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The Timing of Cod Reproduction: Interannual Variability and
the Influence of Temperature

by

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ABSTRACT

We examined interannual variability in the timing of spawning of female cod, *Gadus morhua*, from 1947-1992 in three regions off Newfoundland in the northwest Atlantic. Maturity data, assessed by visual examination of dissected gonads of cod collected by research trawls, were analysed with probit regressions to identify the day of each year at which 50% of females had ceased spawning (which we refer to as spawning time) on the northern (NAFO Division 3L) and southern Grand Bank (3NO) and on St. Pierre Bank (3Ps). Among regions, average spawning time (mean$\pm$SD) varied from day 157$\pm$18 (June 6) and 139$\pm$17 (May 19) on the northern and southern Grand Bank, respectively, to day 135$\pm$24 (May 15) on St. Pierre Bank. Interannual differences in spawning time were significant within 3L (1948-1991), 3NO (1947-1992), and 3Ps (1953-1987) (likelihood ratio tests; $p<0.001$). Interannual variation in spawning time was significantly associated with variation in water temperature prior to spawning in 3L and in 3Ps although the signs of the associations differed between regions, casting doubt on the hypothesis that the timing of cod reproduction represents an adaptive response to temperature change. Cold temperatures were associated with delayed spawning in 3L but were associated with early spawning in 3Ps. The negative correlation between temperature and spawning time in 3L can be explained by the positive influence that temperature has on gonad development. In 3Ps, we attribute the early spawning dates in years characterized by cold bank temperatures (1) to a thermal barrier that sub-zero temperatures impose on spawning migrations from the continental slope to the shelf, and (2) to increased rates of gonad development, and an earlier readiness to spawn, experienced by cod "forced" to prolong their residence in warm slope waters. Our analyses indicate that cod spawning time varies significantly among years, demonstrate how the effects of temperature on cod reproduction depend on regional hydrography, and are the first to separate sampling variability and interannual variation in age structure from true interannual variability in spawning time.

INTRODUCTION

The significance of short-term changes in biological variables is often difficult to assess in the absence of long-term data on the variability of the traits in question. With notable exceptions (e.g. Darwin's finches (Grant 1986); brown trout, *Salmo trutta* (Elliott 1993)), temporal data on variation in life history, morphological, or behavioural traits of organisms in the wild is restricted to a few years (although potentially several generations) at best. The potential causes of long-term temporal variability can be explored when similar time series of one or more environmental parameters are also available. Data on commercially exploited species represent a potentially valuable source of such time series because management usually entails the collection of biological and physical data in a

consistent manner over many years or decades. Using a research data set that spans over 40 years, we examine temporal differences in the timing of reproduction in a commercially important groundfish in three regions of the northwest Atlantic and assess the degree to which this variation is influenced by the environment.

Biological data on Atlantic cod, *Gadus morhua,* have been collected by research trawlers off the island of Newfoundland since 1947. These data include the age, size, sex and state of maturity (assessed by visual inspection of dissected gonads) of random samples, stratified by length of fish, from each trawl. Extensive data are available for Grand Bank off eastern Newfoundland and for St. Pierre Bank south of the island (Fig. 1). Water temperature data are also available for northern Grand Bank and St. Pierre Bank during the time period encompassed by the trawl surveys. Our objectives were (1) to describe interannual variation in the timing of cod reproduction, (2) to determine whether there are significant differences in the timing of spawning among years, and (3) to assess the degree to which interannual variation in the timing of cod reproduction is caused by interannual variation in water temperature.

MATERIALS AND METHODS

Estimation of Annual Spawning Time

Cod have been systematically sampled off Newfoundland by the Canadian Department of Fisheries and Oceans from 1947 to 1992. Prior to 1972, cod were sampled with research otter trawls along line transects. Since 1972, surveys have been randomly stratified by depth. Our analyses are restricted to regions in which ice cover was unlikely to prevent sampling of cod during pre-spawning and spawning periods. These regions were northern Grand Bank (North Atlantic Fisheries Organization, or NAFO, Division 3L), southern Grand Bank (3NO), and St. Pierre Bank (3Ps). Myers et al. (1993) provide a summary of the monthly samples in these regions.

The reproductive state of female cod was assessed at sea, following the classification of Templeman *et al.* (1978), upon the removal and dissection of gonads. Individuals were identified as either *maturing, spawning,* or *spent* according to the following criteria: *maturing* - eggs opaque and visible to naked eye; *spawning* - ovaries containing clear eggs, clarity being indicative of hydration and readiness for release (cf. Kjesbu 1989; Rijnsdorp 1989); *spent* - ovaries whitish-grey or bluish-grey, slack and often wrinkled, residual eggs often present.

We define time of spawning as the day of year on which 50% of mature females are in a *spent* state. We used a maximum likelihood probit regression to describe how the probability that a female will be spent is related to age (time of spawning is positively associated with age in cod; Hutchings and Myers 1993), day of year, and year. To calculate these probabilities, we classified *maturing* and *spawning* females as 0 and classified *spent* females as 1. Thus, the probability, p, of an individual aged a completing spawning on day t of year Y is

$$p = \Phi(\beta_0 + \beta_1 a + \beta_2 t + \beta_Y) \qquad (1)$$

where Φ is the cumulative distribution function for the standard normal distribution, β_0 is the intercept of the probit regression, β_1 and β_2 are the probit regression coefficients for the effects of age (a) and day of year (t), respectively, and β_Y represents the deviation of the regression intercept attributable to the effects of year Y. It is easier to work with the estimated mean spawning time for individuals of a given age than the estimated probit regression coefficients, β_0 and β_Y. Given that $0.5 = \Phi(0)$, estimated mean spawning time in year Y (t_Y) can be calculated for females aged 10 yr (a reasonable historical median age at reproduction in Atlantic cod; cf. Baird et al. 1992) as

$$t_Y = -(\beta_0 + 10\beta_1 + \beta_Y) / \beta_2 \qquad (2)$$

It is unlikely that trawl samples collected by research vessels will be independent of one another because these samples are clustered in space. That is, the proportion of spent females in one trawl sample will not be independent of the proportion of spent females in another trawl sample. Failure to account for cluster structure in such data (i.e. high within-cluster

correlations) can lead to underestimates of the true sampling variance (Rao and Scott 1992). To account for within-cluster correlations, we used the method suggested by Rao and Scott (1992) for the analysis of clustered binary data. Thus, the standard error estimates of β_Y were inflated by an amount equal to the estimated variance due to cluster sampling divided by the estimated binomial variance. Some years were excluded from the analyses because of insufficient sampling during spawning periods. The values of β_Y for these years were characterized by inordinately large standard errors, i.e. 3-5 orders of magnitude greater than all other values. Of the 46 years of available data, sample sizes were sufficient within years to estimate spawning time for 35, 30 and 29 years in 3NO, 3L and 3Ps, respectively. Because t_Y is not linear in the parameter estimates β_0, β_1, β_2, and β_Y, the standard error of t_Y cannot be determined exactly. However, an approximation to the standard error of t_Y can be calculated by using the δ method, i.e. by means of a linear approximation of equation (2).

Water Temperature Data

To assess the effects of water temperature on spawning time, we restricted our analysis to the six month periods most likely to encompass gonad development and reproduction. Based on the information provided by Myers et al. (1993), these time periods were January through June for St. Pierre Bank and southern Grand Bank, and February through July for northern Grand Bank.

The temperature series for St. Pierre Bank was compiled from all available temperature records from the Marine Environment Data Services (MEDS), Department of Fisheries & Oceans, Ottawa, Ontario. We used only those temperatures recorded over the bank that were further than 20 km from the continental shelf break at the 200m depth because of strong temperature gradients at the shelf break. We report the average of all temperatures recorded from January through June at a depth of 50m (there was no detectable seasonal cycle at or below this depth from January to July; Drinkwater and Trites 1986).

Temperature data for northern Grand Bank were those measured at a hydrographic station off St. John's, Newfoundland (Station 27; Fig. 1). This station has been sampled approximately twice monthly since 1946. Temperatures recorded at Station 27 are well correlated with sea temperatures throughout the northern Grand Banks (Petrie et al. 1992). For each year, we averaged all temperatures recorded at depths of 75m and 100m from February through July. We report these data as yearly deviations from the long-term (1946-1992) mean.

The existence of strong temperature gradients prevented us from contructing a reliable time series for southern Grand Bank. Temperatures recorded within weeks of one another between January and June often differed by 5-6°C, regardless of depth (MEDS, 1947-1992). In addition, the bank was not sampled sufficiently to separate annual from geographic variation in temperature.

Water temperature and spatial distribution of cod

Temperature might influence the timing of cod reproduction by affecting their spatial distribution. To investigate this possibility in the northern Grand Bank and St. Pierre Bank regions, we examined the relationship between water temperature and the biomass of cod caught by research trawls on the continental shelf relative to the biomass of cod on the continental slope prior to spawning.

Biomass data for cod on northern Grand Bank (3L) were available for April and May (Baird et al. 1992), the two months immediately preceding the month of peak spawning (Myers et al. 1993). The shelf and slope data included all fish captured in research otter trawls at depths of 57-92m and 276-366m, respectively. Biomass estimates for the shelf and slope waters represented the total biomass of cod captured from all "strata" (survey areas delimited primarily on the basis of depth) sampled in each of the two depth categories. Cod in the shelf and slope waters were sampled randomly from 5 and 6 strata, respectively. Data are available from 1978-1991, although some strata were not sampled during some years. The biomass totals for non-sampled strata were estimated from a multiplicative model which included year and stratum effects (Gavaris 1980). Yearly biomass estimates that include non-sampled strata are termed "incomplete" data in our analyses. The temperature data were those measured at Station 27. Temperature-depth profiles for the shelf and slope off northern Grand Bank were obtained from data recorded along a hydrographic transect extending from St. John's east to Flemish Cap (Fig. 1; data summarized in Templeman 1975).

Biomass and temperature data for St. Pierre Bank were obtained from Canadian and French research data. The Canadian temperature data (which included some data collected by

other countries) were those previously described from MEDS (i.e. average temperature from January to June at 50m depth). The French data were obtained from hydrographic surveys (described by Moguedet and Mahé 1991) that were conducted along the same transect (Fig. 1) from 1978 to 1990 and were sampled at the same time every year (usually mid-March; range for all years was 21 February to 21 March). We used the average absolute temperatures recorded between depths of 0 and 99m on the bank. Temperature-depth profiles for the shelf and slope waters of St. Pierre Bank were also obtained from Moguedet and Mahé (1991). Biomass data from Canadian stratified-random surveys are available from 1972-1991 (Bishop et al. 1991). Shelf and slope waters encompassed depths of 56-90m and 271-365m, respectively. Given that sampling dates varied from late-January to mid-June, we included only those years for which samples were available in the 2 months immediately preceding spawning (i.e. late-January to late-March). Random-stratified surveys by French research vessels were conducted during February and March each year from 1978 to 1991 (Moguedet and Mahé 1991; data available in Bishop et al. 1991). Both the French and Canadian data included years in which strata were incompletely sampled.

Statistical Analyses

Likelihood ratio tests were used to determine whether significant interannual variation in cod spawning time existed within each of the three geographical regions. We calculated the log-likelihood ratios of the probit model with and without the year effects (β_y) and then calculated the G-statistic (whose distribution approximates the χ^2-distribution) which is equal to twice the difference in the log-likelihood ratios (Sokal and Rohlf 1981). Weighted linear regressions were used to analyse the associations between water temperature and spawning date and between water temperature and the ratio of cod biomass on the shelf relative to that on the slope.

RESULTS

Timing of Cod Spawning

There was significant interannual variation in the timing of cod spawning on northern (3L) and southern (3NO) Grand Bank and on St. Pierre Bank (3Ps) (Fig. 2); inclusion of year effects significantly reduced the log-likelihoods of the probit regressions in each of the three regions (3L - $G=181.74 > \chi^2_{[29;\ 0.001]}=58.30$; 3NO - $G=187.67 > \chi^2_{[34;\ 0.001]}=65.25$; 3PS - $G=192.44 > \chi^2_{[28;\ 0.001]}=56.89$). Spawning on northern Grand Bank (mean day of year$\pm$SD: 157$\pm$18, i.e. June 6) occurs significantly later ($F_{[2,91]}=10.29$, $p<0.001$) than spawning on southern Grand Bank (day 139$\pm$17, i.e. May 19) and on St. Pierre Bank (day 135$\pm$24, i.e. May 15).

There are a number of similarities in the ways in which spawning time has varied annually among regions. Spawning was progressively earlier from the either the late-1950s (3NO and 3Ps) or the mid-1960s (3L) until the late-1960s. From the late-1960s to the mid-1970s, spawning became progressively later in each region before occurring earlier again in 3L and 3Ps until the late 1970s. Since the early 1980s, spawning times have changed relatively little in 3L, have become somewhat later in 3NO (particularly in the early 1990s), but have occurred progressively earlier in 3PS.

Water Temperature and Spawning Time

Water temperatures during the months of gonad development and reproduction varied dramatically among years on both northern Grand Bank (3L) and St. Pierre Bank (3Ps) (Fig. 3). Although no long-term pattern is evident on northern Grand Bank, temperatures colder than the 1946-1991 average were most evident in the early and late 1970s and from 1982 to 1991. A long-term decline in temperature of approximately 2°C is evident on St. Pierre Bank from the early 1950s to the late 1960s. Since the late 1960s, St. Pierre Bank has experienced two periods of progressive increases and decreases in temperature with the dramatic reduction from 1982 to 1987 almost matching the entire long-term variation in temperature from 1952 to 1987.

Time of cod spawning on northern Grand Bank and St. Pierre Bank is closely related to water temperatures on these banks prior to cod reproduction (Fig. 3). Interestingly, the general patterns of association between spawning date and temperature differed between regions. In 3L, cold temperatures are associated with delayed spawning; in 3Ps, cold temperatures are associated with early spawning. These relationships are particularly strong

after 1972, the years in which cod sampling was randomly stratified. Including only the post-1972 data (because of the increased reliability of spawning date estimates determined from random samples) and including years in which temperature data existed for at least 5 of the 6 months prior to and including reproduction, there were significant associations between spawning date and water temperatures on northern Grand Bank and St. Pierre Bank (Fig. 4). Spawning date was negatively correlated with temperature in 3L ($F_{(1,16)}$=6.12, r=0.54, p=0.025) but positively correlated with temperature in 3Ps ($F_{(1,14)}$=5.86, r=0.46, p=0.030).

Water Temperature and Spatial Distribution of Cod

From 1978 to 1991, variation about the long-term (1946-1991) mean temperature in 3L (station 27, Feb-Jul at 75-100m) exceeded 0.5°C with generally warmer temperatures evident to 1981 (maximum absolute temperature: -1.05°C in 1979) and the coldest temperature recorded in 1991 (absolute temperature: -1.62°C) (Fig. 5). Although the biomass of cod on the shelf relative to that on the slope differed more than 10-fold from 1978 to 1991 in 3L (Fig. 5), these differences were uncorrelated with water temperature ($F_{(1,10)}$=0.01, r=0.02, p=0.947).

In contrast to 3L, water temperature in 3Ps from 1972 to 1991 was significantly associated with the relative biomass of cod on the shelf (Figs. 6 and 7). The temperature profile in 3Ps is marked by two distinct time periods. Absolute temperatures (Jan-Jun at 50m) from 1972 to 1984 were significantly warmer (mean±SD: 0.82±0.59°C) than they were from 1985 to 1991 (-0.59±0.48; $F_{(1,18)}$=28.90, p<0.001). The 1.4°C decline in temperature between these periods was associated with considerably fewer numbers of cod on the shelf (Fig. 6). The relative biomass of cod on the shelf varied by almost 3 orders of magnitude from 1972 to 1991 (total biomass declined by less than 1 order of magnitude during this period; Bishop et al. 1991). The relative biomass of cod on the shelf increased significantly with shelf water temperatures for the combined Canadian and French data (all data: $F_{(1,25)}$=11.42, r=0.56, p=0.002; complete data only: $F_{(1,12)}$=8.90, r=0.65, p=0.01) (Fig. 7B). The positive association between cod biomass on the shelf and water temperature prior to reproduction was particularly strong for the French data in which biomass and temperature were recorded during the same time period annually ($F_{(1,10)}$=17.20, r=0.80, p=0.002) (Fig. 7C).

DISCUSSION

Interannual Variation in Spawning Time

The timing of spawning by Atlantic cod off Newfoundland differs significantly among years. In general (68% probability, i.e. 2SD), mean spawning time would be expected to vary up to 34 to 48 days on Grand Bank and St. Pierre Bank, respectively. To the best of our knowledge, the existence of statistically significant variation has not been explored in any other analyses of interannual variation in spawning time in fishes. A serious shortcoming of virtually all such analyses is the failure to incorporate the spatial and temporal biasses characteristic of cluster sampling in both marine and freshwater environments (cf. Myers et al. 1986) into variance estimates of spawning time. Many estimates of spawning date are further complicated by the use of commercial catch data (e.g. Cushing 1969) and by inconsistent use of the phrase "peak spawning period" (e.g. Sinclair and Tremblay 1984; Page and Frank 1989).

Given the lack of consistency in the estimation of spawning time, it is difficult to assess the degree to which interannual variability in reproduction is a feature of marine fish populations. An additional complication is the general failure to account for interannual variation in age structure. A 61 year time series (1928-1988) of egg data collected from commercial catches in the Lofoten fjord, Norway, indicates that mean peak spawning date of cod has varied by at least 30 days (Ellertsen and Solemdal 1990). However, for a 7-year period (1976-1982) in the same area, research egg survey data show remarkably little variation in median spawning date (Pedersen 1984). Cushing's (1969) interpretation that the timing of peak catches of cod in Lofoten lacks interannual variation over 75 years (1984-1968) must be tempered by an absence of statistical analysis and by the problematic biasses associated with commercial catch data. Jónsson (1982) documented substantial interannual variation in the beginning of the spawning season of cod off the southwest coast of Iceland. These research data were calculated as deviations from the long-term (1954-1981) mean of

the percentage of cod with "running" gonads from March 1 to April 15. Of 12 herring, *Clupea harengus*, populations for which several years of egg survey data are available (Sinclair and Tremblay 1984), peak spawning periods within populations can differ up to 45 days among years (e.g. southern Gulf of St. Lawrence population for which 27 years of data were available; see also Lambert 1987). Page and Frank (1989) document different levels of interannual variation in time of peak spawning in two stocks of haddock, *Melanogrammus aeglefinus*, off eastern Canada and provide a summary of interannual variation in spawning time for other north temperate and high latitude fish populations.

The existence of interannual variability in spawning time has both ecological and management implications. Cushing (1969) postulated that spawning time should be relatively invariant from year to year so that "the population has the best chance of profiting by the variability of the production cycle (Cushing 1969: 91). A corollary of this hypothesis is the suggestion that, in the presence of low temperatures, delayed reproduction represents an adaptive response which increases the likelihood that larval emergence will match a presumeably delayed zooplankton bloom (Sætersdal and Loeng 1987; Ellertsen and Solemdal 1990). These hypotheses are not supported here given the different signs of the significant correlations between temperature and spawning time, and because of the low correlation that exists between bottom and surface temperatures (Drinkwater and Trites 1986) in the northwest Atlantic. From a management perspective, it has generally been assumed that spawning time is roughly constant among years and that closure of commercial fisheries during spawning would be an effective means of increasing the number of reproducing females and, hence, recruitment to the fishery. The existence of significant interannual variation in the timing of spawning suggests that such a management policy may have limited success for Atlantic cod off Newfoundland.

Effects of Water Temperature on Spawning Date

The influence of water temperature on the timing of cod reproduction off Newfoundland differs between regions. In 3L, spawning on northern Grand Bank is delayed in cold years. Yet in 3Ps, colder temperatures on St. Pierre Bank prior to reproduction are associated with earlier spawning. This discrepancy in the effects of temperature on spawning date can be attributed to regional differences in the thermal gradient between shelf and slope waters. We contend that water temperature acts as a thermal barrier to spawning migrations and as a physiological regulator of the rate of gonad development. We illustrate the relative importance of these migration and energetic constraints on cod spawning with reference to the 3L and 3Ps NAFO divisions off Newfoundland.

Cod spawn primarily on the continental shelf, rather than the continental slope, off Newfoundland (Hutchings et al. submitted). Tagging studies in 3Ps indicate that cod overwinter in slope waters before migrating onto adjacent St. Pierre Bank to spawn (Templeman 1962; Templeman and Fleming 1962). In 3L, cod spawning on northern Grand Bank overwinter either on the shelf or on the slope (Templeman 1979). Thus, spawning migrations, where they exist, occur from slope to shelf waters. If slope waters are generally warmer than shelf waters in late winter and early spring, steep thermal gradients between these waters could delay migration to spawning areas. In 3Ps, as indicated by the hydrographic profiles of Moguedet and Mahé (1991), thermal gradients between shelf (depth 56-90m) and slope (271-365m) waters vary greatly among years (Table 1). In general, thermal gradients during cold years (1985-1990, as determined from Fig. 6) were twice as steep as thermal gradients in warm years (1978-1984). Late-winter temperatures on the shelf were often either well below 0°C (1985, 1987, 1989, 1990) or well above 0°C (1978, 1981, 1983, 1984). In contrast, thermal gradients between the shelf and slope in 3L are relatively weak, in large part because of the Labrador Current which generally maintains temperatures below 0°C on the shelf and below 4°C on the slope throughout the year (Templeman 1975; Drinkwater and Trites 1986). The average thermal gradient between shelf (57-92m) and slope (276-366m) from 1951 to 1971 (July data) is approximately 3.5°C (Templeman 1975) and varies little between warm and cold years. More importantly, temperatures on the shelf at 75-100m depth rarely exceed 0°C. For example, in 1979 (March), a warm year, the temperature difference between shelf (0° to -1°C) and slope (3.3° to 3.4°C) was about 4°C (MEDS data base). This temperature difference is slightly greater than the thermal gradient of approximately 2°C in a very cold year such as 1977 (July) (shelf: 0.7° to -1.6°C; slope: 1.7° to 1.9°C) (MEDS data base).

It seems unlikely, then, that temperature will act as a thermal barrier to migration in 3L because thermal gradients are generally low and they vary little from year to year. Furthermore, given that cod that overwinter on the shelf are exposed to sub-zero temperatures for much of the year, the presence of such cold water at any specific time would not be

expected to act as a significant deterrent to movement. The lack of a significant correlation between temperature and the shelf/slope biomass of cod supports this notion. However, low temperatures on northern Grand Bank would be expected to slow the maturation process, thereby delaying spawning, by reducing the rate of gonad development (Calder 1984; Davenport 1992). Cold temperatures also appear to be the most important factor responsible for delayed spawning in herring (Lambert 1987; Ware and Tanasichuk 1989) and in caplin, *Mallotus villosus*, (Carscadden et al. 1992). Thus, we attribute the negative correlaton between temperature and spawning time in 3L to the energetic constraint that low temperatures impose on physiological processes.

We propose that cold temperatures (i.e. <0°C) on the shelf act as a thermal barrier to cod migrating from the slope in 3Ps and that the positive association between temperature and spawning time on St. Pierre Bank is due to increased rates of gonad development experienced by cod "forced" to prolong their residence in warm slope waters. During those years identified as cold years in 3Ps (i.e. 1985-1990), temperatures on St. Pierre Bank did not exceed 1°C, being less than or equal to -1°C in 4 of the 6 years (Table 1). In contrast, temperatures of at least 0°C (often as high as 3-5°C) always existed on St. Pierre Bank during the warm years (i.e. 1978-1984). The hypothesis that cold temperatures deter migration from the slope to the shelf is supported by the observation that, relative to the slope, cod biomass on the shelf during the cold post-1984 years was, on average, one order of magnitude less than cod biomass on the shelf during the warm pre-1985 years. This difference in relative shelf cod biomass was highly significant (combined Canadian and French data: mean $\log_{10}$-shelf/slope biomass ($\pm$ SD) from 1978-84 and 1985-91 was 0.13 ± 0.37 and -0.85 ± 0.68, respectively; $F_{[1,21]}=15.64$, p=0.001). In all likelihood, these differences in biomass reflect true changes in the timing of migration to spawning areas. Changes in biomass cannot be attributed to changes in abundance because the numbers of cod (shelf and slope data combined) did not differ between the warm and cold year periods. This is true for both the French and Canadian research data: French abundance estimates (mean$\pm$SD) for 1978-1984 and 1985-1991 were 6699 ± 5832 and 6532 ± 5430, respectively ($F_{[1,12]}=0.01$, p=0.96); Canadian abundance estimates for the same time periods were 5503 ± 1075 and 9106 ± 6031, respectively ($F_{[1,12]}=2.42$, p=0.15).

During periods of cold ($-1.7°<x<0°C$) temperatures on St. Pierre Bank, cod appear to delay their spawning migration onto the shelf and to prolong their time of residence in slope waters. By remaining in the considerably warmer slope waters, gonad development would occur at a faster rate, leading to an earlier date at which females would be physiologically capable of spawning and presumably to an earlier date of spawning. This would account for the positive correlation observed between water temperature and spawning date in 3Ps. This raises the possibility that, if slope waters are always warmer than shelf waters, cod may always mature in the warm slope waters prior to migrating onto the shelf to spawn. However, the data suggest otherwise. If cod normally spend the months immediately preceding spawning in slope waters, we would expect either no correlation to exist between either spawning time or shelf/slope cod biomass and temperature, or we would expect to find negative (physiological constraint) and positive (migration constraint) associations, respectively. Neither set of associations were documented here. Thus, in the absence of changes in cod abundance, we conclude that the observed changes in cod biomass between shelf and slope waters with changes in water temperature provide strong evidence that cold temperatures ($-1.7°<x<0°C$) on St. Pierre Bank during late winter and early spring act as a thermal barrier to cod migration and result in longer residence times by cod in the warm slope waters prior to spawning on the shelf.

Avoidance of sub-zero degree temperatures on St. Pierre Bank by mature cod may be related to their ability to produce plasma antifreeze glycoproteins (to prevent freezing of tissue fluids; Fletcher et al. 1987) and the potential physiological costs of doing so. Exposure to temperatures less than 0°C are required before adult cod will produce antifreeze glycoproteins (Fletcher et al. 1987). Given that it may take up to 2 months for plasma ionic concentrations to attain a new equilibrium (Fletcher 1981; Fletcher et al. 1987), the physiological costs of migration into sub-zero degree water may be prohibitive. The limited ability of adult cod to prevent freezing at temperatures less than -1.2°C (Goddard et al. 1992) should also favour avoidance of the extremely cold temperatures that dominate St. Pierre Bank in some years (e.g. 1985, 1987, 1989, 1990; Table 1). On the basis of these experiments and on Bull's (1936, 1951) demonstration that cod can distinguish temperatures differing by 0.05°C, Goddard et al. (1992) hypothesized that the high sensitivity of cod to the thermal characteristics of their surroundings should enable them to detect and, where the option exists (e.g. in 3Ps but perhaps to lesser degrees in 3L), avoid very cold water. The data on temperature and shelf/slope cod biomass documented here for 3Ps are consistent with this hypothesis.

The influence of temperature on both spawning date and the biomass of cod on the shelf, relative to that on the slope, in conjunction with experimental work on the production of plasma antifreeze proteins in cod provides strong evidence for the conclusion that cold temperature can act as a thermal barrier to mature migrating cod and as an energetic constraint on the rate of gonad development. Where steep thermal gradients exist between shelf and slope waters (e.g. St. Pierre Bank spawning cod in 3Ps), cold temperatures (<0°C) on the shelf force cod to undergo gonad development in very warm slope waters (6-9°C). As a consequence, individuals attain a readiness to spawn earlier than they would if they had undergone most of their gonad development at the 0-3°C they would have experienced on the shelf in years in which thermal barriers to cod migration were absent. In areas in which steep thermal gradients between shelf and slope waters are rare, or in areas in which temperatures vary little on a seasonal basis (e.g. northern Grand Bank spawning cod in 3L), the opportunity for fish to avoid particularly cold temperatures will be limited, thus reducing the ability of temperature to act as a thermal barrier to migration and increasing the likelihood that the rate of gonad development will be highly dependent on ambient water temperature. In summary, our analyses indicate that the timing of cod reproduction varies significantly among years off Newfoundland, demonstrate how the effects of temperature on cod reproduction depend upon the hydrography of the region, and are the first to separate sampling variability and interannual variation in age structure from true interannual variability in spawning time.

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Table 1. Interannual variability in the range of temperatures on the continental shelf (56-90m depth) and continental slope (271-365m) in NAFO division 3Ps. Data are from hydrographic surveys conducted by French research vessels along a single transect (Fig. 1) and are described in detail by Moguedet and Mahé (1991).

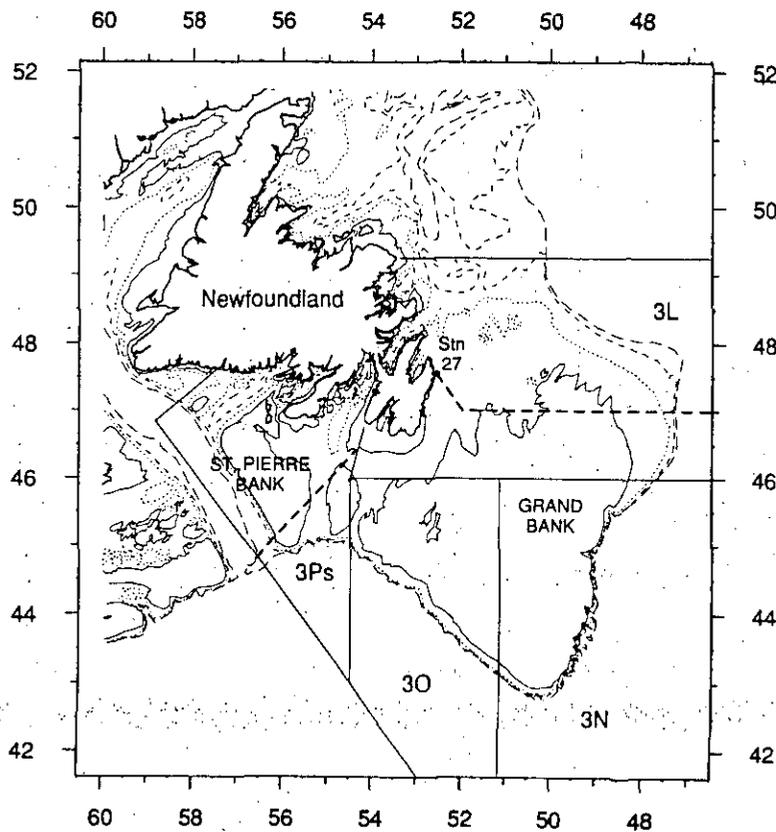| Year | Date | Temperature Range (degrees Celsius) | |
		Shelf	Slope
1978	March 14-19	$-1° < x \leq 5°$	$7° \leq x < 9°$
1979	March 7-8	$-1° < x \leq 0°$	$6° < x \leq 7°$
1981	March 11-21	$1° \leq x \leq 3°$	$7° \leq x < 9°$
1982	March 12-19	$-1° \leq x \leq 0°$	$3° < x < 5°$
1983	February 26 - March 2	$0° \leq x \leq 3°$	$5° < x < 6°$
1984	March 15-18	$1° \leq x \leq 4°$	$6° \leq x < 9°$
1985	March 13-14	$x < -1°$	$6° < x \leq 7°$
1986	February 21-22	$-1° < x < 0°$	$6° < x < 8°$
1987	March 5-6	$x \leq -1°$	$6° \leq x < 7°$
1988	March 7-8	$0° \leq x \leq 1°$	$4° \leq x \leq 6°$
1989	March 9-10	$x \leq -1°$	$3° < x < 5°$
1990	March 12-13	$x \leq -1°$	$6° \leq x \leq 7°$

Figure 1. Map of the study region, including NAFO divisions. Hydrographic transects in divisions 3L and 3Ps are indicated by thick dashed lines.
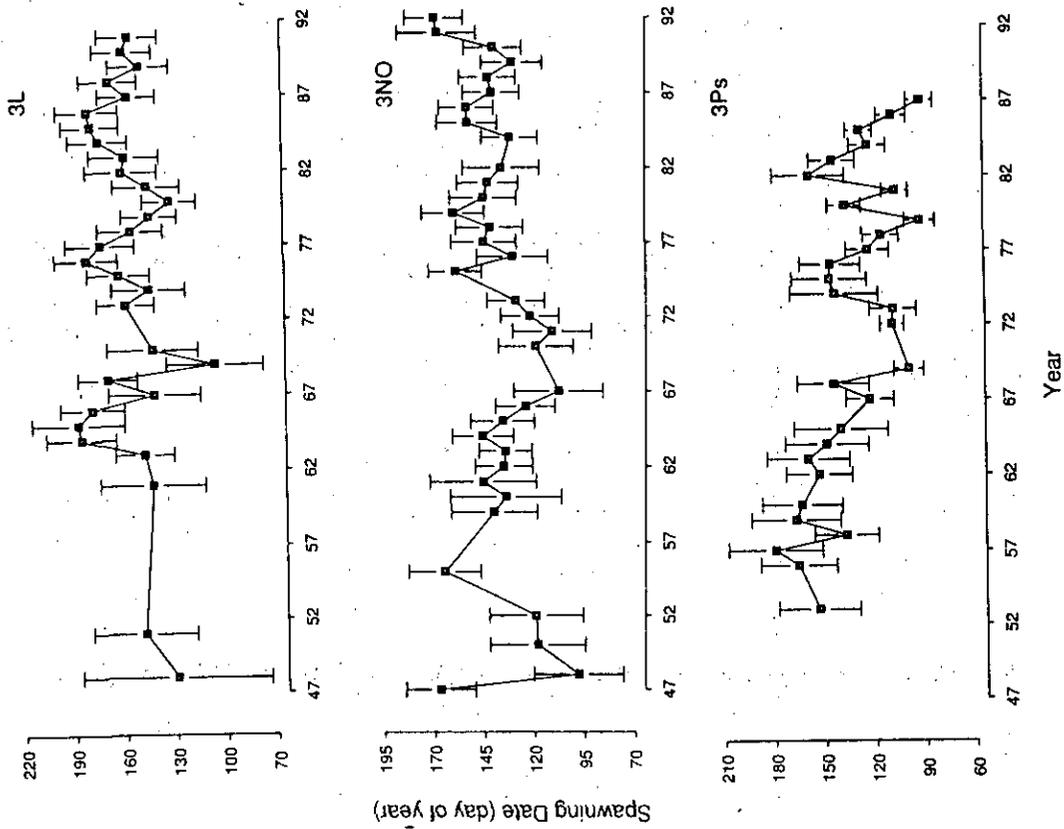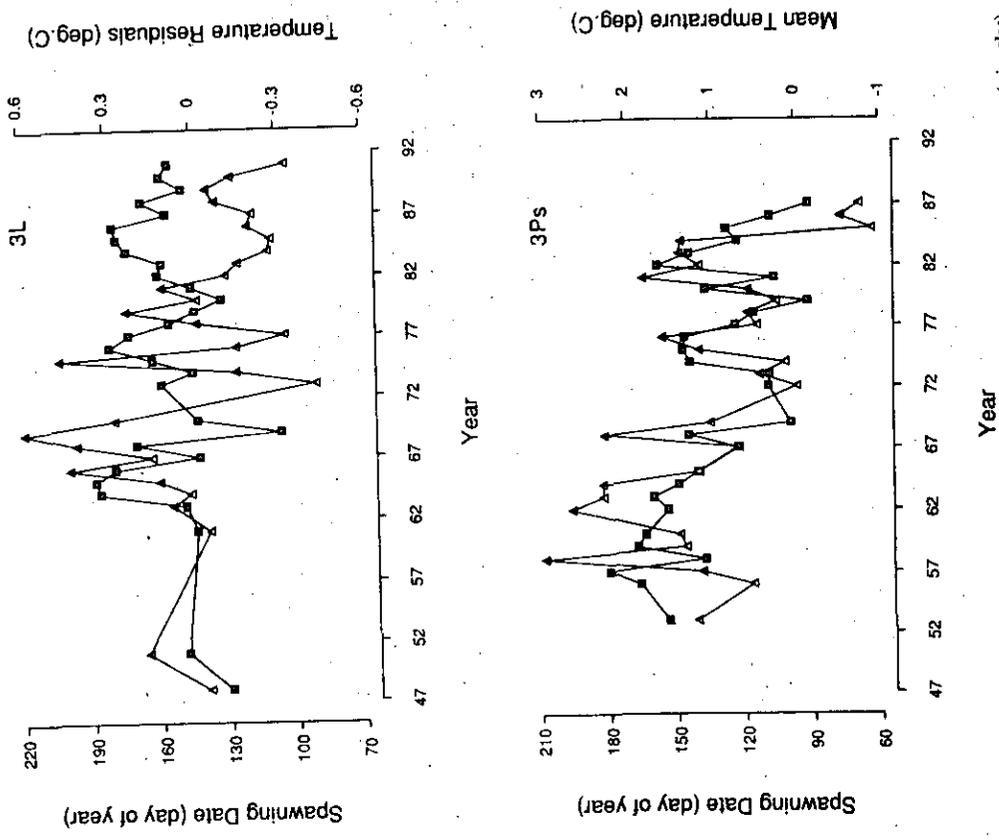
- 11 -

Figure 3. Interannual variation in spawning time (squares) and water temperature (triangles) during gonad development and reproduction of Atlantic cod in NAFO divisions 3L (northern Grand Bank) and 3Ps (St. Pierre Bank). Water temperature data in 3L were recorded at Station 27 (see Fig. 1) and represent the annual average deviation from the long-term (1946-1992) mean of all temperatures recorded at 75 and 100m from February to July. Water temperature data in 3Ps (St. Pierre Bank) represent the annual means of all temperature records at 50m from January to June (data from the Marine Environment Data Services).

Figure 2. Interannual variation in spawning date (time at which 50% of reproductive females are in a spent state) of Atlantic cod in NAFO divisions 3L (northern Grand Bank), 3NO (southern Grand Bank), and 3Ps (St. Pierre Bank) (data are means ± 1 SE).

Figure 4. Relationship between spawning date of female Atlantic cod and water temperature during gonad development and reproduction in 3L (northern Grand Bank) and 3Ps (St. Pierre Bank). Data for 3L are from 1973-1991; data for 3Ps are from 1972-1987.
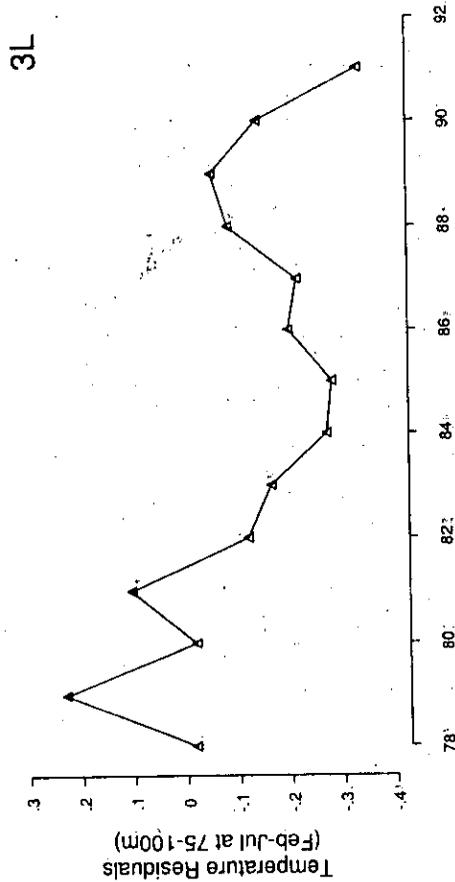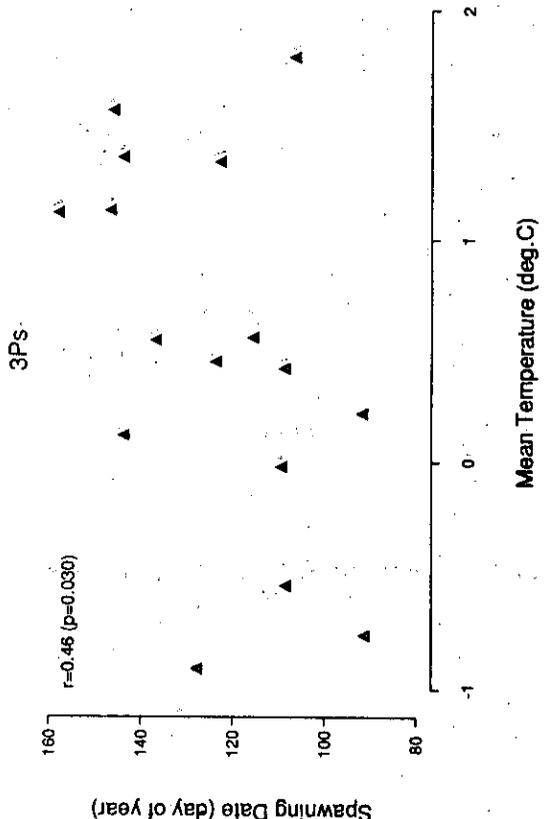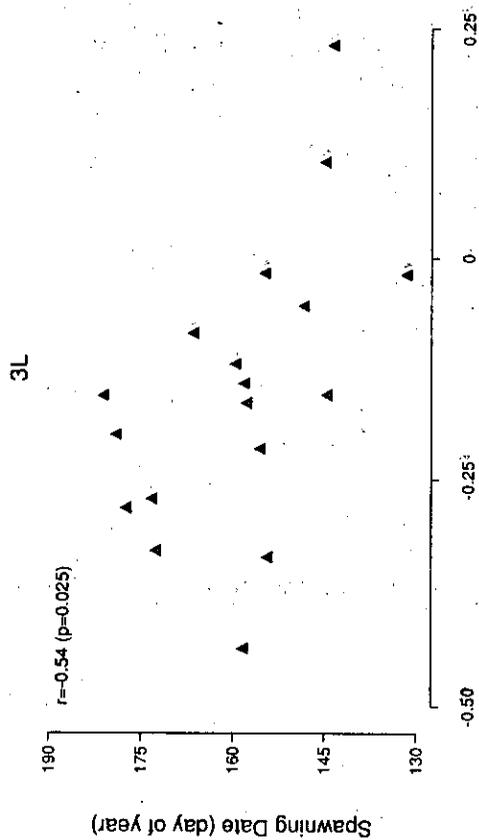
Figure 5. Interannual variation in water temperature and the biomass of Atlantic cod on the continental shelf (57-92m) relative to that on the continental slope (276-366m) in NAFO division 3L (northern Grand Bank). Biomass data are from Canadian research surveys (definitions of complete and incomplete data are in the Methods section).
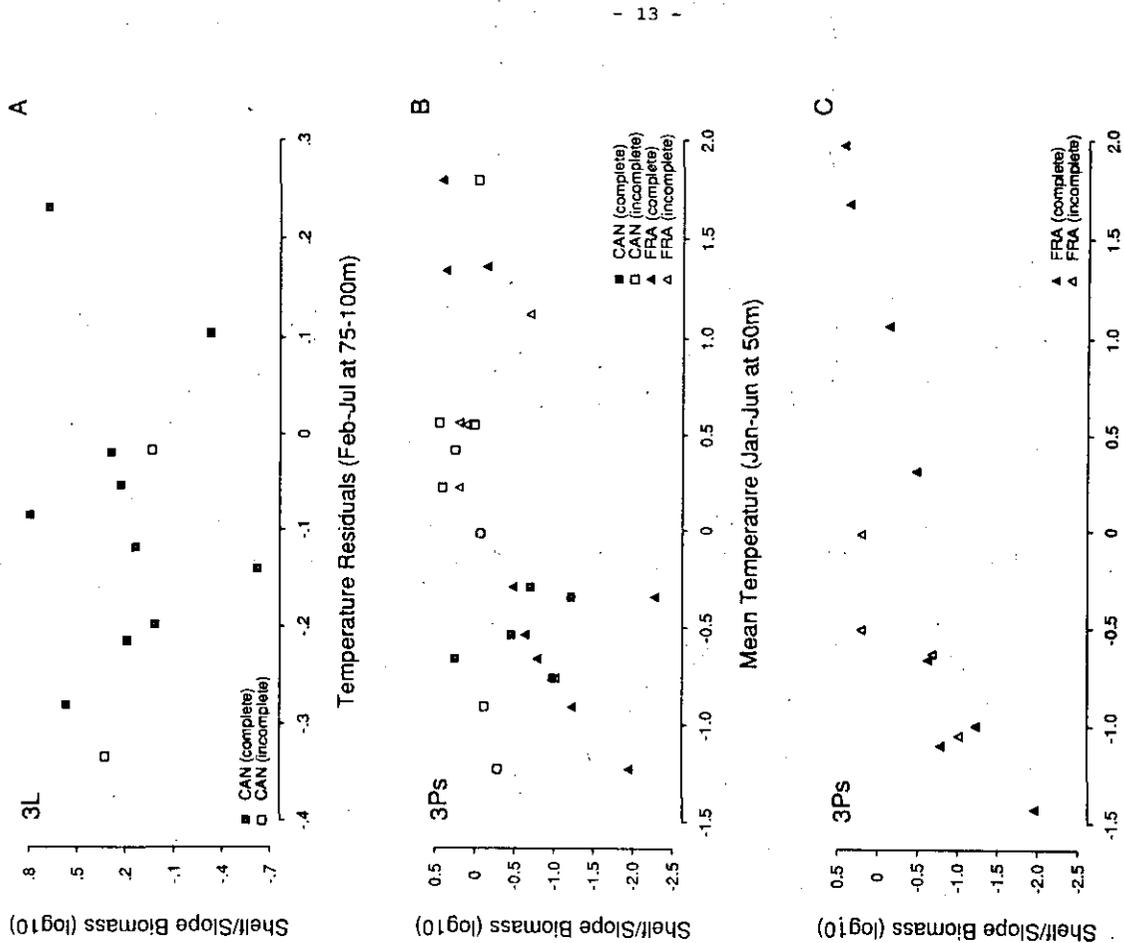
Figure 7. Relationships between biomass of Atlantic cod on the continental shelf relative to that on the slope and water temperature prior to reproduction. A. Data for 3L (northern Grand Bank) from 1978-1991. B. Canadian and French data for 3Ps (St. Pierre Bank) from 1972-1991. C. French data collected during February-March of each year in 3Ps from 1978-1990.
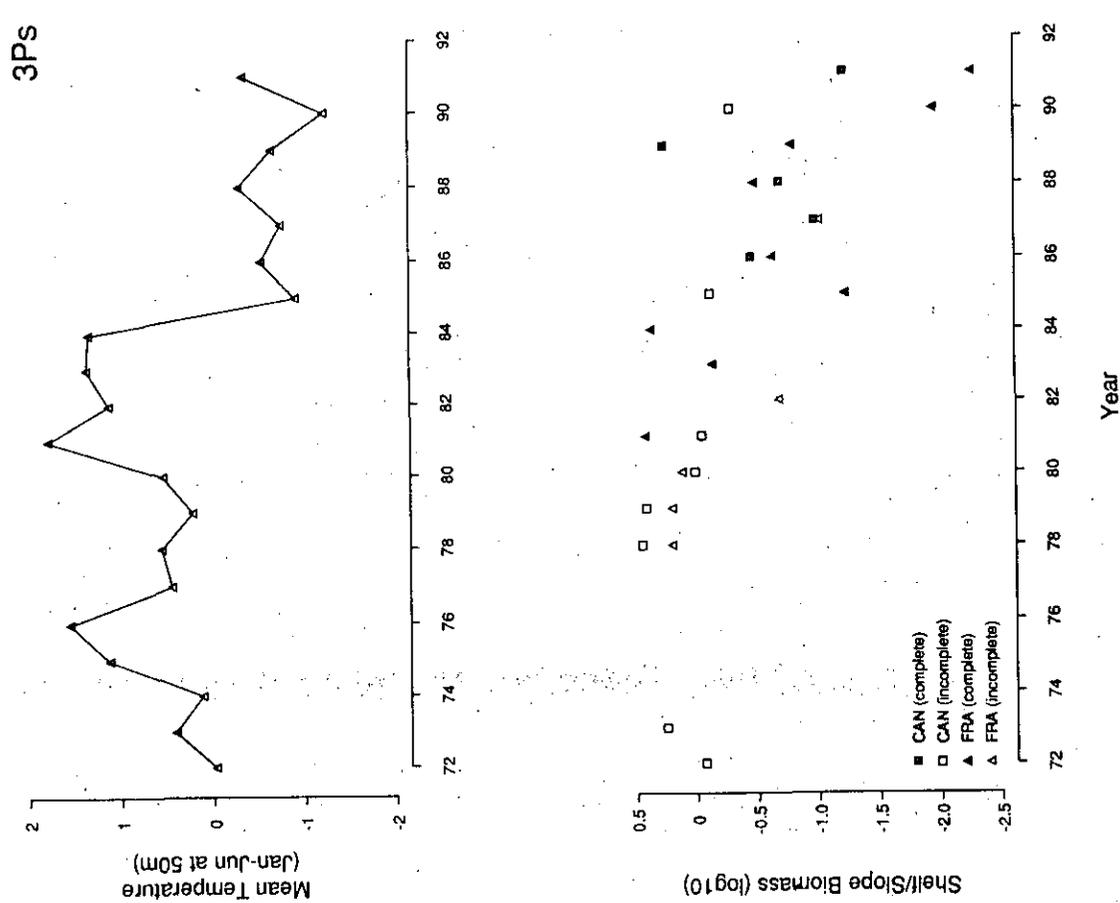
Figure 6. Interannual variation in water temperature and the biomass of Atlantic cod on the continental shelf (56-90m) relative to that on the continental slope (271-365m) in NAFO division 3Ps (St. Pierre Bank). Biomass data are from Canadian and French research surveys (definitions of complete and incomplete data are in the Methods section).