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Timing of Atlantic cod (*Gadus morhua* L.) seasonal migrations in the southern Gulf of St Lawrence: interannual variability and proximate control

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The objective of this study was to identify likely proximate cues to the seasonal migrations of cod, *Gadus morhua* L., in the southern Gulf of St Lawrence. We computed a migration timing index across several years using commercial fishery (1970–1992) and sentinel survey (1995–1999) catch rate data, and closely monitored the seasonal changes in temperature, dissolved oxygen, food intake, and energy stores between 1995 and 1998. The inter-year variability in the timing of the seasonal migrations was relatively low (s.d. = 8 d for spring migration, 10 d for autumn migration), suggesting that photoperiod was involved in the control mechanism of migration. However, other factors were also implicated in the control mechanism, given that cod initiated the autumn migration progressively earlier in the late 1980s and 1990s. At the onset of the autumn migration, dissolved oxygen concentrations were above levels known to induce avoidance behaviour in this species, and food resources were considered to be relatively abundant. Similarly, cod did not initiate the autumn migration at a specific temperature or following a particular temperature regime experienced during summer. However, cross correlation function analysis indicated that a widespread cooling of near bottom waters preceded the mid-1980s shift in migration timing by one to two years, suggesting that the cooling event was linked in some way to the change in migration dates. Other correlations showed that the earlier migrations coincided with older cod becoming more abundant and smaller in size, and also with their principal fish prey (herring and capelin) increasing in number. These results suggest that older cod played a key role in launching the early autumn migrations. One plausible interpretation is that their decline in body size and lipid-rich diets led to a rapid build up of energy reserves over summer grounds, and thus to an earlier readiness to engage in the autumn migration. We discuss the potential impact of earlier departures on stock productivity.

Keywords: Atlantic cod, energy reserves, food intake, migration, oxygen, photoperiod, temperature.

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Introduction

Many of the world's most commercially important cod (*Gadus morhua* L.) populations perform extended seasonal migrations (up to 1000 km, Woodhead, 1975). In spring, migratory cod generally move from offshore to inshore areas (McKenzie, 1956; Jean, 1964; Harden Jones, 1968; Woodhead, 1975; Templeman, 1979; Lear and Green, 1984) where preys are abundant (e.g. see Ponomarenko, 1996; Lambert and Dutil, 1997a;

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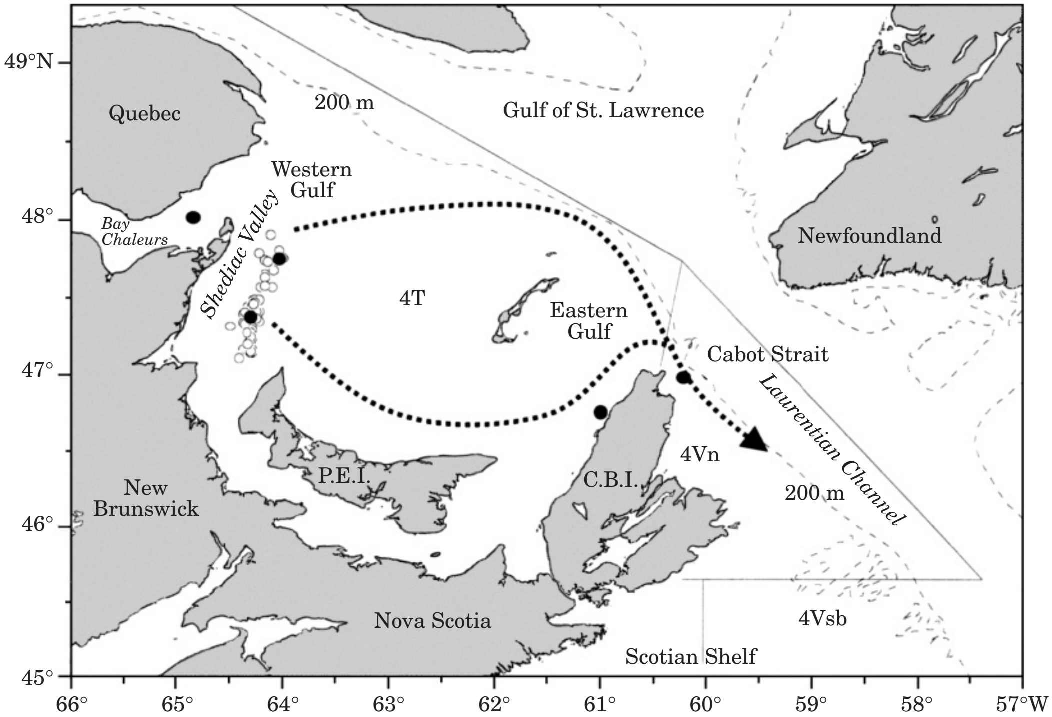

Figure 1. Likely migration routes (Sinclair and Currie, 1994; G. A. Chouinard, unpublished data) between the southern Gulf of St Lawrence (summer) and the Cabot Strait (winter) grounds. The (●) symbols show the locations of temperature recorders deployed on sea bottom. The (○) symbols show sites where near bottom water samples were collected for measurement of dissolved oxygen. NAFO divisions 4T, 4Vn, and 4Vsb are shown.

Schwalme and Chouinard, 1999; O'Driscoll *et al.*, 2000). In autumn, cod may return offshore to avoid what will ultimately be near freezing waters in their summer habitat. While cod can produce plasma antifreeze glycopeptides (Hew *et al.*, 1981; Fletcher *et al.*, 1987), adult cod do not have the capacity to survive water temperatures below about −1.2°C (Kao and Fletcher, 1988).

To ensure that the evolutionary benefits of migration outweigh the risks, a safe and reliable control mechanism must be in place so that migratory movements are initiated at the appropriate times within the physiological and environmental cycles. However, our current understanding of the control mechanism of cod migration is limited. For instance, the question as to whether the migrations are cued by the seasonal changes in water temperature remains open. Temperature has been correlated with cod distribution in several studies (Jean, 1964; Scott, 1982; Rose and Leggett, 1988; Smith *et al.*, 1991; Swain and Kramer, 1995; Castonguay *et al.*, 1999), and temperature changes alone were shown to modify swimming behaviour in captive cod (Claireaux *et al.*, 1995a). Yet, empirical analyses relating *in situ* temperature changes to actual onset of migration are lacking, although such reports already exist for some anadromous species (Jonsson and Ruud-Hansen, 1985; Bohlin *et al.*, 1993) and marine pelagic species (Ogawa and Ishida, 1989; Castonguay *et al.*, 1992; Wilson *et al.*, 2001). Other plausible but yet untested environmental factors that may cue cod migrations include photoperiod (Woodhead and Woodhead, 1965), dissolved oxygen concentrations (D'Amours, 1993), and food supply (Templeman, 1965). With respect to food, an alternate hypothesis is that an annual cycle in appetite (see Fletcher, 1984; Wootton, 1990) regulates migrations to and from feeding grounds. Similarly, it may be that internal changes in temperature preference (Clark and Green, 1991; Despatie *et al.*, 2001), as opposed to environmental changes in temperature, trigger cod migrations.

Identifying the proximal cues to migration and thus being able to predict the onset of seasonal migrations has practical applications for fisheries management, particularly in cases where the timing of migrations are used to set the duration of mixed-stock fisheries. The southern Gulf of St Lawrence cod stock (Figure 1) provides a striking example in which seasonal migrations result in a mixed-stock fishery. During the spring-summer period, southern Gulf cod are found inside the Gulf of St Lawrence [Northwest Atlantic Fisheries Organisation (NAFO) division 4T] (Jean, 1964; Paloheimo and Kohler, 1968) where they reproduce (May–July), feed intensively, and accumulate energy reserves (Schwalme and Chouinard, 1999). The type of prey consumed inside the Gulf in recent years has been primarily herring (*Clupea harengus* L.) and capelin (*Mallotus villosus* Muller) (Schwalme and Chouinard, 1999). In autumn, cod leave their feeding grounds and migrate distances up to 650 km (Hanson, 1996) to overwinter along the southern edge of the Laurentian Channel in the Cabot Strait (NAFO 4Vn) and the eastern Scotian Shelf (NAFO 4Vsb) where they are mixed with stocks from these areas (Lambert, 1993; Campana *et al*., 1999; Swain *et al*., 2001). In spring, they migrate back to their spawning and feeding grounds inside the Gulf, thus completing their annual migration cycle.

The southern Gulf cod population, like several other cod populations from the Northwest Atlantic, has declined to low abundance in the early 1990s, and the directed 4T cod fishery has been closed since 1993 (Chouinard *et al*., 2000). Factors that can potentially explain the poor stock performance in recent years include a large-scale temperature anomaly and its negative impact on growth (Dutil *et al*., 1999), a high rate of natural mortality (Sinclair, 2001), and intense foraging of cod pre-recruits by pelagic fishes (Swain and Sinclair, 2000). A change in migration schedules might have also been detrimental to the population. For example, Castonguay *et al*. (1999) reported a southerly shift in the winter distribution of neighbouring stock, the northern Gulf of St Lawrence cod, and suggested these cod may have left their feeding grounds earlier in the late 1980s and early 1990s. This interpretation implies that the autumn feeding season was shortened, with possible negative consequences on condition and winter survival.

The objectives of our study were to document the actual timing of seasonal migrations, and then to identify the likely variable(s) cueing these migrations. As a first step in this process, we estimated the timing of migrations in southern Gulf cod for the years between 1970 and 1999. We then assessed whether the seasonal migrations are relatively constant from year to year, a result that would support a photoperiod trigger mechanism. We also compared migration timing with changes in environmental temperature and dissolved oxygen, and with the naturally occurring cycles in food intake, energy storage, and prey abundance on summer grounds. Finally, we discuss how the mechanism triggering cod migrations might be linked to environmental and physiological cycles, and comment on the implications of earlier departures from feeding areas.

Material and methods

Migration timing

We used three mobile gear (seine and otter trawl) data sets to infer migration timing: personal logbooks, official logbooks, and sentinel surveys. The "personal logbooks" are those that skippers traditionally maintain to document catches; they are not the type submitted to regulatory agencies such as the Canadian Department of Fisheries and Oceans (DFO), and therefore not subject to intentional misreporting. We were successful in obtaining the personal logbooks from 11 different vessels. These logbooks represented a total effort of 30 681 sets carried out in the eastern Gulf of St Lawrence between 1970 and 1992, after which there was a moratorium on the directed cod fishery. For any given season and year, only some of the 11 vessels in the data set were useful to infer migration timing: the number of vessels that made frequent trips into the eastern Gulf of St Lawrence ranged from a single vessel (1970–1972; 1979–1980) to ten vessels (1990), with the 1970–1992 mean being equal to four (s.e. = 0.5) vessels. In addition to their personal notes, skippers maintain a separate set of logbooks, commonly termed "official logbooks" that are regularly submitted to DFO. The available data set covers a relatively short period (1986–1992) but includes many vessels (mean = 20) for any given season and year in both the eastern and western Gulf. Lastly, sentinel surveys helped determine the timing of the autumn migration from 1995 to 1999. Sentinel surveys consist of periodic sampling excursions on traditional fishing grounds (as opposed to entire southern Gulf) following a stratified-random protocol. Trips were carried out between July and November, and were generally two to three days in duration with a maximum of one trip per week. On site, seiners conducted regular fishing sets whereas otter trawlers performed one-hour sets. We used the data from two sentinel survey vessels in the western Gulf, and two other vessels in the eastern Gulf.

In keeping with the understanding that migrating cod form large and dense aggregations (Rose, 1993), which make them more vulnerable to mobile fishing gear, we used the day of peak catch rates as an index of migration timing. As a first step in the calculation of the timing index, trip or daily means of catch rates were produced for each vessel. The means reflected a substantial effort: about ten sets per trip for the sentinel series, 13 h per day for the official logbooks, and five sets per day for the personal logbook series. Then, for each vessel, the time-series of catch rates was visually inspected for a single peak in either spring or autumn. The peak in catch rate was generally unambiguous. For instance, when compared with the previous three days on record, the peak represented an increase in catch rate of 190% (s.e. = 25%) in spring and 246% (s.e. = 27%) in autumn (based on personal logbooks). Finally, for any given season and year, a mean date corresponding to the peak in catch rate was computed using all available vessels. With respect to the spring timing index, we excluded the years characterized by late ice retreat (e.g. 1991 and 1992), since a delayed start of the fishery would have skewed the index.

Environment

Bottom water temperatures were monitored between 1995 and 1998 by deploying temperature recorders at five locations within the study area (Figure 1, filled circles). No surface floats were attached to the moorings, thereby allowing the recorders to remain on station during the ice period. Using differential GPS technology, we recovered the moorings by dragging a grapnel over the stations. During the study, the recorders (Minilogs, Vemco Ltd, Canada) logged bottom temperature every 3 h with an estimated accuracy of 0.2°C. Weekly means and standard deviations were calculated for each site separately. In the western Gulf, near bottom water samples were regularly collected at two to five sites arbitrarily selected for dissolved oxygen measurements (Figure 1, open circles). Oxygen concentrations were measured in duplicate using the Winkler titration procedure (Aminôt and Chaussepied, 1992). Oxygen concentrations are reported as trip means.

Fish collection and nutrition indices

A total of 1613 adult cod (fork length = 52.5 ± 0.3 cm) were collected as part of research and sentinel survey expeditions in 1995, 1996 and 1997. The number of fish collected each month ranged from 21 to 209 and both sexes were generally well represented. The sampling interval ranged from one to two weeks during the summer and autumn and from one to two months during the winter and spring. The exact sampling area varied according to the seasonal migrations of the cod. During the summer and autumn, samples were collected inside the Gulf of St Lawrence, particularly in the western region where a large fraction of the population resides at this time of year (Chouinard *et al.*, 2000). During the winter and spring, samples were collected in the Cabot Strait along the southern edge of the Laurentian Channel. Stock mixing estimates based on elemental composition of otoliths (Campana *et al.*, 1999) and vertebral number (Swain *et al.*, 2001) indicated that cod overwintering in this area were almost entirely from the southern Gulf stock.

Relative (to body mass) food intake was reported as the stomach fullness index, representing the weight of the stomach content as a percentage of the carcass weight (Schwalme and Chouinard, 1999). The carcass weight was calculated as the total weight of the fish less the combined weight of the liver, gonads, and the stomach with content. To provide an estimate of absolute food intake, we computed a standardized (50 cm fork length) stomach content weight index analogous to that of the Fraser-Lee procedure described in Carlander (1981) and Campana (1990). For each trip, we produced a regression equation relating the stomach content weight and fork length. The regression intercept (b) was then incorporated into the following equation to determine the standardized stomach content weight:

$$\mathrm{Stom}_{50\ \mathrm{cm}} = \mathrm{b} + (\mathrm{Stom}_{\mathrm{c}}^{-1} - \mathrm{b})\mathrm{L}_{\mathrm{c}}50$$

where $\mathrm{Stom}_{50\ \mathrm{cm}}$ is the standardized stomach content weight, L_{c} is the fish length at capture, and $\mathrm{Stom}_{\mathrm{c}}$ is the weight of the stomach content at capture. Energy reserves were measured using two indices, the Fulton's condition factor (K) and the hepatosomatic index (HSI). Both indices were calculated as in Lambert and Dutil (1997b):

$$\mathrm{K} = 100\mathrm{WL}^{-3}$$

$$\mathrm{HSI} = (\mathrm{LW} \cdot \mathrm{W}^{-1})100$$

where W represents the somatic weight in grams, L is the fish length in centimetres, and LW is the liver weight in grams. Somatic weight was calculated as the total weight of the fish minus the combined weight of gonads and stomach content.

Statistics

Sample means were compared using nonparametric statistics: the Mann–Whitney test for two samples, and the Kruskal–Wallis test for several samples. Trend lines were fitted to time series using either an iterative locally weighted least-squares (LOWESS) method or a centred moving average approach. In the latter case, missing data points in series were replaced with computed values (linear interpolation) prior to the calculation of the moving averages. Cross-correlation function (CCF) analysis was used to examine whether changes in migration timing lagged environmental changes. Standard correlation analysis was used to quantify the extent to which migration timing co-varied with other factors. We tested for autocorrelation by correlating series with lagged values of itself. We accounted for autocorrelation, when present, by computing an effective sample size (n_{eff}) in correlation analyses. This corrective procedure reduces the changes of incorrectly concluding that a correlation is significant (Type I error). The equations used to compute n_{eff} are those found in Dutil *et al.* (1999, equations 1 and 2) and incorporate the weighting factor proposed by Pyper and Peterman (1998). Note also that the corrective procedure requires the use of continuous time series. Because of this restriction, we had to limit our analyses to years between 1979 and 1992 (instead of 1970–1992) when accounting for autocorrelation.

Results

Migration timing

The spatio-temporal patterns in catch rates were consistent with the formation of dense aggregations of cod during migration events. In spring, as cod were moving towards summer grounds, peak in catch rates were recorded first in the eastern Gulf, and subsequently in the western Gulf (Figure 2a and b); in autumn, a reverse pattern was obvious when cod migrated out of the Gulf (Figure 2c and d). The time difference between the appearance of the western and eastern peaks provided an estimate of the duration of the migrations inside the Gulf. From 1986 to 1990 (official logbooks), the time difference between the two regional peaks was on average 25 d (s.e. = 7 d) in spring and 25 d (s.e. = 4 d) in autumn. From 1995 to 1999, sentinel surveys in autumn also showed a duration of migration of 25 d (s.e. = 4 d).

In the eastern Gulf, the peak catch rates in spring were logged on 3 May with a standard deviation of only 8 d between 1970 and 1992 (Figure 3a, filled circles, personal logbooks). The autumn timing index was slightly more variable (s.d. = 10 d), and more importantly, started a declining trend in 1986 (Figure 3b, filled circles, personal logbooks). Peak catch rates were logged on 30 November in 1970–1985 and on 14 November in 1986–1992. The 16 d difference between the two periods was highly significant (Mann–Whitney test, $p<0.001$). In more recent years (1995–1999), peak catch rates in sentinel surveys were recorded on 1 November. The 14 November and 1 November means were also significantly different (Mann–Whitney test, $p<0.01$).

We examined the possibility that the declining trend since 1986 was due to changes in the fishing fleet composition, since the number of vessels included in the personal logbook dataset tended to increase with time. A small subset ($n=2$) of vessels that fished most years during the entire period was thus inspected: the outcome was similar, with a definite tendency for earlier timing in 1986–1992. Peak catch rates occurred on average 13 d earlier than in 1970–1985 (Mann–Whitney test, $p<0.02$). Moreover, there were no strong indications that the early peaks were caused by the shortening of the autumn fishery due to quota reductions. The peaks during the 1986–1992 period were logged on average 7 d (s.e. = 1 d) before the last fishing trip in autumn and, perhaps more importantly, there was a tendency towards low or null catch rates soon after the peak catch rate event. The tendency for catch rates to be at a minimum in early autumn, and thus for early departure of cod, has been obvious since 1986 in both commercial and sentinel surveys. In 1990, for instance, the catch rates from two commercial vessels quickly fell in early autumn (Figure 4); by comparison, in 1982, the catch rates from the two same vessels remained elevated in early autumn. Finally, it does not appear that the early timing results since 1986 were due to a shift in the fishing area. Figure 5 shows that vessels recorded their peak catch rates consistently in the same region during the study period.

Migration in relation to the environment, food intake, and energy storage

In spring, the bottom-water temperatures inside the Gulf increased above the lower limit for cod distribution (~ -0.5°C, Rose and Leggett, 1988; Swain and Kramer, 1995) (Figure 6). The thermal barrier (< -0.5°C) first disappeared in the eastern Gulf, which is consistent with the spring migration route. The breakdown of the thermal barrier also coincided with the historical peaks in catch rates (see EG and WG in Figure 6). In autumn, cod departed the western Gulf when temperatures were increasing (Figure 7a–c). For each recording station, the temperature at the onset of the autumn migration was significantly different between years ($p<0.0001$, Kruskal–Wallis test applied to weekly samples). The temperature in any of the three weeks preceding the onset of migration was also different between years ($p<0.0001$, Kruskal–Wallis test applied to weekly samples). Moreover, migration timing showed no consistent pattern in relation to within-week temperature variability (Figure 7d–f), and did not coincide with a specific number of degree-days (Table 1).

With respect to dissolved oxygen, a trend towards low concentration values was evident on summer grounds. However, the lowest concentrations occurred about 30 d prior to the onset of the autumn migration (Figure 8). Oxygen concentrations were increasing and ranged between 8 and 9 mg ml^{-1} when cod departed the western Gulf.

The stomach fullness index indicated that cod were feeding intensively as they entered the Gulf in spring, but that they fed little while leaving the Gulf in autumn (Figure 9). Condition indices followed another trend. The condition factor and HSI values were low as cod moved into the Gulf in spring, but progressively increased on summer grounds and eventually peaked in autumn. The HSI, in particular, consistently peaked at (or just prior to) the onset of the autumn migration, and the magnitude of the peaks was similar among the investigated years (Kruskal–Wallis test, $p>0.05$).

A cruise-by-cruise analysis for the western Gulf provided further insight into the relationship between food intake, energy reserves, and the autumn migration. From 1995 to 1997, the stomach content weight represented between 6 and 7% of the carcass weight at the beginning of summer, but only between 1 and 2% at the onset of the autumn migration (Figure 10a). Absolute stomach content weight showed a similar trend: in 1995, for instance, the stomach content weight

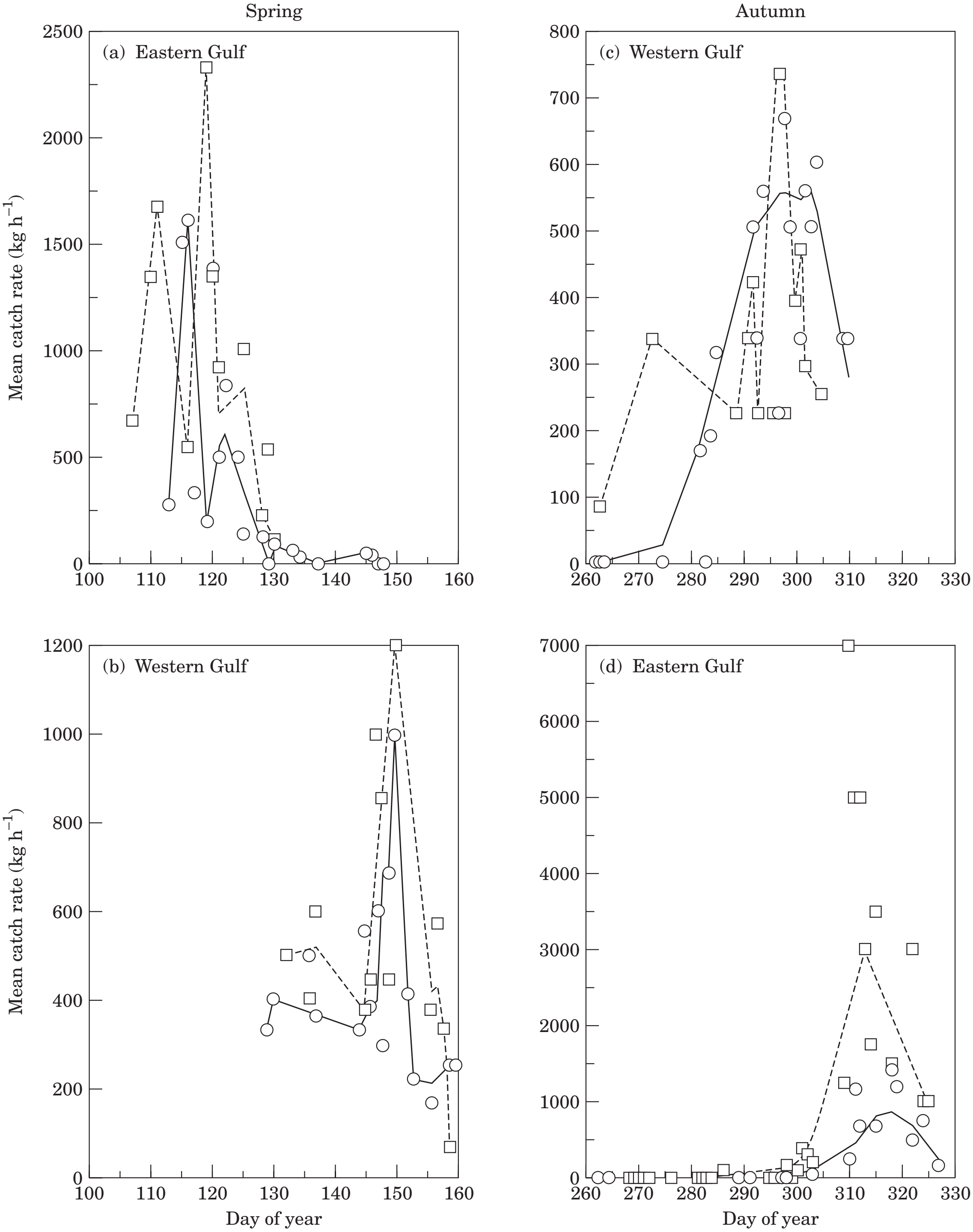

Figure 2. Examples of the changes in catch rates in spring (1990) and autumn (1989). Data points are from the official logbook series and represent daily means of individual mobile gear vessels (two vessels, (○) and (□), shown per graph). Trend lines show locally weighted least-squares regression.

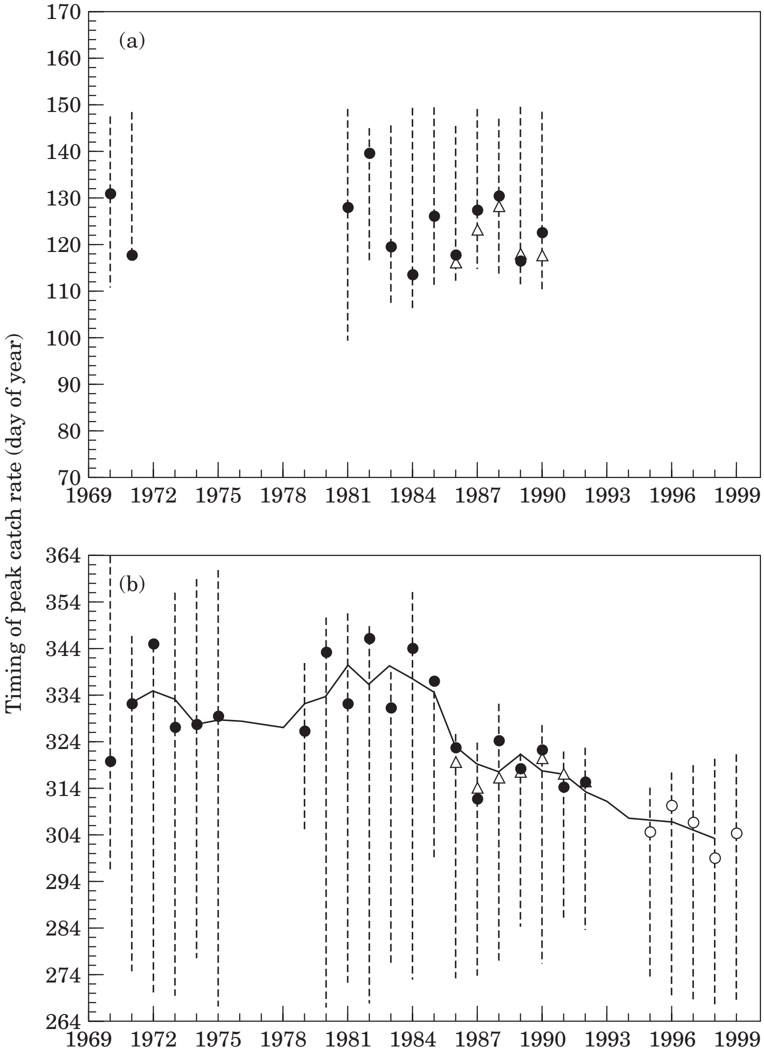

Figure 3. Timing of the (a) spring and (b) autumn peaks in catch rate in the eastern Gulf of St Lawrence. (●)=personal logbook series, (△)=official logbook series, (○)=sentinel series. Vertical broken lines show duration of autumn fishery: lower limit marks the average day when boats began fishing within season, and upper limit shows the average day when the fishery ended within season. Trend lines show three-year running mean.

of a 50 cm cod declined from 81 g (s.e.=9 g) in early summer to only 8 g (s.e.=4 g) at the onset of migration. Interestingly, a small fraction of the population was still present in the western Gulf in late October. In this group, food intake indices were significantly higher compared to cod sampled in early October (Table 2). Condition indices, and particularly the HSI, were in turn relatively low. The late departing cod were thus in poor condition but feeding intensively.

In the longer term (1970–1992), the autumn migration tended to occur earlier as temperatures declined in the cold intermediate layer (CIL) (Figure 11a). However, the correlation between the two variables was non-significant, even after the removal of the 1984 outlier. CCF analysis suggested that changes in migration schedules lagged behind changes in temperature. Significant correlations were found only when the timing index lagged the CIL index (Figure 11a) by one year ($r=0.51$, $n=19$, $p<0.05$) and the bottom water temperatures (Figure 11b) by two years ($r=0.62$, $n=17$, $p<0.01$). There was no significant correlation between timing and the areal extent of cold bottom waters (Figure 11c).

We next examined whether the changes in migration timing were correlated with changes in cod population attributes. For these analyses, the data were first $\log_{10}$ transformed to create normal distributions and improve linearity in correlations. This transformation did not remove autocorrelation, and consequently an effective

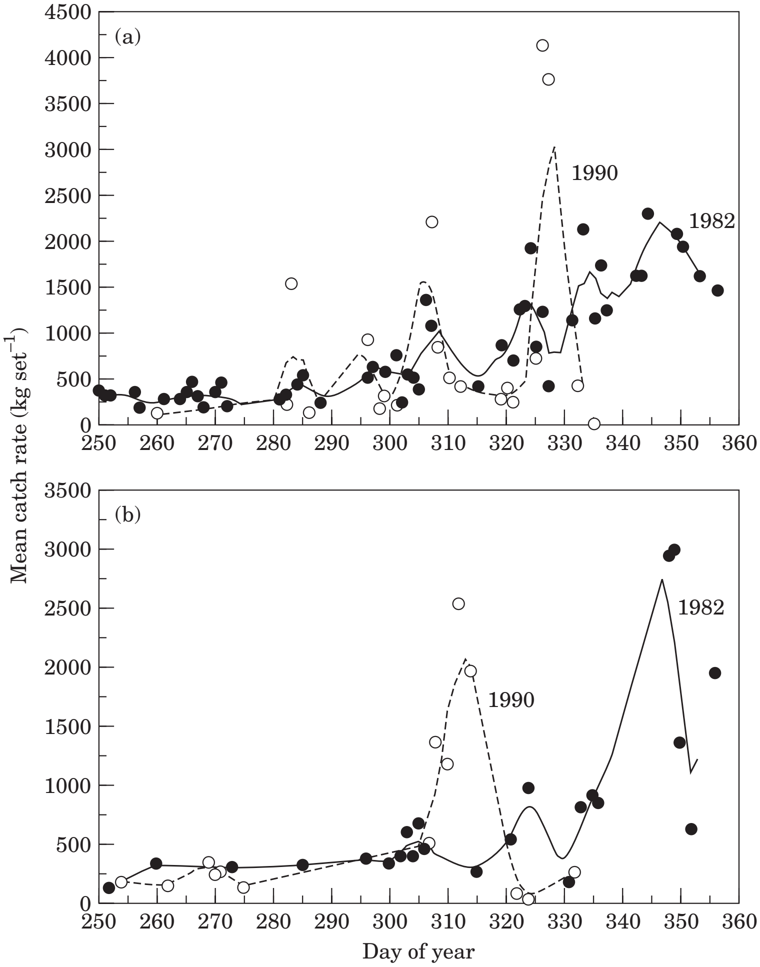

Figure 4. 1982 (●) and 1990 (○) autumnal catch rates (daily means) in the eastern Gulf. Graph (a) represents one fishing vessel and graph (b) another vessel, both from the personal logbook series. Trend lines show five-day running mean.

sample size was calculated for statistical inference. No significant correlations were found between timing and cod population abundance (Figure 11d). However, negative correlations were found between timing and the abundance of older cod, namely those of age 13 ($r = -0.76$, $n = 14$, $n_{eff} = 6$, $p < 0.05$, Figure 11e) and age 14 ($r = -0.66$, $n = 14$, $n_{eff} = 7$, $p < 0.05$). In the same way, timing was positively correlated with the body size (fork length) of older cod only, specifically those of age 11 ($r = 0.71$, $n = 14$, $n_{eff} = 6$, $p < 0.05$), age 12 ($r = 0.93$, $n = 14$, $n_{eff} = 6$, $p < 0.01$, Figure 11f), and age 13 ($r = 0.72$, $n = 14$, $n_{eff} = 7$, $p < 0.05$). It is also noteworthy that migration timing was negatively correlated with the abundance of herring and capelin inside the southern Gulf of St Lawrence ($r = -0.77$, $n = 14$, $n_{eff} = 6$, $p < 0.05$, Figure 12). Therefore, the mid-1980s shift in migration timing coincided with older cod becoming more abundant and smaller in size, and also with cod's principal fish prey becoming more abundant on summer grounds.

Discussion

Environmental cue

The timing of cod migrations varied little between 1970 and 1992, with standard deviations ranging from 8 d (spring) to 10 d (autumn). Although there are no analogies in the marine groundfish literature, similar but slightly lower (s.d. 2–6 d) interannual variation estimates have been reported for some salmonid (Jonsson and Ruud-Hansen, 1985; Bohlin *et al.*, 1993) and avian (Berthold, 1996) species. In the latter group, the low interannual variation estimates were interpreted to indicate that photoperiod plays an important role in the mechanism cueing the seasonal migrations (Berthold,

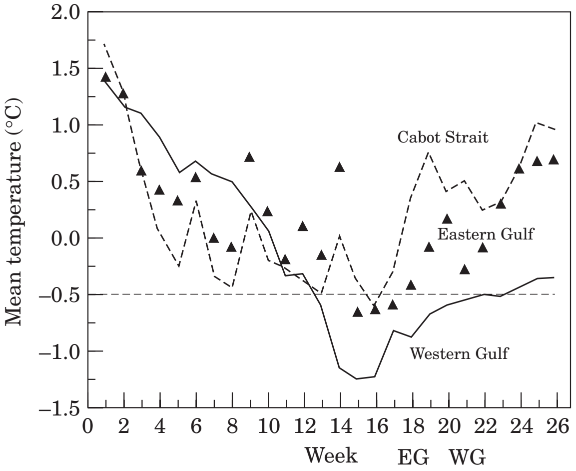

Figure 6. Weekly mean (1997–1998) bottom water temperatures in the western Gulf (continuous line), eastern Gulf (▲) and Cabot Strait (broken line) during the first half of the calendar year. EG and WG indicate week when catch rates peaked in the eastern and western Gulf respectively (official logbooks, 1986–1990). Depth of temperature recording stations ranged from 84 to 88 m.

1996). For cod, however, the autumn migration has occurred progressively earlier since 1986, indicating that photoperiod could not have been an exclusive stimulus to migration. The reported trend in migration timing is consistent with the view of sentinel fishers, who commented that southern Gulf cod were migrating out of the Gulf noticeably earlier during the 1990s (Chouinard *et al.*, 1999b). Castonguay *et al.* (1999) suggested that a neighbouring stock, the northern Gulf of St Lawrence cod, also performed the autumn migration earlier during the late 1980s and early 1990s. Therefore, it appears that the mid-1980s shift in the timing of the autumn migration was real and widespread inside the Gulf of St Lawrence.

It is unlikely that low oxygen concentrations motivated southern Gulf cod to migrate early. At the onset of the autumn migration, the oxygen levels in near bottom waters were increasing and well above those believed to induce physiological stress and avoidance behaviour in this species (<5 mg ml^{-1}, Claireaux and Dutil, 1992; D'Amours, 1993; Claireaux *et al.*, 1995b). The lack of association between oxygen cycling and onset of migration was not surprising, since animals migrating in response to low oxygen levels will most likely end up in an environment with improved oxygen concentrations.

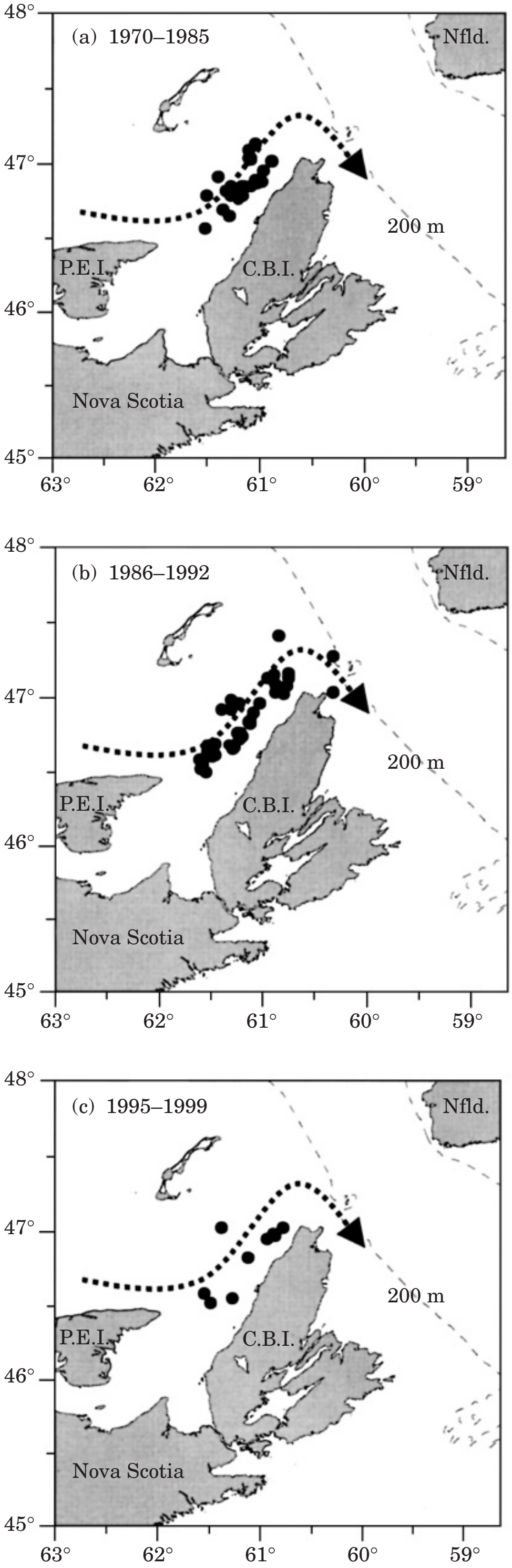

Figure 5. Locations (●) of autumnal peaks in catch rates for individual vessels. Personal logbook data shown in panels (a) and (b); sentinel data shown in panel (c). Arrow line shows likely migration route in autumn.

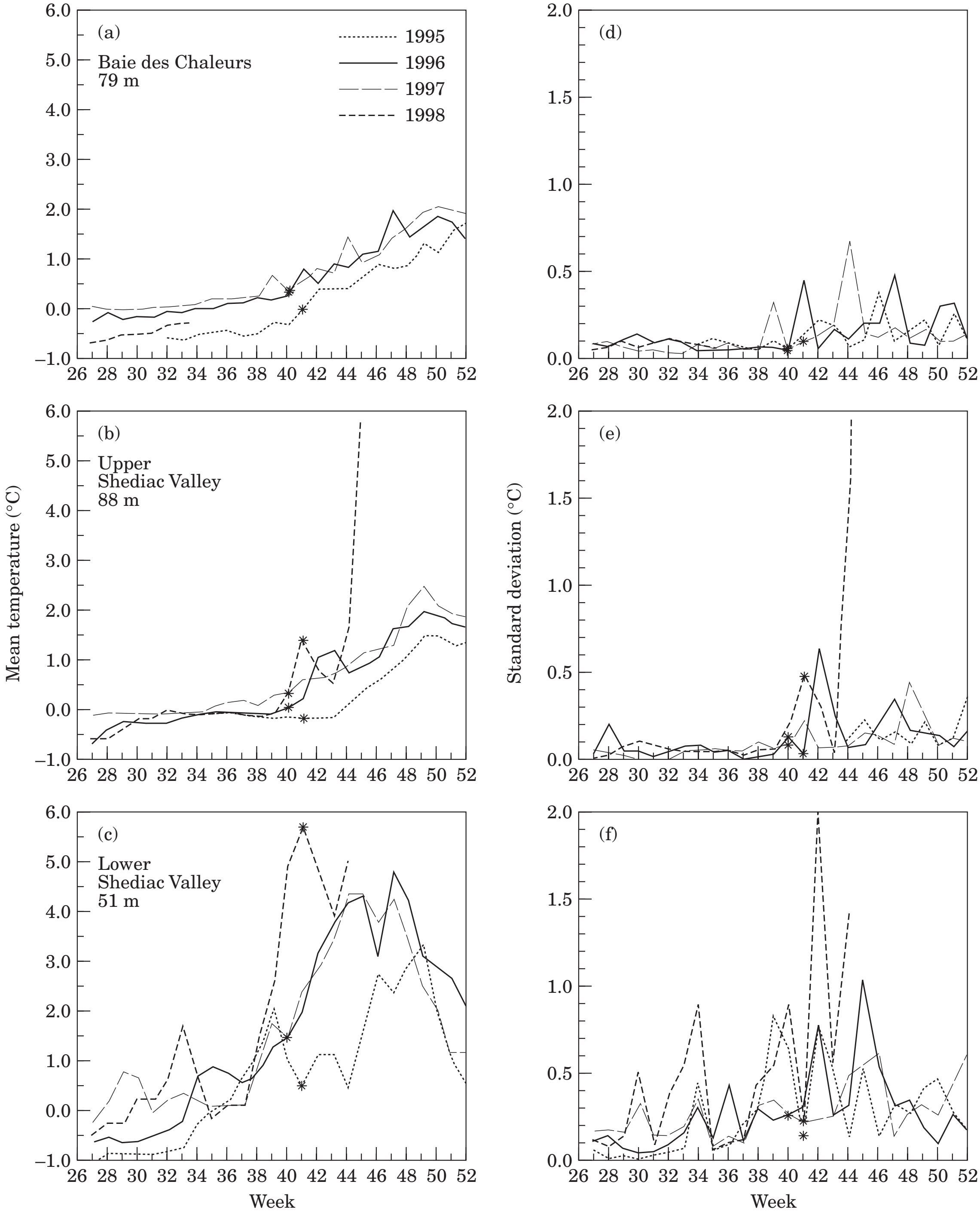

Figure 7. Bottom water temperatures (weekly means, left side of page) and corresponding standard deviations (right side) during the second half of the calendar year. Star symbols indicate week when catch rates peaked in sentinel surveys.

Cod, on the other hand (ultimately) overwinter in deeper and hence less oxygenated waters. They also occupy comparatively warm waters in winter (Swain *et al*., 1998), whereas ectothermic animals facing hypoxia are expected to seek a colder environment to acquire physiological advantages, namely to reduce metabolic rate

Table 1. Degree-days between 1 July and onset of migration in the western Gulf. Calculated using data from moored temperature recorders in upper and lower Shediac Valley.

	Upper Shediac Valley				Lower Shediac Valley			
	Number of days with temperature (°C) above							
Year	0.0	0.5	1.0	1.5	0.0	0.5	1.0	1.5
1995	No data				43	27	14	6
1996	3	0	0	0	49	39	17	3
1997	31	0	0	0	72	33	11	6
1998	15	7	3	2	67	42	36	27
Range	28	—	—	—	29	15	25	24

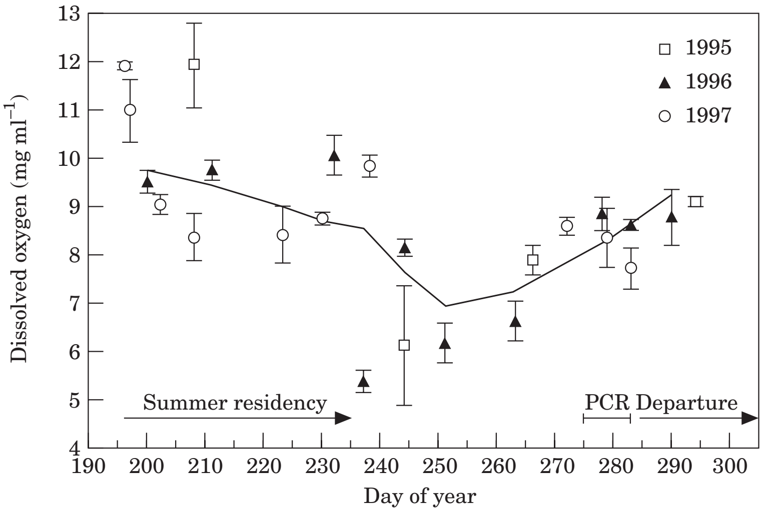

Figure 8. Bottom water oxygen concentrations in the western Gulf. PCR = Peak catch rates. Mean of two to five sites and corresponding s.e. bars are shown. Sampling depths varied from about 40 to 88 m. Locally weighted least-squares line was fitted to 1996 data.

(Brett, 1971) and to increase blood oxygen affinity (Riggs, 1970; Alberts, 1970; Weber *et al.*, 1976; Boutilier *et al.*, 1988).

We found little evidence that limiting food resources triggered the autumn migration. On one hand, cod initiated their autumn migration when food intake (assessed in terms of relative and absolute stomach content weight) was low. On the other, food intake continued to decline during the autumn migration and reached a minimum on winter grounds. Moreover, some individuals extended their summer residency inside the western Gulf: these cod were feeding extensively, suggesting that food was abundant in the Gulf throughout autumn. Therefore, it seems unlikely that a lack of food could have been the principal motivator for the early departures from summer grounds.

Regarding temperature, our results are consistent with the view that the warming of the coastal shelf environment in spring regulates the *progression* of the shoreward movements (Konstantinov, 1965; Chen *et al.*, 1994; Hutchings and Myers, 1994; Colbourne *et al.*, 1997). Our temperature recorders indicated that the return of cod into the southern Gulf coincided spatially (eastern Gulf vs. western Gulf) with the temperatures rising above a lower limit for cod distribution. However, a closer examination of temperature changes during the autumn period suggested that temperature does not function as a proximate signal for the onset of migration. When cod initiated migration in the western Gulf, temperatures were rising but remained well within the median values occupied by this stock in September [0.3–7.5°C (age 5); Swain and Kramer, 1995]. Also, during the four-year monitoring effort, cod did not initiate migration at a specific temperature or following a particular temperature regime (e.g. degree-days) during the previous summer. These results suggest that temperature is not the initiating stimulus for migratory behaviour.

In their study of northern Gulf of St Lawrence cod, Castonguay *et al.* (1999) suggested that early autumn migrations were linked to an oceanic cooling event (Gilbert and Pettigrew, 1997). In the present study,

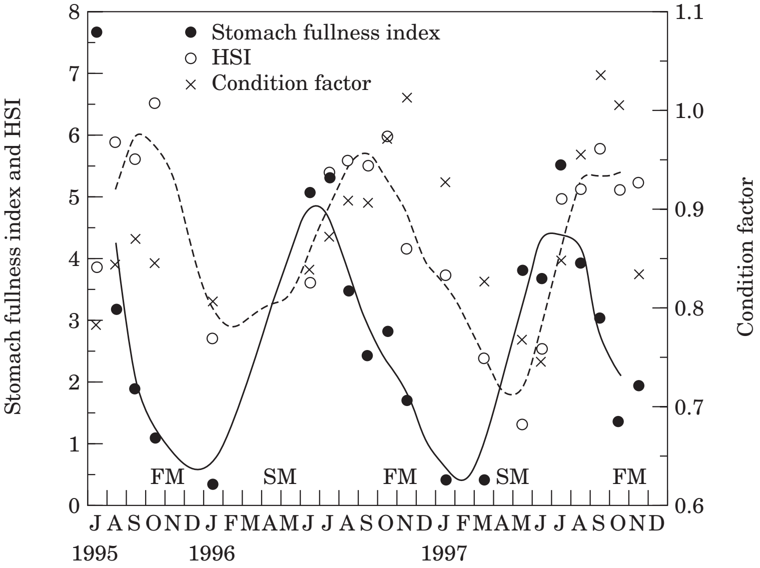

Figure 9. Seasonal changes in the stomach fullness index ((●) symbol, continuous trend line), HSI ((○) symbol, broken trend line), and condition factor ((×) symbol). FM = Fall Migration; SM = Spring Migration. Trend lines represent three-point centred moving averages.

significant correlations between the actual onset of the autumn migration and long-term temperature data support that view. However, according to our CCF analysis the response to the oceanic cooling was not instantaneous, since the earlier migrations occurred only one to two years after the temperature anomaly had begun. This offset time suggests that temperature had no direct influence on the mechanism triggering migration, consistent with the temperature recorder data presented above. A plausible interpretation is that the cooling of water masses changed migration schedules by acting on other key variables. According to fish bioenergetics, the colder temperatures would have lowered the metabolism and feeding rates, and therefore growth rates and size-at-age (see Krohn *et al.*, 1997; Dutil *et al.*, 1999). Also, the colder temperatures may have widened the distribution of fish prey such as capelin well into the southern Gulf (see Frank *et al.*, 1996), and therefore induced a change in the cod diet (Schwalme and Chouinard, 1999). These events deserve special attention because they were simultaneously correlated with the earlier autumn migrations. Below we discuss the physiological mechanism of migration, and examine how the changes in fish prey abundance and size-at-age might have triggered early departures from summer grounds.

Physiological cue

Annual cycles in food consumption and energy deposition/mobilization have been described for both southern and northern Gulf cod (Lambert and Dutil, 1997a; Schwalme and Chouinard, 1999). We examined these physiological cycles in relation to migratory behaviour over a three-year period. We found that the HSI, a good indicator of the total lipid reserves in cod (Lambert and Dutil, 1997b), reached extreme values during migration events. In spring, cod entering the Gulf had recently begun the task of re-building lipid reserves through intense feeding. This general synchronism evidently does not demonstrate a causal relationship between lipid depletion and migration. On the other hand, it allows for the formulation of specific hypotheses regarding the physiological control of cod migration. For instance, it could be hypothesized that lipid depletion in spring enhances appetite (Metcalfe and Thorpe, 1992; Jobling and Miglavs, 1993; Simpson *et al.*, 1996) and in doing so motivates cod to return to their feeding grounds. Others may postulate that lipid depletion triggers migratory behaviour by changing the thermal preferendum, since previous laboratory work has shown that low ration or starved fish (cod included) select colder temperatures compared to well-fed individuals (Javaid and Anderson, 1967; Stuntz and Magnuson, 1976; Mac, 1985; Morgan, 1993; Despatie *et al.*, 2001). Our temperature recorders indicated that Gulf waters in spring, especially those in the western Gulf, tend to be colder than those in the Cabot Strait area. By migrating into the western Gulf, the starved fish would benefit from low-metabolic costs at low temperature (see Swain and Kramer, 1995; Swain, 1999; Despatie *et al.*, 2001).

In autumn, the bulk of the population departed the western Gulf in early October when lipid reserves (HSI) peaked. A small fraction of the population, however,

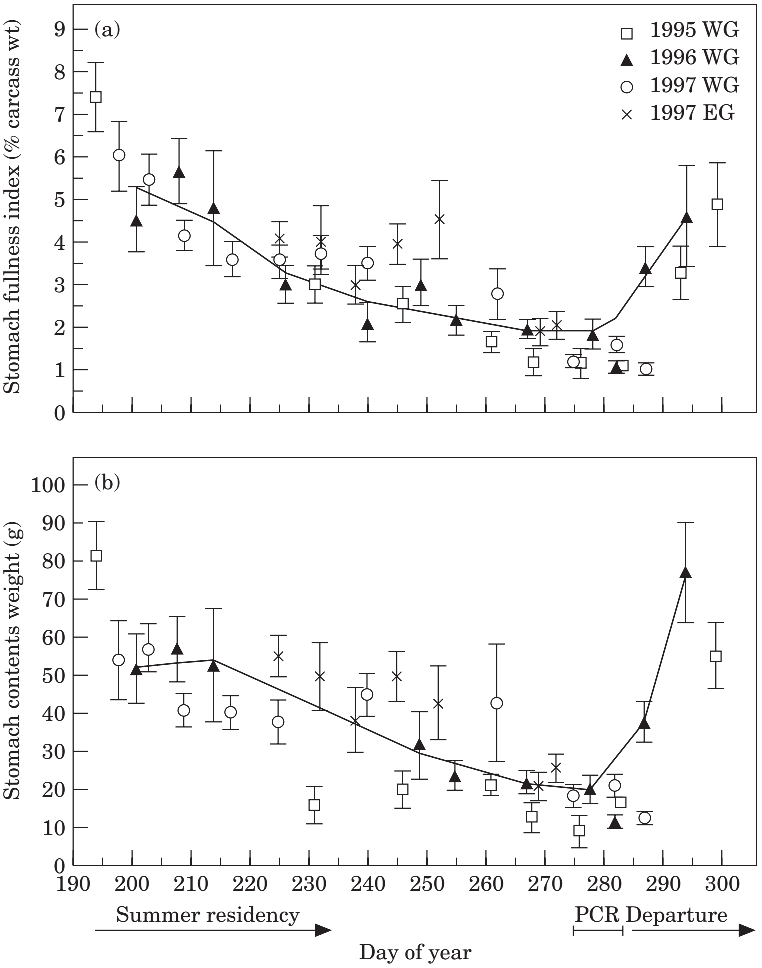

Figure 10. (a) Stomach fullness index and (b) standardized stomach content weight (for 50 cm cod) in western Gulf (WG) and eastern Gulf (EG). PCR = Peak catch rates. Locally weighted least-squares line was fitted to 1996 data.

Table 2. Food intake and energy reserves in western Gulf cod collected in early and late October. Values are expedition means.

	1995		1996	
	10 Oct	26 Oct	5 Oct	20 Oct
A. Food Intake				
Stomach content weight (g)	15.8	54.6***	19.5	76.1***
Stomach fullness index	1.1	4.8	1.8	4.5***
B. Energy Reserves				
Carcass weight (g)	1015	978**	1009	1010^{ns}
Condition factor	0.92	0.87*	0.90	0.84^{ns}
Hepatosomatic index (HSI)	6.3	4.6	6.6	3.1***

Note: The number of fish in samples ranged from 14 to 30. The carcass and stomach content weights were standardized for a 50 cm cod. Asterisks indicate significant difference between the two October samples (Mann–Whitney: *$p<0.05$, **$p<0.01$, ***$p<0.001$, ns = non-significant). Data from 1997 have been omitted due to poor coverage in late October.

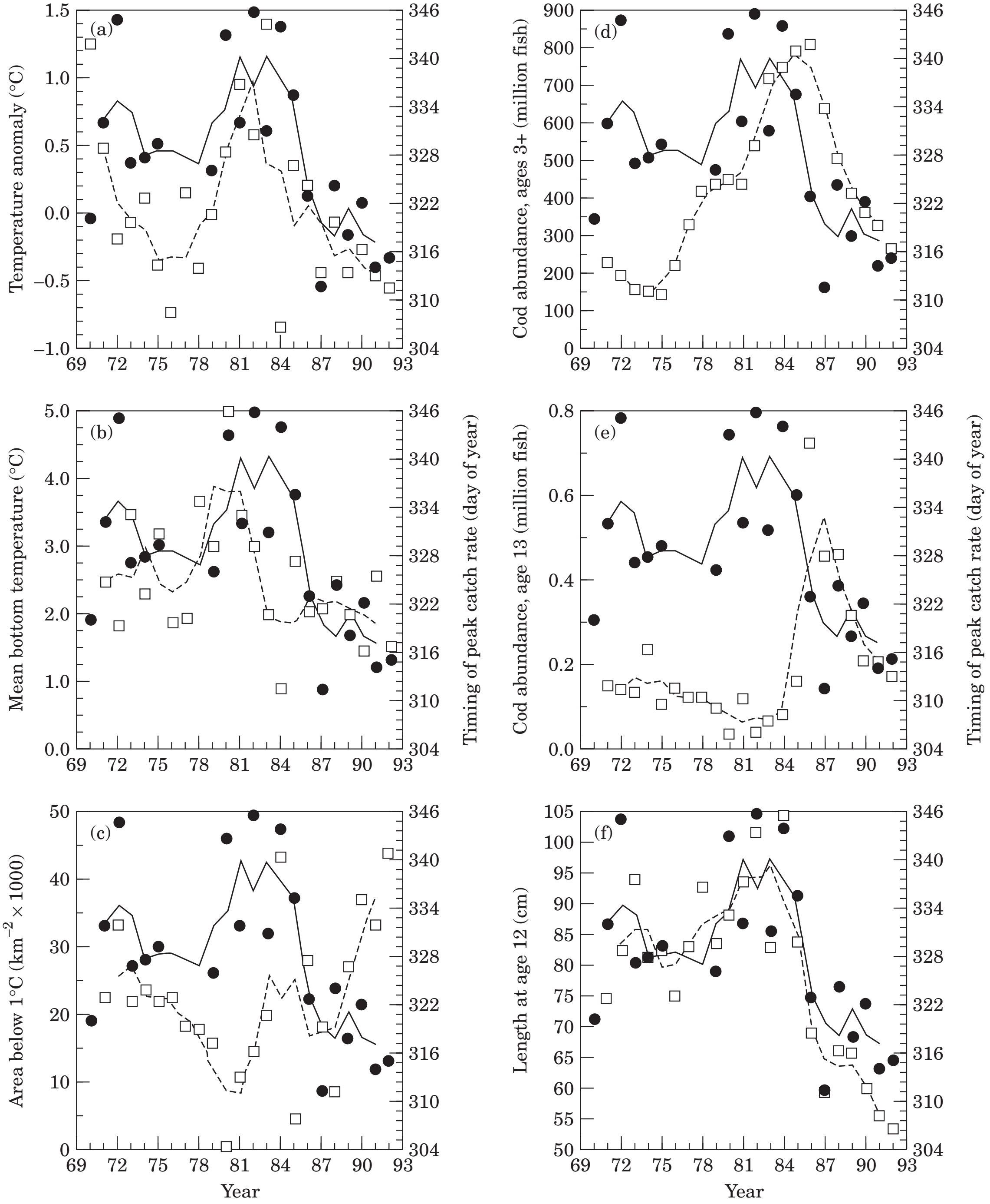

Figure 11. Timing of autumnal peaks in catch rates in the eastern Gulf ((●), personal logbook series) in comparison to long term temperature anomalies ((□), graph (a)), mean bottom temperatures, ((□), graph (b)), areal extent of cold bottom waters ((□), graph (c)), cod abundance ((□), graphs (d) and (e)), and length-at-age ((□), graph (f)). The temperature anomalies represent deviations from the 1948–1994 mean temperature minimum in the CIL (taken from Gilbert and Pettigrew, 1997; southern Gulf, extrapolated to 15 July). Mean bottom temperatures and areal extent of cold waters data were taken from Swain (1993) and reflect the thermal conditions during the month of September. Population abundance and length at age data were taken from Chouinard *et al.* (1999a). Trend lines show three-year running mean.

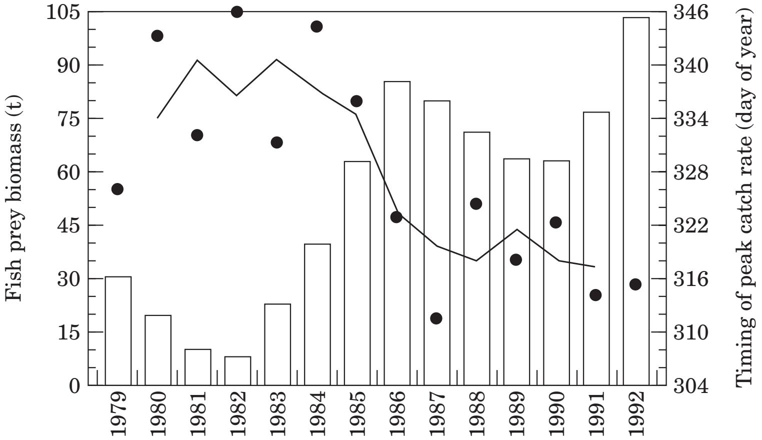

Figure 12. Timing of autumnal peaks in catch rates in the eastern Gulf ((●), personal logbook series) in comparison to the combined abundance of herring and capelin (open bars). Herring abundance surveys started in 1978. The herring data (spring spawners) were taken from Claytor and LeBlanc (1999). The capelin data were taken from Frank *et al*. (1996).

extended their stay in the western Gulf. The late departing fish had a poor feeding history, which raises the question as to whether the migration to winter grounds is conditional upon a certain degree of fatness. In the Russian literature, a close link between lipids and the timing of migration has been reported for the Black Sea sprat and the Azov anchovy (Shulman and Love, 1999). Anchovies that manage to accumulate maximum lipid reserves on summer grounds will gather into vast shoals and leave the Azov Sea in early autumn, while those that accumulate fewer lipids will delay their migration. This model predicts that the timing of the autumn migration will be inversely correlated with the availability of food resources on summer grounds, and more specifically with the availability of fish prey since they represent an important source of lipids for cod (Black and Love, 1986). We found such a correlation using the combined abundance of herring and capelin in the southern Gulf ($r = -0.77$, $p<0.01$). Other investigators have noted the fish prey became more prominent in the diet of southern Gulf cod in recent years: in 1980, for example, the proportion by weight of fish in the diet of large cod was 28%; in 1992, however, this figure increased to 74%, the highest reported since the mid-1950s (Schwalme and Chouinard, 1999). We suggest that the increased proportion of fish in the cod diet accelerated the annual process of lipid deposition on summer grounds. Considering the documented link between lipids and migration (Schulman and Love, 1999), an intriguing question is whether the shift in the cod diet resulted in an earlier readiness to engage in the wintering migration.

We also find interesting that southern Gulf cod performed the autumn migration earlier as the older individuals in the population became more abundant ($r = -0.66$ to -0.76). This result suggests that the older fraction of the population had a significant influence on migration. This interpretation is in agreement with echosounding data showing that the larger cod lead the migratory aggregations (Rose, 1993). The exact significance of this hierarchical structure during seasonal migrations is not known. It could mean that older fish sustain migratory routes and behaviours, with younger fish having nothing to do but follow and learn (Rose, 1993). Such a mechanism seems applicable to herring stocks off the coast of Norway (Dragesund *et al*., 1980), and has been suggested for the Barents Sea cod (Woodhead, 1975) and more recently for the eastern Newfoundland cod (Rose, 1993). For southern Gulf cod, the mid-1980s increase in the number of older individuals might have heightened that leadership, possibly resulting in quick formations of migratory aggregations and expeditious movements out the Gulf. Interestingly, we also found significant correlations between timing and the body size of older cod, with the autumn migration occurring progressively earlier as the older cod became smaller ($r = 0.71$–0.93). Owing to their smaller body size and presumably lower food requirements, it may be that the older cod reached their critical level of fatness for winter survival earlier than normal, thereby triggering earlier departures. Regardless of the exact underlying mechanism, however, the fact that these correlations were significant only for the older fraction of the population suggests that the larger cod determine migration schedules for the entire population.

Implications of earlier autumn migrations

The trend in the autumn migration may explain changes in the distribution of cod observed in the annual demersal fish survey in the southern Gulf of St Lawrence. This survey has always been conducted in September, a few weeks prior to the peak in catch rates in the west (upper Shediac Valley) for recent years. Swain (1995) observed that the proportion of cod survey biomass found in the eastern Gulf increased steadily since the beginning of the survey in 1971 and particularly since the mid-1980s. Recent observations (Poirier *et al*., 2000) indicate that this trend has continued. The changes in the distribution of cod in the survey, particularly the low abundance observed in the most westerly area near the Gaspé coast (Québec), is consistent with the trend for an earlier migration of cod found in this study.

The evolutionary implications of earlier migrations are not clearly understood. Since gonadal recrudescence in southern Gulf cod begins in autumn (Schwalme and Chouinard, 1999; Comeau *et al*., 2001), an obvious advantage for leaving summer grounds as quickly as possible could be the enhancement of gonadal development in warm slope waters (see Hutchings and Myers, 1994). On the other hand, it does not appear that cod are capable of returning into the Gulf sooner the following spring, given the presence of ice (Fréchet, 1990) and cold waters described earlier. It seems that an early arrival on winter grounds increases the time spent where food resources are scarce or inaccessible due to vertical separation of cod and its fish prey (Schwalme and Chouinard, 1999). Unfortunately, for southern Gulf cod, the historic records on post-winter condition are limited to the 1990s (Schwalme and Chouinard, 1999; this study), and thus it is difficult to assess whether or not the extended stay in the winter area resulted in lower condition than normal. One could argue that the lipid-rich diets in recent years favoured an extended period of residence in the winter area, and more specifically controlled the risk of death from energy depletion (see Dutil and Lambert, 2000; Lambert and Dutil, 2000). Certainly, lipids are by far the most efficient vehicles for storing chemical energy, and it seems that avian species at least accumulate more lipids than are needed to cover the cost of migratory activities (Berthold, 1996). Also, on a broader perspective, the idea that a lipid-rich diet can trigger early departures (Shulman and Love, 1999), but that these are ultimately detrimental to the population, raises an evolutionary paradox. Therefore, the earlier departures from feeding grounds may not necessarily be a factor contributing to the slow recovery of the southern Gulf cod population.

Summary

This study has shown that the inter-year variability in the timing of the spring and autumn migrations was relatively low for southern Gulf cod, which raises the possibility that photoperiod was somehow involved in the control mechanism of migration. However, since cod initiated the autumn migration progressively earlier starting in the mid-1980s, it seems unlikely that photoperiod was an exclusive stimulus to migration. CCF analysis indicated that a widespread cooling of near bottom waters preceded the mid-1980s shift in migration timing by one to two years. Correlative analysis in turn indicated that early migration coincided with (1) an increase in the abundance of fish prey (herring and capelin) on summer grounds and (2) older cod, i.e. the ones that presumably lead migratory aggregations, becoming more abundant and smaller in size. The lipid-rich diets coupled to the decline in body size/food requirement may have led to a rapid build-up of energy reserves on summer grounds, and thus to an earlier readiness to engage in the autumn migration.

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