



Spatio-temporal variations in invertebrate–cod–environment relationships on the Newfoundland–Labrador Shelf, 1995–2009

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ABSTRACT: We examined spatial and temporal relationships between snow crab *Chionoectes opilio*, shrimp *Pandalus* spp., Atlantic cod *Gadus morhua* and the environment (depth, temperature and salinity) on the Newfoundland–Labrador Shelf from 1995 to 2009 using autumn multi-species trawl survey data. First, the core habitat of snow crab and shrimp was determined based on cumulative distribution functions of species abundance over depth and bottom temperature. On average, this method predicted the presence of crab and shrimp at 95 and 99% of trawl locations, respectively, and indicated 90% of crab and shrimp inhabited temperature ranges of –1 to 4 and 0 to 4°C and depths of 100 to 500 and 150 to 450 m, respectively. Then geographically weighted regressions, based on trawl stations where species presence was predicted, indicated spatial non-stationarity between invertebrates and explanatory variables at scales <200 km. Snow crab abundance was best predicted by environmental variables, suggesting bottom-up influences are important, whereas shrimp abundance was influenced by both the environment and cod (predator) abundance. We discuss how averaged ecological relationships within large marine ecosystems central to fisheries management mask processes operating at smaller scales, with reference to the northern cod ecosystem under present conditions of warming waters and increasing cod.

KEY WORDS: Spatial ecology · *Gadus morhua* · *Chionoectes opilio* · *Pandalus borealis* · Northwest Atlantic · Geographically weighted regression · Species interactions

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INTRODUCTION

The need for accurate distribution models of commercial marine species is universal (Planque et al. 2011) and increasingly important under global fishing pressures (Worm et al. 2009) and changing climates (Brander 2007, Halliday & Pinhorn 2009, Lenoir et al. 2011). In the Northwest Atlantic region, marine ecosystems have undergone dramatic changes

in recent decades with concurrent large-scale shifts in the abundance and distribution of many species. Following years of sustained overfishing, high mortality, and a period of unusually cold ocean temperatures, the historically important and widely distributed northern cod *Gadus morhua* stock off southern Labrador and eastern Newfoundland, Canada, declined severely in the early 1990s to the point of commercial collapse (Drinkwater 2002, Lilly 2008). This

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decline coincided with a contraction and southward shift in the distribution of the cod stock (deYoung & Rose 1993, Atkinson et al. 1997, Rose et al. 2000) and was mirrored by declines and distributional shifts in several non-commercially exploited species (e.g. capelin *Mallotus villosus*) on the Newfoundland–Labrador Shelf (Gomes et al. 1995, Carscadden et al. 2001). A moratorium on directed cod fishing over most of the range has been in place since July 2, 1992.

The decline of the northern cod stock coincided roughly with a large increase in the abundance of snow crab *Chionoecetes opilio* and northern shrimp *Pandalus borealis* (Lilly 2000), which have comprised the most important fisheries in this region since the mid-1990s. These invertebrate species are favoured by cold ocean regimes (Parsons & Colbourne 2000, Dawe et al. 2008), where their geographic distributions are hypothesized to be largely determined by bottom-up influences requiring colder temperatures (Foyle et al. 1989) and specific habitat requirements for different life stages (Tremblay 1997, Dionne et al. 2003). Additionally, both shrimp and snow crab are prey for cod (Bailey 1982, Lilly 1984, Parsons 2005, Chabot et al. 2008), and top-down predatory control may also influence the distribution and abundance of these species. These population dynamics combined with climate fluctuations have fuelled discussion regarding the relative importance of predation and environmental factors on the abundance and distribution of invertebrates in this region (Worm & Myers 2003, Frank et al. 2006).

A region-wide spatial scale has typically been used to study trends between crustacean–predator and crustacean–environment relationships off Newfoundland–Labrador (Lilly 2000, Worm & Myers 2003, Frank et al. 2006, Boudreau et al. 2011), and, while this approach may elucidate important correlations between factors, it may also mask significant geographic variation (i.e. spatial non-stationarity) in the relationships under study (Windle et al. 2010). Spatial stationarity implies that the parameters of a process (e.g. variance and mean) are independent of location or direction, and is an important assumption for spatial statistics calculated over large regions (Fortin & Dale 2005). Observed spatial patterns of individual marine species and assemblages are the outcome of multiple environmental (exogenous) and biological (endogenous) processes that may operate on different spatial and temporal scales (Planque et al. 2011). The choice of scale is important in ecology, as different spatial patterns and relationships may result from varying the spatial extent and resolution of the ana-

lysis (Wiens 1989, Fortin & Dale 2005, Ciannelli et al. 2008). Spatial variation of species–environment interactions within a management area could have important implications for building reliable predictive models as well as for understanding the role of various factors thought to be associated with invertebrate abundance and distribution on a local scale.

Geographically weighted regression (GWR) is a relatively new statistical technique for investigating spatially varying relationships (Fotheringham et al. 2002). GWR differs from other spatial analysis methods such as autoregressive models and regression kriging because it allows model coefficients to vary with location (Fortin et al. 2012). A local regression is performed at each observation point by applying a spatial kernel that gives more weight to nearby observations than to those farther away, and a set of local coefficients and model performance statistics is subsequently generated for each sampling location. Significant variation in the GWR parameter estimates can be indicative of spatial non-stationarity and used to sub-divide a study area for further analysis (Fotheringham et al. 2002). GWR can also be used to explore the scale dependency of ecological interactions by systematically varying the bandwidth size of the spatial kernel at each observation. This technique has been applied to determine the scale at which a species–environment relationship becomes stationary (Osborne et al. 2007, Windle et al. 2010, Miller & Hanham 2011, Gao et al. 2012) and is potentially an important step in building multi-scale predictive models (Graf et al. 2005).

Marine fisheries data are characterized by zero-inflated counts, patchiness, scale dependency, and spatial correlation, all of which present challenges to traditional statistical methods (Ciannelli et al. 2008, Webley et al. 2011). Zero-inflated data distributions, which can result from spatial patchiness within preferred habitat or sampling outside the range of a species, are difficult to normalize using linear transformations and can result in serious violations of statistical assumptions such as normality, homoscedasticity, and parameter inference (Cunningham & Lindenmayer 2005). In the case of linear GWR analysis, non-normal data distributions may conceal spatial non-stationarity of parameter estimates (Yu et al. 2009), and curvilinear relationships between variables may result in false patterns of spatial non-stationarity (Austin 2007). A 2-stage modelling approach has been increasingly used in the ecological literature to cope with zero-inflated data counts, whereby presence/absence is modelled in the first step and abundance is modelled in the second step,

conditional on predicted presence being greater than zero (Barry & Welsh 2002, Cunningham & Lindenmayer 2005, Martin et al. 2005, Rooper & Martin 2009, Taylor et al. 2011). When presence/absence and abundance are modelled on important ecological niche limits for survival and growth, the results of both stages can be interpreted in a biologically meaningful way (Guisan & Thuiller 2005, Rooper & Martin 2009).

The goal of this work was to investigate spatio-temporal patterns of invertebrate–predator–habitat associations within the large and heterogeneous seascape of the southern Labrador and eastern Newfoundland Shelf, and to identify characteristic scales at which these relationships achieve spatial stationarity. This study expands on previously published work (Windle et al. 2010) to apply GWR to a 15 yr time series (1995 to 2009) of fisheries survey data in Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J and 3K. We used a 2-stage modelling approach to compensate for the patchy distribution and zero-inflated catches of species in the study area and to improve the linearity of relationships by focussing the analysis on areas where species were expected to be present. Given evidence of the importance of environmental conditions to snow crab and pandalid shrimp distributions (Foyle et al. 1989, Parsons & Lear 2001), as well as the hypothesized top-down control of these invertebrates by large ground-fish species (Worm & Myers 2003, Frank et al. 2006, Boudreau et al. 2011), the objectives of this study were to: (1) model crab and shrimp presence and abundance as a function of predator abundance, depth, bottom temperature, and bottom salinity; (2) estimate the spatio-temporal variability of the GWR coefficients; (3) determine scale effects of invertebrate–predator–environment relationships over time; and (4) compare model performances using non-spatial and spatial methods. We interpret the observed spatio-temporal relationships within the context of historical changes on the Newfoundland–Labrador Shelf and existing hypotheses on top-down versus bottom-up influences on snow crab and northern shrimp distribution and abundance.

MATERIALS AND METHODS

Study area

Relationships between invertebrates and explanatory variables were investigated off the eastern coast of Newfoundland–Labrador within the NAFO man-

agement divisions 2J, 3K, and 3L (Fig. 1). This region includes a large area (>300 000 km²) of continental shelf extending from southern Labrador to the northern part of the Grand Banks of Newfoundland, and is characterized by relatively shallow outer banks intersected by several large troughs. The oceanographic regime is heavily influenced by the cold Labrador Current that flows southwards along the Labrador and Newfoundland coastline and at the edge of the continental shelf. Average bottom temperatures over most of the shelf range are from -1.0 to 0.0°C inshore to $>3.0^{\circ}\text{C}$ in the deeper trenches and on shelf slopes (Colbourne et al. 1997).

Distributions of cod *Gadus morhua*, crab *Chionectes opilio* and shrimp *Pandalus borealis* within the study area vary seasonally, although all 3 species have overlapping habitat preferences. In the 2J3KL area, snow crab are widely distributed across the shelf over a broad range of depths (Dawe & Colbourne 2002) and are generally associated with bottom temperatures between -1 and 4°C . Northern shrimp prefer near-bottom temperatures in the range of 2 to 6°C and muddy substrates (DFO 2010a), and are found in high-density aggregations in the northern range of the study area (2J3K). Atlantic cod are found throughout the study area at low densities, with denser aggregations forming during winter and spring in certain regions (Mello & Rose 2010, Rose et al. 2011) and have a tolerance for large ranges of

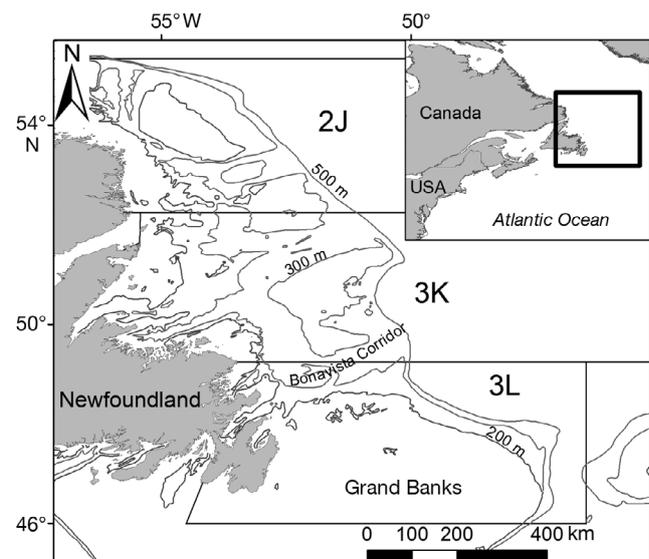


Fig. 1. The continental shelf off Newfoundland and Labrador, Canada (with 200, 300, and 500 m contours identified), showing the locations of the Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K and 3L, the Grand Banks of Newfoundland, and the Bonavista Corridor. The inset shows the location of the study area

depth (10 to >500 m) and temperatures (−1 to 10°C) (Rose 2005). The highest remaining concentrations of cod are found in the Bonavista Corridor, which spans the border between 3K and 3L (DFO 2010b).

Data sources

Fisheries scientific survey data (1995 to 2009) were obtained from the Department of Fisheries and Oceans Canada (DFO) and were collected during fall multispecies bottom-trawl surveys in NAFO Divisions 2J, 3K, and 3L. The survey employed a Campelen 1800 research bottom trawl and followed a stratified random design (Brodie 2005). Trawl catch weights (kg) and abundances of cod, snow crab, and northern shrimp were standardized according to the area swept (0.8 nautical miles in 15 min with a wing spread of 16.84 m), while mean bottom depth (m), temperature (°C), and salinity (ppt) were recorded for each set. Species weights and abundances were log-normalized to adjust for skewed distributions prior to statistical analyses.

Statistical analyses

The data analysis consisted of 2 steps: (1) identifying the core habitat of crab and shrimp by establishing the important environmental niche dimensions of each species; and (2) modelling the abundances of snow crab and northern shrimp within the identified core areas using bottom temperature, bottom salinity, depth, and Atlantic cod abundance as explanatory variables.

Core habitat identification

Niche theory assumes that a species occupies a theoretical ecological space that is limited by environmental determinants (fundamental niche) and that this niche is reduced further by competition, predation, and disturbance (realized niche) (Hutchinson 1957). Depth and temperature are known to be key factors that determine invertebrate distribution and survival (Foyle et al. 1989), and as such, these variables were chosen to define the habitat models for both species.

To increase the robustness of core habitat identification given the species patchiness, the cumulative distribution function (CDF) of crab and shrimp abundance was randomly resampled over depth

and bottom temperature (1000 replicates with replacement) as suggested by Rooper & Martin (2009). The average resampled CDFs were then used to generate habitat limits for each environmental variable for each year to account for changes in species abundance and climate over time. The potential effects of sampling error and outliers were avoided by narrowing the habitat limits to the 5th and 95th percentiles of the cumulative distribution for each species. Trawl locations falling within these percentiles for depth and temperature were considered to be the core habitat of the species over which abundances were modelled in the second stage of the analysis.

Species modelling

GWR was applied to investigate spatial patterns and scale dependency of relationships between invertebrate species and variables hypothesized to be important to their distribution off Newfoundland–Labrador. The abundances of snow crab and northern shrimp within the identified core areas were modelled separately for each year of the time series using bottom temperature, bottom salinity, depth, and Atlantic cod abundance as explanatory variables. The analysis for snow crab abundance used data from 2J, 3K and 3L, while the analysis for northern shrimp was limited to 2J and 3K, due to the more northern distribution of this species at the time of this study. Given the highly correlated relationships between bottom temperature, depth, and salinity, the relationships between crustaceans and predictor variables were paired separately in univariate models to avoid the effects of interactions and multicollinearity on the coefficient estimates (Graham 2003, Wheeler 2007).

The GWR model represents an extension of the traditional linear regression by incorporating a set of geographic locations for each observation point, such that:

$$Y_i(u_i, v_i) = \beta_0(u_i, v_i) + \beta_1(u_i, v_i)x_1 + \beta_2(u_i, v_i)x_2 + \varepsilon_i(u_i, v_i) \quad (1)$$

where Y_i is the dependent variable, β_0 is the intercept coefficient, x_1 and x_2 are explanatory variables, β_1 and β_2 are the parameter coefficients, ε is the error term, and (u_i, v_i) are spatial coordinates for each location i in space. The statistical background and methodology of GWR is detailed in Fotheringham et al. (2002). The radius of the local GWR model can be determined by a fixed Euclidian distance–decay function or an adaptive kernel function that uses a

minimum number of nearest neighbours. A fixed spatial kernel (bandwidth) of 100 km was selected based on optimization of a corrected Akaike information criterion (AICc) (Fotheringham et al. 2002) and was applied to every GWR model to ensure consistency in the time series. The AICc is a relative measure of model performance corrected for the number of parameters, where the model with the smallest AIC represents the closest approximation to reality, and differences in values >3 are assumed to represent a significant improvement (Fotheringham et al. 2002). The bi-square distance decay function took the form:

$$w_{ij} = \exp[-(d_{ij}/b)^2]^2 \quad (2)$$

where d_{ij} is the Euclidean distance between the 2 observation sites i and j and b is the bandwidth in map units.

GWR assumes linear relationships between response and predictor variables, and when this assumption is not met, it can result in spatial patterns of coefficients that are the outcome of model misspecification rather than real ecological phenomena (Austin 2007). Given that species often exhibit curvilinear, skewed, or bimodal responses along environmental gradients that define their habitat (Austin 2002), we investigated this potential source of statistical bias by testing for nonlinear relationships using generalized additive models (GAMs). GAMs represent an extension of the generalized linear model (GLM), and have previously been used in fisheries research for a wide range of species–environment modelling exercises (Murase et al. 2009). A GAM fits a smoothing curve through the data and allows nonlinear response curves to be modelled. In a GAM, a smoothing function (f_i) is used in place of the coefficient β_i , such that:

$$y_i = \beta_0 + f_i x_i + \varepsilon_i \quad (3)$$

where f_i is a non-parametric function describing the effect of x_i on y_i . A Gaussian GAM was fitted using an identity link function and penalized regression splines with automatic smoothness selection (Wood 2006). GAM analyses were carried out in R v. 2.8.1 (R Development Core Team 2012), using the ‘mgcv’ package V. 1.5-5 (Wood 2006).

In the case where a significant ($p(\chi) < 0.05$) nonlinear relationship was identified in a GAM univariate model, a second-order polynomial transformation was applied to the dependent variable and subsequently tested in the GWR in addition to the log-transformed predictor variable (Miller & Hanham 2011). While it is recognized that species–environ-

mental response curves can take many forms (Austin 2002), our nonlinear analysis was limited to the second-order polynomials as niche theory assumes a symmetric bell-shaped response curve that is more easily interpretable than more complex polynomial transformations. The GWR results from the linear (log) and nonlinear (polynomial) transformations were compared using the AICc.

Maps of GWR coefficient estimates were generated for both the shrimp and crab time series to show how the associations between response and predictor variables varied across the study area and over time. A subset of the time series was chosen to compare the spatial patterns of GWR coefficients during contrasting periods of relatively high/low species abundances and ocean temperatures. These years also had to meet the criteria of having no significantly nonlinear relationships between response and predictor variables. Only significant coefficients ($>95\%$) were displayed, as determined by t -values for each local regression (Mennis 2006). GWR analyses were performed in R v. 2.15.0 (R Development Core Team 2012), using the ‘spgwr’ package (Bivand & Yu 2012), and the results were imported into ESRI’s ArcGIS (v. 9.3) for spatial analyses and mapping.

Spatial stationarity in the relationships between invertebrates, temperature, and cod can be expected to vary according to spatial scale. Using progressively larger increments of GWR bandwidth (50, 100, and 200 km), the spatial scale of these relationships was investigated using a spatial stationarity index, where the interquartile range of a given GWR coefficient was divided by twice the standard error (SE) of the same variable from the equivalent global ordinary least-squares regression (Fotheringham et al. 2002). Given that 68% of the global values are within ± 1 SE and 50% of the GWR values are within the interquartile range, ratio values >1 suggest spatial non-stationarity between the independent and dependent variables. Stationarity indices for each bandwidth were plotted over time to compare within-year scale differences as well as differences through time.

Finally, the overall ability of GWR models to predict local crab and shrimp abundances per year was tested by combining all explanatory variables in multivariate GWR models at a 100 km bandwidth. The overall spatial patterns of model performance were explored visually by mapping local coefficients of variation (R^2) from all multivariate models per species and creating an interpolated surface using inverse distance-weighting techniques.

RESULTS

Exploratory analysis of mapped species distributions over the time series revealed general geographic trends within the study area. Atlantic cod *Gadus morhua* were widely distributed in low numbers, but concentrated in the Bonavista Corridor area, at the offshore border between NAFO Divisions 3K and 3L (Fig. 1). Crab *Chionoecetes opilio* were also widely distributed, with higher concentrations in 3K and along the northern slopes of the Grand Banks in 3L, with overall capture rates of 79% over the time series. Shrimp *Pandalus borealis* were found in very high densities in the northern extent of the study area (2J and 3K), and were captured in 83% of the trawls in 2J/3K from 1995 to 2009. Pooled catches for crab and shrimp were both positively skewed across all years (skewness = 8.24 and 9.74, respectively) and were dominated by several large catches and many samples without catches or low numbers.

The CDFs, pooled over the time series (1995 to 2009), revealed that 90% of crab were found between -1 and 4°C and at depths between 100 and 500 m, while 90% of shrimp were found between 0 and 4°C and depths of 150 to 450 m (Fig. 2). Over the time series, 88 to 99% of the stations within the core

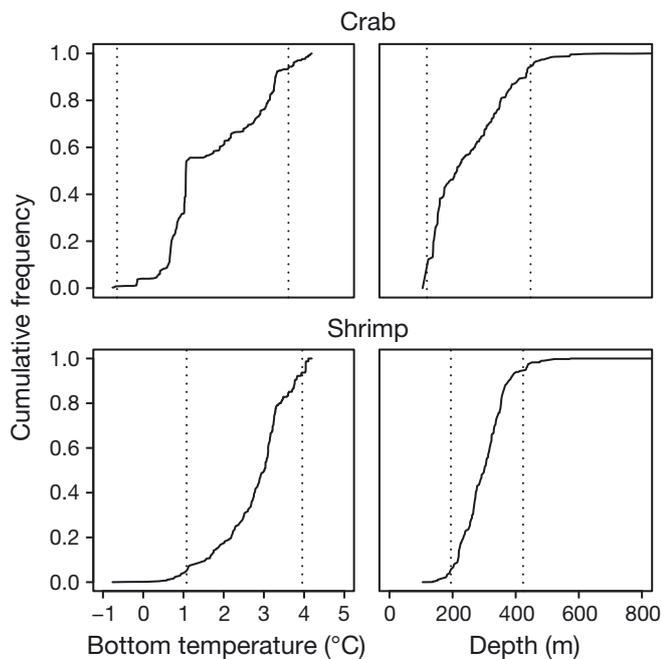


Fig. 2. *Chionoecetes opilio* and *Pandalus borealis*. Examples of the cumulative frequency of snow crab and northern shrimp abundance as a function of bottom temperature ($^{\circ}\text{C}$) and depth (m), with 5th and 95th percentiles indicated by dotted lines. Data were derived from the 2001 fall multi-species bottom trawl surveys in Northwest Atlantic Fisheries Organization Divisions 2J, 3K, and 3L

area had crab present (mean = 95%). The percentages of shrimp found at core area locations were similarly high at 96 to 100% (mean = 99%). Habitat models for both species were weak in accurately predicting the absence of each species at trawl locations outside the core areas. This was likely a result of the cumulative distribution functions not accounting for 10% of overall species abundance; therefore, the calculated environmental niche limits were narrower than the actual species tolerances for depth and temperature. However, the habitat models reflected the overall niche dimensions for the majority (90%) of catches for each species, and this was likely the cause of the relatively high percentages of species occurrence within the core areas.

GAM and GWR models were fitted to each of the 4 univariate relationships (bottom temperature and salinity, depth, cod abundance) per invertebrate species per year, resulting in a total of 120 models for each of the regression methods. The overall incidence of nonlinearity between crustacean abundance and predictor variables was relatively low for shrimp (6 out of 60 univariate GAM models) and higher for crab (15 out of 60 univariate GAM models). However, out of the 15 models of crab with nonlinear transformations, only 3 performed significantly better (AICc difference > 3) than the equivalent linear model in the GWR analysis (Table 1a). For shrimp, 5 of the 6 nonlinear models performed significantly better than the equivalent linear model (Table 1b). The incidence of nonlinear relationships was spread evenly between crab and environmental predictors over the time series, with no nonlinear relationships found between crab and cod. Of the few nonlinear relationships found between shrimp and the predictor variables, most were found with bottom temperature and salinity and none were found with depth.

Depth was consistently the best, or equivalent to the best, predictor for crab abundance in 13 of 15 yr in the time series (Table 1a). No crab–cod pairings resulted in the best model for any year. Of the 6 crab–depth models with nonlinear relationships, only 2 of the polynomial transformations resulted in significantly better models compared to models using standard linear transformations. Bottom temperature was the most consistently superior predictor of shrimp abundance in 8 out of 15 yr (Table 1b). Cod also performed well as a predictor of shrimp abundance relative to the other variables in 5 of the survey years.

Average GWR coefficients of crab models over the time series revealed a mostly negative relationship with cod abundance, bottom temperature and salinity, and a very weak positive relationship with depth

Table 1. *Chionoectes opilio* and *Pandalus borealis*. Comparison of fit for univariate geographically weighted regression models used to predict (a) snow crab and (b) northern shrimp abundance in Northwest Atlantic Fisheries Organization Divisions 2J, 3K, and 3L from 1995 to 2009. Relative corrected Akaike information criterion (AICc) values are shown for linear (L) and nonlinear (NonL: second-order polynomial transformation) models, with values relative to the lowest AICc score per year. Independent variables included Atlantic cod *Gadus morhua* abundance, bottom temperature (°C; Temp), bottom salinity (ppt; Sal), and trawl depth (m). Models not used indicated by dash (–)

Year	n	Relative AICc							
		Cod		Temp		Sal		Depth	
		L	NonL	L	NonL	L	NonL	L	NonL
<i>Chionoectes opilio</i>									
1995	172	14.2	–	0	–	8.26	3.95	5.08	–
1996	257	37.27	–	10.23	–	7.12	12.17	0	5.45
1997	263	26.83	–	28.56	–	20.05	–	0	–
1998	242	22.52	–	17.7	–	5.8	0	10.86	–
1999	253	12.32	–	5.56	–	0	1.91	1.99	–
2000	186	5.92	–	6.62	–	7.11	–	0	–
2001	251	32.06	–	21.73	–	24.57	23.84	0	0.94
2002	238	0.32	–	9.36	11.49	11.64	–	0	–
2003	261	14.8	–	3.86	0	3.12	–	0.71	–
2004	243	13.17	–	8.59	11.47	6.2	–	0	–
2005	308	39.74	–	27.7	–	45.27	–	6.35	0
2006	260	67.34	–	50.53	–	86.2	–	12.32	0
2007	218	49.41	–	39.28	–	65	–	0	2.31
2008	209	37.01	–	27.39	–	38	–	0	–
2009	228	47.59	–	30.34	31.99	55.07	–	0	5.46
<i>Pandalus borealis</i>									
1995	83	6.85	–	0	–	4.4	–	1.38	–
1996	95	18.53	–	6.99	–	8.37	–	0	–
1997	123	39.71	–	38.2	21.35	38.79	0	51.6	–
1998	121	13.75	–	7.43	–	0	–	13.27	–
1999	104	5.16	–	2.21	–	0	–	3.52	–
2000	107	27.87	–	6.86	0	7.69	8.15	25.23	–
2001	122	0	–	11.49	–	10.76	–	8.59	–
2002	125	21.72	–	9.33	–	11.75	–	0	–
2003	122	16.86	–	0	–	4.16	–	3.87	–
2004	114	4.64	–	0	–	5.45	–	2.18	–
2005	136	0	–	4.11	–	5.14	–	5.15	–
2006	119	46.83	0	78.7	–	88.4	–	84.1	–
2007	118	0	–	0.33	–	7.78	–	3.52	–
2008	114	51.79	–	23.01	0	42.33	–	31.13	–
2009	101	1.59	–	0	–	8.36	–	11.49	–

(Fig. 3a). In contrast, GWR coefficients of shrimp models revealed mostly weak positive relationships with temperature, salinity, and depth, and a mostly negative relationship with cod (Fig. 3b). Mean shrimp–cod relationships appeared to alternate between positive and negative coefficients every 3 to 4 yr (Fig. 3b). For both species, salinity and temperature coefficients had the highest variability, while depth and cod coefficients had the lowest over the time series. GWR salinity coefficients showed a marked decrease in variability after 2004 for both species.

The spatio-temporal variation of GWR parameter coefficients was explored visually for each species, resulting in a series of maps that contrast invertebrate–habitat associations in years of different ocean climate conditions and relative overall abundance.

GWR coefficients for crab models were mapped for the 1997 and 2008 surveys, which contrasted periods of relatively high/low crab abundance, cooler/warmer bottom temperatures, and lower/higher cod abundance, respectively (Fig. 4). In both periods, the spatial pattern of GWR cod coefficients revealed a very weak and mostly non-significant relationship with crab throughout the study area. Crab–depth associations were positive in the inshore areas of 2J and 3K as well as offshore 3K in 2008, and negative on offshore slopes of the Grand Banks in 2008. GWR salinity and temperature coefficients followed a similar spatial pattern as depth in both years, although these relationships were mostly non-significant. GWR coefficients for shrimp models were mapped for the 1998 and 2007 surveys in 2J and 3K, which contrasted periods of relatively low/high shrimp abundance, cooler/warmer bottom temperatures, and lower/higher cod abundance, respectively. Spatial patterns of coefficients differed greatly between the 2 periods, with mostly weak positive or non-significant relationships between shrimp and predictor variables in 1998, and weak negative or non-significant relationships in 2007 (Fig. 5).

Spatial scaling of the GWR bandwidths (i.e. gradually expanding the local regressions until they approached a global model) revealed that the relationships between both invertebrate species and predictor variables became spatially stationary on average between 100 and 200 km (Fig. 6). The spatial stationarity of GWR cod coefficients was relatively constant in crab models at 100 km, while shrimp–cod associations varied over the time series and achieved stationarity at scales of <100 km in many years. Large fluctuations in spatial non-stationarity were found for relationships with environmental variables at smaller (50 km) and medium (100 km) scales, making it difficult to establish a clear pattern or trend for either species. Nearly all relationships became stationary at the largest bandwidth tested (200 km) (Fig. 6).

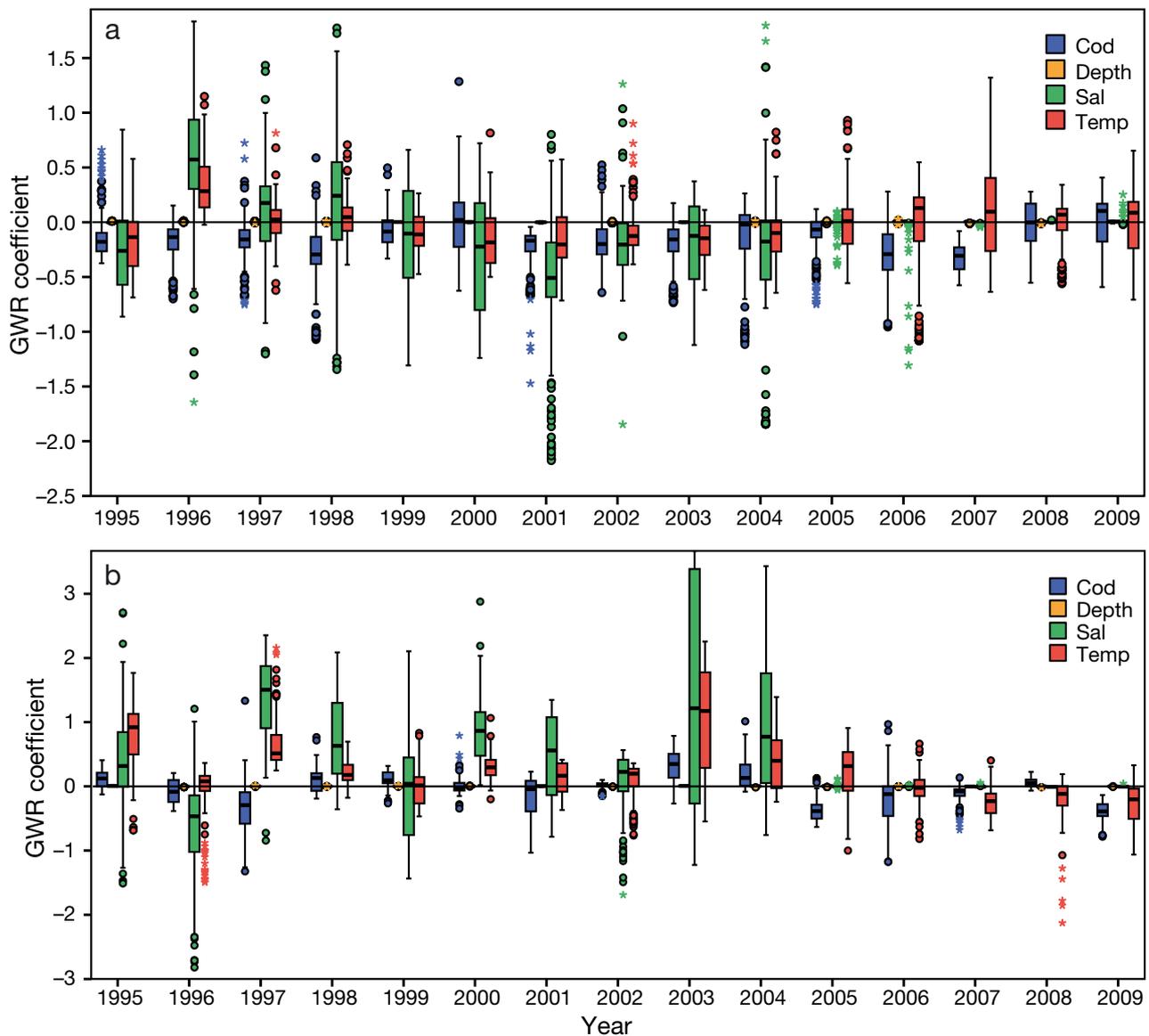


Fig. 3. *Chionectes opilio* and *Pandalus borealis*. Non-standardized coefficients for univariate geographically weighted regression (GWR) models of (a) snow crab and (b) northern shrimp abundance predicted by cod *Gadus morhua* abundance, depth, bottom salinity (Sal) and bottom temperature (Temp) at 100 km bandwidths. Boxplots show the mean, lower and upper quartiles, and outliers of each GWR coefficient per year for the 1995 to 2009 timeline with outliers shown by star symbols

When all explanatory variables were combined, the amount of variance explained by the GWR models at 100 km bandwidths averaged 37% for crab and 35% for shrimp models over the time series (Fig. 7). Model performance for predicting crab abundance appeared to follow a repeating cycle of higher and lower R^2 values every 6 yr, although our ability to establish a clear pattern is limited by the length of the time series. Performance of shrimp models peaked in 1997, with a mean explained variance of 67%, although much lower R^2 values (22 to 26%) were observed in other

years (Fig. 7). The spatial variability of local R^2 estimates was explored by mapping these results for all years, and revealed that, on average, crab models performed best near the fringes of the study area and more poorly near the centre (Fig. 8). Shrimp models performed best near the inshore area in 3K and throughout 2J, and more poorly throughout the remainder of 3K. Overall, the predictor variables used in this study were better able to model crab compared to shrimp distributions, with higher levels of explained variance throughout the study area.

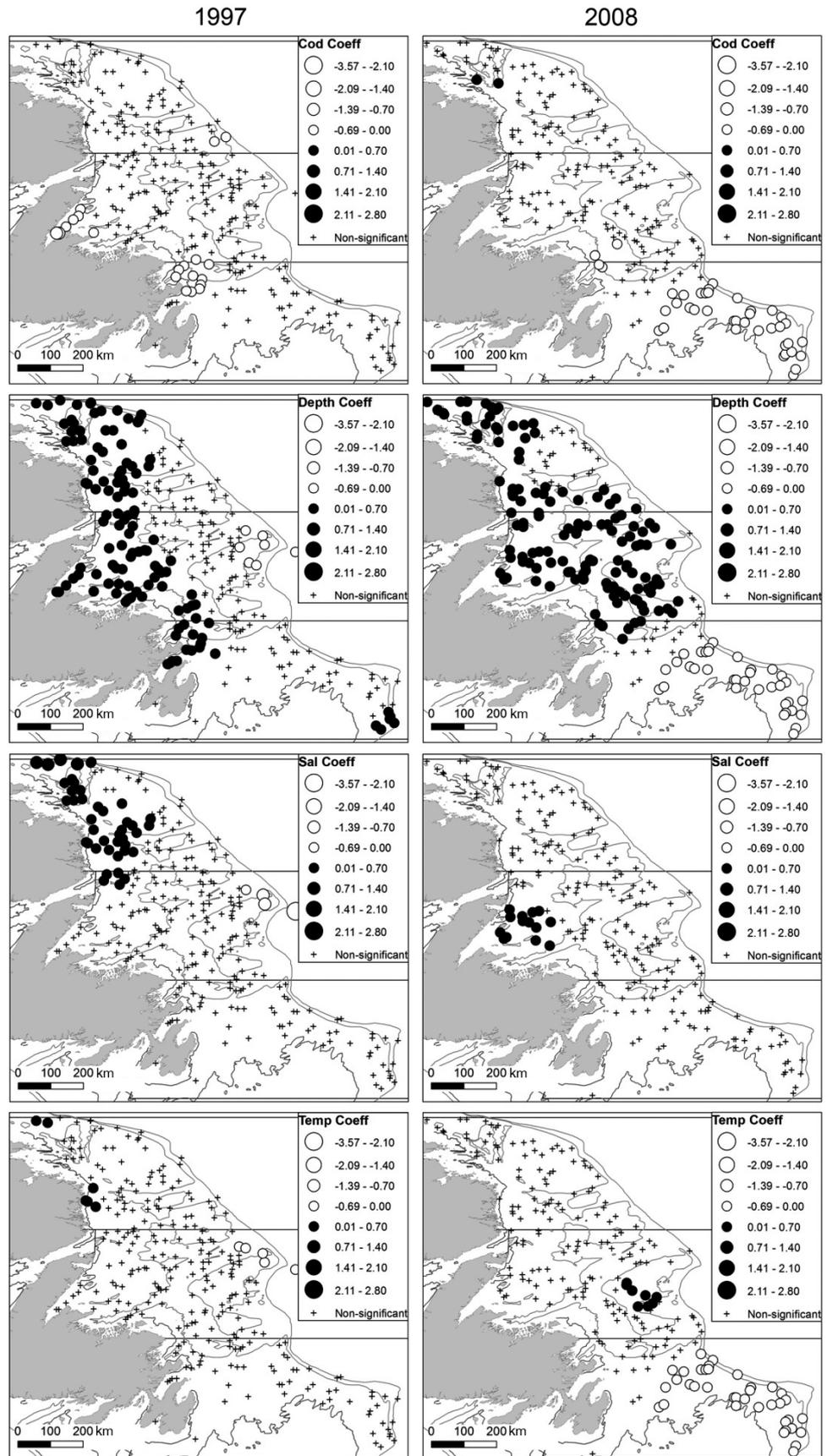


Fig. 4. *Chionoecetes opilio*. Spatial distribution of geographically weighted regression coefficients that were significant in predicting snow crab abundance in 1997 and 2008. The 2 years contrast periods of relatively high/low crab abundance, cooler/warmer bottom temperatures, and lower/higher cod *Gadus morhua* abundance, respectively. Open circles: negative coefficients; closed circles: positive coefficients; crosses: non-significant values. Horizontal lines are NAFO divisions (see Fig. 1)

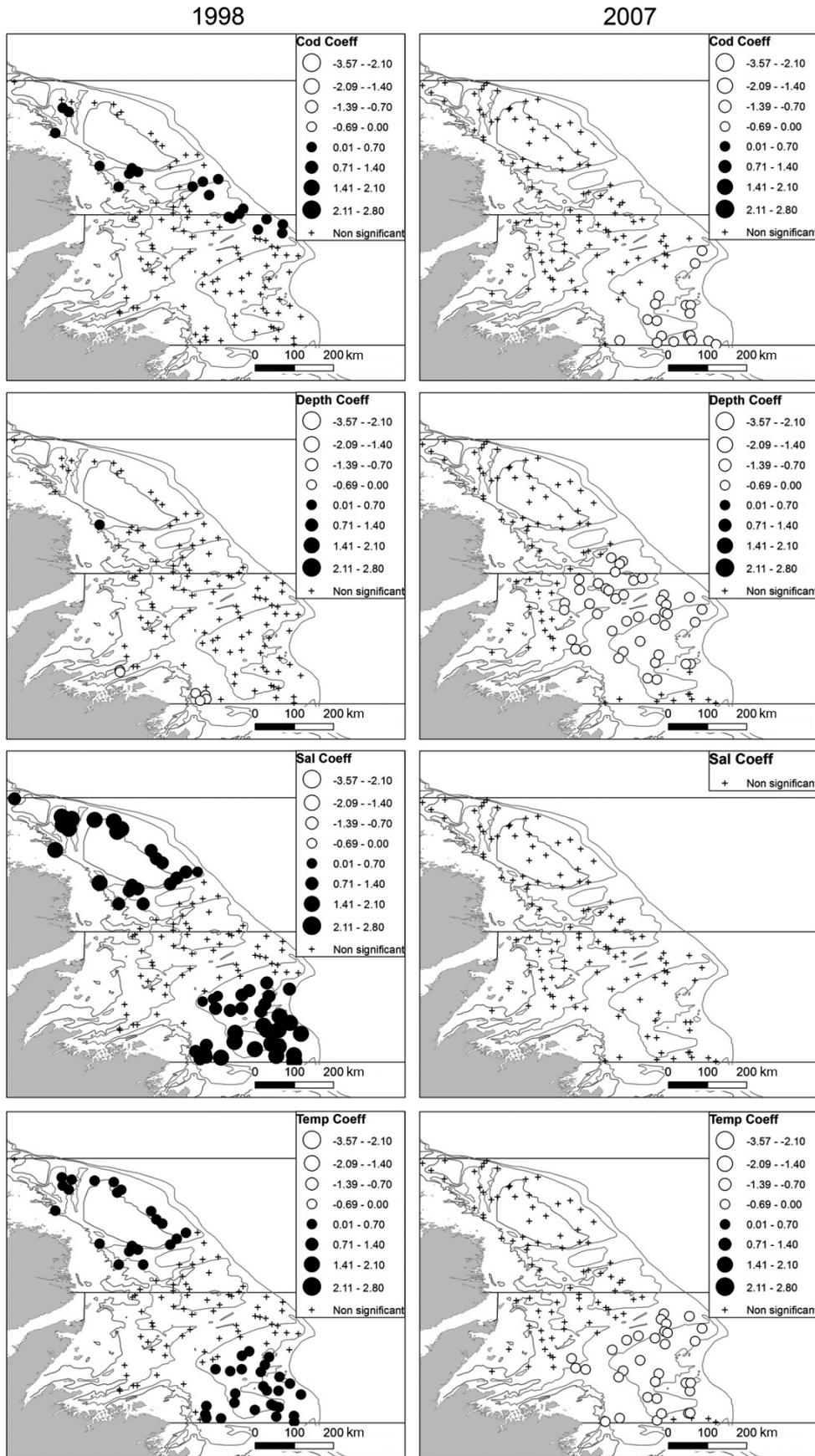


Fig. 5. *Pandalus borealis*. Spatial distribution of geographically weighted regression coefficients that were significant in predicting northern shrimp abundance in 1998 and 2007. The 2 years contrast periods of relatively low/high shrimp abundance, cooler/warmer bottom temperatures, and lower/higher cod *Gadus morhua* abundance, respectively. Open circles: negative coefficients; closed circles: positive coefficients; crosses: non-significant values. Horizontal lines are NAFO divisions (see Fig. 1)

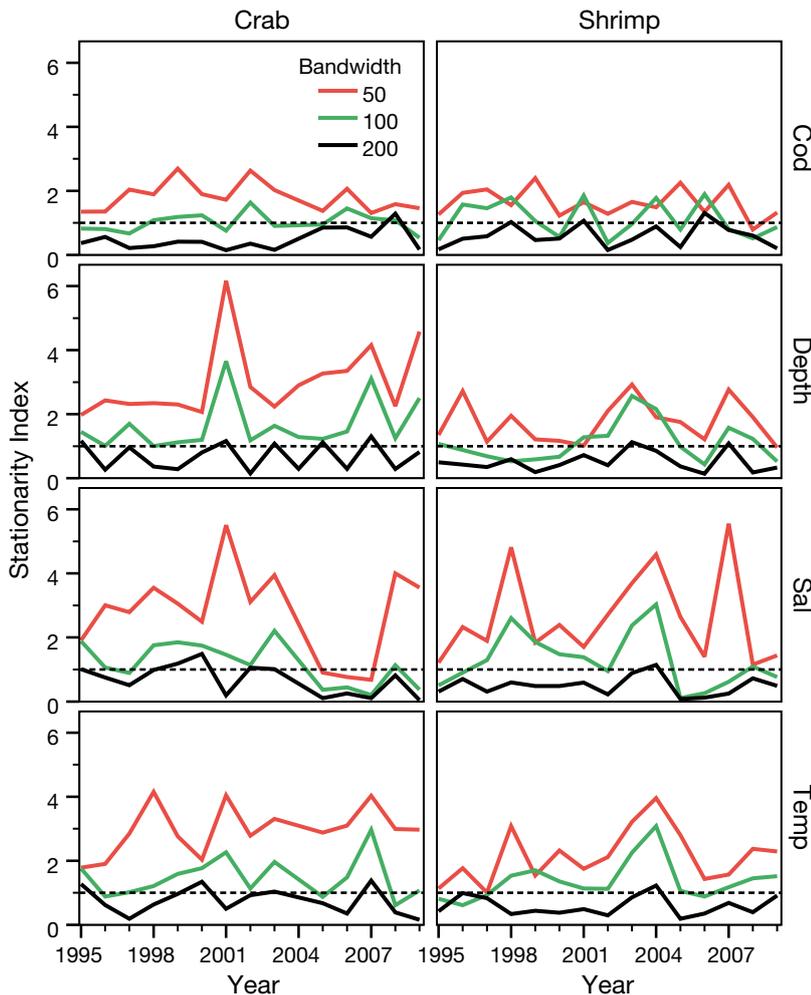


Fig. 6. *Chionoecetes opilio* and *Pandalus borealis*. Spatial stationarity index for geographically weighted regression (GWR) coefficients of cod *Gadus morhua*, depth, and bottom salinity (Sal) and bottom temperature (Temp) used to model snow crab and northern shrimp abundance over multiple bandwidths, from 1995 to 2009. The index is calculated by dividing the interquartile range of a GWR regression coefficient by twice the SE of the same parameter estimate from the global model. Spatial non-stationarity is suggested by values >1 (below dashed line)

DISCUSSION

Our models of spatio-temporal variation of snow crab *Chionoecetes opilio* and shrimp *Pandalus borealis* in the Newfoundland–Labrador region, accounting for both putative top-down (predation by cod) and bottom-up (indexed by depth, temperature, and salinity) factors, indicated both commonalities in factors and differences, and strong spatial dependence. For snow crab, depth was the best predictor of distributions in both linear and nonlinear models, being a proxy for several environmental variables (temperature, salinity, pressure, and sediment type) and consistently outperforming cod *Gadus morhua* as a pre-

dictor of crab distribution and abundance. This predominance of environmental effects supports the importance of bottom-up processes for this species (Foyle et al. 1989, Dawe & Colbourne 2002, Dawe et al. 2008, Boudreau et al. 2011). The results of GWR univariate models of shrimp were less definitive in terms of bottom-up and top-down control, as cod was the best predictor of shrimp distribution from 2005 to 2009 in most cases, but environmental factors also were influential. An increasing abundance of cod in the region since 2005 (DFO 2010b), as well as recent warming trends that would impact the availability of suitable habitat for shrimp, may have influenced this result.

GWR time-series analysis revealed that the regression relationships between crab, shrimp, environmental parameters, and cod were spatially non-stationary and varied through time. Hence, globally averaged relationships are likely to mask important spatial variability that occurs across the Newfoundland–Labrador Shelf. Depth, temperature, and salinity are generally strongly correlated in this region (Colbourne et al. 2009), and mapped GWR parameter estimates for these variables tended to follow similar spatial patterns. Where significant, crab tended to have stronger positive associations with nearshore environmental variables and weaker negative associations with offshore environmental parameters. This weak negative association with temperature was more widely distributed in the south during relatively warm years. These patterns fit with the average distribution of bottom temperatures across the shelf, with the cold inshore branch of the Labrador Current flowing south along the coast and over the top of the Grand Banks, and warmer temperatures in the deeper offshore water (Colbourne et al. 1997). Given that crab are seldom found at temperatures >5 to 6°C , the positive association with cold ($<0^{\circ}\text{C}$) inshore waters is consistent with their temperature range. In contrast, the warmest waters of the offshore basins and trenches have typically been around 4°C , and in recent years have increased to near 5°C (Colbourne et al. 2009),

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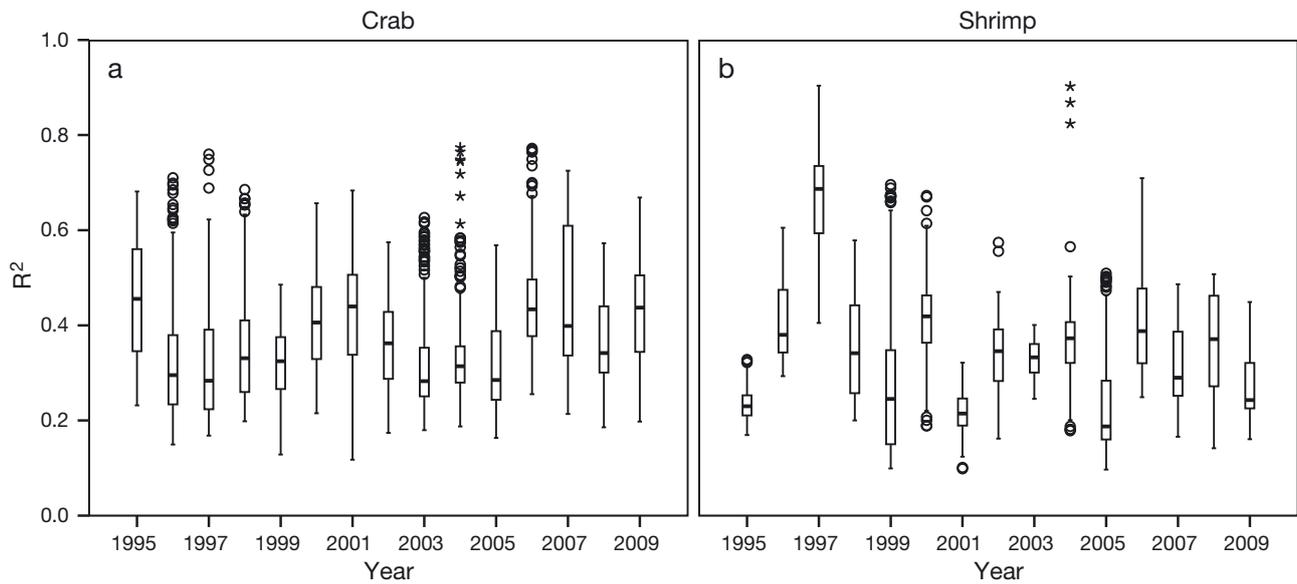


Fig. 7. *Chionoecetes opilio* and *Pandalus borealis*. Explained variance (local R^2) values from geographically weighted regression multivariate models of (a) crab and (b) shrimp abundance as a function of cod *Gadus morhua* abundance, depth, and bottom salinity and bottom temperature, for the period from 1995 to 2009

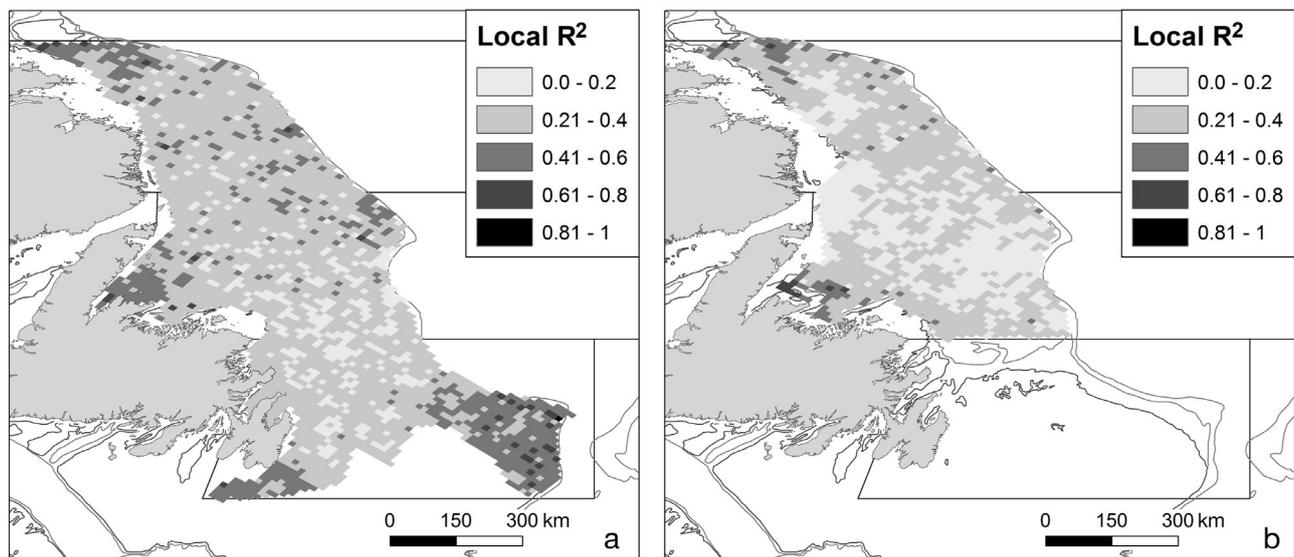


Fig. 8. *Chionoecetes opilio* and *Pandalus borealis*. Mapped distribution of the average explained variance (local R^2) of geographically weighted regression multivariate models of (a) crab and (b) shrimp abundance as a function of cod *Gadus morhua* abundance, depth, and bottom salinity and bottom temperature, for the period from 1995 to 2009. Resolution is at the 10 km \times 10 km scale. Black lines show NAFO divisions (see Fig. 1)

which is near the upper range for these crustaceans. We note that crab had a more negative relationship with temperature in the southern offshore area during a relatively warm period and a more positive relationship in the northern inshore area during a cooler period and that this may be indicative of temperature constraints near the edges of preferred habitat. Overall, the temporal and spatial patterns of

crab–environment relationships are consistent with known species tolerances and reinforce the importance of ocean climate on the distributions of this species (Foyle et al. 1989). The spatial patterns of shrimp and environmental relationships differed greatly between the beginning and end of the time series, although they tended to follow similar patterns within years. These differences may be the

result of an overall warming trend in the ocean conditions over the time series (Colbourne et al. 2009), as well as a large increase in shrimp abundance in this region over the same period (DFO 2010a).

Interpreting predator–prey relationships requires consideration of the environmental variability that may influence overlap between species and potential contact scales (Rose & Leggett 1990, Bailey et al. 2010). Coincident catches of various species may represent similar habitat preferences rather than predator–prey dynamics, and as such we interpret the spatial relationships between invertebrates and cod as complementary to more direct evidence. Diet studies have shown that in the 1970s and 1980s, when cod were more abundant than at present, snow crab comprised a minor proportion of prey for cod (0 to 8% by mass) in most seasons in regions of the Newfoundland–Labrador Shelf (Lilly 1984). In the 1990s and 2000s, the much reduced cod stocks have shown a similar low incidence of feeding on snow crab (Sherwood et al. 2007). Consistent with the diet data, we found that crab and cod had a relatively weak and mostly negative spatial relationship throughout the study area.

The models of spatial association between cod and crab would have benefited from size- or sex-partitioned data, because predation by cod on snow crab is size and sex dependent. Small cod likely avoid the larger male crab, and larger cod feed mainly on smaller size classes of crab, which are mainly females (Chabot et al. 2008). Hence, some of the spatial patterns observed could have resulted from differences in the overlap between size classes of each species. Furthermore, there is evidence that smaller crabs are not always effectively sampled by survey bottom trawls, depending on surficial geology (Dawe et al. 2010), which could bias analyses of crab distribution. Nevertheless, our findings of stronger relationships between crab and environmental predictors and mostly non-significant relationships between crab and cod throughout the study period do not lend support to the theory of a top-down control on snow crab by cod, at least not in the size ranges of crab sampled by the scientific survey.

In contrast to crab, shrimp are a frequent prey item for cod in 2J, 3K and 3L (Parsons 2005, Sherwood et al. 2007). Spatial patterns of GWR coefficients showed an alternating pattern of positive and negative relationships between cod and shrimp throughout the time series, although this association was mostly negative during the warmest years (2005 onwards). On average, the shrimp–cod relationships were negative and were consistent with previously

found trends in cod and shrimp interactions (Worm & Myers 2003). Cod and shrimp have similar habitat preferences, and this relationship may indicate opportunistic predation by cod. It is interesting to note that GWR cod coefficients predicting shrimp were mostly non-significant or positive in the northern range during a year of lower shrimp and cod abundance and cooler bottom temperatures and mostly non-significant or negative during a later period of higher shrimp and cod abundance and bottom temperatures. The negative shrimp–cod relationship in 2008 was mostly found near the Bonavista Corridor, where the offshore cod population is concentrated and has increased in recent years (DFO 2010a). Hence, our findings are consistent with the notion that shrimp have been subjected to some degree of top-down control by cod in this relatively simple food web (Worm & Myers 2003, Frank et al. 2005).

The combined ability of all explanatory variables to predict crab and shrimp abundance was generally poor over the time series, suggesting an incomplete set of predictors in the models. Other factors for which data were not available almost certainly influence crustacean distribution and abundance, especially bottom substrate (Tremblay 1997, Dionne et al. 2003). Moreover, both known and unknown factors are almost certain to interact. For example, a suitable substrate becomes an unsuitable habitat if local temperatures diverge from the physiological range of tolerance for the species. Such appears to be the case on the Newfoundland–Labrador Shelf in recent years for the cold-adapted crustaceans as a consequence of a warming ocean, as evidenced by negative temperature relationships in warm years along the southern extent of the study area.

Central to the findings of this study, spatial information and analyses (GWR) enabled the identification of region-wide patchiness not only in species distributions but in the relationships among species, environmental determinants, and predators that would have been masked by traditional global regression methods. Both crab and shrimp had non-stationary relationships with predictor variables at small and medium bandwidths, and generally achieved stationarity at the largest GWR bandwidths, suggesting that an appropriate scale of analysis for these variables is between 100 and 200 km. Spatial non-stationarity was higher at smaller scales for invertebrate–environment relationships compared to invertebrate–cod relationships. This may have resulted from spatial variability in the underlying processes affecting invertebrate distributions,

as well as the consistently low abundance of cod throughout the study area during the fall surveys used in this study. It is unclear why certain years exhibited increased non-stationarity at multiple scales compared to multi-year averages. For example, spatial non-stationarity of crab–environment relationships increased from 2000 to 2001 and from 2007 to 2009, perhaps as a result of survey-derived bottom temperatures showing a relatively large decrease in 2000 and an increase from 2006 to 2009. The increased spatial non-stationarity of shrimp–environment relationships in 2004 may be due to reduced survey coverage for this year. We note that shrimp–cod relationships showed an alternating pattern of spatial non-stationarity over the time series, which may be related to the recruitment of shrimp cohorts occurring on similar cycles (DFO 2010a). Spatial and temporal patterns in GWR coefficients such as these could help identify areas for more focused species distribution modelling. In addition, our finding that the scale of stationarity was dynamic over space and time highlights the difficulty of translating locally observed predator–prey interactions to the scale of populations and regions in ecological models (Hunsicker et al. 2011). These results emphasize the utility of GWR as an exploratory method for revealing spatial trends in a dataset that can subsequently be analyzed using other statistical tools more appropriate for inference testing.

Time-series analyses revealed dynamics in abiotic and biotic relationships over a 15 yr period from 1995 to 2009 that are likely to continue if waters continue to warm and cod (and capelin) continue to increase and crustaceans decline. We believe that the 2-stage analysis employed in this paper holds promise to disentangle these relationships, by addressing both the statistical and ecological challenges inherent in modelling such large-scale species distributions and their dynamics. In addition, estimating cumulative abundance frequencies over biologically relevant environmental variables aided the establishment of habitat limits (Rooper & Martin 2009). The cumulative frequency method led to improved predictions of the presence of invertebrates, normality of distributions, and analysis of species distributions in areas with appropriate habitat.

As a final comment, it is worth emphasizing that predator associations with potential prey, and hence any suggestion of top-down control by cod in these large marine ecosystems, were not universal and differed among prey species. Previous studies of cod interactions have focussed on only a single prey, be it shrimp (e.g. Worm & Myers 2003) or crab (Boudreau

et al. 2011) and, hence, could not make inter-species comparisons. Unfortunately, spatial data on capelin, formerly and still in some regions the chief prey of cod in Newfoundland–Labrador ecosystems (Link et al. 2009), are not available, but existing survey data indicate that capelin biomass collapsed about the same time as that of cod did, in the early 1990s (DFO 2011). Moreover, diet and isotope studies indicate that cod that formerly fed on capelin switched to shrimp in the 1990s (Sherwood et al. 2007). These findings alone indicate that cod could not have had a top-down influence on their chief prey but that the lack of capelin likely resulted in an increase in shrimp consumption. Overall, these findings suggest that trophic interactions are seldom simple or universal and cannot be expressed for an ecosystem in terms of relationships among a single pair of species. Only a multi-species spatial ecosystem model has the potential to quantify these influences simultaneously, but the present work demonstrates the likelihood that these complexities exist.

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