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Dispersal and growth of pelagic juvenile Arcto–Norwegian cod (*Gadus morhua*), inferred from otolith microstructure and water temperature

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Dispersal of pelagic juvenile cod (*Gadus morhua*) off northern Norway from the main Lofoten spawning grounds to the western Barents Sea is regulated by the north-easterly circulation of the Norwegian coastal current (NCC). In July 1988 the smallest cod occurred within the spawning area (25.2 mm standard length, SL), but offshore small cod consistently occurred furthest from, rather than nearest to, the spawning area. The average SL of cod was 37 mm just offshore from the spawning area near Lofoten, 35 mm on the main post-larval nursery area on Tromsøflaket, and 33 mm in the western Barents Sea. Otolith microstructure analysis revealed no comparable difference in age, the mean age of cod ranging between 61–65 days post-hatch throughout the offshore distribution.

Cod offshore of Lofoten were distinguished from other cod by significantly greater length at age, higher condition factor (dry weight adjusted for length), and a different growth history. Change in SL back-calculated from the summed width of seven daily increments of the otolith, for each of 6 weeks before capture, revealed significantly greater growth for cod offshore from Lofoten which was correlated with water temperature. The slightly slower growth of cod in the western Barents Sea is consistent with transport in the colder NCC from the Lofoten spawning ground, while faster growth of cod offshore of Lofoten is consistent with transport in warmer Atlantic Ocean water, originating from the southern Møre coast spawning areas.

Key words: Arcto–Norwegian pelagic juvenile cod, dispersal, water temperature, otolith microstructure, condition factor, growth.

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Introduction

The stock of Arcto–Norwegian cod (*Gadus morhua*) has historically been the largest in the north Atlantic, with average landings pre-1979 of more than 50% of all the east Atlantic stocks (Garrod, 1988). As part of the management of this fishery, extensive pelagic juvenile cod surveys off north-eastern Norway extending over 16 000 km^2 have been conducted since 1977, to obtain an abundance index of 0-group recruitment (Ellertsen *et al.*, 1989; Sundby *et al.*, 1989). Pelagic juveniles are generally more abundant in the north-east, and are assumed to have drifted from the main Lofoten spawning area in the south-west (Fig. 1a, b). However, an analysis of the size distributions over the survey area in 1983–1985 revealed that, on average, pelagic juveniles were 2–4 mm smaller in the north-east than those close to the main spawning area (Bjørke and Sundby, 1987). The north-eastern pelagic juveniles should, indeed, have been larger (and older) if they had originated from the earlier part of the spawning period and drifted from the main south-western spawning area.

Bjørke and Sundby (1987) suggested that the growth rates were not uniform. The smaller, northern pelagic juveniles may have experienced lower temperatures, and consequently slower growth in contrast to the larger, southern pelagic juveniles from southern, warmer spawning areas. Alternatively, the smaller, northern pelagic juveniles could be younger, having hatched from small areas of local spawning (Sundby and Bratland, 1987). In this paper, these two hypotheses are tested through age and growth analyses using otolith microstructure and measurements of condition factor from the July 1988 survey. Additionally, the rate of otolith increment formation and relative increment widths are examined in pelagic

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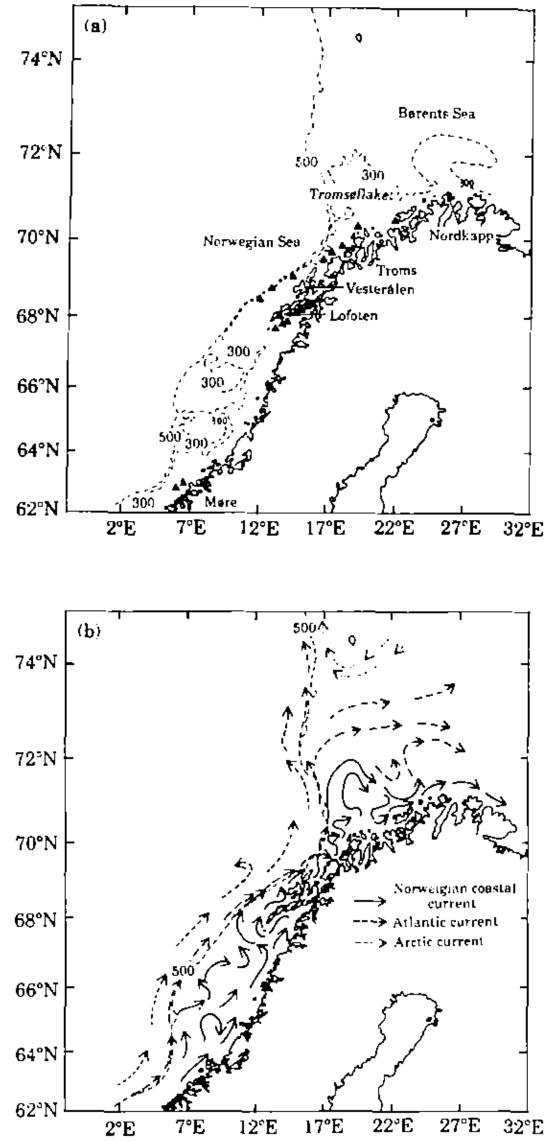

Figure 1. (a) Study area off northern Norway indicating geographic names used in text, and main cod spawning areas (▲, Godø and Sunnanå, 1984; Sundby and Bratland, 1987); and (b) principle circulation (after Sundby, 1984).

juvenile cod that were raised in a mesocosm above the Arctic Circle, under a natural 24-h daylight regime.

Materials and methods

Study area, spawning areas

The spawning areas are distributed in the Norwegian coastal current (NCC) off mid and north Norway, along a 1200 km coastline. The spawning sites are the same every year, although the magnitude of the spawning at individual sites may vary. Approximately 70% of spawning occurs along a rather limited part of the coastline in Lofoten and Vesterålen, between 67°30'N and 69°N (Sundby and Bratland, 1987, Fig. 1a). The rest occurs to the south in the Møre region off mid Norway, and to the north in the Troms region (Godø and Sunnanå, 1984). There is a remarkable constancy in the timing of spawning among years; it starts during the first days of March, reaches a maximum intensity during the first week of April and declines by the first half of May (Ellertsen *et al.*, 1987, 1989). The spawning period is delayed by about 2 weeks at the northernmost spawning field (Troms) relative to the Lofoten area (Sundby and Bratland, 1987).

The eggs and larvae are initially spread north-eastwards in the NCC, and gradually mix into the Atlantic water which also flows parallel to the coast along the shelf break. The spreading is strongly influenced by the bank topography creating clockwise vortices, which in turn reduce the speed of the north-eastward advection (Sundby, 1984). The most north-easterly and largest bank is Tromsøflaket (Fig. 1b), which is often associated with large concentrations of pelagic juvenile cod (Bjørke and Sundby, 1987).

Spawning coincides approximately with the annual temperature minimum of the year, and the early life stages are generally subjected to a linearly increasing temperature into July as they are spread north-east. The temperature increase is caused by summer heating of the upper layer, and advection of the larvae offshore towards the Atlantic water mass, which at this time of the year is warmer than the NCC (Sundby, 1984; Bjørke *et al.*, 1989). Thus, the temperature generally decreases north-eastwards along the coast, and increases strongly offshore towards the shelf break where the core of the Atlantic water is found.

Cruise dates and sampling gear

A pelagic juvenile survey was conducted annually off the north-western coast of Norway, between 62°N and 74°N. In 1988, 248 stations were sampled between 1–26 July by two vessels starting in the north-east of the sampling grid. The sampling gear was a pelagic trawl with a 29 × 29 m mouth opening, tapering to a cod-end with 5-mm mesh. The trawl was towed for 30 min at 2.5 knots (±0.5), as a stepped oblique tow at 40 m, 20 m, and surface. On deck, all pelagic juvenile cod were counted, and the standard length (SL) of up to 50 individuals per tow was measured to the nearest 0.5 mm. A random sub-sample was taken at 49 stations for otolith analysis and preserved in 80% ethanol, buffered with 6.6 ml/l of a saturated solution of tris (hydroxymethyl) aminomethane. Upon inspection of the pelagic juvenile abundances, 21 stations were

Table 1. Summary of sampling and length and age results, from the July 1988 survey. n = number.

Region	n stations	Total catch	n aged	n dry wt.	Mean SL*	Mean age in days	Mean hatch-date
1	4	73	26	45	29.4	65	10 May
2	8	1152	63	69	32.3	65	10 May
3	5	429	38	84	38.5	61	14 May
4	4	266	32	60	27.2	53	22 May

*Length not adjusted to mean cruise date.

selected from within four centres of abundance for length, dry weight, and age analysis (Table 1).

Daily increment formation and width from the mesocosm samples

Cod larvae were reared in a large enclosure pond (37 500 m^3 – see Pedersen *et al.*, 1989, for details) near Tromsø (69°51′N 18°52′E). The median hatching date was 20 April 1989 ($\pm$1.5 days). Larvae were fed natural zooplankton pumped from outside the enclosure, supplemented with dry artificial feed after about 30 days post-hatch (PH). At hatching the day length was 18 h, and by 30 days PH there was 24 h daylight. On 12 July (54 days PH) four cod were sampled, and a further five sampled on 16 July (58 days PH). The otoliths were extracted, labelled so as not to indicate the age to the otolith reader, and treated as below.

In the laboratory, 258 pelagic juvenile cod from the ocean were measured (SL), oven-dried at 60°C for 48 h and weighed to the nearest 0.5 mg. They were then rehydrated, the lapilli extracted under a binocular microscope using polarized light, and affixed to microscope slides using clear, fast-setting glue. Of the three pairs of otoliths, the lapillus is initially the fastest growing up to 25 days PH (Bergstad, 1984), and is therefore not only the most suitable for counting the relatively narrow larval increments, but is also the thinnest with a regular shape, making polishing of the otolith to the nuclear plane the easiest (Campana, 1989; Campana and Hurley, 1989). For 159 cod, one lapillus was then polished on one side to the nuclear plane using 10-μm lapping film, and increments counted at 1000 × magnification as described by Campana and Hurley (1989). Counts were repeated by the senior author until a consistent age was obtained. The increment counts of 12 otoliths were checked by a Canadian, and others were examined by a Norwegian colleague, and were found to be within 5–10%. Daily increments were measured from the periphery to the hatch check, using a digitizer interfaced with a Macintosh computer (see Anderson and Moksness, 1988, for details).

Analysis

Lengths of pelagic juvenile cod were adjusted to the mean date of the cruise (14 July) by adding or subtracting 0.5 mm day^{-1} (Bjørke and Sundby, 1987). This growth rate was determined from back-calculated growth rates (this study), and is similar to that determined from mesocosm studies (Pedersen *et al.*, 1989; Olsen *et al.*, 1991). Ages were also adjusted to 14 July for the inter-region comparison, such that ages of pelagic juveniles from the north-east early in the cruises were increased by up to 6 days, and from the south-west ages were reduced by up to 5 days. Length and age frequency distributions among regions were then compared with a Kolmogorov–Smirnov (KS) test. Length at age and dry weight at length were compared among regions by an analysis of covariance (ANCOVA). The condition analysis required dry weight and length to be transformed to natural logarithms.

To reconstruct the average temperature history along possible drift trajectories, we assumed that from hatch to capture the sum of the temporal and spatial temperature changes increased linearly. As a first approximation, the linear spatial increase in temperature is justified from inspection of temperature contour plots off the Norwegian coast during July 1988 (Bjørke *et al.*, 1989) and other studies (Sundby, 1984). The temperature at hatch was recorded at 20 m depth in the Lofoten, Møre, and Troms areas, which are routinely collected by the Institute of Marine Research in Bergen. The temperature at capture was taken as the mean temperature at 20 m depth within the 100 juveniles trawl hour^{-1} contour.

The weekly growth in SL was back-calculated from the summation of seven daily increment widths, for 6 weeks before capture (after Suthers *et al.*, 1989), using the biological intercept method for back-calculation (Campana, 1990). Change in SL was compared between the four areas of abundance using ANCOVA, for each of the six weeks. The independent variable for this analysis was the back-calculated standard length at the end of each week. There were no apparent trends in the residual plots for each of the six analyses. For this analysis, the daily growth was not adjusted to the same day to adjust for different sampling days (as above), because the growth between

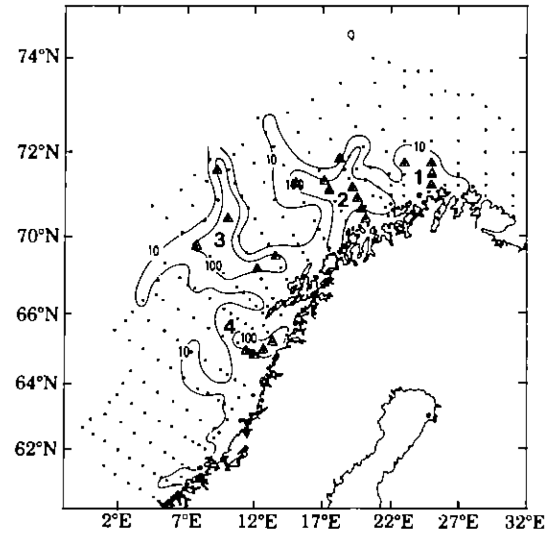

Figure 2. Spatial distribution of pelagic juvenile cod in July 1988 (after Bjørke *et al.*, 1989), indicating with large numerals the four regions, and the stations within each region that were sampled for otoliths are outlined with a triangle. Contour levels (no. trawl h^{-1}) are drawn by eye.

regions was of interest, regardless of the precise day, along with the inclusion of temperature on the day of capture.

Results

Spatial distribution and size

Four regions of pelagic juvenile cod abundance (as determined by the 10 cod trawl $hour^{-1}$ contour) were apparent in July 1988 (Fig. 2). The most northerly and farthest from the spawning area occurred off Nordkapp (region 1). The highest densities occurred in region 2, on Tromsøflaket, and covered the largest area constituting 42% of the total abundance index. Further south-west, region 3 extended offshore into the Norwegian Sea and comprised 35% of the total abundance index. This patch was not associated with any bottom topographic feature, and appears to be unusual in comparison to the distribution in other July surveys (Bjørke and Sundby, 1987; Bjørke *et al.*, 1989). Region 4 occurred close to the coast, just south of the main spawning grounds at Lofoten.

The temperature–salinity (T–S) plot for each of the four regions shows each is associated with different water masses (Fig. 3). The cod in region 3 is completely mixed into Atlantic water, whereas the cod in region 4 are found in NCC water. Regions 1 and 2 are in a mixture of the two water masses, with the former being 2°C cooler.

The adjusted SL frequency distributions for each region all differed significantly from each other, except regions 1 and 2 (Fig. 4, Table 2). The mean SL decreased from region

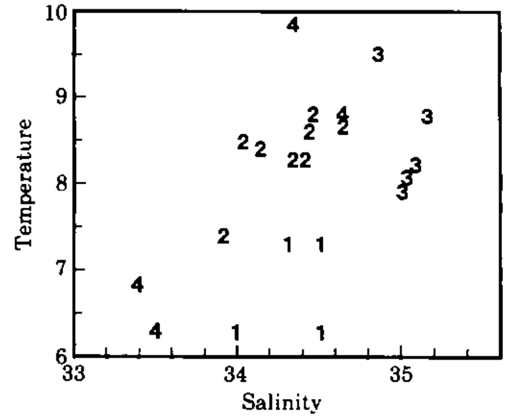

Figure 3. Temperature–salinity plot (at 20 m) of stations sampled for otolith analysis from the four regions, with the relevant region number indicating the data point.

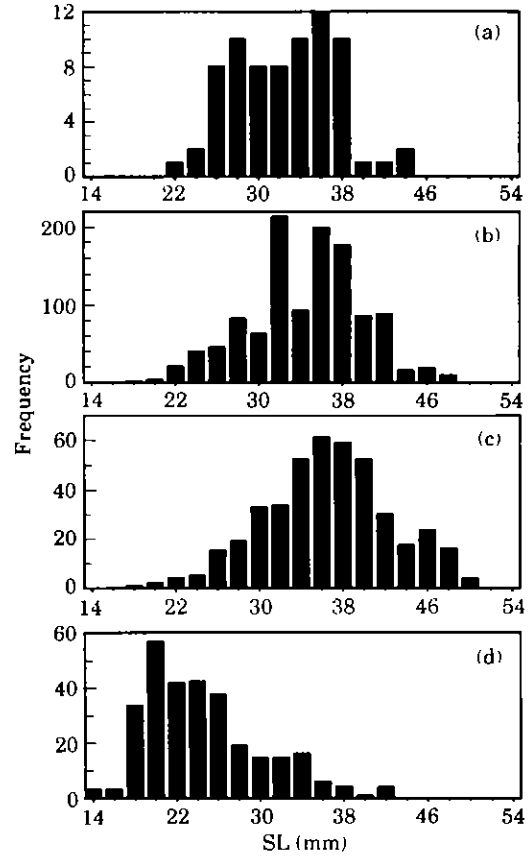

Figure 4. Adjusted standard length frequency distribution (SL) of pelagic juvenile in July 1988. Standard lengths were adjusted by 0.5 mm day^{-1} to the mid-cruise date on 14 July. (a) Region 1, 33.1 mm; (b) region 2, 35.1 mm; (c) region 3, 37.0 mm; (d) region 4, 25.2 mm.

Table 2. Table of Kolmogorov-Smirnov two-sample test probability levels. Above the diagonal is the comparison of SL between regions (Fig. 4), and below the diagonal is the comparison of age between regions (Fig. 5).

	Region 1	Region 2	Region 3	Region 4
Region 1	–	0.162	<0.001	<0.001
Region 2	0.961	–	<0.001	<0.001
Region 3	0.055	0.055	–	<0.001
Region 4	<0.001	0.001	<0.001	–

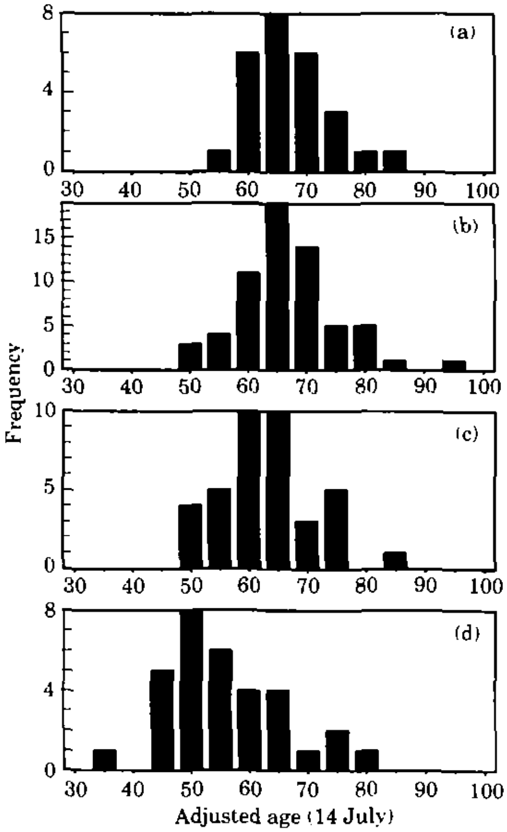

Figure 5. Age-frequency distribution of pelagic juvenile cod, adjusted to the mid-cruise date on 14 July 1988. (a) Region 1, 65 days; (b) region 2, 65 days; (c) region 3, 61 days; (d) region 4, 53 days.

3 off the main spawning area (37.0 mm), to region 2 (35.1 mm) to region 1 (33.1 mm) in the north-east. However, the most south-westerly region had the smallest mean length, near the main spawning area (region 4, 25.2 mm). The length frequency distribution for region 4 indicated extrusion through the mesh of larvae less than 18 mm SL (Fig. 4d), and thus underestimated the mean length.

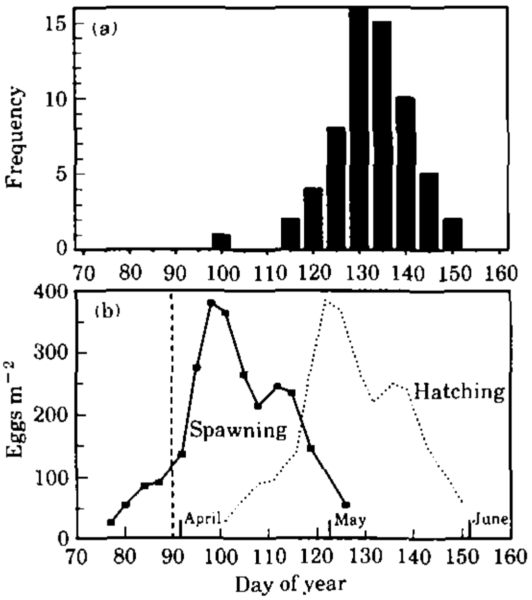

Figure 6. (a) Hatch-date frequency distribution calculated for region 2. (b) Spawning intensity curve at the Lofoten spawning grounds during Spring 1988 (solid line), and the subsequent hatching curve (dotted line, calculated from temperature-dependent egg development rate, with no mortality component). The vertical dashed line indicates day of 50% spawning (31 March, mean from 1976–1983, Ellertsen *et al.*, 1987). The otolith-derived hatch-date distribution is approximately 1 week later than the hatching curve. See text for details.

Age, growth, and condition

While the otoliths showed no evidence of poor preservation, they were often difficult to read. The increment structure appeared faint, with many fine irregular lines. Approximately 28% were therefore discarded as unreadable, which was not associated with size or station, leaving 159 readable.

The adjusted age frequency distributions were not significantly different between regions 1 and 2 (mean age 65 days, Table 2, Fig. 5a, b), which were both not significantly different from region 3 (mean age 61 days, Table 2, Fig. 5c). The smallest larvae in region 4 near the main spawning area were also the youngest (mean age 53 days, Table 2, Fig. 5d).

The hatch-date distribution was calculated for region 2 (which had the largest cod concentration) by subtracting each age from the capture date. The mean hatch date was 10 May, with the majority of hatch dates between 15 April and 29 May (Fig. 6a). Alternatively, the hatch-date distribution was determined independently from the spawning intensity curve recorded at Lofoten in the spring of 1988 (Fig. 6b, P. Solemdal, pers. comm.), and then calculating the subsequent hatching curve using the procedure of Ellertsen *et al.* (1987). The hatching curve is calculated from cod egg development rates, average April

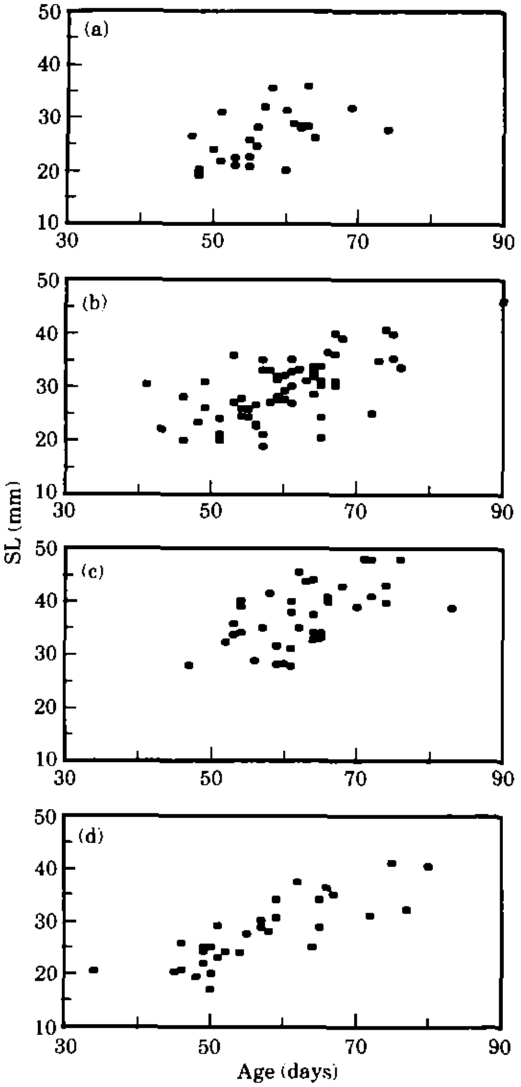

Figure 7. Scatter plot of standard length on age for all regions (Table 3a). *SL = −1.050+0.530 × age, $r^2 = 0.44$, n = 159. (a)* Region 1, n = 26; (b) region 2, n = 63; (c) region 3, n = 38; (d) region 4, n = 32.

Table 3. ANCOVA table of: (a) SL on age between regions (slopes n.s.); and (b) log dry weight on log (SL) between regions. d.f., degrees of freedom; MS, mean square; F, F ratio; p, probability; *, $p < 0.05$.

Source	d.f.	MS	F	p
(a) Age	1	2252	121	<0.01*
Region (intercept)	3	483	26	<0.01*
Residual	154	19		
(b) *SL*	*1*	*80.19*	*11 966.1*	*<0.01**
Region (intercept)	3	0.02	3.6	0.01*
Region × SL (slope)	3	0.03	3.9	0.01*
Residual	301	0.01		

water temperature (3.0°C, range 2.6–3.4, resulting in approximately 24 days incubation), and assuming equal egg mortality all through the spawning season. The peak period of hatching calculated from the spawning curve is about 1-week earlier than the peak hatch-date frequency, back-calculated from the otolith ages (Fig. 6).

The growth rate indicated by the slope of SL on age was *significantly greater in region 3 than elsewhere (Fig. 7,* ANCOVA, Table 3). Overall, during weeks 1 and 2 before capture, cod grew at 0.65 mm day^{-1}. Similarly, the condition index, indicated by the slope of log dry weight on log SL was significantly greater for pelagic juveniles at region 3 (Fig. 8c) than the other three regions which were not significantly different from each other (Fig. 8, ANCOVA, Table 3).

Growth history from the otolith

The growth history in region 3 appears different from the other regions. Region 3 had a significantly greater weekly growth than the other regions, in the back-calculated increase in SL during weeks 1, 2, 3, and week 6 before capture (Fig. 9, Table 4). During weeks 4 and 5, weekly growth did not differ from the other regions (Fig. 9, Table 4).

To determine if the temperature recorded at capture (20 m depth) influenced pelagic juvenile growth, the back-calculated change in SL over the first week before capture was reanalysed. Region was removed from the ANCOVA model in Table 4, and replaced with temperature, which as a covariate with SL was significantly correlated with weekly growth (multiple regression model, $p = 0.05$).

Integrated temperature–growth model

The relationship between size at capture and the integrated temperature history (in days × °C), also indicates that the cod from region 3 have a different origin from the other regions (Fig. 10). In this analysis we assumed juveniles from regions 1 and 2 originated from the Troms or Lofoten spawning areas, which had equal temperatures at hatch. Region 4 juveniles appear to have originated from Lofoten spawning because of their younger age and proximity to the spawning area (Fig. 2). However, region 3 juveniles *may have originated from either Lofoten or Møre, and* both possible integrated temperature histories were calculated (Fig. 10). There is a higher correlation between size at capture and degree-days if region 3 juveniles originated at the Møre spawning grounds rather than the Lofoten area.

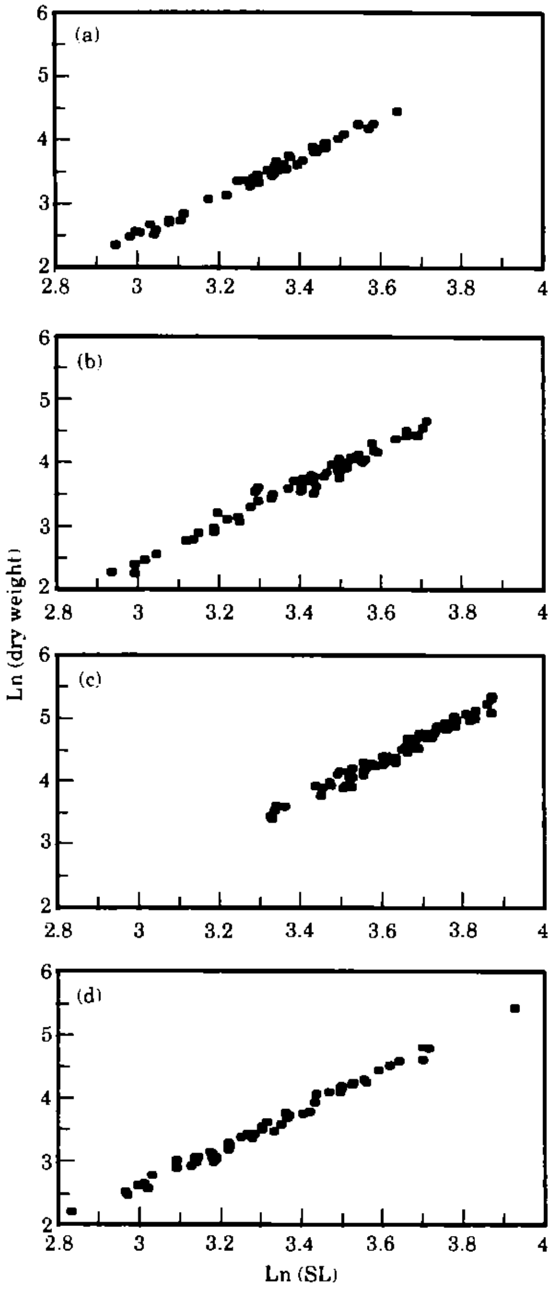

Figure 8. Log–log plots of dry weight on SL for each region. Region 3 is significantly different from the other regions (Table 3b). (a) Region 1, $\ln(DW) = -6.68 + 3.06 \times \ln(SL)$; (b) region 2, $\ln(DW) = -6.61 + 3.02 \times \ln(SL)$; (c) region 3, $\ln(DW) = -7.43 + 3.27 \times \ln(SL)$; (d) region 4, $\ln(DW) = 6.58 + 3.06 \times \ln(SL)$.

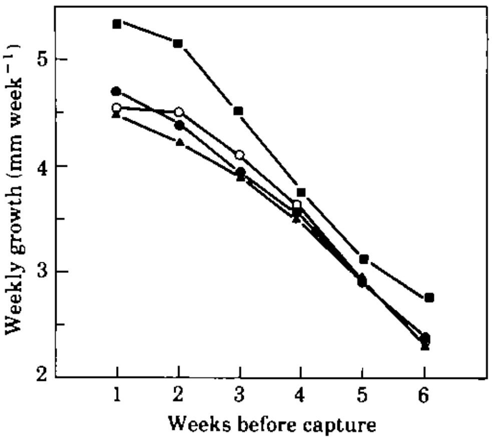

Figure 9. Average back-calculated weekly growth in SL (ANCOVA adjusted for size, Table 4), for weeks 1–6 before capture. ▲ = region 1, ● = region 2, ■ = region 3, ○ = region 4.

Table 4. Final ANCOVA table of the six analyses, with back-calculated weekly change in SL as the dependent variable for each week pre-capture. The region X SL interaction term (slopes) was not significant in all analyses and was removed from the model. *, $p < 0.05$.

Week	Source	d.f.	MS	F	p
1	SL at capture	1	47.26	65.49	<0.01*
	Region	3	3.82	5.29	<0.01*
	Error	154	0.72		
2	SL week 1	1	55.11	82.57	<0.01*
	Region	3	4.14	6.20	<0.01*
	Error	154	0.67		
3	SL week 2	1	54.66	97.86	<0.01*
	Region	3	0.21	5.83	0.02*
	Error	154	0.56		
4	SL week 3	1	64.36	170.13	<0.01*
	Region	3	0.42	1.11	0.35
	Error	154	0.38		
5	SL week 4	1	58.97	251.53	<0.01*
	Region	3	0.34	1.43	0.24
	Error	154	0.23		
6	SL week 5	1	63.05	315.98	<0.01*
	Region	3	1.09	5.46	<0.01*
	Error	150	0.047		

Rate and width of otolith growth increments of reared cod

Validation of age, as determined from otolith microstructure, was made on reared pelagic juveniles since the daily increment formation of Arcto–Norwegian cod may be biased by the natural 24-h daylight regime. The ages of the reared pelagic juveniles were on average within ±3 days (range 0–11 days) of the true age (i.e. ±5%, range 0–20%). The number of increments of the 54-day PH juveniles ranged between 54–63 increments, and of the 58-day PH juveniles between 57–64 increments, as outlined below:

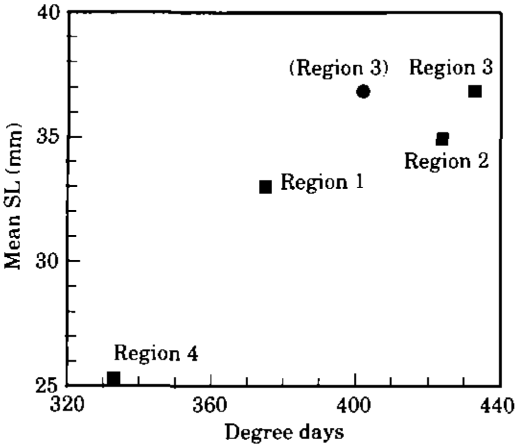

Figure 10. Mean SL at capture plotted on integrated temperature history (degree days from hatch) for each region. Region 3 (■) is calculated from Møre origin, (●) from Lofoten origin.

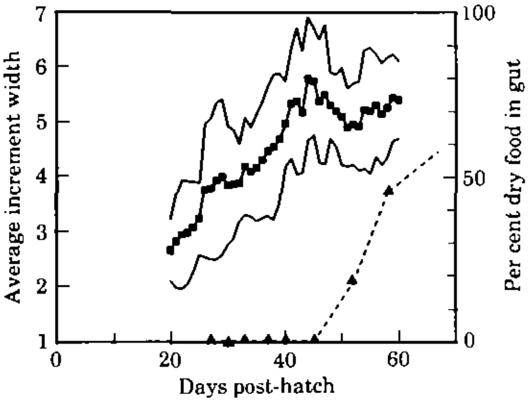

Figure 11. Plot of average daily growth increment width of the otolith (± 1 S.D.) from cod reared in the Tromsø mesocosm (n = 9). The percentage of gut content containing dry food (data from Olsen, 1989) indicates that the natural food was insufficient after 45 days PH. See text for details.

Mean SL (±S.E.)	Actual age (±1.5 days)	No. increments (±S.E.)
38.8 (1.5)	54	57 (2.1)
35.4 (3.1)	58	59 (1.3)

The daily averaged increment width increased until 42 days PH, and then decreased until 51 days PH (Fig. 11). This corresponds to a period of starvation when the abundance of natural zooplankton was insufficient and the incidence of cannibalism increased (T. Pedersen, pers. comm.). The diet of cod changed from 100% zooplankton to nearly 50% dry feed between 45 days PH and 58 days PH due to insufficient zooplankton (Olsen *et al.*, 1991, Fig. 11).

Discussion

The spatial distribution of pelagic juvenile cod off northern Norway during July 1988, when four broad regional concentrations were observed, appears due to variable transport of larvae in the NCC from Lofoten (where 70% of spawning occurs), and also from Møre in the NCC and Atlantic current. Those larvae caught by the clockwise circulation above banks are temporarily retarded, while in other regions they are subjected to rapid transport by coastal jets (Sundby, 1984; Bjørke and Sundby, 1987).

The smaller northern juveniles are not younger, as we hypothesized – possibly being derived from small areas of later local coastal spawning – as there were only slight differences in mean age (except region 4 that was almost on the Lofoten spawning area). The inverse size gradient of pelagic juveniles noted in this study and in other years (Bjørke and Sundby, 1987) is due to slower growth in the northern regions, in comparison to the greater size at age in region 3. In addition to size, two factors that can most likely account for growth differences are water temperature (e.g. Laurence, 1978; Campana and Hurley, 1989; Pepin, 1991) and food (e.g. Laurence, 1974; Bailey, 1989; Suthers *et al.*, 1989), although region-specific removal of slow-growing larvae by predators is also a possibility. Temperatures were routinely collected during the 1988 survey, but zooplankton biomass was not. Over broad spatial and temporal scales (100s km, months), water temperature appears to be the dominant effect in the growth of ocean-caught larvae (Campana and Hurley, 1989). However, over smaller spatial and temporal scales (10s km, weeks), prey abundance can have a demonstrable effect on growth and condition of cod larvae in the open ocean (Koslow *et al.*, 1985; Bailey, 1989; Suthers *et al.*, 1989; Karakiri *et al.*, 1989). Rearing experiments show that after 5 weeks the weight of larval cod reared at 10°C is approximately twice that of cod reared at 7 or 4°C (Laurence, 1978). However, after 5 weeks the body weight of larval cod increases seven-fold when reared at food densities of 500 versus 3000 copepods l^{-1} (Laurence *et al.*, 1981). A six-fold increase in dry weight occurs in 12-day-old sea-trout larvae (*Cynoscion nebulosus*) when reared at 24 or 32°C, but an approximately 10-fold increase when reared at food densities of 25 or 5000 copepods l^{-1} (Taniguchi, 1981). Rearing experiments indicate the scope for growth under extremes of food level, particularly when at Lofoten maximum gut fulness of cod larvae is found at food densities of 10 nauplii l^{-1} (Ellertsen *et al.*, 1987), while temperatures ranged over the study area between 6–10°C (Fig. 3). The simplest hypothesis to account for the growth differences observed in this study is the effect of temperature, which finds some support from our analyses.

The juvenile cod from region 3 significantly exceeded the growth rates of the other three regions, in terms of size at age, the condition factor, and the greater growth history over 6 weeks before capture. Region 3 juveniles have a separate origin probably further south off Møre, shown by their different growth history (Fig. 9). The extent to which this is temperature-mediated growth is supported by the degree–day relationship (Fig. 10), and by the significant effect of temperature on growth during the week before capture. The modified ANCOVA analysis, in replacing the region factor with the temperature variable, is limited, with only 21 stations, requiring more detailed knowledge of the spatial and temporal changes in temperature experienced by the larvae. In the growth history analysis we assume that cod otolith growth responds within days to environmental changes in temperature and food (e.g. Bailey, 1989). We also assume each station's average temperature at 20 m is representative of the temperature experienced by cod during the week before capture. However, cod larvae and juveniles are generally concentrated in the upper 20 m, above the thermocline (Ellertsen *et al.*, 1984). The spatial distribution of zooplankton food biomass may also be correlated with temperature (or biomass of the relevant size fraction), and this awaits further analysis.

Water temperature, zooplankton, and recruitment are linked since the date of peak copepod production is temperature-dependent, and yet cod spawning period is relatively fixed (Ellertsen *et al.*, 1989). Year-class strength of Arcto–Norwegian cod at age 3 years can vary by a factor of 15, and high water temperature during the early life stages is a necessary condition to form a strong year-class. Survival of cod larvae may therefore depend on the match of their abundance with copepod production (Ellertsen *et al.*, 1989; Cushing, 1990). Interestingly, the peak hatch date derived from the spawning curve was about 1 week earlier than the back-calculated peak hatch date of pelagic juveniles from region 2, Tromsøflaket (Fig. 6). This assumes that there was no net avoidance by older and larger pelagic juveniles that could possibly shift the hatch-date distribution to earlier in the year. This is unlikely considering the large size of the sampling gear. Alternatively, the latter part of cod spawning may include the commencement of haddock spawning (as the early egg stages of the two species cannot be distinguished), but the addition of the trailing ends of two distributions is unlikely to affect the modal, or peak, hatch date. In 1988, therefore, the survival rate of eggs to pelagic juvenile stage spawned in the latter half of the spawning period (> 12 April) appears greater than survival of the early eggs. As water temperature at spawning was about average (3°C), reasons for the apparent increased mortality of the early-spawned larvae are unknown.

Our age and growth analyses depend on the assumption that growth increments of the otolith form daily, despite the 24-h daylight/twilight north of Lofoten, which commences a few weeks after peak hatch (Suthers and Sundby, in prep.). In the laboratory, daily increment formation persists after transfer to 24-h light (Campana and Neilson, 1985), but rearing of eggs in 24-h daylight through to hatch and beyond produced a confused pattern (Dale, 1984). The daily formation of increments was substantiated by the validation of pelagic juvenile cod from north of Lofoten (this study), consistent with other accounts of larval Arcto–Norwegian cod – albeit from more southern regions (Bergstad, 1984; Dale, 1984; Gjøsæter and Tilseth, 1982). Furthermore, the width of otolith increments in pelagic juvenile cod appears temporally related to their food supply (Fig. 11; Bailey, 1989; Karakiri *et al.*, 1989). However, up to three times the otoliths were found to be unreadable compared with west Atlantic pelagic juvenile cod (Suthers *et al.*, 1989), possibly due to the long daylength. This may increase the daily duration of feeding, and therefore growth, relative to more southern stocks (Pedersen *et al.*, 1989; Ellertsen *et al.*, 1980; Suthers and Sundby, in prep.). Nevertheless, a cascade of events is released by the effect of water temperature at spawning, extending through to the formation of the year-class strength itself (Ellertsen *et al.*, 1989; Sundby *et al.*, 1989). This study shows that water temperature, either proximally or distally, can influence the growth of pelagic juveniles, and thus form part of that recruitment process.

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References

Andersen, T., and Moksness, E. 1988. Manual for reading daily increments by the use of a computer program. Flødevigen meldinger no. 4–1988. English version.

Bailey, K. M. 1989. Interaction between the vertical distribution of juvenile walleye pollock *Theregra chalcogramma* in the eastern Bering Sea, and cannibalism. Marine Ecology Progress Series, 53: 205–213.

Bergstad, O. A. 1984. A relationship between the number of growth increments on the otoliths and age of larval and juvenile cod, *Gadus morhua* L. *In* The propagation of cod *Gadus morhua* L., pp. 251–273. Ed. by E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal. Flødevigen Rapportser, 1. 895 pp.

Bjørke, H., and Sundby, S. 1987. Distribution and abundance indices of postlarval and 0-group cod. *In* The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea. Proceedings of the third Soviet-Norwegian symposium, Murmansk, 26–28 May 1986, pp. 127–144. Ed. by H. Loeng. Institute of Marine Research, Bergen. 250 pp.

Bjørke, H., Ellertsen, B., Hansen, K., and Bakkeplass, K. 1989. Yngelundersøkelser i juli-august i 1988 og 1989 utenfor norskekysten. Institute of Marine Research egg and larval program no. 28. (In Norwegian.)

Campana, S. E. 1989. Otolith microstructure of three larval gadoids in the Gulf of Maine, with inferences on early life history. Canadian Journal of Zoology, 67: 1401–1410.

Campana, S. E. 1990. How reliable are growth back-calculations based on otoliths? Canadian Journal of Fisheries and Aquatic Sciences, 47: 2219–2227.

Campana, S. E., and Hurley, P. C. F. 1989. An age- and temperature-mediated growth model for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in the Gulf of Maine. Canadian Journal of Fisheries and Aquatic Sciences, 46: 603–613.

Campana, S. E., and Neilson, J. D. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences, 42: 1014–1032.

Cushing, D. H. 1990. Hydrographic containment of a spawning group of plaice in the Southern Bight of the North Sea. Marine Ecology Progress Series, 58: 287–297.

Dale, T. 1984. Embryogenesis and growth of otoliths in the cod (*Gadus morhua* L.). *In* The propagation of cod *Gadus morhua* L., pp. 231–250. Ed. by E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal. Flødevigen Rapportser, 1. 895 pp.

Ellertsen, B., Solemdal, P., Strømme, T., Tilseth, S., and Westgård, T. 1980. Some biological aspects of cod larvae (*Gadus morhua* L.). Fiskeridirektoratets Skrifter Serie Havundersøkelser, 17: 29–47.

Ellertsen, B., Fossum, P., Solemdal, P., Sundby, S., and Tilseth, S. 1984. A case study on the distribution of cod larvae and availability of prey organisms in relation to physical processes in Lofoten. *In* The propagation of cod *Gadus morhua* L., pp. 453–477. Ed. by E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal. Flødevigen Rapportser, 1. 895 pp.

Ellertsen, B., Fossum, P., Solemdal, P., Sundby, S., and Tilseth, S. 1987. The effect of biological and physical factors on the survival of Arcto-Norwegian cod and the influence on recruitment variability. *In* The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea. Proceedings of the third Soviet–Norwegian Symposium, Murmansk, 26–28 May 1986, pp. 101–126. Ed. by H. Loeng. Institute of Marine Research, Bergen, 1987. 250 pp.

Ellertsen, B., Fossum, P., Solemdal, P., and Sundby, S. 1989. Relation between temperature and survival of eggs and first feeding larvae of northeast Arctic cod (*Gadus morhua* L.). Rapports et Procés-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 191: 209–219.

Garrod, D. J. 1988. North Atlantic cod: Fisheries and management to 1986. *In* Fish population dynamics, 2nd edn, pp. 185–218. Ed. by J. A. Gulland. J. Wiley & Sons. 422 pp.

Gjosæter, H., and Tilseth, S. 1982. Primary growth increments in otoliths of cod larvae (*Gadus morhua* L.) of the Arcto-Norwegian cod stock. Fiskeridirektoratets Skrifter Serie Havundersøkelser, 17: 287–295.

Godø, O. R., and Sunnanå, K. 1984. Spawning area and distribution of 0-group cod *Gadus morhua* L., on the More coast. *In* The propagation of cod *Gadus morhua* L., pp. 519–532. Ed. by E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal. Flødevigen Rapportser, 1. 895 pp.

Karakiri, M., Berghahn, R., and von Westernhagen H. 1989. Growth differences in 0-group place *Pleuronectes platessa* as revealed by otolith microstructure analysis. Marine Ecology Progress Series, 55: 15–22.

Koslow, J. A., Brault, S., Dugas, J., Fournier, R. O., and Hughes, P. 1985. Condition of larval cod (*Gadus morhua*) off southwest Nova Scotia in 1983 in relation to plankton abundance and temperature. Marine Biology, 86: 113–121.

Laurence, G. C. 1974. Growth and survival of haddock (*Melanogrammus aeglefinus*) larvae in relation to planktonic prey concentration. Journal of the Fisheries Research Board of Canada, 31: 1415–1419.

Laurence, G. C. 1978. Comparative growth, respiration, and delayed feeding abilities of larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as influenced by temperature during laboratory studies. Marine Biology, 50: 1–7.

Laurence, G. C., Smigielski, A. S., Halavik, T. A., and Burns, B. R. 1981. Implications of direct competition between larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in laboratory growth and survival studies at different food densities. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 178: 304–311.

Olsen, R. E, Henderson, R. J., and Pedersen, T. 1991. The influence of dietary lipid classes on the fatty acid composition of small cod *Gadus morhua* L. juveniles reared in an enclosure in northern Norway. Journal of Experimental Marine Biology and Ecology, 148: 59–76.

Pedersen, T., Eliassen, J. E., Eilertsen, H. C., Tande, K. S., and Olsen, R. E. 1989. Feeding, growth, lipid composition, and survival of larval cod (*Gadus morhua* L.) in relation to environmental conditions in an enclosure at 70° in northern Norway. Rapports et Procés-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 191: 409–420.

Pepin, P. 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Canadian Journal of Fisheries and Aquatic Sciences, 48: 503–518.

Sundby, S. 1984. Influence of bottom topography on the circulation at the continental shelf off northern Norway. Fiskeridirektoratets Skrifter Serie Havundersøkelser, 17: 501–519.

Sundby, S., and Bratland, P. 1987. Spatial distribution and production of eggs from northeast-Arctic cod at the coast of northern Norway 1983–1985. Fisken Hav., 1: 1–58. (English abstract.)

Sundby, S., Bjørke, B., Soldal, A. V., and Olsen, S. 1989. Mortality rates during the early life stages and year-class strength of northeast Arctic cod (*Gadus morhua* L.). Rapports et Procés-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 191: 351–358.

Suthers, I. M., Frank, K. T., and Campana, S. C. 1989. Spatial comparison of recent growth in post-larval cod (*Gadus morhua*) off southwestern Nova Scotia: inferior growth in a presumed nursery area. Canadian Journal of Fisheries and Aquatic Sciences, 46(Supplement 1): 13–124.

Taniguchi, A. K. 1981. Survival and growth of larval spotted seatrout (*Cynoscion nebulosus*) in relation to temperature, prey abundance and stocking densities. Rapports et Procés-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 178: 507–508.