Atlantic cod (*Gadus morhua*) distribution response to environmental variability in the northern Gulf of St. Lawrence

Jonathan L.W. Ruppert, Marie-Josée Fortin, George A. Rose, and Rodolphe Devillers

Abstract: Atlantic cod (*Gadus morhua*) distribution patterns and the behavioral (site fidelity), biotic (prey and predators), and environmental factors that determine them are fundamental to cod's historic importance as a commercial species in the North Atlantic. Using classification and regression tree analysis (CART), we compared two periods (1991–1995 and 1998–2004) with contrasting bottom temperature and salinity regimes to determine regional factors that best explained cod distribution and catch weight per tow from summer surveys in the northern Gulf of St. Lawrence (the feeding period of cod). The classification tree analysis indicated that the presence or absence of cod was chiefly determined by depth in both of these periods. In contrast, the regression tree analysis determined that cod catch weight distributions were explained by different variables in each period. In the colder period (1991–1995), the distribution of catch weights was explained well by environmental variables (bottom temperature, salinity, depth); however, in the warmer period (1998–2004), distributions were best explained by variables from the previous year. These results indicate that the spatiotemporal dynamics of environmental conditions are likely to influence the loyalty of cod to specific feeding grounds and imply that cod responses to the environment could be susceptible to long-term environmental (e.g., bottom–habitat) and climate change.

Résumé : Les patrons de répartition géographique des morues franches (*Gadus morhua*) de l'Atlantique et les facteurs comportementaux (fidélité au site), biotiques (proies et prédateurs) et environnementaux qui les déterminent sont des éléments essentiels pour comprendre l'importance historique de la morue comme espèce d'intérêt commercial dans l'Atlantique nord. Une analyse des arbres de classification et de régression (CART) a servi à comparer deux périodes (1991–1995 et 1998–2004) qui diffèrent par leur température au fond et par leur régime de salinité, afin d'identifier les facteurs régionaux qui expliquent le mieux la répartition des morues et la masse de la capture par passage de l'engin de pêche dans les inventaires d'été dans le nord du golfe du Saint-Laurent (la période d'alimentation de la morue). L'analyse des arbres de classification indique que la présence ou absence des morues est déterminée principalement par la profondeur durant les deux périodes. En revanche, l'analyse des arbres de régression détermine que la répartition des masses de capture des morues s'explique par des variables différentes dans chacune des périodes. Dans la période plus fraîche (1991–1995), la répartition des masses des captures s'explique bien par les variables du milieu (température au fond, salinité, profondeur), alors que, durant la période plus chaude (1998–2004), les répartitions s'expliquent mieux par celles de l'année précédente. Ces résultats indiquent que la dynamique spatiotemporelle des conditions du milieu influence vraisemblablement la fidélité des morues à des sites d'alimentation spécifiques et laissent croire que les réactions des morues à l'environnement pourraient être affectées par des changements à long terme du milieu (par ex., fond–habitat) et du climat.

[Traduit par la Rédaction]

Introduction

Predictions of distribution changes in any species under rapidly evolving environmental conditions require that patterns of change be quantified and linked to underlying ecological processes (Lekve et al. 2002). Hence, distribution change related to habitat changes must be interpreted relative to both ongoing physical and biological variability, and long-term environmental change (e.g., climate change). In marine fisheries ecosystems, making predictions is challenging because short-term spatiotemporal dynamics of species responses to environmental conditions are confounded with longer-term climate change, and species selection pressures

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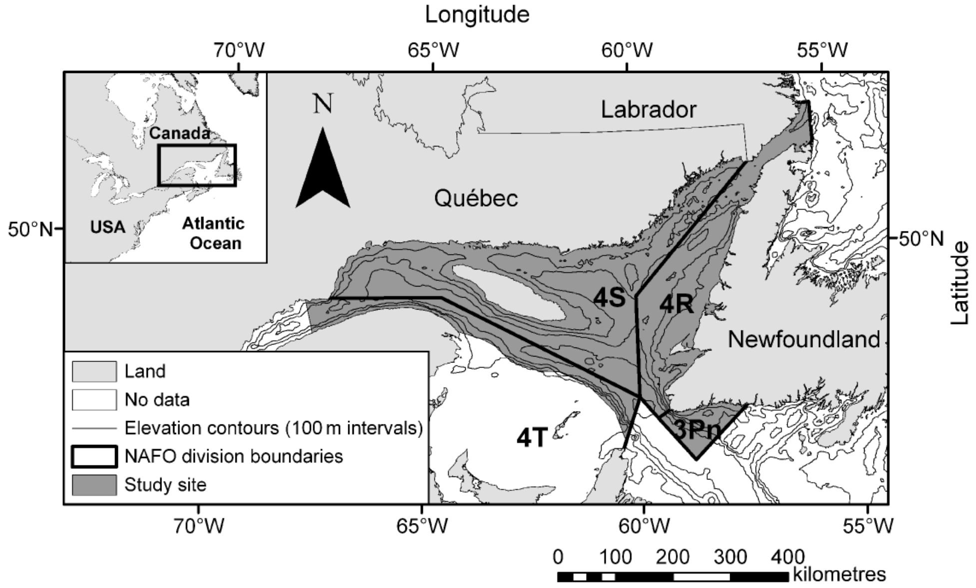
Fig. 1. The study area in the northern Gulf of St. Lawrence, which includes NAFO management units 4SR, 3Pn, and a small portion of 4T.



are likely influenced by population size (Robichaud and Rose 2004; Drinkwater 2005; Hutchings and Rowe 2008).

Many Atlantic cod (*Gadus morhua*) stocks in the northwestern Atlantic have experienced extreme population declines due to overexploitation and environmentally induced changes in productivity (Dutil et al. 1999). In the northern Gulf of St. Lawrence, overexploitation was likely the chief factor contributing to the decline of cod (Rothschild 2007), but during the very cold years of the early 1990s, low recruitment and increases in adult mortality likely played a role, although these conditions have largely abated over the past decade (Dutil et al. 1999; Dutil and Lambert 2000). Despite recent evidence of more favourable environmental conditions for cod and apparent increases in some prey species such as snow crab (*Chionoecetes opilio*) and shrimp (*Pandalus* spp.) — there is no reliable data on the key prey species capelin (*Mallotus villosus*) — it remains unclear why this stock has not rebounded more rapidly towards historic population distributions and numbers. One reason may be that most studies of cod distribution have considered only one or two factors at a time, with other conditions assumed to be homogeneous within the environment (Johnson and Gillingham 2005). Atlantic cod respond to many environmental factors that influence their distribution including temperature, salinity, currents, depth, latitude, ice coverage, time of year, and distribution of prey (Rose and Leggett 1988; Frechet 1990; Sherwood et al. 2007). Thus, an analytical approach that includes as many pertinent abiotic and biotic factors as possible is better suited to explain and predict the distribution and abundance of cod over space and time.

The purpose of this study is to quantify patterns of cod summer distribution and catch weight per tow with respect to abiotic and biotic environmental conditions within the northern Gulf of St. Lawrence during two periods with contrasting conditions: a cold period of rapid population decline (1991–1995) and a warm period of moderate population rebuilding (1996 – early 2000s) (Drinkwater and Gilbert 2004; Fisheries and Oceans Canada (DFO) 2008). Cod distribution is characterized by site fidelity to spawning grounds (e.g., Robichaud and Rose 2001) and to feeding areas (e.g., Wright et al. 2006), but few tests of such loyalty have been made over decadal variations in environmental conditions. We propose a null hypothesis that despite differences in environmental conditions between the periods, site fidelity in cod (stability in occupied regions) does not change, because abiotic conditions across both periods in the northern Gulf were within their preferred optimal range (temperatures of 3–7 °C and salinities of 30–35.5 psu; see Hedger et al. 2004). Classification and regression tree analyses (CART) were employed (Breiman et al. 1984) to determine relationships between cod distribution and environmental variation over space and time .

Materials and methods

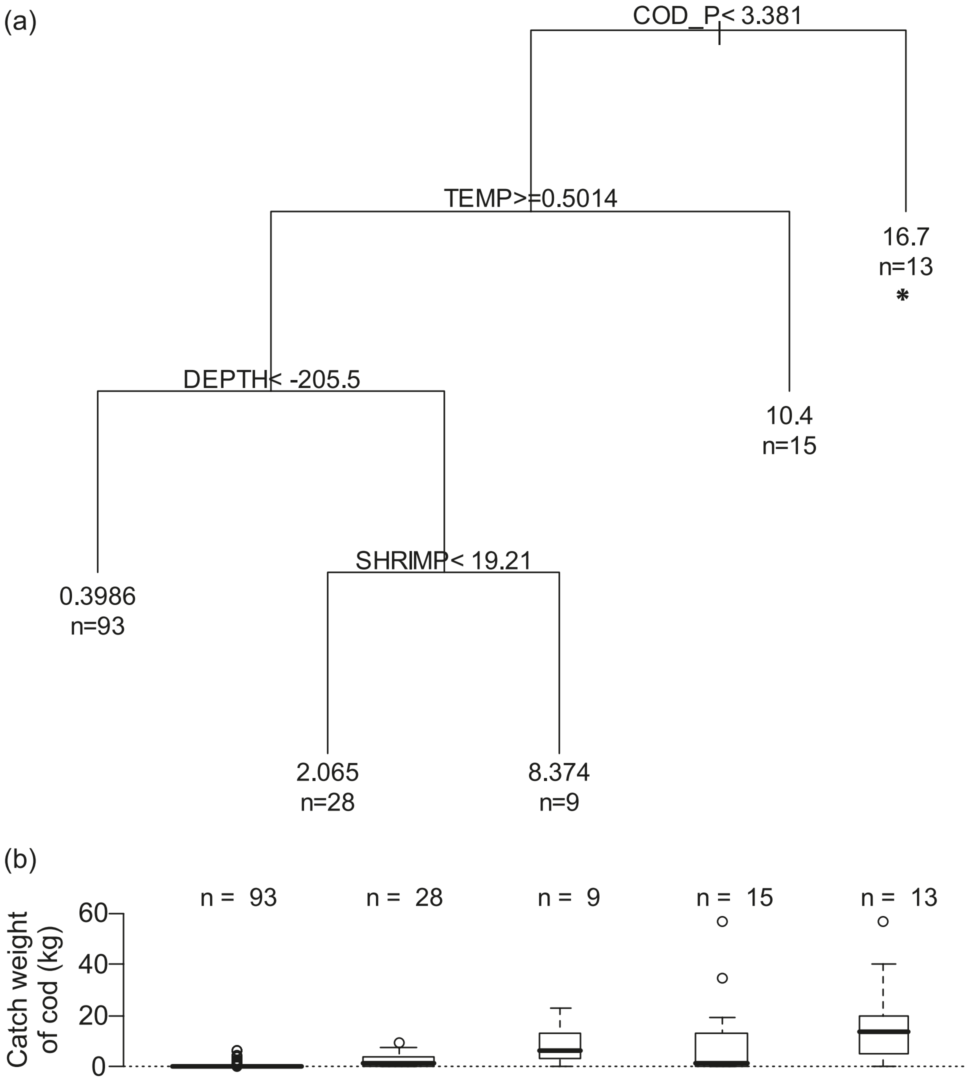
Study area

The northern Gulf of St. Lawrence is a semi-enclosed sea (area of 130 000 km^2) located in eastern Canada between the Canadian provinces of Newfoundland and Labrador and Québec (this includes Northwest Atlantic Fisheries Organization (NAFO) fisheries management zones 4SR and 3Pn; Fig. 1). The area used within this study includes NAFO divisions 4RS, 3Pn, and a small portion of 4T. The Gulf ranges in depth to about 500 m, with complex bathymetry dominated by relatively shallow coastal shelves but deep trenches bisecting both the eastern and northern extensions. It is also characterized by strong interannual variability of water and ice properties (Smith et al. 2006).

Data

Cod abundance data were obtained from annual DFO Québec bottom trawl scientific surveys (BTS). The BTS follow a random depth-stratified design and are conducted during August and early September each year (Doubleday 1981; Gagnon 1991). BTS for years 1991–1995 and 1998–2004 were included in this study and standardized to 15-min tow lengths. The 1991–1995 and 1998–2003 surveys were conducted by CCGS *Alfred Needler* using URI shrimp

Fig. 2. (*a*) The 1994 regression tree for the bottom trawl survey predicting the average Atlantic cod (*Gadus morhua*) catch weight (kg) per tow. The leaves of the tree indicate the average catch weight per tow of cod given the conditions stipulated by the splits. Here COD_P and SHRIMP are species' catch weights (kg) per tow, TEMP is the bottom temperature (°C), and DEPTH is the bathymetric depth of the survey location (m). "_P" indicates that the parameter used pertains to the previous year's value. Further, the number of observations associated with each of the leaves is denoted by "n". (*b*) Box plots show the catch weights per tow of the samples associated with each of the groupings at a given leaf. The number "n" on the tree corresponds to the number "n" on the box plot. (*The highest average catch weight per tow of cod is 16.7 kg and this is found in areas with ≥3.381 kg of cod catch weight in the previous year.)



trawls, and the 2004 survey was conducted by the CCGS *Teleost* using a Campelen 1800 shrimp trawl. Differences in catch efficiency between the vessels have been corrected for by DFO Québec. Despite accounting for this, catch weight predictions using CART should still be interpreted as qualitative (i.e., CART predictions reflect relative and not absolute cod catch weight) because predictions are averages of catch weights. Finally, the gap in the analysis (1996 and 1997) is a result of the absence of temperature and salinity measurements in the 1996 survey (because the previous year's measurements are used within the models).

BTS data sets included information about the location (latitude, longitude, and depth), cod catch weight per tow, bottom temperature, bottom salinity, and date of cod capture (here as day of the year). Depth, slope, and orientation were derived from the 1-min world bathymetric grid from the General Bathymetric Chart of the Oceans (GEBCO 2003). Prey species, including snow crab (*Chionoecetes opilio*), capelin (*Mallotus villosus*), and northern shrimp (mainly *Pandalus borealis*), were also recorded in the BTS. These three species represent a large component of the cod diet within the northern Gulf of St. Lawrence (Savenkoff et al. 2006). We also used Fisheries Observer Program (FOP) data from DFO Québec, which are recorded by independent DFO-accredited technicians who document catches on board commercial vessels. The FOP tracks catches, mostly in NAFO 4S region, on participating commercial vessels throughout the entire year (i.e., from several months of the year with varying proportions of sampling effort in the summer or winter seasons depending on the year; DFO 2007). The FOP records were used as a proxy for fishing effort within the Gulf. Finally, the previous year's values,

Table 1. The number of samples (n) and total catch weight (kg) of cod per year for the bottom trawl survey (BTS) records.

Year	Sample size (n)	Total catch weight (kg)
1991	205	2534
1992	220	1325
1993	203	279
1994	158	543
1995	152	385
1998	199	1630
1999	220	939
2000	208	1572
2001	209	790
2002	172	468
2003	147	1567
2004	113	6360

which change from year to year at a given location (e.g., temperature), were included in the analysis to predict the current year's cod presence or absence and catch weight per tow. The previous year's conditions were derived from interpolated BTS catch and environmental records (this includes records from the 1990–1994 and 1997–2003 BTS surveys) using universal kriging methods (Cressie 1993).

Statistical analysis

To determine the degree of the relationship between the environmental variables, Spearman correlation coefficients were computed and tested for significance. Further, to test for differences between the periods of 1991–1995 and 1998–2004 on the annual average bottom temperature and bottom salinity, Wilcoxon–Mann–Whitney tests were conducted. Both Spearmen correlation analysis and Wilcoxon–Mann–Whitney tests were chosen because they are robust methods for data that are not normally distributed (Rosner 2000).

The relationship between the environmental variables and cod is investigated using CART: classification tree analysis with cod presence or absence data and regression tree analysis with cod catch weights. CART analysis divides (or splits) a set of samples via recursive partitioning into mutually exclusive groupings in which a variable and an associated threshold of the selected variable are chosen to form subsets that become increasingly homogeneous (Kent 2006; e.g., Fig. 2). The resulting grouping is illustrated using a tree structure, which is a nonlinear format and allows for interactions between environmental variables. An important characteristic of CART analysis used with spatial data is that the procedure is able to identify explanatory variables that operate at broader spatial scales within the first couple of splits of a tree and variables used in subsequent splits of the tree that operate at finer spatial scales (Moore et al. 1991). This characteristic of CART analysis results from the declining number of observations associated with each split. Through the process of growing a tree, all samples start at the root (or the top of the tree) and the first couple of splits in a tree have more observations than subsequent splits. This means that the first couple of splits explain more variation than subsequent splits that are formed. CART analysis also originally creates an oversized tree, and a method is needed to discern the most parsimonious result (i.e., the size of the tree with the lowest prediction error). Cross-validation can be used as a means of getting a measure of prediction error for a given tree size and can accurately determine prediction error with smaller data sets (n < 1000) (De'Ath 2007). Using the results of cross-validation, the one-standard-deviation rule can then be employed (Maindonald and Braun 2007) to determine the most suitable model (see Supplementary material)[2]. Still, a possible weakness with this approach results from the number of samples and cod catch weights being highly variable through the years, which could influence the ability of CART analysis to model the data (Table 1, in particular 1991). Despite this, the cross-validation analysis showed consistent results for model prediction errors, indicating that sample size and variability in catch weights are not a major problem within this analysis (Supplemental Table S1)[2]. The CART analysis was run for each year analyzed in this study using RPART in R Software for Statistical Computing (Therneau and Atkinson 1997).

Results

As expected, for all of the years analyzed, Spearmen correlations between depth, bottom salinity, and bottom temperature were significant (p < 0.001; Fig. 3). A significant correlation, with a coefficient greater than 0.8 or less than –0.8, was viewed as indicating high collinearity between these variables. All relationships demonstrated a large degree of collinearity by either meeting or coming consistently close to the ±0.8 benchmark. Mean bottom temperatures over the 1991–1995 period were significantly colder than during the 1998–2004 period (W = 5, df = 10, p = 0.030; Fig. 4) and the 1991–1995 period had significantly lower mean bottom salinity than the 1998–2004 period (W = 3.5, df = 10, p = 0.011; Fig. 4).

Classification tree analysis for the BTS data showed that depth was the most prevalent parameter used in the models across all years and was consistently selected within the first split of trees, suggesting that depth chiefly describes broad-scale patterns of the presence or absence of cod (Table 2). In 1992 and 1995, salinity was attributed to the first split of the tree, but as aforementioned, salinity is highly correlated with depth. In general, the pattern that emerges across all years is that depths that were on average greater than 223 m had few cod during the survey period (Fig. 5). Patterns within subsequent splits of the classification trees showed inconclusive results for fine-scale variation of cod presence or absence.

Regression tree analysis for the BTS data showed that the previous year's cod catch weight was the most prevalent parameter within the first two splits of the models considered across all years (Table 3). Despite being the most prevalent parameter, the previous year's cod catch weight was not

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[2] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3943. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html.

Fig. 3. Spearman correlation coefficient values showing the degree of association between the environmental conditions bottom salinity (*S*), bottom temperature (*T*), and depth (*D*) within the study area. The association between *S* and *T*, *D* and *T*, and *D* and *S* are indicated by solid triangles, shaded circles, and solid squares, respectively. These values are all significant ($p < 0.001$) correlation coefficient values.

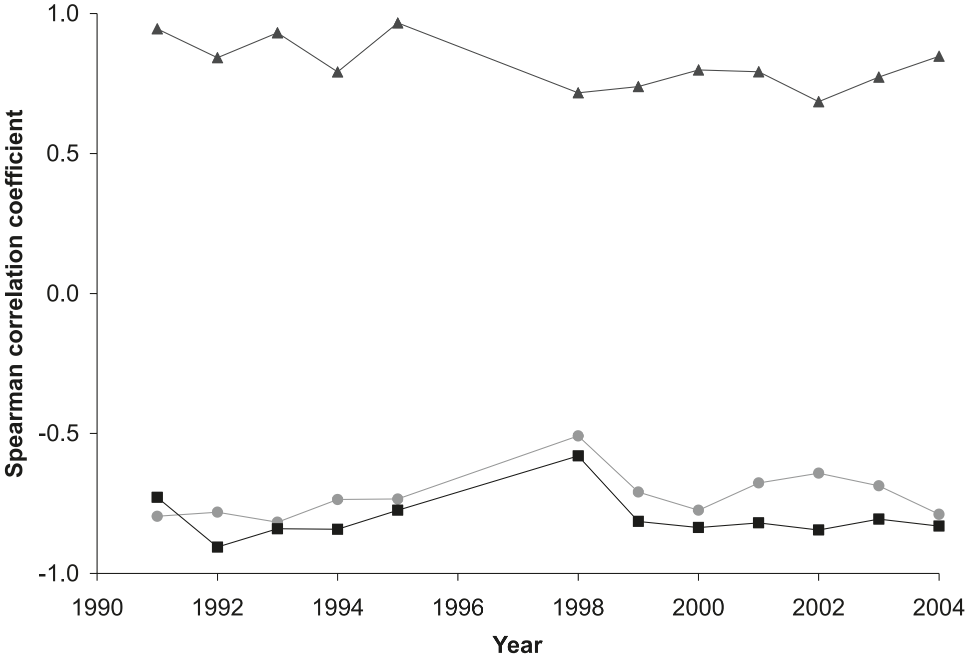
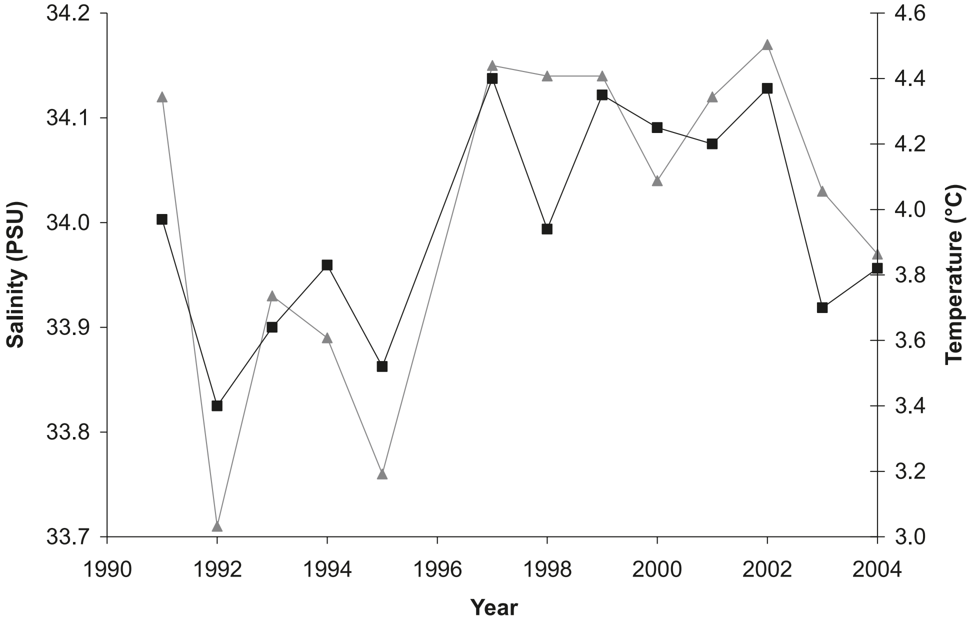


Fig. 4. Average bottom temperature (°C; solid squares) and average bottom salinity (psu; shaded triangles) from summer season measurements on bottom trawl surveys within the study area.



used as a variable at any split level in models for the very cold years of 1991, 1992, and 1993, making the previous year's cod catch weight less important during the early 1990s compared with the later period. Instead, the most prevalent parameters in the early 1990s were depth, bottom salinity, and bottom temperature, which accounted for almost all of the variation. Furthermore, across all years, these parameters are just as prevalent as the previous year's cod catch weight in the models (Table 3). Looking at the subsequent splits in trees, patterns of variable selection were more elusive, suggesting that variables that operate at smaller scales were not revealed in this analysis. Overall, the predictions of the regression tree models for scientific surveys show a predominance of previous year's cod catch weight, bottom salinity, bottom temperature, and depth within the first two splits of all years analyzed (Fig. 5). Distribution changes over time were also apparent. Of particular note was that in the most recent years (2003 and 2004), higher concentrations of cod were predicted to occur in the coastal area off western Newfoundland than in any of the earlier years.

Table 2. The thresholds and variables used in classification tree splits for the bottom trawl surveys of Atlantic cod (*Gadus morhua*) distribution (presence or absence).

Year	1st Split	2nd Split	3rd Split	4th Split
1991	DEP ≥ –222.5			
1992	SAL < 33.9			
1993	DEP ≥ –206.5			
1994	DEP ≥ –205.5			
1995	SAL_P ≥ 33.7, SAL_P < 33.7	TEM < 3.4, DAY < 241.5	SAL ≥ 33.5, TEM_P ≥ 2.0	
1998	DEP ≥ –235	DAY ≥227.5, DAY < 227.5	CAP < 0.03, ASP ≥ 129.9	CRA ≥0.4
1999	DEP ≥ –227	COD_P ≥ 1.4		
2000	DEP < –227.5, DEP ≥ –227.5	DEP ≥ –264		
2001	DEP ≥ –233.5	DAY < 223.5		
2002	DEP ≥ –222			
2003	DEP ≥ –225.5	SHR_P < 28.7		
2004	DEP ≥ –225			

Note: The splits are ranked 1st, 2nd, etc., based on order of occurrence in the tree. The presence of cod occurs when the condition stipulated at the split is satisfied. CAP, capelin (kg); CRA, crab (kg); COD, cod (kg); SHR, shrimp (kg); DEP, depth (m); TEM, temperature (°C); SAL, salinity (psu); DAY, day of the year (days); ASP, aspect (°); SLO, slope (°); OBS, observer trawl frequency.

Discussion

Classification analyses of BTS records indicated that the presence or absence of cod within the summer range was largely a function of depth and that the threshold of depth used to determine the presence or absence of cod showed no significant trend from year to year. The classification analyses showed a consistent response of cod to depth, despite the 1991–1995 period showing conditions of significantly lower average bottom temperatures and salinities within the northern Gulf of St. Lawrence. These environmental conditions coincided with higher ice area coverage within the Gulf of St. Lawrence and a lower cod biomass (Drinkwater 2004; DFO 2008). The regression tree analysis of the BTS records for the 1991–1995 data showed that bottom temperature, bottom salinity, and depth were the main conditions that best described broad-scale patterns of cod catch weights within their summer range. These three variables were also found to be highly collinear, and thus it should be noted that these variables could be considered together when predicting patterns within the northern Gulf of St. Lawrence. The selection of variables differed for the BTS regression tree analyses in the 1998–2004 period, wherein the previous year's cod catch weight explained broad-scale patterns of cod catch weight in the majority of the models. The 1998–2004 period also showed significantly higher bottom salinities and temperatures that coincided with below-average ice area coverage and a slightly increased cod biomass (Drinkwater 2004; DFO 2008). Thus, these results show a shift in the response of cod in the northern Gulf of St. Lawrence that is associated with the environmental conditions of the period. Overall, the results from all analyses are consistent with the understanding that cod presence or absence and abundance in the northern Gulf is related to several abiotic and biotic conditions, including temperature, salinity, currents, depth, latitude, ice coverage, time of year, and distribution of prey (e.g., Rose and Leggett 1988; Fréchet 1990; Sherwood et al. 2007).

The differences between the regression and classification analyses are thought to reflect differing influences of abiotic and biotic factors on distribution assessed by either spatially explicit survey catch weights or presence or absence. According to our analyses, cod catch weights were influenced strongly by both abiotic and biotic conditions that varied from year to year and between cold and warm periods. It is important that during the warm period, when conditions may be more favourable to cod than in the cold period, distribution largely reflected the previous year's catch weight, suggesting that when conditions are good, cod will return to the same summer feeding grounds year after year. Such site fidelity has been shown in cod for spawning areas (e.g., DFO 2005; Robichaud and Rose 2006; Windle and Rose 2007) and also for feeding areas, as in the present study (e.g., DFO 2005; Wright et al. 2006). When environmental conditions were less favourable, however, distribution patterns were not related to those of the previous year but to abiotic factors of the environment, in particular temperature, salinity, and depth. Hence, cod shifted their distribution as environmental conditions changed and may be expected to do so under climate change (e.g., Rose 2005). Such responses are consistent with reports of distribution shifts in feeding habitat distribution in the adjacent "northern" cod stock on the northeastern Newfoundland and Labrador shelf (deYoung and Rose 1993) and also in the Barents Sea (Loeng 1989), off Iceland (Vilhjálmsson 1997), and in the North Sea (Hedger et al. 2004). Our results confirm that distribution shifts of cod in the northern Gulf are similar to those in other regions and stress that changes to temperature and (or) salinity are likely to impact distributional responses of Atlantic cod within these and other boreal marine ecosystems.

It is of particular importance to management that distribution changes noted in our models, particularly for 2003 and 2004, lead to higher concentrations of fish in the nearshore waters along the western coast of Newfoundland. Such distribution changes may help to explain the divergent views of fishermen and stock assessments on the abundance of fish in the stock, as fishermen have encountered increasing numbers of fish in the coastal region, but this may not reflect equivalent increases in stock-wide abundance (Rose 2007). Stock assessments for the region indicate that the stock is recovering slowly, but the large abundance of cod encountered by fishermen along the stock range has triggered a degree of optimism, allowing for larger increases in quotas for

Fig. 5. The average catch weight (kg) per tow of Atlantic cod (*Gadus morhua*) as combined regression tree (average catch weight per tow) and classification tree (presence or absence) model predictions using the scientific survey data from the years 1991–1995 and 1998–2004. These maps show the average catch weight (kg) per tow of cod at a 100 km^2 resolution given the measured summer season environmental conditions. Areas outside of the study extent or missing data are indicated by white on the maps.

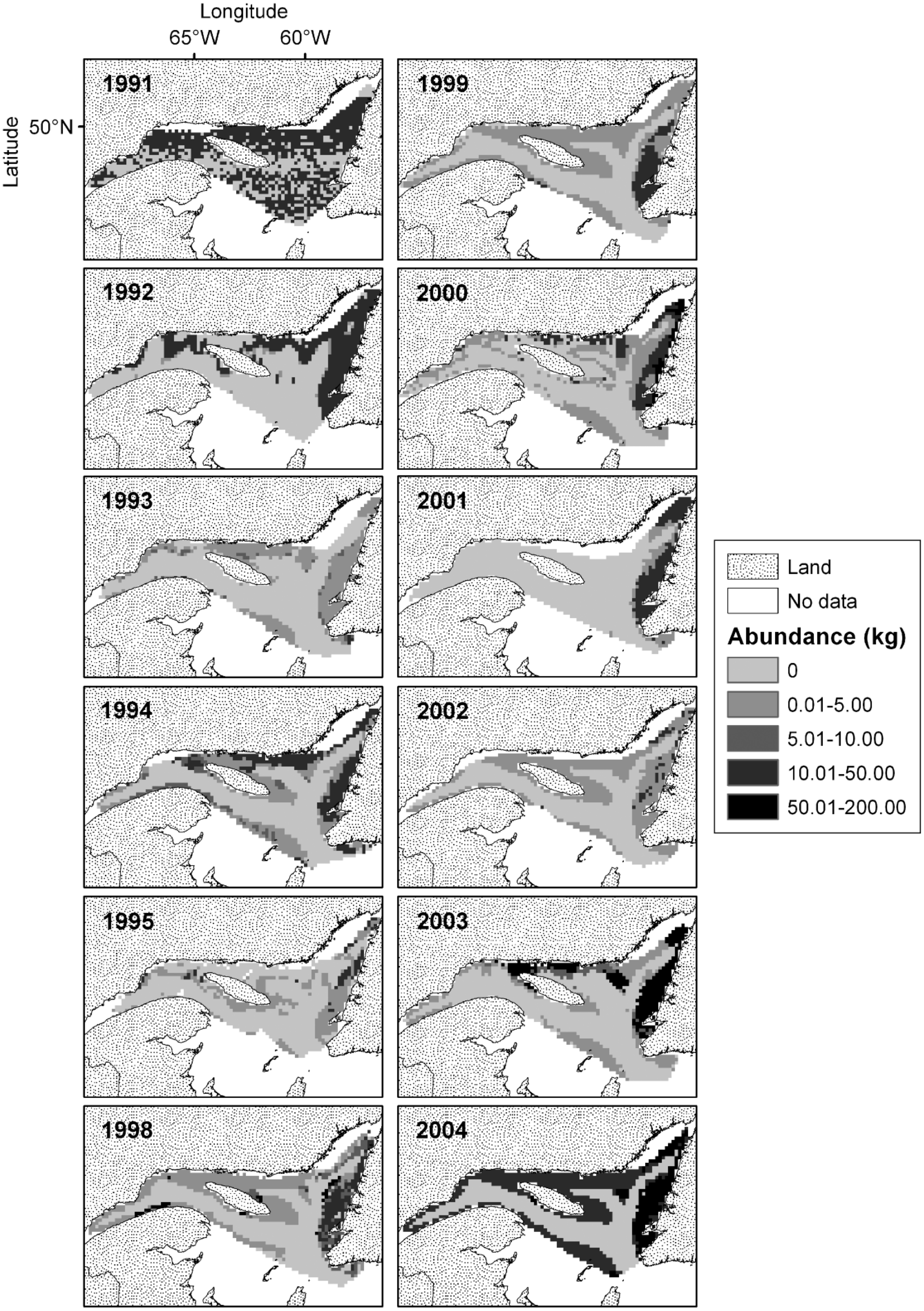


Table 3. The thresholds and variables used in regression tree splits for bottom trawl surveys of Atlantic cod (*Gadus morhua*) catch weight (kg) per tow.

Year	1st Split	2nd Split	3rd Split	4th Split
1991	CAP_P ≥ 6.4	DEP ≥ –217		
1992	SAL < 31.7	SAL < 33.8		
1993	TEM_P ≥ 5.3	DEP ≥ –195.5	DEP < –173	
1994	COD_P ≥ 3.4	TEM < 0.5	DEP ≥ –205.5, SHR ≥ 19.2	
1995	COD_P ≥ 14.5			
1998	SHR_P ≥ 111.4	COD_P ≥ 3.8	ASP ≥ 262.6	CAP_P ≥ 0.1
1999	TEM < 3.8	SHR < 0.2	DAY < 224.5	SLO ≥ 0.4
2000	COD_P ≥ 21.9	TEM < 3.1		
2001	ASP ≥ 279.2	SHR < 3.0, SLO ≥ 0.6	SAL < 33.8, SHR < 6.9	
2002	COD_P ≥ 25.4			
2003	COD_P ≥ 6.6	SAL < 33.6	COD_P ≥ 1.7	
2004	COD_P ≥ 7.5			

Note: The splits are ranked 1st, 2nd, etc., based on order of occurrence in the tree. If the condition stipulated at the split is satisfied, then a larger cod catch weight per tow would be expected by the model. See key for variables and units in Table 2 caption.

the fishery (from 5500 tonnes in 2006 to 7000 tonnes in 2007; Rose 2007). If quotas are increased when the stock is performing poorly, there is an increased risk of slowing or limiting stock rebuilding (Shelton et al. 2006). Other processes not revealed within this study, especially at smaller spatial scales, are likely to influence cod distributions. Given the coarseness of scale of our environmental variables, the CART analyses provide a similarly coarse overview of stock-wide dynamics. Nonetheless, the CART models indicate that within the northern Gulf of St. Lawrence, the distribution of the cod stock has been dynamic and that observed increases have not been uniform over the full range of the stock.

Finally, this study demonstrates a means to effectively model species responses to their environment, which is becoming increasingly more important in fisheries science. Classification and regression tree analyses both have several strengths for analyzing fisheries data to attain robust predictions. Perhaps most importantly is that CART analysis has no a priori assumption of structure in the data, which means that it does not have any assumptions regarding the form of relationships between species and their environment (De'Ath 2002). With fisheries data, which are inherently right-skewed because of a majority of samples with small catch weights and zero inflation, transformations are not required when using CART analysis. This reduces the chance of introducing artifacts into the analysis. Standard transformations of data in this study also did not meet normality assumptions in data structure required for generalized linear models (GLM). Further, due to zero inflation present in the data, generalized additive models (GAM) were not appropriate. CART models can also handle a large number of variables and can parse out variables that contribute the most to observed patterns of species. This means that CART can give a parsimonious assessment of species–environment relationships by considering all potentially important relationships with variables entered into the model. Comparisons of CART with other methods, including GLMs and GAMs, have also suggested that CART was superior by having lower prediction errors (Franklin 1998; Vayssières et al. 2000). Thus, given its assumptions and low prediction error, CART analysis can be a robust option for modeling species–environment relationships in fisheries science.

In conclusion, this study has demonstrated the importance of both abiotic conditions and site fidelity in broad-scale spatiotemporal patterns of cod abundance. Most importantly, the response of cod at broad scales seems to be driven by two very different climatic circumstances within the northern Gulf of St. Lawrence. In the cold period of the 1990s, cod distribution and abundance were largely determined by abiotic factors, but during the more favourable warmer period that followed, site fidelity became the most important factor in explaining year-to-year distribution. Such distributional shifts as shown by this study are important to future management decisions and imply that long-term environmental changes such as those brought about by climate change are likely to influence distribution patterns of cod in boreal ecosystems.

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