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

Hacène Tamdrari, Martin Castonguay, Jean-Claude Brêthes, and Daniel Duplisea

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 D_1 and D_2, forced mainly by environmental heterogeneity, and models D_3 and D_4, in which individual behaviour is influenced by local density. Over the entire area, the cod population follows the D_2 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 (D_4) 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).

H. Tamdrari and J-C. Brêthes: Institut des Sciences de la mer de Rimouski, Université du Québec à Rimouski, 310 allée des Ursulines, Rimouski, Québec, Canada G5L 3A1. M. Castonguay and D. Duplisea: Fisheries and Oceans Canada, Institut Maurice-Lamontagne, 850 route de la mer, PO Box 1000, Mont-Joli, Québec, Canada G5H 3Z4. Correspondence to H. Tamdrari: tel: +1 418 723 1986; fax: +1 418 724 1842; e-mail: hacene.tamdrari@uqar.qc.ca.

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 Benoît, 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 (Blondel, 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; Lévêque, 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

optimally targeted fishing effort would remove an increasingly larger proportion of the population, i.e. catchability increases with decreasing population size (Atkinson *et al.*, 1997; Swain and Benoît, 2006). This underscores the importance of conducting spatially explicit assessments of fisheries to support the implementation of appropriate management measures. The implications for the conservation of fish stocks then become obvious, and the classic economic argument in fisheries science theory that nonprofitability of fisheries with decreasing stock size will limit the overexploitation of stocks (Paloheimo and Dickie, 1964) could then become flawed.

The northern 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 (Savenkoff *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 trawlable 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 $z = \text{cpue}/s$ (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.
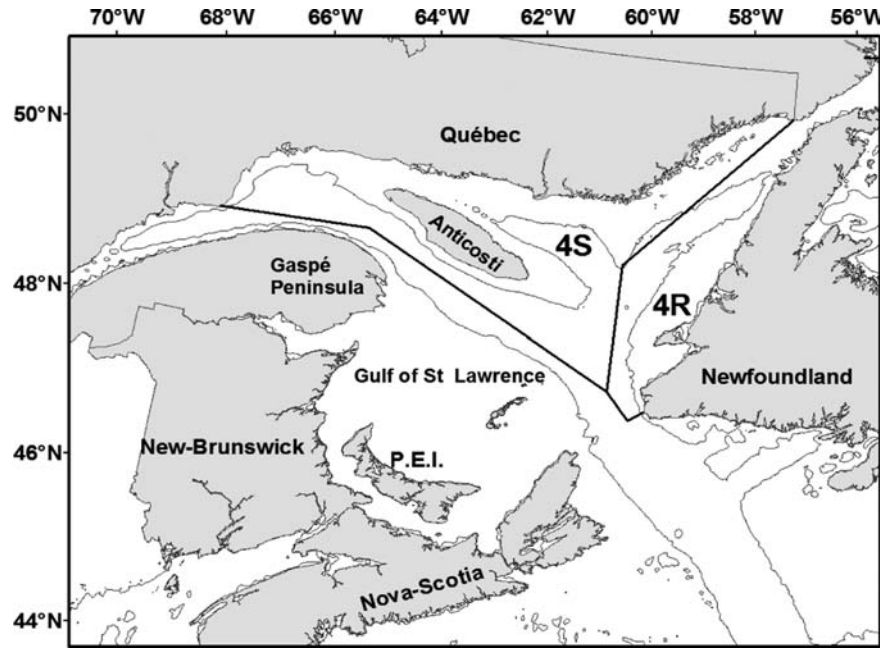
Figure 1. The study area in the Gulf of St Lawrence (NAFO Divisions 4R and 4S).

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 D_1—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 D_2—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 D_3—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 D_4—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 D_1 and D_2 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 D_3 and D_4 imply a density-dependent geographic distribution, i.e. the area of distribution is positively correlated with total abundance. Model D_4 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 × stratum area a_i) are cumulated to obtain the cumulative biomass:

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

The corresponding cumulative proportion of biomasses is then

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

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

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

$Q(z_p)$ 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_{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:

$$\text{Ssp} = 2 \times \left[\sum_{i=1}^{n} \left(\frac{P(T)_{i+1} + P(T)_i}{2} \times \frac{T_{i+1} - T_i}{2} \right) \\ - \sum_{i=1}^{n} \left(\frac{P(T)_{i+1} + P(T)_i}{2N} \times \frac{T_{i+1} - T_i}{2} \right) \right]. \tag{4}$$

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 D_1 dynamic, Ssp increases when population size increases, but for a D_2 dynamic, the Ssp index remains constant and does not vary with population abundance. In contrast, Ssp increases when population size decreases for both D_3 and D_4 dynamics, and $Q(T)$ curves are used to distinguish between D_3 and D_4 (Petitgas, 1998). For the D_3 model, the $Q(T)$ curves have the same origin, but for the D_4 model, $Q(T)$ curves are separated at the origin. Figure 2 of Petitgas (1998) provides a graphic explanation of the way 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 D_2 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 (D_2) 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 (Bez, 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

$$\text{CG} = \frac{\sum_{i=1}^{n} x_i s_i z_i}{\sum_{i=1}^{n} s_i z_i}, \tag{5}$$

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

$$I = \text{Var}(x) = \frac{\sum_{i=1}^{n} (x_i - \text{CG})^2 s_i z_i}{\sum_{i=1}^{n} s_i z_i}. \tag{6}$$

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, $<0.90 \times 10^3$ 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 (D_2) 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 D_2 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, $p = 0.13$).
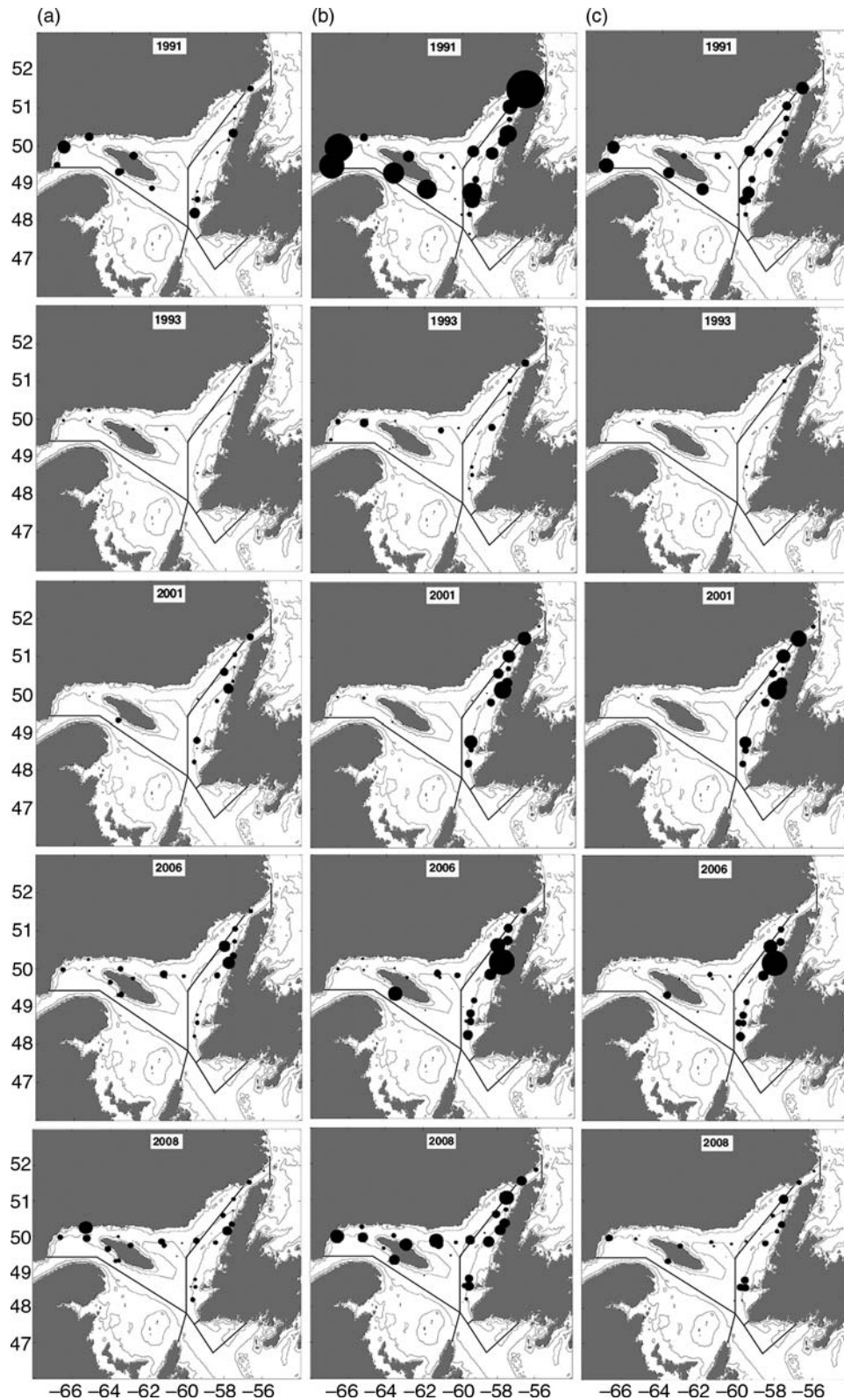
Figure 2. Relative densities of cod age groups (a) <4 years, (b) 4–6 years, and (c) >6 years for 1991, 1993, 2001, 2006, and 2008. Circle diameters are proportional to fish density divided by the maximum density (7.76×10^3 kg km^{-2}) in the survey for all years.

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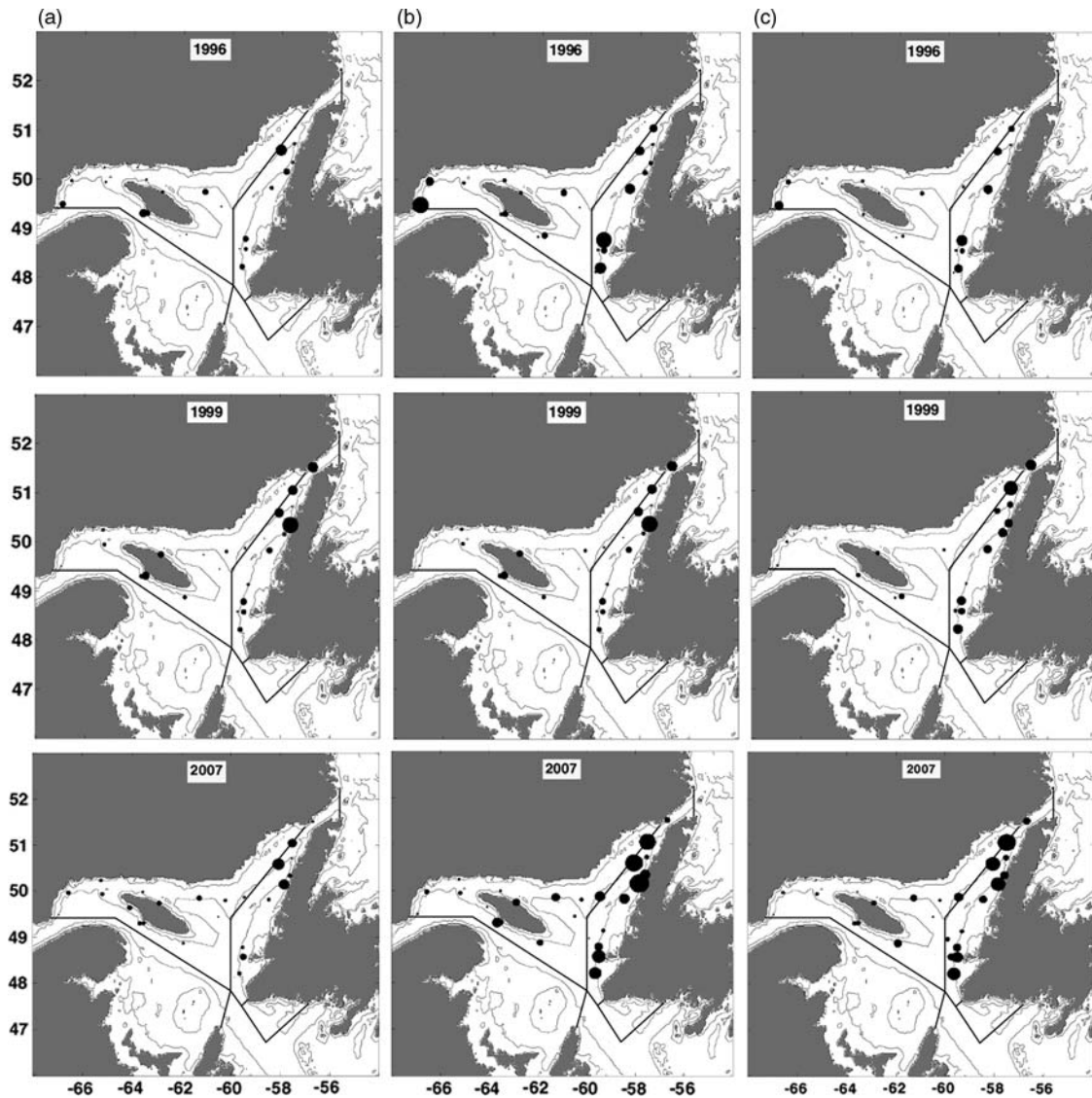
Figure 3. Relative densities of cod age groups (a) <4 years, (b) 4–6 years, and (c) >6 years for 1996, 1999, and 2007. Circle diameters are proportional to fish density divided by the maximum density (2.5×10^3 kg km^{-2}) in the survey for all years.

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

		Year								Confidence interval		
Area	Age group (years)	1991	1993	1996	1999	2001	2006	2007	2008	Lower bound	Mean	Upper bound
Area 4RS	<4	0.941	0.943	0.918	0.927	0.932	0.915	0.912	0.903	0.893	0.930	0.955
	4–6	0.918	0.927	0.923	0.921	0.936	0.910	0.900	0.915	0.888	0.922	0.948
	>6	0.892	0.919	0.925	0.915	0.941	0.915	0.894	0.917	0.889	0.921	0.946
Area 4R	<4	0.880	0.895	0.890	0.883	0.879	**0.833**	0.867	0.850	0.846	0.915	0.942
	4–6	0.877	0.880	0.871	0.852	0.871	**0.823**	0.845	0.858	0.844	0.902	0.938
	>6	0.840	0.859	0.881	0.843	0.877	**0.826**	**0.822**	0.853	0.838	0.886	0.930

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.

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

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).

Year	1991	1993	1996	1999	2001	2006	2007
1993	$D_2/D_2/D_2$						
1996	$D_2/D_2/D_2$	$D_2/D_2/D_2$					
1999	$D_2/D_2/D_2$	$D_2/D_2/D_2$	$D_2/D_2/D_2$				
2001	$D_2/D_2/D_2$	$D_2/D_2/D_2$	$D_2/D_2/D_2$	$D_2/D_2/D_2$			
2006	$\mathbf{D_1/D_1/D_3}$	$\mathbf{D_4/D_4/D_4}$	$\mathbf{D_4/D_4/D_4}$	$\mathbf{D_1/D_1/D_3}$	$\mathbf{D_1/D_1/D_1}$		
2007	$D_2/D_2/\mathbf{D_3}$	$D_2/D_2/\mathbf{D_4}$	$D_2/D_2/\mathbf{D_4}$	$D_2/D_2/\mathbf{D_1}$	$D_2/D_2/\mathbf{D_1}$	$\mathbf{D_3/D_3}/D_2$	
2008	$D_2/D_2/D_2$	$D_2/D_2/D_2$	$D_2/D_2/D_2$	$D_2/D_2/D_2$	$D_2/D_2/D_2$	$\mathbf{D_4/D_4/D_4}$	$D_2/D_2/\mathbf{D_4}$

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

expanded west into 4S. In 4R, the $Q(T)$ curves for 2006 and 2007 are similar near the origin, but the $P(T)$ curve for 2007 lies above the curve for 2006 (Figure 4). This suggests that the constant density model D_3 is appropriate, because local density did not change at the same rate as population abundance (Table 2). The S_{sp} values were higher in 2007 than in 2006 for the two youngest age groups (Table 1), showing that cod in 4R were concentrating in specific locations even as the biomass increased. The basin model was observed between 2006 and 2008, i.e. the balance of 4R biomass in 2008 was very concentrated into relatively small and specific areas.

For the age group >6 years, we observed the same dynamics as for younger fish except in the recent period (2006–2008), where all four models applied (Table 2, Figure 4). In 2007, the S_{sp} index (0.822) was lower than that for 2008 (Table 1), suggesting that cod in the later year were more habitat-selective or more aggregated while the biomass was decreasing in area 4R.

The latitude of the centre of gravity and inertia of cod densities was relatively stable for all age groups and years (Figure 5). The centre of gravity for all age groups between 1991 and 2001 was displaced to the east, whereas inertia decreased, indicating a range contraction in the range of population. However, from 2006 to 2008, the centre of gravity shifted west and the inertia increased for all age groups (Figure 5).

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 S_{sp} 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 S_{sp} 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), 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_1 and D_3 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
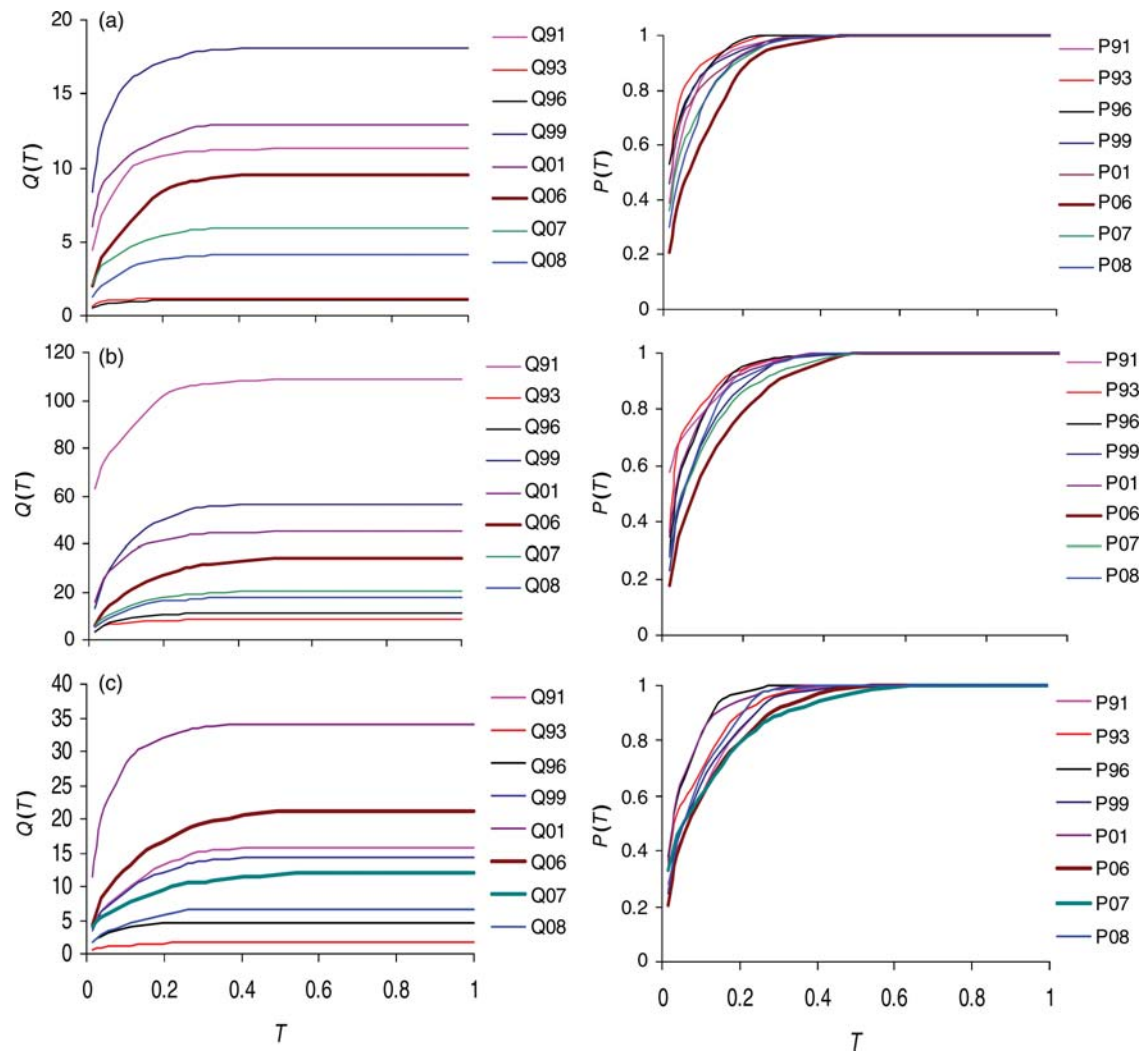
Figure 4. Geostatistical aggregation curves for cod age groups (a) <4 years, (b) 4–6 years, and (c) >6 years at the small scale (area 4R). $Q(T)$ curves are on the left and $P(T)$ on the right. $Q(T)$ curves are adjusted to the average density, so the scales differ among panels. The units for $Q(T)$, T, and $P(T)$ are kg, proportion of the area occupied, and proportion of abundance in kilogramme, respectively. Years with different dynamics are shown emboldened.

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 Benoît, 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 Québec'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
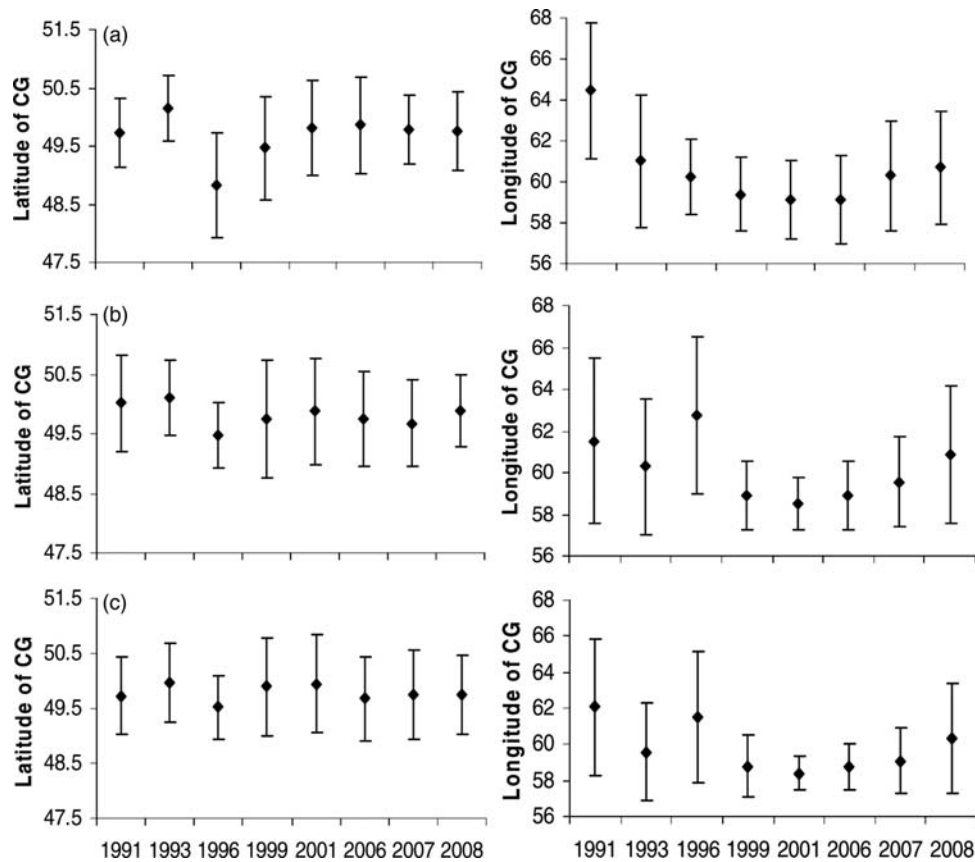
Figure 5. Geographic coordinates of the centre of gravity (CG, ± square root of the inertia) of cod densities for age groups (a) <4 years, (b) 4–6 years, and (c) >6 years.

groundfish populations to achieve density-dependent habitat selection.

References

Anderson, J. T., and Gregory, R. S. 2000. Factors regulating survival of northern cod (NAFO 2J3KL) during their first 3 years of life. ICES Journal of Marine Science, 57: 349–359.

Anneville, O., Cury, P., Le Page, C., and Treuil, J. P. 1998. Modelling fish spatial dynamics and local density-dependence relationships: detection patterns at a global scale. Aquatic Living Resources, 11: 305–314.

Atkinson, B. D., Rose, G. A., Murphy, E. F., and Bishop, C. A. 1997. Distribution changes and abundance of northern cod (*Gadus morhua*), 1981–1993. Canadian Journal of Fisheries and Aquatic Sciences, 54(Suppl. 1): 132–138.

Babcock, E. A., Pikitch, E. K., McAllister, M. K., Apostolaki, P., and Santora, C. 2005. A perspective on the use of spatialized indicators for ecosystem-based fishery management through spatial zoning. ICES Journal of Marine Science, 62: 469–476.

Bailey, K. M. 1997. Structural dynamics and ecology of flatfish populations. Journal of Sea Research, 37: 269–280.

Bakun, A. 2001. School-mix feedback: a different way to think about low frequency variability in large mobile fish populations. Progress in Oceanography, 49: 485–511.

Barange, M., Coetzee, J., Takasuka, A., Hill, K., Gutierrez, M., Oozeki, Y., van der Lingen, C., *et al.* 2009. Habitat expansion and contraction in anchovy and sardine populations. Progress in Oceanography, 83: 251–260.

Bez, N. 1997. Statistiques individuelles et géostatistique transitive en écologie halieutique. Thèse de doctorat en géostatistique, École Nationale Supérieure des Mines de Paris. 276 pp.

Blondel, J. (Ed). 1995. Biogéographie. Approche écologique et évolutive, Masson, Paris. 297 pp.

Bourdages, H., Savard, L., Archambault, D., and Valois, S. 2007. Results from the August 2004 and 2005 comparative fishing experiments in the northern Gulf of St Lawrence between the CCGS Alfred Needler and the CCGS Teleost. Canadian Technical Report of Fisheries and Aquatic Sciences, 2750. 66 pp.

Castonguay, M., Rollet, C., Fréchet, A., Gagnon, P., Gilbert, D., and Brêthes, C. 1999. Distribution changes of Atlantic cod (*Gadus morhua* L.) in the northern Gulf of St Lawrence in relation to an oceanic cooling. ICES Journal of Marine Science, 56: 333–344.

Chouinard, G. A., and Fréchet, A. 1994. Fluctuations in the cod stocks of the Gulf of St Lawrence. ICES Marine Science Symposia, 198: 121–139.

Cote, D., Moulton, S., Frampton, P. C. B., Scruton, D. A., and McKinley, R. S. 2004. Habitat use and early winter movements by juvenile Atlantic cod in a coastal area of Newfoundland. Journal of Fish Biology, 64: 665–679.

Cushing, D. H. 1972. The production cycle and the numbers of marine fish. Symposium of the Zoological Society of London, 29: 213–232.

D'Amours, D. 1993. The distribution of cod (*Gadus morhua*) in relation to temperature and oxygen level in the Gulf of St Lawrence. Fisheries Oceanography, 2: 24–29.

DFO. 2009. Assessment of the cod stock in the northern Gulf of St Lawrence (3Pn,4RS) in 2008. Canadian Science Advisory Secretariat, Science Advisory Report, 2009/010. 15 pp.

Dieckmann, U., Law, R., and Metz, J. A. J. (Eds). 2000. The Geometry of Ecological Interactions: Simplifying Spatial Complexity. Cambridge University Press, Cambridge, UK. 564 pp.

Doebeli, M., and Killingback, T. 2003. Metapopulation dynamics with quasi-local competition. Theoretical Population Biology, 64: 397–416.

Doray, M., Petitgas, P., and Josse, E. 2008. A geostatistical method for assessing biomass of tuna aggregations around moored Fish Aggregating Devices with star acoustic surveys. Canadian Journal of Fisheries and Aquatic Sciences, 65: 1193–1205.

Ehrich, S., Stelzenmüller, V., and Adlerstein, S. 2009. Linking spatial pattern of bottom fish assemblages with water masses in the North Sea. Fisheries Oceanography, 18: 36–50.

Fernandes, P. G., and Rivoirard, J. 1999. A geostatistical analysis of the spatial distribution and abundance of cod, haddock and whiting in North Scotland. *In* Geoenv II—Geostatistics for Environmental Application, pp. 201–212. Ed. by A. S. Gomez-Hernandez, and R. Froidevaux. Kluwer Academic, Dordrecht.

Fréchet, A., Gauthier, J., Schwab, P., Lambert, Y., le Bris, A., Tournois, C., Way, M., *et al.* 2009. The status of cod in the Northern Gulf of St Lawrence (3Pn, 4RS) in 2008. Canadian Science Advisory Secretariat Research Document, 2009/090. 100 pp.

Fréon, P., Drapeau, L., David, J. H. M., Moreno, A. F., Leslie, R. W., Oosthuizen, W. H., Shannon, L. J., *et al.* 2005. Spatialized ecosystem indicators in the southern Benguela. ICES Journal of Marine Science, 62: 459–468.

Fréon, P., and Misund, O. A. 1999. Dynamics of Pelagic Fish Distribution and Behaviour: Effects on Stock Assessment. Blackwell/Fishing News Books, London. 348 pp.

Fretwell, S. D., and Lucas, H. L. 1969. On territorial behaviour and other factors influencing habitat distribution in birds. 1. Theoretical development. Acta Biotheoretica, 19: 16–36.

Fromentin, J-M., Myers, R. A., Bjornstad, O. N., Stenseth, N. Ch., Gjosaeter, J., and Christie, H. 2001. Effects of density-dependent and stochastic processes on the regulation of cod populations. Ecology, 82: 567–579.

Gaertner, J. C., Bertrand, J. A., Samani, D., and Souplet, A. 2005. Spatio-temporal organization patterns of demersal assemblages of the east-coast of Corsica (Mediterranean Sea). Vie et Milieu, 55: 81–89.

Gagnon, P. 1991. The effects of set to strata allocation adjustments. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document, 1991/062. 8 pp.

Hilborn, R., and Walters, C. J. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York. 570 pp.

Iles, T. D., and Sinclair, M. 1982. Atlantic herring stock discreteness and abundance. Science, 215: 627–633.

Koutitonsky, V. G., and Bugden, G. L. 1991. The physical oceanography of the Gulf of St Lawrence: a review with emphasis on the synoptic variability of the motion. *In* The Gulf of St Lawrence: Small Ocean or Big Estuary?, pp. 57–90. Ed. by J-C. Therriault. Canadian Special Publication of Fisheries and Aquatic Sciences. 113 pp.

Lévêque, C. 1995. L'habitat: être au bon endroit au bon moment? Bulletin Français de la Pêche et de la Pisciculture, 337–339: 9–20.

MacCall, A. D. 1990. Dynamic Geography of Marine Populations. Washington Sea Grant Press, Seattle, WA. 153 pp.

Matheron, G. 1981. La Sélectivité des Distributions, note N-686. Centre de Géostatistique. Ecole des Mines de Paris, Fontainebleau, France.

Maury, O., Gascuel, D., Marsac, F., Fonteneau, A., and De Rosa, A. L. 2001. Hierarchical interpretation of nonlinear relationships linking yellowfin tuna (*Thunnus albacares*) distribution to the environment in the Atlantic Ocean. Canadian Journal of Fisheries and Aquatic Sciences, 58: 458–469.

Morris, D. W. 1987. Spatial scale and the cost of density-dependent habitat selection. Evolutionary Ecology, 1: 379–388.

Morris, D. W. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia, 136: 1–13.

Myers, R. A., and Stokes, K. 1989. Density dependent habitat utilization of groundfish and the improvement of research surveys. ICES Document CM 1989/D: 15. 17 pp.

Neuenfeldt, S., and Beyer, J. E. 2003. Oxygen and salinity characteristics of predator–prey distributional overlaps shown by predatory Baltic cod during spawning. Journal of Fish Biology, 62: 168–183.

Paloheimo, J. E., and Dickie, L. M. 1964. Abundance and fishing success. Rapports et Procès-Verbaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer, 155: 152–163.

Petitgas, P. 1994. Spatial strategies of fish populations. ICES Document CM 1994/D: 14. 7 pp.

Petitgas, P. 1996. Geostatistics and their application to fisheries survey data. *In* Computers in Fisheries Research, pp. 113–141. Ed. by B. A. Megrey, and E. Moksness. Chapman and Hall, London.

Petitgas, P. 1997. Sole egg distributions in space and time characterized by a geostatistical model and its estimation variance. ICES Journal of Marine Science, 54: 213–225.

Petitgas, P. 1998. Biomass-dependent dynamics of fish spatial distributions characterized by geostatistical aggregation curves. ICES Journal of Marine Science, 55: 443–453.

Robichaud, D., and Rose, G. A. 2006. Density-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in Placentia Bay, Newfoundland. ICES Journal of Marine Science, 63: 766–774.

Resetarits, W. J. 2005. Habitat selection behaviour links local and regional scales in aquatic systems. Ecology Letters, 8: 480–486.

Rivoirard, J., Bez, N., Fernandes, P., Foote, K., and Simmonds, J. 2000. Geostatistics for Estimating Fish Abundance. Blackwell Science, Oxford. 206 pp.

Saucier, F. J., Roy, F., Gilbert, D., Pellerin, P., and Ritchie, H. 2003. Modeling the formation and circulation processes of water masses and sea ice in the Gulf of St Lawrence, Canada. Journal of Geophysical Research, 108(C8): 32–39.

Savenkoff, C., Castonguay, M., Chabot, D., Hammill, M. O., Bourdages, H., and Morissette, L. 2007. Changes in the northern Gulf of St Lawrence ecosystem estimated by inverse modelling: evidence of a fishery-induced regime shift? Estuarine, Coastal and Shelf Sciences, 73: 711–724.

Shepherd, T. D., and Litvak, M. K. 2004. Density-dependent habitat selection and the ideal free distribution in marine fish spatial dynamics: considerations and cautions. Fish and Fisheries, 5: 141–152.

Smith, S. J., and Somerton, G. A. 1981. STRAP: a user-oriented computer analysis system for groundfish research trawl survey data. Canadian Technical Report of Fisheries and Aquatic Sciences, 1030. 70 pp.

Spencer, P. D. 2008. Density-independent and density-dependent factors affecting temporal changes in spatial distributions of eastern Bering Sea flatfish. Fisheries Oceanography, 17: 396–410.

Stephens, D. W., and Stevens, J. R. 2001. A simple spatially explicit ideal-free distribution: a model and an experiment. Behavioral Ecology and Sociobiology, 49: 220–234.

Swain, D. P., and Benoît, H. P. 2006. Changes in habitat associations and geographic distribution of thorny skate (*Amblyraja radiata*) in the southern Gulf of St Lawrence: density-dependent habitat selection or response to environmental change? Fisheries Oceanography, 15: 166–182.

Swain, D. P., and Castonguay, M. 2000. Final report of the 2000 annual meeting of the fisheries oceanography committee including the report of the workshop on the cod recruitment dilemma. DFO Canadian Stock Assessment Secretariat Proceeding Series, 2000/17. 113 pp.

Swain, D. P., Chouinard, G. A., Morin, R., and Drinkwater, K. F. 1998. Seasonal variation in the habitat associations of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) from the southern Gulf of St Lawrence. Canadian Journal of Fisheries and Aquatic Sciences, 55: 2548–2561.

Swain, D. P., and Morin, R. 1996. Relationships between geographic distribution and abundance of American plaice (*Hippoglossoides platessoides*) in the southern Gulf of St Lawrence. Canadian Journal of Fisheries and Aquatic Sciences, 53: 106–119.

Swain, D. P., and Wade, E. J. 1993. Density-dependent geographic distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St Lawrence. Canadian Journal of Fisheries and Aquatic Sciences, 50: 725–733.

van der Veer, H. W., Ruardij, P., van den Berg, A. J., and Ridderinkhof, H. 1998. Impact of interannual variability in hydrodynamic circulation of egg and larval transport of plaice (*Pleuronectes platessa* L). Journal of Sea Research, 39: 29–40.

Winters, G. H., and Wheeler, J. P. 1985. Interaction between stock area, stock abundance and catchability coefficient. Canadian Journal of Fisheries and Aquatic Sciences, 42: 989–998.

Woillez, M., Poulard, J. C., Rivoirard, J., Petitgas, P., and Bez, N. 2007. Indices for capturing spatial patterns and their evolution in time, with application to European hake (*Merluccius merluccius*) in the Bay of Biscay. ICES Journal of Marine Science, 64: 537–550.

Yvelin, J-F., Fréchet, A., and Brêthes, C. 2005. Migratory routes and stock structure of cod from the Northern Gulf of St Lawrence (3Pn, 4RS). Canadian Science Advisory Secretariat Research Document, 2005/055. 50 pp.