The dispersal pattern and behaviour of Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence: results from tagging experiments

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Abstract: We examined how the distribution of Atlantic cod (*Gadus morhua*) is influenced by abiotic (temperature, salinity, depth, suitable habitat) and biotic (stock biomass) factors based on tagging–recapture data collected from 1995 to 2008 by the Department of Fisheries and Oceans Canada in the northern Gulf of St. Lawrence. We calculated a centre of gravity index and a dispersion index using only individuals recaptured more than 1 year after tagging during the summer. The centre of gravity showed a northward expansion and eastward contraction in recent years, reflecting both fish distribution and changes in fishing effort. The dispersion index was significantly related to temperature, habitat suitability, and biomass but not to salinity or depth. These results indicate that interannual fluctuations of temperature and stock abundance both influence the dispersion pattern of cod. This new information could influence spatio-temporal fisheries management strategies for northern Gulf cod.

Résumé : Nous examinons comment la répartition de la morue franche (*Gadus morhua*) est influencée par les facteurs abiotiques (température, salinité, profondeur, habitat convenable) et biotiques (biomasse du stock) d'après les données de marquage-recapture accumulées de 1995 à 2008 par Pêches et Océans Canada dans le nord du golfe du Saint-Laurent. Nous calculons un indice du centre de gravité et un indice de dispersion en utilisant seulement les individus recapturés plus d'un an après le marquage pendant l'été. L'indice du centre de gravité montre une expansion vers le nord et une contraction vers l'est au cours des dernières années, ce qui reflète à la fois la répartition des poissons et les changements dans l'effort de pêche. L'indice de dispersion est relié significativement à la température, à la présence d'habitats convenables et à la biomasse, mais non à la salinité, ni à la profondeur. Ces résultats indiquent que les fluctuations entre les années de la température et de l'abondance du stock influencent toutes deux les patrons de dispersion de la morue. Cette nouvelle information pourrait affecter les stratégies spatio-temporelles de la gestion des pêches des morues du nord du Golfe.

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Introduction

Atlantic cod (*Gadus morhua*) is widely distributed in the North Atlantic and supports important commercial fisheries throughout its range. Because of the broad distribution and historical importance of the species, the movements and migratory behaviour of cod populations at a large scale have been well studied (Templeman 1979; Robichaud and Rose 2004; Windle and Rose 2005). However, the migratory behaviour and dispersion patterns at a small scale have not been examined closely. Factors affecting those patterns, such as environment, at a small scale are not well characterized and are temporally variable. Previous studies have suggested that environmental conditions, such as temperature or salinity, may influence the distribution, recruitment, migration, and behaviour of fish such as cod (Castonguay et al. 1999; Rose 2005; Ruppert et al. 2009) or capelin (*Mallotus villosus*) (Huse and Ellingsen 2008). Cod aggregation patterns also vary seasonally with respect to both feeding (DeBlois and Rose 1996; Wright et al. 2006) and spawning (Rose 1993; Robichaud and Rose 2001) behaviour.

Knowledge of the effect of environmental factors on the movements, migratory behavior, and dispersion patterns of fish is important. This knowledge is essential for the development of plans for rebuilding and conserving depleted stocks. Climate change is already affecting ice melt and ocean currents in eastern Canada, and the impacts of the changing environment on cod needs to be understood to mitigate climate impacts. The response of fish populations to climate change has been documented in the past. For instance, in the North Atlantic, northward shifts have been reported for demersal fishes, such as cod and haddock (*Melanogrammus aeglefinus*)

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(Perry et al. 2005; Rose 2005; Drinkwater 2009), as a response to climate forcing, primarily via water temperature. Therefore, temperature is one of the primary factors, along with food availability, depth, salinity, shelter, and suitable spawning and nursery grounds that determines the large-scale distribution patterns of many fish populations (Ottersen et al. 1998; Perry et al. 2005; Rijnsdorp et al. 2009).

The northern Gulf of St. Lawrence Atlantic cod stock (Northwest Atlantic Fisheries Organization (NAFO) Divisions 3Pn4RS) was at one time one of the largest cod stocks in North America, with as much as 100 000 t of cod harvested in some years (Chouinard and Fréchet 1994). Largely because of overfishing, the stock collapsed in the early 1990s to ~10% of the historical peak abundance, which had been recorded just 10 years earlier (Savenkoff et al. 2007). In parallel with the decline of biomass, there was also a contraction of the geographic distribution: cod is now rare on the north shore of the Gulf of St. Lawrence (Division 4S) and is concentrated mainly along the west coast of Newfoundland (Division 4R) (Fig. 1). Northern Gulf cod has shown little sign of recovery, and the loss of spawning components has been suggested as one reason (Swain and Castonguay 2000; Yvelin et al. 2005).

The migration pattern of cod in the northern Gulf of St. Lawrence (Divisions 3Pn4RS; Fig. 1) is well known. Generally, cod overwinter in Division 3P, on the northern side of Cabot Strait off the southwest coast of Newfoundland, including Burgeo Bank (Campana et al. 1999; Méthot et al. 2005), move to the northern Gulf (Divisions 4R and 4S) in spring for spawning (Ouellet et al. 1997), and remain there during the postspawning feeding period, when they may be found inshore. They migrate back to the northern side of Cabot Strait (Division 3P) in late autumn and early winter (Chouinard and Fréchet 1994; Castonguay et al. 1999; Yvelin et al. 2005). However, the migratory behaviour may vary with respect to both feeding and spawning season and depends on the abundance of the cod stock and environmental conditions (Moguedet 1994; Kulka et al. 1995). Moreover, cod spatial dynamics are linked to both spatial scale and biomass (density dependent) as well as environmental factors such as temperature, salinity, or depth (density independent) (Tamdrari et al. 2010).

A recovery strategy and good fisheries management should consider dispersal and migratory behaviour patterns at a small scale. Our objective was to analyse dispersal patterns of cod in the northern Gulf of St. Lawrence (Divisions 4R and 4S) inferred from tagging experiments performed from 1995 to 2008 by the Department of Fisheries and Oceans (DFO) Canada. This study considers only fish that completed at least a full migration cycle, i.e., fish recaptured in the same year that they were tagged were excluded. It also focused exclusively on recaptures made during summer, when most recaptures are made. Where dispersal patterns among recaptured cod were obviously different, potential underlying factors responsible for the differences were explored, such as environmental factors. Finally, we examined how such dispersal patterns covary with biotic (biomass) and abiotic (temperature, salinity, and depth) factors. This information is critical for improved understanding of the behaviour and dispersal patterns of the cod stock in the northern Gulf of St. Lawrence and will lead to more informed fishery management in the future.

Materials and methods

Study area

The study area was the northern Gulf of St. Lawrence (NAFO Divisions 4R and 4S), covering a total area of 103 812 km^2 (Fig. 1). The northern Gulf is characterized by highly variable bathymetry, with a maximum depth of about 500 m, and is dominated by shallow coastal shelves with deep channels that bisect both the eastern and northern extensions (Koutitonsky and Bugden 1991).

Tagging and recapture data

From 1995 to 2008, over 70 000 tagged cod were released in the Gulf of St. Lawrence. The tagging program operated annually from February to December in Division 3Pn and from June to December in Divisions 4R and 4S. Fish were captured by a fixed-gear commercial fishery (long lines, feathered hooks, and cod traps). Only cod >43 cm long and in good condition were tagged. Further details concerning tagging methods are presented in Bérubé and Fréchet (2001).

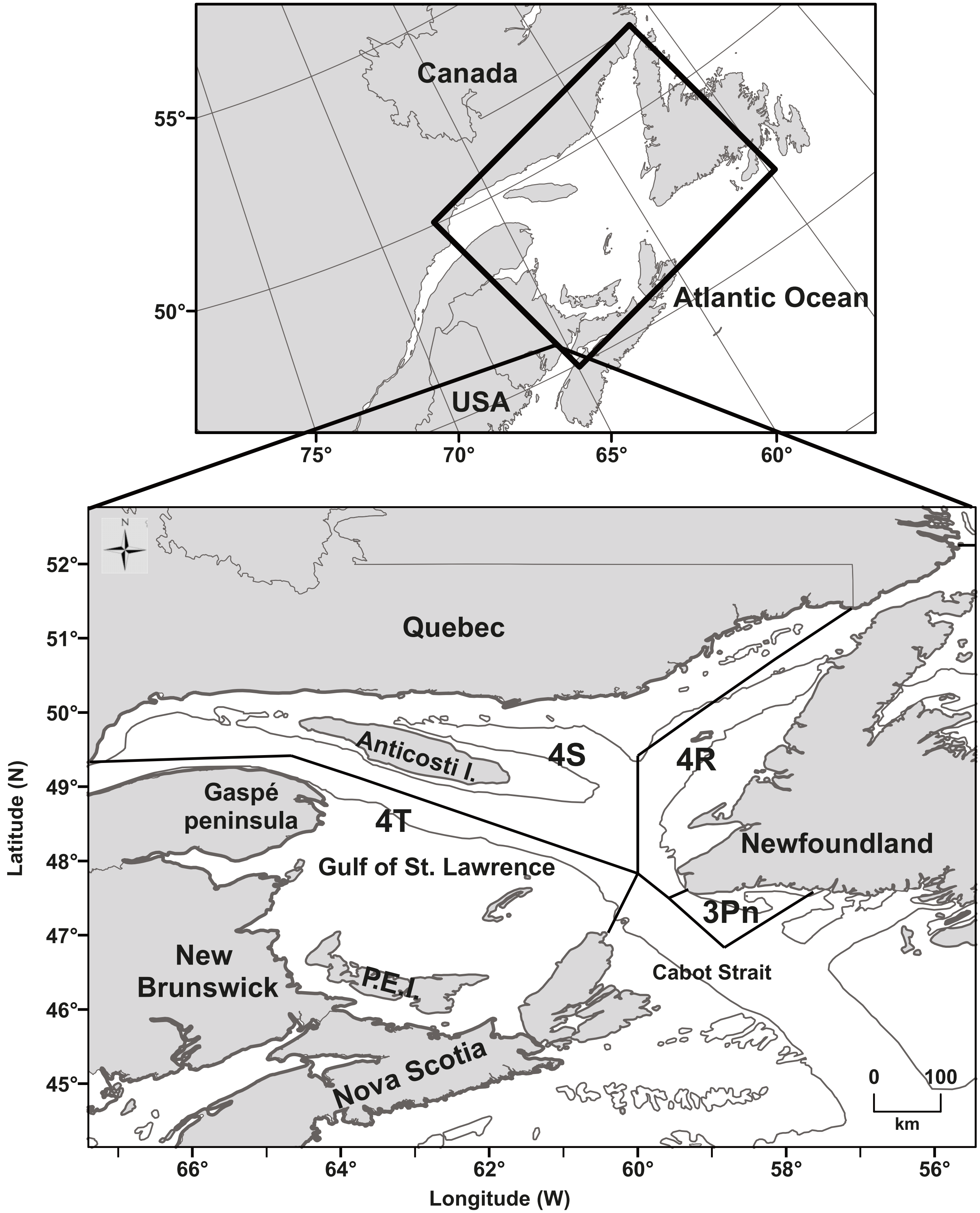
In the northern Gulf of St. Lawrence (Divisions 4R and 4S), only 5.1% of tags were recovered between 1997 and 2008. This reporting rate seems low considering the fishing mortality observed since 1997, which was generally higher than 0.20 (Fréchet et al. 2009). This low rate may be linked not only to natural and fishing mortality, but also to the low reporting rates of tags by fishermen (Cadigan and Brattey 2006, 2008). The majority of tagged cod (78.7%) were recaptured during summer (July, August, and September), reflecting that most fishing activity for this stock occurs then.

The present study considers only fish that had made a complete migration cycle and was restricted to summer, when most of the recaptures occurred and when cod are known to disperse on feeding grounds. Because there was a fishing moratorium in 1995, 1996, and 2003, these years were excluded from the analysis. Stock biomass data were obtained from a sequential population analysis (Fréchet et al. 2009).

Environmental variables

Because cod is a demersal species, bottom temperature at the recapture location is assumed to reflect the ambient temperature of the individual fish. Temperature and salinity were estimated on the sea bottom and within the water column for each sampling year using the following methods. First, all available CTD (conductivity–temperature–depth) casts sampled by the DFO in the Gulf of St. Lawrence during August of each year were assembled and bin-averaged at 1 m intervals (typically 250 or more casts for each year). For each 1 m depth interval, the binned CTD temperature and salinity were interpolated onto a 2 km resolution grid data using the Barnes algorithm as described in Galbraith (2006). To prevent the extrapolation of horizontal temperature and salinity gradients to unreasonable values, the grid interpolations were then bound by the layer minimum and maximum values found in each of nine oceanographic subareas of the Gulf (Galbraith et al. 2010). Temperature and salinity interpolations were thus discarded for waters deeper than the

Fig. 1. Gulf of St. Lawrence showing North Atlantic Fisheries Organization (NAFO) divisions. The grey line indicates the 200 m isobath.



deepest available data in each of the nine subareas. To fill these deep gaps, the vertical temperature (and salinity) gradient at these grid points was calculated by linear regression on the deepest 10 m of available interpolations. Its slope was projected through deeper missing bins to the bottom if the regression accounted for more than 50% of the variance (R^2 > 0.5); otherwise the mean temperature (or salinity) in that deepest 10 m was used for all deeper missing bins. Lastly, bottom temperature and salinity were estimated at each grid point by looking up the interpolated temperature and salinity at the depth level corresponding to a bathymetry grid obtained from the Canadian Hydrographic Service.

Since cod captures occurred at different periods of the year, and knowing that the top 150–200 m of the water column is affected by seasonal variability (e.g., Galbraith et al. 2010), the August interpolations described above were adjusted to the capture dates using a climatological seasonal cycle. This cycle was derived for all longitudes, latitudes, and depths of the Gulf using the harmonic analysis method of Ouellet et al. (2003), whereby the mean annual cycle of all available historical CTD data is least-squares fit to a sum of oscillations with periods of 1 year, 6 months, and 4 months (J. Chassé, DFO, Institut Maurice-Lamontagne, Mont-Joli, Que., personal communication, 2010).

We also estimated the areas of suitable habitat based on cod temperature preferences, for the summer of each year and for depths shallower than 100 m (3–7 °C; Hedger et al. 2004; Lafrance et al. 2005). In this study, we used area (km^2) of suitable thermal habitat as an index of habitat suitability (i_s) for cod.

In the present work, we used the bathymetry at the position of recapture as the depth, because fishermen did not record recapture depths.

Spatial indices

Two spatial indices were used to investigate dispersal patterns: the centre of gravity (with its inertia) (CG, *I*), and the dispersion index (D_m). These parameters are useful for detecting changes in spatial patterns of fish populations (Bez 1997; Woillez et al. 2007). CG represents the mean location (latitude or longitude) of a population in the field. Inertia is the mean square distance between individual recaptured fish and the CG; it describes the dispersion of recaptured cod along latitudinal or longitudinal axes. In the absence of fishing effort data, the total catch of cod per month per unit area (the smallest area available) was used as a proxy for fishing effort to weight the index. This method has previously been used for tagging data by Lawson and Rose (2000) and Brattey et al. (2002).

The centre of gravity (CG) is calculated as

$$\text{(1)} \qquad \mathrm{CG} = \frac{\sum_{i=1}^{n} x_i C_i}{\sum_{i=1}^{n} C_i}$$

where x_i is the location of each recaptured fish i (either latitude or longitude in decimal degrees) and C_i is the recorded landing for the month and the subarea of recapture.

Equation 2 shows how the inertia (*I*) is calculated with variables x_i and C_i as described above.

$$\text{(2)} \qquad I = \mathrm{Var}(x) = \frac{\sum_{i=1}^{n} (x_i - \mathrm{CG})^2 \times C_i}{\sum_{i=1}^{n} C_i}$$

The dispersion index, D_m, reflects the mean geographical position of individuals, while the mean square error of those positions appears as an index of dispersion or concentration. Mathematical formulations of this index were originally proposed by Dagnelie and Florins (1991). We have adapted them to recapture data. D_m was calculated for the summer period of each year according to the following equation:

$$\text{(3)} \qquad D_m = \sqrt{\frac{1}{n}\sum_{i=1}^{n}[(x_i - \bar{x})^2 + (y_i - \bar{y})^2]}$$

where n is the number of recaptured fish, x_i and y_i are the latitude and longitude of recapture, respectively, and $\bar{x}$ and $\bar{y}$ are the means of the longitude (x_i) and latitude (y_i).

Statistical analysis

We tested interannual variations at recapture locations of mean summer bottom temperature, salinity, and depth by performing one-way analyses of variance (ANOVAs) using year as the fixed factor. The relationships between the dispersion index (D_m) and mean bottom temperature, salinity, depth of recapture, the index of suitable habitat, and the biomass of cod 5 years and older was investigated. As explanatory variables are not independent, autocorrelation was tested within each variable, and no autocorrelation was observed (P > 0.05). Therefore, the independence of observations was assumed. To take into account errors on both *x*- and *y*-axes, the relationship was tested using an orthogonal regression function (model II linear regression), (Legendre and Legendre 1998). The function of the regression corresponds to the standard major axis (Legendre and Legendre 1998). Analyses were done with R software.

Results

A total of 1175 tagged cod were recaptured in summer between 1997 and 2008. Only fish that had made at least a complete migration cycle or more were considered. Most tagged cod (87.4%) were recovered in Division 4R area as opposed to Division 4S (Table 1).

Centre of gravity , dispersal patterns, and environmental factors

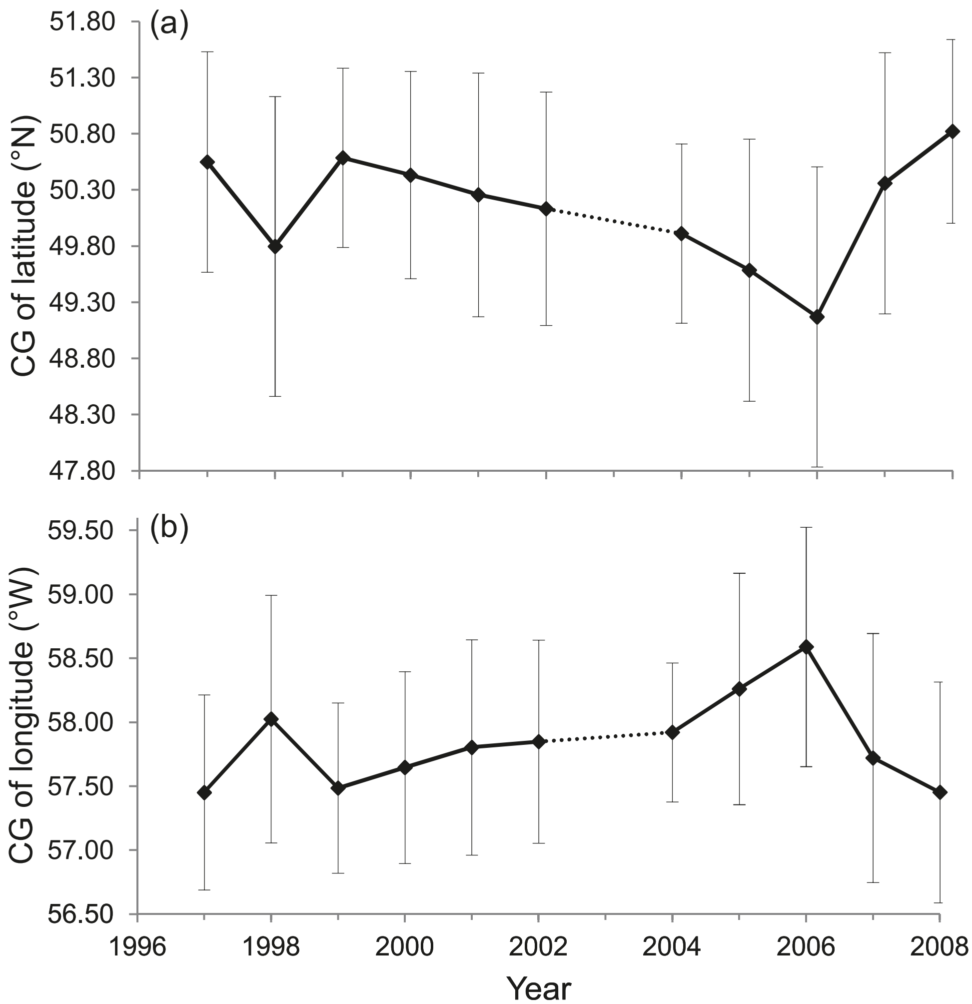
From 1997 to 2006, the mean latitude of recaptures moved southward by more than 1.5° (Fig. 2). During the same period, the mean longitude moved westward by about 1°. This southwestward displacement of the cod population was followed by a northward movement from 2006 to 2008, with a difference in mean latitude of almost 2°. This northward shift was associated with a contraction along the Newfoundland coastline as the mean longitude moved eastward.

Table 1. Summary of recoveries of cod tagged in the northern Gulf of St. Lawrence.

	Recovery year											
Recovery area	1997	1998	1999	2000	2001	2002	2004	2005	2006	2007	2008	Total
4R	40	45	95	90	133	147	33	81	137	146	80	1027
4S	11	13	15	21	22	32	14	5	2	2	11	148
All (4R and 4S)	51	58	110	111	155	179	47	86	139	148	91	1175

Note: Only tags with precise recovery information (location and date) recovered in summer and at large for 1 year or longer were used.

Fig. 2. Geographic coordinates of the centre of gravity (CG, ± square root of the inertia) of recaptured cod: (*a*) CG of latitude; (*b*) CG of longitude.



Interannual variation in the dispersion index (D_m) did not show any particular trend (Fig. 3*a*). However, 1997 and 1998 had the highest dispersion indices, 1.78 and 1.56, respectively. The years 1999 and 2006 had the lowest indices (1.20 and 1.21, respectively), indicating a higher cod concentration. The dispersion index for other years varied between 1.39 and 1.50, reflecting the large variability in cod concentration. From 2006 to 2008, the dispersion index increased slightly.

Temporal variations in the mean bottom temperature at recapture locations were significant among years (ANOVA, $P < 0.001$). The years 1997 and 1998 were characterized by the coldest mean temperatures (2.95 and 2.92 °C, respectively), while 1999 was the warmest (~5 °C) (Fig. 3*b*). From 2000 to 2004, temperatures were relatively stable, with a mean of about 3.7 °C. From 2005 onward, we observed an increasing trend in the mean bottom temperature, from 3.85 to 4.54 °C (Fig. 3*b*).

Similarly, mean salinity at cod recapture locations varied significantly among years (ANOVA, $P < 0.001$). Two broad periods can be identified: 1997–2004, when salinity varied slightly from 32.0 to 32.3, and then an increase to 32.6 was observed in 2005, after which salinity declined (Fig. 3*c*).

Temporal variations of mean depths at recapture locations are also significantly different among years (ANOVA, $P <$ 0.001) (Fig. 3*d*). From 1997 to 2000, the mean recapture

Fig. 3. Interannual variation in the dispersion index (*a*) and mean bottom temperature (*b*), salinity (*c*), and depth (*d*) at recapture locations. Error bars indicate 95% confidence intervals. There are no data in 2003 because the fishery was under moratorium.

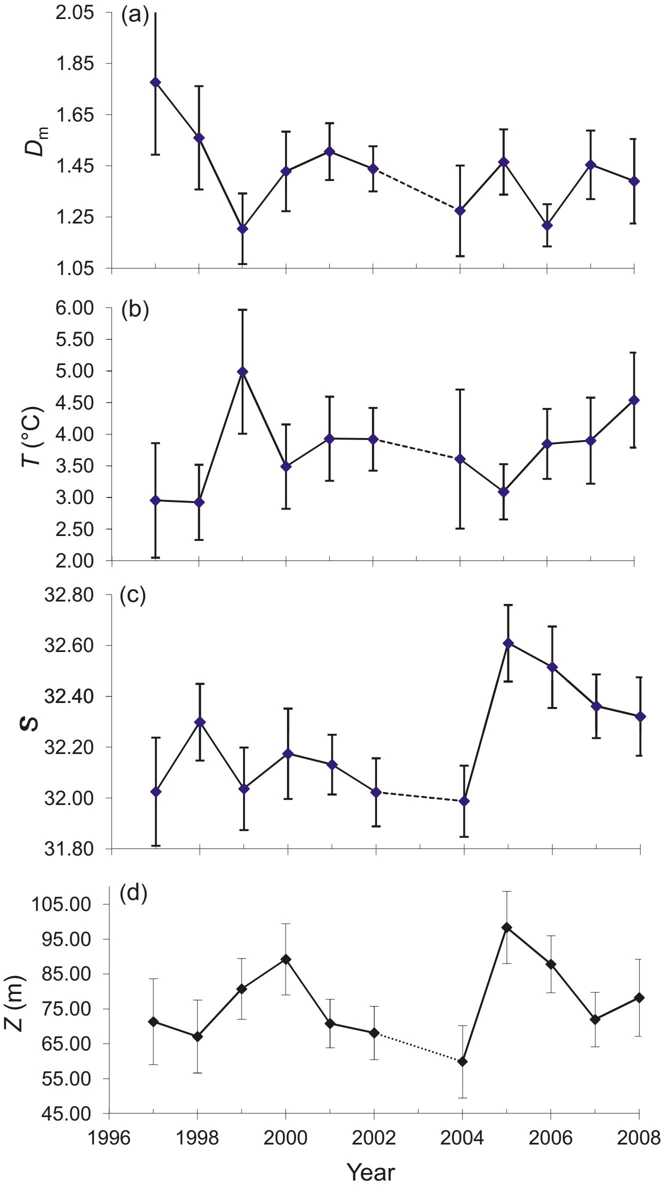
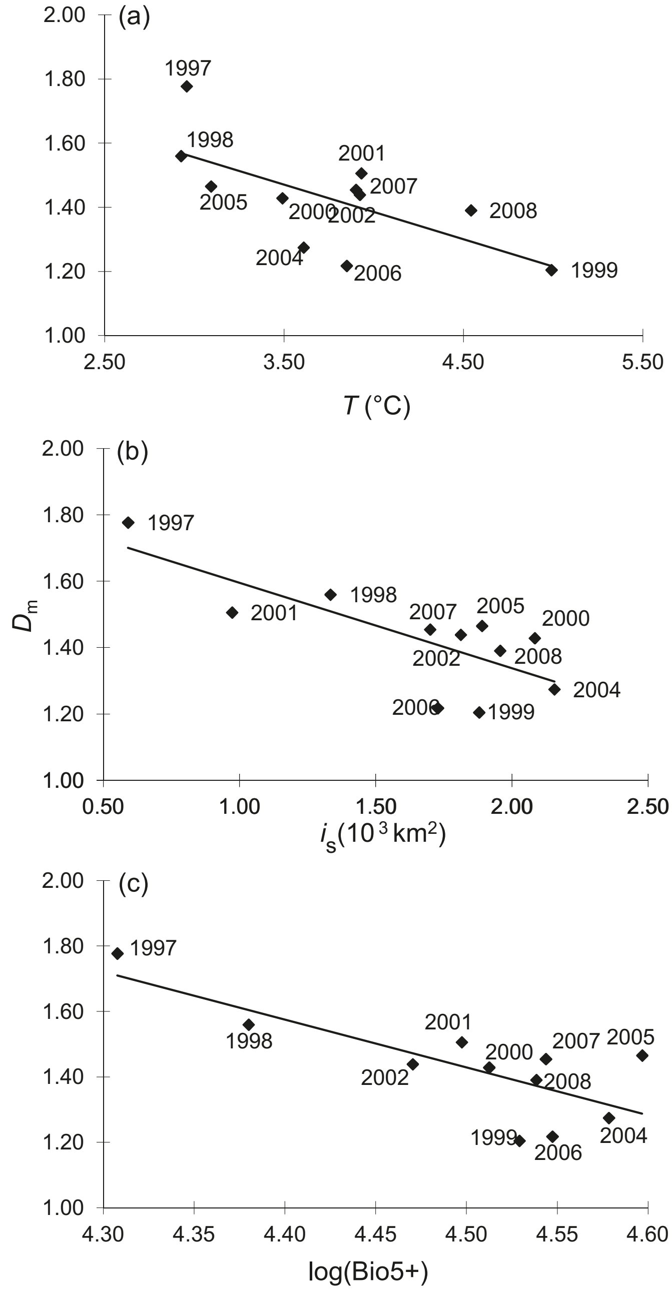


Fig. 4. Relationships between the index of dispersion and mean bottom temperature (*a*), an index of suitable thermal habitat (*b*), and cod biomass age 5+ years (*c*).



depth increased from about 67 to 89 m, followed by a decrease to 60 m until 2004. In 2005, the mean recapture depth was the highest (98 m) and decreased thereafter until 2008.

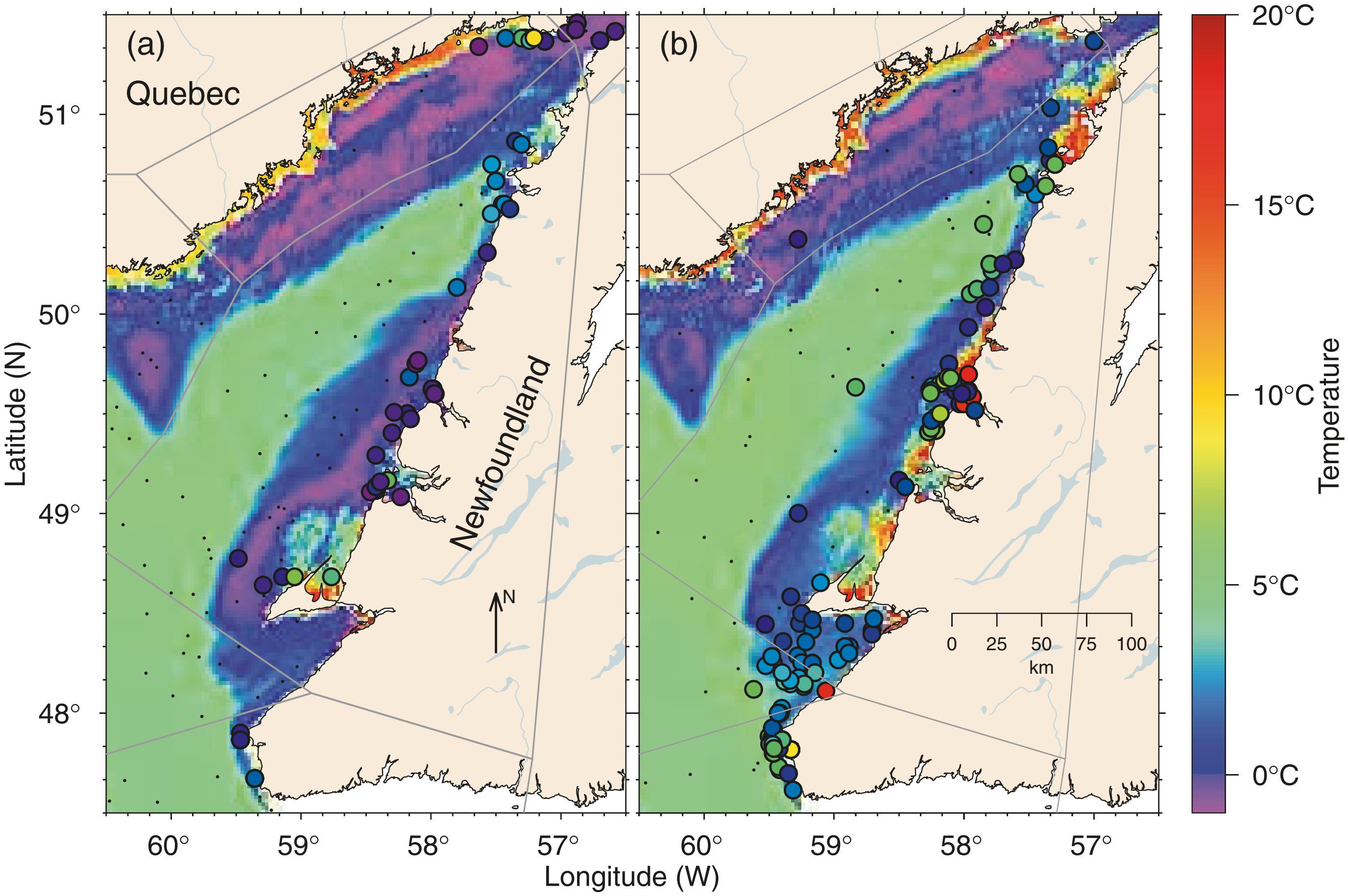
Relationships among the dispersion index, environmental factors, and biomass

The dispersion index of recaptured cod varied negatively with bottom temperature ($D_m = 2.361–0.247T$, $R^2 = 0.467$, $P = 0.02$, Fig. 4*a*). Cod were dispersed at low temperatures (1997 and 1998), while they were more concentrated at higher temperatures (1999 and 2006). This pattern is observed when comparing distributions between the coldest (1998) and one of the warmest years (2006) (Fig. 5). In 1998, cod were more dispersed at temperatures below 3 °C, whereas in 2006 we observed different patches or aggregates of cod at temperatures >3 °C along the west coast of Newfoundland (Fig. 5). The influence of temperature on dispersal behaviour suggests a density-independent dynamic.

The dispersion index of recaptured cod in the northern Gulf of St. Lawrence varied significantly with the index of suitable habitat ($D_m = 1.968–0.326i_s$, $R^2 = 0.617$, $P = 0.004$, Fig. 4*b*). Cod were widespread when suitable habitat conditions were not available, as observed in 1997 and 1998, while they tended to be more aggregated when habitat was more suitable, as observed in 2004 and 2006.

As with temperature, a significant negative relationship between biomass and the dispersion index was observed ($D_m = 9.702 – 1.837 \log_{10}$ (Bio5+), $R^2 = 0.610$, $P = 0.004$, Fig. 4*c*):

Fig. 5. Bottom temperatures in August (*a*) 1998 and (*b*) 2006. The positions of conductivity–temperature–depth casts used for the interpolation are shown (dots) as well as the positions of cod recaptures (circles), colour-coded according to temperatures interpolated at these positions (colour scale). The gray outlines represent the oceanographic subareas used to limit temperature and salinity extrapolations at each 1 m depth layer.



cod aggregated when biomasses were higher. The years 1997 and 1998 had the lowest biomass and highest dispersion index, while the reverse was true for 2004 and 2006. This result suggests a direct effect of abundance on dispersion pattern, that is, a density-dependent dynamic.

No statistically significant relationship was observed between the dispersion index and salinity (D_m = 25.565 – 0.748S, R^2 = 0.010, P = 0.82), which is probably due to the low interannual variability (32.0–32.6) of salinity during the study period. Recapture depth was not a significant factor affecting dispersion (D_m = 2.497 – 0.013Z, R^2 = 0.04, P = 0.59), which primarily reflects the inshore concentration of fishing effort rather than a purely behavioural response.

Discussion

Using tagging data collected over a 10-year period and environmental data at the precise locations of recaptures, this work shows that the dispersal behaviour of northern Gulf of St. Lawrence cod is driven by both abiotic and abiotic factors, acting together.

There was a southwestward displacement in the centre of gravity of recaptured fish from 1997 to 2006. Owing to the shape of the northern Gulf of St. Lawrence, the westward movement is offshore and towards areas where cod were once historically abundant, suggesting hints of a recovery. However, cod have shown a northeastward movement since 2006, which coincided with increasing mean bottom temperatures and decreasing mean salinity and depth in this region. The evidence that the centre of distribution of cod along the coast shifted northward in recent years can be attributed not only to warmer conditions but also to the two stronger year classes that were produced in 2004 and in 2006 (Department of Fisheries and Oceans 2009) and a density-dependent dispersal (Tamdrari et al. 2010). Similar movements have been also observed in the North Sea for some demersal fish (Hedger et al. 2004; Perry et al. 2005). The geographic contraction of cod to the east in recent years is contrary to data collected during the summer (August) bottom trawl research survey, which covers the entire northern Gulf of St. Lawrence except for the nearshore region (<37 m) (Tamdrari et al. 2010). This contraction could be attributed to the spatial distribution of fishing effort deployed in these areas. It is also possible to consider that fishermen concentrate their effort in areas of high cod abundance, responding to shifts in cod distribution through fish movement or local depletion (Rose and Leggett 1991), and therefore that effort is indicative of the presence of cod.

Temperature was one of the most important factors affecting the spatial distribution and dispersal behaviour of cod.

During summer, cod tend to disperse at a lower temperature (<3 °C), seeking areas of preferred warmer temperatures while they are more concentrated at temperatures near 4 °C. As stated by Hedger et al. (2004), the preferred temperature range of cod is between 3 and 7 °C. Lafrance et al. (2005) experimentally determined that cod prefer temperatures between 3 and 7 °C according to age. Nevertheless, cod have been observed over a much wider range of temperatures (less than –1 to 20 °C) (Wroblewski et al. 1994; Ottersen et al. 1998; Rose 2005). Several studies have examined whether temperature change can affect the distribution patterns of cod in the Gulf of St. Lawrence (Rose and Leggett 1988; Swain et al. 1998; Castonguay et al. 1999). Their findings suggest that cod change their spatial distribution in response to interannual changes in shelf water temperatures, which is also what we found in this study. The same behaviour has been reported for cod on Georges Bank (Mountain and Murawski 1992), on the Newfoundland and Labrador Shelf (deYoung and Rose 1993), and also for other species in the North Sea such as sole (*Solea solea*), plaice (*Pleuronectes platessa*), and flatfishes (Engelhard et al. 2011; van Hal et al. 2010), and in the Pacific Ocean for Pacific hake (*Merluccius productus*) (Ressler et al. 2007).

It is important to note that in warm years, cod exhibited a different dispersion pattern than in cold years, suggesting that cod will aggregate on the same summer feeding grounds year after year when conditions are good. This pattern also seems to be influenced by the availability of suitable habitats and probably other factors such as food availability. The most important prey is capelin, and when capelin is abundant, cod will abandon thermal preferences to prey on it (Rose and Leggett 1989). The temperatures observed in this study are in the range of cod preferences, and, if food had an effect, it did not seem to create distortions in the observed patterns.

As with temperature, cod exhibited two different patterns: more aggregated in the most suitable thermal habitats and dispersed in poor thermal habitats; this is unlike what was observed in earlier studies, which found an influence of depth and salinity on the spatial distribution of cod in the northern Gulf of St. Lawrence (Ruppert et al. 2009) and in the North Sea (Hedger et al. 2004). This could be due to the low interannual variation in recapture depth and salinity in this study and to all recaptured cod being located in inshore areas where there is fishing effort. Fisheries in the northern Gulf of St. Lawrence are presently exclusively coastal and exploited with fixed gear.

The respective levels of influence of biomass and temperature, as they covary, cannot be discriminated to explain the spatial distribution patterns of northern Gulf cod. For instance, Swain and Kramer (1995) reported that the median temperature of cod distribution in the southern Gulf of St. Lawrence tends to be colder at high levels of biomass, a trend not observed in the present study. Results indicate that biomass and temperature act together on the dispersal behaviours, and their common effects suggest a dynamic that is both density dependent and density independent. The dynamics of density independence are more influenced by temperature than by other abiotic factors, such as depth and salinity in our case. Tamdrari et al. (2010) noted that in the northern Gulf of St. Lawrence, the proportional density model — a density-independent model — best described cod spatial distribution patterns at a large scale, while both density-independent and density-dependent models described distribution patterns on a smaller scale. Furthermore, density-dependent habitat selection at the local level is not always detectable when considering a large spatial scale (Anneville et al. 1998). The abundance and spatial scale can covary with other factors such as temperature. Therefore, the best model might consider both density-dependent and -independent effects, as suggested by Cushing (1972) and more recently by Shepherd and Litvak (2004) and Tamdrari et al. (2010).

The dispersion pattern or spatial dynamics of marine fish populations may be more complex than as presented in theoretical models. Cod spatial dynamics in the northern Gulf of St. Lawrence are largely controlled by the 4R substock. However, 2006 seems to be pivotal because it coincides with the northward movement, a slight increase in the cod population dispersion, an increase in mean bottom temperature, and a decrease in mean salinity and depth of recapture. Two independent data sources, bottom trawl surveys (Tamdrari et al. 2010) and tagging data (this paper), have shown that changes in spatial dynamics appear to have started in 2006. Moreover, this 2006 change in spatial dynamics was observed in all age groups (Tamdrari et al. 2010).

There is evidence that collapsed fish stocks may concentrate; this has been seen for northern cod (Taggart et al. 1994; Atkinson et al. 1997; Rose and Kulka 1999), haddock (Marshall and Frank 1994; Casini et al. 2005), and pelagic shoaling fish such as anchovy (MacCall 1990; Bertrand et al. 2004). This means that even the remnants of once-large stocks can be exploited profitably until exhaustion of stocks. If stocks are to recover to previous levels and once again expand the fill the historical stock area, the recovery must come from the remnant populations. Clearly, understanding the spatio-temporal distribution and dispersal behaviour of northern Gulf of St. Lawrence cod in relation to their environment and density-dependent dynamics is important for assessing the potential consequences of management actions. The present study provides an indication of some important factors affecting the spatial distribution and dispersal behaviour of cod. As such, it forms a basis for exploring the subpopulation dynamics underlying recent stock declines and potential recovery.

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