Environmental analysis of Atlantic cod (*Gadus morhua*) migration in relation to the seasonal variations on the Northeast Newfoundland Shelf

E. Colbourne, B. deYoung and G. A. Rose

Abstract: Comparison of historical (1930–1989) and recent (1990–1993) oceanographic data from the Northeast Newfoundland Shelf reveals a significant phase lag in the normal seasonal cycle of temperature and salinity. Atlantic cod (*Gadus morhua*) migrating along hypothesized circular routes during the early 1990s experienced temperatures up to 1.0°C below average, particularly at depths typical of the inshore cod fishery. Cod likely spent up to three times longer in subzero °C water during the early 1990s than was typical for the years 1930–1989. The time spent in subzero °C water during normal and warm years was relatively independent of timing of the migration, but even a delay of 1 mo during the early 1990s put cod in subzero °C water twice as long as normal. In contrast, no net salinity anomaly was experienced along the tracks. Temperatures experienced by cod along migration routes have a much larger range and a mean value up to 1.0°C higher than the vertically averaged temperatures at Station 27. In addition, the interannual average temperature along the migration routes, while exhibiting similar trends, was up to an order of magnitude higher (≈3.0 versus ≈0.3°C) than the vertically averaged temperatures obtained from a fixed point on the shelf (Station 27).

Résumé : La comparaison de données océanographiques anciennes (1930–1989) et récentes (1990–1993) pour la partie nord-est de la plate-forme de Terre-Neuve révèle un déphasage important dans le cycle saisonnier normal de la température et de la salinité. Les morues (*Gadus morhua*) qui, au début des années 90, empruntaient les voies de migration circulaires qu'on leur attribue ont été soumises à des températures qui tombaient jusqu'à 1,0°C au-dessous de la moyenne, particulièrement aux profondeurs auxquelles se pratique la pêche côtière à la morue. Les morues ont probablement passé jusqu'à trois fois plus de temps dans des eaux à moins de 0°C au début des années 90 que dans les années 1930 à 1989. Le temps passé dans des eaux à moins de 0°C au cours des années normales et chaudes était relativement indépendant de l'époque de la migration; mais, au début des années 90, un retard de 1 mo seulement obligeait les morues à passer deux fois plus de temps que d'habitude dans des eaux à moins de 0°C. Par contraste, aucune anomalie nette de la salinité n'a été observée le long des voies. Les températures auxquelles sont soumises les morues le long des voies de migration s'étendent sur une plage beaucoup plus large que les températures mesurées sur la verticale à la Station 27, et leur valeur moyenne est plus élevée, l'écart pouvant atteindre 1,0°C. De plus, la température moyenne le long des voies de migration, calculée sur plusieurs années, présentait des tendances similaires mais était plus élevée d'un ordre de grandeur (≈3,0 par rapport à ≈0,3°C) que la moyenne des températures mesurées sur la verticale en un point fixe sur la plate-forme (Station 27).
[Traduit par la Rédaction]

Introduction

Recent studies have suggested that environmental conditions (temperature, salinity, currents, etc.) on the continental shelf of Atlantic Canada may influence the distribution, recruitment, migration, and behaviour of migrating fish such as northern cod (*Gadus morhua*) (deYoung and Rose 1993; Myers et al. 1993; Rose et al. 1994; Taggart et al. 1994). A common approach in such studies is to relate different indices of fish biology, such as biomass, recruitment, growth, or condition factors, to time series of environmental indices, such as volume or area of subzero °C water, bottom temperatures, or vertically averaged temperature or salinity obtained from observations made at some fixed point like Station 27 (Fig. 1). Although there is high spatial coherence between the temperatures at Station 27 and across the shelf over the same depth range (Petrie et al. 1991; deYoung et al. 1994), this approach assumes that station conditions mimic the environment experienced by cod during seasonal migrations from the deep waters offshore to the inshore bays along Newfoundland.

During the Northern Cod Science Program (NCSP) and the Ocean Production Enhancement Network (OPEN), oceano-

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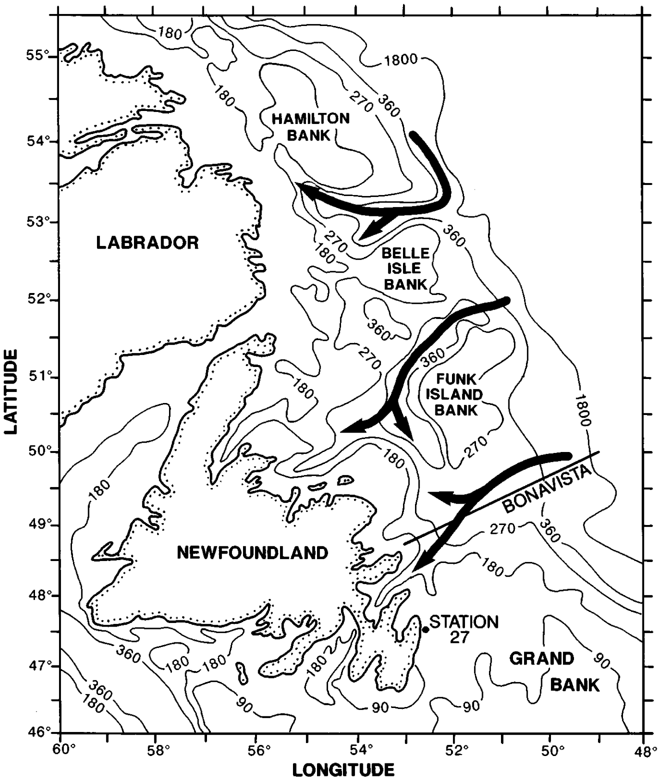


Fig. 1. Location map of the study area showing the positions of the standard Bonavista transect, Station 27, and the cod migration routes predicted by Rose (1993). Isobaths are in metres. Redrawn from Rose (1993).

graphic surveys were carried out at approximately monthly intervals on the Northeast Newfoundland Shelf from early May to November from 1990 to 1993. These data, combined with oceanographic observations made during fisheries research and assessment surveys, have made it possible to resolve the seasonal cycles in the oceanographic environment during the early 1990s over large spatial areas on the Northeast Newfoundland Shelf. As a result, a more realistic approach to ecosystem research is possible, particularly as it pertains to migrating fish such as northern cod. From 1930 to 1989, an extensive temperature and salinity data set available from the Marine Environmental Data Service (MEDS) in Ottawa, Canada, and from archives at the Northwest Atlantic Fisheries Center (NAFC) readily establishes the long-term mean seasonal cycle (Colbourne et al. 1994; deYoung et al. 1994).

Tagging studies, biological indicators, and data from the commercial fishery have been used to describe general patterns of the migrations of cod from the offshore areas of the continental shelf to the inshore feeding grounds (Templeman 1966; Lear 1984). Tagging studies carried out over several decades support the existence of migratory circuits that are to a large extent spatially repeated from year to year (Templeman 1979; Lear 1984; Rose 1993; Taggart et al. 1995). More recently, combined acoustic tracking and tagging studies have identified specific migration corridors wherein cod move from the offshore to inshore areas along deep cross-shelf trenches that transect the continental shelf (Rose 1993; Rose et al. 1995). These corridors are probably used by cod because, being deeper, their bottom waters are warmer because the topography "cuts through" the three-dimensional temperature field. These various data have been used to define the approximate spatial extent of migrating cod throughout a full seasonal cycle.

We infer a circular migratory circuit from the offshore to inshore areas in the south, then north along the east and northeast coast of Newfoundland to southern Labrador, and eventually offshore to deeper water during the autumn where overwintering occurs along the edge of the continental shelf, as suggested by Rose (1993). We also examined other smaller scale migratory circuits from the shelf edge in spring through the Bonavista migration corridor (southern most route, Fig. 1) to the bays along the Avalon Peninsula and offshore along the same path during autumn.

The aim of this paper is to review the seasonal character of the oceanography on the Newfoundland Shelf during the period 1990–1993, with specific reference to the long-term mean, and to investigate the potential effects of oceanographic conditions on migrating cod. We develop a cod migration model utilizing both recent and historical oceanographic data sets to simulate the environmental conditions cod experience as they move along their migration routes. The representativeness of data from a fixed point on the continental shelf, specifically Station 27, to conditions along the simulated migration tracks is also evaluated.

Methods

Station 27 is one of the most frequently monitored hydrographic stations in the Northwest Atlantic Ocean. Data collected at this site have been used in several environmental monitoring and ocean climatic studies (e.g., Petrie et al. 1992; Colbourne et al. 1994; Drinkwater 1994). The position and frequency of occupation of this station make it well suited for determining the phase and amplitude of the seasonal cycle in temperature and salinity in the inshore branch of the Labrador Current in both the upper layer and the center of the cold intermediate layer (CIL) (Petrie et al. 1991; Colbourne et al. 1994).

Following the general methods of Smith (1983), Petrie et al. (1991), and Myers et al. (1990) and detailed descriptions in Colbourne et al. (1994) and Colbourne and Fitzpatrick (1994) the seasonal cycle in the temperature and salinity fields at selected water depths was determined by fitting a least-squares regression of the form $\cos(\omega t - \phi)$ to the historical 1930–1989 and the 1990–1993 data sets, where ω is the frequency of the annual cycle and its harmonics, t is the time of the year, and ϕ is the phase. The two independent sets of regression coefficients were then used to calculate the seasonal cycles for temperature and salinity for the two time periods at depths typical of the inshore portion of the cod migration cycle.

While the Station 27 data set enables a temporal analysis of the oceanographic conditions at a fixed location on the Newfoundland Shelf, the standard Bonavista transect (Fig. 1; Anonymous, 1978), one of the most frequently monitored transects of the Labrador Current in the Northwest Atlantic, enables both a temporal and spatial analysis of oceanographic indices across the continental shelf (Colbourne and Senciall 1993). The historical (1930–1989) and the 1990–1993 data sets along this transect were quality controlled, linearly interpolated to 5.0-m depth intervals, and analyzed on a monthly basis. The area of subzero °C water (CIL) along the transect for each month was determined by projecting all temperature profiles within $\pm 25'$ of latitude of the standard Bonavista transect line onto a 5.0 km horizontal by 5.0 m vertical grid. The data were then averaged and the area inside the 0.0°C contour measured using a digital planimeter.

To examine the environmental conditions along cod migration routes, all data on the Newfoundland Shelf from 46 to 55°N latitude were grouped in the year ranges 1930–1989, 1977–1980, 1986–1988,

Fig. 2. Vertical cross-section of the summer (July–August) cold intermediate layer (CIL) of subzero °C water along the standard Bonavista transect for a warm year (1986), a cold year (1991), and the long-term mean (1930–1989).

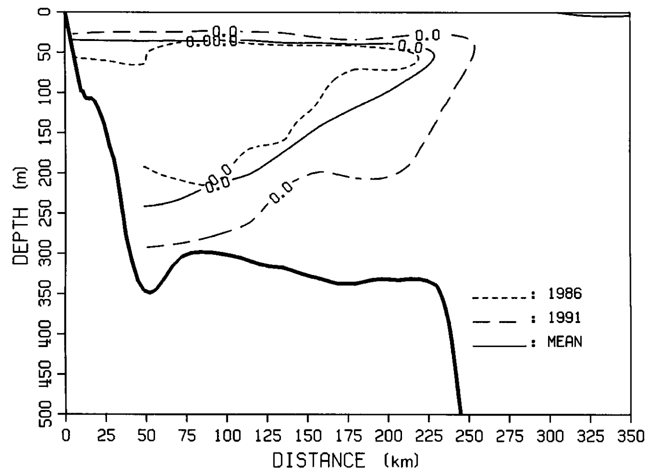
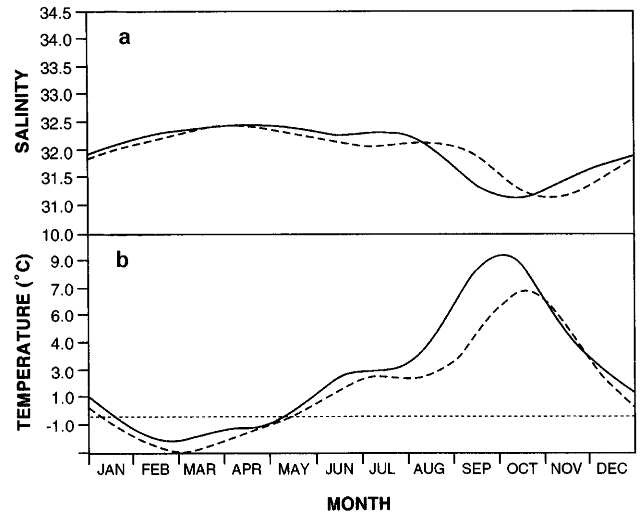


Fig. 3. Seasonal cycle of (*a*) salinity and (*b*) temperature at 30 m depth at Station 27 calculated from the least-squares regressions of all data from 1930–1989 (solid line) and 1990–1993 (broken line).



and 1990–1993 and then averaged into square projections of 0.25° latitude by 0.38° longitude and the mean for each month computed. Data were available at a sufficient number of grid points for each month for these years along the migration tracks used in our analysis, thus enabling the calculation of a temperature and salinity value at any time of the year on the shelf by linear interpolation in both space and time; any missing grid points were interpolated from nearest neighbours. A comprehensive analysis and description of the environmental data base in this area is found in deYoung et al. (1994), Colbourne and Senciall (1993), Colbourne and Fitzpatrick (1994), and Colbourne and Foote (1994). Once the temperature field $T(x,y,x,t)$ and salinity field, $S(x,y,z,t)$ (x and y are the horizontal spatial coordinates, z is the vertical or depth coordinate, and t corresponds to time of year) were known, the simulation of oceanographic conditions experienced by migrating fish was possible.

The simulations were performed by initiating the start time and position of the fish in the spring along the edge of the continental shelf off Cape Bonavista. The fish were then moved along migration routes near the bottom towards the coast through the Bonavista migration corridor at a constant speed. After the fish arrived inshore, they were allowed to either move northward along the coast at a constant depth or remain in the same general area until autumn, after which they moved offshore along the bottom to the edge of the shelf (see Fig. 5*b*). As the fish moved through both time and space the temperature and salinity values they experienced were calculated using the linear model described above.

Seasonal oceanography

The dominant feature of the temperature structure on the continental shelf throughout most of the year, except the winter months when the thermal stratification breaks down, is the large volume of subzero °C water trapped between warmer surface and bottom continental slope water, commonly referred to as the cold intermediate layer (CIL) (Petrie et al. 1988). The summer (July–August) CIL bounded by the 0.0°C isotherm shows significant variability from the mean in the offshore extent, maximum depth, and cross-sectional area between a warm year (1986) and a cold year (1991) (Fig. 2). A discussion of the interannual variability of various CIL indices is presented in Colbourne et al. (1994) and Colbourne and Senciall (1993). Subzero °C water occupies a significant portion of the total volume of water on the continental shelf, with subzero °C water always present from the bottom of the seasonally heated upper layer (30–50 m in summer) to the bottom nearshore (depths >50 m) to about 50 km offshore (depths >250 m) depending on local bathymetry.

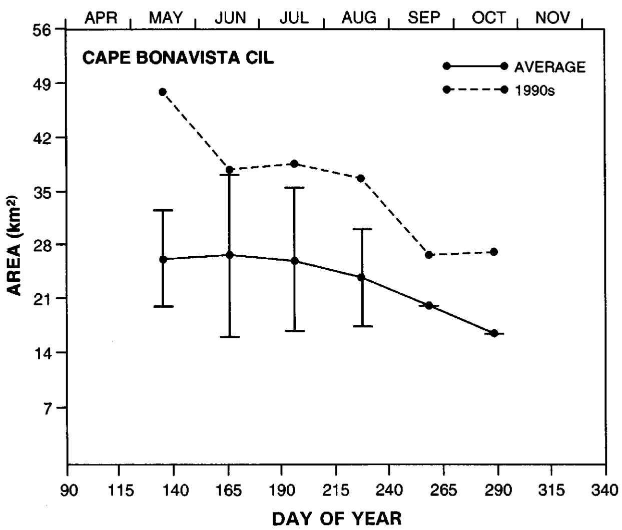
The seasonal cycles in the temperature and salinity fields on the Newfoundland Shelf were first investigated by Bailey (1961) and modeled by Petrie et al. (1991). As described earlier, we fitted harmonic regressions to the recent (1990–1993) and historical (1930–1989) data sets. This analysis allowed us to investigate in detail the effect of cold years on the phase and amplitude of the seasonal cycles and the possible implications for the fishery.

Winter and spring salinities at Station 27 during the early 1990s were near normal at 30 m depth, below normal by about 0.25 psu during late spring and early summer, and up to 0.5 psu above normal from midsummer to early autumn (Fig. 3*a*). These anomalies were likely the result of a delayed upstream runoff and ice melt during the spring. Surface salinity normally reaches a minimum at Station 27 in late September (Myers et al. 1990), but this minimum was not observed until early November during the period 1990–1993, up to 5 wk later than normal.

During the winter months of the early 1990s the 30 m depth temperature was up to 0.5°C below normal and up to 3.0°C below normal during the summer and early autumn. By late October, temperatures rebounded and were near the long-term average for the remainder of the year (Fig. 3*b*). The amplitude of the seasonal temperature cycle which normally reaches its maximum by late September was delayed by up to 3–4 wk during the early 1990s. These observed phase shifts in both the temperature and salinity seasonal cycles were the result of anomalously cold air temperatures (Findlay and Deptuch-Stapf 1991), above-normal spring ice coverage, and delayed ice melt experienced on the Newfoundland Shelf since the late 1980s to 1993 (Prinsenberg et al. 1997).

The seasonal variation in the area of the CIL for the two time periods shows a relatively constant area of subzero °C

Fig. 4. Seasonal variation in the cold intermediate layer (CIL) of subzero °C water along the Bonavista transect based on all data from 1930–1989 (solid line) and 1990–1993 (broken line). Vertical bars represent SD.



water along the Bonavista transect from May to July after which it shows a gradual decrease during early autumn, reaching its minimum by November after which it increases again due to the onset of winter cooling (Fig. 4). During the early 1990s, this area was significantly larger (by 30–40%) than the long-term average. It is clear from this analysis that the oceanographic conditions on the Newfoundland Shelf during the early 1990s were anomalous in both amplitude and phase.

Cod migration

Historically the northern cod stock was believed to consist of several overlapping and intermingling populations over an area from the northern Grand Banks to northern Labrador (Harris 1990). These populations undertook seasonal migrations from the warmer slope water offshore to the inshore areas and bays along the coast of Newfoundland and Labrador during spring and summer to feed on mainly caplin (*Mallotus villosus*), a species also undergoing an annual migration (Lear and Green 1984). The southernmost cod migration route observed by Rose (1993) through the Bonavista corridor between the northern Grand Bank and southern Funk Island Bank (Fig. 1) was the target of intensive cod migration and oceanographic studies in the springs of 1990, 1991, and 1992 (Rose 1993; Rose et al. 1995; DeBlois and Rose 1995). In addition, under the NCSP, this route was monitored at approximately monthly intervals during spring and summer of 1992 and 1993 to resolve the seasonal variations in the oceanographic conditions.

During the studies of the Bonavista corridor, cod were tracked acoustically along the route for up to 36 d (Rose et al. 1995). Up to 6500 cod were tagged from the migrating aggregations each year (G.A. Rose, unpublished data). The general patterns of tag returns during 1990 and 1991 (a moratorium was declared on fishing in July 1992; hence, tag returns declined to near nil) were described by Rose (1993). Here, we repeat details essential to the present study. Tags were returned from the inshore regions along the Avalon Peninsula and the east coast of Newfoundland during July and along the northeast Newfoundland coast to St. Anthony during August. Later returns were received from southern Labrador to September and near the edge of the shelf the following winter (Fig. 5*a*). The pattern is suggestive of a circular migration cycle from the offshore to inshore in the spring, north along the coast during summer, and offshore during late autumn (Fig. 5*b*). We infer that this route approximates the maximum range of migrating cod during recent years. In keeping with the south–north movement patterns over a longer time period, Chen et al. (1994) used the inshore commercial cod landings between 1974 and 1991 to show a spatial pattern in the timing of the inshore fishery, with the fishery starting along the Avalon Peninsula in late June but not until August in southern Labrador.

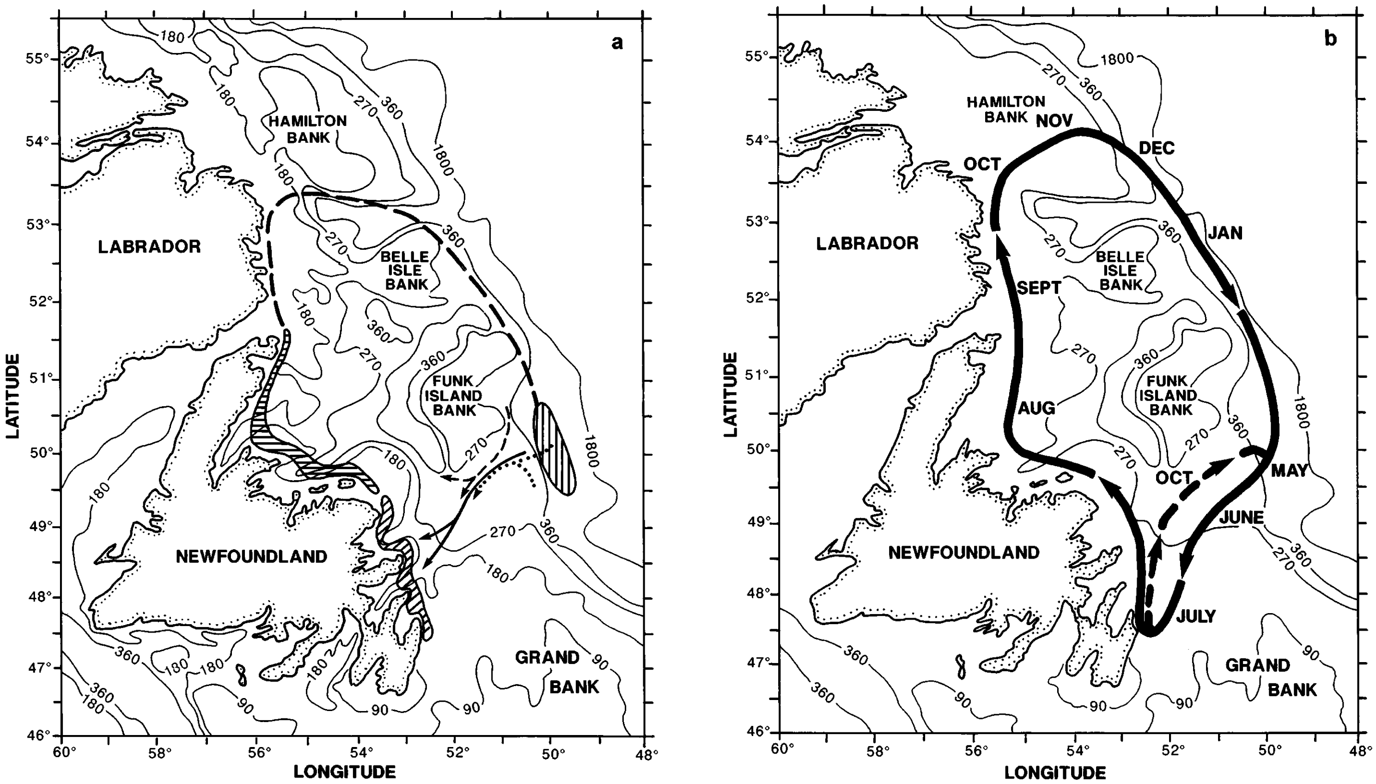
In this study, we used the circular routes (Fig. 5*b*) to examine the oceanographic conditions experienced by fish as they undertook their seasonal migrations. However, we emphasize that other more northerly migration routes (Fig. 1) lead directly to the northerly inshore zones and may have been the chief migration routes of some cod in former years. Nevertheless, the southernmost route was utilized by the bulk of northern cod in the early 1990s during their inshore migrations, and the circular route we used was supported by tagging from 1990 to 1992 and hence is the most reliable circuit upon which to base our initial simulations.

The basic assumptions we used in our simulations were that cod migrate along the routes near the bottom across the shelf into shallower water near the coast. The along-shore summer migration was fixed at a constant 30 m depth. This depth was chosen to correspond to the approximate median depth of the inshore commercial cod trap fishery. The average migration speeds along the cross-shelf (spring) leg and the inshore northward (summer) leg were fixed at about 8 km/d and about 5 km/d during the autumn offshore migrations. These speeds were necessary to match the timing of the tag returns and the timing of the inshore commercial fishery and are within the range of the groundspeeds observed acoustically on the cross-shelf leg during spring. The mean groundspeed observed during the acoustic tracking experiments of 1992 was about 9 km/d and the average during all three years ranged from 7 to 24 km/d. A detailed analysis of these cod migration speeds in relation to ambient currents on the Northeast Newfoundland Shelf is given in Rose et al. (1995).

Results

To examine the oceanographic conditions cod experience on their migration routes, we started the model simulations in mid-May near the edge of the continental shelf off Cape Bonavista at the seaward end of the Bonavista migration corridor. To evaluate the sensitivity of the timing of the migration cycle to the oceanographic conditions, we also ran simulations starting in mid-April and mid-June. Fish migrating shoreward along the external route (Fig. 5*b*), starting in mid May, through the Bonavista corridor in water depths ranging from 500 to 1000 m experience average (1930–1989) temperatures decreasing from about 3.5°C near the shelf edge to 2.0°C near the center of the corridor and to –1.0°C as they move onto the Grand Bank in about 100–200 m depth (Fig. 6). Temperatures

Fig. 5. (*a*) Migration patterns of northern cod observed in June and July (solid line, 1990; broken line, 1991; dotted line, 1992). Hatching indicates areas of inshore tag returns in July (diagonal hatching), August (horizontal hatching), and the following winter (vertical hatching). The heavy broken line indicates the boundary of the migration route indicated by Rose (1993). Adapted from Rose (1993). (*b*) Migration routes considered in this study showing the timing of the migration. Bathymetry in metres.



rise again as the cod move into shallower water near the coast and into the bays, decrease as they migrate northward along the coast during early July, and increase as they move north to southern Labrador from early August through to September. By early autumn the seasonal warming reaches its maximum near bottom in water depths typical of the inshore cod trap fishery. From late September to early October the fish begin to move offshore across Hamilton Bank in roughly 0.0°C water which then increases to between 3.0 and 4.0°C as they move along the shelf edge during the winter months. Cod migrating along this route experience an average temperature of 2.0°C throughout the year.

Similarly, the average salinity decreases from about 34.8 psu in the deep water at the shelf edge to 33.0 psu on the Grand Bank to 32.3 psu near the coast in water depths of about 30 m. The salinity then gradually decreases from south to north from about 32.3 psu along the Avalon Peninsula to about 31.7 psu off southern Labrador and increases again to near 34.8 psu along the shelf break.

During the period 1990–1993, cod experienced slightly below-normal temperatures along the edge of the continental shelf in water depths below 300 m and in the deep trench along the Bonavista migration corridor. Significant negative temperature anomalies ranging from 0.5 to 1.0°C below normal were experienced across the Grand Bank and Hamilton Bank and from 1.0 to 3.0°C below normal along the coast of Newfoundland and Labrador in water depths typical of the inshore cod trap fishery (Fig. 6). During this period, migrating cod experienced an average temperature of 1.1°C, about

Fig. 6. Depth, salinity, and temperature encountered by cod as they migrate along the external migration route shown in Fig. 5*b* based on all data from 1930–1989 (solid line) and 1990–1993 (broken line).

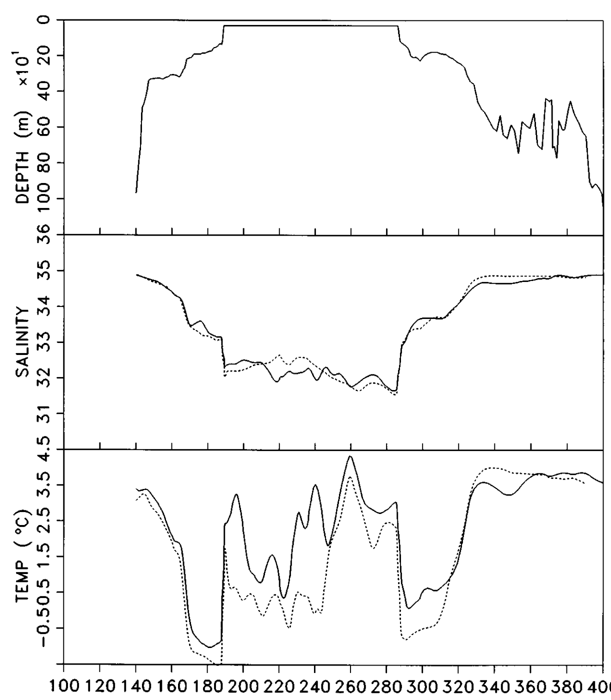
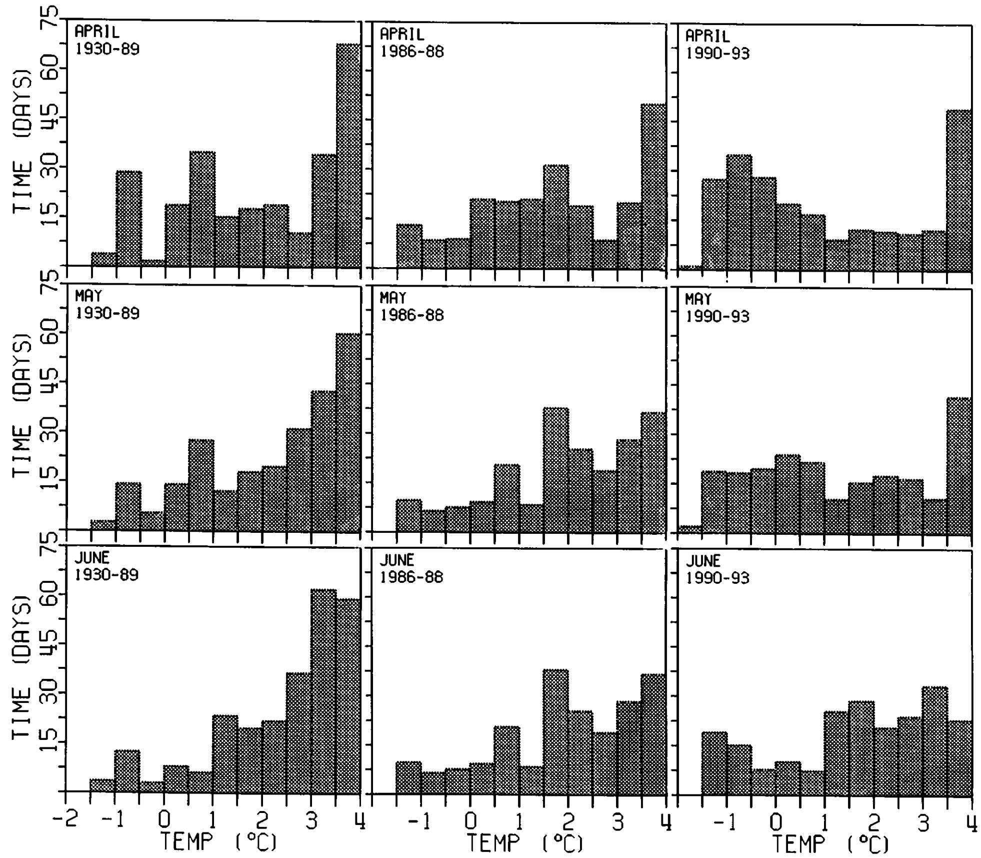


Fig. 7. Histograms of the time that cod occupied various temperature ranges along the migration route for migration start times of April, May, and June based on the average of all available data from 1930–1989, 1986–1988, and 1990–1993.



1.0°C below the 1930–1989 average. Salinities during the same period showed no significant departures from normal in the offshore regions but fluctuated by about 0.3 psu above and below the mean in the inshore regions.

The environmental conditions experienced by migrating cod along tracks over smaller spatial scales show very similar trends. However, the inshore portion of the time series has a higher mean temperature corresponding to the latitudinal gradient in the summer temperature in the inshore regions of the continental shelf (Colbourne and Foote 1994). For example, if cod started their migration at the edge of the continental shelf in May (Fig. 5*b*) and moved inshore through the Bonavista corridor to the Avalon Peninsula by July, staying inshore at approximately the same latitude until September and then finally migrating offshore along a similar path during autumn, they would encounter an average temperature of 5.2°C in the inshore region compared with 2.3°C along the inshore portion of the external migration route discussed above.

The large volume of subzero °C water that is present year-round on the Northeast Newfoundland Shelf, even during warm years (Fig. 2), forces fish migrating along or near the bottom from the offshore to the inshore to transit approximately 30 km of subzero °C water, even more during cold years. As a result the time that migrating fish spend in various temperature ranges along their routes depends on the environmental conditions (e.g., average 1930–1989, warm 1977–1980 and 1986–1988, and cold 1990–1993 periods) as well as their migration start times (Fig. 7). The migration start times simulated here (April, May, and June) refer to the month cod started their shoreward migration leg from the edge of the continental shelf. For a start time in May, on average, cod would spend up to 60% of their time in water from 2.0 to 4.0°C during average and warm years but only about 40% during the cold period of the early 1990s and the remainder of the time in colderwater.

For average (1930–1989) and warm (1977–1980 and 1986–1988) periods, with normal migration start time (May), cod would spend about 8% of their time in water below 0.0°C compared with 21% during the cold years of the early 1990s, almost three times longer than normal (Fig. 8). If migration had been delayed by one month during the 1990s the time in subzero °C water, although reduced would still have been greater than average by a factor of two. During warm years, time spent in subzero °C water is almost independent of migration delay times from April to June.

In general, the percentage of time migrating fish would occupy various salinity ranges during average and cold periods shows a somewhat different distribution (at a salinity bin resolution of 0.5 psu); however, there was little difference in the total time spent in high-salinity water (>33.0 psu), about 65%, and low-salinity water (<33.0 psu), about 35% (Fig. 9). The difference in the distributions in the salinity range of 32.5–33.0 psu is the result of the higher than normal salinity experienced in August and September in the inshore region (water depths from 0 to 50 m) during the period 1990–1993 (Figs. 3*a* and 6).

Fig. 8. Histograms of the percentage of time cod spent in subzero °C water for migration start times of April, May, and June for average conditions (1930–1989), cold conditions (1990–1993), and two warm periods (1977–1980 and 1986–1988).

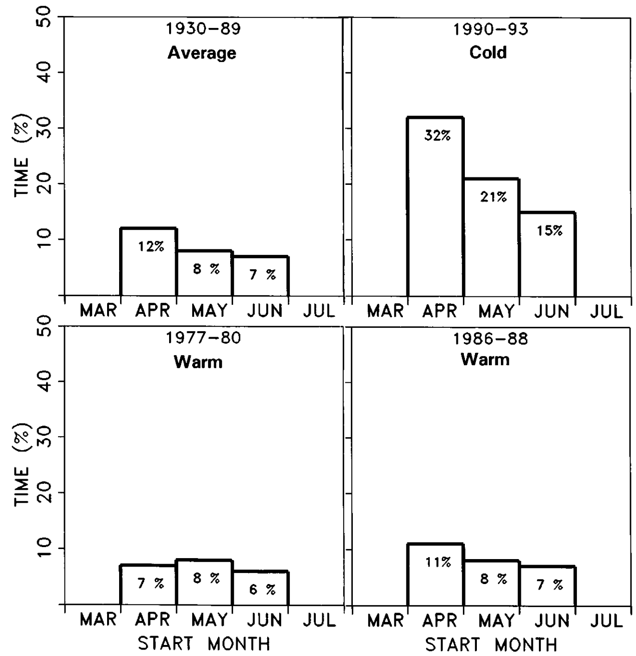
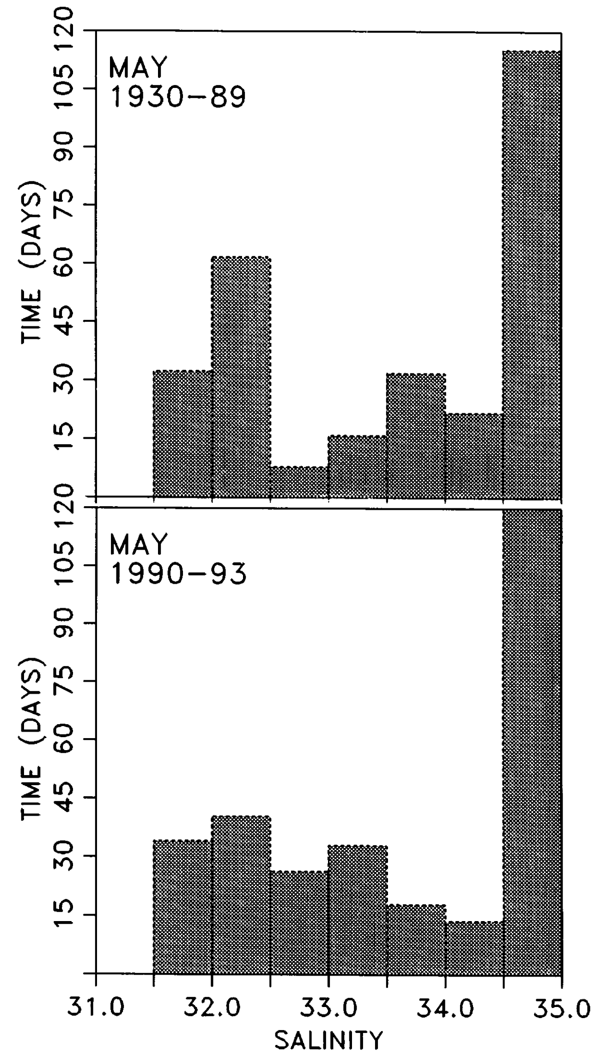


Fig. 9. Histograms of the time that cod occupied various salinity ranges along the migration route for a migration start time in May based on the average of all available data from 1930–1989 and 1990–1993.



Comparison with static conditions

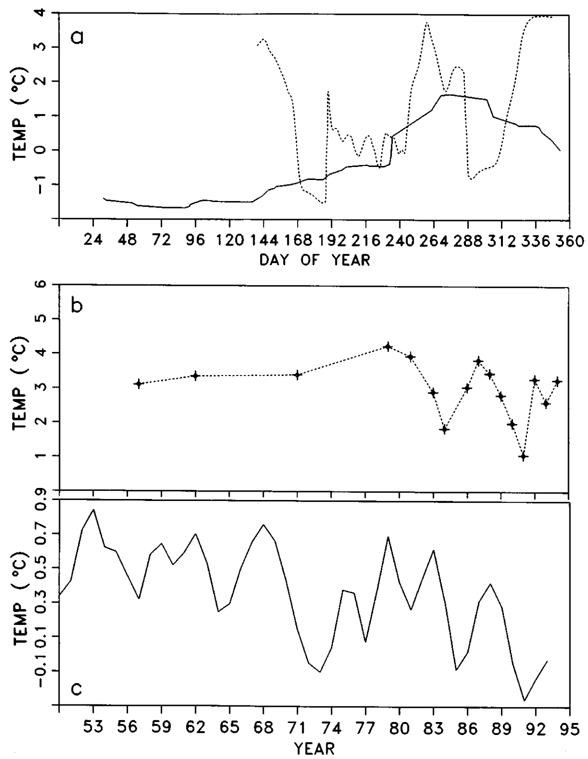
As shown, cod migrating from offshore (water depths >500 m) to the inshore regions (depths ≈30 m) typically encounter temperatures ranging from >3.0°C in deep water and along the coast to between 0.0 and –1.5°C in the depth range from approximately 50 to 100 m depth nearshore and on the banks. How does a time series of fish–temperature (the water temperature experienced by moving fish) over this depth range differ from a time series obtained at a single point (e.g., Station 27, Fig. 1) on the continental shelf? Since migrating fish integrate the ocean environment over significant depth ranges, vertically averaged data probably represents, the best overall measure from a fixed point with which to evaluate oceanographic influences in general. A comparison of the annual vertically averaged (0–176 m) Station 27 temperature and the fish–temperature (along the external migration path presented in Fig. 5*b*) time series shows different trends and ranges over the same time period (Fig. 10*a*). The mean vertically averaged temperature at Station 27 from mid-May to December during 1991 was –0.1°C compared with 1.1°C along the migration track for the same time period. The temperature at Station 27 ranged from –1.7 to 1.8°C, and along the migration track, during the same period, the temperature ranged from –1.5 to 3.8°C. Thus for a given year, migrating fish experience a much greater range and higher mean temperature than that indicated by the vertically averaged Station 27 data.

To examine interannual variability in migration path temperatures the small-scale migration path (Fig. 5*b*) offered the best data coverage. Even in this case, it was necessary to group the historical data, particularly for earlier periods, to obtain adequate spatial coverage throughout the year. Thus the fish temperatures are for 1955–1959, 1960–1964, 1970–1972, 1979–1980, 1981, 1983, 1984, 1986, 1987, 1988, 1989, 1990, 1991, 1992, 1993, and 1994. The annual average fish temperatures (Fig. 10*b*) along this path are higher than the mean temperature along the external route shown in Fig. 5*b* and the vertically averaged Station 27 temperature (Fig. 10*c*). The two time series show similar interannual variations, corresponding to periods of colder than normal conditions (Colbourne et al. 1994, 1997). However, the vertically averaged Station 27 time series has a much smaller range, and the amplitude in a given year, such as 1991, differs by as much as 1.0°C. Additionally, we find that the long-term average fish temperature is greater than the vertically averaged Station 27 temperature by an order of magnitude, a large and potentially significant difference, especially for applications involving cod growth models.

Discussion

Recent tagging, acoustic tracking, and the commercial inshore landings data indicate that northern cod generally follow circular migration routes from wintering areas near the

Fig. 10. (*a*) Vertically averaged temperature at Station 27 during 1991 (solid line) and the temperature cod encountered during the season along the external migration route shown in Fig. 5*b* during the early 1990s (broken line); (*b*) average annual temperature encountered by cod along the southern small-scale migration route shown in Fig. 5*b*; the crosses are centered at the time period of data availability; (*c*) time series of the annual vertically averaged Station 27 temperature.



edge of the continental shelf shoreward through the deep cross-shelf trenches containing warm slope water. The large-scale migration route chosen for investigation in this paper is based on these data and is intended to represent the maximum areal migration of the southern component of northern cod (Rose 1993). Other migration routes no doubt are possible, particularly for the historical stock which was much larger in numbers and covered a much greater geographical area (deYoung and Rose 1993). In keeping with this interpretation, Wroblewski et al. (1995) have shown that cod move along the shelf edge northward and southward between Hamilton Bank and the Grand Bank in the winter prior to spawning. Nevertheless, we believe that the routes we have used are sufficiently realistic to allow us to compare oceanographic conditions experienced by migrating fish during different climatic periods. Our results indicate that cod migrating along these routes during the early 1990s experienced significant negative temperature anomalies, particularly in the inshore region at depths typical of the inshore fishery.

The delay in the normal seasonal cycle during the 1990s may have affected the normal migration and spawning patterns of northern cod and could have been responsible for a redistribution of the stocks. Rose (1993) observed delays in spawning and migration inshore along the Bonavista corridor, especially in 1991 and 1992. In keeping with these delays, the inshore fishery began several weeks later in the early 1990s than was historically typical. In particular, Chen et al. (1994) showed that in 1991, which was characterized by very cold conditions, the delays in the onset of the inshore fishery were the longest ever observed. Additionally, the normal migration and spawning of caplin, the chief prey of cod, to the beaches along the east coast of Newfoundland had been delayed by up to 1 mo since 1991 (Nakashima and Winters 1995; J. Carscadden, Department of Fisheries and Oceans, St. John's, NF A1C 5X1, personal communication). This is consistent with the observed phase shift in the normal seasonal temperature cycle reported here. Our results also show that the time fish spent in very cold water (<0.0°C) along the migration path during the 1990s would have been significantly reduced by delaying their onshore migration by 1 mo. We suggest that the confounding influences of a poor environment and a disrupted food supply (mainly caplin) contributed to recent observed changes in northern cod migration and distribution.

The effects of severe environmental conditions on the general condition and behaviour of cod warrant further comment. During the period 1990–1993, cod had approximately 35% less heat available along their migration routes relative to 0.0°C than during average conditions from 1930 to 1989. Resultant reductions in metabolic rates due to the decline in water temperature integrated along migration tracks coupled with a decreased food supply could have caused delays in the attainment of peak prespawning condition normally reached during late autumn (Taggart et al. 1994). Consequently, the timing of spawning and post-spawning migrations may have been affected. Such reactions to cold are consistent with the delayed spawning and the general southerly shift in spawning aggregations observed during the early 1990s (deYoung and Rose 1993).

To conclude, this work presents a first attempt to quantify at large spatial and temporal scales the oceanographic conditions that cod are likely to experience along their seasonal migration routes from offshore to the shores around Newfoundland. Our results may be useful particularly in relation to cod growth models and condition studies, as they provide biologically relevant time series of temperatures experienced by migrating cod.

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References

Anonymous. 1978. List of ICNAF standard oceanographic sections and stations. ICNAF Selected Pap. No. 3.

Bailey, W.B. 1961. Annual variations of the temperature and salinity in the Grand Banks region. Fish. Res. Board Can. MS Rep. Ser. No. 74.

Chen, X.H., Shelton, P.A., and Bath, A.J. 1994. Relationships between temperature and landing patterns in the southern Labrador and eastern Newfoundland inshore cod fishery. Fish. Oceanogr. **3**: 191–196.

Colbourne, E.B., and Fitzpatrick, C. 1994. Temperature, salinity and density at Station 27 from 1978 to 1993. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 159.

Colbourne, E.B., and Foote, K.D. 1994. Spatial temperature and salinity fields over the shelves of Newfoundland and Labrador. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 160.

Colbourne, E.B., and Senciall, D. 1993. Temperature, salinity and density along the standard Bonavista Transect. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 150.

Colbourne, E.B., Narayanan, S., and Prinsenberg, S. 1994. Climatic change and environmental conditions in the Northwest Atlantic during the period 1970–1993. ICES Mar. Sci. Symp. **198**: 311–322.

Colbourne, E., deYoung, B., Naryanan, S., and Helbig, J. 1997. Comparison of hydrography and circulation on the Newfoundland Shelf during 1990–1993 with the long-term mean. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

DeBlois, E.M., and Rose, G.A. 1995. Effect of foraging activity on the shoal structure of cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **52**: 2377–2387.

deYoung, B., and Rose, G.A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. Can. J. Fish. Aquat. Sci. **50**: 2729–2741.

deYoung, B., Perry, F., and Greatbatch, R. 1994. Objective analysis of hydrographic data in the Northwest Atlantic. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 130.

Drinkwater, K.F. 1994. Overview of environmental conditions in the Northwest Atlantic in 1993. NAFO SCR Doc. 94/20, Ser. No. N2385.

Findlay, B.F., and Deptuch-Stapf, A. 1991. Colder than normal temperatures over northeastern Canada during the 1980s. Clim. Perspect. Apr. Mon. Rev. **13**: 9–12.

Harris, L. 1990. Independent review of the state of the northern cod stock. Department of Fisheries and Oceans, Ottawa, Ont.

Lear, W.H. 1984. Discrimination of the stock complex of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland, as inferred from tagging studies. J. Northwest Atl. Fish. Sci. **5**: 143–159.

Lear, W.H., and Green, J.M. 1984. Migrations of the “northern” Atlantic cod and the mechanisms involved. In Mechanisms of migration in fishes. *Edited by* J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill. Plenum Press, New York. pp. 309–316.

Myers, R.A., Akenhead, S.A., and Drinkwater, K. 1990. The influence of Hudson Bay runoff and ice-melt on the salinity of the inner Newfoundland Shelf. Atmos.- Ocean, **28**: 120–157.

Myers, R.A., Drinkwater, K.F., Barrowman, N.J., and Baird, J.W. 1993. Salinity and recruitment of Atlantic cod (*Gadus morhua*) in the Newfoundland region. Can. J. Fish. Aquat. Sci. **50**: 1599–1609.

Nakashima, B.S., and Winters, G.H. 1995. Caplin in SA2 + Div. 3KL. DFO Atl. Fish. Res. Doc. 95/70, Chap. 5. pp. 72–80.

Petrie, B., Akenhead, S., Lazier, J., and Loder, J. 1988. The cold intermediate layer on the Labrador and Northeast Newfoundland shelves, 1978–1986. NAFO Sci. Counc. Stud. **12**: 57–69.

Petrie, B., Loder, J., Akenhead, S., and Lazier, J. 1991. Temperature and salinity variability on the eastern Newfoundland Shelf: the annual harmonic. Atmos.-Ocean, **29**:14–36.

Petrie, B., Loder, J., Lazier, J., and Akenhead, S. 1992. Temperature and salinity variability on the eastern Newfoundland Shelf: the residual field. Atmos.-Ocean, **30**: 120–157.

Prinsenberg, S.J., Peterson, I.K., Narayanan, S., and Omoh, J.U. 1997. Interaction between atmosphere, ice cover, and ocean off Labrador and Newfoundland from 1962 to 1992. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Rose, G.A. 1993. Cod spawning on a migration highway in the north-west Atlantic. Nature (Lond.), **366**: 458–461.

Rose, G.A., Atkinson, B.A., Baird, J., Bishop, C.A., and Kulka, D.W. 1994. Atlantic cod distributional changes and thermal variations in Newfoundland waters, 1980–1992. ICES Mar. Sci. Symp. **198**: 242–252.

Rose, G.A., deYoung, B., and Colbourne, E. 1995. Cod (*Gadus morhua*) migration speeds and transport relative to currents on the Northeast Newfoundland Shelf. ICES J. Mar. Sci. **52**: 903–913.

Smith, P.C. 1983. The mean and seasonal circulation off southwestern Nova Scotia. J. Phys. Oceanogr. **13**: 1034–1054.

Taggart, C., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P. 1994. Overview of cod stocks, biology, and environment on the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Mar. Sci. Symp. **198**: 140–157.

Taggart, C.T., Penny, P., Barrowman, N., and George, C. 1995. The 1954–1993 Newfoundland cod-tagging database: statistical summaries and spatial–temporal distributions. Can. Tech. Rep. Fish. Aquat. Sci. No. 2042.

Templeman, W. 1966. Marine resources of Newfoundland. Bull. Fish. Res. Board Can. No. 154.

Templeman, W. 1979. Migration and intermingling of stocks of Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas from tagging in 1962–1966. ICNAF Res. Bull. **14**: 5–50.

Wroblewski, J.S., Kulka, D., Narayanan, S., Oake, A., Collier, A., and McGrath, B. 1995. Winter distribution and movement of northern Atlantic cod (*Gadus morhua*) along the Newfoundland–Labrador continental shelf edge derived from observations on commercial trawlers. Fish. Oceanogr. **4**: 128–146.