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Distribution changes of Atlantic cod (*Gadus morhua* L.) in the northern Gulf of St Lawrence in relation to an oceanic cooling

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Research vessel trawl survey data were examined to investigate age-by-age changes in the distribution of Atlantic cod (*Gadus morhua* L.) with respect to depth, temperature, and latitude in the northern Gulf of St Lawrence (Canada) in both winter (1978–1994) and summer (1984–1995) in relation to a water cooling event. We used a cumulative distribution function method that statistically compares distributions of sampled variables with those occupied by fish. There was no evidence that the ambient temperatures occupied by cod changed with the cooling. On average, cod occupied waters with temperatures of 4.4–5.9°C in winter and of 1.4–3.5°C in summer, with no temporal trend. However, major distribution shifts occurred in winter: the median latitude of the geographic distribution in 1993 was 2° (220 km) south of that in 1985, and cod were also distributed 200 m deeper in the 1990s. Even though stock abundance decreased drastically during the time period considered, abundance in the deepest stratum surveyed (>365 m) increased. The median latitude of distribution in winter was correlated with an index of temperature anomaly in the cold intermediate layer during the previous summer ($r=0.85$, $p<0.05$, corrected for autocorrelation). This indicates that the cooling at mid-depth influenced cod distribution and resulted in an earlier wintering migration. Cod responded to a change in their habitat by changing their migration and distribution patterns.

Key words: cod, depth, temperature, and latitudinal distribution, migration timing, cold intermediate layer, research vessel surveys.

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Introduction

The Gulf of St Lawrence has been experiencing below normal water temperatures in the cold intermediate layer (CIL), since the mid-1980s. The CIL is a layer of cold water sandwiched between warmer and fresher surface waters and warmer and saltier bottom waters. It is a relic of winter cooling typically found in the summer from about 30 to 100 m in the Gulf of St Lawrence. Seven of the eight coldest years of the 50-year CIL record in the Gulf of St Lawrence occurred since 1986 (Gilbert and Pettigrew, 1997; Figure 1a). The low temperatures are due to the cold winters the NW Atlantic has experienced over the same period (Drinkwater, 1996). This cooling has also been felt on the Newfoundland Shelf (Colbourne *et al*., 1994; Drinkwater, 1996) and the eastern Scotian Shelf, but not further south (Page and Losier, 1994; Drinkwater, 1996).

The Gulf of St Lawrence also experiences interannual temperature fluctuations of its deep waters (200–300 m) (Bugden, 1991), but these changes are uncorrelated with CIL temperature variations (Gilbert and Pettigrew, 1997). In contrast to CIL temperatures, deep-water

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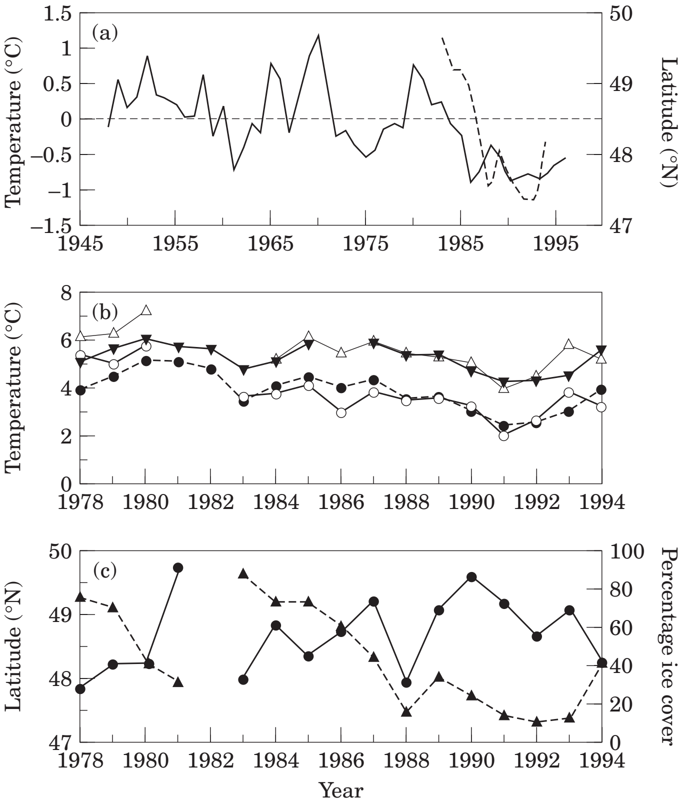

Figure 1. (a) Deviations from the 1948–1994 mean cold intermediate layer (CIL) minimum temperature (solid line) in the Gulf of St Lawrence extrapolated to 15 July (redrawn from Figure 6 of Gilbert and Pettigrew, 1997) and median latitude (dashed line) of the geographic distribution of cod in January; (b) temperature fluctuations at depths of 150–200 m (—○—, Petrie 2; – –●– –; Petrie 3) and 200–250 m (—△—, Petrie 2; —▼—, Petrie 3) [corresponding to southern and northern 4R (see Figure 2), respectively] (Petrie, 1990) from 1978 to 1994; and (c) median latitude of the cod distribution in January (dashed line), and corresponding percentage of the 3Pn4RS area covered by ice (solid line), as determined from the ice map closest to the median date of the survey.

temperatures in Cabot Strait (Figure 2) were relatively high (5.5–6.5°C) during the late 1980s and early 1990s (Gilbert *et al.*, 1997). The uncoupling of temperatures between the Gulf's CIL and its deep water is due to different forcing mechanisms affecting the two layers, the CIL being under the influence of winter atmospheric temperature and flow through the Strait of Belle-Isle (Figure 2) (Petrie *et al.*, 1988; Gilbert and Pettigrew, 1997) while deep-water temperatures depend on varying proportions of Labrador and Gulf Stream waters at the shelf edge (Bugden, 1991).

Atlantic cod (*Gadus morhua* L.) from the northern Gulf of St Lawrence stock [Northwest Atlantic Fisheries Organisation (NAFO) divisions 3Pn4RS shown in Figure 2] typically over-winter in southern 4R or 3Pn, on the northern side of Cabot Strait, enter the northern Gulf in spring for spawning, and remain there during the post-spawning feeding period, when they may be found inshore (Ouellet *et al.*, 1997). They migrate back to Cabot Strait in late autumn/early winter (Templeman, 1978; Chouinard and Fréchet, 1994). Since 1989, the distribution of cod has been deeper in January, as shown by research vessel trawl surveys conducted annually from 1978 to 1994. While the proportion of cod biomass trawled deeper than 360 m was always less than 20% before 1988, it increased to over 90% in the early 1990s (Fréchet and Gagnon, 1993; Chouinard and Fréchet, 1994).

In this study, we relate changes in the winter and summer distribution of juvenile and adult cod from the northern Gulf of St Lawrence to the recent cooling of the Gulf. Our objective is to perform an age-disaggregated comparison of depth, temperature, and latitudinal distribution changes that occurred in winter and in summer in relation to the progression of the cooling event. We wished to determine whether the recent cooling of Gulf CIL waters exposed cod to colder water temperatures in winter or summer, which would provide a straightforward mechanism to explain declines in condition and growth of cod in the northern Gulf

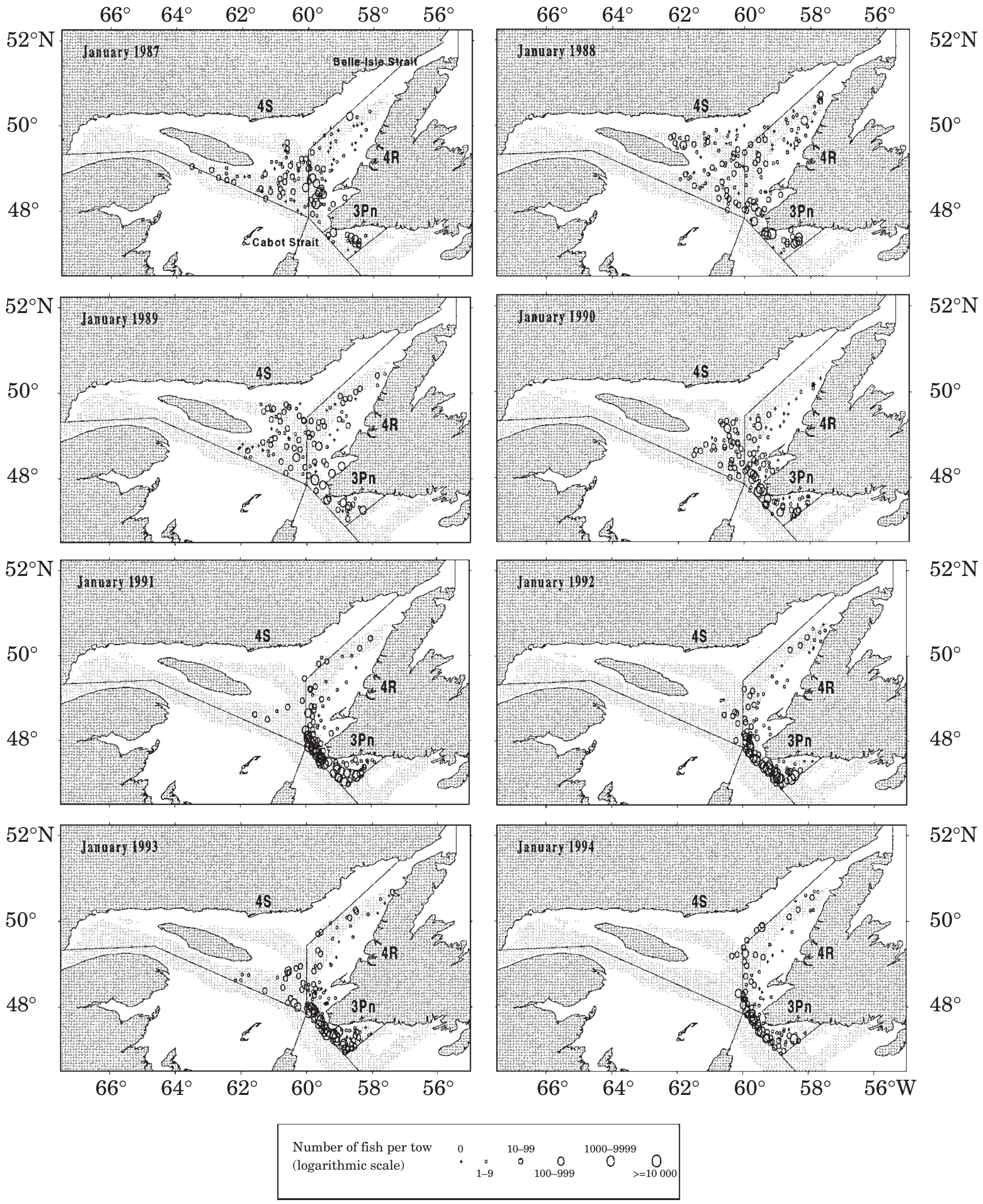

Figure 2. Spatial distribution of catches (number of cod per tow) during the winter survey in the northern Gulf of St Lawrence from 1987 to 1994. Sampling coverage differed among years due to variability in weather and ice cover. The grey area shows depths >200 m.

reported by Lambert and Dutil (1997) and Dutil *et al.* (1999). These authors argue that, in addition to the dominant influence of fishing, an environment-driven decline in condition and growth also contributed to the demise of the northern Gulf of St Lawrence cod stock.

Changes in the distribution of the northern Gulf cod stock in the 1980s and 1990s have to be interpreted in light of a drastic concurrent reduction in abundance that culminated in the closure of the fishery in January 1994 (Anon., 1994). Stock size (biomass of age 3 fish and older) was estimated from virtual population analysis to be only 32 000 t in 1994, which represents only 7% of the historical average, calculated from 1974 to 1986 (Fréchet and Schwab, 1998). Size-at-age has also been steadily declining since the early 1980s and, except for the large 1987 year class, recruitment has been average to poor in this stock during the 1980s and early 1990s (Chouinard and Fréchet, 1994).

Materials and methods

Cod catch data were analysed from two series of research vessel trawl surveys carried out by the Canadian Department of Fisheries and Oceans in the northern Gulf of St Lawrence and Cabot Strait (Divisions 3Pn4RS). The winter survey was conducted on board the MV "Gadus Atlantica" from 1978 to 1994, excluding 1982. The survey usually took place in January but was about 3 weeks later than usual in 1980 (27 January–11 February) and 1981 (29 January–17 February). This survey included on average 147 stations (range: 84–207) of 30-min duration. The summer survey was carried out from 1984 to 1995 in August/early September (July in 1984) and comprised a mean number of 195 stations (range: 108–233). This survey was conducted by the MV "Lady Hammond" between 1984 and 1989 (30-min tows) and by the RV "Alfred Needler" (24-min tows) thereafter. The winter survey used an Engel-145 bottom trawl with a 30 mm liner while the summer survey employed a Western IIA otter trawl with a 32 mm liner (MV "Lady Hammond") and a URI shrimp trawl with a 19 mm liner (RV "Alfred Needler"). Differences in gear selectivity between the MV "Lady Hammond" and the RV "Alfred Needler" will not affect interannual distribution comparisons based on catch for all ages combined but they may affect age-by-age comparisons; results will be examined keeping this caveat in mind.

For both surveys, a depth-stratified design was used whereby sets in a given depth stratum are chosen randomly with the number of sets being approximately proportional to the stratum area (Doubleday, 1981), except that since 1992 for the summer survey an optimal allocation of sets to strata based on variance has been used (Gagnon, 1991). Cod catch-at-age, calculated for each tow, were then expanded to the surface area of the various strata using a program (STRAP) developed for analysis of groundfish research trawl survey data (Smith and Somerton, 1981). Near-bottom temperatures were measured either with Sippican XBT, Applied STD, Guildline CTD, or Sealogs. Temperature data were quality-controlled by checking every value $\geq 7°C$ against mean and s.d. values for the corresponding month and area from Petrie (1990). We excluded from all analyses tows for which the near-bottom temperature was missing or fell outside the range defined by Petrie's mean ± s.d. Not using a common data set would have made it risky to compare conclusions for a variable that is never missing (depth or latitude) with those for a variable that is sometimes missing (temperature). Tows with missing temperatures represented a small proportion of total (13% on average) except for the 1992 winter survey (52%, due to equipment failure).

Neither survey covered the entire distribution area of the northern Gulf stocks in all years. Shallow (37–91 m) depths were not sampled before 1991 during the summer surveys. To standardize the analyses of the 1984–1995 summer survey data, we excluded tows from depths <92 m (such tows represented 11% of total on average). We examined the impact of excluding shallow strata on temperature distribution of cod by comparing from 1991 to 1995, temperatures that cod occupied when shallow stations were included or excluded. Moreover, after 1988, part of the winter distribution was outside the survey area (south and east of 3Pn) (Rollet *et al*., 1994) and hence was not sampled. Finally, two shallow strata in Division 4S, representing 6% of the total 3Pn4RS area, could not be sampled on either survey because of the rough bottom.

For both surveys, we compared (for all ages pooled and disaggregated, ages 2 to 8+) distributions of sampled and occupied (i.e. sampled weighted by abundance expressed as number of fish caught) temperatures, depths, and latitudes among years. For every year we plotted the 2.5, 50, and 97.5% values of sampled and occupied cumulative distribution functions (CDF) of temperatures, depths, and latitudes, following Swain and Kramer's (1995) method of graphical representation. As the only age difference in distribution was between ages 2–3 (juveniles) and ages 4 and older (a mixture of juveniles and adults at age 4 and largely adults for older ages) (not shown), we only report here distributions for ages 3 and 6 as well as for all ages pooled. We then tested for differences between sampled and occupied CDF of the above three parameters using a computer program called Habitat developed by one of the authors of this paper (P.G.). Habitat implements a randomization test developed by Perry and Smith (1994). It tests the null hypothesis of a random association between fish distribution and habitat conditions. The test is based on a statistic that is the maximum absolute difference between the CDF of the parameter and the abundance-weighted CDF, which represents the occupied distribution. This statistic is compared with values typical of a random association between the parameter and the abundance. The program calculates 2000 such values from random pairings of observed parameters and abundance. The probability of random association is estimated as the proportion of simulated values greater than the observed one. The main advantage of the CDF method used here is that it takes into account survey design and allows statistical comparisons between occupied and sampled habitat variables to be calculated. Details of the method and its rationale can be found in Perry and Smith (1994).

The above distribution analyses cannot distinguish between shifts in habitat associations of individual fish and selective disappearance (mortality) of fish from one region of their habitat in a context of declining stock size. For example, a shift to deep water from one winter to the next may reflect a genuine shift in abundance to deep water of fish that previously overwintered in shallow water, or it may result from the selective disappearance of shallow-water fish. To examine this issue, we compared trawlable numbers of fish (i.e. number of fish caught by the trawl expanded to the surface area of the stratum using the STRAP program) per depth stratum for the winter survey over the years when the depth shift took place (1985–1990). Increases in numbers of fish at depth over time would indicate an actual shift to deep waters of individual fish that were previously distributed in shallow waters rather than a selective disappearance of shallow-water fish. Stock abundance (age 3 and older) decreased by 65% from 1985 to 1990, from 540 000 to 187 000 t (Fréchet and Schwab, 1998).

To quantitatively relate environmental change to fish distribution, we calculated a Pearson's coefficient of correlation between the CIL summer temperature anomaly and the median latitude of the geographic distribution of cod in the following winter. The correlation was corrected for autocorrelation following a method described in Ebisuzaki (1997; his Equation 2), which calculates an effective sample size (n_{eff}). Not accounting for autocorrelation would make the statistical tests less stringent. We also calculated correlations corrected for autocorrelation between mean annual temperatures in the northern Gulf at depths of 150–200 and 200–250 m (Figure 1b) and median January latitudinal distribution of cod. Although these temperatures were measured in summer, a comparison with fish distributions in winter is valid here because there is no seasonal temperature signal below 150 m (D. Gilbert, unpubl. data). Fréchet (1990) sampled both inside and outside the ice field and reported that, in winter, cod from the northern Gulf of St Lawrence concentrate in the marginal ice zone but do not usually occur inside the ice field. We examined how the median latitude of the cod distribution in winter is correlated (corrected for autocorrelation) with the percentage of the 3Pn4RS area covered with ice (Figure 1c). To calculate the percentage of ice cover, we digitized ice maps corresponding to the median survey date provided by the Atmospheric Environment Service of the Canadian Department of Environment. All the above correlations could be calculated only between 1983 and 1994 because the method that corrects for autocorrelation requires continuous series and there was no winter survey in 1982.

Results

Winter changes in cod distribution and the environment

Starting in the late-1980s, adult cod were gradually found deeper in January (Figure 3). Juveniles also shifted depths but to a lesser extent (Figure 3). Before 1989, the median depth occupied by adults in January varied from 125 to 250 m, with particularly shallow distribution from 1978 to 1981. From 1989 to 1991, cod shifted to deeper waters and remained at about 450 m from 1991 to 1994. The upper (2.5%) and lower (97.5%) bounds of the depth distribution also shifted deeper and the median converged towards the lower bound (Figure 3), reflecting the observation that most fish were located within a narrow depth range (at the bottom of Cabot Strait). Before 1989, cod occupied depths significantly shallower than sampled depths in 5 out of 10 years (Habitat, $p<0.05$). After 1988, occupied depths were significantly deeper than sampled ones in 5 out of 6 years (Habitat, $p<0.01$).

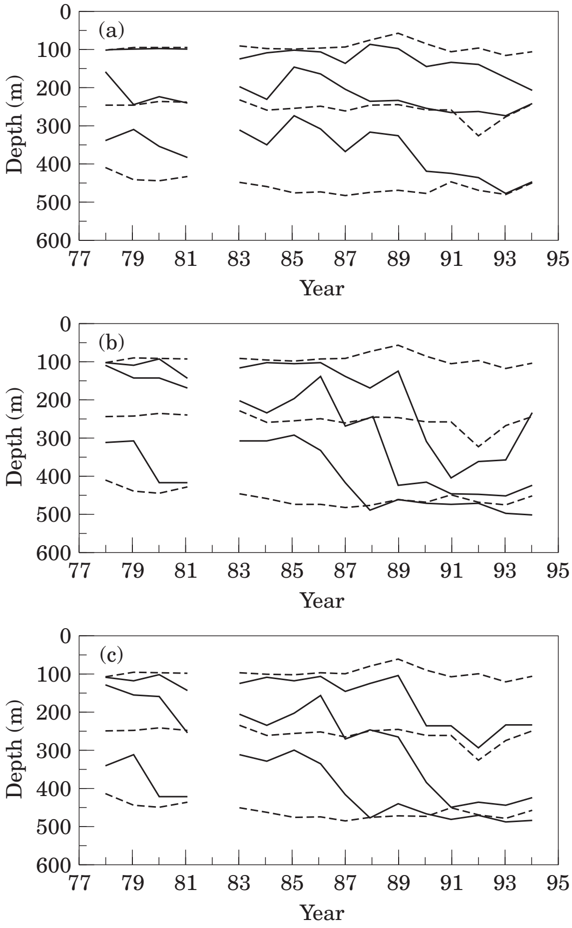

Figure 3. Cumulative distribution functions (CDFs) of depths (expressed as 2.5, 50, and 97.5 percentiles) occupied by (a) juvenile cod (as shown by age 3), (b) adult cod (as shown by age 6), and also for (c) pooled ages, vs. those sampled by the trawl during the winter survey, from 1978 to 1994. The 2.5, 50, and 97.5 percentiles of occupied depth CDFs are represented by the top, middle, and bottom solid lines, respectively. The 2.5, 50, and 97.5 percentiles of sampled depth CDFs are represented by the top, middle, and bottom dashed lines, respectively.

Table 1. Estimates of cod abundance (millions of fish age 3 and over) per depth stratum in the 3Pn4RS survey area in January from 1985 to 1990. Fish abundance estimated from the winter survey is scaled to stratum area using the STRAP program. The depth stratum with the largest abundance is shown in bold.

Depth stratum (m)	1985	1986	1987	1988	1989	1990
<92	0.4	0	2.0	1.0	0.1	0.2
92–183	63.0	**97.9**	8.1	3.5	7.6	0.5
183–273	**75.3**	39.6	**13.6**	**38.1**	15.3	10.3
274–365	4.8	81.7	13.5	4.5	3.6	15.8
>365	1.0	3.1	3.9	12.5	**17.4**	**27.3**

Comparisons of the estimated numbers of cod in each survey depth stratum indicate that despite the fact that stock abundance declined by 65% in the 1985–1990 period, the abundance in the deepest (>365 m) stratum sampled steadily increased, from an estimated 1 million fish in 1985 to 27 million fish in 1990 (Table 1).

The depth distribution change was not accompanied by a corresponding change in median occupied temperature, which remained in the 4.4–5.9°C range (mean of medians: 4.9°C) throughout the winter survey series except in 1978, when it was only 2.3°C (Figure 4). However, the lower (cold) bound of the temperature distribution started to converge towards the median at the time of the depth shift (1989/1990), indicating that cod then experienced a more uniform temperature field and did not occupy cold water. There was no detectable age-related difference in temperature exposure (Figure 4). Interestingly, the small magnitude of the depth shift in juveniles (Figure 3) did not result in the occupation of colder water after 1988. In most cases (12 out of 16 years), Habitat did not detect significant differences between occupied and sampled temperatures (ages pooled) even though their plots (Figure 4) seemed quite different. This is because the test's statistical power to detect a non-random distribution is weak when most of the abundance comes from a small number of sets, i.e. when fish are highly aggregated.

Starting in 1986, the distribution of cod in January progressively shifted to the south, such that the median latitude of their geographic distribution in 1993 was located 2° (220 km) south of their median latitude in 1985 (Figure 5). The shift was more pronounced in adults than in juveniles: by 1993, the median latitude occupied by juveniles was still located inside the Gulf (i.e. north of 48°), about 1° to the north of the adult median latitude, which was outside the Gulf (Figure 5). The southerly trend was reversed in 1994. It is noteworthy that cod were distributed more to the south in 1980 and 1981, the 2 years when the survey was conducted 3 weeks later than normal. In 10 out of 16 years, cod (ages pooled) were significantly more abundant in southern latitudes than expected under a uniform distribution hypothesis (Habitat, p<0.01). For the other 6 years, there was no difference between latitudes occupied by cod and sampled station latitudes. The southerly upper bound of occupied latitudes in 1992 represent a sampling artefact caused by the exclusion of many northerly stations with missing near-bottom temperature in that year, as shown by the change in sampled station latitudes for that year (Figure 5). The exclusion of these northerly stations in 1992 did not change medians and ranges of observed depths (Figure 3) and temperatures (Figure 4).

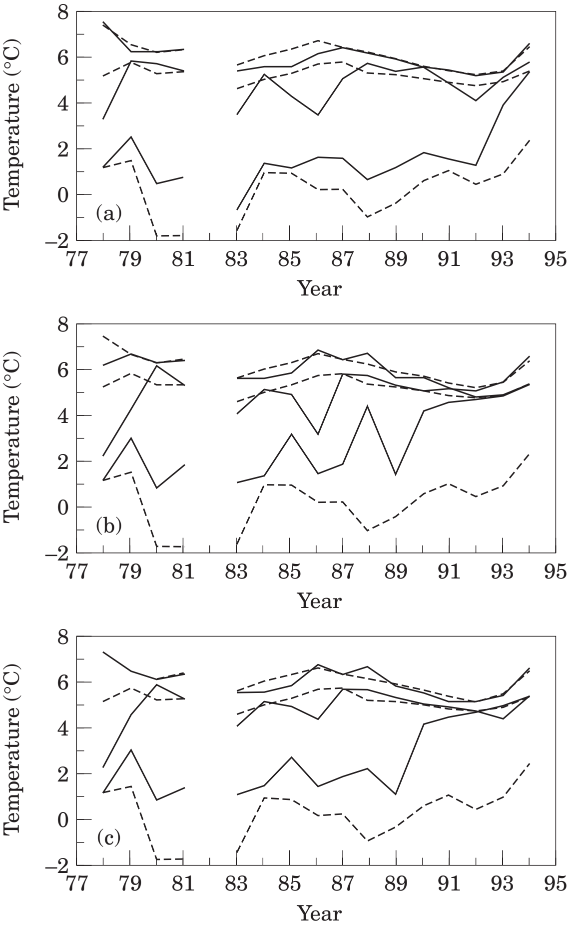

Figure 4. Cumulative distribution functions (CDFs) of temperatures (expressed as 2.5, 50, and 97.5 percentiles) occupied by (a) juvenile cod (as shown by age 3), (b) adult cod (as shown by age 6), and also for (c) pooled ages, vs. those sampled by the trawl during the winter survey, from 1978 to 1994. The 2.5, 50, and 97.5 percentiles of occupied temperature CDFs are represented by the bottom, middle, and top solid lines, respectively. The 2.5, 50, and 97.5 percentiles of sampled temperature CDFs are represented by the bottom, middle, and top dashed lines, respectively.

The shift to deeper waters and more southerly latitudes in January could have been strictly due to an earlier start of the wintering migration. To control for a

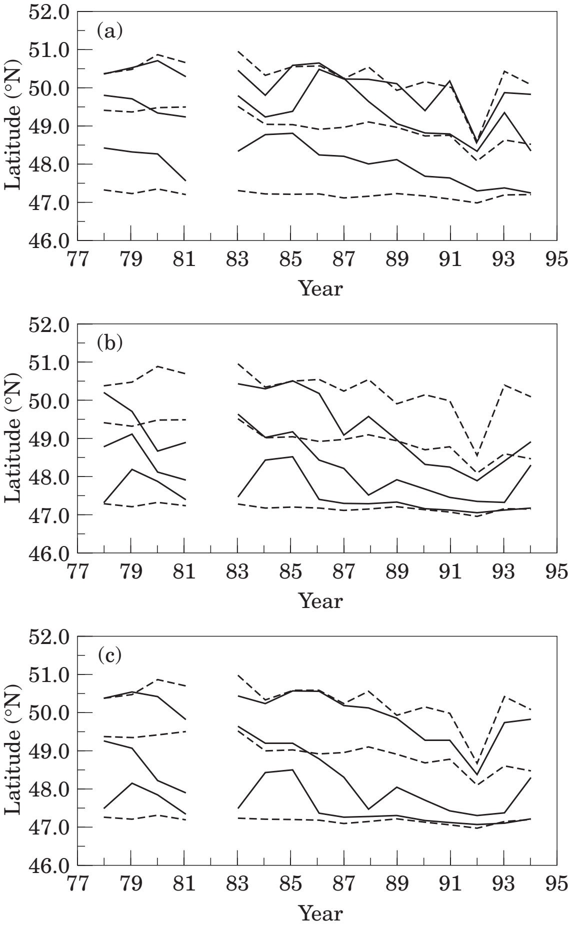

Figure 5. Cumulative distribution functions (CDFs) of latitudes (expressed as 2.5, 50, and 97.5 percentiles) occupied by (a) juvenile cod (as shown by age 3), (b) adult cod (as shown by age 6), and also for (c) pooled ages, vs. those sampled by the trawl during the winter survey from 1978 to 1994. The 2.5, 50, and 97.5 percentiles of occupied latitude CDFs are represented by the bottom, middle, and top solid lines, respectively. The 2.5, 50, and 97.5 percentiles of sampled latitude CDFs are represented by the bottom, middle, and top dashed lines, respectively.

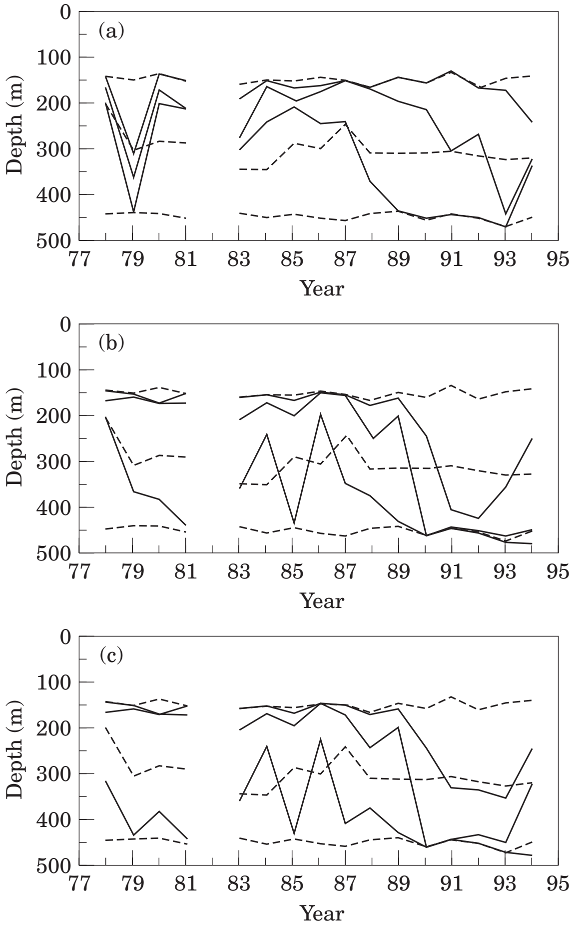

Figure 6. Cumulative distribution functions (CDFs) of depths (expressed as 2.5, 50, and 97.5 percentiles) occupied by (a) juvenile cod (as shown by age 3), (b) adult cod (as shown by age 6), and also for (c) pooled ages, vs. those sampled by the trawl during the winter survey, from 1978 to 1994, including only 3Pn sampling stations. The 2.5, 50, and 97.5 percentiles of occupied depth CDFs are represented by the top, middle, and bottom solid lines, respectively. The 2.5, 50, and 97.5 percentiles of sampled depth CDFs are represented by the top, middle, and bottom dashed lines, respectively.

migration timing effect, we compared changes in depth distributions for fish caught only in 3Pn, i.e. those fish whose migration should be mostly completed by the time of the survey (Figure 6). Starting in 1990, cod median depth in 3Pn shifted from about 200 to 450 m, indicating that the stock's over-wintering location shifted to deeper waters (i.e. further offshore and more to the south). Hence, results suggest that in addition to performing the autumn migration to wintering grounds earlier, cod also over-wintered in deeper waters.

There was a significant positive correlation (corrected for autocorrelation) between the median latitude where cod was found in January and the index of CIL temperature anomaly in the previous summer ($r=0.85$, $p<0.05$, $n=12$, $n_{eff}=6$, d.f.$=4$) (Figure 1a). Latitude was also significantly correlated with the CIL index of two summers before ($r=0.89$, $p<0.05$, $n=12$, $n_{eff}=6$, d.f.$=4$) but not with any other lag of the CIL index. The negative CIL temperature anomalies that started in 1986 (Figure 1a) were not felt at typical depths (150–250 m) and locations (4R) occupied by the stock, although temperatures there did become colder in 1991 and 1992 by as much as 1.3°C (Figure 1b). Correlations of cod median latitude in January with the 150–200 m or the 200–250 m temperature series or with ice cover were not significant for any lag after accounting for autocorrelation ($p>0.05$).

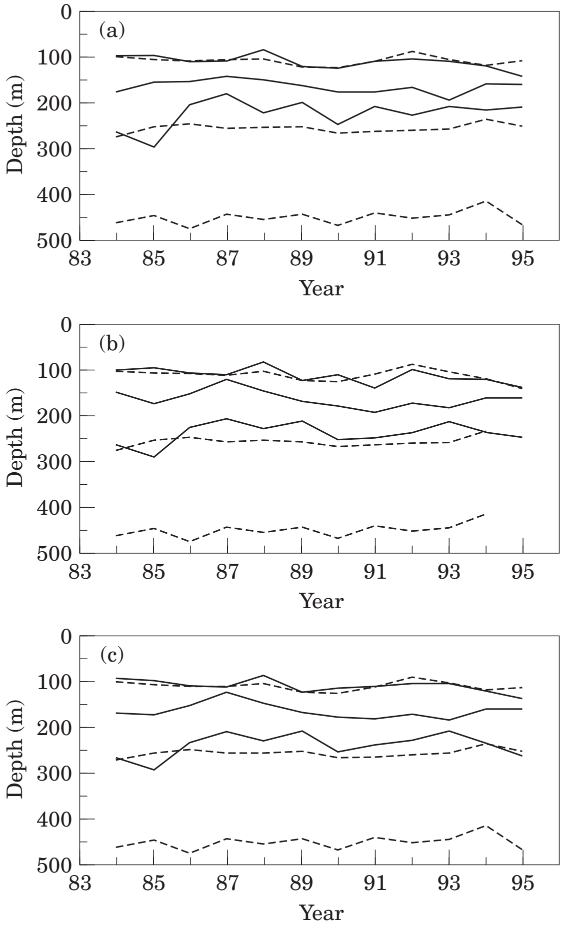

Figure 7. Cumulative distribution functions (CDFs) of depths (expressed as 2.5, 50, and 97.5 percentiles) occupied by (a) juvenile cod (as shown by age 3), (b) adult cod (as shown by age 6), and also for (c) pooled ages, vs. those sampled by the trawl during the summer survey from 1984 to 1995. The 2.5, 50, and 97.5 percentiles of occupied depth CDFs are represented by the top, middle, and bottom solid lines, respectively. The 2.5, 50, and 97.5 percentiles of sampled depth CDFs are represented by the top, middle, and bottom dashed lines, respectively.

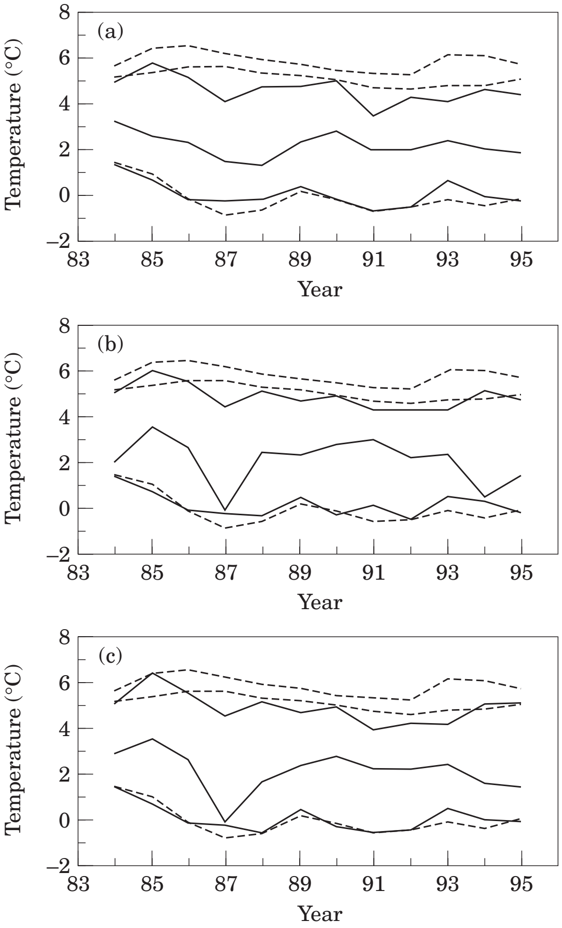

Figure 8. Cumulative distribution functions (CDFs) of temperatures (expressed as 2.5, 50, and 97.5 percentiles) occupied by (a) juvenile cod (as shown by age 3), (b) adult cod (as shown by age 6), and also for (c) pooled ages, vs. those sampled by the trawl during the summer survey from 1984 to 1995. The 2.5, 50, and 97.5 percentiles of occupied temperature CDFs are represented by the bottom, middle, and top solid lines, respectively. The 2.5, 50, and 97.5 percentiles of sampled temperature CDFs are represented by the bottom, middle, and top dashed lines, respectively.

Summer changes in cod distribution

We detected little depth, temperature, or latitudinal changes in cod distribution in summer for that portion of the stock surveyed in water deeper than 91 m. The median occupied depth in August did not exhibit trends and remained in the 144–181 m range (ages pooled), except for 1987 when it was only 119 m (Figure 7). There was no apparent age-related difference of depth distribution in summer (Figure 7). The mean median occupied temperature across years was 2.1°C. Excluding 1987, the median occupied temperature fluctuated between 1.4 and 3.5°C without any evidence of a temporal trend (Figure 8). As with depth, the cold median temperature of −0.1°C occupied by cod in 1987 was atypical. In that year, 47.5% of the fish were caught at the bottom of the CIL in waters whose temperatures ranged from −0.3 to −0.1°C (Figure 8). The latitudes where fish were found in summer fluctuated little among years or between juveniles and adults (Figure 9). The median latitude occupied by the stock varied from 49.4 to 50.1°N. No pronounced difference in depth, temperature, or latitude distribution was detected for any age in 1990, when the change in vessel and trawl took place (not shown), suggesting that the change did not affect age by age comparisons. Occupied depths were significantly shallower than sampled ones (Figure 7), and occupied near-bottom temperatures were significantly colder than sampled ones (Figure 8) in all years

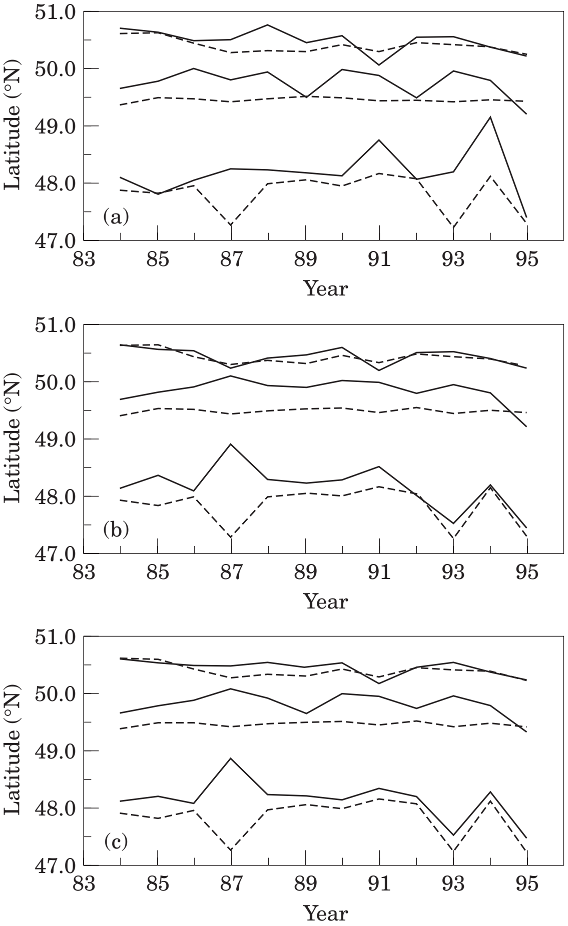

Figure 9. Cumulative distribution functions (CDFs) of latitudes (expressed as 2.5, 50, and 97.5 percentiles) occupied by (a) juvenile cod (as shown by age 3), (b) adult cod (as shown by age 6), and also for (c) pooled ages, vs. those sampled by the trawl during the summer survey from 1984 to 1995. The 2.5, 50, and 97.5 percentiles of occupied latitude CDFs are represented by the bottom, middle, and top solid lines, respectively. The 2.5, 50, and 97.5 percentiles of sampled latitude CDFs are represented by the bottom, middle, and top dashed lines, respectively.

and for both juveniles and adults (Habitat, $p<0.05$). Cod (ages pooled) were significantly more abundant in northern latitudes than expected under a uniform distribution hypothesis in 8 of 12 years (Figure 9; Habitat, $p<0.01$). For the 4 other years, there was no difference between occupied and "sampled" latitudes.

Table 2. Temperature (°C) (expressed as 2.5, 50, and 97.5 percentiles of the cumulative distribution functions) occupied by cod on the summer survey when the 37–91 m depth stratum is included (bold) or excluded from the analysis.

Year	**2.5**	2.5	**50**	50	**97.5**	97.5
1991	**−1.7**	−0.6	**2.1**	2.2	**3.7**	3.9
1992	**−0.7**	−0.5	**2.7**	2.2	**5.1**	4.2
1993	**−0.5**	0.5	**1.9**	2.4	**4.1**	4.1
1994	**−1.1**	0	**1.6**	1.6	**6.1**	5.0
1995	**−0.2**	−0.2	**1.4**	1.4	**5.1**	5.1

The most important question regarding the exclusion of waters <92 m in summer is how it affected cod distribution with respect to temperature. We examined this using results from the 1991–1995 surveys, when shallower waters were sampled. The percentage of fish numbers (scaled to strata areas) in the 37–91 m depth stratum was 32, 43, 32, 40, and 15 for 1991–1995, respectively. Hence, adding the shallow strata to the survey increased the proportion of the stock that was sampled by approximately 50%. However, for those years, the impact of excluding waters <92 m on the estimation of median temperatures that cod occupied was minimal (Table 2). Even though the range of occupied temperatures became larger, the median occupied temperature was either smaller, equal, or larger when the shallow stratum was included and, on average, it was identical whether shallow stations were included or not. In years when >30% of the total estimated number of fish were in 37–91 depths (1991–1994), the 2.5 percentile of temperature was colder when shallow strata were included than when they were not (Table 2).

Plots of sampled depths and latitudes through time (the dotted lines of Figures 3, 5, 7, and 9) show that the surveys' sampling effort remained constant through time. Hence changes in sampling effort could not have biased observed trends in distribution.

Discussion

There was no evidence that cod were exposed to colder water temperatures as a result of the cooling of the Gulf of St Lawrence's CIL. There was no temporal trend in the median temperature occupied by juveniles or adults in either January or August. This suggests that declines in weights-at-age (Dutil *et al.*, 1999), condition (Lambert and Dutil, 1997) and increases in natural mortality (Dutil and Lambert, 1999) experienced by northern Gulf cod in the 1980s and 1990s were not caused by direct exposure to colder water.

Although cod may not have been exposed to colder water as a result of the cooling, it seems that their spatial distribution was affected. The significant correlation between the Gulf's summer CIL temperature anomaly and cod spatial distribution during the following winter suggests a cause–effect relationship between the two variables. The southerly latitudinal shift in winter and the striking depth shift (>200 m) that accompanied it, together with the absence of latitude change in August, suggest that cod performed the overwintering migration earlier and that this change of timing was due to the cooling at mid-depth. This and the absence of change in exposure temperatures suggest that cod modified their spatial distribution to remain within a range of preferred temperatures. The fish responded to changes in their habitat by altering their migration and distribution patterns. Cod may have modulated their spatial distribution more in response to changes in CIL thickness and/or volume than in CIL temperatures, but CIL minimum temperature and volume of waters below 0°C are negatively correlated in the Gulf ($r = -0.74$, $n = 14$, $neff = 12$, $p < 0.05$; D. Gilbert, pers. comm.). The earlier migration to wintering grounds inferred by this study may have shortened the duration of the autumn feeding season of northern Gulf cod, which may have contributed to the declines in size-at-age and condition mentioned earlier. Northern cod (NAFO Divisions 2J3KL) may also have been distributed further south and deeper in the autumn in recent years, perhaps in response to the oceanic cooling (Rose *et al.*, 1994; Atkinson *et al.*, 1997; see also Hutchings, 1996).

The absence of a significant correlation between ice cover and cod distribution in winter reported in this study does not contradict Fréchet's (1990) conclusion that progression in the formation of ice influences the timing and the extent of the winter migration of 3Pn4RS cod. The correction for autocorrelation resulted in low degrees of freedom and the ensuing low statistical power. Furthermore, the ice variable used here (percentage ice cover) may have been too crude to adequately measure the dynamic relationship between catch rates and the marginal ice zone reported by Fréchet (1990).

Even though stock abundance was rapidly declining during the latter half of the 1980s (Anon., 1994; Fréchet and Schwab, 1998), the abundance in the deepest stratum surveyed was actually increasing, suggesting that individual fish that previously over-wintered inshore were increasingly distributed deeper and further offshore. This offshore shift coincided with and presumably explains the failure of the winter (January to March) fixed-gear cod fishery off southwestern Newfoundland (3Pn) from 1990 onwards, reported by Fréchet and Gagnon (1993). This fishery took place in depths <180 m.

The conclusion that the temperatures occupied by cod did not differ during the cooling period is weakened by the caveat that shallow (<92 m) nearshore waters had to be excluded from the analysis of the summer survey while summer is the season when cod typically forage in nearshore waters. On the basis of the 1991–1995 surveys, the sampling coverage of the population was increased by about 50% when the shallow 37–91 m depth stratum was included. A comparison of temperature distribution of cod for those years (Table 2) shows that median occupied temperatures change little whether the shallow stratum is included or not but we do not know if this conclusion would hold had the above comparison been carried out earlier (1984–1989), when the cooling took place. However, data from the southern Gulf of St Lawrence summer survey do not indicate a cooling of temperatures occupied by cod after the onset of the Gulf cooling (i.e. after 1985), even though this survey extends coverage to a depth of 20 m (Swain and Kramer, 1995). This and the comparison of Table 2 suggest that our conclusion of no change in occupied temperatures is not greatly affected by the exclusion of shallow waters. Cod use their habitat in three dimensions: there is also the possibility that vertically-migrating fish (Beamish, 1966) would have been more exposed to the colder and thicker CIL at night as a result of the cooling episode, but there are no data to examine this possible effect. Clay and Castonguay (1996) also observed that in springtime, northern Gulf cod migrate vertically at night to as much as 80 m off bottom. This emphasizes the limitations of a study which assumes that the temperature near the bottom represents the fish's ambient temperature.

Even though we were fortunate enough to have both summer and winter surveys available for analysing distribution changes, such surveys are nevertheless only "snapshots" in time. Important distribution changes of northern Gulf cod with respect to temperature may have occurred other than in August and January. To integrate seasonal variability, Colbourne *et al.* (1997) incorporated effects of seasonal cycles on cod migrations over large spatial scales and determined that northern cod migrating along hypothetical circular routes in the early 1990s experienced waters up to 1°C below average, particularly in the inshore zone. A thorough understanding of environmental effects on stock productivity will require modelling representative annual thermal histories of individual fish based on adequate validation. Brander (1995) calculated a growth–temperature relationship across stocks that indicates that a 1°C increase in the mean annual temperature that cod are exposed to will produce a 30% increase in mass. This emphasizes the importance of accurately measuring stock-specific annual ambient thermal histories to reliably assess impacts of oceanic variability on fish distribution and growth patterns. The present study, which describes annual variations in thermal exposure of cod in both January and August is a useful first step. Data storage tags, which measure temperature at frequent and regular intervals (Metcalfe and Arnold, 1997) represent a promising tool with which to derive integrated annual thermal budgets in fishes.

Temperatures occupied in summer by cod from the southern Gulf of St Lawrence in the 1980s and 1990s also exhibited little interannual changes but were approximately 1°C colder than those of the northern Gulf cod stock for the same season (Swain and Kramer, 1995). However, these authors, who had access to a longer survey series, also showed that median temperatures occupied by cod in summer varied by more than

1.5°C between the 1970s and the 1980s. Comparisons of depth distributions of cod in summer based on the northern and southern Gulf surveys must account for differences in sampling coverage: the northern survey samples to a depth of 37 m while the southern survey begins at 20 m. Nevertheless, the results suggest different depth distributions since the median depths occupied by southern and northern Gulf cod are 40–50 m (Swain, 1993) and 143 m, respectively [143 m represents the mean of median occupied depths of 1991–1995 summer surveys, including stations in the 37–91 m depth range (data not shown)]. This difference in depth distribution implies different habitat preferences, although such comparisons have to account for the large differences in bathymetry between the deep northern and the shallow southern Gulf of St Lawrence. For example, the mean of median depths of tows in the northern Gulf during the 1991–1995 summer survey, including stations <92 m, is 222 m while the mean depth of tows in the southern Gulf, averaged from 1971 to 1991, is only 87 m (Swain, 1993).

As is the case with southern Gulf cod (Swain *et al.*, 1998), temperatures occupied by northern Gulf cod in winter are much warmer than those in summer even though selecting warm water is energetically costly. One possible explanation is that warm temperatures are required in winter for gonad maturation to proceed properly in time for spring spawning. Female cod held at 6°C in the laboratory started spawning about 2 months before females held at 2°C (Y. Lambert and P. Ouellet, Institut Maurice-Lamontagne, pers. comm.). By selecting warm waters, cod also avoid a reduction of locomotor activity and swimming speed that would result from exposure to cold water during the over-wintering period and the spawning migration (Castonguay and Cyr, 1998).

As mentioned before, the distribution changes described in this study occurred concomitantly with a steep decline in abundance of the northern Gulf cod stock that culminated in the closure of the fishery in January 1994 (Anon., 1994). Even though aforementioned sampling caveats prevented us from adequately measuring this population's range, Figure 2 nevertheless strongly suggests that its winter range shrank in the 1990s. Atkinson *et al.* (1997) found that northern cod's range is positively correlated with abundance and suggested that cod exhibited hyperstability during their decline, in that local densities remained relatively constant over a range of abundance levels (Hutchings, 1996; Atkinson *et al.*, 1997). Hilborn and Walters (1992) define "hyperstability" to describe stocks with distribution properties such that catch per unit of effort remains high as abundance declines. Northern Gulf cod may have exhibited hyperstability during their decline in abundance that led to increased catchability in the winter fishery.

We conclude that starting in the mid-1980s, the distribution of northern Gulf cod has been more southerly and deeper in winter and that the latitudinal shift is correlated with the cooling of the northern Gulf at mid-depth. However the temperatures experienced by cod during the cooling were not different from those before the cooling. Cod responded to a change in their habitat by altering their migration and distribution patterns.

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