HATCH DATE AND 0-GROUP GROWTH RATE COMPARISONS FOR COD (Gadus morhua) IN NEWFOUNDLAND WATERS: SUPPORT FOR THE MATCH HYPOTHESIS

DAVID L. PINSENT

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HATCH DATE AND 0-GROUP GROWTH RATE COMPARISONS FOR COD (*Gadus morhua*) IN NEWFOUNDLAND WATERS: SUPPORT FOR THE MATCH HYPOTHESIS

by

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ABSTRACT

Lapillus otoliths of 0-group cod (*Gadus morhua*) were used to determine the day of hatching and length at age of individuals collected along the northeast coast of Newfoundland and on the southern Grand Bank in 1989 and 1991. Spatial pattern in the distribution of hatch dates was examined for latitudinal trends analogous to those of the spawning times in the area. Length at age analysis allowed the identification of specific areas and times where 0-group growth was greatest.

Geographic distribution of cod hatching dates is neither consistently synchronous nor sequential in Newfoundland waters. A homogeneous pattern of hatch date distributions existed from the northeast coast of Newfoundland to southern Grand Bank in 1989, a year with average spring and summer water temperatures. In contrast, hatching dates during 1991, a year with below average spring and summer temperatures, exhibited a latitudinal progression from south to north. Hatching in the early part of a site-specific distribution resulted in first-feeding-larvae emerging at the onset of *Calanus* peak abundance. These larvae were characterized by a prolonged period of relatively slow growth. Those which began feeding later maintained rapid instantaneous growth for a short period. The result was that slower-growing, "early" larvae were actually larger than faster growing, "later" feeding larvae, by the end of their first year. Consequently, those that hatch early achieve a larger size at the end of one year.

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This work is dedicated to my grandfathers,
the late Albert Pinsent of New Harbour
and Edward Follett of Grand Bank,
both skilled sport
fishermen. They
thaught me at a young
age that eating fish
was good for your
health, but the
opportunity
to go
fishing was
just as good.

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Chapter 1

INTRODUCTION

1.1 - Overview

The success of a year class can depend largely on the number of fish that survive their first year of life (Hjort 1914; Pennington 1979; Houde 1987; Bradford 1992). Understanding how the biotic and abiotic conditions are associated with survival of the 0-group may improve estimates of year class strength. These conditions can be parameterized if the precise timing of a specific event, such as the hatching period, is identified. The hatching date may be especially useful because, when combined with water temperature, critical events such as the time of first feeding and spawning time are easily calculated. Growth of the 0-group may also play an important role in determining year class strength because mortality decreases as size increases (Peterson and Wroblewski 1984; McGurk 1986; Houde 1987; Pepin 1991). Both survival and growth of fish larvae have been correlated with food quality and quantity (Lasker 1975; Lasker and Zweifel 1978), especially at the time of first feeding (Frank and Leggett 1986).

Previous efforts to identify the hatch dates of Atlantic cod *(Gadus morhua)* in Newfoundland waters have been inferred from work on adults. Egg hatching times have been estimated by shifting the entire spawning date distribution forward. Myers *et al.* (1994a) calculated hatch date distributions to test whether first feeding larval abundance coincided with peak *Calanus* nauplii abundance. Templeman's (1981) estimates of hatching times defined a segment of the sequence in the egg and larval distribution pattern around Newfoundland. Also primarily inferred from work with adult cod is the latitudinal cline of 0-group size at age. The age-specific size of adult cod is known to increase from Labrador to the southern Grand Bank (Fleming 1960; May *et al.* 1965). There is little information on the geographic trends of 0-group growth, but previous inferences of increasing size from north to south have some empirical foundation (Templeman 1966: p52).

Because there is little relevant empirical data for 0-group cod in Newfoundland waters, I begin with a review of the peak spawning times and locations believed to be applicable in this study. The dispersion patterns of eggs and larvae are then applied to determine the spatial or temporal origins of post-larval samples (Templeman 1981; Lear and Wells 1984). Egg and larval transport in coastal and offshore waters around Newfoundland is reviewed accordingly. Finally, background on growth throughout the early life history of cod is given as a basis for discerning the significance and possible source of any variability between collections.

1.2 - Spawning; Spatial and Temporal Considerations

1.2.1 - Spawning Areas

In a summary of previous literature, Templeman (1981) defines the upper continental slope off Labrador as the major spawning ground for what he terms the Labrador-East Newfoundland stock (2GHJ and 3KL, see Figure 1.1). In addition, the eastern edges of the Belle Isle and Funk Island Banks on the Northeastern Newfoundland Shelf are identified as major spawning grounds for this stock. This widely accepted and established view of the most productive spawning locations for cod around Newfoundland and Labrador has been challenged recently. Hutchings *et al.* (1993), in a comprehensive examination of research trawl data from 1946-1992, show that the slope and banks of the continental shelf are not the primary location for cod spawning, and instead:

> "the relative abundance of spawning individuals on the shelf is highest: (i) off northeast Newfoundland, (ii) within 100km of the Newfoundland coast from Cape Freels to Cape Race, (iii) on the central Grand Bank, and (iv) on the St. Pierre Bank. Slope spawning is largely restricted to the eastern slope of Hamilton Bank and Funk Island Bank."

Also in contrast to previous reports is the identification of the central Grand Bank as the primary area of spawning on the Grand Banks. Helbig *et al.* (1992) and Templeman

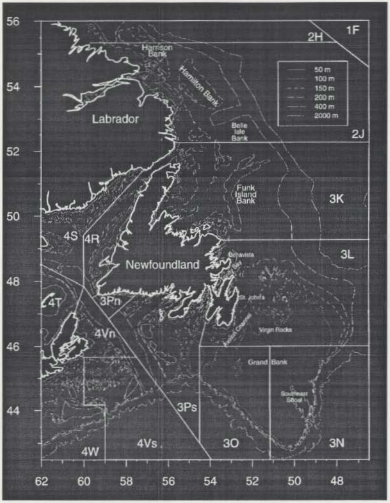

Figure 1.1 Map of bays, banks and NAFO Divisions mentioned throughout the text.

(1981) reason from Serebryakov's (1968) egg and yearling surveys that the principal spawning grounds are the Southeast Shoal, as well as the eastern and southern flanks of the Bank. However, as it tracks the continental slope, the Labrador Current passes over these areas making it possible for Serebryakov's samples to have originated from areas north of the southern Grand Bank. In brief, cod spawning has been shown to occur over a wide spatial range in the Newfoundland region, throughout the shelf and along the slope, as well as areas close inshore (Hutchings *et al.* 1993). While there is no particular or select spawning ground for cod, the existence of stock-specific spawning sites cannot be ruled out.

1.2.2 - Spawning Times

The spawning times of cod off Newfoundland and Labrador were recently reviewed by Myers *et al.* (1994a). Spawning data spanning 45 years were analyzed to show that mean spawning times were progressively later moving from northern Labrador to northern Grand Bank. Spawning on the southern Grand Bank may either coincide with or occur earlier than that on the northern portion of the bank. Templeman (1981) described similar patterns but in more qualitative terms (Table 1.1).

Table 1.1 - Spawning times of cod in the Newfoundland region. Spawning dates are presented as ranges or as means with one standard deviation.

AREA	SPAWNING TIME
2GHJ slope	mainly March-April [a]
2GH	April 6 ± 29 [b]
Hamilton Bank	April 7 ± 20 [b]
Belle Isle Bank	April 20 ± 28 [b]
3K south to Funk Island Bank	mainly April-early May [a]
Funk Island Bank	May 18 ± 36 [b]
NE Grand Bank	mainly April - June [a]
northern Grand Bank	mainly April and May [c]
northern Grand Bank (3L)	June 9 ± 37 [b]
northern Grand Bank	June 6 ± 18 [d]
southern Grand Bank	later half of April-early June [a]
southern Grand Bank	last half of May [c]
southern Grand Bank (3N and O)	May 13 ± 28 and 17 ± 41 [b]
southern Grand Bank	May 19 ± 17 [d]

Source

a Templeman, 1981
b Myers *et al.*, 1994a
c Fitzpatrick and Miller, 1979
d Hutchings and Myers, 1994

The temporal trends described by these authors are subject to both annual and long-term variability. Interannual variability for the northern and southern Grand Bank is statistically significant and the northern portion appears to be correlated with temperature (Hutchings and Myers 1994). More long-term changes in the time of reproduction may be the result of a reduced age structure within the cod population. Older individuals of this batch-spawning species tend to begin spawning later and spawn for a longer period than the younger individuals. Selective removal of older individuals by intensive fishing over time could result in the earlier and shorter spawning periods observed today (Hutchings and Myers 1993).

1.2.3 - Inshore Spawning

Scientific literature from as early as the 1890's indicates cod spawning around inshore Newfoundland (Nielsen 1895). More recently, scientific evidence has been accumulating to suggest that a considerable number of cod spawn in coastal waters around Newfoundland. There have been no reports of either actual or relative abundance of spawning individuals inshore, but Hutchings *et al.* (1993) speculate that coastal populations "...may provide a considerably larger contribution to recruitment than has previously been believed."

Based on research gill net surveys from the mid-to-late 1960s, Hutchings *et al.* (1993) reported cod in spawning condition (i.e. hydrated females, expected to spawn within three days) in the inner and outer reaches of St. Mary's, Placentia, Trinity and Bonavista bays, as well as along southeastern Labrador and near St. Anthony. In separate studies, hydrated females (Smedbol 1994) as well as "actively spawning" males and females (Wroblewski *et al.* 1994) were sampled near Random Island, Trinity Bay.

The temporal sequence of cod spawning events around inshore Newfoundland has not been accurately determined, but for each bay mentioned by Hutchings *et al.* (1994), the percentage of spawning individuals during the May/June sampling period was higher than during the April/May sampling period. Wroblewski *et al.* (1994) documented fish in ripe or spawning condition on April 22, and from July 2 to July 7 a "spawning aggregation" was identified in Trinity Bay. The abundance of hydrated females and first stage eggs reported by Smedbol (1994) peaked from the end of June to the beginning of July. There was also evidence that spawning extended into September.

1.3 - Oceanographic Influences on Egg and Larval Transport

Cod eggs and larvae drift passively in the upper 25-30m of the water column (mixed layer) throughout their development (Wiborg 1948, 1950; Page and Frank 1989). Egg and larval drift patterns in Newfoundland waters have been inferred from oceanographic studies (Templeman 1981; Lear and Wells 1984). Satellite-tracked drifter buoys and drift simulation models, for example, have been used to estimate the spatial and temporal distribution of eggs and larvae in Newfoundland-Labrador waters (Helbig *et al.* 1992).

This work suggested that the path of eggs and larvae from each postulated spawning area is very distinctive.

Eggs spawned on the slope off the Labrador Shelf and the slope off the Northeast Newfoundland Shelf (i.e. the eastern edges of Hamilton, Belle Isle and Funk Island Banks, see Figure 1.1) are subject to the flow of the offshore branch of the Labrador Current. Templeman (1981), in reference to these areas, states "...the Labrador Current turns shoreward as it passes southward and brings large numbers of cod larvae into the large bays and numerous inlets of eastern Newfoundland...". However, Helbig *et al.* (1992) demonstrated that the main or offshore branch of the Labrador Current is held over the slope off the Northeast Newfoundland Shelf and runs onto the eastern and southern edges of the Grand Banks. Therefore, eggs and larvae in or near the Labrador current would be forced onto the shelf only with persistent, favourable wind or storm conditions (Helbig *et al.* 1992). The inshore branch of the Labrador Current seems to pass over the Northeast Newfoundland Shelf and through the Avalon Channel rather than entering the bays of northeastern Newfoundland. The Northeast Newfoundland Shelf is a more likely nursery ground for eggs and larvae originating from the west or middle portions of Hamilton, Belle Isle or Funk Island Banks (Helbig *et al.* 1992).

Given that significant numbers of cod spawn on the Northeast Newfoundland Shelf (Hutchings *et al.* 1993), in an area to the west of the major banks, the fate of these eggs and larvae must be considered. Particle drift modelling (Helbig *et al.* 1992) suggests that eggs and larvae spawned over central areas of the shelf would remain on the shelf. Also, passive drifters originating from other areas of the shelf (e.g. portions to the northeast of the Northern Peninsula) have the potential to enter the larger northern bays, e.g. White Bay, Notre Dame Bay and Bonavista Bay.

The southern Grand Banks (NAFO Divisions 3NO), however, are oceanographically isolated from the Northeast Newfoundland Shelf. The offshore branch of the Labrador Current runs north to south along the perimeter of the Grand Bank (Petrie and Anderson 1983; Loder *et al.* 1988; Helbig *et al.* 1992) without flowing across the bank itself. There is considerable biological (Templeman 1979, 1981; Frank *et al.* 1992) and oceanographic data (Petrie and Anderson 1983; Loder *et al.* 1988; Helbig *et al.* 1992) to indicate that the eggs and larvae found on the southern Grand Banks originated on the Grand Banks, not the Northeast Newfoundland Shelf or Slope.

1.4 - Variability in First Year Growth

It has been proposed that an increased rate of early development (Pepin 1989, 1991) and larger size at age (Peterson and Wroblewski 1984; McGurk 1986; Houde 1987; Pepin 1991) are associated with increased survival (Anderson 1988, for a review). As eggs and yolk-sac larvae drift, the ambient water temperature of the mixed layer is fundamental to the rate of development. The time required for eggs to hatch (Page and Frank 1989, and references therein) and the number of days until yolk sac absorption (Campana 1989; Pepin 1991) are inversely proportional to water temperature. The variables influencing growth or development become more complex and growth rate becomes less sensitive to temperature after yolk sac absorption (Pepin 1991). Variability of larval and postlarval cod growth rates *in situ* has been associated with differences in water temperature (Bolz and Lough 1983; Buckley 1984; Campana and Hurley 1989; Myers *et al.* 1994a), year class size (Lett and Doubleday 1976; Lett 1978; Beacham 1980), prey abundance (Anderson 1982; Suthers 1989) and interspecific competition (Beacham 1981). Ultimately, identifying conditions conducive to relatively high growth might lead to a better knowledge of the variability in year class strength.

A combination of factors influencing growth results in increased variability of size with age because surviving individuals and populations encounter different environmental conditions as they develop (Campana and Hurley 1989). For example, a larval cod can settle to demersal habitat at a length of 25-35mm (Methven and Bajdik 1994) or, under other conditions, remain pelagic at 67mm (Anderson and Dalley 1993). The potential differences between pelagic and demersal environments are likely to influence growth (Brett 1979), resulting in variability in size at age. The general consensus seems to be that temperature and food intake are the two parameters to which first year growth is most sensitive.

1.5 - Rationale and Objectives

Two assumptions are inherent in studies that estimate hatch dates from the time of spawning (Templeman 1981; Myers *et al.* 1993). First, in directly shifting forward the entire spawning distribution to represent the hatching distribution, temporal variation in egg mortality is ignored. Furthermore, shifting the complete spawning range equally, assumes incubation occurred at a constant temperature throughout the entire spawning duration. This supposition is doubtful given the range of spawning times at one location (Myers *et al.* 1994a). The work reported here does not require these assumptions because the hatch date information was directly determined using otoliths. These data will provide as a first objective, a basis for determining whether hatching times within a year in the Newfoundland region are synchronous, or whether they follow a latitudinal trend as documented for spawning times in the area (Templeman 1981; Myers *et al.* 1994a). Second, some indication of the variability in hatch dates associated with a cold year (1991) and an average year (1989) will be determined.

Growth rates are often difficult to evaluate if estimated from age or length frequencies which may be skewed by immigration/emigration, selective mortality, or a prolonged spawning period (Campana and Hurley 1989, and references therein). On the other hand, otolith microstructure is very effective in determining daily growth rates (Campana and Neilson 1985, for a review). Developing a model to describe 0-group growth potentially permits its use as a predictive tool in estimating fish age given length. The model's accuracy depends on its flexibility both spatially and temporally, given a variety of environmental conditions. A growth model may also provide specifics on when food requirements are greatest by determining when growth rate is maximum. Furthermore, when growth data are available over geographic or temporal ranges, environmental conditions conducive for growth may be identified and employed to better predict survival of the first year class.

Chapter 2

MATERIALS AND METHODS

2.1 - Sampling

Two distinct environments were sampled, a coastal zone habitat along the northeast coast of Newfoundland and an offshore area, the southern Grand Bank. Inshore (coastal) sites were Springdale, Halls Bay; Centreville, Bonavista Bay; and Bellevue, Trinity Bay. Offshore (southern Grand Bank) sites refer to sampling stations in NAFO Division 3O. These diverse areas provide an opportunity to compare how contrasting environments may effect the hatching times and growth of 0-group cod. Location of samples sites are indicated in Figure 2.1.

Samples from the coastal sites were collected using a 30m beach seine of 7mm mesh. The seine was deployed perpendicular to the beach. One person was stationary at the water's edge while the other walked in a semicircular path to approximately cover a 90 degree arc, ending back on the beach where the seine was hauled onto shore. All samples were collected after sunset to reduce gear avoidance by the cod. The offshore samples were collected by the R/V Wilfred Templeman using a Yankee 80/104 shrimp trawl with a cod end of 6.5mm bar mesh. This gear is a bottom trawl but does fish obliquely in the water column while being retrieved. A complete list of gears and collection dates appears in Table 2.1.

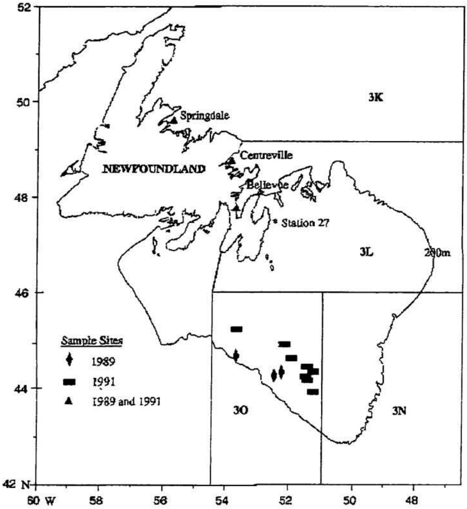

Figure 2.1 - Location of collection sites in 1989 and 1991

Table 2.1 - Summary of Sampling Sites, Dates and Gears

Collection Site	Year	Collection Date	Gear
Springdale 49°34´8˝N 55°57´8˝W	1989	October 3	30m beach seine
	1991	November 4	
Centreville 49°01´1˝N 53°52´2˝W	1989	October 2	30m beach seine
	1991	October 28	
Bellevue 47°38´1˝N 53°44´0˝W	1989	September 26	30m beach seine
	1991	September 17, 18, 19, 24, 25 October 1, 2, 3, 4, 7, 8, 22	30m beach seine and a 4.9m bottom trawl
Southern Grand Bank NAFO Div. 3O	1989	September 3, 4, 15	Yankee 80/104 Shrimp Trawl
	1991	September 4, 5, 6, 7, 9, 12, 13, 14	

All samples were frozen at -20° or -70°C soon after collection, but were thawed for 3 hours before recording standard length and removing the otoliths. A total of 400 fish were chosen for aging such that the range of standard lengths for each collection overlapped as much as possible. Standard length was measured as the distance from the tip of the snout to the base of the caudal peduncle. Length shrinkage during freezing was not accounted for due to lack of an adequate conversion factor for cod of this size range (50-110mm). However, 40 to 60mm cod frozen for 3 months, have been estimated to shrink ca. 2-5% of standard length (D. A. Methven, Ocean Sciences Centre, Memorial

University of Newfoundland, A1C 5S7; unpublished data). Shrinkage should be considered if the growth model is to be used as a predictive tool, but should not affect comparative growth analysis.

2.2 - Otolith Preparations

Lapillus otoliths were dissected from the fish by removing the top portion of the skull. The parietal, pterotic, epiotic and supraoccipital bones were removed with an anterior to posterior frontal section. The utricular vestibule was then visible and could be identified by the pigmentation on its exposed surface. (This membranous sac of epithelial tissue contains the lapillus and is located posterior and lateral to the midbrain and medial to the hyomandibular bone). The vestibule was extracted with forceps. Insect pins were used to separate the otolith from the membrane. The otolith was then allowed to air dry. Each lapillus was mounted on a glass slide using CrystalBond ™, a thermoplastic glue. A small drop of glue, approximately 1mm in diameter, was placed on the slide and the otolith was mounted (convex lateral surface exposed) on top of the glue. The slide was warmed by placing it on a hot plate which allowed the otolith to be set into the glue as level as possible. It was necessary to keep the exposed surface of the otolith free of glue and debris at this stage. The otolith used for aging (either left or right) was randomly selected as there is no significant difference in the number of increments between the lapilli of the same fish (Campana 1987; Campana and Hurley 1989).

To make the daily increments visible, it was necessary to remove the lateral surface of the lapillus to the midplane of the otolith. This was done by grinding the otolith over 3.0μm lapping film until rings from the core to the margins of the otolith were moderately visible. Then, much finer 0.3μm lapping film was used to polish the surface and make the rings more discernable. Over-grinding, for the most part, was prevented by placing a stripe of labelling tape over the edges of the lapping film and gliding the outer portions of the slide along the tape. This procedure helped keep the slide level during grinding. A linear (back-and-forth) movement was used for both grinding and polishing. Polishing was ceased when increments around the primordia (core) of the lapillus were discernable, since these increment widths are the narrowest.

2.3 - Ageing The Fish

One of two growth axes was selected for counting. The growth axes were defined by Secor *et al.* (1992) as "...axes within the microstructure where increment widths are greatest". Enumeration started at the outer margin of the otolith and ended at the hatch check (Figure 2.2), counting every discontinuous zone (dark ring) determined to be a daily increment. Daily increments were distinguished from sub-daily increments following criteria set out by Campana (1992). A complete count along the growth axis was not always possible due to regions of poor clarity caused by confluent increments, cracks and/or preparation quality. In this case, counts were made to a check or other identifiable mark, then the counting axis was shifted to a clearer section. Checks were

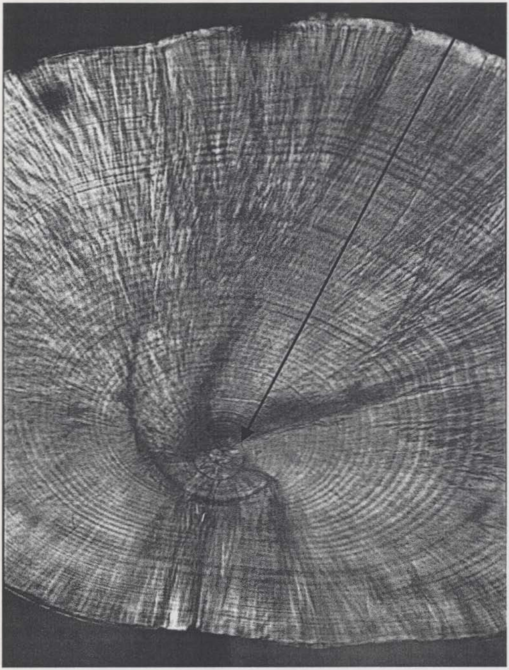

Figure 2.2 - Lapillus otolith prepared for increment counting. Tip of the arrowhead identifies the hatch check. Body of the arrow runs through a growth axis.

defined by Bolz and Lough (1983) as "thicker, darker, discontinuous zones".

All increment counts were made using an Olympus BH-2 microscope at 450 or 1000x magnification, depending on the size of the otolith. Generally, 1000x oil emersion was used for the perinuclear zone (around the hatch check). A polarizing filter, substage condenser lens, and an aperture diaphragm were helpful in distinguishing daily and sub-daily rings. Refraction proved to be a useful property with the right filter and position of the condenser. The microscope eyepiece was used to count otolith rings instead of a monitor because of its higher resolution and field of view. Counts were enumerated using a hand-held counter which eliminated bias between sequential counts of the same otolith. At least three counts were made for each otolith. If the three counts of the same otolith ranged by more than 10 percent of the lowest count, the otolith was eliminated from the data set. This criterion resulted in less than 5 percent being discarded (13 of 322). Fish from each site were aged in sub-sets of 10-15 to avoid any bias due to preparation or reading quality, which was expected to improve during the study. All checks as well as the outer margin of the otolith were included in the increment count.

2.4 - Age Validation

Daily growth increments in larval and postlarval cod otoliths have been validated as accurate and precise indicators of age in many studies (Radtke and Waiwood 1980; Bergstad 1984; Dale 1984; Campana and Neilson 1985 for a review; Campana 1989).

With careful preparation of the lapillus otolith, the discontinuous and incremental zones become discernable and the daily age from the day of hatching can be determined. The first distinct ring is deposited on the otolith of cod within 24 hours of hatching (Radkte and Waiwood 1980; Bergstad 1984; Dale 1984).

Because previous reports have not confirmed daily increment formation in the lapilli of cod from Newfoundland waters, it was deemed necessary to validate this point. To confirm the rate of increment deposition and the timing of hatch check formation, the number of discontinuous rings on the lapillus otolith of known age larvae were counted. The larvae from a resident brood stock population were incubated and hatched at Memorial University's Ocean Sciences Centre in Logy Bay. From the day of hatch, five larvae were taken every three days for eighteen days. The number of post-hatch days in relation to the increment count are given in Figure 2.3. Lapillus increment counts were not significantly different from the actual post hatch age of the fish.

To measure the degree of otolith reader bias, a random subsample of fish was aged by an independent reader. These otoliths were prepared and read initially by the author, then a second reader, who knew only the specimen number of each fish. The independent counts were done by an individual who has aged hundreds of 0-group cod (Cynthia Mercer, Fisheries Ecology, Department of Fisheries and Oceans, St. John's). A plot of first and second mean counts shows no significant difference (Figure 2.4).

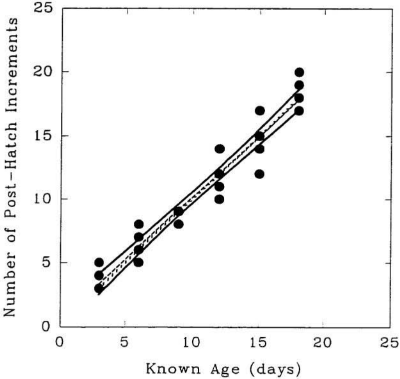

Figure 2.3 Lapillus increment counts of known age larval cod. The 95 % limits (—) for the regression (---) of the actual data contained the line representing a 1 to 1 match (⌝).

Counting the increments around the periphery of the otolith was difficult. Even with the daily deposition of rings and precise enumeration, the results may be inaccurate due to the uncertainty of discriminating between daily and subdaily increments (see Campana 1992). Around the outer one-fourth to one-eighth of the otolith (depending on its size) there are generally several successive wide, dark bands. Using magnification of 1000x or more these bands appeared as composites of narrower, lighter increments.

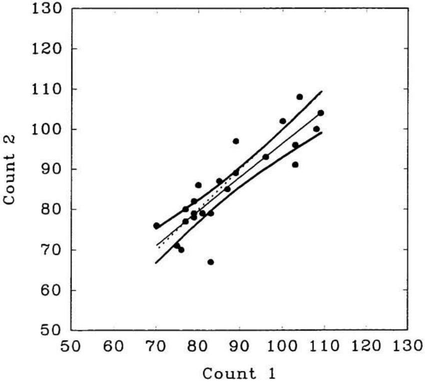

Figure 2.4 Comparison of mean otolith increment counts from independent readers. A 1-to-1 relationship (...) lies within the 95% interval (—) for the regression (-) of count 1 and count 2.

To investigate which were the true daily increments, the outer margins of select otoliths were photographed using a Scanning Electron Microscope (Figure 2.5). It appears that the daily increments are indeed the wider, darker increments, a finding in agreement with the pattern observed in Gulf of Maine cod (Steve Campana, Department of Fisheries and Oceans, Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia; pers. comm.).


000005 20KV X600 40um


000006 20KV X3.00K 8.0um

2.5 - Statistical Analysis

2.5.1 - Hatch Date Distribution Analysis

The date of egg hatching was determined by subtracting the number of lapillus post-hatch increments from the date of collection. Hatch date frequency distributions were then plotted for each collection site. An objective of this study was to detect spatial or temporal differences in mean hatch dates among the collection sites. However, repeated use of the data from each site quickly eliminated the available degrees of freedom. Therefore, in an exploratory capacity, a least significant difference (LSD) criterion was applied to all possible pair combinations (Sokal and Rohlf, 1981). The significance level, α, was set at 0.05 and the LSD of the mean hatch dates was calculated by SAS statistical software (GLM Procedure, SAS Institute Inc. Version 6.03).

2.5.2 - Length at Age Data

A linear regression was not adequate to describe the standard length at age data due to frequent pattern of residuals and unequal variance. Given the life history stage of these individuals, and the previous application of an exponential curve (Campana and Hurley 1989), that was the next model tested. The residuals from the exponential model also exhibited pattern and much of the variance was not explained.

The next logical step was to test an S-shaped curve for appropriate fit. The Gompertz growth model has been effective in describing fish growth during early life history stages (Zweifel and Lasker 1976; Pennington 1979; Bolz and Lough 1988). The curve may take the integral form:

(Eq. 2.1)

$$SL = SL_0\, e^{k(1-e^{-gt})}$$

where SL is the standard length at any point along the curve, SL_0 is standard length in millimeters at time $t = 0$; k is a dimensionless parameter; and g is the rate of decrease in instantaneous growth ($k*g$). To stabilize the variance, the natural log of the equation was taken, to give:

(Eq. 2.2)

$$\ln SL = \beta_0 + \beta_1(1-e^{(-\beta_2 age)})$$

where β_0 = lnSL at hatching ($t = 0$); β_1 is now the dimensionless parameter; and β_2 is the rate of decline in instantaneous growth. Following the example of Bolz and Lough (1988), the standard length at hatching was fixed at 4.01mm, a reliable approximation of the length at hatch for cod (Fahay, 1983).

Growth of the 0-group cod was considered from two perspectives, relative instantaneous growth and standard length attained at the end of one year. Both growth indices were calculated from Equation 2.2. Instantaneous growth (% day^{-1}) was determined by the product of $\beta_1 * \beta_2$ and maximum length (mm) at the end of the first year was estimated by including 365 as AGE in this equation. As will become apparent in Chapter 3, a higher instantaneous growth rate does not necessarily result in a larger fish at the end of the first year. Parameters β_1 and β_2 were estimated using the Non-Linear Procedure of SAS statistical software (SAS Institute Inc. Version 6.03). Models were accepted only if parameter estimates were significantly different from 0 and there was no obvious pattern in the residuals.

2.6 - Temperature Data

Temperature has long been considered as a determinate of growth rate in fishes. However, the relationship is not always directly proportional, or even linear (Brett 1979). Temperature's effect on growth is further complicated by its inverse relationship with asymptotic length (Ricker 1979). Since an objective here is to compare growth rate and asymptotic length (at the end of one year) of 0-group cod both spatially and temporally, the influence of temperature must be considered.

Temperature data were not available from all collection sites in 1989 and 1991. Mean monthly temperatures from Station 27 (47°33′N 52°35′W, 4 km east of St. John's harbour) were chosen to represent all coastal sites. Matched with the available thermograph data at 10 meters from each site, Station 27 mean monthly temperature at

10 meters was highly correlated ($r^2 = 0.71$). A ten meter depth was selected as an indicator of the average depth at which a 0-group cod would be found, considering diel migrations and changes in habitat during early life history. Temperatures used for the southern Grand Bank were long-term mean monthly averages of NAFO Division 3O from 1910 to 1982, but 85 percent of the data was recorded after 1950 (Drinkwater and Trites 1986).

Chapter 3

RESULTS

3.1 - Hatch Date Distributions

The pattern of hatch date distributions among collection sites in 1989 was quite unlike the pattern in 1991. There was also considerable variability between the two years for three of the four sites. These observations will be discussed, accordingly, as differences among collection sites within a year (spatial variability) and as differences within a site between years (spatial variability).

3.1.1 - Spatial Comparisons in 1989

Hatching among all sites in 1989 appeared synchronous (Figure 3.1). The range of hatching dates for each site was identical when grouped into 10 day bins. The mode for each site, except Bellevue, was within the Julian day 180 (June 29) bin. The sample size for Bellevue was relatively small but suggested bimodality, with one peak at day 180 and one at day 200 (July 19). The mean hatch dates ranged from June 19 on the southern Grand Bank to July 2 at Bellevue (Table 3.1).

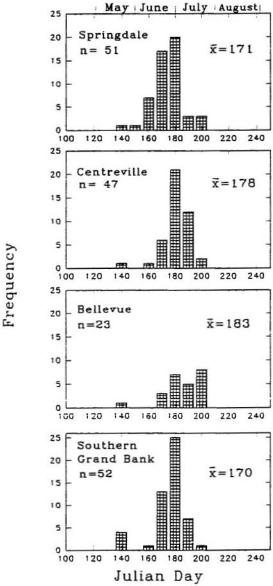

Figure 3.1 Hatch date distributions in 1989. Sample sites are plotted north-to-south.

Table 3.1 - Mean Hatch Dates for Each Site in 1989

Collection Site	Mean Hatch Date (Julian Day)	Standard Deviation	Standard Error
Springdale	June 20 (171)	9.4	1.3
Centreville	June 27 (178)	8.0	1.2
Bellevue	July 2 (183)	10.1	2.1
Southern Grand Bank	June 19 (170)	18.5	2.6
Coastal Sites	June 25 (176)	10.1	0.9

The null hypothesis for spatial comparisons was that mean hatch dates between sites were not different. A t-test was used to calculate the least significant difference (LSD) between two means. Difference in means above the LSD was termed significant, only if the variance about the mean was equal (Table 3.2). If the variance between the sites were unequal, the certainty about the means being significantly different would decrease, especially if the difference were close to the LSD. For example, the mean hatch dates between Centreville and Bellevue differed by 4.82. According to the LSD (4.99) criteria these sites were not significantly different. However, because the variance of these two samples was unequal, the LSD was calculated based on reduced degrees of freedom (37.3 instead of 63.0, which would have been used had the variances been equal). Mean hatch date comparisons will therefore be referred to only as different or not different. A summary of all possible paired comparisons is given in Table 3.2.

Table 3.2 - Difference in Mean Hatch Dates in 1989

LSD = 4.99	Centreville	Equal Variance	Bellevue	Equal Variance	Southern Grand Bank	Equal Variance
Springdale	6.8	yes	11.7	No	0.9	No
Centrevile			4.8	Yes	7.8	No
Bellevue					12.6	No
Coastal Group					5.7	No

3.1.2 - Spatial Comparisons in 1991

The sequence of hatch dates in 1991 began at the southern Grand Bank and became later proceeding northward (Figure 3.2). The distributions overlapped much less than in 1989 (Figure 3.1). The means ranged from May 18 at the southern Grand Bank to August 12 at Springdale (Table 3.3).

Table 3.3 - Mean Hatch Dates for Each Site in 1991

Collection Sites	Mean Hatch Date (Julian Day)	Standard Deviation	Standard Error
Springdale	August 11 (223)	8.2	1.5
Centreville	August 1 (214)	6.4	1.0
Bellevue	July 6 (188)	16.0	2.5
Southern Grand Bank	May 19 (139)	13.5	2.1
Coastal sites	July 26 (207)	18.9	1.8

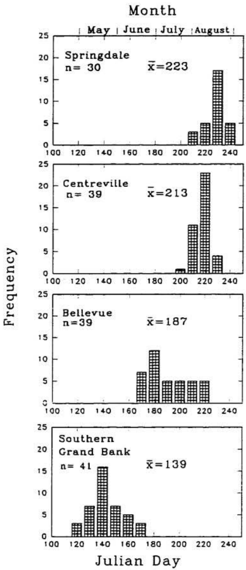

Figure 3.2 Hatch date distributions in 1991. Sample sites are plotted north-to-south.

The southern Grand Bank sample mean hatch date was different from each of the coastal sites. As in 1989, the offshore cod eggs hatched earlier than the coastal sites. Mean hatch dates were different for all paired comparisons (Table 3.4).

Table 3.4 - Difference of Mean Hatch Dates for in 1991

LSD = 6.39	Centreville	Equal Variance	Bellevue	Equal Variance	Southern Grand Bank	Equal Variance
Springdale	9.3	Yes	36.1	No	84.3	No
Centreville			26.8	No	75.0	No
Bellevue					48.2	Yes
Coastal Group					67.9	No

3.1.3 - Spatial Comparisons Between Years

Figure 3.3 illustrates the annual variability of the hatch date distributions for each site between 1989 and 1991. Each distribution was smoothed by a spline function. The southern Grand Bank sample mean hatch date was a month earlier in 1991 (May 19), relative to the samples of 1989 (June 19). In contrast, Centreville's and Springdale's peak hatching occurred more than a month later in 1991, with few dates in common with the 1989 distribution. The less normally-shaped distributions from Bellevue overlapped substantially between the two years and their means were not different. Figure 3.3 also shows mean monthly temperature plots associated with each collection site. It was

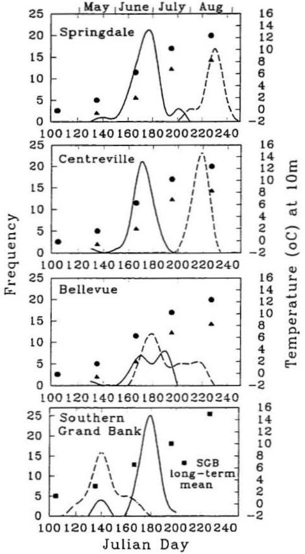

Figure 3.3 Spline hatch distribution curves for 1989(—) and 1991 (--). Temperatures (°C) are from Station 27 at 10m in 1989(●) and 1991(▲). Long-term mean temperatures(■) are from division 30.

apparent that the temperature at peak hatch for the survivors of each distribution except southern Grand Bank in 1991 was between 6-8°C.

3.2 - Spatial and Temporal Variability in Growth

The Gompertz growth model appropriately described the $\log_e$ standard length at age data of 0-group cod in the Newfoundland region. Parameter estimates, residual plots, r^2 and error sum of square values are given for each curve in Appendix A. This growth model was tested with a fixed length at hatch of 4.02 mm. However, the size at hatch may vary from 3.3 - 5.2 mm and the model's parameters would not be significantly different from the current parameters. The 95% confidence interval for each parameter would overlap for any length at hatch within this range. As mentioned in Chapter 2, two aspects of growth comparisons will be addressed, instantaneous growth rate and maximum length attained at the end of the first year.

3.2.1 - The Gompertz Curve Fit

A total of 173 fish were aged in 1989. Standard length at capture ranged from 43.2 to 108mm with an age range from 62 to 160 days post-hatch. The plot of $\log_e$ standard length at age was well described by a Gompertz growth model (Figure 3.4). More than 99 percent of the variance was explained by the curve $\ln Sl = 1.3915 + 3.68(1-e^{(-0.016AGE)})$, with no apparent pattern in the residuals (Appendix A).

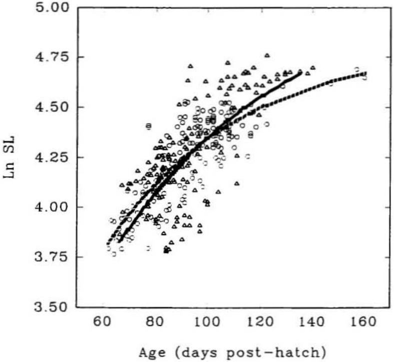

Figure 3.4 Gompertz growth model (lines; 1989(—) and 1991(- -)) fitted to all data in 1989 (△) and 1991(○).

In 1991, 149 individuals were aged, ranging in standard length from 35.8 to 116.7mm, and in age from 66 to 140 post-hatch days. Despite more variance, the Gompertz model $\ln SL = 1.3915 + 3.42(1-e^{(-0.020AGE)})$ fit the scatter plot adequately (Figure 3.4), with over 99 percent of the variance was explained and no obvious residual pattern (Appendix A).

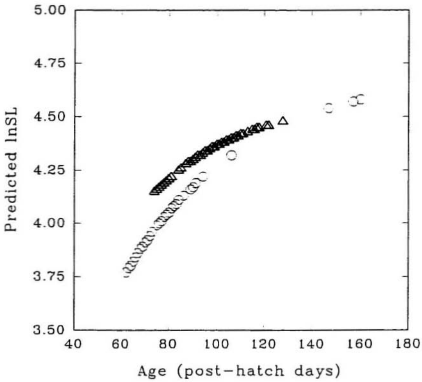

Figure 3.5 Growth curves of coastal(△) and offshore (○) 0-group cod in 1989.

3.2.2 - Spatial Variability in 1989

Fish samples were grouped as coastal or offshore fish (according to site of collection) to determine if there was geographic variability in growth between the two regions. Figure 3.5 shows the predicted length at age plot for 1989 coastal and offshore samples using the Gompertz growth model described above. Over the size range of the fish collected, the inshore cod were predicted to be larger at any given age than the offshore cod. The growth curves are distinct up to about post-hatch day 100, after which time the curves begin to merge. The coastal fish seemed to have decreased their rate of instantaneous growth more sharply than offshore fish, resulting in both groups reaching the same size by day 130. However, on average, the coastal fish were larger at age and had a higher instantaneous growth rate than the offshore fish. Growth parameters and instantaneous growth rates for each group are given in Table 3.5.

3.2.3 - Spatial Variability in 1991

Growth curves for coastal and offshore collections in 1991 (Figure 3.6) were not as homogeneous as in 1989. As well, contrary to the circumstance in 1989, coastal fish in 1991 were much smaller at age than their counterparts from the southern Grand Bank. Even though the instantaneous growth rate of the coastal group was higher than the offshore group (Table 3.5), the coastal length at age curve declined much earlier and more rapidly than the offshore curve (Figure 3.7). Length at age for coastal samples increased very little after post-hatch day 90. The offshore fish displayed a longer duration of slower growth, and as a result, were larger than the coastal fish after post-hatch day 80.

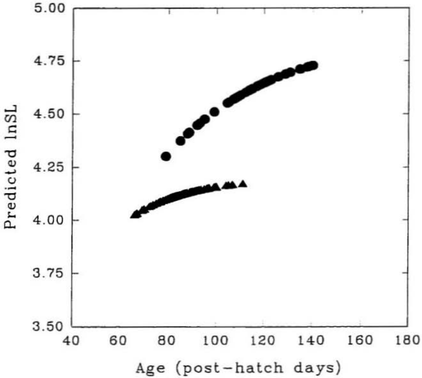

Figure 3.6 Growth curves of coastal (▲) and offshore (●) 0-group cod in 1991.

3.2.4 - Temporal Variability

All fish used in this study were old enough to have passed the point of maximum growth, i.e. the inflection point of the growth curve. Therefore, length at age points generated from these fish portray the period of decline in instantaneous growth. It was consequently apparent that a relatively high rate of instantaneous growth does not dictate larger length as the fish ages. Figure 3.8 demonstrates how the relative position of length at age curves changed as size within each group increased. The coastal fish in 1991 had the highest instantaneous growth (Table 3.5), but after about day 90 they were the smallest at age of any group. Similarly, the offshore fish from 1991 attained the largest size at age by day 80, but had the next to lowest growth rate. This is possible because the growth rate declined at a slower rate (β_2).

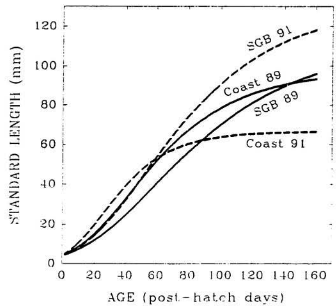

Figure 3.7 Growth curves extrapolated to length at hatch. Curves were generated by the Gompertz growth equation for coastal and offshore fish in 1989 (—) and 1991 (- -).

Table 3.5 - Growth Statistics for 1989 and 1991

Parameter/ Area	β_1 **(S.E.)**	β_2 **(%/day) (S.E.)**	**Growth Rate (day^{-1}) (± 1 S.E.)**	**SL$_{max}$ (mm)**	**Inflection Point (days)**
Coastal 1991	2.806 (0.073)	0.042 (0.010)	0.118 (0.087-0.150)	66.33	24.4
Coastal 1989	3.191 (0.051)	0.027 (0.002)	0.086 (0.078-0.094)	97.49	35.9
SGB 1991	3.477 (0.079)	0.023 (0.002)	0.079 (0.071-0.089)	129.77	47.8
SGB 1989	3.314 (0.075)	0.020 (0.001)	0.067 (0.063-0.070)	110.25	40.6

Chapter 4

DISCUSSION

4.1 - Variability in Hatch Date Distributions

Geographic distribution of cod hatching dates is neither synchronous nor sequential in the Newfoundland region. There was substantial annual variation in hatch date distributions between a cold year and an average year (Figure 4.3). Within the year of average spring and summer water temperatures (1989), a homogeneous pattern of hatch date distributions existed spatially, whereas a cold year (1991) produced a latitudinal delay in hatch dates from southern Grand Bank to northern Newfoundland. A causal effect between temperature and hatching date cannot be deduced from these results, however, the hypothesis does deserve consideration because annual variation in the spawning time of cod has been correlated with annual temperature difference for the NAFO divisions 3L and 3Ps (Hutchings and Myers 1994). Although, the effect of temperature on spawning time was not unequivocal; the effect differed among spawning areas.

Temperature's effect on hatching time also seems to vary geographically. During cold years, spawning (Hutchings and Myers 1994) as well as hatching (Figure 3.3) on the Northeast Newfoundland Shelf was delayed, but these events occurred earlier in more southerly areas (3Ps for spawning and 3O for hatching). The present study indicates that the variability in hatching time is due to the spatio-temporal fluctuations in spawning time rather than variation in incubation period. Since peak hatching in all but one instance occurred between 6° and 8°C, temperature-mediated differences in incubation time are unlikely to account for the observed differences in the hatch dates. Furthermore, because these hatch dates were determined from individuals that survived to the early juvenile stage, the 6°- 8°C range during hatching seems conducive to survival.

Spawning times for each coastal site in 1989 and 1991 were backcalculated from hatching dates (by subtracting the incubation period); each distribution occurred within one standard deviation of the mean spawning time for division 3L (Figure 4.1). Springdale and Centreville, in 1991 (Figure 4.1b), were exceptions as both calculated distributions occurred in the later tail of the observed spawning distribution. Estimated spawning times of the fish collected from 3O in both years were entirely within one standard deviation of the observed mean in the area (Myers *et al.* 1994a).

Even though backcalculated spawning distributions of coastal sites fit the observed mean spawning times in 3L, one cannot necessarily conclude that 3L is the area in which these 0-group cod were spawned. It is likely however, that these offspring were produced at a time coinciding with 3L spawning. Given the oceanographic conditions of the Northeast Newfoundland Shelf (Helbig *et al.* 1992) and the spawning times of areas north of 3L (Myers *et al.* 1994a), the other logical spawning locations of the samples collected in Springdale, Centreville and Bellevue would be areas near the coast or within the bays themselves.

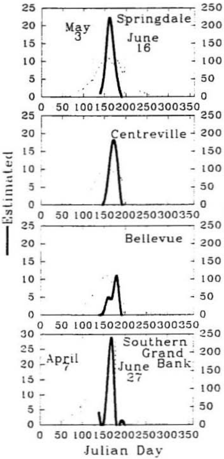

Figure 4.1a Observed(- -) and estimated(-) spawning times in 1989. Observed distributions are generated from a randomized frequency distribution based on the mean and 1 SD (⁝) of Division 3L (<200m) (top three panels) and 3NO (bottom panel) (Data from Myers *et al.* 1994a). Estimated spawning distributions are backcalculated from hatch dates at each collection site.

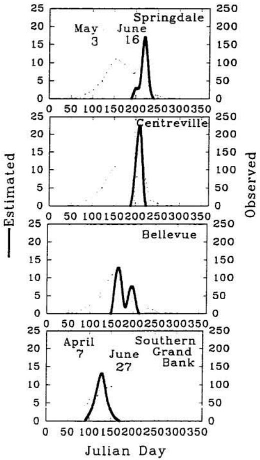

Figure 4.1b Observed(- -) and Estimated(-) Spawning Times in 1991.

The hatch date distribution of Springdale, Centreville and the southern Grand Bank appear quite normal for each year (Figure 3.3), suggesting their origin as a single spawning distribution. The hatching distributions for Bellevue in each year do not approximate normality. In 1989 there is a hint of bimodality and in 1991 there is a peak followed by a plateau. A study done at another site in Trinity Bay supports the idea of protracted modes of recruitment into the area. There seems to be more than one pulse of 0-group cod settling in Trinity Bay during late summer and autumn (Pinsent and Methven, submitted). However, the observed plateau of 1991 may be the result of a two-week range in collection times at Bellevue that year. With each successive day of sampling it is more likely that "late arrivers" will be sampled at a particular site. Undoubtedly, all recently settled juveniles from one spawning event do not arrive at the same site during the same day. It is also reasonable to assume that the lag in arrival times is partly due to the range of spawning distribution dates. Therefore, fish collected over several days would result in more variance about the estimated mean hatch or spawning date.

The degree that the back-calculated hatch date distribution is normally distributed may also be an indication of the level of mortality from hatching to the time of collection. A skewed hatching distribution may result if the risk of mortality for each individual from hatching to collection was not equal. Obviously, if there is extreme mortality for any amount of time the hatch dates for fish from this period will not appear frequently in the hatch date distribution. The site specific distributions in Figures 3.1 and 3.2 are not intended to represent the entire range and relative frequency of hatch dates for each year. These figures are simply an estimate of the hatch date distribution for cod that survived to the early juvenile stage.

If areas within divisions 3K and 3L are considered possible larval habitats for the coastal fish, estimated first-feeding larval abundance would coincide quite well with mean peak abundance of the copepod, *Calanus* (stages I-IV). First-feeding larval emergence time can be calculated using Pepin's (1991) equation for yolk-sac stage duration (19.9 days x $e^{(-0.017T)}$) and temperatures (T, °C) from Station 27. *Calanus* abundance in 3K peaks once in June and again in August, while in division 3L a strong pulse starts in July and is maintained through to September (Myers *et al.* 1994b). First-feeding larvae from each of the coastal sites in 1989 and 1991 emerge during the peak *Calanus* abundance in 3L (Figure 4.2)) more so than in 3K. *Calanus* abundance on the southern Grand Bank (3NO) initially peaks in February and then again from June to July (Myers *et al.* 1994b). First-feeding larval appearance times, calculated from 3O collections in 1989 and 1991, fall directly within the June-July window of peak *Calanus* nauplii abundance. If copepod emergence was delayed in a cold year (i.e. 1991) (Sætersdal and Loeng 1987; Ellertsen *et al.* 1987; Ellertsen *et al.* 1989) only the magnitude of optimum feeding times would change.

Myers *et al.* (1994a) found that *Calanus* abundance was the only biotic or abiotic parameter correlated with the time of cod spawning in the Northwest Atlantic. However, because cod display a latitudinal sequence in spawning times (Myers *et al.* 1994a), the match/mismatch hypothesis of Cushing (1974, 1982, 1990) does not explain the spawning strategy of cod. Match/mismatch regards the time of fish spawning as being relatively fixed from year-to-year to coincide auspiciously with the annual variability of plankton peak abundance. The coincidence of first-feeding larval cod and *Calanus* abundance is more aptly explained by the match hypothesis of Brander and Hurley (1992), which states that ". . .timing of spawning is coupled to timing of plankton production".

The fact that almost every individual fish sampled for this study was determined to have started feeding during peak *Calanus* abundance (Figure 4.2) is further evidence to support the match hypothesis of Brander and Hurley (1992). Furthermore, since first feeding times were calculated from survivors of the larval stage, the time of first feeding seems fundamental in 0-group cod survival.

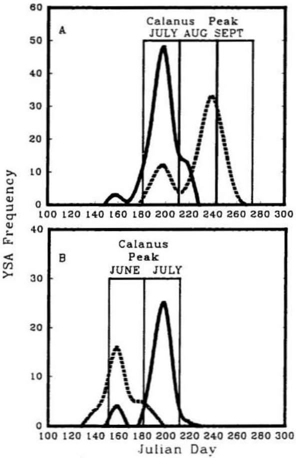

Figure 4.2. Comparison of yolk-sac absorption (YSA) time and long-term mean peak *Calanus* abundance. Panel A depicts the yolk-sac absorption time of the coastal fish from 1989 (—) and 1991 (- -) along with the months of mean peak *Calanus* abundance in 3L. Panel B is the yolk-sac absorption time for the southern Grand Bank fish from 1989 (—) and 1991 (- -) compared to the peak Calanus abundance in 3NO.

4.2 - Comparison of 0-Group Growth

Despite the heterogeneity of standard length at age among sample sites, the general form of the Gompertz non-linear growth model was useful in describing the growth of cod between 2 and 5 months of age. Generally, the model expresses an exponential rate of increase in length at age, coupled with an exponential rate of decrease. However, the model is not recommended as a predictive tool for estimating age in days from standard length across large spatial or temporal scales. The spatio-temporal variability in parameter estimates established from these data (Table 3.5) implies significant error if one set of estimates were used to predict age from a sample collected elsewhere or at another time. However, if a size-representative subsample from a single collection in a given year were aged for parameter estimation, the model may be useful in predicting age from length. The accuracy of the predictions would essentially depend on the amount of variability in length at age within that single sample.

Sampling at one site over prolonged periods also increases the variability in length at age. As observed from the hatch date estimates, standard deviation of the mean hatch date increased if samples used for the estimate were collected over a week or more. The increased variance was the result of fish arriving at the collection site on sequential days. If each fish required equal time to arrive at the site, a lag of 3 days in arrival time, for example, would translate into a difference of 3 days in hatch dates. This lag would also increase variability in length at age. Fish from a wide range of hatch dates are more likely to experience different abiotic or biotic conditions, causing variability in growth rates (Brett 1979; Campana and Hurley 1989). Because a range in hatch dates produces fish of variable size, a size effect on growth is also created. The Gompertz growth model reveals that instantaneous growth rate decreases exponentially after the inflection point of the growth curve (Figure 3.8). Therefore, a collection containing a wider range of fish size results in more variance in growth rate and growth parameters.

In an attempt to explain the variance in length at age and growth rate between collections, the effect of temperature seemed an obvious place to begin. Temperature's effect on growth varies with age (Ricker 1979). For example, Pepin (1991) concluded that temperature is less influential on growth after yolk sac absorption. Since the size range of the fish used for this study includes life history events which may be affected differently by temperature, I will examine the stage at which Campana and Hurley (1989) determined ". . . temperature exerted its most significant effect. . . " on cod larval growth, i.e. when growth was most rapid.

The stage of most rapid growth for larval cod is at the inflection point given by the Gompertz model (Figure 3.8). Instantaneous growth rate at this point is indicated by the parameter β_2 (Table 3.5), because the rate of change is approaching zero. The southern Grand Bank fish, for both years, were the slowest growing at this point but temperatures

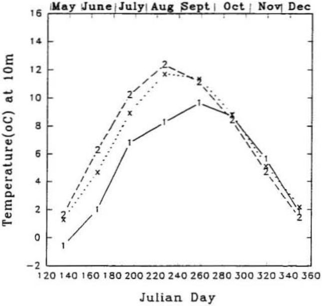

Figure 4.3 Station 27 mean monthly temperatures at 10m. ¯X¯ long-term monthly mean from 1946-1992; -1- mean monthly in 1991; --2-- mean monthly in 1989.

throughout the year on the Northeast Newfoundland Shelf were colder than on the southern Grand Bank (Drinkwater and Trites 1986). In addition, coastal 1991 fish had the highest instantaneous growth rate but experienced the coldest temperatures of any group until October (Figure 4.3).

Nevertheless, there is a degree of direct association between temperature and maximum length attained after one year. The southern Grand Bank fish in both years reached larger lengths at the end of the first year than did the coastal fish. Coastal 1991 fish exhibited the lowest asymptotic length of any group. However, the southern Grand Bank fish of 1991 presumably experienced temperatures colder than the fish from 1989, but their asymptotic length was larger.

Temperature differences do not appear to adequately explain differences in growth rates or maximum length reached at the end of one year. The temperature differences believed to be experienced by each group of fish are based on regional monthly means. The Northeast Newfoundland Shelf and the southern Grand Bank are known to display spatial and temporal temperature patchiness (Petrie *et al.* 1991) on small scales. The degree of this variability and its effect on growth is difficult to assess without knowing the exact location of spawning and the route leading to the collection site.

An analysis of temperature differences offers no adequate explanation for the variability in growth or length at age of 0-group cod in Newfoundland waters. This leaves the suggestion that food is a fundamental factor in determining growth. Consistently, food abundance has been determined to influence growth rate (Laurence 1974; Laurence *et al.* 1981; Hawkins *et al.* 1985). In this study, however, food consumption was not monitored and could not be correlated with instantaneous growth. Instead I examined the effect of feeding duration on the maximum length attained at the end the first year.

As discussed in section 4.1, estimated first feeding times for coastal and 3O sites in both years coincided well with average *Calanus* peak abundance in the respective areas. This match seems a likely strategy considering that food requirements are maximum during the period of maximum growth (Campana and Hurley 1989), which is around the inflection point of the growth curve (Table 3.5). The difference between these coastal and offshore 0-group cod in 1989 and 1991 was the duration of time that they were able to encounter optimal feeding. Referring to Figure 4.2, it seems as if most of the coastal larvae in 1991 and the offshore larvae from 1989 were approaching the end of the *Calanus* peak when their food requirements were greatest (24.4 and 40.5 days, respectively). The result was an earlier decline in the rate of increase in length at age soon after peak *Calanus* abundance. By the end of the year, the coastal 1991 and offshore 1989 groups were smaller at age than fish from the other year in the same area. More favourably, the offshore 1991 and coastal 1989 fish would have had plenty of food for 50-70 days. These groups showed a relatively slower rate of declining growth and were larger at the end of their first year. Posuarvae of this size have already begun to settle (Methven and Bajdik 1994), but are known to continue to feed on pelagic zooplankton in Newfoundland waters (Lomond 1994) and in the northeast Atlantic (Bowman 1981; Hop *et al.* 1994). Therefore, it seems that length at age for cod over this size range is a function of feeding duration, not simply food abundance on a shorter time scale. It is also logical to start feeding earlier in order to provide intraspecific competitive advantage over those arriving later. One would be larger, a more accomplished predator, and a have better chance of survival. To paraphrase, the early bird gets lots of worms.

In conclusion, identification of cod hatch date distributions provided confirmation of times and conditions which were at least adequate for larval and early juvenile cod to survive. There was significant spatial and temporal variation in hatch dates between the two years. Neither instantaneous growth rates nor maximum length at age for 0-group cod was found to be associated with mean monthly temperature. Length at age at the end of the first year was greatest when first-feeding larvae emerged around the onset of the peak *Calanus* abundance. Larger size was achieved by a relatively slower growth rate over a longer period. Identification of 0-group cod which are larger or faster growing has a practical application because these fish are known to have a better chance of survival (Anderson 1988; Pepin 1991; Pepin and Myers 1991) and, therefore, recruitment to commercial fisheries.

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Appendix A

Model Parameter Estimates

Coastal Sites - 1989

```
Non-Linear Least Squares Summary Statistics
Dependent Variable LNSL

Source              DF   Sum of Squares    Mean Square

Regression            2      2193.3441       1096.6720
Residual            114         1.3692          0.0120
Uncorrected Total   116      2194.7134

(Corrected Total)   115         2.0314    ERRORSS=1.3693
```

```
                       Asymptotic     Asymptotic 95 %
Parameter   Estimate   Std. Error   Confidence Interval
                                     Lower      Upper

B1          3.1913     0.0513       3.0896     3.2930
B2          0.0270     0.0021       0.0228     0.0312
```

```
        Asymptotic Correlation Matrix

Corr            B1            B2
------------------------------------------
B1              1             -0.9893
B2              -0.9893       1
```

Plot of growth model residuals for the coastal sites in 1989.

A = 1 obs, B = 2 obs, etc.

```
RESIDUALS
0.4+
   |
   |
   |
   |
   |        B             A
0.2+                     AA
   |                   A       A
   |                  A AA      A A       AA                     A
   |               A         B A  AA         A
   |                A   AA     AAA  C E     A AAAA          A
   |            B      AA       AB   A  A      A      AA     A
0.0+---------AAA--------------AA-------A---B--CA----A-----------------
   |      A          A   A      A A    AAAA      C    A     A    A
   |           A      A        A   BBA       AA A      B
   |       AA A                  A       A
   |       A                     A    A      A
   |                                 A         A
0.2+                      A     A       B
   |                A
   |                A     A      A
   |
   |               A
   |
0.4+
   --+---------+---------+---------+---------+---------+-------
    70        80        90        100       110       120    130

                          AGE (days)
```

Southern Grand Bank Stations - 1989

Non-Linear Least Squares Summary Statistics
Dependent Variable LNSL

Source	DF	Sum of Squares	Mean Square
Regression	2	810.2509	405.1254
Residual	48	0.4354	0.0091
Uncorrected Total	50	810.6862	
(Corrected Total)	49	1.9997	ERRORSS=0.4353

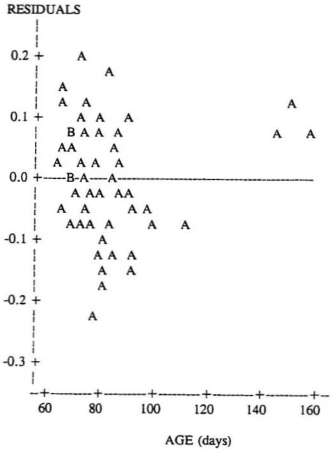
Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95 % Confidence Interval Lower	Upper
B1	3.3141	0.0747	3.1639	3.4643
B2	0.0203	0.0011	0.0180	0.0227

Asymptotic Correlation Matrix

Corr	B1	B2
B1	1	-0.9740
B2	-0.9740	1

Plot of growth model residuals for the offshore sites in 1989.

A = 1 obs, B = 2 obs, etc.



Coastal Sites - 1991

```
Non-Linear Least Squares Summary Statistics
Dependent Variable LNSL

  Source              DF   Sum of Squares   Mean Square

  Regression           2   1828.6987          914.3494
  Residual           106      4.0183            0.0379
  Uncorrected Total  108   1832.7170

  (Corrected Total)  107      4.1115      ERRORSS=4.0183


                            Asymptotic    Asymptotic 95 %
  Parameter    Estimate     Std. Error    Confidence Interval
                                          Lower      Upper

   B1          2.8061       0.0731        2.6612     2.9511
   B2          0.0420       0.0102        0.0217     0.0622


                  Asymptotic Correlation Matrix

          Corr      B1              B2
          ----------------------------------------
           B1       1               -0.9644
           B2       -0.9644         1
```

Plot of growth model residuals for the coastal sites in 1991.

A = 1 obs, B = 2 obs, etc.

```
RESIDUALS
    |
 .50+
    |
    |
    |
 .25+                      A   A       AA     A
    |                    AAA A  A      BB     B
    |              A    A AB  C BAAA A       B   A     A
    |         A AB  A   AAAA ABBCBAA A  B AA  A
  0 +------------------------AA-A--AAA--A-A--------------------
    |         A            B  B A            A        A      A
    |              A  A    A      A       AB
    |        A                  A   A                   A
 .25+                    A      A   A
    |                        B  A   A
    |                     B    A  A  A
    |                        A        A    A
 .50+
    |
    |
    |
 .75+
    |
    ------+---------+---------+---------+---------+-----------
         60        70        80        90       100       110

                      AGE (days)
```

Southern Grand Bank Stations - 1991

```
Non-Linear Least Squares Summary Statistics
Dependent Variable LNSL


   Source              DF  Sum of Squares  Mean Square

   Regression           2  863.6681           431.8341
   Residual            39    0.4237             0.0108
   Uncorrected Total   41  864.0918

   (Corrected Total)   40    0.8485      ERRORSS=0.4238



                           Asymptotic     Asymptotic 95 %
   Parameter  Estimate     Std. Error    Confidence Interval
                                         Lower       Upper

     B1       3.4768       0.0792        3.3167      3.6371
     B2       0.0229       0.0023        0.0181      0.0278



             Asymptotic Correlation Matrix

           Corr         B1           B2
         -------------------------------------
           B1           1            -0.9747
           B2          -0.9747        1
```

Plot of growth model residuals for the offshore sites in 1991.

A = 1 obs, B = 2 obs, etc.

```
RESIDUALS
.4+
  |
  |
  |
  |
  |
.2+                     A
  |                                  A                   A
  |                     A      A               A
  |                  A                                A
  |                       A         A A   A  AAA A
  |                               A  AA
 0+----------------------------------A---A-A------A---A--A---
  |                                   A  A A  A  A  A A A   A
  |                    A       A        A                  A
  |                                    A
  |                 A        A              A
  |                                            A
.2+
  |
  |
  |
  |
  |
.4+
  ------+---------+---------+---------+---------+---------+----
       70        80        90       100       110       120
                             AGE (days)
```

All Sites Combined - 1989

```
Non-Linear Least Squares Summary Statistics
Dependent Variable LNSL

  Source               DF   Sum of Squares    Mean Square

  Regression            2   3003.1134         1501.5567
  Residual            164      2.2862            0.0139
  Uncorrected Total   166   3005.3996

  (Corrected Total)   165        7.7452   ERRORSS=2.2862


                                  Asymptotic   Asymptotic 95 %
  Parameter  Estimate             Std. Error   Confidence Interval
                                               Lower      Upper

    B1       3.4171               0.0527       3.3128     3.5213
    B2       0.0200               0.0008       0.0182     0.0218


                 Asymptotic Correlation Matrix

            Corr     B1             B2
           ---------------------------------------
            B1       1              -0.9784
            B2      -0.9784          1
```

Plot of growth model residuals for all sites in 1989.

A = 1 obs, B = 2 obs, etc.

```
RESIDUALS
     |
     |          B
     |
     |
     |               C
     |              A
 0.2 +            A  A A
     |             AA  BA
     |      A     B A A  AA B B
     |   A    A BA A  BA BABA AA
     |   A  A     A   ABAD  BB        A
     |     AAA B   A A B  BAA A  A                  A
 0.0 +---AAA---CAAA--A---AA-AC-C-A-AA-A------------A------
     |  A A A A   B     A  AAAC  A                  A
     |    A A    A      A AB BA
     |   A  AAAA  AA    A  A  A  A BA A
     |     AAA  A     A A    B  A
     |         A  A  A     C
-0.2 +          AAAA AA  A       A
     |          AA   A  A
     |        A
     |
     |
     |
-0.4 +
   --+---------+---------+---------+---------+---------+--
     60        80       100       120       140       160

                        Age (days)
```

All Sites Combined - 1991

Non-Linear Least Squares Summary Statistics
Dependent Variable LNSL

Source	DF	Sum of Squares	Mean Square
Regression	2	2690.3323	1345.1661
Residual	147	6.4765	0.0440
Uncorrected Total	149	2696.8088	
(Corrected Total)	148	11.6298	ERRORSS= 6.4765

Parameter	Estimate	Asymptotic Std. Error	Asymptotic 95 % Confidence Interval Lower	Upper
B1	3.6872	0.1410	3.4084	3.9659
B2	0.0162	0.0014	0.0134	0.0191

Asymptotic Correlation Matrix

Corr	B1	B2
B1	1	-0.9876
B2	-0.9876	1

Plot of growth model residuals for all sites in 1991.

A = 1 obs, B = 2 obs, etc.

```
RESIDUALS
     |
     |
     |
     |
     |
 0.5 +
     |                AA
     |               A
     |    A B A  AB      A  A   AB
     |    A A A ABABABAA   A   A  A ABA AAAA  A
     |        AABDED B  D AA     AA A AA AAAA A A
 0.0 +----A----A-BAB-ADABAC-A-AB-A-----AA---A---A-A-A--A-AA
     |        A  AA  A AB A  A        A
     |        A  A   A  A    A
     |            AA
     |          B BA  AA  AB A   A
     |           AA AA
-0.5 +              A        A
     |           A    A A
     |                 A
     |
     |
     |
-1.0 +
     |
     -+---------+---------+---------+---------+--
     60        80        100       120       140

                   AGE (days)
```