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SPAWNING AND RECRUITMENT OF NORTHERN COD AS MEASURED BY PELAGIC JUVENILE COD SURVEYS FOLLOWING STOCK COLLAPSE, 1991-1994

by

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Abstract

Pelagic juvenile cod sampled during trawl surveys in the late summer and early fall demonstrated significant variations in geographical distributions, abundance, spawning period and growth from 1991-1994. In 1991 cod were located at only a few locations within the inshore areas whereas in 1992-1994 cod were observed frequently throughout the inshore areas. Sampling effort offshore varied among years making direct comparisons among years difficult. Generally, few cod occurred in the offshore areas sampled over the southern portion of the Northeast Newfoundland Shelf and northern Grand Bank in 1991-1993. In 1994 cod were observed frequently offshore on the Northeast Newfoundland Shelf. Very few cod were observed on the northern Grand Bank in 1994 whereas a distinct concentration was observed over the southern Grand Bank. The 1991 year-class appeared to be weak while the 1994 year-class appeared to be relatively strong. Mean cod abundances (10,000m^{-3}) were significantly greater ($P < 0.01$) in 1994 in both inshore and offshore areas compared to the earlier years. Mean abundance in 1992 was significantly greater inshore than in 1993 ($P < 0.01$), whereas offshore there was no significant difference. Successful spawning (eggs and larvae that survived to become pelagic juveniles) occurred relatively late in 1992 and 1993 compared to 1994 which was closer to the historical median spawning time. Back calculation based on micro-otolith structure indicated that larvae hatched primarily during July and August in 1992 and 1993 compared to larvae which hatched primarily in June in 1994. Growth rates were statistically greater in 1992 and 1993 (0.65 mm d^{-1}) than in 1994 (0.48 mm d^{-1}) ($P < 0.015$). The lower growth rate in 1994 may have resulted from an earlier hatching in seasonally colder waters. It is hypothesized that observed differences in distributions, abundance and spawning periods may be linked to changing environmental conditions in spring.

Résumé

Les échantillonnages de morue juvénile pélagique réalisés durant les relevés de recherche au chalut à la fin de l'été et au début de l'automne révélaient d'importantes variations dans les distributions géographiques, l'abondance, la période de frai et la croissance de 1991 à 1994. En 1991, on n'avait trouvé de la morue que dans quelques endroits de la zone côtière, tandis que de 1992 à 1994, elle apparaissait fréquemment dans l'ensemble de cette zone. Les opérations d'échantillonnage en haute mer ayant varié d'une année à l'autre, il est difficile de faire des comparaisons directes. Généralement, la morue était rare dans les échantillonnages du large dans le secteur sud de la plate-forme du nord-est de Terre-Neuve et sur le nord des Grands Bancs de Terre-Neuve de 1991 à 1993. En 1994, la morue était fréquente dans les eaux du large de la plate-forme du nord-est de Terre-Neuve, mais très rare sur le nord des Grands Bancs de Terre-Neuve, tandis qu'une concentration distincte était observée dans le secteur sud de ces bancs. La classe d'âge de 1991 semblait faible, mais celle de 1994 relativement forte. L'abondance moyenne (10 000m^{-3}) était considérablement plus grande ($P<0,01$) en 1994, tant dans les eaux de la côte que dans celles du large, que les années précédentes. En 1992, elle été notablement plus grande dans le secteur côtier qu'en 1993 ($P<0,01$), tandis que dans les eaux du large elle était comparable à celle des années antérieures. L'aboutissement du frai (oeufs et larves ayant atteint le stade de juvéniles pélagiques) s'est produit relativement tard en 1992 et 1993 par rapport à 1994, où il était plus proche de la durée de frai moyenne historique. Des calculs rétrospectifs fondés sur la structure des micro-otolithes ont révélé que les larves sont arrivées à éclosion surtout en juillet et août en 1992 et en 1993, mais en juin en 1994. Du point de vue des statistiques, les taux de croissance étaient plus élevés en 1992 et 1993 (0,65 mm d-1) qu'en 1994 (0,48 mm d-1) ($P<0,015$). La baisse du taux de croissance en 1994 est peut-être due à une éclosion plus précoce dans les eaux plus froides en raison de la saison. On émet l'hypothèse que les différences observées dans les distributions, l'abondance et les périodes de frai peuvent être liées à des changements dans les conditions environnementales au printemps.

Introduction

The pelagic juvenile stage of cod occurs following the period of egg and larval drift, beginning with metamorphosis from the larval to juvenile stage at (approximately 20-25 mm total length, Fahey 1983) and ending with settlement to a demersal habitat. Sampling populations of pelagic juvenile cod can provide important measurements of cod population dynamics relating to stock structure, spawning times and survival. Geographic distributions of pelagic juvenile cod can delineate major nursery areas in relation to spawning populations (Riley and Parnell 1984, Sundby et al. 1989, Suthers and Frank 1989, Suthers and Sundby 1993). These distributions can vary significantly among years due to variations in ocean circulation affecting egg and larval drift which can significantly effect subsequent recruitment to the fishery in different stocks (Frank 1992, Schopka 1994, Polachek et al. 1992). Abundance estimates made during the pelagic juvenile stage of cod have demonstrated that it is often an early indication of subsequent recruitment to the spawning stock (Sundby et al. 1989, Campana et al. 1989, Assthorsson et al. 1994, Jakupsstovu and Reinert 1994). These studies have indicated that survival of a year-class is primarily determined during the egg and larval stages of cod. While measuring abundance during the pelagic juvenile stage can provide an early indication of recruitment, measuring biological characteristics of the pelagic juveniles, such as age, growth and condition, can provide important clues to causal factors influencing survival.

Historically cod have spawned throughout the offshore and inshore areas of Newfoundland and Labrador (Templeman 1981, 1989, Hutchings et al. 1994). However, the relative importance of inshore spawning, compared to offshore has not been determined (Halliday and Pinhorn 1990, Hutchings et al. 1994, Anderson et al. 1995). Modelling studies of egg and larval drift have demonstrated that eggs spawned on the shelf will remain largely on the shelf, although significantly downstream of their spawning sites (Helbig et al. 1992, Davidson and deYoung 1995). Some eggs and larvae may drift to the inshore but this is predicted to be of relatively minor importance except under specific conditions of wind forcing (op. cit.). These drift predictions have been corroborated by field observations of pelagic juveniles during the 1980's a period in which spawning cod were distributed throughout the area and pelagic juvenile cod were found distributed extensively offshore (Anderson et al. 1995). Pelagic juveniles which occurred inshore in the autumn may have accounted for less than ten percent of all eggs spawned (op. cit.).

It has been hypothesized that the northern cod spawning population may shift its distribution south in response to changing ocean climate, in particular cold temperatures (deYoung and Rose 1993). Such a shift would have a significant effect on the dispersal of eggs and larvae, which may be detrimental to survival (op. cit.). Similarly, when fish populations collapse due to overfishing there may be significant changes in both the spawning period and location where cod spawn. Under these circumstances we can expect a significant changes in the geographic distribution, abundance and age structure of pelagic juveniles.

The purpose of this study was to measure the geographic distributions and abundances of pelagic juvenile cod following the collapse of the northern cod stock in the early 1990's (Harris 1990, Bishop et al. 1993). Of particular interest were the locations of juvenile nursery areas and the evaluation of the relative contributions of inshore and offshore spawning components to these areas. In addition, we wanted to estimate the spawning periods and growth rates of the juvenile cod each year to evaluate relative differences among years. Such measurements will assist in the development of comprehensive pre-recuit indices critical to measurements of population growth during the period of recovery for the northern cod population.

Methods

The sampling program was designed as series of synoptic inshore/offshore surveys. During the first three years of the program, 1991-93, sampling was carried out using one ship targeting the inshore areas along the northeast coast of Newfoundland and the offshore area of the southern Northeast Newfoundland Shelf and northern part of the Grand Bank (Figure 1). Previous studies had indicated these areas would cover the primary geographic distribution of pelagic juvenile cod (Helbig et al. 1992, Davidson and deYoung 1995, Anderson et al. 1995). Surveys were carried out from late September to the middle of October (Table 1), to precede the main period of settlement of the pelagic juvenile stage of cod. Settlement is thought to occur at approximately 60-80 mm length (Perry and Neilson 1988, Godo et al. 1989) and primarily from late October through November (Anderson and Dalley 1993, Methven and Bajdik 1994), although cod may settle earlier at smaller lengths in coastal habitats (Olsen and Soldal 1989, Methven and Bajdik 1994). In 1994 the survey was expanded to cover the entire area from Labrador to the southern tip of the Grand Bank using two ships simultaneously (NAFO Divisions 2J3KLNO, Figure 1). The change to a broader survey area was to cover the entire geographic range of pelagic cod, which was not being adequately sampled by the single ship surveys. The shift to an earlier time in 1994 was to minimize any bias due to possible early settlement in some years. However, there was no indication that substantial settlement of juvenile cod had occurred prior to the 1991-93 surveys (Anderson and Dalley 1993).

A survey grid at 54 km (30 nautical mile) station spacing was used. This design is equivalent to a systematic stratified sampling design, where the first station is selected randomly from within a 54x54 km stratum with subsequent stations spaced systematically at 54 km (Snedcor and Cochrane 1967). Within the inshore bays stations were positioned to lie approximately 30 nautical miles apart along a line running through the centre of each bay at maintain a comparable sampling effort over space within the inshore areas to that offshore. When a line of stations within a bay was not possible, such as Notre Dame Bay and Bonavista Bay, then an approximate 54 km spacing was systematically chosen spread within each bay.

Two trawls were used during these surveys, a 4.5 m^2 Tucker trawl (Harding et al. 1987) and the International Young Gadoids Pelagic Trawl (IGYPT) (Koeller and

Carrothers 1981, Koeller et al. 1986). In 1991 the survey was carried out using the Tucker trawl. In 1992 both Tucker and IGYPT trawls were used but both trawls were not used at each station. In 1993 and 1994 only the IGYPT trawl was used. The Tucker trawl was towed at 1.25-1.5 m s^{-1} using a double oblique haul 0-100 m . The mesh size was 3.2 mm in the main portion of the net, while the cod end was 0.505 mm Nitex netting. The Tucker trawl was instrumented to transmit data in real time, including electronic flowmeters, net angle and a CTD. The IGYPT trawl is a 10x10 m pelagic mid-water trawl designed to catch pelagic juvenile cod. In the 1992-93 surveys it was towed at 1.25-1.5 m s^{-1} for 30 minutes with the head rope positioned at approximately 50-60 m depth. In 1994 the IGYPT trawl was towed between 20-50 m depth. Depth and net configuration were monitored in real time using acoustic net sensors (Scanmar) to measure net depth, net opening, wing and door widths. For both trawls, the net performance data were used to estimate the volume of water (m^3) filtered during the tow.

Due to logistical problems the IYGPT and Tucker trawls were not used at all stations in 1992. A comparison of the standardized catch rates (number of cod m^{-3}) for stations sampled by both trawls demonstrated higher values for the Tucker trawl (Anderson and Dalley 1993). Based on this comparison, the standardized catch rates of the Tucker trawl were multiplied by a factor of 0.27 for direct comparisons to IGYPT trawl data.

The trawl catches were processed at sea identifying all fish to species level where possible and recording total length for Atlantic cod. Atlantic cod were preserved in 95% ethanol and returned to the laboratory where the otoliths (sagittae and lapillae) were removed and mounted. Lapillae were polished and aged under a light microscope with the assistance of an image analysis system. Samples for otolith age analyses were stratified across all length groups and for different geographic areas.

Comparison between means was based on the t-test, where the approximate *t*-statistic for unequal variances was used if the folded F statistic demonstrated the variances between data sets were unequal (SAS 1988). Distributions were contoured based on spatial interpolation of abundances ($\log_{10}$ number 10,000m^{-3}) using the kriging technique (Keckler 1994).

Results

Distributions and Abundances

The pattern of distributions observed during the four years, 1991-94, indicated a trend of expanding spatial distribution, both within the inshore areas and extending to the shelf areas offshore (Figure 3). In 1991 pelagic juvenile cod were caught only at a few locations inshore and none were observed offshore. In 1992 cod were distributed throughout most of the inshore areas and on adjacent shelf areas while a few cod were observed on the northern Grand Bank. By 1993 cod were again distributed widely within the inshore areas and on the adjacent shelf. However, they were also distributed more widely on the northern Grand Bank than in 1992.

No cod were caught on the the southern portion of the Northeast Newfoundland Shelf sampled in the vicinity of Funk Island Bank during the first three years of this study. In 1994 cod were distributed throughout the inshore areas but were also observed over most of the sampled area of the Northeast Newfoundland Shelf, extending as far north as southern Labrador and over sampled portions of Belle Isle Bank and Funk Island Bank. The greater offshore distribution on the Northeast Newfoundland Shelf in 1994 was evident when comparing 1994 stations in this area with corresponding ones from 1993. Few cod were caught on the northern Grand Bank in 1994, although a distinct concentration was sampled on the southern Grand Bank.

Comparison of abundances among years is confounded by the different gears used and the different extent of offshore sampling each year. In 1991, only the Tucker trawl was used and the number of cod captured was very low; only 15 cod were captured at 13 of 55 locations sampled. In 1992, both the Tucker and IGYPT trawls were used, but both trawls were not used at each location. The very low abundance of cod sampled in 1991 is reinforced when comparing catches in the Tucker trawl at the same locations sampled in 1992 where, on average, five times more cod were caught. Abundances (excluding zero catches) in the IGYPT trawl averaged 1.9 (range 0.4-1.9) cod 10,000m^{-3} in 1992, 0.8 (range 0.5-3.8) cod 10,000m^{-3} in 1993 and 6.3 (range 0.5-85.7) cod 10,000m^{-3} in 1994.

It is possible to compare mean abundances from the IGYPT trawl within inshore and offshore areas from sample locations common between years (including zero catches). Mean abundance was highest in 1994, both inshore and offshore, and lowest in 1993 (Table 2). It is noteworthy that the maximum abundance sampled inshore in 1994 was almost an order of magnitude greater than in either 1992 or 1993, and offshore it was approximately three times greater. Comparison of abundances for commonly sampled inshore areas demonstrated that cod were significantly more abundant in 1994 and were lowest in abundance in 1993 (Table 3). Offshore cod were more abundant in 1994 while there was no statistical difference in abundance between 1992 and 1993 (Table 3). These statistical differences, combined with the apparent broad offshore distribution of cod in 1994, indicate that 1994 was a relatively large year-class compared to the previous three years. In contrast, year-class strength in 1991 appeared to be extremely low. While mean abundances were higher inshore in 1992 than 1993, the broader distribution of cod offshore over the northern Grand Bank in 1993 may sum into a greater total number of cod offshore than in 1992.

Lengths

The length ranges of cod sampled each year were similar, although there were notable differences in the modes. In 1991 cod ranged in length from 38 to 81 mm length, although there were too few cod caught to determine any length frequency modes (Figure 4). In 1992 cod ranged in length from 32 to 72 mm with a single mode centered at 46 mm. In 1993 there was a broader range of lengths sampled, from 26 to 88 mm with a dominant mode at centered 45 mm and a second mode centered at 65-66 mm. In 1994 there was again a single mode with a peak at 45 mm and lengths ranging from 30 to 73 mm.

Given the broad geographic area sampled in 1994, we examined lengths among the different areas in which cod were found. Cod ranged primarily between 31 and 64 mm length in all areas with no apparent differences among areas. Inshore, cod averaged 43.4 to 46.7 mm (range 31-60 mm) length among all bays except Conception Bay. In Conception Bay only five cod were caught and two of these cod were 93 and 101 mm length while the smallest cod was 40 mm. Cod off southern Labrador averaged 43.2 mm length (range 33-56 mm) and on the Northeast Newfoundland Shelf averaged 43.2 mm length (range 32-58 mm) while on the southern Grand Bank cod averaged 49.6 (range 35-88) mm length. While the mean value on the southern Grand Bank was slightly greater, it was inflated by by two fish of 73 and 87 mm length. The majority of fish measured on the southern Grand Bank ranged between 35-64 mm length.

Age and Hatch Dates

Cod averaged 67 days of age in 1992, 69 days in 1993 and 80 days in 1994. The small number of fish captured and the poor quality of otoliths in 1991 precluded any ageing from these samples. Based on ages and the known date of capture, the hatch date of fall survivors in 1992 ranged from the middle of July to the middle of August with a peak during the first two weeks of August (Figure 5). Hatching occurred from the end of June to the latter half of August in 1993, with two distinct modes. One mode occurred during the first two weeks of August and the second occurred during the middle of July. In 1994 hatching occurred significantly earlier than in 1992 and 1993, extending from the middle of May to the first of July and was highest throughout June.

Adjusted Lengths

Growth rate averaged 0.65 mm d^{-1} in 1992, 0.65 mm d^{-1} in 1993 and 0.48 mm d^{-1} in 1994 (Table 4). Comparison of slopes demonstrated no statistical difference in growth rate between 1992 and 1993, but that growth rate was significantly slower in 1994 than in either 1992 or 1993 (Table 4). There was no statistical difference in intercepts between 1992 and 1993 (Table 5).

Based on the measured growth rates, the length frequencies of data collected in 1992-94 were adjusted to match the mid-date (14 September) of a survey carried out in 1981 (Anderson et al. 1995). This adjustment allowed for a direct comparison of cod lengths from the 1990's to the only historical data available from the offshore region. Compared to the length frequency distribution sampled in 1981, cod collected during 1991-94 fell within the historically sampled length range, from approximately 15 to 70 mm (Figure 6). Lengths sampled in 1992 match the length frequencies associated with the smallest fish sampled in 1981, which equate to those fish which spawned latest in the season. In 1993 the cod lengths compared with the historic distribution of 1981, although the dominant peak in 1993 matched that observed for the late spawning period in 1981. In 1994 the length frequency distribution matched the largest fish sampled in 1981 and, therefore, cod which spawned earliest in the season.

Discussion

Year-Class Strength

Year-class strength is routinely measured during the pelagic juvenile stage for a number of cod stocks in the North Atlantic, and in each case the abundance indices have been related to recruitment measured at older ages (Sundby et al. 1989, Assthorsson et al. 1994, Jakupsstovu and Reinert 1994). However, in some cases high year-class strength measured during the pelagic juvenile stage does not result in high recruitment, apparently due to density dependent predation occurring after settlement (Bogstad et al. 1994). For the northern cod stock (NAFO 2J3KL) we expect that abundance measured during the pelagic juvenile stage will also measure year-class strength in most years. Further, we propose that there are three important measurements required to index year-class strength during the pelagic juvenile stage: abundance, size and distribution. High abundance will indicate relatively high survival from spawning, and may be linked to spawning stock biomass (Myers et al. 1993, Bogstad et al. 1994). Relatively large sizes following the pelagic period may result in higher survival during the first year of life, both in relation to size dependent predation (Ware 1975) and better condition for survival during the first winter (eg. McLean et al. 1981). Finally, spawning distributions relative to dispersal of cod eggs and larvae have been hypothesized as important to survival and recruitment in the northern cod (deYoung and Rose 1993). Specifically, spawning off southern Labrador is thought to be an important requirement for high recruitment in northern cod (op. cit.).

The results from this study indicate a trend of increasing year-class strength among four years, 1991-1994. The extremely low abundances and limited distribution of cod in 1991 indicated that year-class abundance was weak. In contrast, year-class strength in 1994 was significantly stronger than the preceding three years, both inshore and offshore. In addition, cod were observed distributed widely over the northern part of the Northeast Newfoundland Shelf, demonstrating that significant spawning occurred off southern Labrador in 1994. While the northern part of the Northeast Newfoundland Shelf was not as extensively sampled in the previous three years, comparison to the northern most stations sampled in 1993 indicated that juvenile cod were not broadly distributed over the shelf, compared to 1994. Finally, cod in 1994 exhibited a larger adjusted size than in 1992 or 1993 (Figure 6). Although growth rate was lower in 1994 than either 1992 or 1993, juvenile cod in 1994 would still have been larger by mid-November. Together, the greater abundance, larger size and broad distribution over the Northeast Newfoundland Shelf in 1994 indicate that eventual recruitment may be greater than the previous three years.

It is difficult to compare abundances sampled in 1994 to those measured in 1981 (Anderson et al. 1995) due to differences in sampling gear and methods. However, several factors indicate the abundance of pelagic juvenile cod sampled in 1981 was much larger. Cod were distributed throughout the southern part of the Northeast Newfoundland Shelf and northern Grand Bank sampled in 1981 (op. cit.), whereas cod were not observed abundantly over the same area in 1994. In addition, there was a much broader range of lengths sampled in 1981, indicating a longer spawning period which would originate from a larger spawning stock and age structure (Taggart et al. 1994). Finally, 1981 was one of the largest year-classes produced during the 1980's (Bishop et al. 1993).

Strength of the 1992 and 1993 year-classes may not have been significantly different. Although mean abundance in 1992 was greater inshore than 1993, there was no statistical difference offshore, whereas the broader distribution in 1993 would integrate into a greater abundance. In addition, the presence of larger, older cod in 1993 would equate to more fish than in 1992 as a result of a greater cumulative mortality since hatching. Based on these considerations, we nominally rank year-class strength as $1994>1992\leq1993>1991$. The high ranking of the 1994 year-class and the low ranking of the 1991 year-class agrees with estimates from bottom trawl surveys for these four years (Dalley and Anderson, submitted) and from an index of year-class strength from beach seine surveys (Ings et al., submitted).

Spawning Periods

Pelagic juveniles represent the survivors of spring spawning. When abundances, distributions, sizes and ages vary among years, it is difficult to distinguish between interannual differences in the spawning period of adults versus differential survival during the egg and larval period, based on a single survey. However, there is evidence that both factors may have been important in effecting differences observed in the pelagic juvenile cod during the period 1991-94.

In 1991 the broad distribution of lengths from 38 to 82 mm suggests that spawning may have occurred throughout an extended period in the spring. However, the low abundances restricted to a few locations inshore indicate that the spawning was largely unsuccessful.

In 1992 there was one dominant mode in the length frequency distribution, demonstrating there was a single successful spawning period which occurred relatively late in the season. Furthermore, in 1993 the larger length and age frequency distributions indicated successful spawning occurred through a longer period in spring. However, in 1993 the predominant period of successful spawning appeared to have occurred relatively late in the season, while in 1981 spawning would have occurred throughout the spring with a peak in April-May (Anderson et al. 1995). If the spawning period was comparable in 1992 and 1993 then the length frequencies suggest differential survival, where survival was greater earlier in the year in 1993.

Unfortunately, there are no direct observations on spawning and, therefore, it is also possible that adults simply spawned over a longer period of time in 1993 than in 1992.

In 1994 there was again a single period of successful spawning, although this occurred much earlier. Assuming egg development times of 25-30 days (Anderson and deYoung 1995), then spawning appeared to have occurred primarily in April-May. This period coincides with the primary peak estimated for 1981 (Anderson et al. 1995). The earlier spawning period of the pelagic juvenile cod in 1994 appears to have resulted from a significant shift in spawning to an earlier time (April-May) and not from differential survival; there was no evidence of late spawning (June-July) in 1994 as occurred in 1992 and 1993, based on bongo samples collected throughout the pelagic juvenile survey (J. Anderson, unpub. data). A significant shift in spawning time contrasts with a stable spawning period which only varied by a few days, and hatching which only varied by two weeks, over many years for the Arcto-Norwegian cod stock (Ellertsen et al. 1989). However, a contracted spawning period is consistent with the collapsed age structure of this stock (Taggart et al. 1994). A shift in spawning time may be an adaptive strategy for a small population of cod with a reduced age structure, when spawning conditions change among years. Spawning in 1994 coincided with the historical median period of spawning for the Northeast Newfoundland Shelf (Myers et al. 1993), whereas in 1992 and 1993 it coincided with the latest period of spawning recorded for the northern Grand Bank. Was there evidence of changing ocean environmental conditions among the four years of this study?

A dominant feature in spring off the coasts of Newfoundland and Labrador is the presence of sea ice (Cote 1989). The extent and duration of this sea ice varies significantly among years (Colbourne et al. 1994). Extensive ice coverage in the spring will significantly reduce the amount of light energy reaching surface waters, and will delay both the seasonal heating cycle and the onset of primary production. During the four years of this study, the annual ice coverage varied significantly. In 1991 there was an extensive ice cover which occurred near the extreme southern and eastern limit of the historic distribution throughout spring and early summer, and has been described as the most extensive in 30 years (Colbourne et al. 1994). In 1992 and 1993 ice cover was again significantly above the longterm median, but less severe than 1991 (Colbourne 1993). In contrast, 1994 ice cover from April onwards was much less than 1991-93 (Colbourne and Narayanan 1994). From March 1994 onwards the maximum extent of the ice edge along the inner shelf approximated the longterm median. Offshore the maximum extent exceeded the median but was substantially less than in 1993.

Interannual variations in the occurrence of sea ice off the coasts of Newfoundland and Labrador coincides with variations in the abundance, distribution and spawning period of pelagic juvenile cod sampled each year. When ice coverage was extensive and extended onto the northern Grand Bank late into spring, the cod were distributed primarily within the inshore area and the period of successful spawning was relatively late in the season. However in 1994, when ice conditions were closer to the longterm median, pelagic juvenile cod were found extensively over the Northeast Newfoundland Shelf in relatively high abundance from an earlier spawning period. We attribute the lower average growth rates in 1994 to an earlier spawning in seasonally colder waters than occurred in 1992 and 1993.

Together, these observations suggest a mechanism whereby spring production of plankton is delayed by the extensive presence of sea ice into late spring, and in association with cold water temperatures. A delay in the onset of spring production would have a significant effect on the survival of cod larvae if they were spawned and hatched too early to feed on nauplii. Delayed onset of spawning of cod on the northern Grand Bank in association with cold water temperatures is consistent with this hypothesis (Hutchings and Myers 1994). In addition, if extensive ice and cold water conditions in the spring effected a southern distribution of spawning cod, as hypothesized by deYoung and Rose (1993), then we would have expected few pelagic juvenile cod to have occurred offshore on the Northeast Newfoundland Shelf and northern Grand Bank during 1991-93, as observed.

Inshore vs Offshore Spawning

Historically the primary spawning areas of the northern cod stock were reported to occur along the shelfbreak in association with the major offshore banks (Serebryakov 1967, Templeman 1981, deYoung and Rose 1993). However, the existence of local populations of cod within the inshore areas was recognized in early attempts to define management units for cod in the Newfoundland and Labrador region (Halliday and Pinhorn 1990). Recently, Hutchings et al. (1994) reported the occurrence of inshore spawning and that it may have represented a significant component of spawning historically. Comprehensive studies of spawning by northern cod have been hampered by the seasonal occurrence of sea ice (Cote 1989) which typically occurs throughout much of the geographical range of northern cod during the spawning season.

The early life history of northern cod was first described as spawning which occurred primarily offshore followed by drift of eggs and larvae to the inshore where they settled to the bottom as juveniles, cod eventually returning to the offshore areas as older juveniles (Templeman 1981, Lear and Green 1984). However, this simple description is not supported by models of egg and larval drift nor by historical data on pelagic juvenile cod. Existing models of egg and larval drift predict that cod eggs spawned offshore will largely remain offshore (Helbig et al. 1992, Davidson and deYoung 1995). While some eggs and larvae spawned to the north on the inner shelf may drift inshore (Davidson and deYoung 1995), a significant inshore drift could only occur under specific conditions of meteorological forcing (Helbig et al. 1992). These models are supported by surface drogued drifters, none of which have entered the inshore bays from the offshore shelves (Myers et al. 199?, Pepin and Helbig submitted). Predictions by these models are supported by historical data which demonstrated that historically pelagic juvenile cod were widely dispersed over the Northeast Newfoundland Shelf and northern Grand Bank several months after spawning (Anderson et al. 1995). A circulation model predicts that larvae which occur near the head of Conception Bay would be dispersed within approximately 30 days, or less (deYoung et al. 1994). This prediction is confirmed by observations of capelin which spawn on beaches within the bays along the coast of Newfoundland, where larvae were found widely dispersed offshore within a few weeks of release during 1991-94 (J. Anderson, unpubl. data). The dispersal of larval capelin from the bays does not support the conceptual model of large-scale transport of cod eggs and larvae from the offshore to the inshore bays.

The patterns of distribution observed for pelagic juvenile cod in this study, following the period of egg and larval drift, indicate that significant spawning did not occur offshore in 1991-1993. Only in 1994 were cod observed abundantly over the Northeast Newfoundland Shelf, indicating a significant spawning occurred off southern Labrador. While sampling did not extend as far north in 1991-93 as in 1994, the absence of pelagic juvenile cod in offshore samples during these three years indicates any spawning which may have occurred offshore occurred far to the north. However, successful spawning apparently did occur throughout the inshore areas in 1992-94. Highest abundances occurred within the bays and decreased onto the adjacent shelf areas. These distributions are consistent with spawning occurring primarily inshore within the bays and gradual dispersal of eggs and larvae to the offshore, as predicted by deYoung et al. (1994). While some of the juvenile cod observed inshore may have originated from spawning offshore, this contribution is expected to be small based on modelled predictions of dispersal, the apparent low abundance of adult cod offshore (Bishop et al. 1993) and the offshore distribution of pelagic juvenile cod observed in 1994.

The discrete distribution of pelagic juvenile cod sampled on the southern Grand Bank in 1994 is consistent with a distinct spawning, with retention of eggs and larvae, on the southern Grand Bank. The observed pattern of distribution is similar to that sampled for capelin larvae (Frank and Carscadden 1989) and flatfish larvae and juveniles (Walsh 1991, Frank et al. 1992) which spawn as separate populations on the southern Grand Banks.

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Table 1. Summary of pelagic juvenile cod survey dates and sampling each year 1991-94.

Year	Start Date	End Date	Total Days	Survey Mid-date	Locations Sampled Tucker	Locations Sampled IYGPT
1991	11 October	22 October	12	289	57	
1992	30 September	15 October	16	281	35	32
1993	27 September	20 October	24	281		87
1994	22 August	3 September	13	239		99

Table 2. Mean and maximum abundances (number 10,000m^{-3}) of pelagic juvenile cod caught by the IYGPT trawl within common inshore and offshore locations sampled each year. Means include null catches.

Year	Inshore			Offshore		
	n	Mean	Maximum	n	Mean	Maximum
1992	18	1.066	1.160	15	1.025	1.116
1993	26	1.047	1.126	50	1.017	1.109
1994	23	1.506	9.569	76	1.138	3.378

Table 3. Statistical comparisons between mean abundances ($\log_{10}$ number $10{,}000m^{-3}$) sampled within inshore and offshore locations each year. *t* - refers to the t test statistic; *df* - refers to degress of freedom; *P* - refers to the probability that the means are statistically equivalent.

Comparison	Inshore			Offshore		
	df	*t*	*P*	*df*	*t*	*P*
1992-1993	42	1.8024	0.0787	63	0.9653	0.3381
1992-1994	22.3	-3.3271	0.0030	85	-3.3283	0.0013
1993-1994	22.1	-3.5095	0.0020	77.3	-3.7055	0.0004

Table 4. Average growth rate estimated each year based on linear regressions of age (d) on fish length (mm).

Year	Regression	df	F Value	R^2 (%)
1992	Length $= -0.46 + 0.648$ Age	102	111.18	51.9
1993	Length $= -0.11 + 0.645$ Age	90	245.65	73.1
1994	Length $= +6.86 + 0.476$ Age	100	81.24	45.1

Table 5. Statistical comparison of growth rates among years for all data where age was ≤ 80 days. P Level, refers to the probability of obtaining a greater F value. NA, refers to the test not being applicable.

Years	df	Test	Slopes	Test	Intercepts
		F Value	P Level	F Value	P Level
1992-1993	164	1.26	0.2629	0.05	0.8161
1992-1994	203	4.53	0.0001	NA	NA
1993-1994	191	6.14	0.0141	NA	NA

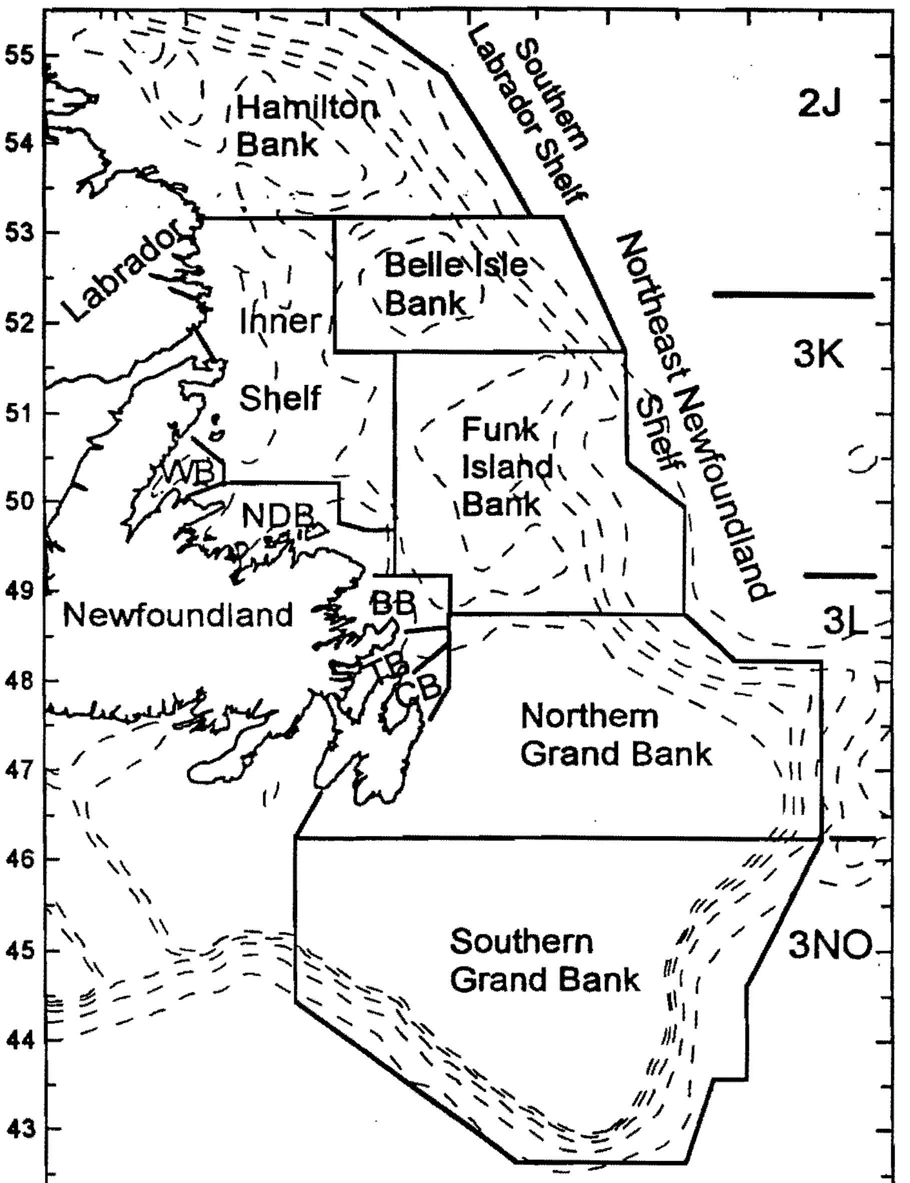

Figure 1. Geographical areas of the southern Labrador Shelf, Northeast Newfoundland Shelf, Grand Banks and inshore bays located along the northeast coast of Newfoundland sampled in this study. WB - White Bay, NDB - Notre Dame Bay, BB - Bonavista Bay, TB - Trinity Bay, CB - Conception Bay.

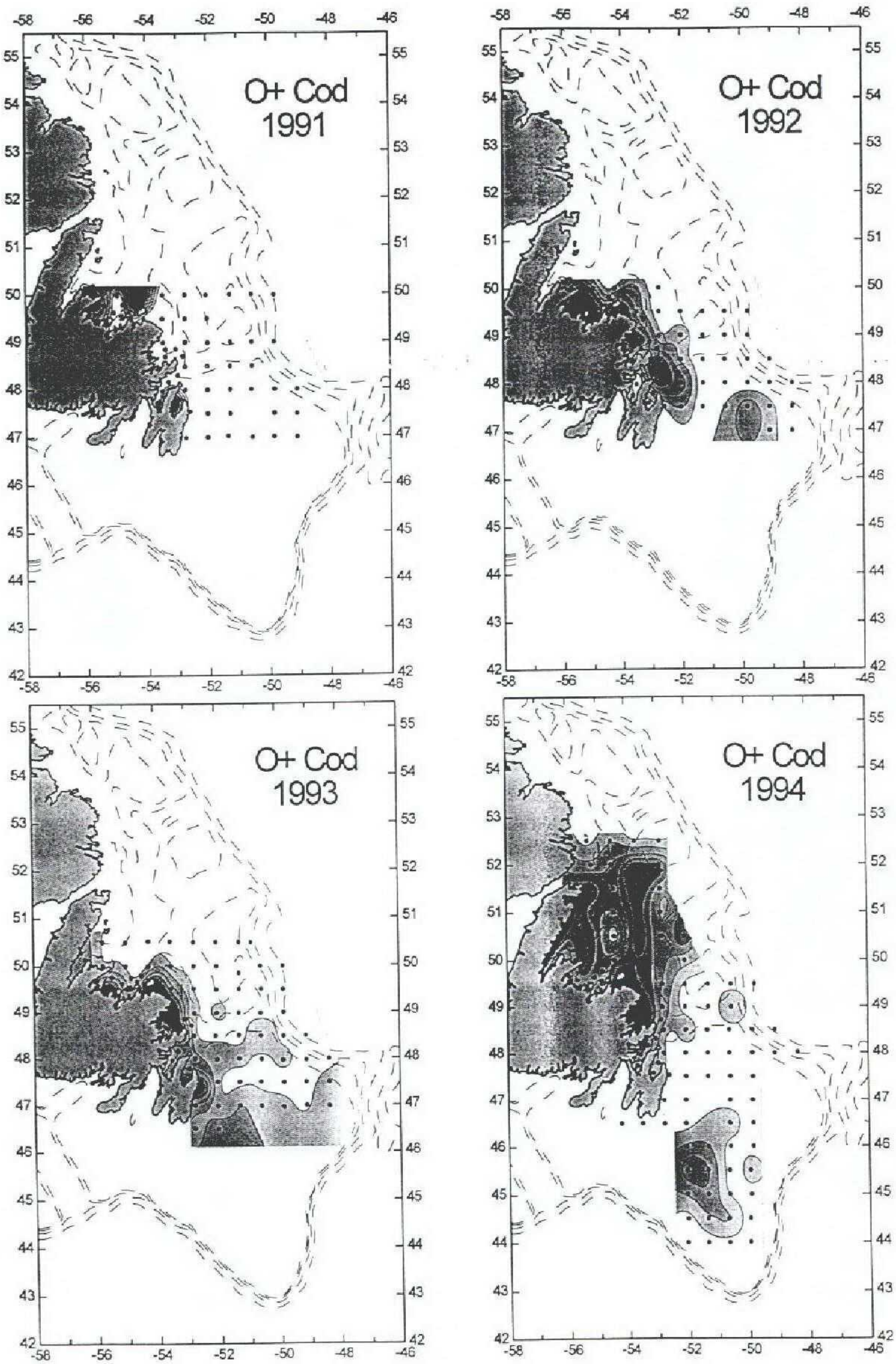

Figure 2. Distributions of pelagic juvenile cod sampled 1991-94. Each year the distributions are contoured based on the abundance ($\log_{10}$ number $10{,}000m^{-3}$), scaled from highest to lowest within each year.

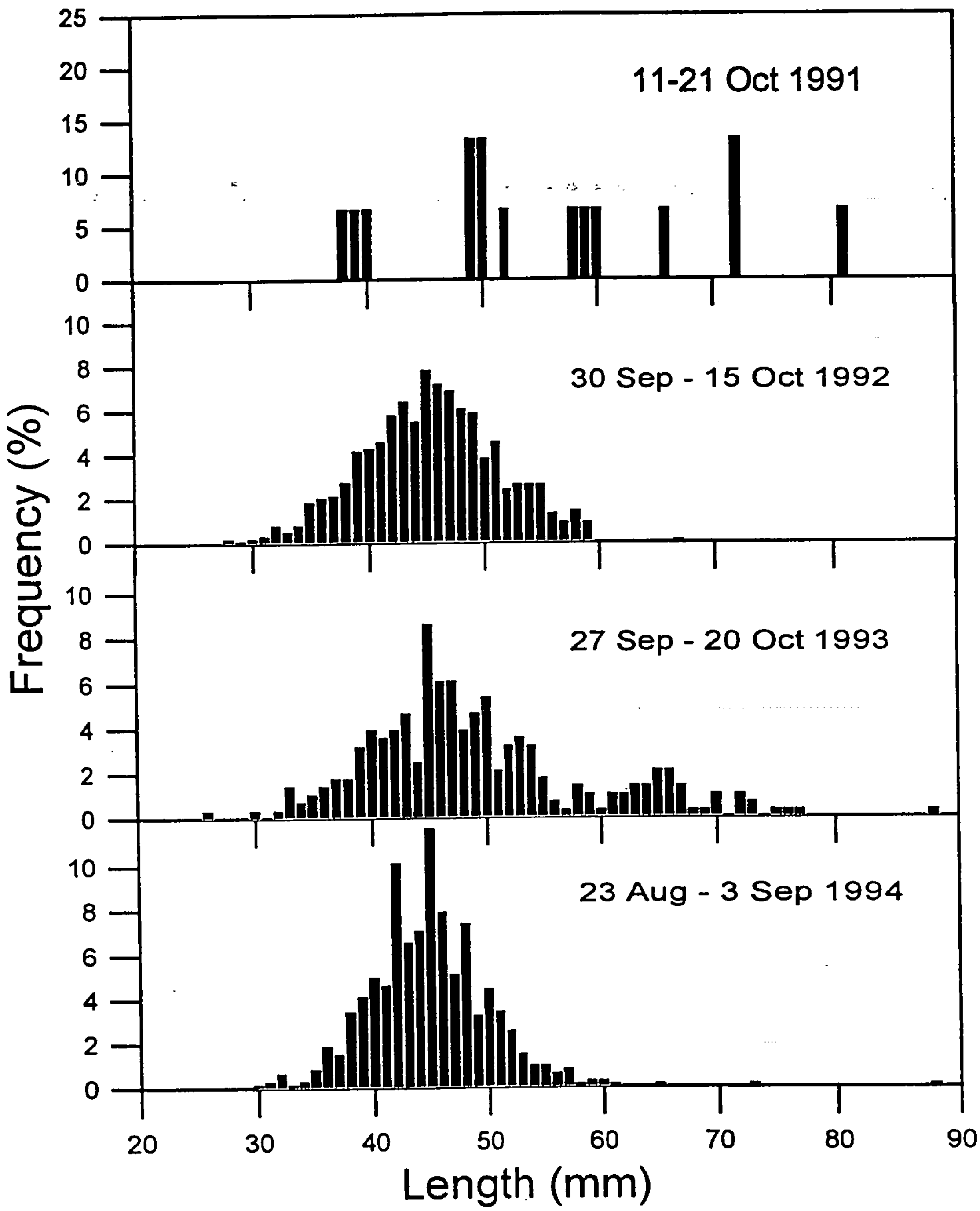

Figure 3. Length frequency distributions (%) sampled each year.

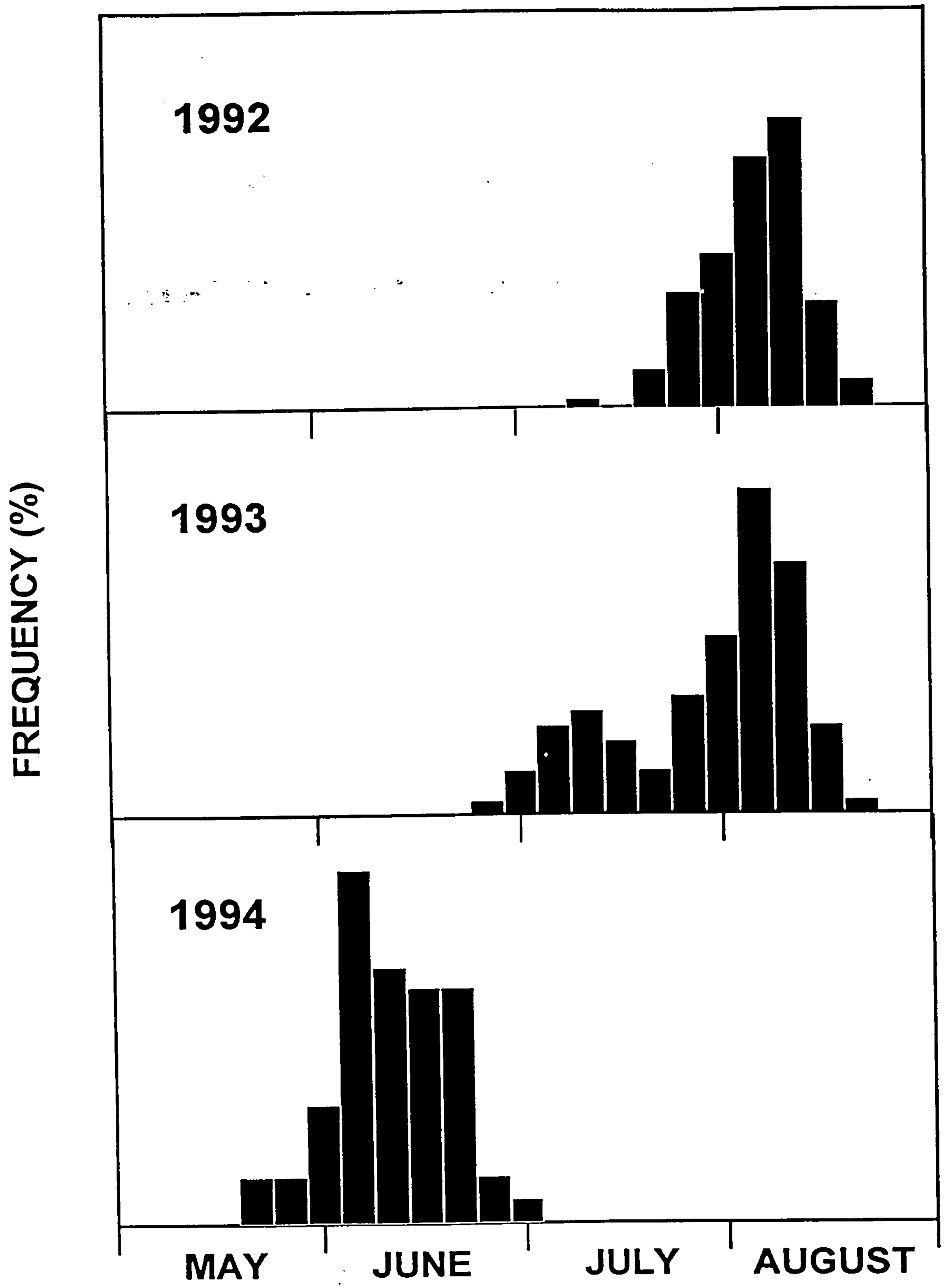

Figure 4. Larval hatch dates estimated from micro-otolith based ages sampled each year, for five day periods.

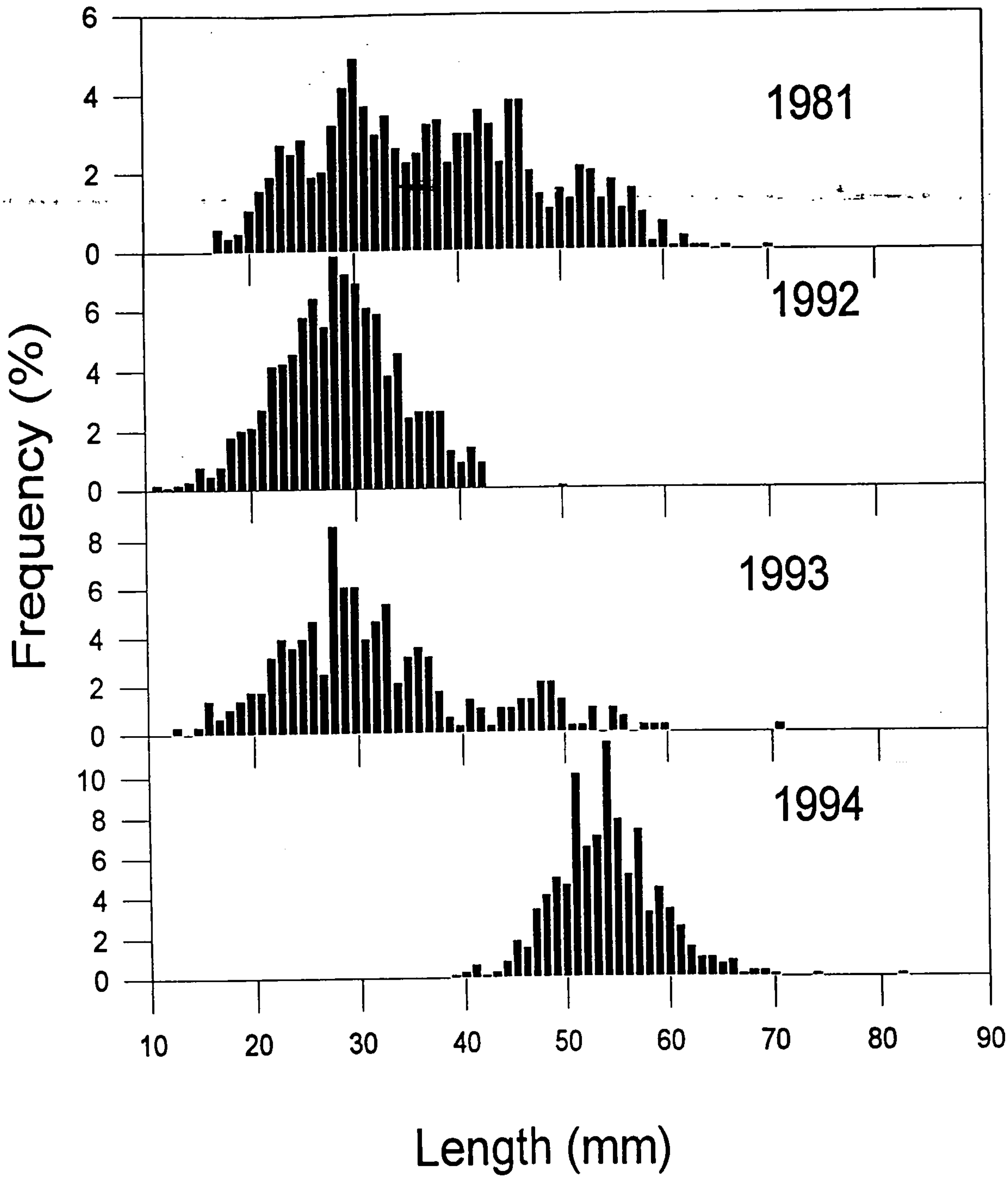

Figure 5. Length frequency distributions adjusted to a common date in September based on measured growth rates in 1992-94, compared to the historic length frequency distribution sampled during September 1981.