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Distribution and Abundance of Pelagic O-Group Cod in Inshore and Offshore Areas for the Northern Cod Stock (NAFO 2J3KL)

by

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Abstract

The Northern cod stock has previously been reported to undergo a large-scale natant-contranatant migration: spawning occurs primarily in the north off Labrador; eggs and larvae are advected southward to the inshore areas along the NE coast of Newfoundland where they settle as juveniles; there is a gradual return migration to the northern spawning areas. We examined abundance distributions of pelagic 0-group cod in the fall, several months after spawning, in both inshore and offshore areas to determine if these fish occurred predominantly inshore following pelagic drift. While the surveys were conducted in different years the distributions appeared to represent general conditions for any given year, independent of interannual differences in stock size. Comparison between areas demonstrated similar abundances and mean sizes occurred in both inshore and offshore areas. These results do not support the concept of large-scale advection of eggs and larvae spawned offshore to inshore areas, but indicate that cod eggs spawned offshore remain offshore. Backcalculations of spawning times indicate the pelagic 0-group fish sampled offshore were spawned predominantly in April, whereas fish caught inshore were spawned predominantly in April-May through to June. Backcalculation estimates of spawning abundance for inshore and offshore areas indicate that the offshore area represented the primary nursery area for northern cod. The inshore areas along the NE coast of Newfoundland may represent $\leq 10\%$ of eggs spawned annually.

1 Introduction

The northern cod stock, the largest and most valuable cod stock in the Northwest Atlantic, has been managed as a single unit bounded by the Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J3KL, stretching over 6 degress of latitude from Hamilton Bank off southern Labrador to the northern part of the Grand Bank. This stock has traditionally been regarded as a stock complex, being made up of a number of spawning units associated with each of the offshore banks (Templeman 1981, 1989; Lear 1984). Formation of the managment unit was based on a description of the biology formulated through several early studies (Halliday and Pinhorn 1990). Central to this description was the understanding that these fish undergo a large natant-contranatant migration during their early life history (Templeman 1979; 1981; Lear and Green 1984). Spawning reportedly occurs primarily in deep water along the slope of the continental shelf off Labrador in March and April (Serebryakov 1965, 1967; Postolaky 1968; Templeman 1981). Following spawning, eggs and larvae develop slowly in cold surface waters for periods of 40-60 days and are thought to be carried south and shoreward 450-750 km by the Labrador Current to the large bays and numerous inlets of eastern Newfoundland where these fish develop and settle to the bottom in the fall (Templeman 1981; Lear and Green 1984). The inshore areas, therefore, serve as the primary nursery areas for these young cod as they grow and develop.

Recent publications have indicated that the above description is too simplistic. Templeman (1989) concluded there was evidence for inshore spawning of cod, which occurred later than for the offshore spawning components. Recently, Heibig et al. (1992) concluded that fish eggs released on the shelf tend to stay there, with no tendency to drift into the inshore bays or onto the Grand Bank. When the effect of storms was included in their model the transport of cod eggs into these bays was further reduced. They concluded that, under mean conditions of circulation, the northeast Newfoundland Shelf would be the nursery area of 2J3KL cod, not the inshore bays as previously described. Juvenile cod (1- and 2-year olds) do appear in research bottom trawl catches from the edges of the Grank Bank (Kuzmin 1991), confirming that young cod occur in the offshore area.

Given the importance of this stock and the current depressed state of the fishery there is interest in being able to predict cod recruitment both at an early age and independent of traditional data sources (Harris 1990). A better knowledge of the early life history is necessary before surveys can be designed to monitor juvenile cod abundance. There have never been synoptic surveys to describe the distribution and abundance of young cod in inshore and offshore areas. However, we did have available the results from several inshore surveys and one offshore survey during the fall of different years in which pelagic 0-group cod were taken. This pelagic occurrence is not unusual since 0-group cod occur in the water column for several months following spawning, settling to the bottom around 7-8 cm in length (Perry and Neilson 1988). The purpose of this paper was to test the hypothesis that the

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the majority of pelagic juveniles do not occur offshore, but inshore as previously described. Our approach was two-fold. First, we compared survey data from inshore and offshore during the month of September to provide a general description of the relative distributions and abundances of pelagic 0-group cod in these areas. Second, using a simple model we estimated the timing of spawning in both areas and made first-order estimates of the relative abundances of cod eggs in the inshore and offshore areas.

2 Methods

2.1 Data Sources

A total of 4 surveys were carried out in September of different years: offshore in 1981; inshore Trinity Bay in 1984 and 1985; inshore Conception Bay 1989 (Figures 1-4). The offshore survey was based on a systematic grid design where stations were approximately 54 km (30 nautical miles) apart. A total of 87 stations were sampled between 45°15'N and 50°15'N latitudes. This survey design is equivalent to a systematic sampling design (Snedcor and Cochrane 1967), assuming that the first station was randomly selected from within a 54 by 54 km² stratum. In Trinity Bay both the 1984 and 1985 surveys were based on a number of selected strata within which each station was selected randomly prior to the survey. For the offshore and Trinity Bay surveys we consider the sample design adequate to estimate the abundance of cod for these areas. In Conception Bay the sampling locations were based on a series of stations that had been selected to represent different sections of the bay and, therefore, statistically cannot be considered as randomly chosen to reflect abundance of cod within Conception Bay. Nevertheless, we feel the spacing of stations throughout the bay was adequate to represent the abundance distribution of pelagic cod.

All data were collected using an 8 m² rectangular mid-water trawl (RMT-8) with a net mesh size of 4.5 mm and a cod end mesh size of 0.505 mm (Clark 1969). During the 1981 offshore survey, each tow was stepped oblique from 200 m depth to the surface with the net being towed for 5 minutes at depths of 150, 100, 50, 25 and 0 m at a speed of approximately 1.0-1.6 m s⁻¹ (2-3 knots) and payout and retrieval rates of 0.5 m s⁻¹. Net depth was monitored with a net sonde transducer mounted on top of the net. When water depth was less than 200 m, then the tow was started from the next greatest depth, i. e. 150 m, 100 m and so on. Total tow time was recorded for each tow. In the 1984 and 1985 inshore surveys a simple oblique tow was done to and from 200 m, or within 10 m of the bottom when bottom depth was less than 200 m. Otherwise, the sampling procedures were the same as 1981. During the 1989 Conception Bay survey two simple oblique tows were done at each location to and from 100 m depth, or within 10 m of the bottom, with one tow being done towards the mouth of Conception Bay and the second tow towards the head. All other sampling procedures remained the same in 1989 as in previous years.

All cod were removed from the samples, counted and measured for total length to the nearest mm. Standardized estimates of abundance $(N, \text{ fish } 100\text{m}^{-2})$ were calculated as:

$$N = \frac{C \cdot D}{8L} \cdot 100 \tag{1}$$

where C is the number of cod collected, D is the maximum sampled depth (m), 8 is the area of the net opening (m^2) and L is the tow path (m). The tow path was estimated from tow time as

$$L = T \cdot S \tag{2}$$

where T is tow time (s) and S is ship speed (m s^{-1}).

2.2 Spawning Backcalculation Model

We constructed a simple model to estimate spawning frequency in spring from the cod size distributions observed during the fall surveys. The model was dependent on stage specific estimates of growth and mortality rates for larval and juvenile stages and temperature dependent development and mortality rates for eggs. All rate estimates were taken from the literature, as summarized in Table 1. Size at hatch was taken as 3.5 mm and metamorphosis from larvae to pelagic juvenile cod was set at 25 mm (Fahay 1983). Water temperatures used to estimate egg development and mortality rates were averaged for 0-20 m depth for 8 different subareas that covered NAFO areas 3K and 3L for May and June, as summarized in Drinkwater and Trites (1986). Based on these backcalculations, estimates of total egg abundance were calculated, one for each fall survey, by simple areal expansion of each area surveyed. Backcalculation estimates were obtained by using different sets of parameter values for all growth, mortality and development rates. An estimate of total eggs spawned in each survey year for the entire 2J3KL cod stock was based on numbers at age estimated each year (Baird et al. MS1991, Table 52), maturity at age assuming a 50/50 sex ratio (C. Bishop, per. comm.) and fecundity at age (May 1967) (Table 2).

The model used to backcalculate the number of eggs spawned in the spring, based on the catch of juvenile fish in the fall was

$$N_{0} = \sum_{i=1}^{n} N_{i} \prod_{j=1}^{3} e^{z_{j} t_{j}}$$

(3)

where N_0 is the number of eggs spawned, Ni represents the standardized number of juvenile fish in each length (mm) category *i* sampled and *j* represents each life history stage such that 1=juveniles, 2=larvae and 3=eggs. *z* represents instantaneous mortality rate for each stage duration t_j , where different juvenile and larval mortality values were selected from Table 1 and egg values were calculated as

$$r_e = 0.03 \exp^{0.18T}$$
 (4)

where T is water temperature (Pepin 1991). t represents the time spent in each stage and is a function of growth rate g_i for juveniles (j = 1) and larvae (j = 2), and water temperature T for eggs, such that

$$t_1 = (J - 24) \cdot g_1^{-1} \tag{5}$$

$$t_2 = (L - 3.5) \cdot g_2^{-1} \tag{6}$$

$$t_3 = 74.131 \cdot T^{-0.82}.\tag{7}$$

 t_3 is after Apstein (1909) and Page and Frank (1989). J is the size of juvenile cod captured at each station, where $J \ge 25$ mm and L is the size of larval cod for each backcalculation, where 3.5 mm < L < 25 mm. Different growth rates for juveniles and larvae were selected from Table 1. The estimated spawning date distribution D_0 was calculated from each length category as,

$$D_0 = D_c - (t_1 + t_2 + t_3) \tag{8}$$

where D_c was the date of capture.

3 Results

3.1 Comparisons of Sampling Differences Among Surveys

Although the same net was used in all four surveys, the net deployment procedure differed between surveys. To compare abundance distributions of pelagic 0group cod in the inshore and offshore areas sampled during the different surveys we evaluated the degree to which sampling differences may have affected standardized catches. In this first section we evaluate possible sampling differences associated with stepped oblique versus simple oblique tows and day versus night samples. The day/night differences were based on data collected only in 1981, whereas the tow comparisons involved data collected in different years. While differences in 0-group abundance are expected to vary among years, the comparison is made nevertheless to test for possible sampling differences due to technique.

Tow times averaged 44.6 minutes (20-52 min.) for the offshore survey in 1981, 12.1 minutes (8-16 min.) combining the two surveys in Trinity Bay in 1984 and 1985, and 12.0 minutes (10-14 min.) in Conception Bay in 1989. The much longer tow times for the offshore survey in 1981 resulted in increased volume of water filtered by the stepped oblique tows, compared to simple oblique tows done in the other surveys. We compared possible abundance differences associated with the stepped oblique tows offshore in 1981 to the simple oblique tows inshore in the other years (1984, 1985, 1989). The stepped oblique tows were longer and filtered considerably more water than the simple oblique tows, when comparing similar tow depths. The simple prediction is that more fish would be caught when more water is filtered. When fish are spread throughout the water column then increased capture of fish is expected with greater amounts of water filtered. In this case standardized abundances of fish from the two sampling methods would be equal. However, when fish abundances for a given location are equal but fish are confined to a specific depth range then standardized abundance estimates from stepped oblique tows may be lower compared to simple oblique tows because relatively large volumes of water will be filtered at depths not containing fish. In this case a comparison of abundances between the different tow methods would not be valid.

Abundance comparisons between surveys were done only for 0-100 m tows to standardize maximum tow depth. In stepped oblique tows offshore in 1981 abundances averaged 4.70 cod 100 m⁻² compared to 4.14 cod 100 m⁻² for simple oblique tows in Conception Bay in 1989. The means were not significantly different (Wilcoxon's test, z=-0.7553, P=0.4501, n₁=17, n₂=15). In Trinity Bay in 1984 and 1985 there were 9 tows to maximum tow depths of 90-110 m, although only 3 of these captured cod. When these data were included in the comparison there was still no statistical difference among abundances (Kruskal-Wallis test, χ^2 =0.75, P=0.6869). From these comparisons we conclude that there was no apparent bias associated with comparing standardized abundance estimates for the stepped oblique tows compared to the simple oblique tows.

In 1981 the sampling was carried out continuously over a 24-h period, however, the inshore surveys were conducted only during daylight hours. To determine if there were day-night differences in catchability, day/night data for 1981 were analyzed for both standardized abundances (cod m⁻²) and size (mm) of cod captured. In each case there were no statistical differences in either \log_{10} abundances (t test, P=0.4079) or mean sizes (t-test, P=0.2241).

3.2 Distribution

Pelagic cod were caught throughout much of the offshore area surveyed in September 1981 (Figure 1). These cod were concentrated in three areas: 1) a broad area

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overlying the NE Newfoundland shelf and the northern Grand Bank (NAFO areas 3KL); 2) the southern Grand Bank (3NO); and 3) near St. Pierre Bank (3Ps). There was some evidence of higher concentrations ($\geq 10 \text{ cod } 100\text{m}^{-2}$) for nearshore areas along the NE coast of Newfoundland as well as along the southern coast of Newfoundland. High numbers of cod were also observed at a number of stations throughout the offshore area, demonstrating that high abundances were not confined to the nearshore areas.

Inshore, the range of abundances was similar to that observed offshore. In both 1984 and 1985 high abundances of cod $(\geq 10 \text{ cod } 100\text{m}^{-2})$ were observed near the head of the Trinity Bay (Figures 2 and 3). Throughout the bay the distribution of cod was irregular with catches ranging from 0 to $> 10 \text{ cod } 100\text{m}^{-2}$. In 1985 the distribution of cod appeared to extend beyond the mouth of Trinity Bay, indicating that this distribution may have continued into the offshore area. In 1984 the sampling did not extend to the mouth, so inferences about offshore distribution cannot be made. Pelagic cod were caught at stations throughout Conception Bay in September 1989, although peak abundances were $< 10 \text{ cod } 100\text{m}^2$ (Figure 4). The only notable spatial pattern in abundances were the zero catches in the northeast corner of the Bay.

3.3 Abundances

For pelagic 0-group cod caught offshore in 1981 abundance averaged 6.4 cod $100m^{-2}$ over all stations that captured cod while the maximum abundance was 56.6 cod $100m^{-2}$ (Table 3). In Trinity Bay abundances averaged 8.2 cod $100m^{-2}$ in 1984 and 11.0 cod $100m^{-2}$ in 1985. Peak abundances were 27.1 and 130.7 cod $100m^{-2}$, respectively. In Conception Bay abundance averaged 4.3 cod $100m^{-2}$ while the maximum abundance was 12.9 cod $100m^{-2}$.

Comparing abundances among inshore and offshore areas is constrained by sampling in different years for each area. Here a comparison is based on mean values estimated for each survey, including only stations where cod were caught. Inclusion of a variable number of stations where cod were not caught would lower the mean and increase the variance, possibly obscuring real differences in abundances. Comparison based on 95%CI's indicate that there were no significant differences in mean abundances among areas (Figure 5). The average inshore abundance (all 3 inshore surveys) was 7.8 cod $100m^{-2}$, which is similar to the mean of 6.4 cod $100m^{-2}$ sampled offshore in 1981.

3.4 Sizes

In 1981 cod sampled offshore ranged from 17 to 70 mm total length and averaged

38.1 mm overall (Table 1). Where cod were abundant (i. e. > 5 cod/tow) mean lengths ranged from 28.3 to 51.2 mm. The length frequency data indicated multiple peaks which ranged from 27 to 60 mm length, with apparent modal values at 30, 45 and 52 mm length (Figure 6). There was no apparent spatial pattern in mean cod lengths at different stations, nor was there a north-south (latitudinal) trend in mean length measured at each station (F=1.2, P=0.2776, df=61). In Trinity Bay mean lengths were 36.5 and 28.4 mm total length in 1984 and 1985, ranging from 7-67 mm and 4-65 mm, respectively (Figures 7 and 8). Note that one large fish captured in Trinity Bay in 1984 at 124 mm length was assumed to be more than one year old and was excluded from the estimate of mean length (Figure 7). In Conception Bay cod averaged 34.1 mm and ranged in length from 12 to 69 mm. Peaks in length occurred from about 25 mm up to 50-60 mm in length for each of the inshore surveys.

Levene's test for homogeneity of variances indicated a significant difference among the 4 data sets (F=4.78, P=0.0027, df=637). A non-parametric test for differences in mean size among the 4 cruises indicated there was a statistical difference in mean sizes (Kruskal-Wallis test, χ^2 =73.71, P=0.0001, df=3). Wilcoxon's test for comparisons among pairs of cruises indicated that mean size offshore in 1981 was not statistically different from Trinity Bay in 1984, but that mean size in Conception Bay was statisitically smaller than either of these cruises and mean size in Trinity Bay in 1985 was smaller than all other cruises (P < 0.05).

3.5 Estimates of Spawning

Three sets of parameter values were used to estimate the spawning curve and absolute abundance of cod eggs spawned in the spring of 1981, based on the spawning backcalculation model. To represent average conditions, median values of temperature, growth and mortality were used (Table 4). To bound the median estimate of spawning time, two sets of alternate parameter values were used. One represents slow growth and development of all 3 stages which also were subjected to high mortality, defined here as "minimum". Alternatively a "maximum" parameter set was used representing fast growth and development with low mortality (Table 4).

Spawning was estimated to have occurred between 6 March and 2 June with a peak in spawning occurring on 23 April 1981, based on the median parameter values (Table 5). From the simulation it appears that peak spawning occurred from early April (day 90) until late April (day 120) and was completed by the end of May (day 150) (Figure 10). The minimum parameter set estimates spawning occurred from

11 January to 12 February, while the maximum parameter set estimates spawning would have occurred from 5 April to 17 June (Table 5). These simulations estimated that 6×10^{14} to 4×10^{19} eggs were spawned in 1981 for the minimum and maximum parameter sets, respectively. The median parameter set estimates that 5×10^{16} eggs were spawned.

For comparison of spawning estimates between inshore and offshore areas only the median set of parameter values were used. From the data collected in Trinity Bay during September 1984, the model estimates that spawning was highest in May (days 130-140) but occurred from March through June (Figure 11). For Trinity Bay in 1985 the model predicted that the main period of spawning occurred during the last half of May and the first half of June (days 140-160) (Figure 12). There was a second distinct peak which occurred in late March (days 80-90). For Conception Bay in 1989 the prediction is that spawning was highest from late March to mid-April (days 80-110) and again in late May (days 140-150) (Figure 13).

Estimated numbers of eggs produced, based on areal expansion of the total number of eggs caught at all stations to the area of Trinity and Conception Bays, were 2.1×10^{14} for Trinity Bay in 1984, 3.1×10^{14} for Trinity Bay in 1985, and 4.7×10^{13} for Conception Bay in 1989. Estimates of the number of eggs spawned each year based on maturity, fecundity and VPA estimates of abundance at age were 1.3×10^{14} eggs in 1981, 1.3×10^{14} in 1984, 1.4×10^{14} in 1985 and 1.5×10^{14} in 1989.

4 Discussion

The occurrence of three areas of high abundances sampled offshore in 1981 is consistent with the present management units of the NE Newfoundland Shelf and northern Grand Bank (2J3KL), the southern Grand Bank (3NO) and St. Pierre Bank (3Ps). Unfortunately, sampling did not extend north of 50°15' N latitude, and did not include the northern area of 3K nor any of area 2J. High concentrations of cod (1-10 cod $100m^{-2}$) observed offshore over much of the NE shelf appear to have extended north of the surveyed area. However, future studies will be necessary to determine the northern extent of this distribution.

High concentrations were observed in several stations sampled immediately offshore of the bays along the NE Newfoundland coast, consistent with the expectations that cod eggs and larvae drift to inshore areas along this coast where they would settle as juveniles. However, sampling did not extend into the bays in 1981. Sampling in Trinity Bay in 1984 and 1985 demonstrated that concentrations of cod within the bay were equivalent to those observed offshore in 1981 (> 10 cod $100m^{-2}$) but their distributions were discontinuous. Each year the highest concentrations were observed near the head of the bay. The location of these high concentrations in Trinity Bay is consistent with large numbers of juvenile cod sampled near beaches over a large geographic area in previous years (Fleming 1963) and in Trinity Bay in recent years (D. Methven, Memorial University of Newfoundland, per. comm.).

Several factors indicate that the majority of cod spawned offshore remain offshore. The extensive distribution of pelagic 0-group cod offshore in September of 1981 compared to the heterogenous distribution of cod within the bays in September of later sampling years indicates that the inshore was not the dominant area for pelagic cod several months after spawning. The existing early life history description for these cod is that drift to inshore bays would have occurred within 40-60 days after spawning. As peak spawning is expected to occur during April and May the majority of the cod eggs spawned should have completed their drift by July, August at the latest. The fact that there were no apparent differences in mean abundances between the offshore and inshore areas further supports the hypothesis that cod spawned offshore do not drift inshore but largely remain offshore as juveniles. This is consistent with the modelled predictions of egg and larval drift for the NE Newfoundland Shelf (Helbig et al. 1992). Further, if we assume Trinity and Conception Bays represent $\sim 1/5$ of all inshore areas and that abundance would be similar, then we only estimate that 1.5×10^{15} eggs would be represented by the inshore areas. Even if we assume the extreme case that Trinity and Conception Bays only represent 1/10 of the inshore areas, our estimates of egg abundance are still < 10% of that from the offshore area in 1981. In addition, the offshore area surveyed in 1981 did not extend north of 50°15'N latitude although the distributions indicated high abundances occurred north of the survey area. Therefore, our estimate of total eggs spawned offshore is conservative. Finally, the similarity of cod sizes caught each year in the inshore and offshore areas is also consistent with the conclusion that there is not a large scale drift of cod from offshore to inshore areas. Assuming similar growth rates, these cod would be approximately the same age. If there was a large scale downstream transport of cod to inshore areas then cod sampled inshore should have been significantly larger, and older. In fact the opposite was observed, where cod were significantly smaller inshore during 2 of 3 years compared to offshore in 1981.

We suggest that, at most, only part of the population of cod eggs spawned offshore would have drifted to inshore areas. An alternate explanation is that the cod observed inshore originated from eggs spawned inshore. This is supported, in part, by the backcalculations of spawning times that were generally later for the inshore areas. Templeman (1979, 1981) reported that inshore spawning was generally later than that offshore. However, our surveys were conducted in different years and a direct comparison of spawning times is not possible. The comparison of mean abundance and size in Trinity Bay each year indicates spawning may have been later in 1985, as fish sampled at the same time of year were both smaller and more abundant.

Interannual differences in the abundance of 0-group juvenile cod will occur due to natural factors. However, we are concerned with testing the hypothesis that the majority of the cod eggs (say on the order of 90%) are transported to inshore nursery areas. This effect should exceed inter-annual differences in abundances. Stock size has fluctuated during the period of observations used in this study. The highest stock size occurred in 1985 (Baird et al., MS 1991). Stock abundance in the other years compared to 1985 were 0.67 in 1981, 0.94 in 1984 and 0.89 in 1989. Assuming there were no significant changes among years in age of maturity and fecundity, then the observations in 1981 were for the smallest number of eggs spawned. This observation supports the argument that the offshore area is the significant nursery ground of the northern cod. Alternatively, year-class size was relatively high in 1981 compared to other years. Compared to 1981, year-class size was 0.38 in 1984 and 0.64 in 1985; data are not available yet for 1989. Therefore, if year-class size was established by September each year then we should have expected higher mean abundances in 1981.

There is a notable discrepancy between the estimates of total egg abundance based on backcalculations from the pelagic 0-group surveys and those based on VPA estimates of abundance. The backcalculation model of spawning times in 1981 using the 3 parameter sets spans the previously reported spawning times for the northern cod. The median parameter set corresponds closely with the expected duration and peak time of spawning for this population. The fact that the simulation tended to overestimate the number of eggs spawned in the spring suggests that mortalities of these juvenile cod may have been over estimated in our model. However, the modelled estimates represent the expected range of growth and mortality rates reported for cod in other regions. Another possible explanation is that our standardized estimates of abundance (cod 100m⁻²) are too high. Alternatively, our estimate of the number of eggs spawned in the spring from VPA estimates of abundance is based on limited information of maturity and fecundity. Significant interannual variability in fecundity has been reported for this area (Pinhorn 1984) and our estimates based on a single set of values may not be representative. 'As well, the estimates of maturity and fecundity are based on data collected during the 1960's when population size was much greater. If age at maturity was less (Xu et al. 1991) or fecundity greater

during the 1980's then we would have under estimated the number of eggs spawned.

Offshore, the lack of a significant north-south cline in cod sizes is not consistent with reports that cod spawn earliest in the north and later in the south. Two facts could account for the similarity of mean sizes observed among all stations sampled offshore in 1981. One is that cod spawned in the north grew slower such that mean sizes were the same in the fall, following several months of growth. However, the large scale coherence of temperatures throughout the offshore area (Petrie et al. 1991) indicates that growth differences would not be expected if temperature was critical. Alternatively, a similar size distribution would occur if there was a downstream transport of cod from north to south over the NE shelf. Helbig et al. (1992) predicted that cod eggs spawned offshore would be transported south, but not off the NE shelf. In this case we would expect a general accumulation and mixing of pelagic cod within the southern area of the NE shelf, and mean sizes would not differ due to a general accumulation and mixing of these cod, even when spawning times may have differed significantly. In this way, the southern area of the NE Newfoundland Shelf would be the primary nursery area for the "northern" cod stock, not the inshore areas.

Significant diel differences in catches of 0-group cod were reported on Georges Bank, attributed to vertical migrations where cod were more abundant in night catches (Perry and Neilson 1988). Pelagic 0-group cod sampled offshore in 1981 did not exhibit any significant diel differences in either abundances or sizes captured. The main difference between these studies is that water depths were ≤ 80 m on Georges bank, whereas water depths were mostly > 100 m, and often > 200 m, in this study. It could be that the much deeper water overlying the NE Shelf inhibits any diel vertical migrations for pelagic 0-group cod. Perry and Neilson (op. cit.) reported that even on bottom during day there was sufficient light for these cod to feed. It is possible that when cod occur over shallower depths they begin their migration to the bottom at smaller sizes and younger ages. However, when water depths are greater this may not occur. Inshore samples in this study were done only during the day. If diel migrations occur for these young cod when water depths are shallower, as reported for Georges Bank, then day sampling may have underestimated abundances inshore.

The simulation model does not account for possible differences in growth and mortality rates for cod spawned during different seasons. As the season progresses cod spawned later might be expected to have higher growth and mortality rates due to warmer temperatures (Houde 1989, Pepin 1991). If growth rate of cod spawned later in the season was significantly greater, then our model predictions of spring spawning will be skewed towards earlier spawning times. However due to higher mortality rates, we should not overestimate an earlier spawning as these fish will represent a proportionately smaller contribution in fall samples. In either case, when growth is faster and/or mortality is greater for eggs spawned later in the season then the contribution of eggs spawned later in the season will be underestimated in our model. However, we expect any such bias to be equal among our estimates for inshore and offshore areas and not to significantly affect our comparison among areas.

Suthers and Frank (1989) reported different distributions of pelagic juvenile cod in different years sampled, and they cautioned about generalizing from one year's sampling. We acknowledge that the abundance distributions may vary substantially in different years. However on the scale we are testing (offshore versus inshore), the extensive distribution of pelagic cod sampled offshore in 1981 is compelling evidence that the offshore is an important nursery area. While the abundance distribution is expected to vary, we expect that the observations offshore in 1981 are representative of general conditions which occurred for this stock during the 1980's, and conclude that the NE Newfoundland Shelf is the general nursery area of cod spawned on the offshore banks.

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Table 1. Reported growth and mortality rates for cod larvae and juveniles used in the simulation model. (1-f refers to estimating differences in length frequencies for different periods of time)

Atea	Lengths (mm)	Growth Rate (mm d ⁻¹)	Data Source	Reference
Irish Sea	5-22	0.49	otoliths, Gulf III	Thompson and Haroup (1991)
Browns Bank	3.6-43.0 3.6-24.8	0.44 0.30	otoliths, bongos	Campana and Hurley (1989)
Flemish Cap	6.0-18.9 6.0-34.1 9.8-18.9	0.24 0.32 0.27	l-f, bongos	Anderson (1982)
Browns Bank	25	0.39-0.59	% growth rates, Tucker trawl & 1 m ring net	Suthers et al. (1989)
Norway	45-90	1.61	l-f. Danish seine	Olsen and Soldal (1989)

Area	Stage	Mortality Rate (d ⁻¹)	Reference
Norway	larvae	0.069-0.153	Sundby et al. (1989)
	iuveniles	0.012-0.053	

Table 2. Maturity and fecundity for ages 1-14 used to estimate the numbers of eggs spawned each year by the Northern cod stock.

n F e	Proportion Mature	Fecundity
0	0	188,632
5	0.05	329,607
0	0.30	508,162
0	.0.70	723,791
2	0.92	976,091
9	0.99	1,264,721
0	1.00	1,589,390
0 .	1.00	1,949,845
0	1.00	2,345,858
0	1.00	2,777,229
0	1.00	3,243,770
0 ·	1.00	3,647,31

Table 3. Summary of mean abundances and lengths for cod collected in offshore and inshore areas during September of different years. Offshore refers to the NE Newfoundland Shelf, Grand Bank and St. Pierre Bank. TB refers to Trinity Bay, CB refers to Conception Bay.

Area	Year	Abundance (100m ⁻²)	be	R	Range (100m ⁻²)	Length (mmTL)	sd	'n	Range (mmTL)
Offshore	1981	6.4	10.16	62	0-56.6	37.6	14.11	467	17-70
Inshore TB	1984	8.2	9.47	16	0-27.1	36.5	12.35	79	7-67
Inshore TB	1985	· 11.0	23.19	32	0-130.7	28.4	12.79	114	4-65
Inshore CB	1989	4.3	3.27	17	0-12.9	34.1	15.67	41	12-69

Table 4. Parameter values used in simulations estimating the spawning period and population abundance of cod eggs spawned for the offshore area sampled in 1981. Temperature (°C), growth (mm d⁻¹), mortality (d⁻¹).

		Eggs	Stage Larvae	Juveniles
Median:	Temperature	2.81		
	Growth		0.27	0.5
	Mortality		0.111	0.033
Minimum:	Temperature	0		
	Growth		0.24	0.40
	Mortality		0.153	0.053
Maximum:	Temperature	6.0		
	Growth		0.30	0.60
	Mortality		0.069	0.012

Table 5. Estimated dates of spawning for cod based on the simulation using three parameter sets. Values are given as both date and day of the year in parentheses.

Parameter	Spawning				
Set	Start	End	Peak		
Median	6 March	2 June	23 April		
	(65)	(153)	(113)		
Minimum	11 January	1 May	12 February		
	(11)	(121)	(4 3)		
Maximum	5 April	17 June	15 May		
	(95)	(168)	(135)		

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COD INSHORE vs. OFFSHORE



Figure 5. Length frequency (%) distribution of cod sampled offshore in September



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Day of the Year

Figure 10. Cod egg spawning distribution estimated by backcalculation of pelagic

0-group cod sampled offshore in September 1981.



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Spawning Conception Bay



