ICES Journal of Marine Science, 57: 1182–1195. 2000
doi:10.1006/jmsc.2000.0880, available online at http://www.idealibrary.com on IDEAL®

Spatial variation in hatch date distributions and origin of pelagic juvenile cod in Icelandic waters

Gudrun Marteinsdottir[1]*, Björn Gunnarsson[1],
and Iain M. Suthers[2]

Marteinsdottir, G., Gunnarsson, B., and Suthers, I. M. 2000. Spatial variation in hatch date distributions and origin of pelagic juvenile cod in Icelandic waters. – ICES Journal of Marine Science, 57: 1182–1195.

Hatch date distributions, local spawning time and incubation temperatures at different spawning sites around Iceland were used to trace the most likely origin of 0-group cod. Length, age and hatch date frequency distributions were obtained from young larvae collected on the main spawning grounds off the south coast in 1995 and from pelagic 0-group cod captured in six nursery regions off the west, north and east coast of Iceland in 1995, 1996 and 1997. Historically, the 0-group cod found in coastal areas north and east of the country are believed to have originated from the main spawning grounds at the south-southwest coast. Contrary to the expected dispersal pattern, both size and age of 0-group cod decreased from west to north, when moving clockwise around the country away from the main spawning grounds in the south. It is shown that this spatial variation in size is not explained by different growth rates but by age. Consequently, the reconstructed spawning periods of surviving 0-group cod captured along the north and the east coast and the recorded spawning time for cod on the main spawning grounds in the south were not congruent. Large proportion of these 0-group cod, especially in 1995 and 1996, appeared to have hatched in June and July or considerably later than the recorded time period of hatching on the main spawning grounds in April and May. Therefore, rather than originating on the main spawning grounds in the south, some of the surviving 0-group cod originated from spawning that occurred in the western, northern and eastern fjords, during either the spring when local water temperatures were 3–4°C colder, or in early summer at a much later time. Spawning females have been observed at these locations over an extended time period (April–June) and protracted incubation periods due to cold waters will result in delayed hatching of larvae. In some years the smaller northern spawning sites, may contribute significantly towards the surviving population of 0-group juveniles, and probably contributing to the relative stability in recruitment experienced by this stock.

Key words: Iceland, pelagic 0-group cod, hatch date distribution, spawning date distribution, growth.

Received 3 November 1999; accepted 9 May 2000.

G. Marteinsdottir, and B. Gunnarsson: Marine Research Institute, P.O. Box 1390, Skulagata 4 Reykjavik, Iceland. I. M. Suthers: School of Biological Science, University of New South Wales, Sydney, 2052 Australia. Correspondence author: Tel. +354-5520240; Fax: +354-5623790; email: runa@hafro.is

Introduction

Many nations conduct pelagic juvenile or 0-group surveys on which they base their first prediction of year class strength (eg. cod, Sunby *et al.*, 1989; Asthorsson *et al.*, 1994; Anderson and Dalley, 1998). Although 0-group abundance indices may provide an early indication of year-class strength, they do not correlate well with recruitment (Asthorsson *et al.*, 1994; Anderson and Dalley, 1998). 0-Group indices are usually assembled for large geographic areas, by averaging abundance in diverse habitats and ignoring the fact that the surviving populations of pelagic juveniles may have originated from different spawning sites characterized by a diverse stock–environmental interactions that may affect growth and survival.

The location and the time of spawning in fishes are thought to be temporally and spatially located so as to provide optimum conditions for newly hatched eggs and larvae (Cushing, 1990). Protracted spawning may

1054–3139/00/041182+14 $30.00/0

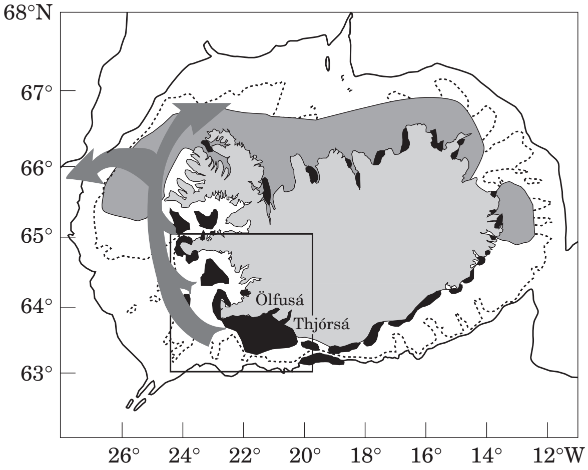

Figure 1. Spawning sites (in black) of cod in Icelandic waters and the expected drift route of eggs and larvae from the main spawning sites at the southwest coast. The dark grey area represents a typical distribution of 0-group cod, although the size of the total area occupied by juvenile cod may vary depending on the year class. Locations (in black) along the west, north and east coast represent areas where samples of spawning cod have been obtained from commercial catches by the Marine Institute since 1979 as well as areas that have been fished historically for spawning cod by local fishermen. The area within the box is shown in Figure 4.

enhance survival by reducing the potential for mismatch between larval occurrence and favourable environmental conditions (Cushing, 1990; Mertz and Myers, 1994). Similarly, more widespread spawning locations may provide greater variety of environmental opportunities to match hatching times and larval food production and to minimize loss of eggs and larvae due to advection (Sinclair, 1988). Cod spawning, in particular, is protracted and occurs over a number of locations, making it difficult to speculate on the key spawning locations.

The main spawning grounds of cod in Iceland are located along the south coast (Saemundsson, 1924). From there the eggs and larvae are believed to drift with the coastal current and the warm saline Atlantic water of the Irminger Current, flowing northward along the West coast (Astthorson *et al*., 1994). The Irminger current then splits into two branches off the Vestfirdir peninsula, one flowing to the west towards Greenland and one continuing northeast on to the northern shelf (Stefansson, 1962, 1981, Fig. 1). In most years, the majority of the pelagic juvenile cod are found in the arcto-boreal waters of the northwest, north, and northeast coast of Iceland (Astthorsson *et al*., 1994). In some years large patches of juvenile pelagic cod are also detected in the western branch of the Irminger current (Astthorsson *et al*., 1994; Begg and Marteinsdottir, 2000). It is therefore generally accepted that most of the juvenile cod, found in west, north and east Iceland, originate from the main spawning grounds in the south (Astthorsson *et al*., 1984) and that in some years considerable fractions of the larvae and juveniles may drift with the other branch of the Irminger current into Greenland waters, later returning as adults to spawn (Frank, 1992; Schopka, 1994).

Contrary to the expected dispersal, the mean length of pelagic juvenile cod has been shown to decline in a clockwise direction from west to east (Astthorsson *et al*., 1994). The decreasing size gradient appears to be present during many of the years since the first 0-group survey conducted in 1970 (Begg and Marteinsdottir, 2000 and references therein). It has been suggested that this size gradient results from temperature-induced growth differences. Astthorsson *et al*. (1994) proposed that larval growth rates may have been enhanced by the warmer water at the west coast and retarded by the cooler waters off the north and the east coasts (the "growth hypothesis"). Alternatively, the decline in the size of juvenile cod from west to east may result from spatial variation in the origin of the 0-group cod. Astthorsson *et al*. (1994) suggested that smaller juveniles originating from a delayed local spawning off the north and the east coasts may generate the smaller average lengths of cod in these areas. The low sea temperatures in the north and in the east may also produce spatial variation in size related age distribution of pelagic juveniles through the prolongation of incubation time of eggs spawned in this region (the "hatch date hypothesis"). Larvae that hatch in the cold coastal water of the northern and eastern fjords are likely to hatch later than those incubated at higher temperatures prevailing on the main spawning ground in the south, even though spawning occurred at a similar time.

Information on the life history and the origin of pelagic juveniles is clearly needed in order to understand the spatial stock structure of Icelandic cod and the mechanism responsible for variable recruitment. Recruitment to this stock has been low for an extended period of time (Marteinsdottir and Thorarinsson, 1998). Since 1985, no year class has exceeded the long term average of 205 million three year olds. The causes for these recruitment failures are not entirely known. Although low stock levels and unfavourable age composition of the spawning stock during these years account for considerable amount of the variation in recruitment (Marteinsdottir and Thorarinsson, 1998), unfavourable environmental conditions may also be responsible. The effects of environmental factors cannot be studied unless the origins of surviving 0-group cod are known.

This study examines the causes for size variation among pelagic 0-group cod in Icelandic waters by resolving the two hypotheses. First, spatial variations in age–length relationships are compared to determine whether geographical size differences are growth related. Second, the most likely origins of 0-group cod are deduced by comparing hatch date compositions and reconstructed spawning distributions, based on regional temperatures during incubation, with available information on spawning times and locations.

Materials and methods

Temperature measurements

Temperatures were obtained from continuously recording thermometers positioned in surface waters at four locations on the west, north and east coasts of Iceland (in regions 1, 2, 4 and 6, respectively; Jonsson, 1999). Temperatures were recorded every two hours and daily temperatures were obtained by averaging all measurements between 0000 and 2400 h. Three of the thermometers broke down in 1997, therefore continuous readings during April through June were only obtained in region 6, in addition to recordings in April in region 4 and in June in region 2. As continuously recording thermometers have not been positioned at locations on the south coast, temperature measurements were obtained from CTD employed during surveys conducted by the Marine Research Institute. Measurements were obtained from 20 m depth at station S2 (63°17′N, 20°32′W) located on the main spawning ground.

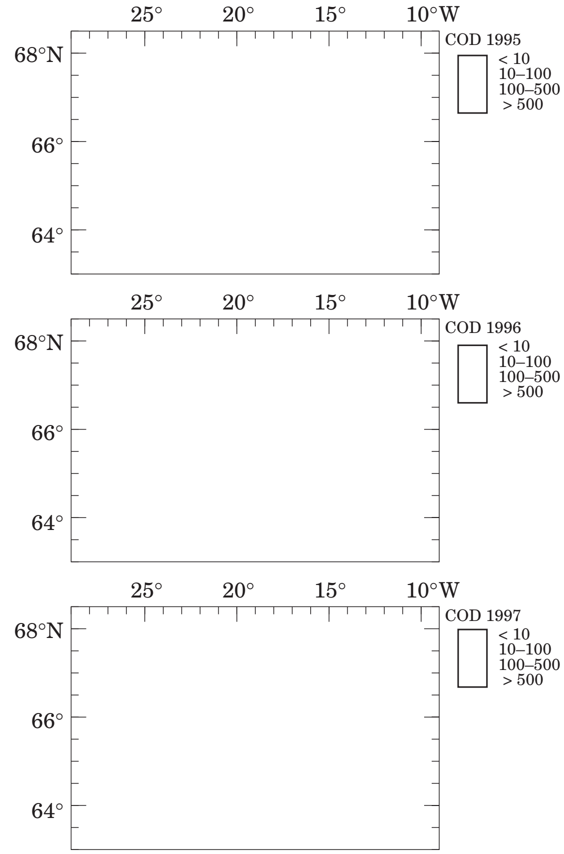

Figure 2. Distribution of 0-group cod in 1995–1997 (Magnusson and Sveinbjornsson, 1995; Sveinbjornsson, 1996; Sveinbjornsson and Jonsson, 1997).

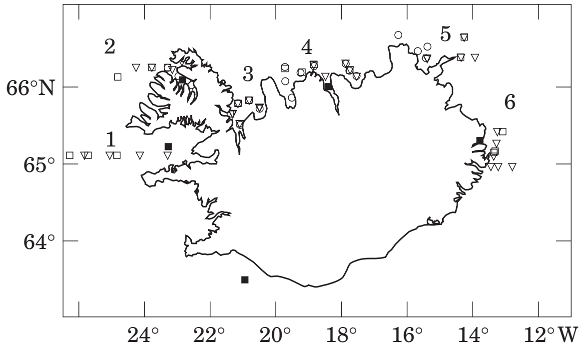

Figure 3. Location of the six regions, and stations sampled for pelagic 0-group cod used for ageing in 1995 (open box), 1996 (open circle) and 1997 (open triangle). Temperatures were obtained at locations shown by the black boxes.

Sampling, otolith preparation and analysis

Samples of pelagic 0-group cod were obtained from the 0-group survey in 1995–1997 (see Astthorsson *et al.* (1994) for methods used in the surveys). At every station, samples of cod were bagged and frozen at − 20°C. Subsequently, by inspection of the abundance distributions (Fig. 2), six regions of abundance were identified and samples were withdrawn for analysis (Fig. 3; Table 1). Sampling of larvae for use in ageing and back calculation of spawning dates at the main spawning grounds, were obtained from a survey conducted on 6–9 June 1995 (Fig. 4). The larvae were collected with a $1 \times 1\ m^2$ Tucker net (333 μm), towed in an oblique path down to 40 m at 2.1 knots.

In the laboratory, specimens were thawed and measured to the nearest 0.1 mm standard length (SL). The lapillar and sagittal otoliths were extracted, cleaned and mounted on glass slides with nail polish. One lapillus from each cod was polished on one side with 6 μm and 3 μm lapping film, to render the hatch check and outer growth increments clearly visible, before viewing the otolith under a 1000 × oil immersion lens. If the cod exceeded 55 mm, the lapillus was removed from the glass slide with acetone and mounted on a new slide with a thermal mounting wax (Christal Bond, item no. 40-8150 by Buehler, 41 Waukegan Road, Lake Bluff, IL 60044-1699, USA) and polished on the other side. Growth increments were counted along the longest radius from the hatch check to the periphery. Counts were repeated until a consistent age was obtained (approximately ± 5%). In 1995 and 1997, respectively,

Table 1. Summary statistics including information on the number of station sampled for ageing, total number of pelagic 0-group cod collected in each Region, number of 0-group cod aged from each Region, mean length of cod sampled at the selected stations in the 0-group survey and the mean length of cod selected for ageing.

Region names	Breidafjordur	Vestfirdir	Hunafloi	Nordurland	Langanes	Austfirdir
Region numbers	1	2	3	4	5	6
			1995			
Number of stations	3	3	5	4	3	3
Number of cod collected in survey	68	55	271	1250	762	340
Number of cod aged	29	37	33	69	33	32
Mean length from survey (mm)	48.6 ± 6.4	46.1 ± 9.4	36.4 ± 6.8	39.1 ± 7.1	29.6 ± 4.7	25.1 ± 6.0
Mean length from aged cod (mm)	50.2 ± 5.9	45.9 ± 9.5	37.7 ± 6.1	39.5 ± 6.9	31.5 ± 4.2	26.1 ± 5.0
			1996			
Number of stations	0	5	4	5	4	0
Number of cod collected in survey	0	54	81	2891	52	0
Number of cod aged	0	31	35	50	44	0
Mean length from survey (mm)		46.9 ± 6.0	40.5 ± 6.1	43.3 ± 6.2	29.9 ± 5.0	
Mean length from aged cod (mm)		44.1 ± 6.1	38.9 ± 6.1	41.7 ± 6.4	29.4 ± 4.8	
			1997			
Number of stations	4	4	5	5	4	6
Number of cod collected in survey	502	2001	10 136	14 986	3538	4363
Number of cod aged	50	49	51	53	50	50
Mean length from survey (mm)	53.0 ± 11.6	48.8 ± 7.6	41.9 ± 7.3	45.1 ± 9.7	46.7 ± 8.9	46.9 ± 11.6
Mean length from aged cod (mm)	51.2 ± 11.2	50.0 ± 6.7	42.2 ± 5.1	47.4 ± 8.8	47.0 ± 8.4	46.4 ± 9.8

20% and 30% of the readings by the two readers (Gunnarsson and Suthers) were compared and found to be within ± 10%. In 1996 all readings by the two readers were compared. Approximately 4% of these readings differed by more than 10% and the otoliths were discarded. In 1997, an inter-comparison of increment counts was made with Dr Steve Campana (Marine Fish Division, Bedford Institute of Oceanography) on 20 randomly selected otoliths and agreement was within 10%. Furthermore, daily increment formation has been validated in 0-group cod reared in northern Norway, hatching at 1–2°C (i.e. in conditions similar to

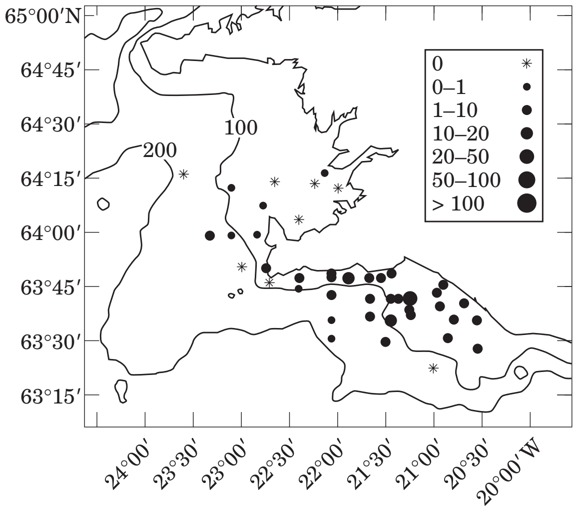

Figure 4. Abundance (number of larvae/100 m^3) and distribution of larvae collected on the main spawning grounds Selvogsbanki SW of Iceland in beginning of June 1995. See Figure 1 for geographical location of the area presented.

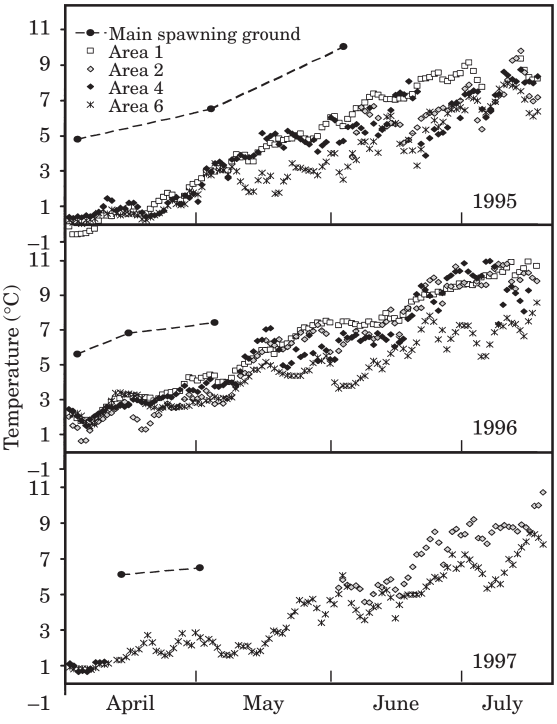

Figure 5. Temperatures on the main spawning ground and in regions 1, 2, 4 and 6.

Table 2. Temporal and spatial comparisons of adjusted mean lengths (± s.d., mm) of 0-group cod (ANOVA on log-transformed data and Student–Newman–Keuls multiple comparisons test). Adjustment of length to a common date (20 August, mid-point of all surveys) is based on mean growth rate of 0.5 mm/d^{-1} for the aged 0-group cod in 1995–1997. Results of the multiple comparisons among areas within each year are indicated by lower case letter (a–e), where means with the same letter were not significantly different from each other. Comparisons among years are indicated with an upper case letter (A–C).

	Year			ANOVA	
Area	1995	1996	1997	F (year)	P (year)
	a		a		
1	46.0 ± 5.8		54.8 ± 11.2		
	A		B	19.4	0.0001
	ab	a	a		
2	43.0 ± 9.5	41.4 ± 5.6	51.8 ± 6.7		
	A	A	C	38.7	0.0001
	bcd	b	bc		
3	35.6 ± 6.0	37.8 ± 6.1	42.5 ± 5.2		
	A	A	B	16.6	0.0001
	bc	a	b		
4	39.2 ± 7.1	41.5 ± 6.3	45.3 ± 8.7		
	A	A	B	8.9	0.0002
	de	c	bc		
5	33.4 ± 7.9	30.9 ± 4.5	42.7 ± 8.4		
	A	A	B	17.6	0.0001
	e		c		
6	29.6 ± 5.0		40.9 ± 9.8		
	A		B	35.3	0.0001
ANOVA, F (area)	18.4	34.8	20.7		
ANOVA, p (area)	0.0001	0.0001	0.0001		

that found in this study, Suthers and Sundby, 1993, 1996).

Length distributions of aged cod and the total cod collected at same stations during the survey were compared with Kolmogorov–Smirnov two-sample test on standard length (SL) where total lengths of 0-group cod measured in field were converted to SL by dividing TL by 1.1 (Thorisson, 1994). Neither of the two distributions from same year and same region differed significantly ($p<0.05$). Standard lengths were further adjusted to the mean cruise date for the three years (20 August), as the duration of each survey was approximately three weeks (starting in the south and moving anti-clockwise around the island in 1995 and 1996 but clockwise in 1997). The adjustment was 0.5 mm day^{-1}, which approximates the overall size-age relationship in this study, and is the same as used in the Norwegian post-larval surveys (Suthers and Sundby, 1993).

Mean length and age were compared with ANOVA (on log-transformed data) and Student–Neuman–Keuls multiple comparison test performed with SAS (SAS, 6.03 edition) between regions, within and among years.

Growth rates

Growth of larvae and 0-group cod was analysed by comparing the slopes of standard length on age relationships. A more detailed analysis, based on the width of daily increments in conjunction with environmental data, will be presented elsewhere. For overlapping length at age data, comparisons were made between regions and between years by analysis of covariance (ANCOVA).

Reconstruction of hatch dates and spawning dates

Hatch date frequency distributions were derived from back-calculated age-class distributions, based on numbers of increments from the hatch check until time of capture. Hatch date distributions of larvae were corrected for mortality but no corrections were performed for the 0-group cod as the samples were collected during the low-mortality juvenile stage (see Campana and Jones, 1992). For the larvae, the numbers in each age class were allowed to increase in numbers from the day of capture backwards to the day of hatching by applying a rate of daily mortality. The specific daily mortality rate (Z_t) was calculated as a power function of larval dry weight (W) (Houde, 1997) using the power relationship derived for haddock by Heath and Gallego (1998):

$$Z_t = 1.5 W_t^{-0.5} \tag{1}$$

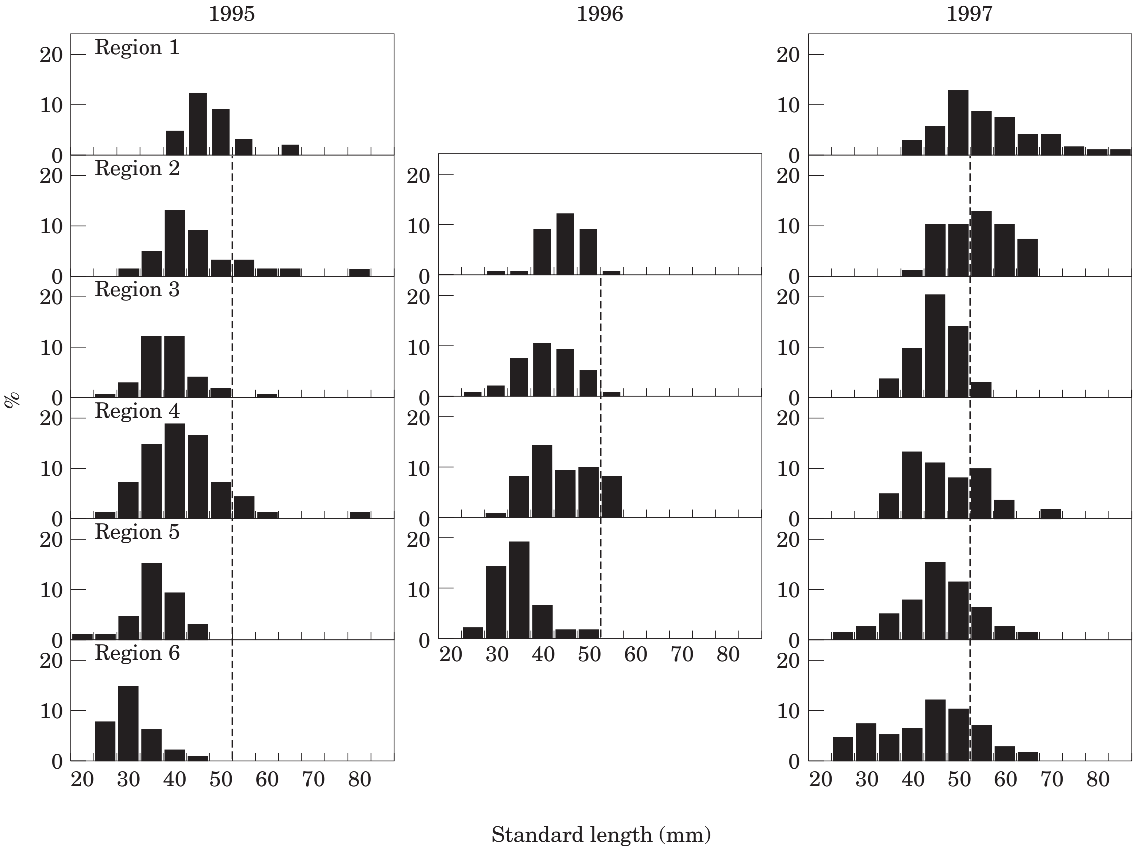

Figure 6. Adjusted (20 August) length distribution of aged 0-group cod in 1995–1997. A dotted reference line is drawn at the length of 50 mm.

As information on dry weight of larvae sampled in 1995 was not obtainable (the larval samples had to be shared with another project), weight (W) of larvae was estimated using the length–weight relationship obtained for larvae in the size range 4–14 mm collected on the main spawning grounds in 1994 ($W_{(\text{in } \mu g)} = 0.455 \times SL^{3.674}$; $n = 397$; $r^2 = 0.86$). The relationship between this estimated dry weight and age of larvae in 1995 ($W = 0.317 \times \text{age}^{2.161}$) was used to estimate weight at age to be used in equation (1). The estimated daily specific mortality ranged from 26% at age 1–5 days to 4% just prior to the age of 30–35 days. The daily mortality rate of 8–14% for ages 13–23 days is consistent with estimated mortality of larvae in the field based on larvae collected along the transport route west of the country (Asgeirsson, T.; Marine Research Institute; pers. com.).

Calculation of incubation periods and spawning dates followed the method described by Pinsent and Methven (1997). Spawning dates were calculated by subtracting the estimated incubation period from the hatching dates. In order to obtain information on incubation periods (T_{hatch}) at those temperatures most likely experienced in the northern and the southern regions (Table 4), T_{hatch} was estimated for four different temperatures (T=1°, 3°, 5° and 7°C, respectively), by the equation of Pepin *et al.* (1997).

$$T_{\text{hatch}} = 46.1e^{-0.17T} \quad (2)$$

Temperatures between 1–5°C were characteristic for incubation during April and early May in the fjord areas on the west, north and the east coasts, while larvae originating on the main spawning grounds experienced 5–7° during same time period (Fig. 5). Therefore, the incubation periods of larvae collected at Selvogsbanki in 1995 (Fig. 4) were estimated by assuming that larvae that hatched in April had experienced temperatures of 5.5°C (Fig. 5), those that hatched during the first half of May had experienced 6.5°C and those that hatched in the second half of May had experienced 7.5°C during the incubation.

Time and duration of spawning

Information on time and duration of spawning on the main spawning grounds was obtained from data

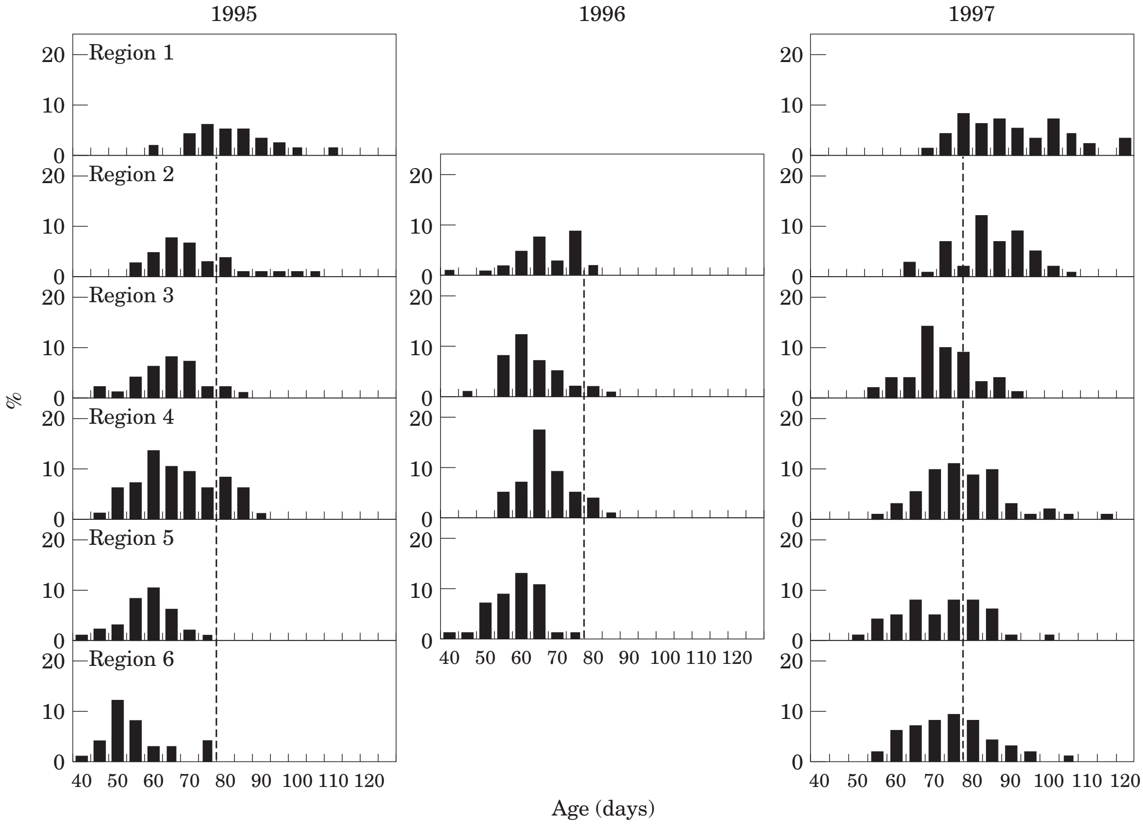

Figure 7. Adjusted (20 August) age distribution of 0-group cod in 1995–1997. A dotted reference line is drawn at the age of 80 days.

described by Marteinsdottir and Petursdottir (1995) and Marteinsdottir and Björnsson (1999). Samples were obtained during research cruises and from commercial sources, several times every week during the spawning periods. All sampled cod were assigned to four maturity stages (immature, maturing, spawning and spent; Powels, 1958) where the ovaries of spawning females contained hydrated oocytes and spawning males were characterized by freely running milt. Additional information on the occurrence of spawning cod at locations in regions 1–6 (Fig. 3) was derived from the Marine Research Institute data base containing all fish samples collected since 1979.

Results

Local water temperatures

In general, temperatures were 2–4°C higher on the main spawning ground at the south coast compared to local temperatures within the fjords on the west, north and east coast (Fig. 5). On the main spawning ground, temperatures rose from approximately 5°C at the beginning of April to 6° or 7°C in early May with, however, notably warmer temperatures in 1996 than in 1995 or 1997. In 1995, temperatures at the south coast exceeded 9°C by the end of May. Temperatures at the west, north and east coast were at or below 1°C at the beginning of April and did not approach 6–7°C until the end of May or the beginning of June.

Size and age of 0-group cod

Average size of pelagic juvenile cod decreased from west to east in all years (Table 2, Fig. 6). In 1995 and 1997 the largest individuals were captured in region 1. The average adjusted length of juveniles in this region was significantly greater than the average length of juveniles captured in regions 5 and 6 off the northeast and east coasts (ANOVA, $p<0.0001$; SNK-multiple comparison test; Table 2). No individuals were found in regions 1 and 6 in 1996. However, juveniles from the other regions (Table 2), declined in length from west to east with juveniles captured in region 2 being significantly larger than juveniles from region 5.

Similar declines from west to east were observed in the age of the pelagic juvenile cod (Fig. 7, Table 3). In 1995 and 1997 the oldest individuals were captured in regions 1 and 2. The average adjusted ages of juveniles in these

Table 3. Temporal and spatial comparisons of adjusted mean age (days, adjusted to 20 August, mid-point of all surveys) of 0-group cod (ANOVA on log-transformed data and Student–Newman–Keuls multiple comparisons test). Results of the multiple comparisons among areas within each year are indicated by lower case letter (a–e), where means with the same letter were not significantly different from each other. Comparisons among years are indicated with an upper case letter (A–C).

	Year			ANOVA	
Area	1995	1996	1997	F (year)	P (year)
1	a 81 ± 11.2 A		a 96 ± 14.1 B	19.4	0.0001
2	b 73 ± 11.9 A	a 68 ± 8.7 B	b 89 ± 11.2 C	38.7	0.0001
3	c 66 ± 8.3 A	a 66 ± 7.8 A	cd 75 ± 8.8 B	17.6	0.0001
4	bc 70 ± 12.4 A	a 69 ± 7.5 A	c 80 ± 11.8 B	16.3	0.0001
5	d 61 ± 7.9 A	b 60 ± 6.7 A	d 73 ± 10.7 B	28.7	0.0001
6	e 55 ± 7.5 A		cd 76 ± 11.1 B	99.0	0.0001
ANOVA, F (area)	27.9	12.2	28.5		
ANOVA, p (area)	0.0001	0.0001	0.0001		

two regions (81 and 73 days in 1995; 96 and 89 days in 1997) were significantly greater than the average age of juveniles in region 5 and 6 (61 and 55 days in 1995; 73 and 76 days in 1997); ANOVA, $p<0.001$, Table 3). Similarly, in 1996 the average age decreased from 68 days in region 2 to 60 days in region 5 (Table 3).

Annual variation in size and age

Inter-annual differences in size and age of pelagic juvenile cod were manifested by the presence of older and larger individuals in all regions in 1997 compared to 1995 and 1996. The differences between 1997 and 1995–1996 were highly significant (ANOVA, SNK, $p<0.001$) while the differences in size or age between 1996 and 1995 were mostly nonsignificant. In region 1 juvenile cod were, on average, 15 days older in 1997 compared to 1995. In the other regions the inter-annual age differences ranged from 11 to 21 days (Fig. 7).

Growth

Growth rates, indicated by the slope of length on age, varied between regions and between years. Overall, growth ranged from $0.36\ \text{mm d}^{-1}$ in region 5 in 1995 to $0.77\ \text{mm d}^{-1}$ in region 4 in 1996 (Table 4, Fig. 8). Analysis of covariance demonstrated significant differences between regions in 1995 and in 1997 ($p<0.0001$). In 1996, no significant differences were detected among regions when either the slopes ($p>0.07$) or the intercepts ($p>0.16$) were compared. In 1995, comparisons between regions 5–6 and regions 1–4 were not possible due to

Table 4. Regressions of age, days, on standard length, mm, of juvenile pelagic cod from the different regions in 1995–1997 (see Fig. 8).

Year/ region	Growth relationships	n	r^2
1995	SL = 0.49 + 0.55 × Age	233	0.85*
1	SL = 7.28 + 0.47 × Age	29	0.80*
2	SL = − 8.99 + 0.57 × Age	37	0.75*
3	SL = − 3.66 + 0.58 × Age	33	0.66*
4	SL = 5.11 + 0.49 × Age	69	0.70*
5	SL = 11.48 + 0.36 × Age	33	0.48*
6	SL = − 2.93 + 0.60 × Age	32	0.79*
1996	SL = 12.0 + 0.75 × Age	160	0.80*
2	SL = 3.10 + 0.55 × Age	31	0.80*
3	SL = − 5.2 + 0.64 × Age	35	0.66*
4	SL = − 11.4 + 0.77 × Age	50	0.67*
5	SL = − 2.2 + 0.55 × Age	44	0.66*
1997	SL = − 6.38 + 0.64 × Age	300	0.69*
1	SL = − 13.1 + 0.73 × Age	49	0.82*
2	SL = 4.47 + 0.53 × Age	49	0.82*
3	SL = 7.57 + 0.46 × Age	51	0.79*
4	SL = − 0.86 + 0.57 × Age	53	0.61*
5	SL = − 12.8 + 0.72 × Age	47	0.87*
6	SL = − 19.31 + 0.75 × Age	50	0.71*

*$p<0.0001$.

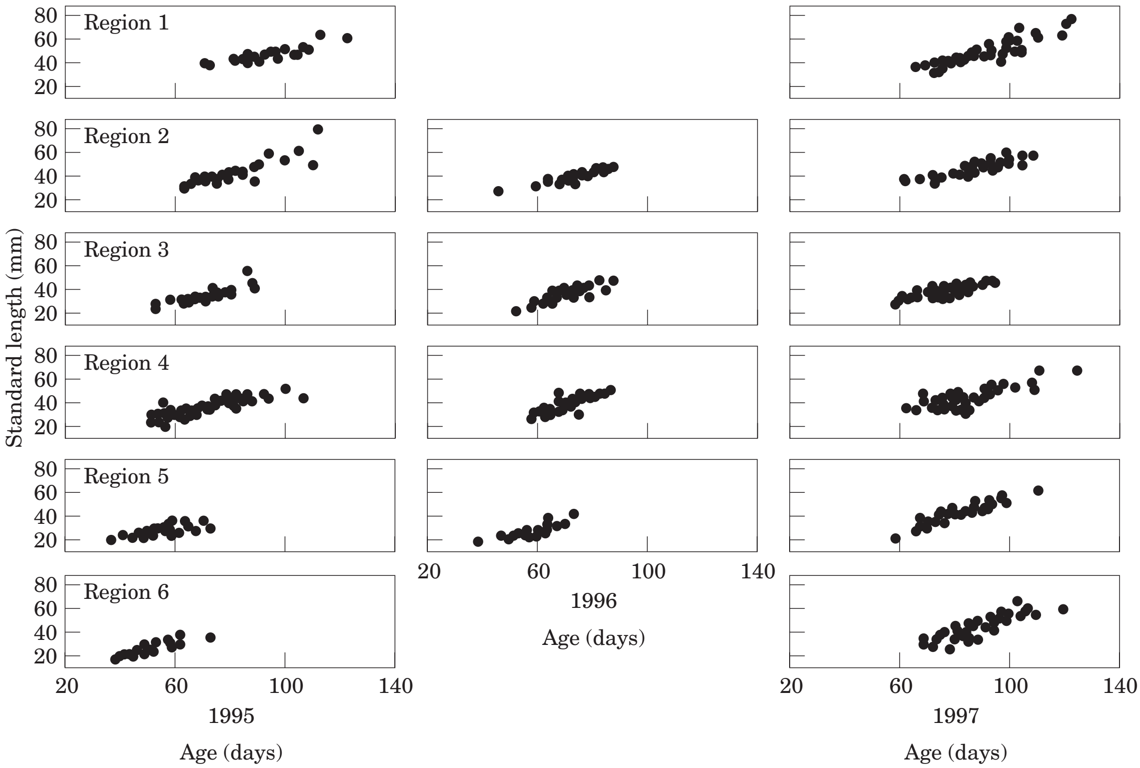

Figure 8. Scatter plot of standard length on age for all regions in all years.

lack of overlap in age between regions. Growth differed significantly among regions 1–4 in 1995 (ANCOVA; F=16.65; df=3; $p<0.001$) with slowest growth in region 4 (0.49 mm d^{-1}). Growth in region 5 was significantly slower than growth in region 6 (ANCOVA; F=9.4, df=1, p=0.003). In 1997, significant differences were detected among all regions (ANCOVA, F=8.1, df=5, p=0.0001). Growth appeared to be slowest in regions 3 and 4, 0.46 and 0.58 mm d^{-1}, and fastest in regions 1, 5 and 6 (0.73–0.75 mm d^{-1}).

Growth was relatively higher in 1996 than in the other two years. This was especially true for regions 3 and 4 (ANCOVA, region 3: F=3.2, df=2, p=0.04; region 4: F=17.3, df=2, p=0.0001). Comparisons between years were not possible for regions 5 and 6 due to lack of overlap in the data.

Hatch date distributions

Both the temporal and the spatial variation in length distributions and corresponding age distributions were reflected in the hatch date frequency distributions. A distinct gradual decline in average time of hatching was detected from west to east (Table 5, Fig. 9). In 1995 most of the juveniles caught in region 1 hatched in late May and early June. In regions 2, 3 and 4 most of the juveniles originated from a hatching period in June. In the two most eastern regions, surviving juveniles hatched in late June and the beginning of July. For those sampled in 1996, birth date distributions appeared to be similar to those observed in 1995, i.e. most of the juveniles in regions 2, 3, and 4 hatched in June and some of the juveniles in region 5 hatched as late as July. In 1997, surviving juveniles originated from an earlier hatch period than in 1995 or 1996. This was particularly true in regions 1 and 2, as juveniles from these regions had mostly hatched in May, on average two weeks earlier than juveniles from same regions in 1995 and 1996 (Fig. 9, Table 5).

The larvae on the main spawning grounds in 1995 (Fig. 4) had a hatch date distribution in April and May with peak hatching around the middle of May (Fig. 10, Table 5). This is in contrast to observations of hatch dates among the juvenile 0-group cod in the same year (Fig. 9) where only a small fraction of the 0-group cod in regions 1 and 2 had hatched in May.

Timing of spawning

Spawning on the main spawning grounds, defined by the presence of hydrated oocytes in the ovaries, started in the middle of March in all years. In 1996 and 1997, spawning terminated in the beginning of May (Fig. 11). In 1995, spawning terminated later and relatively high

Table 5. Mean hatch date of larvae collected on the main spawning grounds in 1995 and mean hatch dates of pelagic juvenile cod in each region in 1995–1997. Also included are estimates of back-calculated spawning dates based on the hatch date distributions and four different incubation temperatures that represent expected temperature during incubation on the main spawning grounds (5–7°C) and in fjords west, north and east of the country (1–5°C) (see Material and methods for methods used to estimate spawning dates).

	Mean hatch date	Range of hatch dates	Mean spawning date			
			1°C	3°C	5°C	7°C
1995						
Main spawning grounds (Larval survey)	19/5	24/4–1/6	9/4	20/4	28/4	4/5
Region 1	28/5	28/4–18/6	19/4	30/4	9/5	14/5
Region 2	6/6	6/5–24/6	28/4	10/5	17/5	23/5
Region 3	13/6	26/5–2/7	26/4	7/5	15/5	21/5
Region 4	10/6	5/5–2/7	30/4	11/5	19/5	25/5
Region 5	19/6	3/6–10/7	11/5	22/5	30/5	5/5
Region 6	24/6	2/6–6/7	16/5	27/5	4/6	10/6
1996						
Region 2	12/6	30/5–11/7	4/5	15/5	23/5	29/5
Region 3	15/6	27/5–2/7	6/5	18/5	26/5	31/5
Region 4	11/6	27/5–24/6	4/5	15/5	23/5	28/5
Region 5	20/6	6/6–11/7	12/5	24/5	1/6	6/6
1997						
Region 1	14/5	11/4–7/6	6/4	17/4	25/4	30/4
Region 2	21/5	29/5–15/6	13/4	24/4	2/5	7/5
Region 3	21/5	16/5–22/6	26/4	7/5	15/5	21/5
Region 4	31/5	22/4–23/6	19/4	30/4	8/5	14/5
Region 5	6/6	10/5–30/6	21/4	2/5	10/5	16/5
Region 6	3/6	3/5–23/6	25/4	7/5	15/5	20/5

frequencies of females with hydrated ovaries were still present in the second and third week of May (Fig. 11; Marteinsdottir and Petursdottir, 1995; Marteinsdottir and Bjornsson, 1999).

Date on spawning at localities on the west, north and east coast are limited. Spawning cod have been detected in samples collected in March–June in regions 1–6 (Table 6). Spawning in region 1 appeared to occur mainly in April and the beginning of May. Spawning on the north and east coasts appeared to occur slightly later, from late April through May. Records of spawning cod later in the season, in June, exist for regions 1–4.

Reconstructed spawning distribution of surviving larvae and juveniles

Except for the spawning date distribution of larvae caught on the main spawning grounds (Fig. 12), few of the other spawning distributions (Table 5) based on back calculated hatch date distributions, appear to coincide with the recorded spawning time on the main spawning grounds (Fig. 11). With the temperatures on the main spawning grounds being generally above 5°C during the incubation period, only parts of the hatch date distributions, e.g. hatch dates in April and May in regions 1, 2 and 4 in 1995 and regions 1, 2, 4 and 6 in 1997 (Fig. 9, Table 5) will, when back calculated into spawning dates, coincide within the same frame demonstrated in Fig. 11. None of the hatch dates in 1996 can be back calculated into spawning distributions that overlap with the spawning period on the main spawning grounds. Based on an incubation temperature of 5°C, the average spawning dates of 0-group cod caught in regions 2–6 during 1996, would be as late as 23–26 May or in early June (Table 5).

In contrast, spawning distributions of 0-group cod that originated from hatching in June and July coincided better with spawning dates at locations on the west, north and east coast (Table 6). For example, if the 0-group cod that hatched in June originated from spawning at the north or east coasts they had, most likely experienced 3–5°C incubation temperatures (Fig. 5), i.e. an incubation period of 20–27 days. Reconstructed spawning dates based on these temperatures indicated considerable spawning in May (Table 5), congruent with the recorded spawning periods of cod at these locations. Those 0-group cod that hatched in July are likely to have experienced higher temperatures (7–9°C, Fig. 5) during their incubation and must therefore have originated from spawning events that occurred considerably late in the season, i.e. in June.

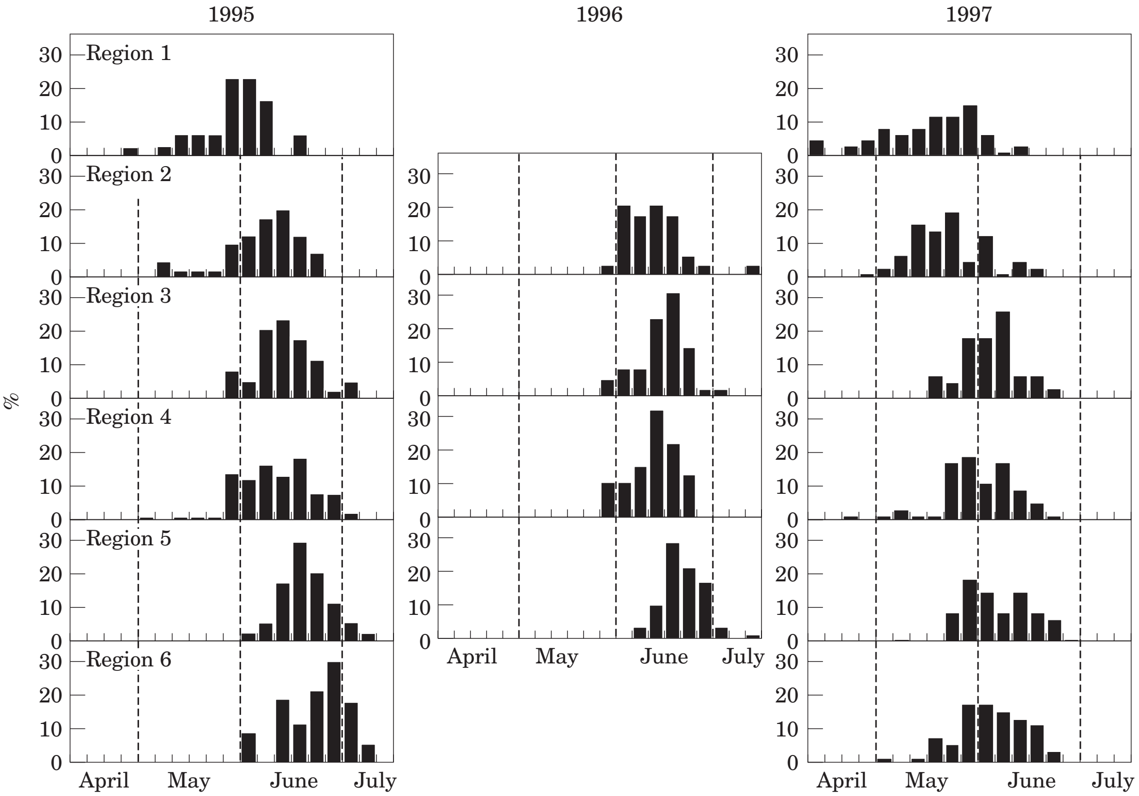

Figure 9. Hatch date distributions of 0-group cod.

Discussion

It has been suggested that, differences in size of 0-group cod from the west to the east coast of Iceland result from temperature-induced growth differences with ocean temperatures off the south and west coasts being higher than those off the north and east coasts (Astthorsson *et al.*, 1994). We reject this growth hypothesis as this study clearly shows that the spatial variation in size is typically age related, with the oldest juveniles captured off the west coast and the youngest juveniles captured off the east coast. Furthermore, the declining clockwise size gradient around the country cannot be explained by differential growth rates, as growth rates of juveniles captured off the north and east coasts were, in many cases, either faster or not significantly different from growth rates of juveniles off the west coast.

The spatial variation in birth date distributions, indicates that the surviving juvenile cod emanate from different spawning grounds. The spawning periods at the main spawning grounds lasts from the middle of March until, in most years, the second or third week of May (Fig. 11; Marteinsdottir and Bjornsson, 1999). The reconstructed spawning distribution (based on the incubation temperature and the birth date distribution) of larvae captured on the main spawning grounds in June 1995 overlapped with the second half of the documented spawning period based on female maturity stages. This distribution may reflect unequal survival of larvae from the beginning and the end of the spawning period. Alternatively, the older larvae may have drifted off the bank by the time of sampling.

In contrast, only parts of the spawning distributions displayed by the pelagic juvenile cod overlapped with the spawning period at the main spawning grounds, if an incubation temperature (5–7°C) specific for the south coast was used to calculate the birth date distribution.

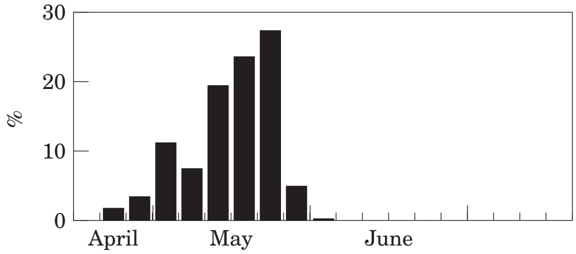

Figure 10. Hatch date distributions of larvae collected on the main spawning grounds (Fig. 4) in the beginning of June 1995.

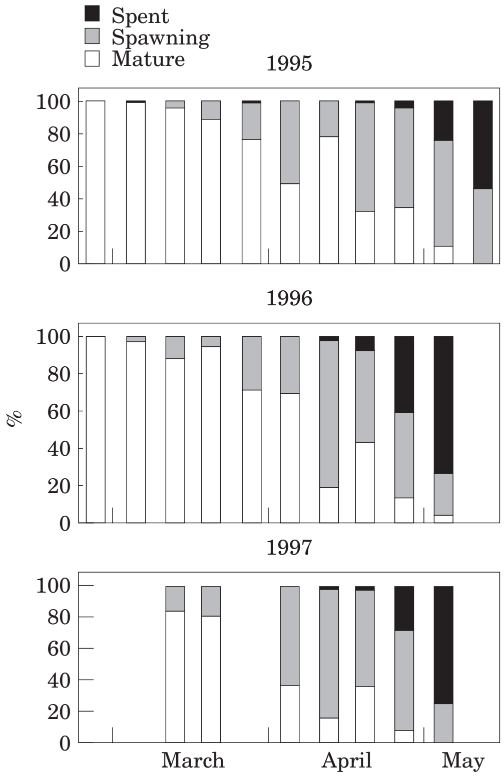

Figure 11. Proportion of maturity stages among cod on the main spawning grounds (Selvogsbanki) in 1995–1997.

Therefore, hatching that occurred in June and July is likely to originate from local spawning within the northern and eastern fjords that occurred at relatively cold temperatures in late April and May or from spawning that occurred at these locations later in the season (end of May and June).

Spawning cod have been reported at several locations around Iceland, although these observations are not as well documented as for the main spawning grounds. For example, in addition to the data presented in Table 5, local spawning has been known to take place in late April, May and even in June on the west and the north coasts (Saemundsson, 1924; Fridgeirsson, 1982; Jonsson, 1982). Spawning cod were caught and tagged at locations on the east coast in April (Thorsteinsson and Marteinsdottir, 1992) and local fishermen state that spawning at the northeast coast occurs during late April, early May and even in the beginning of June. Intense sampling of spawning cod at three locations on the north coast in the last two years, has indicated that considerable spawning does occur in late May and June at these locations (unpublished data from a sampling programme maintained by the authors).

It appears that the surviving juvenile cod did not exclusively originate from the main spawning grounds on the south coast, but also from smaller spawning grounds located all around the island. As a result, each year class is most likely composed of offspring from multiple spawning sites whose relative contribution varies from year to year. Based on the hatch date distribution in 1997, a considerable proportion (e.g. at least those that hatched in April and May) of surviving 0-group cod sampled in most of the regions may have originated from the main spawning grounds. In contrast, relatively few of the surviving 0-group cod in 1995 and 1996 appeared to have originated from the main spawning ground. These observations are concordant with the observed 0-group abundance indices. The index was exceptionally low in 1995 and 1996 (163 and 40, respectively) compared to the long term average of 427. In 1997, it was 1152 (the third highest since the first record in 1970). There are several indications that drift of larvae and juveniles from the main spawning grounds to the nursery area north of the country may have been more pronounced in 1997 than in the previous years. First of all, in 1997 the 0-group cod were widely distributed along the expected track route northwest of the country and occurred in high densities in the area where the Atlantic water flows around the northwest peninsula on to the northern shelf area (Fig. 2). Furthermore, in 1997 a greater influence of warm saline Atlantic water from the southern locations was detected past the Siglunes section in 1997 (located in the middle of region 4 at 18°50′W) compared to 1995 and 1996 (Anon., 1995, 1997, 1999; Sveinbjörnsson and Jonsson, 1997).

Based on the present results, contribution of the main spawning grounds towards the surviving population of 0-group cod appears to be highly variable. This variable contribution may explain some of the variation in year class strength of the Icelandic cod stock. The spatial variation in hatch date distributions and the positive relationship between age and size described in this study, indicate that offspring from the main spawning grounds will be generally larger (and older) than offspring from the smaller local spawning sites at the west, north and east coast. Therefore, contribution of the main spawning ground may be examined by analysing the size distribution of 0-group cod. For example, the average size of 0-group cod in the northern area will be expected to rise when transport from the southern coast has been successful and juveniles from the main spawning grounds are present in some numbers. A preliminary analysis of the relationship between average size of 0-group cod at the north coast (using mean lengths of 0-group cod caught during 1970–1997 in region 4) and recruitment (numbers of three year old from VPA (Anon., 1999)) is shown to be positively significant ($p=0.001$; $r^2=0.31$).

Population richness may be constrained during early life-history stages by the availability of spawning or nursery habitats (Sinclair, 1988). These results indicate that Icelandic cod may spawn at more sites, and over a longer period than previously thought, thus spreading

Table 6. Numbers of samples of spawning cod obtained in each month during the TAC sampling programme in 1979–1997. It should be noted that the data indicate the occurrence of spawning, but not the absence of spawning, as sampling was not performed routinely in each week of the month.

	Week of the month	Region 1	Region 2	Region 3	Region 4	Region 5	Region 6
March	1						
	2	34	4	3	2		
	3	4	1	3	3		1
	4	2		1			
April	1	5	2		1		1
	2	8	1			1	
	3	8			5	8	5
	4	1			5	1	6
May	1	3		2	8	2	
	2	2			1		2
	3				5	3	3
	4	1			2	3	
June	1						
	2		1	1	2		
	3	2					
	4						
July	1	1					
	2						

the risk of larval mortality in time and space and reducing the risk of recruitment failure due to small-scale perturbations. This population richness may be responsible for the relatively low fluctuations in recruitment expressed by the Icelandic cod stock, compared to most other cod stocks in the North Atlantic. Since 1955, the maximum recruitment has been only six or seven times greater than the minimum recruitment (estimating the maximum Icelandic component of the total stocks as 350 million three year olds; Schopka, 1994). In contrast, the range of variation in the North Sea cod stock has been 21 fold (Daan *et al*., 1994), in the Arcto-Norwegian cod stock it has been 18-fold (Nakken, 1994), and in the Faroe Plateau cod it has been 16-fold (Jakubsstovu, 1994).

The results of this study provide new information on how multiple spawning aggregations, whose offspring are exposed to diverse oceanographic features, maintain balanced recruitment levels in the Icelandic cod stock. To fully understand the factors responsible for variable recruitment, future studies should focus on conditions that influence survival of offspring from the main spawning grounds, including transport of eggs and larvae to the nursery sites north of the country.

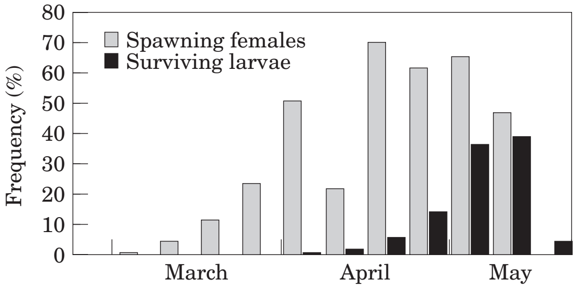

Figure 12. Frequency of spawning females and back calculated spawning dates of larvae collected on the main spawning grounds in June 1995 (Figs 4 and 10).

Acknowledgements

We wish to thank Steve Campana (Bedford Institute of Oceanography, Canada) for all his help regarding the otolith readings. We thank Adalbjorg Jonsdottir for reading the otoliths and Sveinn Sveinbjornsson for samples of the 0-group cod. We also thank Kristin Hardardottir for graphical assistance. The study was supported by the Ministry of Fisheries, the Icelandic Research Council and the Republic of Iceland Anniversary Fund. This study was a part of the EU funded project, FAIR-PL98-4122, "An operational model of the effects of stock structure and spatio-temporal factors on recruitment (STEREO)".

References

Anderson, J. T., Dalley, E. L. 2000. Interannual differences in hatching times and growth rates of pelagic juvenile cod in Newfoundland waters. Fisheries Research, 46: 227–238.

Anonymous 1995. Environmental conditions in Icelandic waters 1995. Marine Research Institute serial no. 44.

Anonymous 1996. State of marine stocks in Icelandic Waters 1995/96. Prospects for the quota year 1996/97. Marine Research Institute serial no. 43.

Anonymous 1997. Environmental conditions in Icelandic waters 1996. Marine Research Institute serial no. 53.

Anonymous 1999. Environmental conditions in Icelandic waters 1997 and 1998. Marine Research Institute serial no. 73.

Astthorsson, O. S., Gislason, A., and Gudmundsdottir, A. 1994. Distribution, abundance, and length of pelagic juvenile cod in Icelandic waters in relation to environmental conditions. ICES Marine Science Symposia, 198: 529–541.

Begg, G. A., and Marteinsdottir, G. 2000. Spawning origins of pelagic juvenile cod inferred from spatially explicit age distributions: potential influences on year-class strength and recruitment. Marine Ecology Program Series. 202: 193–217.

Campana, S. E., and Jones, C. M. 1992. Analysis of otolith microstructure data. *In* Otolith microstructure examination and analysis, pp. 73–100. Ed. by D. K. Stevenson, and S. E. Campana. Canadian Special Publication Fisheries and Aquatic Science, 117.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: and update of the match/mismatch hypothesis. Advances in Marine Biology, 26: 249–293.

Daan, N., Heessen, H. J. L., and Pope, J. G. 1994. Changes in the North Sea cod stock during the twentieth century. ICES Marine Science Symposia, 198: 229–243.

Frank, K. T. 1992. Demographic consequences of age-specific dispersal in marine fish populations. Canadian Journal of Fisheries and Aquatic Sciences, 49: 2222–2231.

Fridgeirsson, E. 1984. Cod larvae sampling with a large pump of SW-Iceland. Flödevigen rapportser, 1: 317–333.

Heath, M. R., and Gallego, A. 1998. Bio-physical modelling of the early life stages of haddock in the North Sea. Fisheries Oceanography, 7: 110–215.

Houde, E. D. 1997. Patterns and trends in larval-stage growth and mortality of teleost fish. Journal of Fish Biology, 51(supplement A): 52–83.

Jákupsstovu, S. H. Í., and Reinert, S. A. 1994. Fluctuations in the Faroe Plateau cod stock. ICES Marine Science Symposia, 198: 194–211.

Jonsson, E. 1982. A survey of spawning and reproduction of the Icelandic cod. Rit Fiskideildar, 6: 45 p.

Jonsson, S. 1999. Temperature time series from Icelandic coastal stations. Journal of the Marine Research Institute, Reykjavik, 16: 23–59.

Magnusson, J., and Sveinbjornsson, S. 1995. Report on the 0-group survey in Iceland and East Greenland waters, August 1995. ICES CM 1995/G: 42.

Marteinsdottir, G., and Björnsson, H. 1999. Time and duration of spawning of cod in Icelandic waters. ICES CM 1999/Y: 34.

Marteinsdottir, G., and Petursdottir, G. 1995. Spatial and temporal variation in reproduction of Icelandic cod at Selvogsbanki and nearby coastal areas. ICES CM 1995/G: 15.

Marteinsdottir, G., and Thorarinsson, K. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua* L.) by including age diversity of spawners. Canadian Journal of Fisheries and Aquatic Sciences, 55: 1372–1377.

Mertz, G., and Myers, R. A. 1994. Match/mismatch predictions of spawning duration versus recruitment variability. Fisheries Oceanography, 3: 4, 236–245.

Nakken, O. 1994. Causes of trends and fluctuation in the Arcto-Norwegian cod stock. ICES Marine Science Symposia, 198: 212–228.

Pepin, P., Orr, D. C., and Anderson, J. T. 1997. Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 54(Suppl. 1): 2–10.

Pinnset, D. L., and Methven, D. A. 1997. Protracted spawning of Atlantic cod (*Gadus morhua*) in Newfoundland waters: evidence from otolith microstructure. Canadian Journal of Fisheries and Aquatic Sciences, 54(Suppl. 1): 19–24.

Powels, P. M. 1958. Studies on reproduction and feeding of Atlantic cod (*Gadus morhua* L.) in the Southwestern Gulf of St Lawrence. Journal of the Fishery Research Board of Canada, 15: 1383–1402.

Saemundsson, B. 1924. Fiskarnir (Pisces Islandiae). Felgasprentsmidjan, Reykjavik, Iceland. p. 583.

Schopka, S. A. 1994. Fluctuations in the cod stock off Iceland during the twentieth century in relation to changes in the fisheries and environment. ICES Marine Science Symposia, 198: 175–193.

Sundby, S., Bjorke, 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., and Sundby, S. 1993. Dispersal and growth of pelagic juvenile Arcto-Norwegian cod (*Gadus morhua*), inferred from otolith microstructure and water temperature. ICES Journal of Marine Science, 50: 261–270.

Suthers, I. M., and Sundby, S. 1996. Role of the midnight sun: comparative growth of pelagic juvenile cod (*Gadus morhua*) from the Arcto-Norwegian and south west Nova stocks. ICES Journal of Marine Science, 53: 827–836.

Sinclair, M. 1988. Marine Populations. An Essay on Population Regulation and Speciation. Washington Sea Grant Program. University of Washington Press, Seattle. 251 pp.

Stefansson, U. 1962. North Icelandic Waters. Rit Fiskideildar, 3: 1–269.

Stefansson, U. 1981. Sjorinn vid Island (The Sea around Iceland). *In* Nattura Islands, pp. 397–438. Ed. by S. Thorarinsson. AB Reykjavik, Iceland (in Icelandic).

Sveinbjornsson, S. 1996. Report on the 0-group fish survey in Iceland and East Greenland waters, August 1996. ICES CM/G: 50.

Sveinbjornsson, S., and Jonsson, S. 1997. Report on the 0-group fish survey in Iceland and East Greenland waters, August–September 1997. ICES CM/G: 04.

Thorisson, K. 1994. Is metamorphosis a critical interval in the early life of marine fishes? Environmental Biology of Fishes, 40: 23–36.

Thorsteinsson, V., and Marteinsdottir, G. 1992. Tagging and recapture of cod in Stodvarfirdi and Gunnolfsvik in 1991 and 1992. Ægir, 2: 3–10 (in Icelandic).