Density-independent and -dependent habitat selection of Atlantic cod (Gadus morhua) based on geostatistical aggregation curves in the northern Gulf of St Lawrence

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Relationships were sought between local density and population abundance of Atlantic cod (Gadus morhua) in the northern Gulf of St Lawrence (Canada) over its entire area (4RS) and also within a subarea (4R) where the stock has concentrated since it collapsed during the early 1990s. Relationships were analysed using geostatistical aggregation curves computed within the two areas between years of contrasting abundance levels. The curves were interpreted in terms of four conceptual models of spatial dynamics: models D1 and D2, forced mainly by environmental heterogeneity, and models D3 and D4, in which individual behaviour is influenced by local density. Over the entire area, the cod population follows the D2 model for all years and age groups, and it is influenced by abiotic factors. Within the subarea, all four models applied, and the density-dependent basin model (D4) dominated from 2006 to 2008. The year 2006 seems to be pivotal because it coincides with the expansion of the cod population into its former area in the western Gulf (4S).

Keywords: depleted groundfish populations, habitat selection, spatial dynamics, stock rebuilding.

Received 10 September 2009; accepted 8 June 2010; advance access publication 30 July 2010.

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Introduction

An important goal in ecology is to understand the distribution patterns of organisms in relation to the available habitat and to determine what spatial structure reveals about ecological processes (Dieckmann et al., 2000; Doebeli and Killingback, 2003). Much work to date has emphasized the importance of considering the spatial component in understanding exploited marine ecosystems as well as the temporal and spatial scales of variations within those ecosystems (Babcock et al., 2005; Fréon et al., 2005). Moreover, the choice of habitat by marine fish depends on a variety of biotic and abiotic factors (Swain et al., 1998; Swain and Benoit, 2006). Hydrodynamics play an important role in the spatial variability of fish populations through the phenomena of drift and retention during the pelagic phase of organism development (van der Veer et al., 1998; Bakun, 2001). Changes in spatial structure may be associated with temperature, depth (Castonguay et al., 1999; Cote et al., 2004; Gaertner et al., 2005), salinity, or oxygen concentration (D’Amours, 1993; Neuenfeldt and Beyer, 2003). Other factors related to individual behaviour affect the spatial distribution at different scales (Fréon and Misund, 1999; Morris, 2003).

Ecological patterns in species distribution and abundance are linked to habitat characteristics, dispersal mechanisms, colonizing abilities, gene flow, and genetic structure (Beldon, 1995; Bailey, 1997). The ability to occupy available habitat depends on how well individuals and populations can minimize the negative factors of competition and predation and optimize the compromises between biological and environmental constraints (Morris, 1987; Lévéque, 1995).

Relationships between abundance and the geographic distribution of populations have been studied using dispersion indices and geostatistical analyses. They can provide information on the underlying mechanisms of habitat selection (Fréon and Misund, 1999). Habitat selection based on density-dependence has been described for pelagic species (MacCall, 1990; Fréon and Misund, 1999) and groundfish (Swain and Wade, 1993; Swain and Morin, 1996; Woillez et al., 2007; Spencer, 2008). The ideal-free distribution theory has been proposed to explain the distribution of fish populations (Fretwell and Lucas, 1969; Stephens and Stevens, 2001). The theory assumes that individuals have a complete knowledge of their environment, being free to move between habitats and to adopt the foraging strategy that maximizes the net energy intake per unit of time. Therefore, if fish populations follow the ideal-free distribution, the expectation is that only the best foraging habitats would be occupied at low abundance. As abundance increases, individuals should start to occupy less optimal habitats, because intraspecific competition would reduce the desirability of the best habitats. As a result of such behaviour, the population range should expand with population size. In a fisheries context, if a population follows the ideal-free distribution, then as population size decreases, a unit of
Density-independent and -dependent habitat selection of Atlantic cod

The Gulf of St Lawrence Atlantic cod (Gadus morhua) stock [Northwest Atlantic Fisheries Organization (NAFO) Division 3Pn4RS] was at one time the second largest cod stock in North America, with as much as 100,000 t of cod taken from it in some years (Chouinard and Fréchet, 1994). Largely because of overfishing, the stock collapsed in the early 1990s to ~10% of historical peak biomass, which had been recorded just 10 years earlier (Savenkov et al., 2007). Biomass then increased through the moratorium that was placed on the fishery (1994–1996) up to about 1999, then was stable at a relatively low level until two stronger year classes were produced in 2004 and especially in 2006 (DFO, 2009). Notwithstanding these two year classes, current biomass remains substantially below the levels of the late 1980s and early 1990s. Along with the collapse, there was a contraction in the area occupied by the stock, and most of the remaining biomass was concentrated along Newfoundland’s west coast (Division 4R). Perhaps, spawning components (substocks) may have been lost (Swain and Castonguay, 2000; Yvelin et al., 2005). Since 1997, the commercial catch from the stock has fluctuated between 3300 and 7200 t (except for 400 t in 2003, when a second moratorium of a single year was in effect). Fréchet et al. (2009) provide more information on the fishery and abundance trends of this stock.

In the context of a recovery strategy and better management of fisheries, it is important to understand how this particular cod stock could return to its previous geographic distribution. Using data from the summer scientific bottom-trawl survey carried out from 1991 to 2008 by the Department of Fisheries and Oceans (DFO), Canada, we here analyse the relationship between local density and total abundance over time for northern Gulf cod with geostatistical aggregation curves (Petitgas, 1998). The dynamics were contrasted at two spatial scales: the entire historical area of the stock and within a subarea where cod have persisted despite notable population fluctuations.

Material and methods

The Gulf of St Lawrence is a semi-enclosed sea connected to the North Atlantic Ocean through Cabot Strait in the southeast and through the Strait of Belle Isle in the northeast. Its bathymetry is dominated by the Laurentian Channel, a glacially deepened trough that divides it into two distinct systems: deep northern and shallow southern (Koutitonsky and Bugden, 1991). The study area here is the northern Gulf of St Lawrence (NAFO Division 4RS), a total surface area of 103,812 km² (Figure 1). The northern Gulf is physically and topographically heterogeneous (Koutitonsky and Bugden, 1991), and it consists of four distinct areas: a shallow shelf (<100 m) on the west coast of Newfoundland, a shelf on Québec’s North Shore characterized by uneven topography, the Laurentian Channel, which extends from Cabot Strait to the centre of the Gulf and is up to 500 m deep, and the Esquiman Channel, which connects the Laurentian Channel to the Strait of Belle Isle to the north, with an average depth of ~200 m.

The circulation in the Gulf is estuarine, governed by freshwater flow from the St Lawrence River and its tributaries and the deep saline water of Atlantic origin flowing upstream in the deepest part of the Laurentian Channel, while waters from the Labrador Shelf penetrate through the Strait of Belle Isle (Koutitonsky and Bugden, 1991; Saucier et al., 2003) and contribute to the formation of intermediate waters. The water column of the Gulf consists of three distinct water masses. The Atlantic deep waters on the bottom are relatively stable, with salinity near 34 and temperatures of 4–6°C. The waters of the cold intermediate layer (CIL) are characterized by low temperature (~2 to 0°C) and salinity between 32 and 33 (Koutitonsky and Bugden, 1991; Saucier et al., 2003). The warmer surface layer, the thickness of which can reach 40 m, has large seasonal variations in temperature and salinity. It forms in spring and disappears during winter. The low temperatures and the thickness of the CIL, which varies between 100 and 150 m, may potentially hinder the migrations of several fish species, including adult cod.

Data sources

Summer research bottom-trawl surveys in NAFO Division 4RS are conducted annually in August by the Department of Fisheries and Oceans, Canada. A stratified random-survey design is used (Gagnon, 1991). Between 163 and 238 fishing stations are occupied each year over 32 strata. From 1990 to 2003, the survey was conducted on board the RV “Alfred Needler” using a URI trawl with a 19-mm liner in the codend (24-min tows). Since 2004, however, the survey has been conducted on the RV “Teleost”, which is equipped with a Campelen 1800 trawl with 13-mm liner (15-min tows). The URI trawl data were converted to Campelen trawl data based on comparative fishing experiments held in 2004 and 2005 (Bourdages et al., 2007). Annual estimates of trowable biomass by divisions are obtained using the STRAP procedure (Smith and Somerton, 1981), which is the common method used by DFO to analyse data from bottom-trawl surveys.

The present work focused on the years 1991, 1993, 1996, 1999, 2001, and 2006–2008 to obtain a maximum biomass contrast and to keep the area sampled constant (30 depth strata covering together 82,327 km²). In all, 30 strata were covered, 85% of the total area (96,565 km²) sampled in the northern Gulf of St Lawrence.

To limit small-scale random variation, the sampling unit was the stratum. An average catch (kg) per tow was calculated for each stratum (catch per unit effort, cpue), considered in this study to be a “sample”. Knowing the average swept-area per tow and per stratum s, the cpue values were transformed into densities z using the relationship z = cpue/s (kg km⁻²)

Theoretical considerations on spatial dynamics

The present work is based on geostatistical aggregation (or concentration) curves, which are statistical tools derived from mining science (Matheron, 1981). Geostatistical tools have been used increasingly in fisheries and marine ecology, either to optimize sampling strategies (Petitgas, 1996) or stock assessment (Fernandes and Rivoirard, 1999; Rivoirard et al., 2000) or to map the distributions and spatial patterns of fish (Petitgas, 1998; Woillez et al., 2007; Doray et al., 2008; Barange et al., 2009). Mathematical formulations of the aggregation curves were originally proposed by Matheron (1981) and further adapted by Petitgas (1998) to fisheries data.
The types of spatial dynamics observed in marine species can be illustrated by four main models (Petitgas, 1998; Shepherd and Litvak, 2004) that describe the distribution patterns of the local population and illustrate the changes in density compared with total abundance. These are outlined below.

Dynamic D1—The area occupied by fish remains constant. An increase in population abundance is associated with an increase in fish density in one or several specific subareas, but densities elsewhere do not vary. In this case, local environmental effects favour an increase in local fish density.

Dynamic D2—The area occupied by fish remains constant. An increase in population abundance is associated with an increase in fish density at all points, but density remains a constant proportion of population abundance. This dynamic was referred to as the proportional density model by Hilborn and Walters (1992). Local fish density changes at the same rate as population abundance.

Dynamic D3—The area occupied by fish increases with population abundance whereas fish density remains constant. This dynamic was referred to by Hilborn and Walters (1992) as the constant density model.

Dynamic D4—The area occupied by fish as well as fish density vary with population abundance. Local density does not change at the same rate as population abundance, and maximum density increases with abundance.

Models D1 and D2 imply that the area occupied by a population is independent of its abundance, i.e. there is no significant correlation between abundance and distribution area. Models D3 and D4 imply a density-dependent geographic distribution, i.e. the area of distribution is positively correlated with total abundance. Model D4 corresponds to the “basin theory” proposed by MacCall (1990).

Geostatistical aggregation curves

To define a population’s spatial dynamics in terms of the theoretical models, curves were built representing the biomass and the proportion of total biomass observed on each surface unit as a function of the proportion of space occupied by the biomass. For this study, the surface unit was the stratum. Knowing cod densities $z_i$ in each stratum $i$, the densities are ranked in descending order, and biomass (density $\times$ stratum area $a_i$) are cumulated to obtain the cumulative biomass:

$$Q(z_p) = \sum_{i=1}^{p} a_i z_i.$$  \hspace{1cm} (1)

The corresponding cumulative proportion of biomasses is then

$$P(z_p) = \frac{Q(z_p)}{Q(z_n)} = \frac{\sum_{i=1}^{p} a_i z_i}{\sum_{i=1}^{n} a_i z_i},$$  \hspace{1cm} (2)

where $n$ is the total number of strata. The proportion of total area corresponding to the $p$ densest strata is given by

$$T(z_p) = \frac{\sum_{i=1}^{p} a_i}{\sum_{i=1}^{n} a_i}.$$  \hspace{1cm} (3)

$Q(z_p)$ measures the maximum fish biomass present in a proportion $T(z_p)$ of the total survey area. It is expressed in kg and ranges between 0 and the total fish biomass in the area ($Q_{\text{max}}$). $P$ and $T$ vary between 0 and 1. $P(T)$ is the cumulative function of the proportion of the biomass $P(z_p)$ for each area proportion $T(z_p)$.

Two types of curve are drawn: $Q(T)$ as a function of $T(z_p)$, and $P(T)$ as a function of $T(z_p)$. The concavity of the $Q(T)$ and $P(T)$ curves is described by a dispersion parameter that characterizes the spatial distribution of abundance, so represents a space selectivity.
index Ssp. Ssp is calculated from the P(T) curves using the following discrete approximation formula:

\[ Ssp = 2 \times \left[ \sum_{i=1}^{n} \left( \frac{P(T)_{i+1} + P(T)_{i}}{2} \times \frac{T_{i+1} - T_{i}}{2} \right) - \sum_{i=1}^{n} \left( \frac{P(T)_{i+1} + P(T)_{i}}{2N} \times T_{i+1} - T_{i} \right) \right]. \]  

(4)

The index Ssp represents twice the area between the diagonal and the curve P(T). From an environmental perspective, a high index in a dynamic process of spatial distribution means a greater capacity for habitat selection, which means a higher concentration of fish in certain habitats that may be the most suitable.

**Variation in the space selectivity index with population size**

For populations that follow a D1 dynamic, Ssp increases when population size increases, but for a D2 dynamic, the Ssp index remains constant and does not vary with population abundance. In contrast, Ssp increases when population size decreases for both D1 and D4 dynamics, and Q(T) curves are used to distinguish between D1 and D4 (Petitgas, 1998). For the D1 model, the Q(T) curves have the same origin, but for the D4 model, Q(T) curves are separated at the origin. Figure 2 of Petitgas (1998) provides a graphical explanation of how the space selectivity varies with population size.

To determine the dynamics in the northern Gulf of St Lawrence, a first step was to estimate Ssp from Equation (4) for each year and spatial scale considered. Calculations were made for the entire population, and also for three age groups (<4, 4–6, and >6 years). In a second step, the values of Ssp obtained for different periods were statistically compared using a bootstrap technique, by simulating a null hypothesis for the D2 dynamic (Petitgas, 1998). Sets of original Q and T data from the different periods were pooled and resampled randomly n times with replacement, thus generating a random set of nQ and nT. This resampling generated k pairs of Q and T. Then, using the equations above, k curves of P(T) were derived and their corresponding Ssp indices calculated. A mean Ssp was obtained for the pooled data for all years, with a confidence interval determined by the bootstrap procedure. When the annual Ssp value for a particular year was outside this confidence interval, the null hypothesis (D2) was rejected for that year. Each Ssp was calculated from 30 pairs of values of P and T (30 strata), then resampled 1000 times.

**Other spatial indices (centre of gravity and inertia)**

The centre of gravity and inertia may be useful in detecting changes in the spatial patterns of fish populations (Bert, 1997; Woillez et al., 2007). The centre of gravity represents the mean location of a population in a field, and inertia is the mean square distance between individual fish and the centre of gravity, describing population dispersion. The centre of gravity (CG) is

\[ CG = \frac{\sum_{i=1}^{n} x_i s_i z_i}{\sum_{i=1}^{n} s_i z_i}, \]

(5)

where \(x_i\) is the location (either latitude or longitude in decimal degrees) in stratum \(i\) weighted by cpue, \(s_i\) the area of influence (stratum surface), and \(z_i\) the cod density. The inertia (I) is then

\[ I = \text{Var}(x) = \frac{\sum_{i=1}^{n} (x_i - CG)^2 s_i z_i}{\sum_{i=1}^{n} s_i z_i}. \]

CG and I were computed for each age group and for all years, by latitude and longitude.

**Results**

**Geographic distribution**

Before the collapse of the northern Gulf of St Lawrence cod stock in the early 1990s, the maximum observed densities were west of Anticosti Island and off northwestern Newfoundland (Figures 2 and 3). Off west Anticosti, the mean density of individuals aged <4 and >6 years in 1991 was double that off northwest Newfoundland. In contrast, the average density of intermediate age groups (4–6 years) was 1.4 times higher off northwest Newfoundland. More than 50% of total-stock biomass was in NAFO Division 4S in 1991. In 1993, the densities were very low across the northern Gulf, <0.90 × 10^3 kg km^-2 for all age groups.

The spatial distribution of cod was similar between 1996 and 2001, with maximum densities between longitudes 56 and 60°W. More than 88% of the biomass was concentrated in area 4R, with densities ranging from <0.33 to 6.24 × 10^3 kg km^-2 for all ages combined. Since 2006, there has been a gradual increase in density. In 2008, almost 60% of total biomass was in 4R and 40% in 4S for age groups <4 and 4–6 years, and 75% of the biomass of the >6 years age group was in 4R and 25% in 4S (Figure 2).

For juvenile cod (age <4 years), the spatial distribution remained unchanged from 1996 to 2001. High densities were localized in area 4R (Figures 2 and 3). Between 2006 and 2008, the density of cod <6 years increased substantially in western 4S, although this increase was more pronounced for ages 4–6 years (Figure 2), a consequence of the relatively strong year classes produced in 2004 and 2006. The density of cod >6 years was still highest along the west coast of Newfoundland (4R) then (Figures 2 and 3).

**Spatial dynamics of age groups**

At the scale of the entire northern Gulf of St Lawrence (4RS), the proportional density model (D2) provided the best description for all age groups and years (Table 1). The Ssp values (range 0.892–0.943) indicated a high concentration of cod, fluctuating between years but without any particular trend. The concentration was slightly higher for the youngest age group and lower for the oldest group, although this difference was not significant (Kruskal–Wallis test, \(p = 0.34\)). This means that at a large spatial scale, local fish density changed at the same rate as total biomass for all age groups, i.e. the density at each point remained a constant proportion of the population abundance.

At the scale of 4R, which is ~40% of the distribution area of the whole stock, dynamic D2 was still dominant because there were no significant differences between the Ssp values between years (Table 1). Ssp values varied between 0.823 and 0.895 and were significantly lower than for the entire area 4RS (Mann–Whitney U-test, \(p < 0.0001\)), which means that the cod population was less habitat-selective at the smaller scale. The same trend in concentration between age groups was more pronounced than for the whole of 4RS, although it was not significant (Kruskal–Wallis test, \(p = 0.13\)).
The period 1991–2001 corresponded to the period when cod biomass contracted into 4R. When 2006 was compared at a small spatial scale (4R) with all other years using bootstrap tests on Ssp values (Table 1) and pairwise comparisons (Table 2), both density-dependent and -independent dynamics were observed for all age groups. Comparing 2006 with the years of
higher local abundance, i.e. higher $Q(T)$ in 1991, 1999, and 2001 (Figure 4), when biomass was decreasing, suggested that the density-independent model $D_1$ was appropriate. However, when the 2006 curve was contrasted with previous years of lower local abundance in 4R (1993 and 1996), the density-dependent basin model ($D_4$) described the spatial dynamics better, because biomass increased in the area occupied by cod (Figure 4). Comparing the 2006 curve with those for 2007 and 2008 suggests that density-dependent models would have been more appropriate (Table 2), because 2007 and 2008 were the years when the biomass

Figure 3. Relative densities of cod age groups (a) $<4$ years, (b) $4-6$ years, and (c) $>6$ years for 1996, 1999, and 2007. Circle diameters are proportional to fish density divided by the maximum density ($2.5 \times 10^3$ kg km$^{-2}$) in the survey for all years.

Table 1. Annual Ssp of cod in the northern Gulf of St Lawrence (4RS) and area 4R alone.

<table>
<thead>
<tr>
<th>Area</th>
<th>Age group (years)</th>
<th>Year</th>
<th>Confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Lower bound</td>
<td>Mean</td>
</tr>
<tr>
<td>Area 4RS</td>
<td>$&lt;4$</td>
<td>0.941</td>
<td>0.943</td>
</tr>
<tr>
<td></td>
<td>$4-6$</td>
<td>0.918</td>
<td>0.927</td>
</tr>
<tr>
<td></td>
<td>$&gt;6$</td>
<td>0.902</td>
<td>0.919</td>
</tr>
<tr>
<td>Area 4R</td>
<td>$&lt;4$</td>
<td>0.880</td>
<td>0.895</td>
</tr>
<tr>
<td></td>
<td>$4-6$</td>
<td>0.877</td>
<td>0.880</td>
</tr>
<tr>
<td></td>
<td>$&gt;6$</td>
<td>0.840</td>
<td>0.859</td>
</tr>
</tbody>
</table>

Emboldened values of Ssp are outside the confidence interval, so allow the rejection of model $D_2$. The null model ($D_2$) is tested by 1000 bootstraps at a significance level of 0.05.
Table 2. Pairwise comparisons of the type of spatial dynamics according to $Q(T)$ curves for cod aged $<4$, $4–6$, and $>6$ years at a small spatial scale (area 4R).

|------|------|------|------|------|------|------|------|

Emboldened values indicate cases where the null hypothesis $D_2$ model was rejected.

Discussion

The objective of this study was to examine the relationship between local density and overall population abundance of *G. morhua* at different scales in the northern Gulf of St Lawrence, using geostatistical aggregation curves (Petitgas, 1998). At the scale of the whole northern Gulf of St Lawrence (NAFO Division 4RS), the proportional density model ($D_2$) was best at describing the spatial distribution pattern for all age groups of Atlantic cod in all years. This pattern has also been reported for Atlantic cod in the North Sea (Myers and Stokes, 1989) and for young hake (*Merluccius merluccius*; Petitgas, 1994) and sole eggs (*Solea solea*) in the Bay of Biscay (Petitgas, 1997). Therefore, when abundance increases, the population use of space also increases to its known bounds, and $Ssp$ remains relatively constant.

On a smaller scale (NAFO Division 4R), all four types of spatial dynamic were found. However, as was the case for the entire stock area, the proportional density dynamic model ($D_2$) dominated. A differential density model ($D_1$) was sometimes found appropriate at this smaller scale. This is a pattern typical of more heterogeneous environments, which often provide a larger niche breadth. Species with the capacity to move freely over a relatively large and diversified area tend to concentrate in the most favourable habitats, which translates into a higher value of $Ssp$ when abundance increases. The constant density dynamic model ($D_3$; Hilborn and Walters, 1992) was occasionally found to apply to area 4R and has been reported previously to represent the dynamics of larval herring (*Clupea harengus*; Iles and Sinclair, 1982).

The results also reveal the presence of the density-dependent dynamic $D_4$, the basin model (MacCall, 1990). For example, this situation was observed when comparing localized abundance in 4R in 2006 with a decreased abundance in 2007, when cod were concentrating in the northeastern Gulf of St Lawrence (Tables 1 and 2). Dynamic $D_4$ has been reported for collapsed fish stocks: Californian anchovy (MacCall, 1990), anchovy and sardine in the southern Benguela and off Japan, California, and Perú (Barange et al., 2009), young cod around Newfoundland (Robichaud and Rose, 2006), and cod in the southern Gulf of St Lawrence (Swain and Wade, 1993). American plaice (*Hippoglossoides platessoides*) in the same area (Swain and Morin, 1996), and flatfish in the eastern Bering Sea (Spencer, 2008). Changes in average density and space occupied by cod are associated with changes in abundance.

Our results show that cod spatial dynamics in the northern Gulf of St Lawrence were largely controlled by the 4R substock from 1993 to 1996, when there was a trend of increasing biomass during the moratorium (Fréchet et al., 2009), unlike the scarcity of cod in 4S (Figures 2 and 3). The change in dynamics from $D_2$ to $D_4$ through $D_3$ and $D_1$ in recent years for all age groups can be associated with the confinement of the stock in area 4R, where there are density-dependent phenomena and geographic expansion attributable to the increase in total biomass (juvenile and adult). These processes are influenced by environmental factors and are linked to year-class strength and the behaviour of different age groups in area 4R. These dynamic changes seem to have started in 2006, coinciding with the relatively strong 2004 year class and an expansion of cod biomass into the western Gulf of St Lawrence (Figure 5). Swain and Wade (1993) noted that the regions with higher densities of juvenile cod in the southern Gulf of St Lawrence were the same at low and high levels of abundance, but that for adult cod (4+ years), the areas of high density varied with abundance levels.

The results discussed above, along with those from this study, suggest that the spatial dynamics of marine fish populations are more complex than as presented in theoretical models such as the ideal-free distribution. As stated by Petitgas (1998), the spatial dynamics supporting the basin model (MacCall, 1990) can be obtained by combining the proportional density model ($D_2$) and the constant density model ($D_3$).

Comparing the results for all age groups for the northern Gulf (4RS) with Division 4R, we found different dynamics (both
Density-dependent and -independent) at the smaller scale and a single dynamic (density-independence) at the larger scale. Density-dependent habitat selection at the local level is not always detectable when looking at a large spatial scale (Anneville et al., 1998). In earlier studies, the distribution of marine populations showing density-dependent habitat selection was approximately several thousands of square kilometres (Winters and Wheeler, 1985; Swain and Benoit, 2006; Spencer, 2008). In keeping with the beliefs of others (Maury et al., 2001; Shepherd and Litvak, 2004; Ehrich et al., 2009), such comparisons lead us to argue that fish spatial dynamics are scale-dependent. At the scale over which most marine fish populations are distributed, it seems unlikely that individuals would be informed adequately much beyond their immediate perceptual range. Even if they could obtain precise information about optimal suitability over the population’s distribution range, the energetic costs of travelling to the optimal habitat may outweigh any benefit that might accrue from doing so (Shepherd and Litvak, 2004). Both abundance and the area of distribution can co-vary with other factors not accounted for by the ideal-free distribution. Therefore, a more reasonable model might consider both density-dependent and -independent effects, as suggested by Cushing (1972) and others more recently (Anderson and Gregory, 2000; Fromentin et al., 2001; Shepherd and Litvak, 2004; Resetarits, 2005).

In area 4R, we observed a change from density-independent ($D_2$) to density-dependent basin model dynamics ($D_4$) in recent years. If spawning components were lost in area 4S, as suggested by Swain and Castonguay (2000) and Yvelin et al. (2005), this suggests that migrant cod from Newfoundland’s west coast (area 4R) might contribute to rebuilding the local remnant subpopulation of Quebec’s north shore (4S area) if density-dependent dynamics persist.

Understanding the consequences of density on distribution patterns is important for managing depleted populations. Fisheries management policies are often based on long-term monitoring of fish density from which trends in abundance are inferred. Variability in density-dependent habitat selection could alter the effectiveness of recovery strategies, especially with respect to rebuilding cod in area 4S. Overall, it is our opinion that it is important to promote growth in biomass of depleted populations.
groundfish populations to achieve density-dependent habitat selection.

Acknowledgements
We acknowledge the advice of Doug P. Swain at the outset of the study, Johanne Gauthier for help with databases, Laure Devine for improving the manuscript, and editor Verena Trenkel and two anonymous referees for thoughtful comments. The study was partly supported by SARCEP, a Species at Risk fund from the Department of Fisheries and Oceans, Canada.

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doi:10.1093/icesjms/fsq108