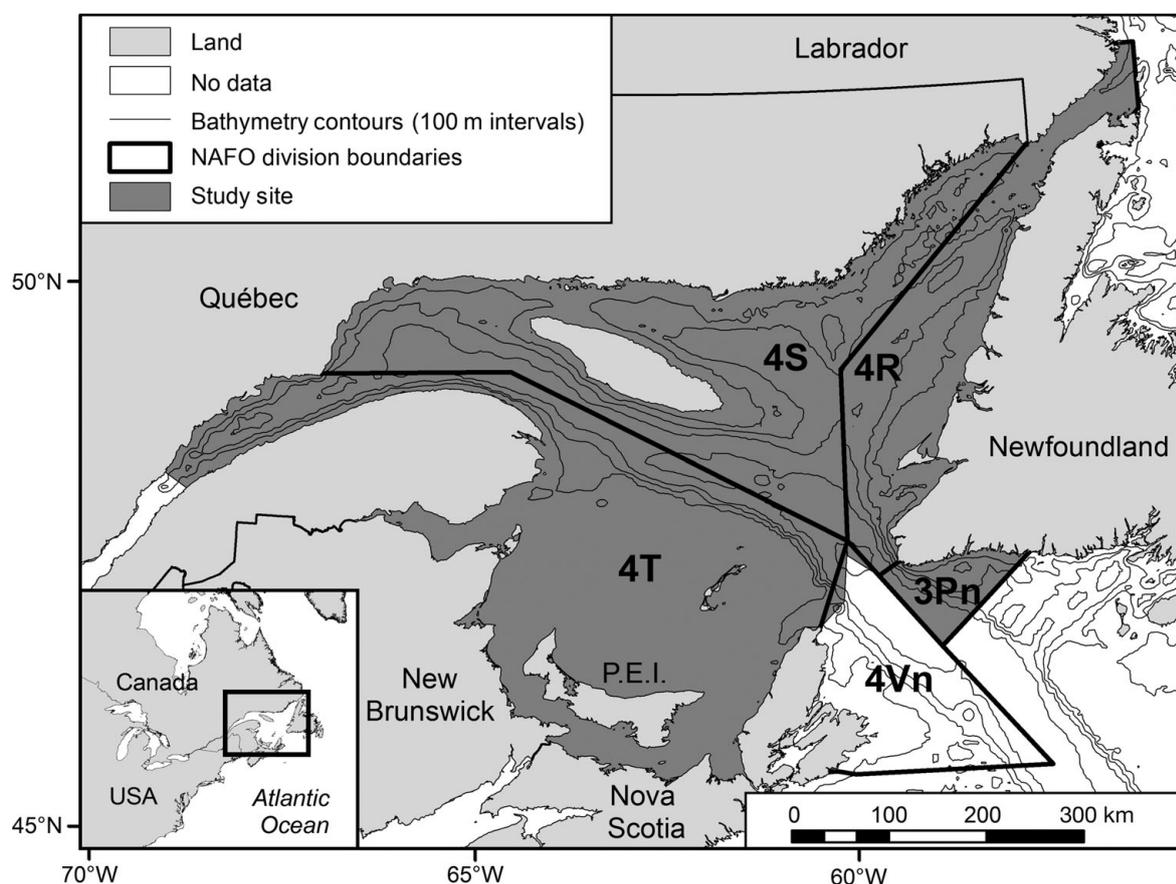


Fig. 1. The Gulf of St. Lawrence and its Northwest Atlantic Fisheries Organization (NAFO) management units. The study area (denoted in dark grey) includes management units 4SRT, 3Pn and a small portion of 4Vn. The contour lines delineate bathymetry at 100 m intervals in depth

villosus catch weight, but, because capelin is a semi-pelagic species, the catch cannot be used to infer relative abundance. As a result any catch weight of capelin was used to only infer its presence. Depth, slope and orientation were derived from the 1 min world bathymetric grid of the General Bathymetric Chart of the Oceans (GEBCO 2003). Surficial sediment data was provided by Natural Resources Canada, which coarsely classifies regions and represents the best available classification and coverage for the entire Gulf region (Fulton 1995). To account for lag responses to the abundance and distribution of a particular species, species catch weight measurements for the previous year were derived from interpolated BTS measurements by universal kriging for cod, shrimp and crab catch weights (Cressie 1993).

Analysis. To determine how the benthic fish community responds to contrasting environmental conditions that reflect a cool, less saline (1991 to 1995) and a warm, more saline (1997 to 2003) period we used an MRT approach (De'ath 2002). Prior to the MRT analysis we verified whether or not temperature and salinity differ significantly between these 2 periods using the Wilcoxon-Mann-Whitney test, because the data are not normally distributed (Rosner 2000). We chose not to pool the data (i.e. all years of data) into a single regression tree, because this would remove much of the yearly variability, and we were interested in how and if community responses changed with respect to changes in environmental conditions through time. This means that a MRT model was created for each year of data analyzed.

MRT analysis is a data-mining technique that uses a recursive partitioning algorithm that subdivides sample sites into 2 groups based on the similarities in community composition (or the dependent variable) and environmental conditions (or the independent variables; Breiman et al. 1984, De'ath 2002). The final output is a tree structure with a root (with all samples together), branches that are formed by splits (based on the selection of an environmental variable and a threshold for that variable) and leaves that form the predictions (Fig. 2). MRT analysis is an extension of the univariate regression tree analysis (i.e. classification and regression tree analysis or CART), with the exception that it has a multivariate prediction. As a result MRT predictions can be viewed as the average

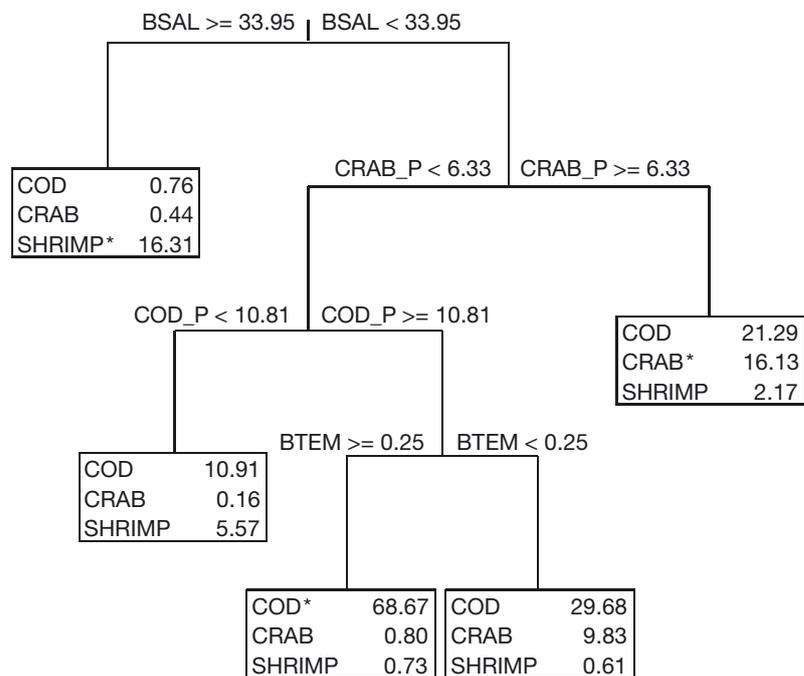


Fig. 2. The multivariate regression tree for 1994 predicting the relative catch weight per tow (kg) for cod *Gadus morhua*, shrimp *Pandalus borealis* and crab *Chionoecetes opilio*. The leaves of the tree indicate the average catch weight per tow of each species given the conditions and thresholds stipulated by the splits. *Catch weights of species that were significantly higher, as per the indicator species index, than in other leaves

response of each species to other species (i.e. a community) as opposed to the average response of a single species without consideration of any community responses (Fig. 2). There are several advantages to MRT analysis, but the most important is that no assumptions are required regarding data structure, in contrast to many other multivariate techniques (De'ath 2002). However, non-targeted fisheries data are generally right skewed and zero-inflated, which means that values need to undergo log-transformation prior to analysis to reduce large disparities between catch values (i.e. large and small catch values). The log-transformation improves the ability of MRT analysis to capture more subtleties of the community–environment relationships, because without log-transformation MRT analysis strictly groups species abundances based on 2 categories: large catch weights and all other catch weights. This approach for regression techniques has proven to be quite robust for non-targeted fisheries data (Ruppert et al. 2009). Another useful property of MRT analysis with spatial data is that explanatory variables that operate at broader spatial scales are designated in trees within the first 2 splits, and variables used in subsequent splits in trees typically operate at finer spatial scales (Moore et al. 1991). This hierarchal

partitioning results in splits near the root of the tree having more observations than those below. This means that explanatory variables closer to the root of the tree explain more variation in the data than subsequent splits in the tree, which have inherently fewer observations. The MRT analyses were run in R Project for Statistical Computing, using the *mvpart* package (De'ath 2007b).

An important aspect of any analysis of multivariate ecological data is to determine how well a model explains variation in the data. With MRT analysis, prediction error is used to assess the fit of a model and to determine the appropriate tree size (i.e. initial MRT models created by this process are often over-sized). A measure of prediction error in the present study was attained through cross-validation, which is not affected by small sample sizes (where $n < 1000$; De'ath 2007a). To delineate an optimal tree size with a consistent minimum deviance (or prediction error), the 1 standard deviation rule was used to determine the appropriate tree size (Maindonald & Braun 2007). Despite the cross-validation analysis, the variability in the sample size and catch weights can present a problem in the ability of MRT analysis to determine appropriate community–environment relationships (Table 1). To test this, cross-validation was bootstrapped 1000 times to judge the precision of the final model (i.e. whether or not the tree and size of tree describe community–environment relationships). If consistency in a regression tree is demonstrated, this would indicate that the sample size or variability in catch weights does not present a problem for the finalized model.

Table 1. Sample size, number of splits and species variation explained by the multivariate regression tree models. The appropriate tree size for multivariate regression trees was determined by the 1 standard deviation rule (Maindonald & Braun 2007), based on 1000 cross-validation runs (see the supplement at www.int-res.com/articles/suppl/m411p189_supp.pdf)

Year	Sample size (n)	Number of splits	Species variation explained (%)
1991	365	7	63
1992	293	4	61
1993	341	8	62
1994	261	4	56
1995	231	11	72
1997	286	7	56
1998	352	13	61
1999	377	7	56
2000	390	11	64
2001	323	6	58
2002	314	27	76
2003	231	4	51

When using MRT analysis there are several aspects to constructing a model that need to be investigated. To assess the degree of collinearity and hence redundancy among variables, Spearman correlation analysis was initially conducted on all variable pairs (Rosner 2000). As MRT is a method of constrained cluster analysis which chooses a tree structure with splits defined (or constrained) by environmental variables, a comparison with an unconstrained method of cluster analysis (i.e. partitioning methods that do not define splits by environmental variables) was conducted to determine whether MRT splits based on the variables used adequately accounted for the potential species variance (De'ath 2002). Finally, to represent predictions of MRT analysis spatially, the multivariate responses or predictions need to be classified using a species indicator index. In the present study the indicator index developed by Dufrêne & Legendre (1997) was used. The index (d) is the product of the relative frequency (f) and relative average abundance (a) of species within clusters. Specifically, for a cluster c in set K the index would look as follows:

$$d_{i,c} = f_{i,c} \times a_i$$

$$f_{i,c} = \frac{\left(\sum_{j \in c} p_{i,j}\right)}{n_c}$$

$$a_{i,c} = \frac{\left(\sum_{j \in c} x_{i,j}\right)/n_c}{\sum_{k=1}^K \left(\sum_{j \in k} x_{i,j}\right)/n_k}$$

where $p_{i,j}$ is the presence/absence of species i in sample j , $x_{i,j}$ is the abundance of species i in sample j , and n_c is the number of samples in cluster c . Species that showed a higher MRT abundance value than expected by chance over 1000 iterations were used to classify the MRT prediction. This index has been used in previous work with MRT analysis and cluster analysis to provide an accurate means to classify and map MRT predictions (e.g. Claudet et al. 2006, DeVantier et al. 2006, Cappelletti et al. 2007; see Fig. 2).

To summarize the similarities and differences between the variable selection of the MRT analysis in the early (1991 to 1995) and late (1997 to 2003) periods, we used CART (Breiman et al. 1984). CART is the univariate form of MRT analysis. For the CART models, the response variable is the period of the MRT model (i.e. early or late), and the explanatory variables are the variables selected by the MRT models to describe the responses of community composition. Using CART in this manner removes potential subjectivity of the interpretation of differences and similarities of variables selected by the MRT model predictions between the early and later period models.

RESULTS

Bottom temperatures were significantly cooler in the Gulf of St. Lawrence between 1991 and 1995 compared to bottom temperatures between 1997 and 2003 (Wilcoxon-Mann-Whitney $W = 1\,121\,171$ and $p < 0.001$; Fig. 3). The bottom environment was also significantly less saline in the 1991 to 1995 period compared to the 1997 to 2003 period ($W = 1\,160\,747$ and $p < 0.001$; Fig. 3). Hence, grouping the periods into 1991 to 1995 (cold, less saline) and 1997 to 2003 (warm, more saline) was justified. Given the strong collinear properties of environmental variables in the marine environment, it was expected that the depth, salinity and temperature of the benthic environment would be redundant variables within the MRT analysis (Nybakken & Bertness 2003), but only depth and salinity had consistently significant Spearman correlation coefficients ($p < 0.001$; see Fig. S1 in the supplement at www.int-res.com/articles/suppl/m411p189_supp.pdf). Neither was removed from the analysis, however, because both have the potential to independently describe important influences on the community dynamics in the Gulf.

Broad-scale variable selection by MRT analysis (i.e. variables assigned to the first 2 splits) during both the

early 1990s (1991 to 1995) and the later period (1997 to 2003) were very different. During the early 1990s broad-scale species variation was explained mostly by salinity in the benthic environment and the previous year's catch weight of crab *Chionoecetes opilio* and shrimp *Pandalus borealis* (Table 1). In contrast, during the later period, the previous year's catch weight of cod *Gadus morhua* and salinity (with depth combined) were both the main determinants of broad-scale species variation for 6 out of 7 yr (Table 1). It was also notable that the previous year's catch weight for crab and shrimp, along with the presence/absence of capelin *Mallotus villosus*, were used in MRT models during the later period to explain broad-scale patterns of community composition, but none of these variables were used consistently.

MRT variable selection for finer scale species variation (i.e. the third, fourth, or fifth splits) displayed no consistent trends or patterns of variable selection between the early 1990s and the later period. The most prevalent finer scale variables in the models for the early 1990s included temperature and the previous catch weight of cod and crab (Table 1). In the later period, the previous catch weight of crab was the most prevalent variable selected, but it only accounted for

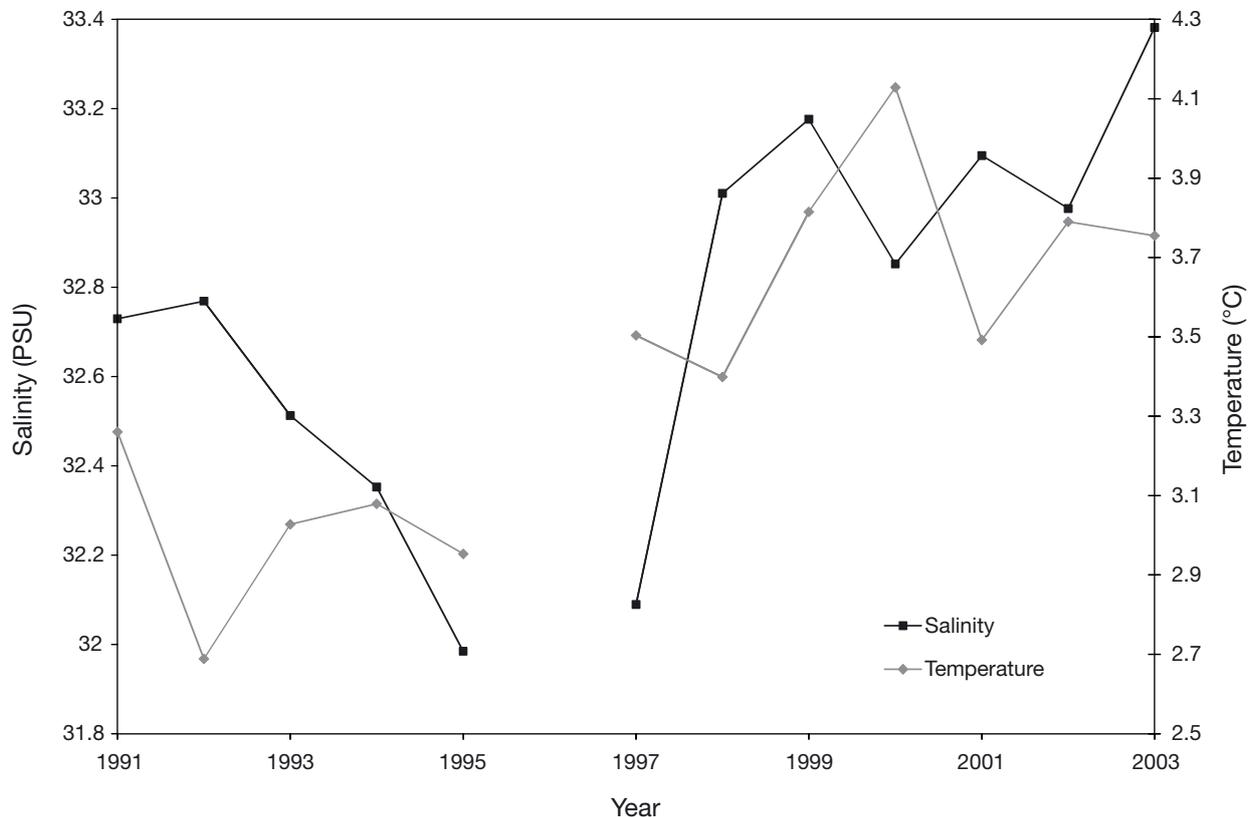


Fig. 3. September/August average benthic temperature and salinity measurements recorded during bottom trawl surveys. The period from 1991 to 1995 displays significantly cooler temperatures and less saline conditions when compared to that from 1997 to 2003 (Wilcoxon-Mann-Whitney $W = 1\,121\,171$, $p < 0.001$; $W = 1\,160\,747$, $p < 0.001$, respectively)

fine-scale species variation in 6 out of 7 yr (Table 1). Other variables that were prevalent in the later period included the previous catch weight of shrimp, cod, capelin, depth and bottom salinity.

Classification tree analysis of the MRT variable selection between the periods showed 2 distinct groupings of the early and later period models by broad-scale variables. If the variable selection is analyzed by split level in the models, the previous catch weight of crab at the second split level and the bottom salinity at the first split level distinguish the models between the two periods with no misclassifications (Fig. 4). Crab catch weight in the previous year was the most important distinguishing variable between these periods, but it was a variable that was largely not selected in later period models (it was only selected by 2 out of 7 later period models; Fig. 5). In the instances where the previous catch weight of crab was chosen by models in the later period, the absence of bottom salinity at the first split level distinguished these later period models from the models of the early 1990s. If the MRT variable selection is interpreted as broad-scale (combining first and second splits) and fine-scale (combining third and fourth splits), then the classification tree changes (Fig. 4). The distinguishing variable between the early and later period models was the previous catch weight of cod at the broad scale. The previous catch weight of cod was consistently selected in the later period models, with the exception of the 2003 model, which was misclassified by the classification tree. The difference in the 2003 model was likely attributable to an upward bias in cod and shrimp abundance estimated by the DFO surveys in the Gulf compared to other abundance indices (DFO 2010a,b). Despite the single misclassification in the second model, the classification tree analysis suggested that there was a strong difference in the model variable selection between the periods that was largely attributable to the previous catch weight of crab and cod at the broad scale.

The cross-validation analysis showed a consistent result for MRT models, which indicated that variability in the sample size and in catch weights were not a major problem within this analysis (see Table S1 in the supplement at www.int-res.com/articles/suppl/m411p189_supp.pdf). Comparisons of MRT models with unconstrained cluster analysis revealed that the within-group variation for groups formed by MRT analysis were very similar to those formed by unconstrained clustering (see Table S2 in the supplement), meaning that the environmental variables used to form trees in MRT analysis adequately accounted for the potential species variance that can be explained, and no other important unobserved variable was likely. Finally, the MRT models explained an average species variation across all years of 61%. None of the models

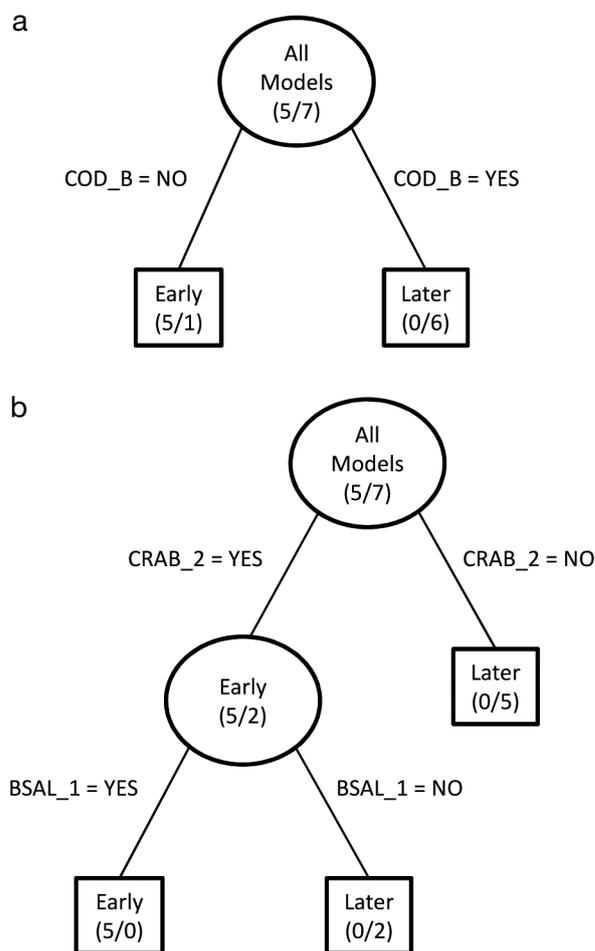


Fig. 4. Classification tree analysis of multivariate regression tree variable selection by (a) split level and (b) broad- and fine-scale splits. ‘_B’ denotes a broad-scale variable and ‘_1’ and ‘_2’ designate variables at the first and second split level, respectively. Predictions are the classification of models as either 1991 to 1995 (early) or 1997 to 2003 (late) based on variable selection. Numbers in parentheses indicate the ratio of early to late period models associated with a given node or split (e.g. early/late)

displayed a poor ability to explain species variation in the data, with the variation explained ranging from 51 to 76% (Table 1).

Thus, applying the indicator species index to the MRT multivariate predictions revealed spatially explicit patterns of community composition throughout the study period (Fig. 6). The indicator species index revealed that cod, crab and shrimp, which were sampled adequately in the BTS, each characterized spatially distinct multivariate response groupings for the majority of years analyzed. The patterns that emerged from these predictions were that regions characterized by shrimp occur within the deeper, more saline regions of the Gulf. Areas that were characterized by crabs

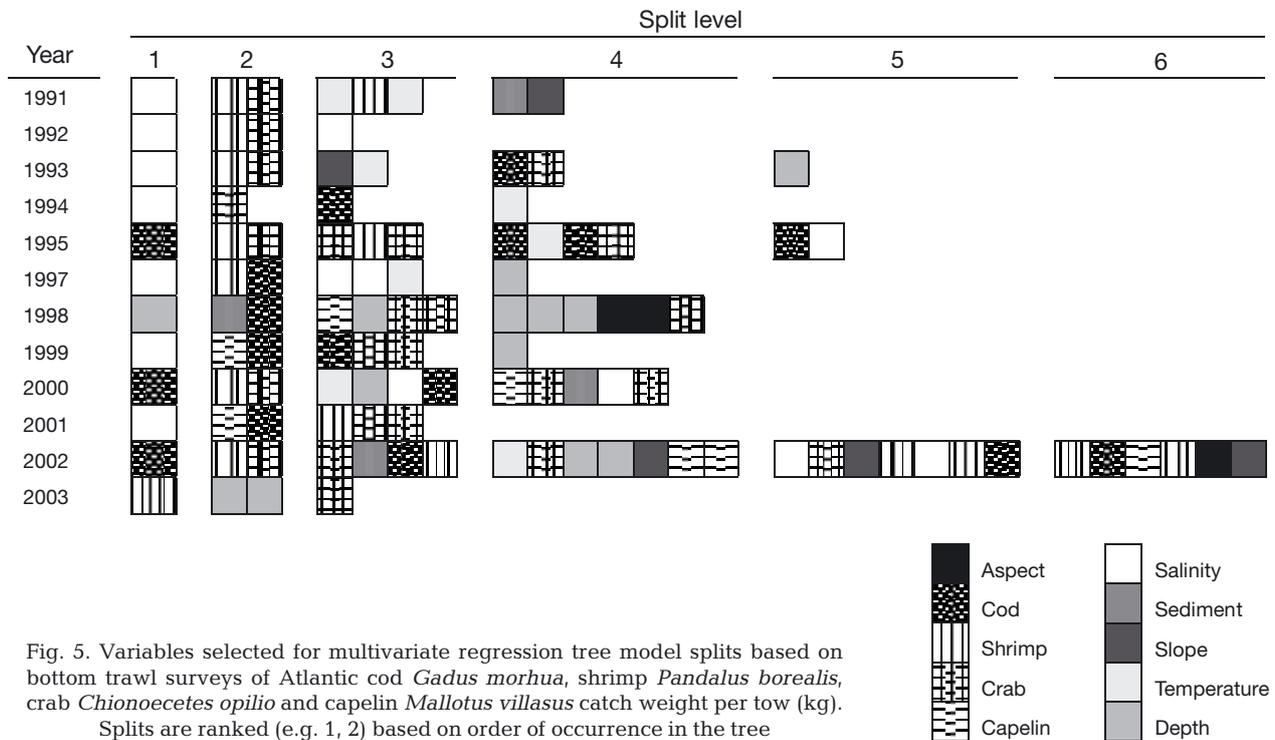


Fig. 5. Variables selected for multivariate regression tree model splits based on bottom trawl surveys of Atlantic cod *Gadus morhua*, shrimp *Pandalus borealis*, crab *Chionoecetes opilio* and capelin *Mallotus villasus* catch weight per tow (kg). Splits are ranked (e.g. 1, 2) based on order of occurrence in the tree

were predominantly found throughout inshore regions of the southern Gulf. Cod were found to characterize the inshore regions throughout the Gulf, but these areas were fairly ubiquitous rather than continuous. Finally, the areas that were not characterized in abundance by a particular species or a combination of species in the analysis were the most spatially prominent (in area) as a prediction by the MRT models.

DISCUSSION

A central objective of the present study was to ascertain how community spatio-temporal dynamics may be influenced by abundances of a given species and changes in environmental conditions. Using MRT analysis, we were able to identify and link community dynamics in the Gulf of St. Lawrence to trends in salinity and temperature. A major advantage of this approach is that it provides a predictive framework of community composition and allows for multiple interactions in dependent and independent variables that contribute to observed patterns (De'ath 2002). Linking this technique with classification tree analysis is beneficial, because it aids in summarizing the differences in community dynamics between 2 different environmental regimes. Another important aspect was coupling of MRT analysis with the species indicator index (Dufrêne & Legendre 1997) to visualize spatio-

temporal patterns of species with significantly high frequency and abundance, as predicted by the models. By taking these steps we are able to delineate which environmental factors characterize spatially explicit patterns of community composition without limiting the potential spatial or temporal scope.

Community dynamics

The findings in the present study demonstrate that well known long-term changes in environmental conditions (Benoît & Swain 2008, DFO 2008, Ruppert et al. 2009) and the previous abundance of crab *Chionoecetes opilio* and cod *Gadus morhua* contribute to spatio-temporal patterns of community composition at regional scales in the Gulf of St. Lawrence. In the cooler, less saline period (1991 to 1995), broad-scale community composition patterns were largely associated with benthic salinity and the previous years' catch weights of shrimp *Pandalus borealis* and crab. This contrasts with the warmer, more saline period (1997 to 2003) during which community composition patterns were similarly associated with benthic salinity, but also associated with the previous years' catch weight of cod. We interpret this to indicate that there is a strong and consistent pattern of community composition influenced by benthic salinity and depth gradients in the

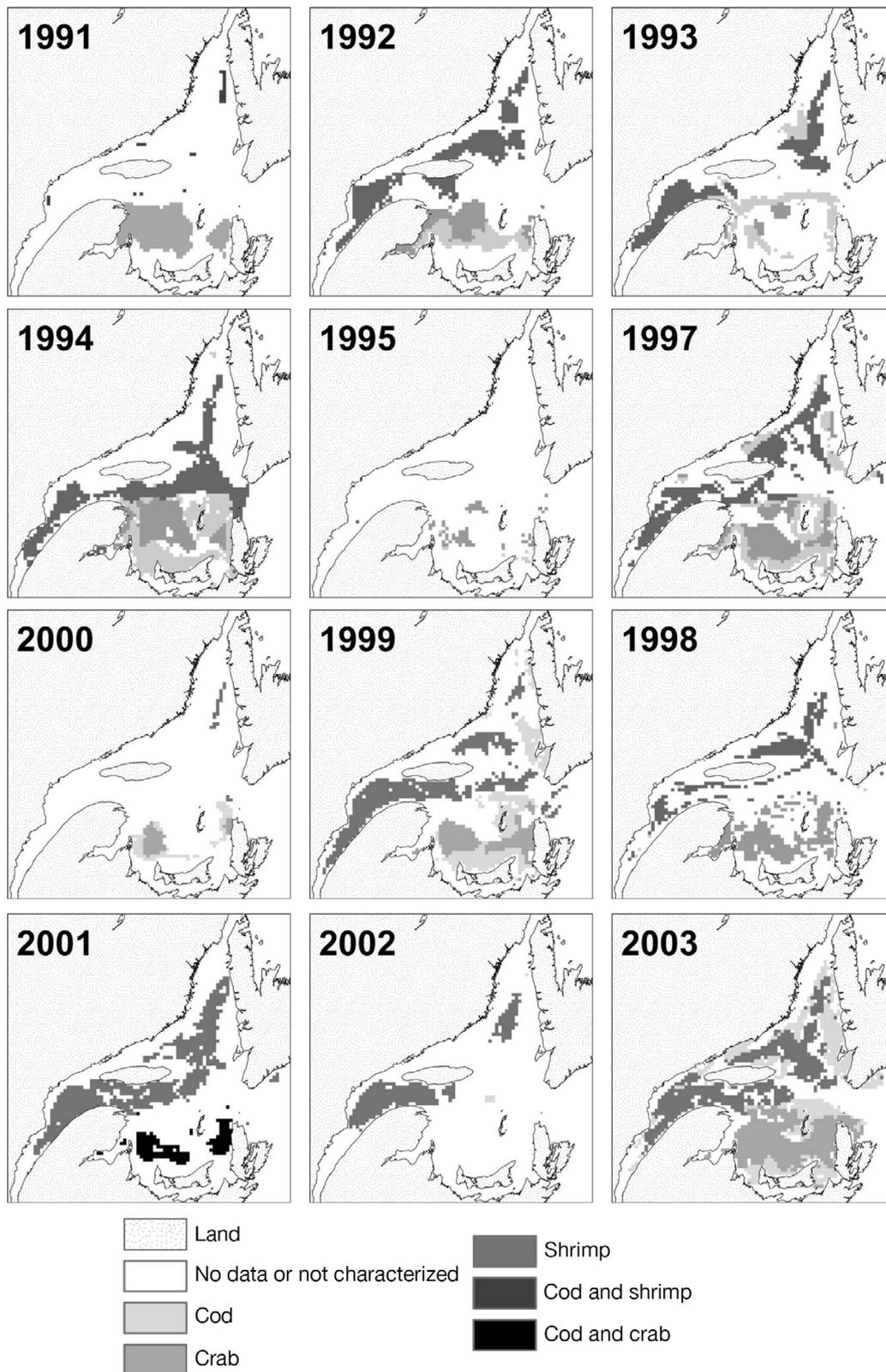


Fig. 6. Maps of multivariate regression tree predictions spanning from 1991 to 1995 and from 1997 to 2003, based on species indicator index classification. These maps show areas with communities that are characterized by a given species (i.e. a species that has a significantly high abundance and frequency) at a 100 km² resolution

Gulf. This association likely reflects both the migration patterns of cod throughout the region and the more sedentary movement and habitat preference of snow crab and northern shrimp (Tremblay 1997, Castonguay et al. 1999, Koeller 2000). The MRT models show areas characterized by cod are typically found in the shallower inshore regions (summer distributions), which is consistent with earlier findings that cod in this region migrate annually between shallow summer feeding areas (largely feeding on capelin *Mallotus villosus*) and deeper over wintering grounds (Rose & Leggett 1988, Campana et al. 1999, Castonguay et al. 1999). Further, the MRT model predictions also consistently associate shrimp and crab with relatively deeper regions having cooler temperatures and more saline conditions, consistent with findings that shrimp prefer areas with bottom temperatures ranging from 1 to 6°C and that snow crab prefer even colder temperatures ranging from -1 to 2°C (Shumway et al. 1985, Tremblay 1997, Koeller 2000).

Environmental factors, however, did not underpin all MRT predictions. Perhaps the most novel finding of the present study was that the previous years' crab abundance was the main biotic factor explaining patterns of community composition during the cold and less saline period of the early 1990s, whereas the previous years' cod abundance explained patterns of community dynamics in the warmer, more saline period that followed. These findings suggest that the influence of individual species on their community may not be constant, but will be mediated by the dynamics of environmental conditions, and, specifically in this case, that in cold periods the community structure will be most influenced by crab abundance, while in warmer periods it will be most influenced by cod. This is consistent with previous findings that cod behaviour may be influenced by the environment, in that fish tend to show less summer site fidelity in colder periods compared to warmer ones (Ruppert et al. 2009). Another factor potentially influencing range changes is abundance, with the expectation of range expansion in some species with increasing abundance (for cod, see Robichaud & Rose 2004). Over the period of our study, there were changes in the abundance of various species throughout the Gulf region. However, the changes appear to be shifts rather than expansions, which indicates that the spatial dynamics shown here reflect behavioural rather than abundance changes (unless asymmetrical range changes exist for various species that, in turn, influence community structure, which is possible but beyond the scope of the present analyses). Other studies have shown that cod and other species will modify their ranges under changing environmental conditions, independent of abundance (e.g. deYoung & Rose 1993, Nye et al. 2009). Another factor

which could influence community dynamics is age structure of long-lived species (here only cod). This factor is unlikely to have been important in our study as the age structures of Gulf cod populations did not change substantially between the 2 periods (DFO 2009, 2010a). What this and other studies demonstrate is that cod and snow crab can strongly influence at least some aspects of community dynamics when environmental conditions are favourable to them, but during unfavourable times their influence likely recedes.

Limitations

Given our approach and the data used within our analysis, we recognize that our findings are limited in several ways. The Gulf of St. Lawrence is a complex ecosystem with hundreds of species (Frank et al. 2006, Benoît & Swain 2008), and our study addresses questions of community composition with reference to only 3 (plus capelin poorly sampled and only used as a predictor of presence/absence). These 4 species, however, do represent some of the most ecologically important components of food web interactions and are also vital to the economic viability of the Gulf region (Worm & Myers 2003, DFO 2005). As no better data were available for the study, we believe that the interactions among these species can act as an index for wider community change within the gulf ecosystem. Another limitation of the data is that crab catch weight can be problematic as an index of abundance with the DFO bottom trawl surveys, because the gear used is biased towards catching larger individuals (generally large males). Thus, it should be noted that the crab abundance provides a sex-specific index of relative and not absolute abundance. In any event, the MRT methodology demonstrated here can accommodate additional and better data as they become available. Other important factors not considered in our study include changes in habitat quality (e.g. Nilsson & Rosenberg 2003), potential food resources (e.g. Savenkoff et al. 2006) and fisheries activities (e.g. Scheffer et al. 2005). We believe that the present work should be viewed as a demonstration of how community structures resulting from the dynamics of these factors can be linked among themselves and to environmental variation, and as a first step towards a more comprehensive community-based model.

Management applications

Notwithstanding the limitations of the present analyses, the approach itself and its findings could be applied to fisheries management and conservation.

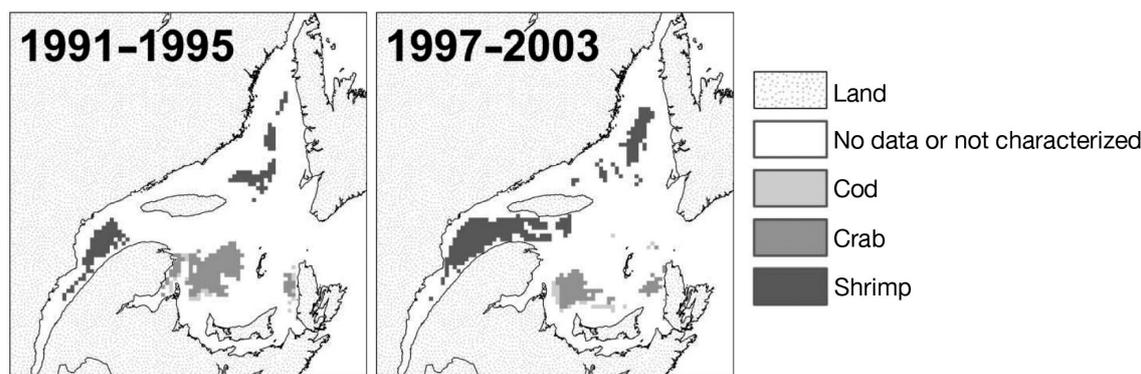


Fig. 7. Combined multivariate regression tree predictions for the 1991–1995 and 1997–2003 periods. These maps show areas that are consistently characterized by a given species during each period (i.e. a species that has a significantly high abundance and frequency) at a 100 km² resolution

Predictive outputs from the MRT analysis could allow fisheries managers to distribute fishing effort (or at least to know where effort is being exerted with respect to community distributions) for both economic and ecological viability of the stocks (Beare et al. 2005). With the understanding that community dynamics differ between cold and warm periods, the yearly MRT predictions could be combined to produce a 'mode' community prediction for each period (Fig. 7). What emerges from this is an overall, spatially explicit assessment of community composition. In the present case, regions within the Gulf of St. Lawrence that are characterized by all 3 focal species (other species could be included if data were available) exhibited slightly different spatial arrangements when comparing the cooler, early 1990s with the warmer, late 1990s/early 2000s.

As a final note, future predictions for the Gulf of St. Lawrence and the North Atlantic are that it will be subject to warmer conditions within the next century (IPCC 2007). The present study has shown that there is a strong link between temperature and community dynamics in the Gulf; hence, temperature changes will expose species to novel conditions, and this could lead to local extirpations, alterations of migration patterns and/or dispersal from traditional sites, which, in turn, could disrupt spatio-temporal community composition patterns. In particular, our study emphasizes the importance of the link between environmental conditions (temperature and salinity) and the influences of specific species (here crab and cod) on community dynamics across broad spatial and temporal scales. Attempts to implement an ecosystem approach to management in fisheries ecosystems should consider the interactions of these environmental and single species effects on marine communities. MRT provides a relatively straightforward method to do that.

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