

Spatial Comparison of Recent Growth in Postlarval Atlantic Cod (*Gadus morhua*) off Southwestern Nova Scotia: Inferior Growth in a Presumed Nursery Area¹

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Spatial variation in distribution, age, and recent growth of postlarval cod (*Gadus morhua*) were examined off southwestern Nova Scotia during the early summer of 1985 and 1986. Ages ranged between 40–120 d posthatch throughout the sampling area, from the spawning grounds on Browns Bank, to nearshore (<55 m depth) and offshore regions 150 km north. The hatch-date distributions during 1986 between cruises 3 wk apart were significantly different in the nearshore, contrary to the age structure on the Bank which appeared more stable. These observations are consistent with retention of cod in the Browns Bank gyre, coupled with episodic leakage and northerly advection in the residual current. Recent growth determined from otolith increment widths was significantly less for those cod sampled at nearshore stations than for cod offshore and on the Bank. Recent growth was significantly correlated with zooplankton biomass in a size range suitable for postlarval cod, while sea temperature was correlated in only one cruise. Nearshore areas had on average 25% of the zooplankton biomass found on the Bank. Recent growth indices of the third and fourth week precapture were not significantly different between the nearshore and offshore, implying that the cod had shared a common environment, and common origin such as Browns Bank.

Les variations spatiales dans la répartition, l'âge et la croissance récente des morues post-larvaires (*Gadus morhua*) ont été étudiées au large du sud-ouest de la Nouvelle-Écosse au début de l'été de 1985 et de 1986. Les âges variaient entre 40 et 120 jours après l'éclosion dans toute la région d'échantillonnage, puis les aires de fraye dans le banc Browns jusqu'à l'avant-plage (55 m de profondeur) et les régions du large à 150 km au nord. Les distributions des dates d'éclosion en 1986 entre les expéditions espacées de 3 sem étaient très différentes dans l'avant-plage, contrairement à la structure d'âge sur le banc, qui semblait plus stable. Ces observations concordent avec le phénomène de retenue des morues dans le tourbillon du banc Browns, couplé aux pertes épisodiques et à l'advection vers le nord des courants résiduels. La croissance récente déterminée à partir de la largeur de l'otolithe était considérablement inférieure chez les morues échantillonnées dans les stations d'avant-plage par rapport aux morues du large et du banc. La croissance récente affichait une corrélation significative avec la biomasse de zooplancton dans la gamme de taille qui convient à la morue post-larvaire, tandis que la température de l'eau n'a pu être corréliée que pour une seule expédition. Les zones d'avant-plage affichaient en moyenne une biomasse de zooplancton équivalente à 25 % de celle du banc. Les indices de croissance récente relevés pendant les troisième et les quatrième semaines précédant la capture ne différaient pas considérablement dans l'avant-plage et au large, ce qui signifie que la morue a partagé un environnement commun et une origine commune, tels que le banc Browns.

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The dispersal of marine planktonic fish eggs and larvae has been viewed as a process serving to enhance the survival of postlarvae by increasing the probability of encountering abundant food (Norcross and Shaw 1984; Doherty et al. 1985), and/or decreasing the risk of predation (Johannes 1978; Zijlstra 1988). Such areas are commonly referred to as nursery grounds and represent the end point of the dispersal process (Harden Jones 1968; Checkley et al. 1988). Many marine fishes,

including Atlantic cod (*Gadus morhua*), spawn offshore while their postlarvae and juveniles can occur in nearshore and estuarine areas (Daan 1978; Pihl 1982; Gødo and Sunnanå 1984; Lear and Wells 1984; Riley and Parnell 1984; MacDonald et al. 1984; Tremblay and Sinclair 1985; Suthers and Frank 1989). Pelagic juvenile cod also occur offshore (Zijlstra 1988), and the consequences for their growth and survival in the nearshore and offshore environments are unknown.

In southwestern Nova Scotia, residual currents flow northwards from Browns Bank (a major spawning area for cod) toward the coast. In the spring of 1985–87, high concentrations

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of postlarval and pelagic juvenile cod occurred on Browns Bank, as well as landward of the 55-m isobath (Suthers and Frank 1989). As there was no discernible larval size gradient between Browns Bank and the inshore areas, the distribution of pelagic juvenile cod appeared to be influenced by processes of both northerly drift in the residual current and retention on the natal bank, while the occasional high inshore abundance of postlarval cod was suggested to be indicative of a nursery ground (Suthers and Frank 1989).

Dispersal from the spawning area to potential nursery grounds is contrary to conclusions from large-scale ichthyoplankton surveys on the Scotian Shelf, that eggs and larvae of groundfish are retained in tidally induced gyres associated with the major offshore banks (Gagné and O'Boyle 1984; O'Boyle et al. 1984; Neilson et al. 1988). Larval retention in a geographically predictable area was argued to be the principal factor regulating success of a stock, rather than favourable growth and survival conditions that might be found in a nursery ground (Iles and Sinclair 1982; Sinclair and Tremblay 1984; Sinclair and Iles 1985). A functional role of nursery grounds can be objectively assessed from condition indices of the postlarvae, or from estimates of growth (Theilacker 1986; Townsend et al. 1987; Buckley and Lough 1987).

This paper extends upon the geographic analysis of larval and postlarval cod size distributions off southwestern Nova Scotia contained in Suthers and Frank (1989), by determining the spatial distribution of age and recent growth in the early summer of 1985 and 1986. Age is an exact measure of larval duration and superior to larval length estimates for examining the dispersal process. We examine the hypothesis that passive drift from the spawning grounds to the nearshore environment typifies the dispersal process of cod yielding older cod inshore relative to those on Browns Bank. Postlarvae from the nearshore were also predicted to exhibit higher growth rates assuming that the inshore environment was a functional nursery ground. We test this hypothesis using a model of recent growth, incorporating food abundance and sea temperature which are the principal determinants of otolith growth in fish (Campana and Neilson 1985; Jones 1986). Recent growth was assessed using the width of the peripheral daily growth increments of the otolith.

Methods

Study Area, Cruise Dates and Sampling Gear

Three ichthyoplankton surveys were conducted during the spring and early summer of 1985 and 1986 in the nearshore and shelf waters of southwestern Nova Scotia over an area of approximately 650 km² (Fig. 1). The region is dominated by strong semi-diurnal tides, with a residual current flowing north from Browns Bank (5–10 km·d⁻¹). A persistent clockwise gyre is situated over the western cap of Browns Bank, with a residence time of 5–25 d (Greenberg 1983; Smith 1983, 1989).

To assess spatial variation in the abundance and age of cod the survey area was divided into four transverse regions and a fifth region to the east (Fig. 1). Region 1 included Browns Bank, which is the principal late winter–early spring cod spawning ground in the area (O'Boyle et al. 1984; Campana and Hurley 1989), and all other stations south of 43.00°N. Regions 2, 3 and 4 were to the north and were divided into inshore (<55 m station depth) and offshore components. In cruise 86-3, region 5 was included, east of 65.00°W (Fig. 1).

During the May 1985 survey, two cruises were conducted at the same time (Table 1). Cruise 85-1 sampled the offshore waters and cruise 85-2 sampled the nearshore (Fig. 1). During cruise 85-1, a Tucker trawl (2 × 2.5 m mouth opening, 1600-μm mesh) was the principal sampling gear. A complete description of this gear type and deployment scheme is contained in Suthers and Frank (1989). In cruise 85-2, a 1.0-m diameter ring net (1000-μm mesh) was towed from the surface to 5 m at 2 m·s⁻¹ for 15 min; filtering approximately 1000 m³. An electronic package towed beneath the net recorded temperature, depth, and towing speed while a TSK (Tsurumi-Seike Co. Ltd) flow meter in the mouth of the net recorded volume filtered.

During the May 1986 survey, cruises 86-1 and 86-2 were conducted during the same time period (Table 1). A Tucker trawl was used at all sampling locations.

In June 1986 (cruise 86-3, Table 1) we sampled the nearshore and offshore with a Tucker trawl with a deployment scheme identical to that in cruise 86-2. Salinity and temperature were determined at the end of the tow with bottle collections and a temperature-depth probe.

Samples from all cruises were preserved in 5% formalin in fresh water, buffered with sodium borate. Within 3–10 d, postlarval cod were transferred to 95% ethanol to preserve the otoliths. All cod were counted and measured (standard length, SL) to the nearest 0.2 mm. Lengths were not corrected for preservation shrinkage.

Zooplankton Collection and Analysis

Zooplankton biomass data for cruises 85-1 and 86-1 (Table 1) were taken from Frank (1988). Zooplankton was collected at each station with a mini-BIONESS (0.25 m² mouth opening, 333-μm mesh). The three most northerly stations in cruise 85-1 were not sampled, so zooplankton biomass (Y , milligrams per cubic metre) was estimated from distance offshore (X , kilometres) using the equation

$$\ln Y = (1.02) \times \ln X - 1.33, \text{ after Frank (1988).}$$

Zooplankton was sampled during cruises 85-2, 86-2, and 86-3 with a 0.5-m diameter, 405-μm mesh ring net (Table 1). Macrozooplankton (jellies, euphausiids) was excluded by rinsing the sample through a 4 or 10-mm mesh sieve before preservation in 5% formalin in freshwater. In the laboratory, zooplankton was divided by sieving into four size fractions; 308–602, 602–860, 860–1050, and >1050 μm. Total zooplankton biomass (principally calanoid copepods, small euphausiids) was estimated as the sum of dry weight fractions, expressed as milligrams per cubic metre.

Otolith Analysis

Cod otoliths form one growth increment per day although two to three narrow increments around the nucleus may go unresolved (Bolz and Lough 1988; Campana and Hurley 1989). All otoliths were polished with lapping film to the nuclear plane and the number of daily increments counted at 1250× magnification (Campana and Neilson 1985). Each otolith was counted three to six times until a consistent age was obtained. If any of the counts differed by more than 10, often on account of poor sample preparation, the otolith was discarded (approximately 6% overall). Increment widths and otolith radius (Fig. 2) were measured on a video screen using an image analysis system (Campana 1987). The most recent, outer increment was

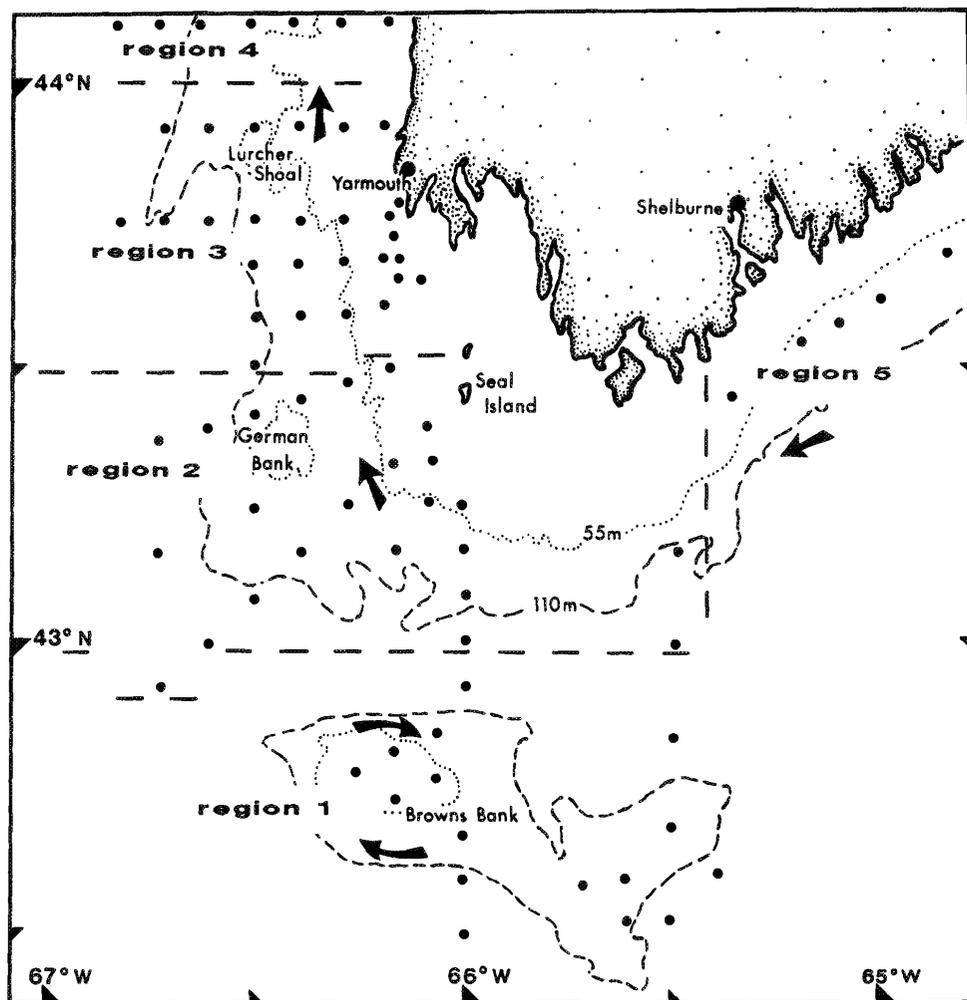


FIG. 1. Stations sampled off southwestern Nova Scotia during May 1985, 1986 and June 1986, and division into five regions. The 55-m isobath (dotted) delineates the offshore from the nearshore. Arrows indicate the mean circulation (Greenberg 1983; Smith 1983).

TABLE 1. Cruise information pertaining to the three survey periods. i = inshore. Key to gear deployed; BN, BIONESS; HM, 0.5-m diameter ring net; 1m, 1.0-m diameter ring net; Tt, Tucker trawl.

Survey	Cruise	Dates	Gear deployed	Stations	Regions covered	Zooplankton sampling gear
May 1985	85-1	9-21 May	Tt	30	1,2,3	BN
	85-2	16-22 May	1m	8	3i	HM ^a
May 1986	86-1	10-18 May	Tt	34	1,2	BN
	86-2	14-23 May	Tt	20	2i	HM
June 1986	86-3	5-11 June	Tt	49	1,2i,3i,4i,5	HM

^aAverage of 10 neighbouring stations.

usually incomplete and was not included in the analysis. The left and right lapilli of 23 cod were analysed to compare the age and increment width measurements. The average difference in age was 7% (range 0-26%) and the average difference in width of the outer 14 increments was 8.6% (range 0-26%).

All cod from cruises 85-1 and 85-2 were aged, using one of the pair of lapillar otoliths chosen at random. The ages and increment widths of cod sampled with the 1.0-m diameter ring net in cruise 85-2 were analysed with the Tucker trawl samples of cruise 85-1 as there was no significant difference in the age-

length relationship (analysis of covariance, ANCOVA $p > 0.5$). Poor preservation of the otoliths at one station in region 3 (cruise 85-1), primarily included those from cod < 15 mm standard length (SL). Therefore an age-length regression from cruise 85-1 was used to estimate the probable age distribution of these smaller fish for region 3 ($\text{age} = 39.6 \times \ln(\text{SL}) - 40.6$, $r^2 = 0.71$).

During 1986, when pelagic juvenile cod were abundant, samples were selected for otolith analysis from stations within regions (Fig. 1) where the greatest densities were recorded.

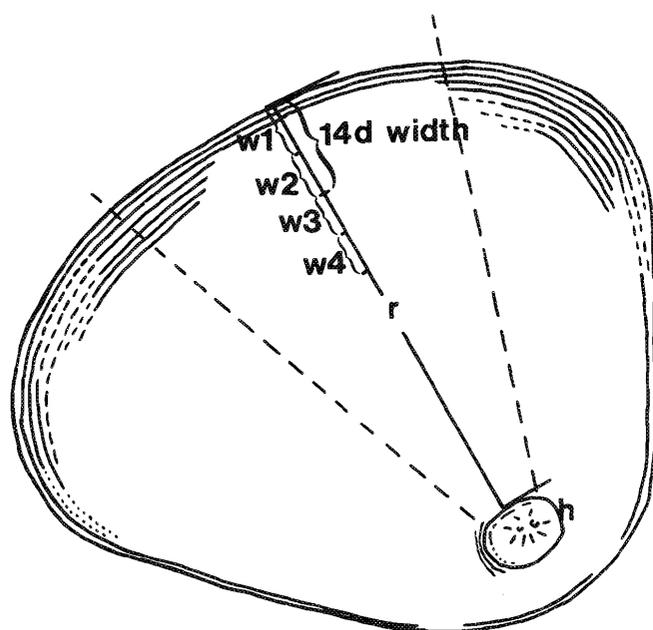


FIG. 2. Diagram of lapillar otolith showing the location of the measurements taken. Measurements were confined to the area between the dashed lines and include: 14-d width, r =radius, h =hatch check, $w1$ – $w4$ are the 7-d widths.

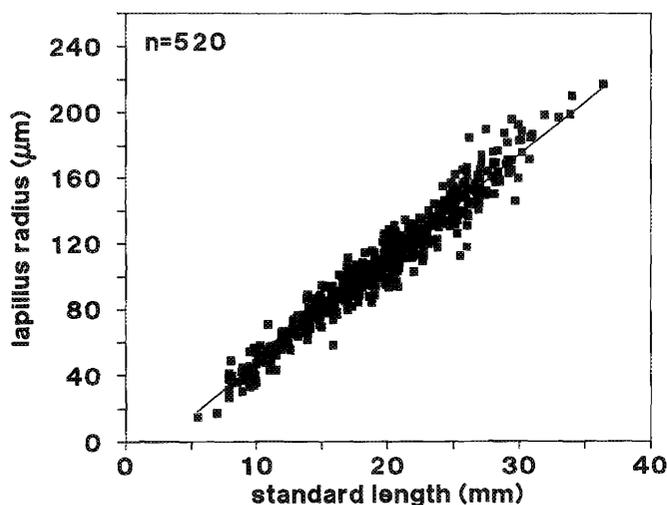


FIG. 3. Linear relationship of lapillus radius (μm) on standard length (mm) for all cruises. The intercepts between cruises were significantly different. Individual cruise regressions: 85-1,2 radius = $-19.82 + 6.40 \times \text{SL}$ $r^2=0.92$; 86-1 radius = $-6.85 + 5.82 \times \text{SL}$ $r^2=0.95$; 86-2 radius = $-16.67 + 6.50 \times \text{SL}$ $r^2=0.96$; overall radius = $-16.08 + 6.34 \times \text{SL}$ $r^2=0.95$.

Occasionally when the station sample sizes exceeded 15 individuals, a random subsample was taken.

In this study, the otolith radius was linearly related to the SL over all cruises (Fig. 3). The slopes were not significantly different among cruises but the intercepts were different ($p < 0.001$). Within a cruise the otolith radius–SL regressions were not significantly different among regions (ANCOVA $p > 0.3$), except for region 2 inshore, cruise 86-2 ($p < 0.01$). The regression equation for this region was radius = $6.66 \times \text{SL} - 23.39$ ($r^2=0.95$). Therefore any increase in otolith radius (i.e. a daily growth increment) of cod in this region would not reflect the same proportional increase in SL

as in other regions, and therefore increment widths for cruises 86-1,2 could not be directly compared between regions as indices of recent growth. A corrected radius was calculated for region 2 inshore by adding the residuals from the radius–SL regression, to the estimated radius derived from the radius–SL regression of regions 1 and 2. The increment widths were altered proportionally (from -5 to $+25\%$).

The cumulative width of the 14 recent growth increments prior to capture was used as an index of recent growth. While otolith size and fish size are strongly correlated, daily otolith growth rate is believed to be a running average of fish growth under average environmental conditions (Fig. 3; see Mosegaard et al. 1988; Reznick et al. 1989; Secor and Dean 1989). The metabolic lag between daily feeding and otolith growth is unknown for cod, although in salmon parr it is 1–2 wk (Wilson and Larkin 1982; Volk et al. 1984). Consequently the summed widths of the 14 most recent daily growth increments was used in this study, both as a conservative measure of recent growth, and as a growth index for the regions where the cod were sampled.

Statistical Analyses

As the cruises extended over 6–10 d, each age was adjusted to a common capture date, corresponding to the mid-date of the cruise (maximum adjustment was ± 4 d). Where regional sample sizes exceeded 30 fish, the regional age frequency histograms were compared with a Kolmogorov-Smirnov test. The probability level of significance for the multiple comparisons was adjusted to $0.05/n$ where n was the number of regions. To test for regional differences in recent growth rate, the cumulative width of the 14 most recent complete daily growth increments for each cruise (Fig. 2) was analysed in two ways, both of which incorporated size (SL) to remove its effect. Inclusion of age in the model did not result in a significant increase in the variance explained and therefore was not included in any of the models. The first test was a linear model to examine the effect of regions on the cumulative 14-d increment width. The second test was a multiple regression model of the cumulative 14-d increment width, as a function of zooplankton and sea surface temperature (1–5 m below surface). This test assumes that food and temperature recorded at capture was representative of the previous 14 d. For each cruise the four outer 7 d widths (Fig. 2) were analysed separately as in the first test above, to examine the effect of regions on the growth history. Variances of otolith increment widths, SL and environmental variables used in these models were not homogeneous (Cochran's C), requiring logarithmic transformations. Residuals in both models were normally distributed. All analyses were performed using SYSTAT (Systat Inc. 1988, Evanston, Il.).

Results

Spatial Distribution in Abundance

Over 80% of the total catch of postlarval cod (>10 mm SL) occurred north of Browns Bank in regions 2 and 3 in May 1985 and 1986 (Suthers and Frank 1989; Fig. 4a and 5a). In May 1985, cod were particularly abundant (>10 per 1000 m^3) in region 3 inshore (3i). In June 1986 (cruise 86-3), conducted 3 wk later than cruises 86-1,2 pelagic juvenile cod were concentrated on Browns Bank, and in region 3i — although sampling was limited offshore in region 2 (Fig. 6a). For the 31 stations common to cruises 86-1,2 and 86-3, there was no

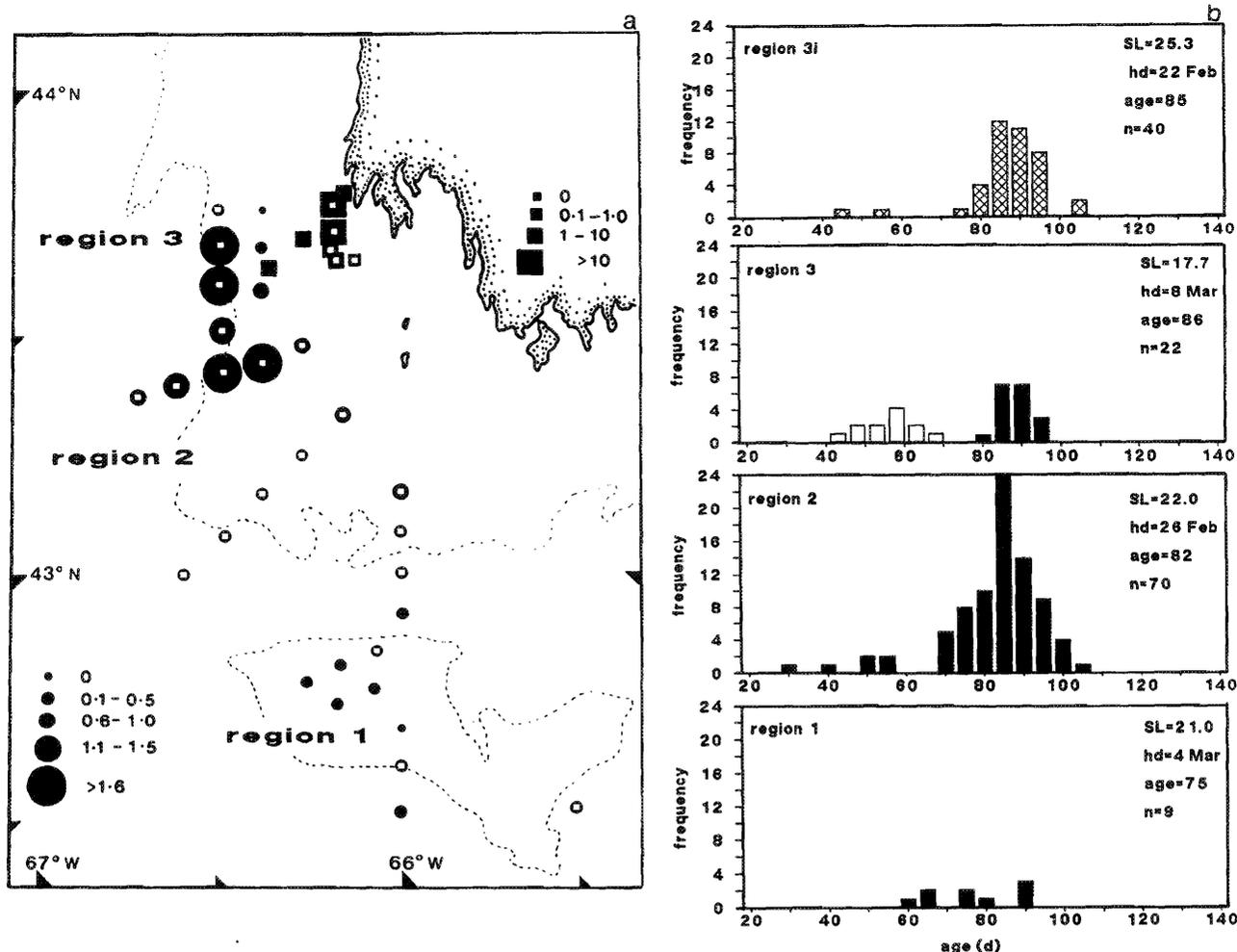


FIG. 4. (a) Expanding symbol plot of postlarval cod concentration ($\text{No.} \cdot 1000 \text{ m}^{-3}$) during cruise 85-1 (circles, data from Suthers and Frank 1989) and during cruise 85-2 (squares). Note different concentration scales for the two cruises. Symbols containing a white square show location of samples used in the age and growth analysis. (b) Regional age frequency histograms adjusted to a common sampling date, 18 May. Cross-hatched histogram refers to cod sampled with the 1.0-m ring net. Open histogram indicates age frequency estimated from length frequency (see Methods). Probability value associated with Kolmogorov-Smirnov comparison of age frequency distributions between regions 2,3i = 0.9. Also shown are regional average standard length (SL), hatch date (hd), age, and sample size.

significant correlation in cod concentration (Spearman's rank correlation $r_s = 0.13$, $p > 0.05$). There was no apparent size gradient from region 1 to region 4i during cruise 86-3, which was also demonstrated in other cruises (Suthers and Frank 1989).

Spatial Distribution of Ages

The age distributions between regions 1, 2, 3, and 3i during cruise 85-1,2 (adjusted to a common capture date, 18 May) showed no gradient in age from Browns Bank to inshore (Fig. 4b). There was no significant difference between the age frequency histograms of region 2 and 3i (Kolmogorov-Smirnov test $p > 0.9$).

During cruises 86-1,2 (Fig. 5b), the age frequency histogram of region 2 was different from regions 1 ($p < 0.001$) and 2i ($p < 0.001$) which, in turn, were not significantly different from each other ($p = 0.94$). Thus cod in region 2 were significantly older with the mean age greater by 10 d — although the age distribution in region 2i appeared polymodal (Fig. 5b).

The age distributions 3 wk later during cruise 86-3 were significantly different between region 1 compared with regions 2i and 5 — to the north and northeast ($p < 0.03$, Fig. 6b). Region

2i was different from region 3i ($p < 0.04$), and region 3i was different from region 5 ($p = 0.01$). Overall, postlarvae in regions 1 and 3i were 10 d older than the other regions, although again the age distributions tended to be polymodal.

Two regions were sampled in cruises 86-1,2 and again in cruise 86-3, permitting an assessment of the similarity of the age structure between regions over the intervening 3 wk. The hatch date distributions for region 1 did not differ significantly between cruises (Fig. 7a and b, Kolmogorov Smirnov test $p = 0.06$), showing a similar range, from early March to mid April (although the distribution appeared polymodal in cruise 86-3). In contrast, the hatch date distribution of region 2i was significantly different between the two cruises (Fig. 7c and d, $p < 0.001$), with later spawned postlarvae appearing in June. The hatch dates at region 2i ranged from mid February to mid April during cruise 86-2 and from mid March to early May in cruise 86-3.

Index of Recent Growth

The index of recent growth was initially analysed with an ANCOVA model (Table 2a), with region a factor and SL a covariate. The slopes of the recent growth index on SL during

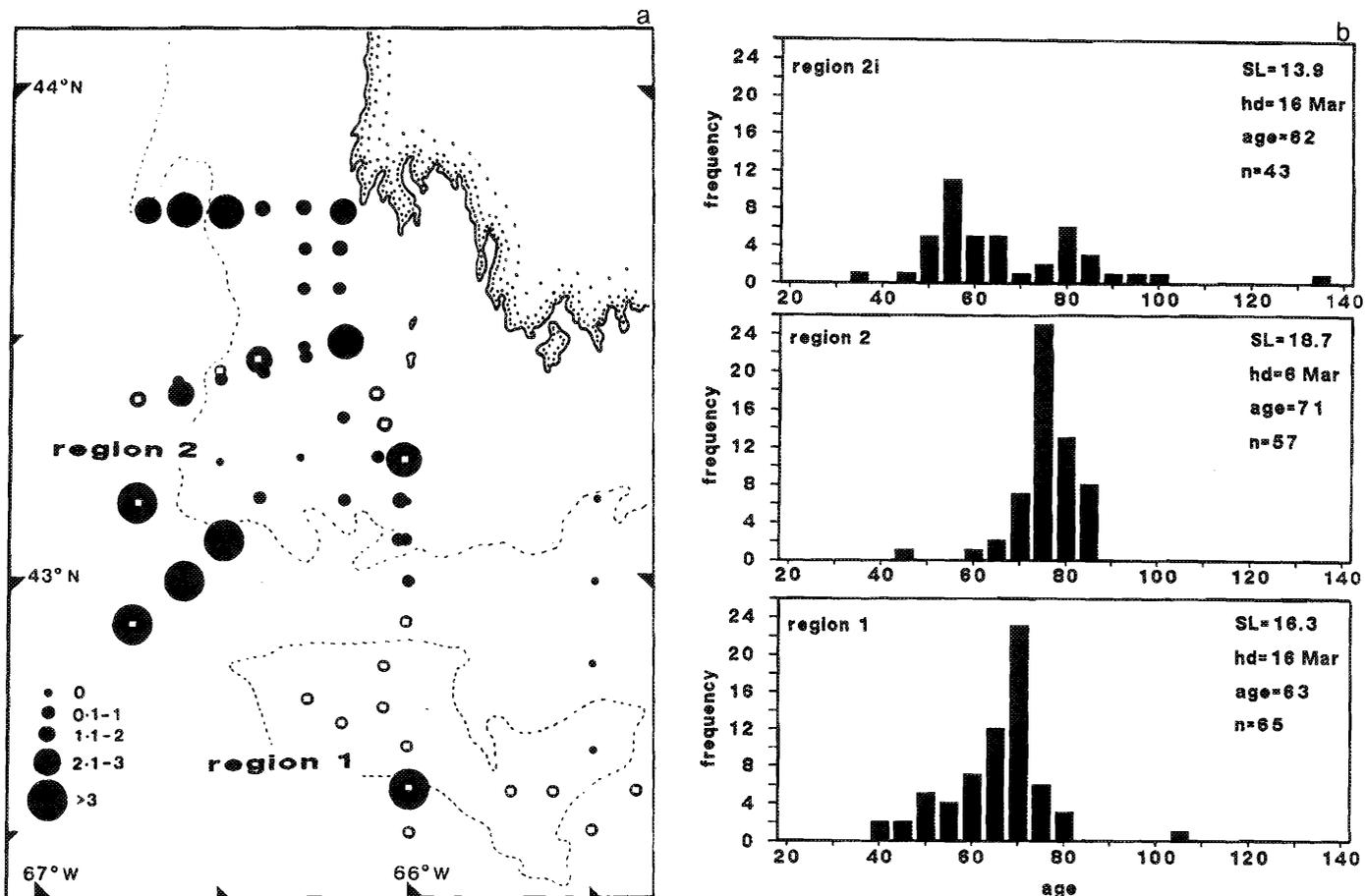


FIG. 5. (a) Expanding symbol plot of postlarval cod concentration ($\text{No.} \cdot 1000 \text{ m}^{-3}$) during May, cruises 86-1,2 (from Suthers and Frank 1989). Symbols and abbreviations as in Fig. 4. (b) Corresponding regional age frequency histograms adjusted to a common sampling date, 18 May. Probability values associated with Kolmogorov-Smirnov comparisons of age frequency distributions between regions 1,2 < 0.001; region 2,2i = 0.001; region 1,2i = 0.94.

May 1985 were significantly greater in regions 1, 2, and 3 than in region 3i (Table 2a, Fig. 8a). For example, offshore cod 25 mm SL grew approximately 25% over the previous 2 wk, compared with 22% inshore. During cruises 86-1,2 the slopes from Browns Bank and region 2 offshore were the same, and significantly greater than that of cod from region 2i (Table 2a, Fig. 8b). Thus in May 1986, 25 mm SL cod offshore grew approximately 33% over the previous 2 wk, compared with 23% inshore. Three weeks later during cruise 86-3, region 1 had the greater slope (Table 2a, Fig. 8c), and was significantly different from the inshore regions. At this time 25 mm SL cod in region 1 grew approximately 29% over the previous 2 wk compared with 24% inshore.

The second model used was a multiple regression model of the recent growth (Table 2b), incorporating SL, total zooplankton (>308 μm) and sea temperature (between 1 and 5 m deep) at each station as independent variables. Total zooplankton concentration and sea temperature were selected because they were considered to have the greatest effect on increment width (Campana and Neilson 1985) and were the least confounded by collinearity.

The multiple regression model explained almost as much of the variance in the recent growth index as the ANCOVA model (Table 2b). The influence of the region factor identified in the ANCOVA model was removed, as the region by region residuals from the multiple regression of each cruise were not significantly different from zero, except for cruise 85-2, region

3i. This exception may be explained by the disparate regional sample sizes, and perhaps the use of a mean zooplankton value for cruise 85-2 (see Table 1). Total zooplankton concentration was significantly and positively correlated with recent growth in all cruises after size was entered into the multiple regression. Sea surface temperature was significantly and positively correlated only in cruises 86-1,2 (Table 2b).

The slope of the recent growth index-SL for each region, and regional average total zooplankton biomass were positively related (Fig. 9). Region 2 and 3 (offshore) and Browns Bank had the greatest zooplankton concentration, tending to form an offshore grouping, distinct from the nearshore. The nearshore had less than 25% of the zooplankton biomass concentration of Browns Bank (Fig. 9).

The four 7-d indices of growth (Fig. 2) were analysed with region as a factor and SL a covariate (identical to the first model above). The increments became narrower and often indistinct towards the nucleus in some specimens, so the sample size was reduced (cruises 85-1,2 95% of the original sample; cruises 86-1,2 72%; cruise 86-3 67%). The SL was back calculated for each week using the cruise otolith radius-SL regression. Analysis of the most recent 7-d otolith growth prior to capture generally showed similar results as the 14-d index except for cruises 85-1,2, which showed there was no effect of regional difference in slopes, although the intercepts were significantly different among regions (Table 3). Overall, the two most recent 7-d widths showed significant effects of region (Table 3), shown in

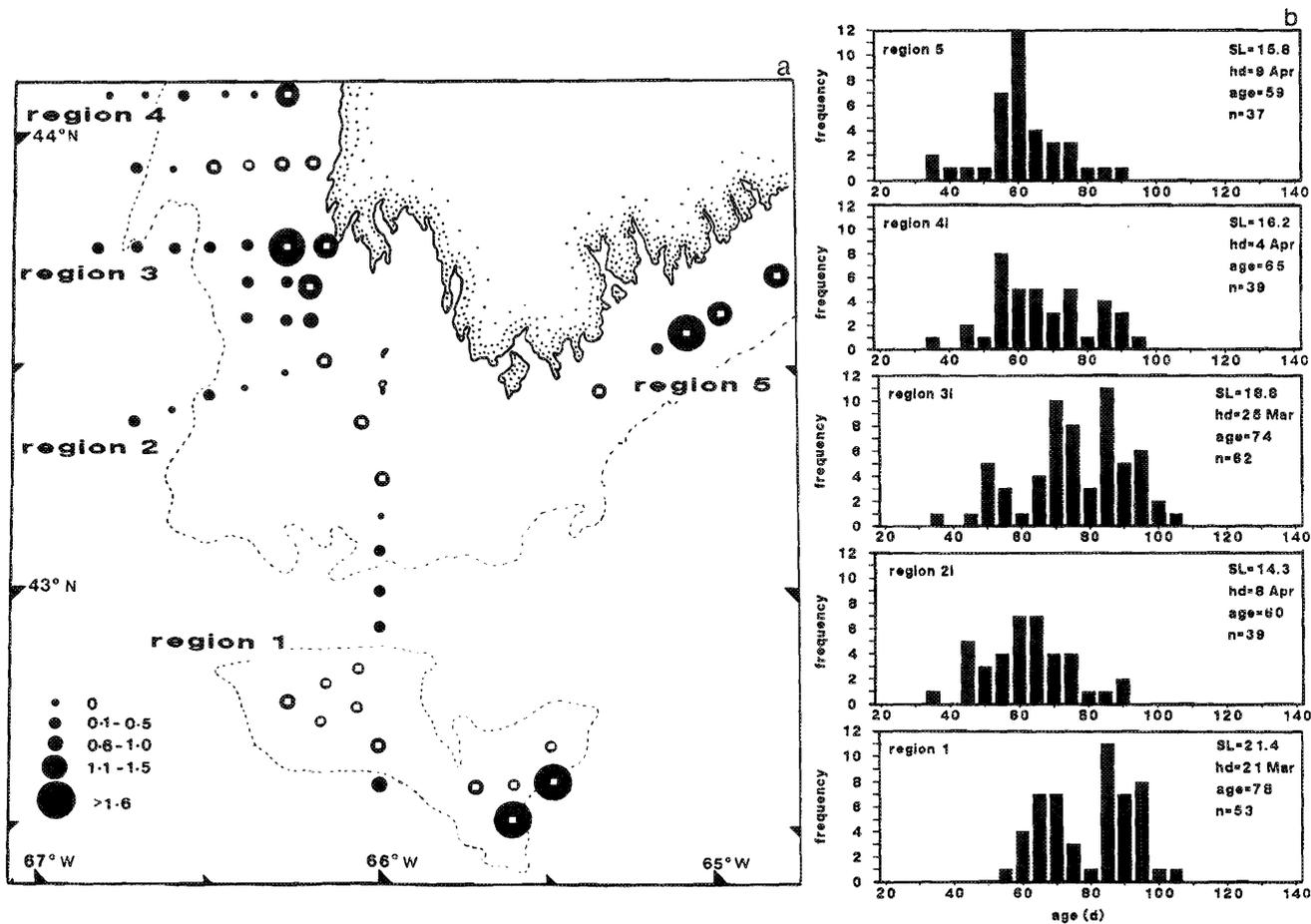


FIG. 6. (a) Expanding symbol plot of postlarval cod concentration ($\text{No.} \cdot 1000 \text{ m}^{-3}$) during June, cruise 86-3. Symbols and abbreviations as in Fig. 4. (b) Corresponding regional age frequency histograms adjusted to a common sampling date, 7 June (20 d after 18 May for comparison with cruises 85-1,2 and 86-1). Probability values associated with Kolmogorov-Smirnov comparisons of age frequency distributions between regions 1,2i = 0.03; region 1,3i = 0.99; region 1,4i = 0.23; region 1,5 = 0.004; region 2i,3i = 0.04; region 2i,4i = 0.99; region 2i,5 = 0.99; region 3i,4 = 0.31; region 3i,5 = 0.01; and region 4i,5 = 0.99.

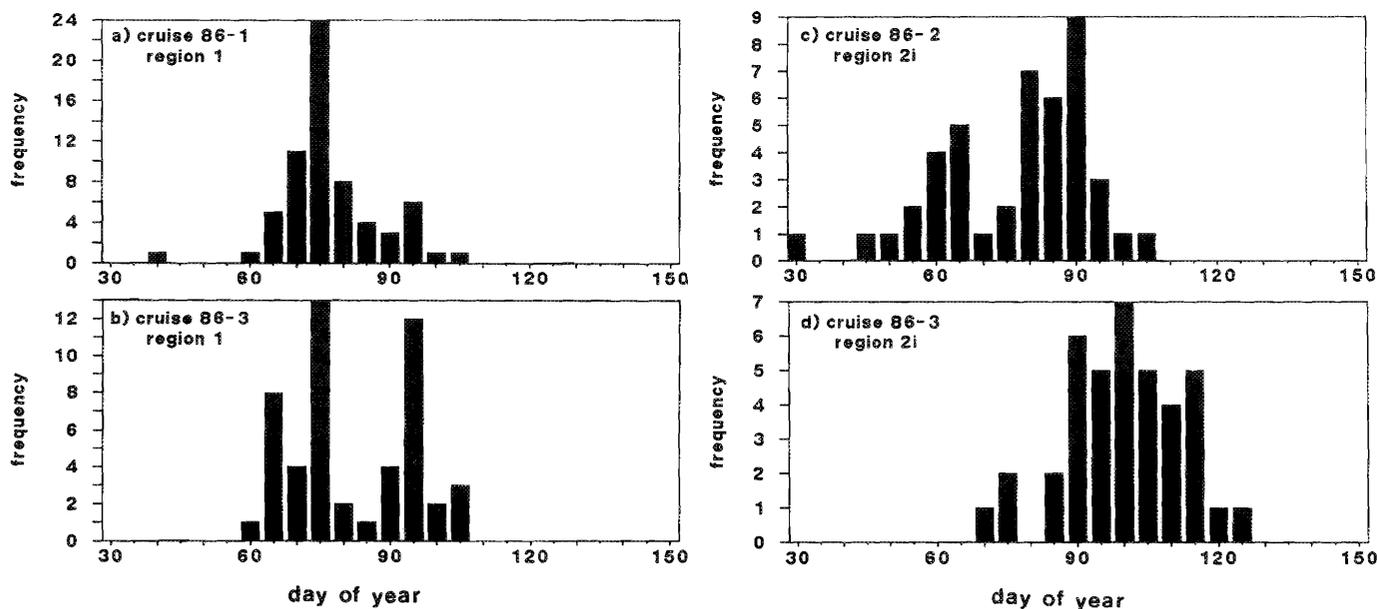


FIG. 7. Hatch date frequency distributions of cod. (a) Cruise 86-1, region 1, (b) cruise 86-3, region 1, (c) cruise 86-2, region 2i, (d) cruise 86-3, region 2i.

TABLE 2. Linear models and parameter estimates resulting from the analysis of the most recent 14-d width of the otolith for each cruise. a) width = constant + region + SL + region × SL b) width = constant + SL + Z + T; SL = standard length, T = sea surface temperature, Z = zooplankton biomass concentration. * 0.005 < p < 0.05, ** p < 0.005.

Cruises	Source	SS	df	MS	r ²	Parameter	Coefficient (SE)	
85-1,2	(a)	SL	1.47	1	1.47**	0.66	region (1) × SL	1.03 (0.17)
		Region	0.09	3	0.03	0.07	region (2) × SL	0.96 (0.07)
		Region × SL	0.12	3	0.04*	0.02	region (3) × SL	1.15 (0.17)
		Error	1.91	131	0.01		region (3i) × SL	0.68 (0.08)
		Model				0.75		
	(b)	Constant				0	constant**	0.81 (0.20)
		SL				0.66	SL**	0.87 (0.05)
		Z				0.04	Z**	0.08 (0.02)
		T				0	T	-0.10(0.08)
		Model	5.28	3	1.48**	0.70		
Error		2.26	135	0.02				
86-1,2	(a)	SL	4.37	1	4.37**	0.71	region(1) × SL	0.88 (0.06)
		Region	0.27	2	0.14**	0.05	region (2) × SL	0.86 (0.08)
		Region × SL	0.37	2	0.19**	0.04	region(2i) × SL	0.46 (0.07)
		Error	1.95	145	0.01			
		Model				0.80		
	(b)	Constant				0	constant**	0.86 (0.15)
		SL				0.71	SL**	0.72 (0.04)
		Z				0.03	Z**	0.03 (0.01)
		T				0.03	T**	0.29 (0.07)
		Model	7.60	3	2.53**	0.77		
Error		2.26	147	0.02				
86-3	(a)	SL	4.35	1	4.35**	0.62	region(1) × SL	0.79 (0.07)
		Region	0.41	4	0.10*	0.01	region(2i) × SL	0.46 (0.05)
		Region × SL	0.46	4	0.12*	0.04	region(3i) × SL	0.39 (0.06)
		Error	3.62	192	0.02		region(4i) × SL	0.46 (0.10)
		Model				0	constant**	1.41 (0.39)
	(b)	SL				0.62	SL**	0.56 (0.03)
		Z				0.02	Z**	0.02 (0.01)
		T				0	T	0.24 (0.19)
		Model	7.05	3	2.35**	0.64		
		Error	4.05	198	0.02			

Fig. 10 by the different adjusted regional mean widths (cruises 85-1,2) and the width-SL slopes (cruises 86-1,2, 86-3). The regional differences reflect the zooplankton biomass characteristics shown above, yet these differences are not maintained in the growth history record of the otolith. The regional differences in all cruises decreased until they were not significantly different by the third and fourth week precapture (Fig. 10). However, cod from region 5, cruise 86-3 tended to show slower growth over the third and fourth weeks precapture compared with the other regions, suggesting these fish were immigrants from outside the study area (Fig. 10c).

Discussion

Age Distribution and Dispersal

The complex spatial distribution of postlarval age between the spawning grounds on Browns Bank and regions to the north confirm earlier analyses of size (Suthers and Frank 1989) and larval age (Campana et al. 1989), that both larval drift and retention influence the dispersal patterns of cod in southwestern Nova Scotia. At residual current speeds of 5–10 km·d⁻¹ (Smith 1989), cod 100–150 km from the Bank should have been 2–4 wk older than those on the Bank. Regional differences in age

were apparent, but were neither large (difference in mean age < 10 d) nor consistent with the direction of the residual flow. The hypothesis that passive, uniform drift occurs from the spawning grounds to the nearshore environment was rejected, because of the lack of an age gradient. The northerly distribution of postlarval cod, and the lack of correlation in the horizontal distribution of postlarval cod between May and June of 1986 is taken as evidence to reject the hypothesis of larval cod retention in geographically discrete areas (O'Boyle et al. 1984; Gagné and O'Boyle 1984). Periodic breakdown of the Browns Bank gyre (Smith 1989) could influence eggs, larvae, and postlarvae by a northward drift causing a variable residence time of cod on the Bank. The persistence of 60–100 d old cod near Browns Bank and their broad distribution to the north during June of 1986, agrees with this interpretation. An alternative hypothesis is that nearshore spawning could obscure an age gradient. Hurley and Campana (1989) showed that between 1983–85, nearshore spawning off southwestern Nova Scotia was relatively minor in comparison to the offshore. The results of the recent growth analysis also show that growth of nearshore cod was less than offshore, with a common offshore growth history (Fig. 10).

The partial retention of the postlarval cod population on the Bank during 1986 was confirmed by the relative stability in the

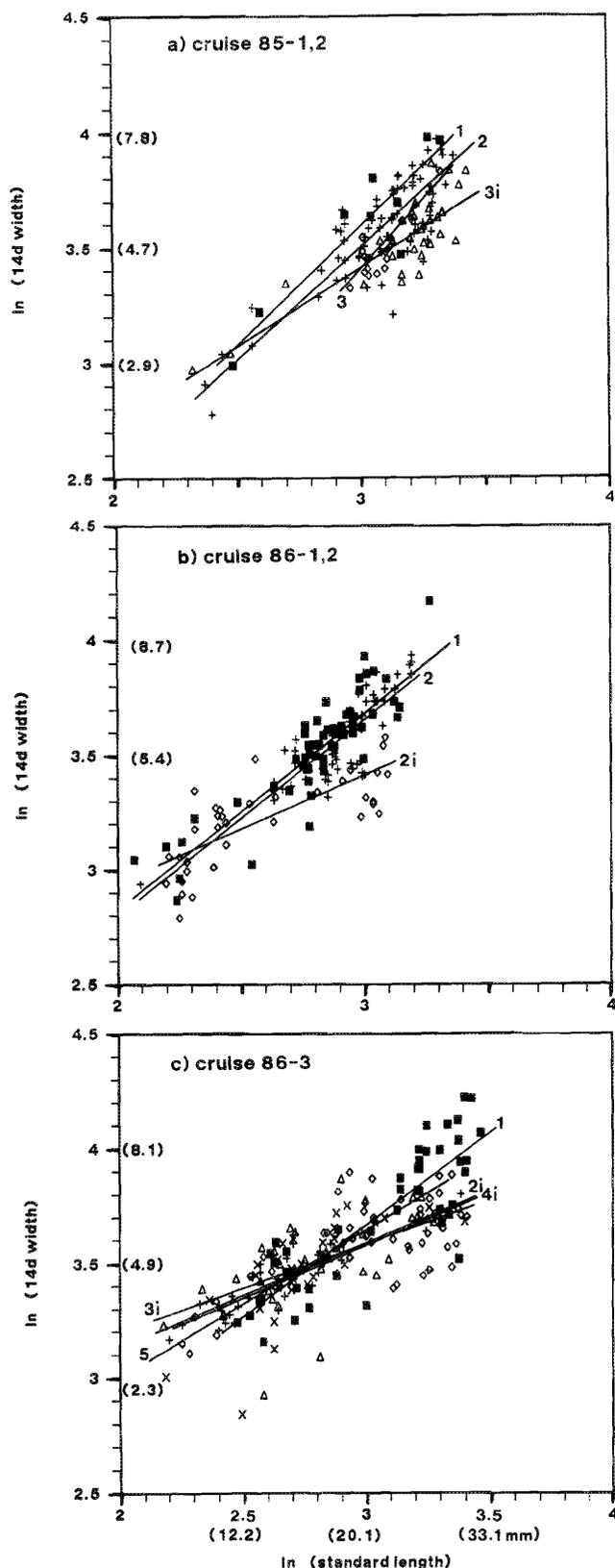


FIG. 8. Log-log plot of the cumulative width of the most recent 14 daily increments on standard length (SL) for each region during (a) cruises 85-1,2; region 1 (■), region 2 (+), region 3 (◇), region 3i (Δ), (b) cruises 86-1,2; region 1 (■), region 2 (+), region 2i (◇), and (c) cruise 86-3; region 1 (■), region 2i (+), region 3i (◇), region 4i

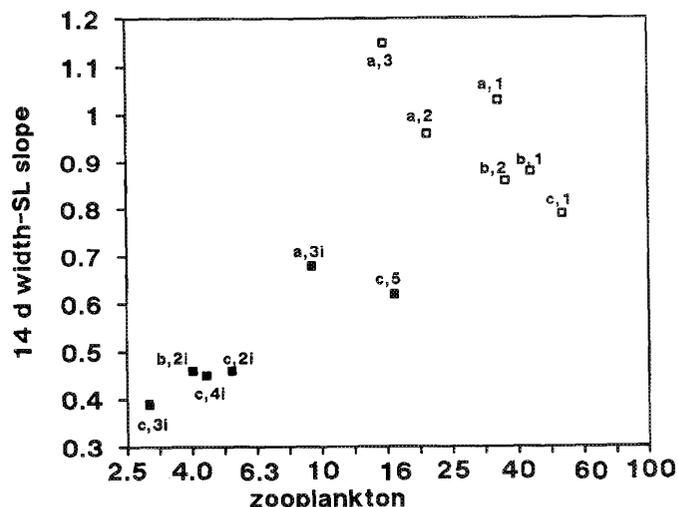


FIG. 9. Scatter plot of the 14-d width-SL slope (from Table 2a), and regional average biomass (log scale, $\text{mg}\cdot\text{m}^{-3}$) of total zooplankton ($>308\ \mu\text{m}$) during cruises (a) 85-1,2; (b) 86-1,2 and (c) 86-3. Points are identified as cruise, region. Closed symbols; inshore stations $<55\ \text{m}$, including region 5, open symbols; offshore stations including Browns Bank.

TABLE 3. Comparison of levels of significance for the region factor (cruise 85-1,2) and regional slope terms (cruises 86-1,2 and 86-3) for each of the four 7-d increment widths from 1 wk to 4 wk precapture (Fig. 10). Complete model was: width = constant + SL + region + region \times SL.

Cruise	Parameter	Week 1	Week 2	Week 3	Week 4
85-1,2	Region	**	**	—	—
86-1,2	Region \times SL	**	**	—	—
86-3	Region \times SL	*	*	—	—

age structure of cod between May and June, compared with the change in age structure inshore at region 2i. The hatch date distributions had changed significantly in region 2i during the intervening 3 wk, with the disappearance of older post-larvae (Fig. 7). Thus the spatial distribution of cod in nearshore regions appeared to be more variable, possibly due to poor survival associated with the slower growth rates there or high rates of advection through this region, or both.

Recent Growth Index and Dispersal

The hypothesis that the inshore region of southwestern Nova Scotia was a functional nursery ground for postlarval cod was rejected. The recent growth index in the nearshore habitat was significantly lower than in the offshore for all cruises in both years. This result is surprising given the high concentration of postlarvae seen in this region. If growth is positively correlated with survival (Anderson 1988), then recruitment could be reduced in years when inshore advection predominates (such as in 1985 compared with 1987, Suthers and Frank 1989) — although other factors such as high zooplankton biomass inshore could ameliorate this affect.

FIG. 8. (continued) (Δ), and region 5 (×). The anti-log of SL is shown in parentheses on the abscissa. Shown on the ordinate in parentheses is the increase in SL over 14 d using the otolith radius-SL relationship for each cruise.

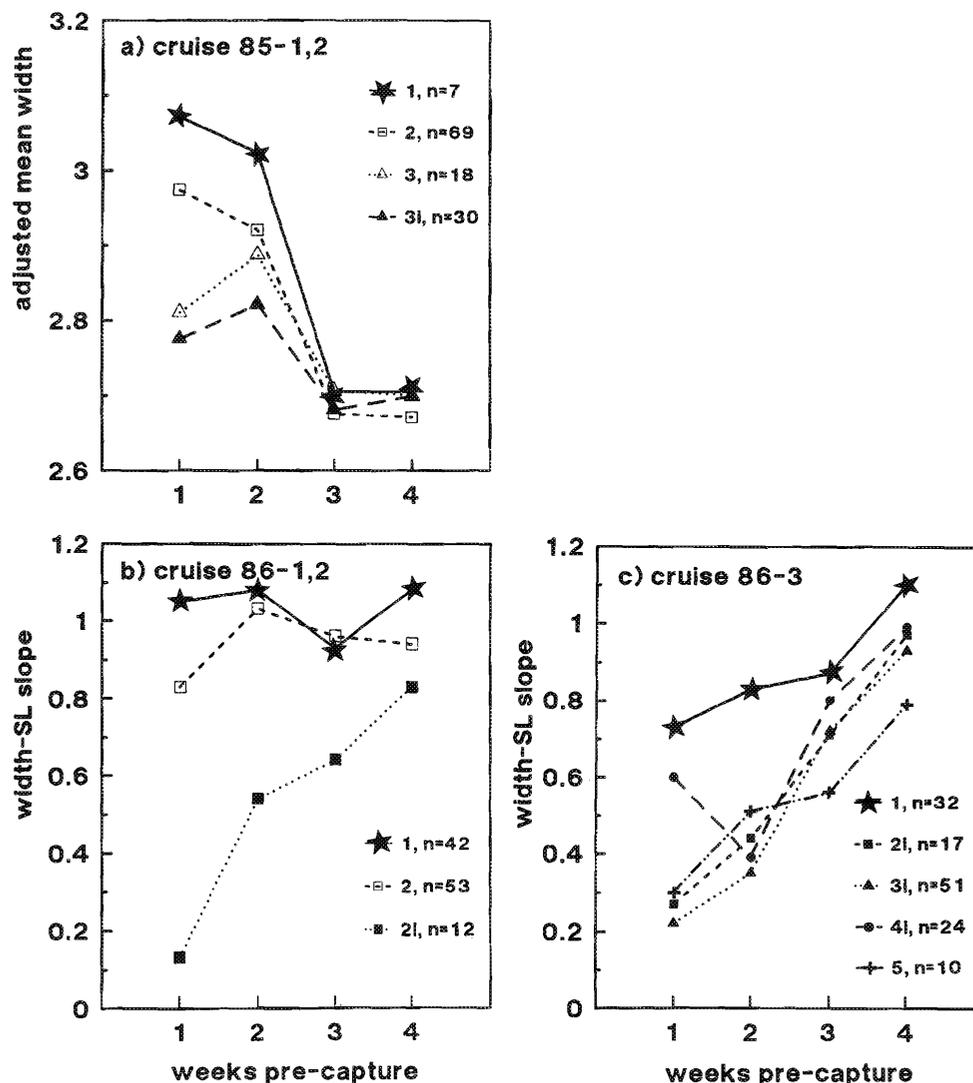


FIG. 10. Regional comparisons of the 7-d increment width-SL regression for weeks 1 to 4 precapture. (a) log mean adjusted widths, cruises 85-1,2 (b) width-SL slopes, cruises 86-1,2 and (c) width-SL slopes, cruise 86-3.

Zooplankton biomass $>308 \mu\text{m}$ was the principal factor that accounted for regional differences in recent growth, assuming that the food and temperature conditions at capture were representative of the previous 14 d. The greatest concentrations of zooplankton occur offshore in the 80–120 m depth range and in the vicinity of Browns Bank (Frank 1988). The gut contents of cod from cruises 85-1,2 largely contained the adult stages of *Calanus finmarchicus* (Budgey 1987). This result is consistent with Marak (1960) who found that the diet of postlarval and pelagic juvenile cod was dominated by copepods, particularly adult *Calanus* (average length 3.5 mm). When the smallest and largest zooplankton size fractions (308–602 and $>1050 \mu\text{m}$) were included in the multiple regression instead of total zooplankton, there was negligible improvement in the fit of the model. Yet if the analysis was confined to cod $>18 \text{ mm SL}$, then the zooplankton size fraction $>1050 \mu\text{m}$ was significantly correlated with the recent growth index ($p < 0.03$ for all cruises), while the 308–602 μm size fraction was not ($p > 0.1$). Thus not only the abundance but also the size relationship between postlarval cod and their prey can explain variation in increment width and recent growth. Prey abundance and quality have a

significant effect on increment width in the laboratory (Volk et al. 1984). Our study presents field evidence of a significant correlation between simultaneous measurements of recent growth and prey abundance of a size suitable for postlarval cod. Similar results using recent otolith growth increment widths, were found in larval Alaskan walleye pollock (*Theragra chalcogramma*) where the highest recent growth over 10 d prior to capture occurred at the station with the greatest zooplankton biomass (Bailey 1989). Current controversies about food availability limiting the growth and survival of larval fish (Anderson 1988; Frank 1988; Sinclair 1988; Taggart and Frank 1989) may largely stem from inappropriate sampling at unsuitable scales. For example length at age is an integrated measure of growth and does not reflect the environmental variables recorded at capture.

Low zooplankton biomass inshore could result from grazing pressure due to high densities of larvae and postlarval fish (up to $6 \cdot \text{m}^{-3}$, including sculpins, sandlance, herring, and other blennioids), and of the ctenophore *Pleurobrachia pileus* that can exceed $50 \cdot \text{m}^{-3}$ (Milne and Corey 1986). In June 1986, ctenophores were 20–30 fold more abundant inshore than on

the Bank, while postlarval fish other than cod were 10–100 fold more abundant (Suthers 1989). At nominal ctenophore densities of $1 \cdot m^{-3}$ the daily consumption of zooplankton would be approximately $4 \text{ mg} \cdot m^{-3}$ assuming a ration of $8.5 \text{ mg} \cdot d^{-1}$ and a feeding incidence of 50% (Frank 1986). Acknowledging the current uncertainty concerning clearance rates of ctenophores (Miller and Daan 1988; Bell 1988), the daily predation of *Pleurobrachia* alone could equal the inshore standing stock of zooplankton.

Seasonal changes in temperature have been shown to affect otolith increment widths in the field (Campana and Hurley 1989). The equivocal effects shown in this study may be due to the small range in temperature encountered ($<3^\circ\text{C}$ range; 85-1,2: $3.5\text{--}5.5^\circ\text{C}$, 86-1,2: $4.0\text{--}7.0^\circ\text{C}$, 86-3: $6.0\text{--}8.5^\circ\text{C}$). Any temperature effect would have been masked by the strong effect of variable feeding conditions that were independent of temperature. Although higher growth rates tended to occur on Browns Bank, water temperature was not always warmer there than inshore.

Growth Indices 4 wk Precapture

The regional differences were more apparent in the most recent 7-d growth index than in the most recent 14-d index. The difference in regional means or width–SL slopes began to diminish before the third week precapture (Fig. 10). This convergence of the growth history suggests a previous mixing of the population between the inshore and offshore, and a common origin on Browns Bank. These growth histories further support the concept that the nearshore cod distributions were not persistent (Fig. 7), but spatially variable at the scale of weeks. The width–SL slopes of region 5 (off Shelburne N.S.) during cruise 86-3 (Fig. 10c) diverged at 3 and 4 wk precapture, suggesting a different origin, perhaps in the northeast (O'Boyle et al. 1984; Campana et al. 1989). Geographical differences have been found in growth histories of fish larvae, corresponding to the local production, and conforming to known subpopulations of adults (Struhsaker and Uchiyama 1976; Nishimura and Yamada 1988). Further analysis of larval growth histories could therefore indicate mixing of larvae of different origin or stocks.

Regional variation in otolith increment widths that was observed is consistent with the findings of other studies that used different techniques to assess the role of food on growth and survival (e.g. O'Connell 1980; Theilacker 1986; Buckley and Lough 1987). For example, Theilacker (1986) found that at stations 350 km offshore in the southern Californian current, nearly 70% of early stage jack-mackerel larvae were starving while only 12% of larvae near coastal banks and islands were starving. These were first feeding larvae, and the geographical differences in condition reflect the stage-specific requirement for copepod nauplii, which were more abundant inshore. The recent growth of cod larvae ($<10 \text{ mm SL}$) was not investigated in this study. However, the distributions of larval and postlarval cod off southwestern Nova Scotia were generally coincident (Suthers and Frank 1989); their distributions reflect the influence of the episodic breakdown of the Browns Bank gyre with subsequent transport by the residual circulation. The biomass of large zooplankton ($>308 \mu\text{m}$) is greatest offshore and on Browns Bank, while landward there is an abundance of smaller ($80\text{--}153 \mu\text{m}$) particles suitable for larvae (Frank 1988). Therefore drift and retention of larval and postlarval cod offshore ($>55 \text{ m}$) in southwestern Nova Scotia, would maintain the early life stages of cod in the vicinity of a range of prey sizes. South-

western Nova Scotia is a highly productive region, through processes such as upwelling (Garrett and Loucks 1976) and a tidal front (Fournier et al. 1984). Distributions of larval herring in eastern Maine (Townsend et al. 1987), and of larval sciaenids in the Gulf of Mexico (Cowan and Shaw 1988) are also coincident with frontal regions. The spawning strategies shown by these fish with regard to dispersal and prey distribution may be quite general and applicable to cod as well.

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