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Cod Spawning in Relation to Physical and Biological Cycles of the Northern Northwest Atlantic

by

R. A. Myers, G. Mertz and C. A. Bishop
Science Br., Department of Fisheries and Oceans
P. O. Box 5667, St. John's, Newfoundland, Canada A1C 5X1

Abstract

All the available, reliable cod (*Gadus morhua*) spawning data for the northern Northwest Atlantic (the Grand Banks of Newfoundland, the Labrador and West and East Greenland Shelves) have been analyzed to update older, often unpublished, reports of spawning dates. The derived spawning times are examined for latitudinal trends and it is shown that no consistent, general pattern exists. The spawning dates are compared to seasonal cycles of plankton abundance, ocean temperature, water column stability and oceanic transport. The latitudinal trends in spawning dates and timing of the plankton peak are found not to correspond.

Keywords: spawning and plankton, spawning and environment, match/mismatch, recruitment

1 Introduction

Temporal and spatial spawning patterns of fish may provide important clues as to their spawning strategies, clues which may be of considerable significance to the understanding of recruitment variability. Consider the prevalence of spring spawning of temperate fish stocks; this characteristic may indicate that egg release is timed to produce larvae when planktonic food is most abundant. It may be further surmised that larval survival and eventual recruitment are determined by the degree of synchrony of the appearance of first-feeding larvae with the abundance peak of zooplankton; this constitutes the match/mismatch hypothesis of Cushing (1990, 1982, 1969). A less stringent version of this scheme is the match hypothesis of Brander and Hurley (1992), viz., "...timing of the spawning is coupled to timing of plankton production".

Sinclair (1988) and Sinclair and Tremblay (1984) have contended that match/mismatch does not explain the spatial patterns of spawning, that in general it has not been demonstrated that there is any correspondence between spawning zones and those of high plankton density. These authors propose that spawning is directly regulated by physical factors, chiefly the requirement that a larval cohort must be retained within a limited area.

Oceanographic influences on food availability, rather than the need for larval retention, may link oceanic features and spawning patterns. For example, Lasker (1975) has noted that the successful foraging of larval fish can depend on the presence of a strong pycnocline (the depth range of maximum stratification) which serves as a zone of vertical concentration for planktonic food. Since vertical stability has a pronounced seasonal cycle at temperate latitudes, spawning time may be selected to match the time of maximum stability. Even if food is abundant larval growth may be limited by low temperature in cold water regimes, implying a possible influence of the seasonal temperature cycle on the determination of spawning time.

In this paper we will update older, often unpublished, reports of cod (*Gadus morhua*) spawning dates for the northern Northwest Atlantic (the

Grand Banks of Newfoundland, the Labrador and East and West Greenland Shelves). We have elected to focus on cod as this is a much studied species, and the required information is available for stocks spanning a great geographic range. The derived spawning dates are examined for latitudinal trends. In order to assess the implications of the analysis for the hypotheses outlined in the three paragraphs above we compare the spawning times to seasonal cycles of plankton abundance, ocean temperature, water column stability and oceanic transport.

2 Data and Methods

The oceanographic data are the most straightforward, and the data sources are given as each variable is introduced. The plankton data, spawning times, and appearance times for larvae require some description, which is given in the following three subsections.

Plankton

The seasonal cycles for zooplankton, based on Continuous Plankton Recorder (CPR) data, are available, from Robinson et al. (1973), for standard areas (Fig. 1): Region 1 – NAFO zones 1A through 1F; Region 2 – NAFO zones 2G, 2H, 2J; Region 3 – NAFO zones 3K, 3L, 3M, 3N, 3O, 3Ps, 3Pn. The data were acquired in the period 1961-1971. We do not have plankton data for East Greenland waters. CPR data for these regions were limited to major ship tracks; Region 3 was sampled fairly broadly, while coverage of Regions 1 and 2 was limited to the stippled areas indicated in Fig. 1. Although CPR data are not ideal, suffering from limited and variable coverage, they can be usefully applied to defining seasonal plankton cycles (e.g., Cushing, 1982).

We will use *Calanus finmarchicus* abundance to represent larval food supply. Pepin (1990), in describing his analysis of North Sea recruitments, notes that "*Calanus* was used as a measure of the availability of planktonic prey because for many species the young fish feed extensively on the eggs, nauplii, and copepodite stages". From the CPR data monthly abundances of *Calanus* I-IV are available and will be utilized here; these data are clearly not ideal as nauplii abundances are not included. However, Brander and Hurley (1992) have shown that the *Calanus* peak does provide a useful temporal reference for comparison to spawning times.

Spawning times

The spawning times were estimated from trawl surveys of maturing fish. These surveys are designed to take close to a random sample of the population, and thus should be more representative of the population than estimates taken from commercial samples. Only data for female fish were examined. The fish were divided into two categories: (1) those that were in prespawing or spawning condition and (2) those that were spent or in post-spawning condition. (The maturity stages are described in Table 1 of Templeman et al., 1978). Table 1 gives the numbers of fish used in the analysis, categorized by region and month. We then used a maximum likelihood probit analysis to estimate the mean and standard deviation of the normal distribution that best described the distribution of spawning (McCullagh and Nelder 1989). The logistic and Gompertz distributions were also fitted to the maturity data. We found that the Gaussian cumulative distribution provided an adequate model of the data; no other distribution consistently provided a superior fit to the data.

Spawning of an individual cod usually occurs in more than one batch, and can be protracted. Hutchings and Myers (1993) estimated from field data that the average duration of spawning for females was 25 days. Kjesbu (1989) obtained similar estimates for labratory experiments. This indicating that our calculated spawning dates will be overestimated by about 2 weeks.

For the East and West Greenland stocks we used maturity data from Serebryakov (1968), data acquired during a series of Soviet fisheries investigations in the Northwest Atlantic, conducted in the 1950s and early 1960s. We also used Serebryakov's data to supplement data for NAFO divisions 2GH, where Canadian sampling was limited.

For the Newfoundland/Labrador Region (NAFO regions 2G, 2H, 2J, 3K, 3L, 3M, 3N, 3O, 3Ps) we combined all research surveys from 1947 to 1991 for the analysis. We separated the NAFO Divisions 2J and 3K into three separate banks (Fig. 1), Hamilton bank in the north, Belle Isle Bank in the middle, and Funk Island bank in the south. The remainder of the data were analyzed by NAFO division.

Fig. 2 displays two fits to the maturity data. In this plot, and in all the plots to follow, monthly tick marks designate the center of each month. In general the probit-based curves plausibly capture the stage progressions. With the data partitions used we encountered no major difficulties in obtaining reasonable fits. Table 2 records the peak spawning times and standard deviations for the spawning curves, by region. The fitted spawning distributions will be broadened somewhat by interannual changes in the period of peak spawning, an effect which will increase the standard deviations. It is not clear whether or not sufficient data exist to allow extraction of the interannual variations. Fig. 3 shows all the fitted spawning curves.

Larval appearance times

In section 4 we will require estimates of the time of appearance of first feeding cod larvae, entailing calculation of the durations of the egg and yolk sac stages. The estimation of these two development times is described in the two following paragraphs.

The hatching times were estimated from Fig. 6 of Page and Frank (1989) (age of stage IV cod eggs versus temperature) using surface temperatures (from the compilation by Drinkwater and Trites, 1986) chosen to represent the period after spawning. These corrections are necessarily imprecise. For the warm water stocks (3M, 3L, 3N, 3O and 3Ps) the hatching periods are in the range 15 to 20 days. For the colder water stocks (West Greenland, 2GH, Hamilton Bank, Belle Isle Bank and Funk Island Bank) the hatching times range from 20 to 30 days; for these stocks, the estimates of hatching intervals are less reliable since the curve determining this quantity as a function of temperature becomes steeper as temperature decreases. However, even for these cold water cases, the hatching times are in reasonable agreement with previous estimates: Templeman (1981) gives the hatching period for cod eggs in -1°C to 1°C water as 40 days, while we have used 30 days as the hatching time for water at 0°C.

The yolk sac stage duration is given by Pepin (1991) as 19.9 days $\times \exp(-0.0177)$ where T is the temperature in °C. The temperature dependence of this interval is weak for the temperatures encountered in our study region, so we have simply approximated this stage-duration as 20 days.

3 Latitudinal trends

We have compared our spawning time estimates to those recorded in earlier studies. Fitzpatrick and Miller (1979) reported a number of noteworthy features in the latitudinal dependence of the spawning times of Newfoundland/Labrador cod. In Fig. 4 we have plotted our derived peak spawning times, with standard deviations, versus latitude. According to Fitzpatrick and Miller (1979), "... unpublished data of the St. John's Biological Station indicate that time of maximum spawning is delayed from north to south, being mainly in April and May on the northern Grand Bank and mainly during the last half of May on the southern Grand Bank ...". According to our analysis peak spawning on the northern Grand Bank (3L) occurs in early June, considerably later than the period given by Fitzpatrick and Miller. For the southern Grand Bank (3N, 3O) we find peak spawning in early to mid-May, in acceptable agreement with the findings of Fitzpatrick and Miller. For St. Pierre Bank (3Ps) we find peak spawning in mid-May while Fitzpatrick and Miller give spawning as occurring "primarily in the months of May and June". Our examination does not support the existence of earlier spawning toward the north on the Grand Bank.

Although spawning on the Grand Bank seems to show some systematic delay toward the north (from 3N, 3O and 3Ps to 3L), it is curious that this trend appears to reverse as one proceeds north of the Grand Bank. From zone 3L, as one progresses north through Funk Island Bank, Belle Isle Bank, Hamilton Bank and zone 2GH, spawning becomes systematically earlier; indeed peak spawning for zone 2GH (early April), Hamilton Bank (early April) and Belle Isle Bank (mid April) is earlier than on the southern Grand Bank (early to mid May). Early spring spawning of southern Labrador cod is supported by Templeman (1981) and Serebryakov (1968).

In Fig. 4 the spawning time for 3M (Flemish Cap) cod is conspicuously early, by about two months, compared to the spawning periods of stocks at similar latitudes. Substantiation for this anomaly is provided by the cod egg survey data presented in Serebryakov et al. (1987); their data show that cod eggs are abundant on Flemish Cap only in March and April, principally March. Templeman (1976) found, during sampling on Flemish Cap, that 84% of the female cod were spent by 20-23 March, also confirming the early spawning for this area. It is also notable that the spawning peak for 3M cod is very narrow compared to the widths of the peaks for the other stocks analyzed here (Figs. 2,3,4), a fact not noted in earlier studies.

4 Spawning and environmental cycles

In this section we will consider the relationship of spawning periods to the seasonality of four biotic or environmental quantities: plankton, temperature, stability, and transport.

Spawning and plankton cycles

In this subsection we will compare the spawning periods and the dates of appearance of first feeding larvae with the times of maximum abundance of *Calanus*. The plankton records are shown in Fig. 5, extracted from Robinson et al. (1973). The *Calanus* peak is about one month earlier in the southerly area (Region 3), compared to the Labrador region (Region 2) and Greenland waters (Region 1).

In Fig. 6a we have plotted the peak of the spawning time versus the peak period for *Calanus*. It is apparent that there is a much greater range of spawning period compared to the range of periods for the *Calanus* maximum. The dashed line in this figure represents equality of the times of spawning and the *Calanus* peak. The northerly stocks, West Greenland, Hamilton Bank and Belle Isle Bank, form a cluster, as do the more southerly shelf stocks 3N, 3O, 3Ps, Funk Island Bank and 3L. Region 3M is clearly distinct. It is important to note, in comparing the two clusters of stocks, that the spawning times show a tendency opposite to that evident in the *Calanus* peak times. That is, the centroid of the spawning times for the northerly stocks is earlier than that for the more southerly shelf stocks, while the *Calanus* peak is delayed from south to north.

In Fig. 6b the same patterns are apparent. The larvae of the northerly stocks appear earlier than those of the southerly shelf stocks (contrary to the trend for the *Calanus* peak), and 3M is again distinct.

Spawning and temperature cycles

The match/mismatch hypothesis assumes that food availability determines larval growth rate. However, in cold water regimes, such as the northern Northwest Atlantic, temperature might limit growth rates (even if food is plentiful). An effect of this nature has been observed for larval coregonids in Lake Constance by Eckmann and Pusch (1989); they find that "Zooplankton abundance is thus no decisive factor for the onset of larval growth. We conclude that surface water temperature determines the rate of early larval growth...". Thus, it is worthwhile to consider the seasonal cycles of surface water temperature in the study region in relation to the spawning periods.

In Fig. 7 we have plotted the seasonal surface temperature cycles, from Drinkwater and Trites (1986), for three representative subregions of our study area: the Northeast Newfoundland Shelf in the NAFO 3J and 3K regions, typifying cold shelf waters; St. Pierre Bank, typifying more southerly, somewhat warmer shelf waters; Flemish Cap, typifying the open ocean domain for these latitudes. The shelf waters are very cold in winter and early spring, remaining cold until April-May. Rapid warming of the shelf waters is evident after May. On and in the vicinity of Flemish Cap the seasonal cycle has the same phase as for the shelf waters, but temperatures do not drop below about 3.5°C at any time of the year.

There is no obvious relationship between spawning or larval appearance time (Fig. 6a,b) and ocean temperature. The 3M stock occupies the warmest waters and spawns earliest. Yet, the northerly stocks, occupying very cold water, spawn earlier than the southerly shelf stocks.

The 3L stock produces first feeding larvae significantly later than the *Calanus* peak (Fig. 6b). Since *Calanus* nauplii occur before this peak, it appears that 3L larvae are mismatched to their food. It is certainly conceivable that this delay is temperature mediated (see lead paragraph of this subsection), as the host waters for this stock are warming rapidly in the June-July period (Fig. 7).

Spawning and stability/wind mixing cycles

Throughout spring and early summer, strong winds prevail over the Newfoundland/Labrador region. This suggests that "Lasker events" (Lasker, 1975), the dilution of larvae and their food by wind mixing, may be common here. Before conclusions about the importance of this effect can be drawn, an examination of the ocean stability (stratification) and wind cycles must be carried out.

In Fig. 8 we have plotted the stability parameter $\Delta\rho = \rho(50\text{ m}) - \rho(0\text{ m})$ (ρ is density of sea water) by month for the three subregions considered in the temperature analysis. The density data were calculated from temperature and salinity data in Drinkwater and Trites (1986). In Fig. 9 we show the seasonal cycle of wind speed (V_w) for the Grand Bank. The stratification parameter can be shown to be proportional to the energy input required to mix the water column. The energy input rate, of the wind to the water column, is proportional to $V_w{}^3$ (e.g., Csanady, 1984). We can thus regard the index $V_w{}^3/\Delta\rho$ as representing the potential for Lasker events.

From May to early July $V_w{}^3$ decreases by about 25%; during this same period $\Delta\rho$ typically increases by about a factor of five in these subregions. Clearly the stratification change controls the potential for Lasker events during this interval. Both variables favor reduced likelihood of occurrences of strong mixing, as spring progresses into summer.

The stability cycles for northerly and southerly shelf waters (Fig. 8) are quite similar and thus it appears that stability cannot be invoked to explain the differences in spawning times. Moreover, there is no indication of an early increase in stability for region 3M (Fig. 8, middle panel) that would explain the conspicuously advanced spawning in this zone.

Spawning and transport cycles

According to Sinclair and Tremblay (1984) and Sinclair (1988) the location and timing of spawning is determined by the potential for retention of eggs and larvae. According to this picture, any seasonality of the current field will influence the selection of spawning time. For example, Parrish et al. (1981) suggest that some fish species off California synchronize their spawning with changes in the the wind-driven currents so as to avoid egg release in the upwelling season when loss to the offshore domain would be likely. Below, we briefly consider three possible advective influences in our study region.

(i) *Ekman drift.* The strong winds found over the study region will produce a significant drift, to the right of the wind, of spawning products in the mixed layer. Myers and Drinkwater (1988) found no significant correlations between interannual anomalies in calculated Ekman drift and recruitment of a number of Northwest Atlantic fish stocks. Helbig et al. (1992) used model simulations to show that the spring wind field and storm pattern over the southern Labrador and Newfoundland Shelves favor drift toward the inner shelf regime; that is, there was no evident tendency toward unfavorable (offshore) drift. Overall, there appears to be little reason to suspect that the seasonal changes of the wind-induced drift exert a significant influence on the selection of spawning time.

(ii) *Gulf Stream rings.* Myers and Drinkwater (1989) have shown that interannual variations in recruitment of a number of Northwest Atlantic fish stocks appear to be correlated with the number of Gulf Stream rings near the shelf. It is presumed that a Gulf Stream ring impinging on the shelf can sweep spawning products into the unsuitable offshore habitat. Region 3Ps cod recruitment showed a fairly convincing negative relationship with an index of Gulf Stream ring activity. Accordingly, in Fig. 10 we have plotted the seasonal cycle of the numbers of Gulf Stream rings influencing the waters of 3Ps, along with the cycles for zones adjacent to 3Ps. (The procedure for extracting the ring index from sea surface temperature maps is described in Myers and Drinkwater, 1989). The seasonal minimum for this general area occurs in spring to early summer. (Note that May is the month of peak spawning of 3Ps cod). The most notable feature of 3Ps cod spawning is the great width of the spawning curve (Figs. 2,3,4). It is possible that this broad window of spawning has been selected to reduce interannual variability in the number of surviving offspring (Gillespie, 1977).

(iii) *Transport by the Labrador Current.* There is no doubt that the Labrador Current carries eggs and larvae over considerable distances (Serebryakov, 1968; Helbig et al., 1992). However, the transport is generally alongshelf, and there is no reason to suppose that any existing egg and larval loss to the offshore domain is influenced by seasonal variations in transport.

Section summary

We will conclude this section by comparing our findings to the results of other studies in the Northwest Atlantic: Sherman et al. (1984), Northeastern U.S.A. shelf; Brander and Hurley (1992), Scotian Shelf.

Sherman et al. (1984) studied the larval occurrence patterns, in relation to plankton distributions, for a number of fish species occupying shelf waters from the Gulf of Maine to Cape Hatteras. They concluded that two spawning strategies prevail: ubiquitous spawning (hakes and sand eel) featuring "...high abundance levels of eggs and larvae over a wide temporal and geographic range..."; targetted spawning (cod, haddock and others) aimed to "...optimize encountering prey with respect to temporal and spatial increases in zooplankton abundance". Their analysis shows that, for cod, the larval abundance peaks about one month earlier than the seasonal maximum of zooplankton. Correspondingly, in Fig. 6b we find that the more northerly group of cod stocks produces larvae earlier than the *Calanus* peak. However, the Grand Bank cod stocks appear to produce larvae either in synchrony with or later than the *Calanus* peak.

Brander and Hurley (1992) compared Scotian Shelf cod egg distributions, in time and space, to those of *Calanus*. They found that a south to north delay in the occurrence of the *Calanus* peak was matched by a retardation in the timing of peak cod spawning. In contrast, (Fig. 6a,b) we have found that, while the *Calanus* peak is later in the north of our study region, the spawning and larval appearance times for the northerly stocks are earlier than they are for the southerly shelf stocks.

Brander and Hurley found that for all of the four subregions of the Scotian Shelf, maximum egg abundance is approximately concurrent with the *Calanus* peak. This latter result is of particular interest as we find that egg production for cod of the northern Northwest Atlantic generally occurs well before the *Calanus* peak (Fig. 6a). The difference in patterns might be attributed to the prevalence of colder waters in our study zone; however, the waters of Flemish Cap (3M) are warmer than those of the Scotian Shelf in spring and early summer.

We have presented spawning dates for cod stocks spanning over 15° of latitude (Fig. 4). There is little evidence of an overall latitudinal trend in spawning period; this is in distinction to the Scotian Shelf where a one month lag in cod spawning, over 3° of latitude (April in the south versus May in the North), was reported (Brander and Hurley, 1992). It is interesting to note that cod spawning toward the southern end of the Scotian Shelf (43°N) is concurrent with cod spawning on Belle Isle and Hamilton Banks (52-54°N) and even West Greenland at 60°N.

5 Conclusions

Our results support the match hypothesis of Brander and Hurley (1992), that "...timing of spawning is coupled to timing of plankton production". In Fig. 6a, for all cases examined, cod spawning occurs prior to the *Calanus* peak, suggesting that there is indeed a link between the spawning and the plankton.

An intriguing feature of the data is that the northerly stocks spawn and produce larvae earlier than the southerly shelf stocks. The 3M stock is a clear anomaly, spawning much earlier than any of the other stocks considered. This aspect of the spawning times cannot be readily explained by latitudinal changes in seasonal cycles of plankton, temperature, stability or transport.

There is no evidence that seasonal changes in retention patterns are an influence on spawning for any of the northern Northwest Atlantic cod stocks (with the possible exception of the 3Ps stock). Indeed, the spawning areas for the stocks considered cannot be regarded as retention areas in any sense. Spawning of 2GH, 2J3KL and West Greenland cod is known to occur in slope waters where strong shelf break currents are found (Serebryakov, 1968; Hermann et al., 1965). These facts argue that the ideas propounded by Sinclair (1988) and Sinclair and Tremblay (1984) cannot be applied to cod of the northern Northwest Atlantic.

Previous explications of the match/mismatch hypothesis have been rather vague as to just how close a match between the appearance of first feeding larvae and the zooplankton peak should be expected. For example, in Cushing (1990) the spawning distributions of seven fish species in the southern bight of the North Sea are used to support the contention that a match is required. Fig. 5 of his paper shows that these seven species exhibit spawning peaks ranging from about mid-February to early May, a span of two-and-half months. Yet, according to Cushing, all these species are targetting the same plankton peak. It would appear that only a general, rather than a precise, correspondence between larval production and planktonic food is required. We believe that our analysis of cod spawning in the northern Northwest Atlantic supports this view. It should be noted that the sufficiency, for larval viability, of a general match implies that recruitment will not be strongly influenced by changes in the timing of the plankton peak, contrary to the assertions of the full match/mismatch hypothesis.

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Table 1. Data used to estimate the spawning distribution. For each region, the number of spent (above) and the total number of fish examined is given for each month. Sampling intensity is low in northern regions in the spring because of ice cover.

Region	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
East	0	0	0	217	82	225	0	0	0	0	0	0
Greenland	0	0	0	701	234	234	0	0	0	0	0	0
West	0	0	60	894	3650	1130	0	0	0	0	0	0
Greenland	0	0	231	2034	4250	1360	0	0	0	0	0	0
2GH	0	26	0	271	0	0	68	397	194	226	32	0
	0	58	0	701	0	0	68	398	194	226	32	0
Hamilton	0	0	7	275	229	158	2	440	334	1832	6977	111
Bank	0	79	107	414	240	161	2	440	334	1832	6977	111
Belle	0	2	14	79	905	45	0	190	332	804	3686	690
I. Bank	56	696	300	178	1072	48 0		193	332	804	3686	690
Funk	0	4	15	0	85	356	67	145	105	29	875	862
Island	0	457	152	0	127	444	67	147	105	29	875	862
3L (<201m)	0	1	1	33	321	317	196	389	310	3044	1906	69
	80	111	51	314	1322	495	230	420	310	3044	1906	69
3M	0	1	85	48	98	0	132	311	107	0	79	0
	417	776	157	49	98	0	132	311	107	0	79	0
3O	0	1	15	294	293	141	15	12	11	0	0	0
	0	17	216	1186	582	201	22	12	11	0	0	0
3N	0	0	6	121	433	226	253	52	98	34	14	0
	0	5	132	398	1108	252	253	53	98	34	14	0
3Ps	0	14	130	128	96	313	3	0	27	6	25	1
	59	569	968	607	252	458	3	0	27	6	25	1

Table 2. The mean spawning times (Julian days) for the cod stocks considered, with standard deviations and 95% confidence limits.

Region	Mean	Stnd dev	Lower	Upper
East Greenland	136.	22.		
West Greenland	105.	49.		
2GH	96.	29.	89.	104.
Hamilton Bank	97.	20.	94.	100.
Belle Isle Bank	110.	28.	96.	121.
Funk Island Bank	138.	36.	131.	145.
3L ($<$201 m)	160.	37.	156.	164.
3M	77.	11.	62.	93.
3N	133.	28.	131	136.
3O	137.	41.	132.	143.
3Ps	141.	52.	136.	148.

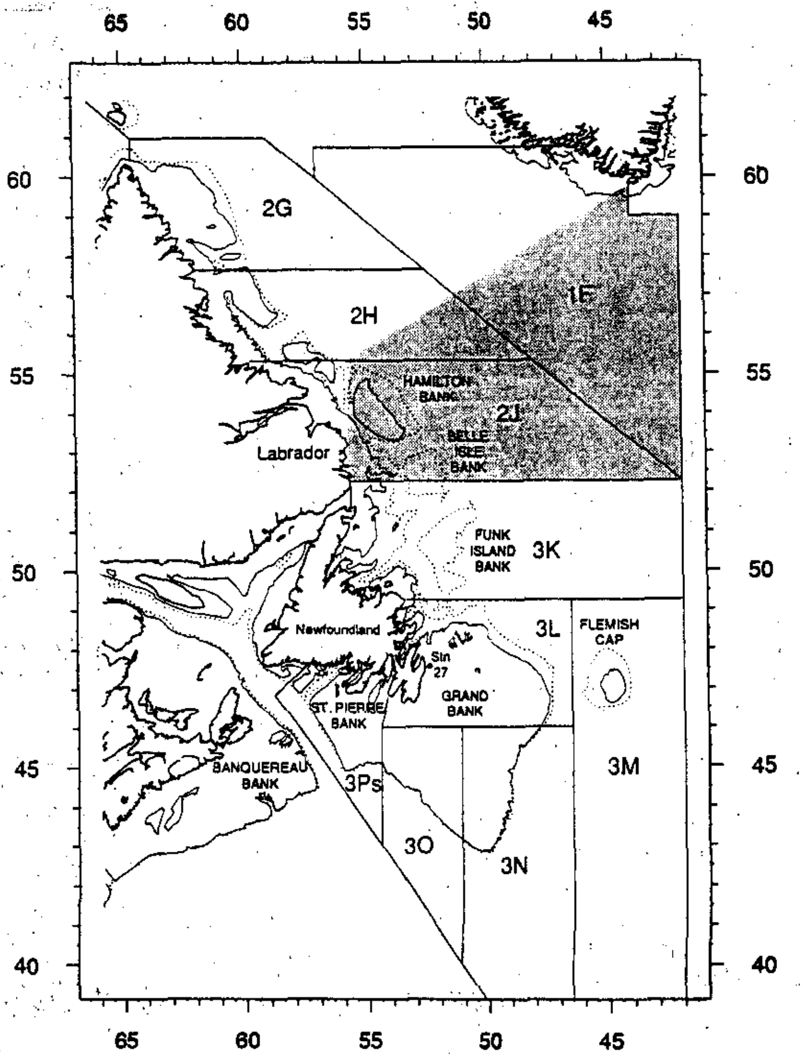


Figure 1. Map of the study region, with the NAFO zones. Funk Island Bank and Belle Isle Bank are conveniently delineated by the 300 m isobath, as indicated here (hatched areas). The stippled areas of Regions 1 and 2 indicate the portions of these zones for which continuous plankton recorder (Robinson et al., 1973) coverage was available.

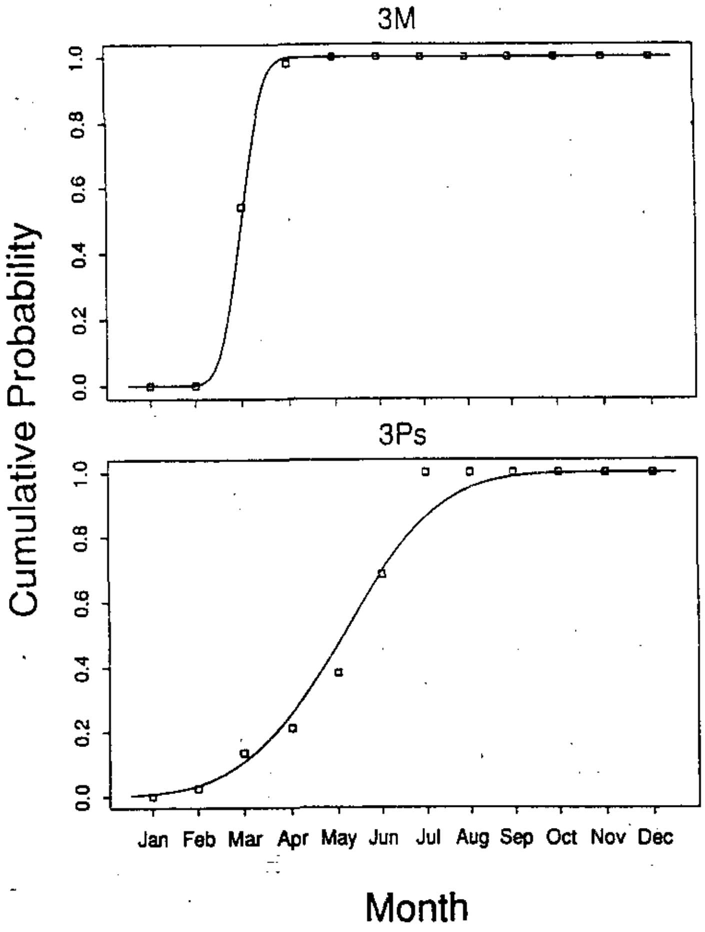


Figure 2. Fitted maturity ogives for two extreme cases: zone 3M (very narrow spawning window); zone 3Ps (very wide spawning window). The squares designate the monthly proportions of the female fish that are spent.

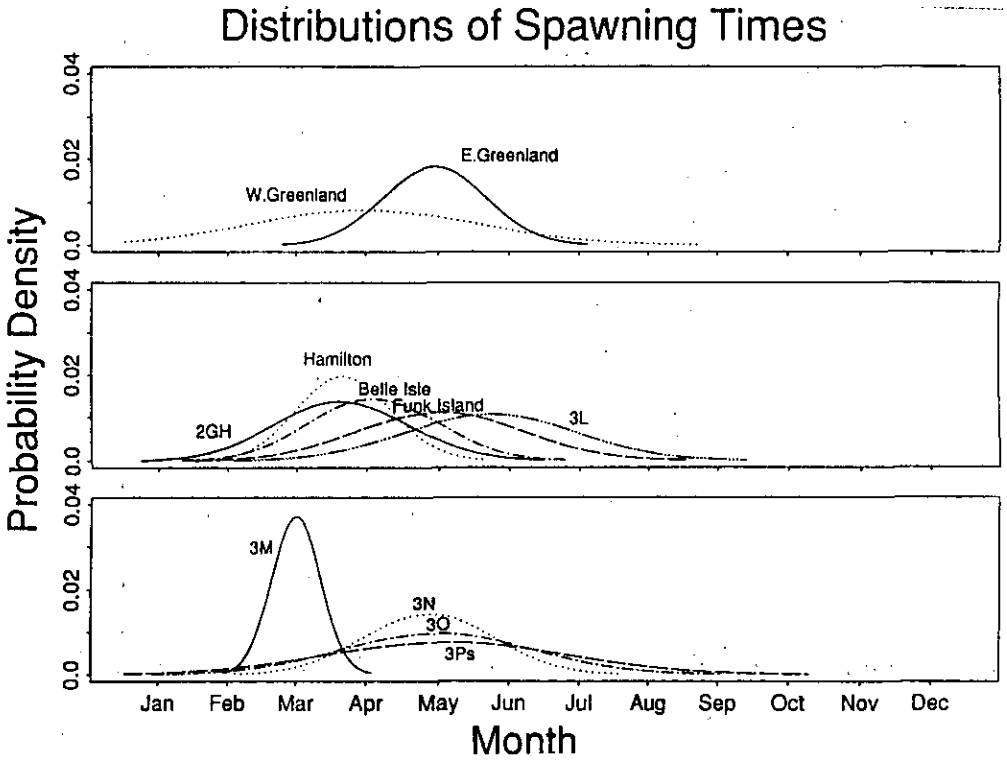


Figure 3. The complete set of egg production curves, derived from the fits to the maturity data as the rate of progression to spent condition. The curves appear as probability density functions, having been normalized to unit area.

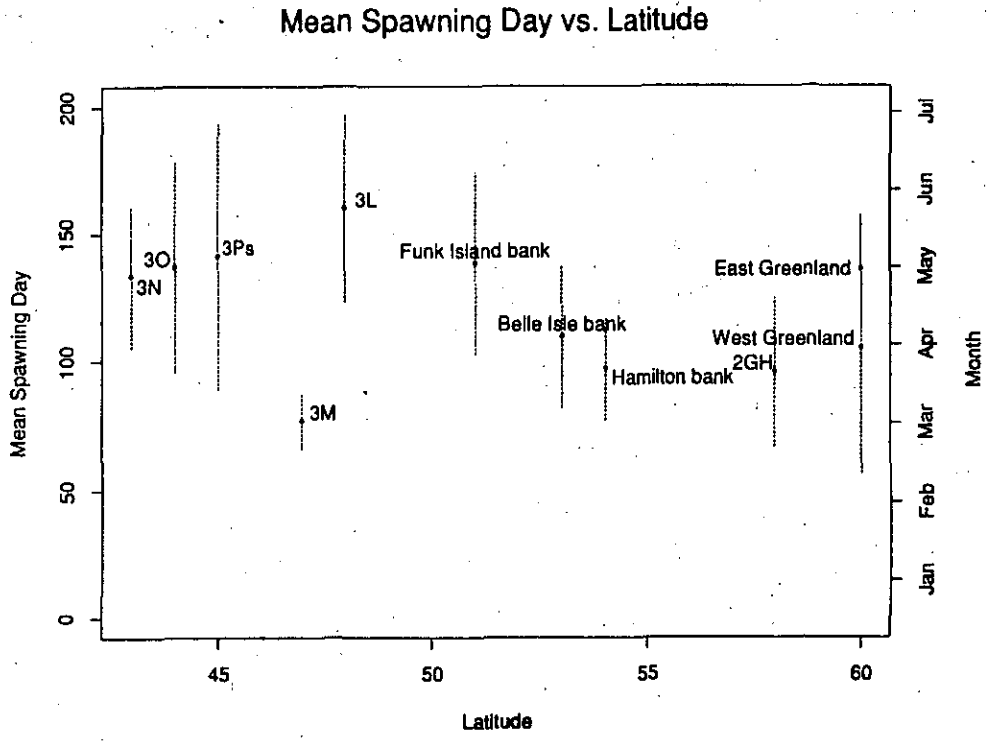


Figure 4. The latitudinal dependence of mean spawning time. The dotted lines indicate the widths (standard deviations) of the spawning distributions.

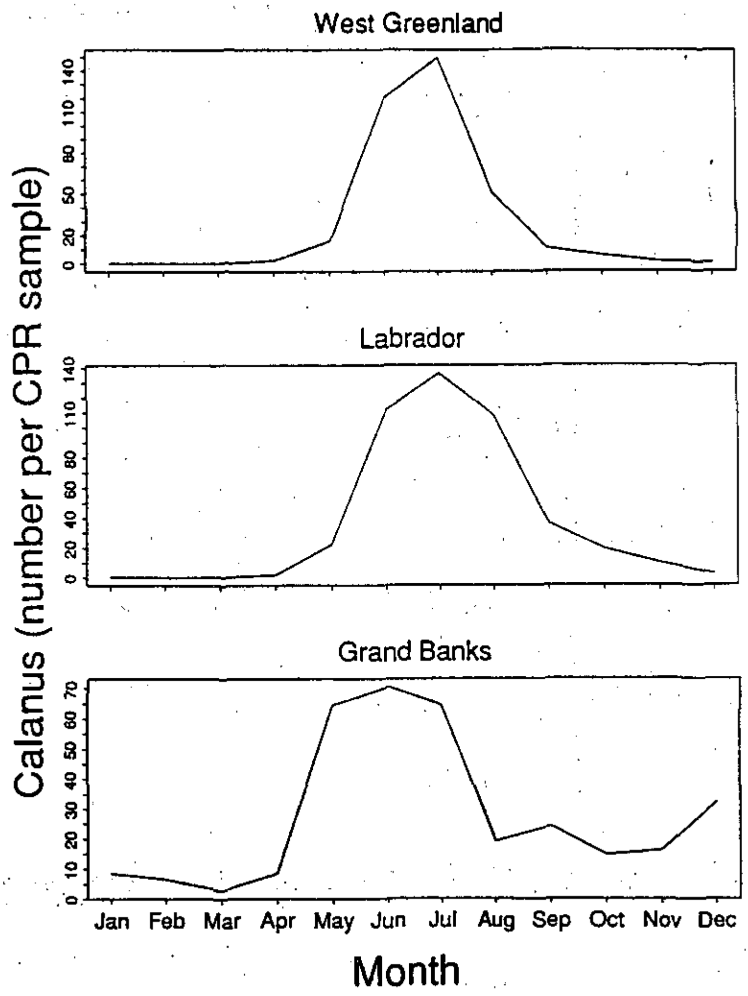
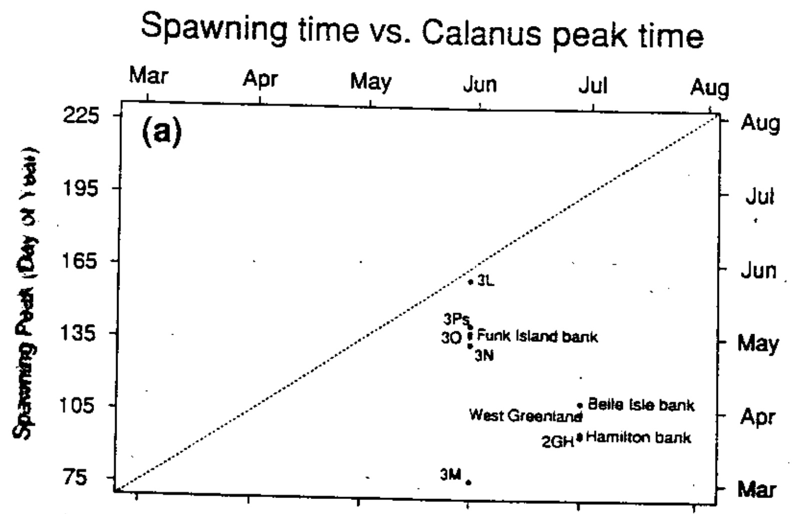


Figure 5. Plots of the estimated abundance (based on CPR data) of *Calanus finmarchicus* I-IV for West Greenland (Region 1), Labrador (Region 2) and the Grand Bank (Region 3) waters, from Robinson et al. (1973).



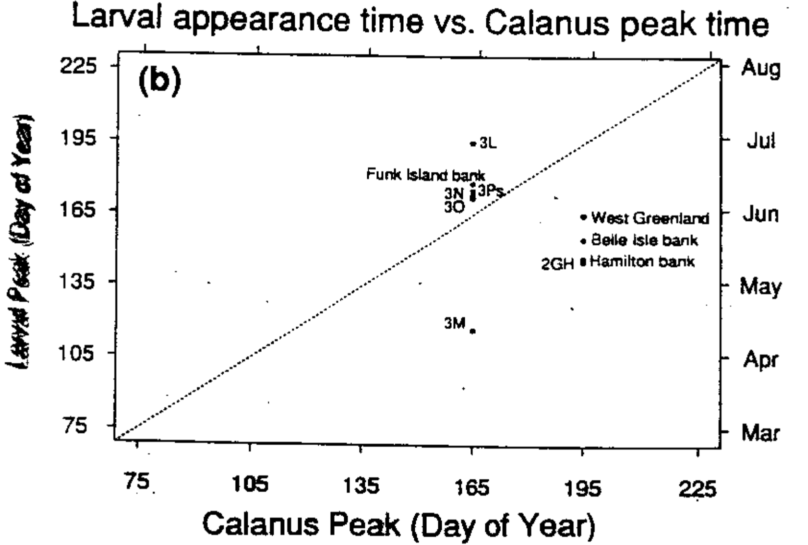


Figure 6a. Mean spawning time versus the date of the peak for *Calanus finmarchicus* I-IV. The dashed line indicates direct proportionality with unit slope.

Figure 6b. The estimated time of appearance of first feeding larvae versus the date of the peak for *Calanus finmarchicus* I-IV. The dashed line indicates direct proportionality with unit slope.

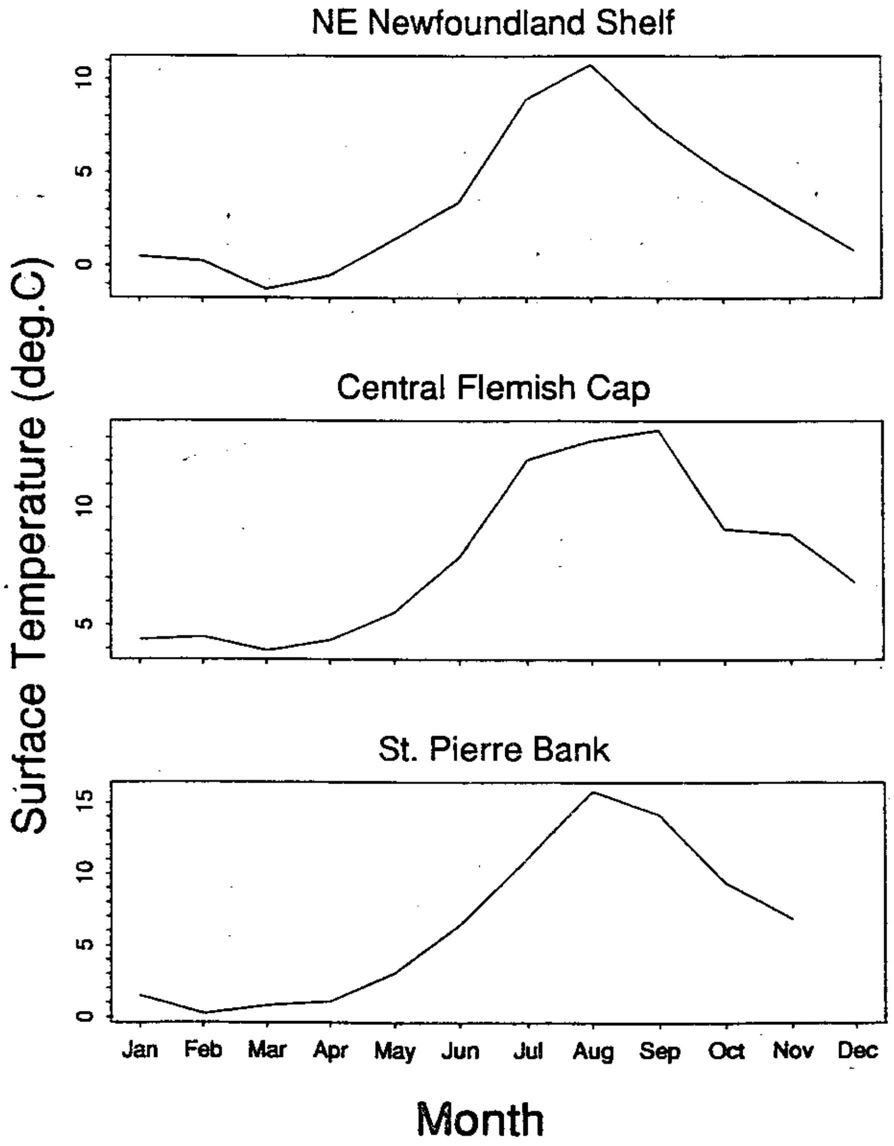


Figure 7. Monthly mean surface temperatures (°C) for three representative areas.

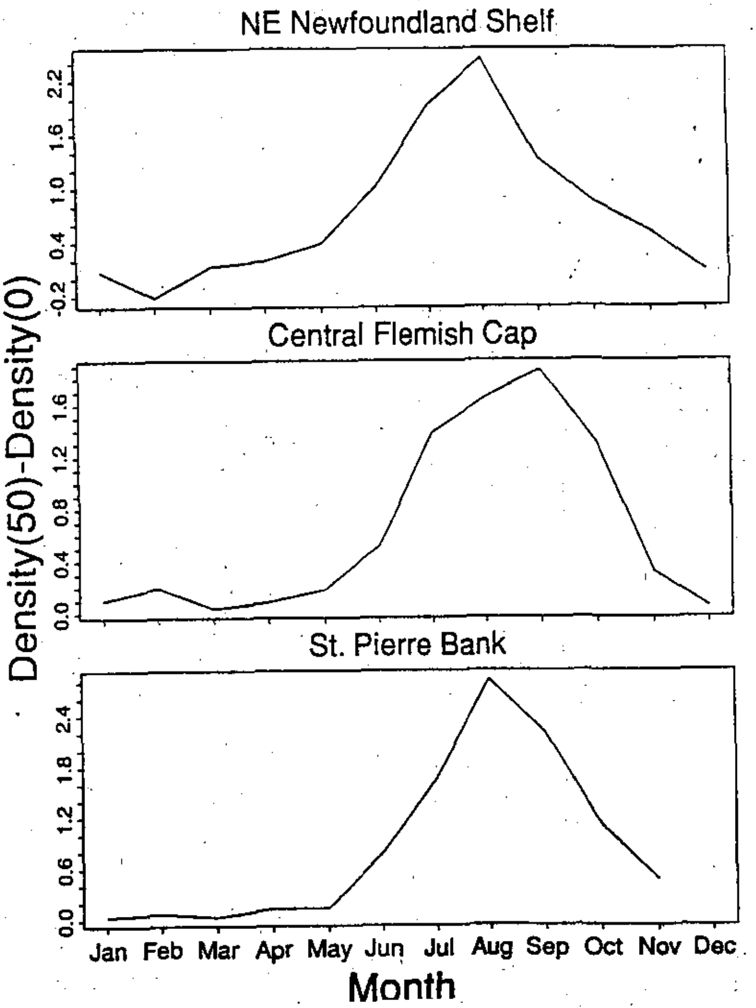


Figure 8. Monthly means of $\rho(50\ \mathrm{m}) - \rho(0\ \mathrm{m})$, where ρ is the density of seawater in $\mathrm{kg/m^3}$, for three representative regions.

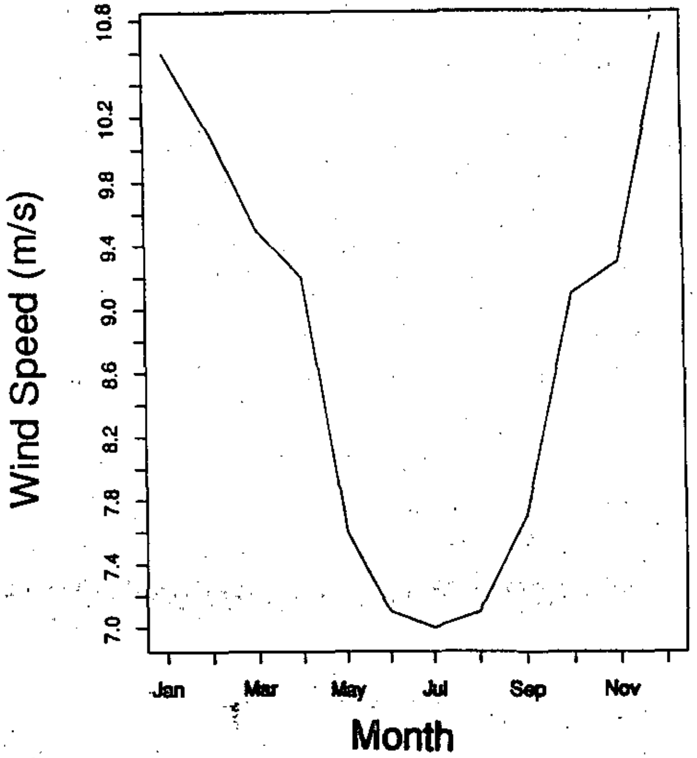


Figure 9. Monthly means of wind speed ($\mathrm{m\ s^{-1}}$) for the Grand Bank (from Isemer and Hasse, 1987).

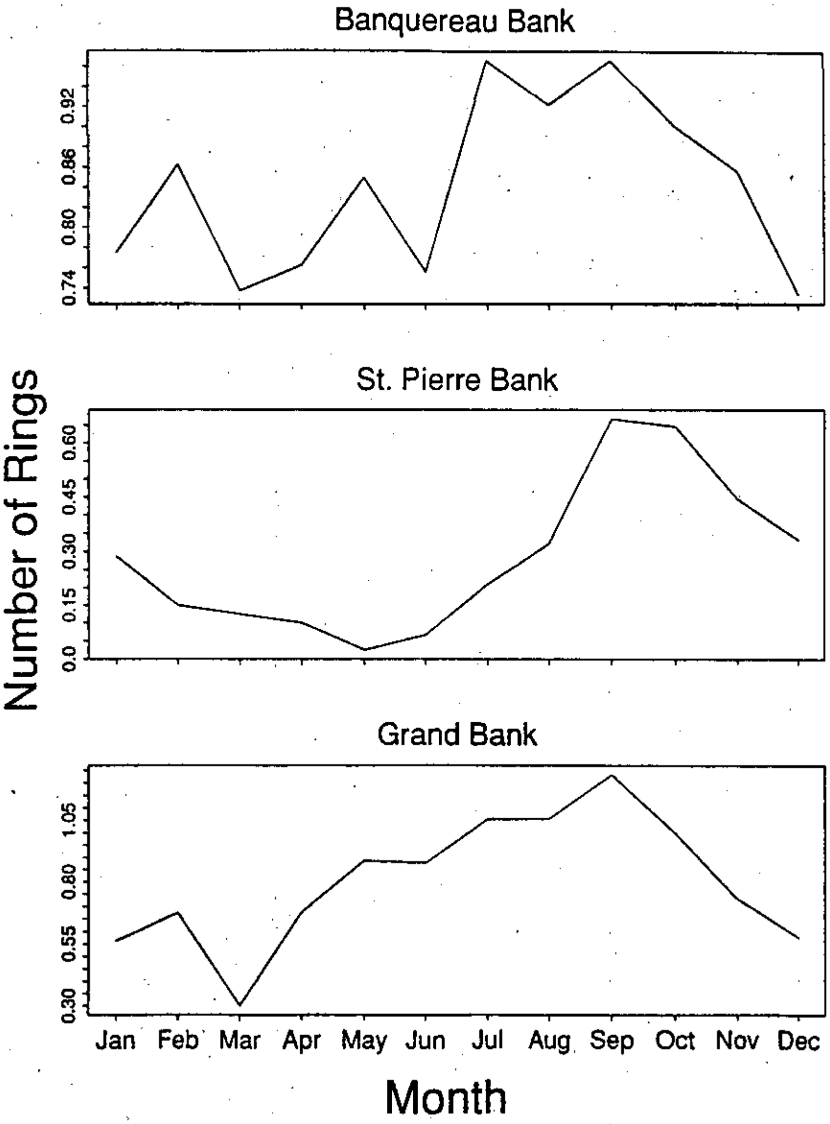


Figure 10. Monthly means of the number of Gulf Stream rings influencing the waters of the northeastern Scotian Shelf (Banquereau), zone 3Ps and the southern Grand Bank (the shelf portions of zone 3NO).