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Variation in hatch date distributions, settlement and growth of juvenile plaice (*Pleuronectes platessa* L.) in Icelandic waters.

By

Björn Gunnarsson and Thór H. Ásgeirsson

ABSTRACT

Hatch date distribution, larval phase and subsequent growth of juvenile plaice (*Pleuronectes platessa* L.) in different regions around Iceland were determined by otolith microstructure analysis. Length, age and hatch date frequency distributions were obtained from juveniles captured in a 1 m beam trawl on 30 stations at 0.5-1 m depth all around Iceland in July 2006. The main spawning has generally been assumed to take place on the south and southwest coasts. Eggs and larvae are then distributed by currents along the west and north coasts. Contrary to expected dispersal pattern, both size and age of juvenile plaice decreased from south to north. The results indicates that the observed spatial variation in size of the juveniles is not explained by different growth rates but by age. The juveniles at the south coast hatch earlier than juveniles on the north and east coasts, have a shorter larval period, and higher growth rates. The study provides evidence that the juvenile plaice population may in fact originate from multiple spawning sites located not only along the south and southwest coasts, but along the entire coast of Iceland. The findings are discussed in relation to currents and temperature in Icelandic waters.

Key words: *Pleuronectes platessa*, juvenile, age, hatch date.

Björn Gunnarsson, Thór H Ásgeirsson: Marine Research Institute, P.O.Box 1390, Skulagata 4 Reykjavik, Iceland [tel: +354 575 2000, fax: +354 575 2001, e-mail: bjogun@hafro.is; thoras@hafro.is

INTRODUCTION

Identifying fish stocks, discriminating among them, and determining the stock composition of mixed stocks are integrated elements of fishery management (Waldman, 1999). Consequently, understanding origin and dispersal of juvenile fish and their subsequent distribution is vital for understanding the processes underlying population structure (Hanson, 1996). Failure to account for stock diversity can lead to erosion of spawning components, detrimental local effects and loss of biological diversity (Bailey, 1997). Furthermore, the understanding on how growth and survival of early life stages affect stock structure will facilitate understanding of recruitment variability and lead to better estimates of the stock-recruitment relationship (Begg and Marteinsdottir, 2002)

The European plaice (*Pleuronectes platessa*) is found on the continental shelf around Iceland, most abundantly in the warmer waters to the south and west of the country (Solmundsson et al., 2005). The main spawning grounds are located along the south and the west coasts and the spawning begins in late February, peaks in March and April and is mostly finished by the middle of May (Saemundsson, 1926; Sigurdsson, 1989; Solmundsson et al., 2003). Pelagic eggs and larvae are believed to drift from spawning areas clockwise around the country with the coastal current and the warm saline Atlantic water (Tåning, 1929, Gunnarsson et al., 1998). (See Fig. 1). The Atlantic water of the Irminger Current flows towards the south coast of Iceland. South of Iceland the Irmingar Current splits and one branch flows along the southeast coast eastwards to Faroese waters (Valdimarsson and Malmberg, 1999). The larger branch follows the bottom contours along the west coast, and splits into two branches west of Iceland's Westfjord peninsula (Stefansson, 1962). The largest part of the Irminger Current flows west towards Greenland, but a smaller branch continues north onto the shelf north of Iceland. This northward flow is often interrupted by the East Greenland Current, which originates in the Arctic Ocean and transports cold water south along the east coast of Greenland. The collision of warm and cold water masses causes considerable variability in hydrographic conditions of the north Icelandic waters and influences the local biological productivity (Malmberg et al., 1996; Guðmundsson, 1998; Jónsson and Valdimarsson, 2005). Although not well documented, spawning of plaice has been reported at several locations all around the country. Tåning (1929) and Saemundsson (1926) reported that spawning of plaice

occurred on the northwest, north and east coasts but concluded that it was limited compared to the main spawning grounds. Furthermore, Solmundsson et al. (2005) showed that spawning plaice is to be found all around the island (Fig 2).

Little is known about the general biology of the juvenile stages of plaice in Icelandic waters. Tåning (1929) summarized investigations from the first three decades of the 20th century on settled 0-group plaice. He showed that plaice settle on sandy beaches on the west-, north- and east coasts, starting at the end of June on the western coast and continuing for up to two months along the northern and eastern coastlines. He also notified a decline in size of the juveniles clockwise around the country, from west to east, and proposed that this was mainly due to temperature induced growth differences and only partly due to difference in spawning time. The larval and juvenile growth rates may have been enhanced by the warmer water on the west coast and retarded by the cooler waters off the north and east coasts.

In recent years, the Icelandic plaice stock has been severely depleted (Anon., 2007). Despite the economic and ecological importance of the species, studies on the population structure, dynamics, and origin are few. Consequently, further information on the life history of the juvenile plaice is clearly needed in order to improve our understanding on the spatial stock structure.

In this study, we make the first attempt to analyse the origin of juvenile plaice in Icelandic waters by estimating the hatch date distributions by means of otolith microstructure. Spatial variations in age-length relationships are then analyzed to determine whether geographical size differences are growth related. The present analysis provides information on the larval duration.

MATERIAL AND METHODS

Sampling

The coastline of Iceland is estimated to be roughly 6500 km in length, excluding tidal flats. The greatest portion of the coastline consists of moderately steep rocky shores (approximately 4900 km), while very steep shores, including vertical cliffs, are estimated to be about 600 km in length. Exposed apparently barren, sandy

shores are estimated to be about 560 km in length (Ingolfsson, 2006). The sampling sites (stations) were selected based on shore type (unvegetated sandy substrates) and accessibility by a 4-wheel drive vehicle. A total of 30 stations were sampled during a 12-day period in July 2006, covering virtually all the main coastal areas of Iceland (Fig 3). Sampling was done with a 1 m beam trawl during two hours around neap tide. The 5.5 m long trawl is equipped with a tickler-chain and 8 mm mesh size in the main body and 7 mm in the cod end. The towing speed was kept as constant as possible during sampling, at an average of 35 m min⁻¹. The gear was pulled parallel to the beach by two persons for approximately three minutes. GPS equipment was used to record the distance covered and the surface area sampled was approximately 100 m². The average depth at each station ranged from 0.5 to 1 m. On each occasion, two or three replicate hauls were made. Samples were stored in plastic buckets and sorted within a few hours in the laboratory. The juvenile flatfish were identified to species, counted, and the total length was measured to the nearest 0.1 millimetre, and then preserved in 96% ethanol until extraction of otoliths. When converting the catch to numbers per 100 m², no correction was made for gear efficiency.

Temperatures were obtained from continuously recording thermometers positioned in surface waters at five locations in regions 1 – 5 (Fig. 3). In region 1 the thermometer was located on the island of Heimaey. The temperature observed there are believed to represent the temperature conditions in regions 1 and 2 (Malmberg et al. 1996). Temperatures were recorded every two hours and daily temperatures were obtained by averaging all measurements between 0000 h and 2400 h.

Data analysis

Otolith microstructure analysis was used to determine growth rates, larval phase duration and age in days of plaice juveniles from the different regions around Iceland. To statistically assess the spatial variation, the survey area was divided into six regions (Fig. 3). Juveniles from stations within every region were pooled together and samples were randomly drawn for analysis. The sagittal otoliths were removed, cleaned and mounted on microscopical slides, sulcus up, with cyanoacrylate glue. The otoliths were polished on both sides with metallurgical lapping film until the accessory primordia and the increments were visible. The final polishing was done with alumina powder (0.3 µm). Approximately 100 otoliths were analysed from each region. Counts were repeated three to five times by the first

author until a consistent age was obtained. If any of the counts differed more than +/- 10%, often due to poor sample preparation, the otolith was discarded (approximately 7% overall). The increment counts of 20 randomly selected otoliths were checked by a second reader, and were found to be within 10%. Lengths of juvenile plaice were adjusted to the mean date of the sampling period (22 July) by adding or subtracting the mean growth rate (mm day^{-1}) within each region. The inner most accessory primordia was determined as the settlement mark (Modin et al. 1996; Alhossaini et al. 1989) and provides an estimate of the timing of settlement to benthic habitat. Growth rate (mm d^{-1}) was calculated as follows:

$$G = (\text{TL}_{\text{catch}} - \text{TL}_{\text{metamorphosis}}) / \text{age after metamorphosis}$$

In which TL is the total length at the time of catch and at metamorphosis, respectively. TL at metamorphosis used for the calculations was 12 mm (Ryland, 1966; Modin et al. 1996). Length at post larval age was compared among regions by an analysis of covariance (ANCOVA). Hatch date frequency distributions were derived from back calculated age class distributions, based on number of increments from the hatch check until time of capture. No corrections were made for mortality. Length, hatch date, and larval phase frequency distributions among regions were then compared with a Kolmogorov-Smirnov (KS) test.

RESULTS

Temperature measurements

In general, temperatures in March - May were 2 - 4°C higher on the south coast compared to local temperatures within the fjords on the west, north and east coasts (Fig. 4). On the south coast, temperatures rose gradually from approximately 6°C in the beginning of April to 8°C in end of May, exceeding 10°C at the end of July. Temperatures on the west, north and east coasts were at or below 2°C in March and approached 6°C in the beginning June. At the end of July, temperatures on the west and north coasts had reached the same temperatures as on the south coast while the temperatures on the east coast was about 1°C lower.

Spatial distribution and size

Density of plaice ranged from 0 to 1034 ind. 100 m⁻² among the investigated stations, with an overall average density in the study area of 140 ind. 100 m⁻² (Fig. 5). The highest densities occurred in region 3 and 6 constituting 43% and 30% of the total abundance index respectively.

Because the length-frequencies were generally skewed and not normally distributed, the median length was estimated rather than the mean length. The adjusted total length (TL) frequency distributions for each region all differed significantly from each other (Fig. 6, Table 2). The median TL decreased from region 1 (32.2 mm) on the southwest coast, clockwise around the country to region 5 on the east coast who had the smallest median length (18.8 mm). In region 6, on the southeast coast, the median length increased again (28.5 mm) (Fig. 7, Table 1).

Growth

An ANCOVA test on the log length as a function of age showed that size at age was significantly different among all regions ($F = 12.6$, $df = 5$, $5p < 0.001$). The overall growth rate estimated for the present study was 0.44 mm d⁻¹. The mean post-settlement growth rate, estimated from count of increments deposited during the juvenile stage, ranged from 0.35 mm d⁻¹ in region 5 to 0.52 mm d⁻¹ in region 6 (Table 1, Fig. 8). However, when analysing plaice ≤ 30 mm and plaice > 30 mm separately from all regions their growth rates were significantly different, 0.36 d⁻¹ and 0.57 d⁻¹, respectively.

Hatch date distribution and larval period

The back-calculated hatch distributions of the juvenile plaice from the otolith microstructure analysis are presented in Fig. 9. The spatial variation in length distributions were reflected in the hatch date frequency distributions. A distinct gradual delay in average time of hatching was detected from west to east (Table 1, Fig 8). Most of the juvenile plaice caught in regions 1, 2 and 3 hatched in mid- to late April. In regions 4 and 5 the juveniles hatched on average two to three weeks later. Some of the individuals in region 5 hatched as late as mid June. In region 6, on the southeast coast, the mean hatch date was 24 April ranging from late March to early June. The hatch date distributions all differed significantly from each other except in regions 1 and 2 (Table 2).

There was no significant difference between the length of the larval phase in the southern regions, 1 and 6 (Kolmogorov-Smirnov test $p>0.10$). The plaice in these regions had a larval phase of 52 days on average, ranging from 46 days to 64 days. The plaice in regions 2 to 5 settled later and had significantly ($p<0.001$) longer larval period than in region 1 and 6, or about 60 days on average, ranging from 50 – 76 days which, in turn, were not significantly different from each other ($p>0.10$).

DISCUSSION

The geographic comparison revealed significant differences in size distribution of juvenile plaice. In contrast to the expected dispersal pattern of the coastal and Irminger currents (Malmberg et al. 1996), the clockwise gradient of juvenile plaice from the south to the east coasts, with decreasing length distributions, has previously been considered to result mainly from temperature-induced growth (Tåning, 1929). Post-settlement growth rates, estimated by otolith microstructure analysis, ranged from 0.35 d^{-1} in region 5 to 0.52 d^{-1} in region 6 (The mean growth rate of plaice, for all regions, from 11 mm to 62 mm was 0.44 d^{-1}). These values are within the range of growth rates reported in the literature for a number of other nursery grounds: 0.38 mm d^{-1} for plaice $\leq 30\text{ mm}$ and 0.61 d^{-1} for plaice $>30\text{ mm}$ on the French coast of the Eastern Channel (Amara and Paul, 2002), $0.19\text{-}0.62\text{ mm d}^{-1}$ in the port Erin Bay Nursery (Nash et al. 1994), $0.56\text{-}0.66\text{ mm d}^{-1}$ in the eastern Wadden Sea areas (Berghahn et al., 1995), $0.23\text{-}0.45\text{ mm d}^{-1}$ along the Swedish Skagerrak archipelago (Pihl et al., 2000) and 0.6 mm d^{-1} in Icelandic waters (Hjörleifsson and Pálsson, 2001). In this study, further comparison of growth rates of juvenile plaice from the warmer regions (regions 1 and 6) and plaice from the colder regions (regions 2-5) revealed similar growth rates for similar size classes. The growth rate for juvenile plaice $\leq 30\text{ mm}$ was 0.38 mm d^{-1} in the warmer regions and 0.36 mm d^{-1} in the colder regions. Similarly, the growth rate for plaice $>30\text{ mm}$ was 0.57 mm d^{-1} in the warmer regions and 0.54 mm d^{-1} , in the colder regions. The significant difference between regions in the length as a function of age may therefore only be a reflection of the different size ranges measured among regions (e. g. very few individuals $\leq 30\text{ mm}$ in region 1 - Fig. 8). This indicates that growth rate had only a small effect and cannot explain the declining clockwise size gradient around the country. Size differences of

juvenile plaice (adjusted to a common date) were primarily a function of hatch date, with earlier hatching resulting in bigger fish (Fig. 9). To examine this, juvenile plaice should be collected continuously in the different regions from early spring to late summer to range over the whole size spectrum in addition to and further otolith increment analysis.

Distinct differences in incubation temperatures prevail between plaice spawned in waters off the north and east coasts and those plaice spawned in the south. The duration of development of plaice eggs is between 13 and 26 days (Apstein, 1909), and thus temperature could cause a few days difference in development times. Furthermore, the development time of larvae is also temperature-dependent with increasing sea temperature generally decreasing the pelagic stage duration (Hyder and Nash, 1998). The present study reveals that plaice from the warmer southern regions 1 and 6 had significantly shorter (54 days on average) larval phase compared with plaice in regions 2-5 (60 days on average) and most likely shorter egg duration. The differences indicate that these plaice originated from different spawning grounds with different temperature regime. These values are within the range of larval phase reported by Karakiri et al. (1991) but differ somewhat from Ryland (1966) who reported larval phase of 60 – 70 days.

Logeman and Harms (2006) developed a high resolution model of the North Icelandic Irminger current (Fig. 1). Preliminary examination of the current speeds in Icelandic waters suggests that they are not high enough to transport plaice eggs and larvae from the south of Iceland into the shelf north of Iceland. According to the model, a drift from region 1, 5 km south of Olfusaros, to Latrabjarg section (Fig.4) would on average take 120 days. Since plaice larvae are known not to be able to delay metamorphosis for any considerable time (Gibson and Batty, 1990), they would have switched from the pelagic phase and settled before entering the northern shelf. The observed spatial gradient in age is likely due to differences in the spawning location of juvenile plaice, with older individuals originating in spawning grounds in the south and younger juveniles farther north and east. It is likely that the contribution from the main spawning grounds in the south and southwest decreases with clockwise distance from the source region and probably non-existent on the northern and the eastern shelf of Iceland.

The spatial variation in hatch date distributions illustrated in this study, clearly indicates that the surviving juvenile plaice originate from different spawning grounds

but not exclusively from the main spawning grounds on the south coast. Only parts of the hatch date distributions displayed by the juveniles in the north and the south overlapped with the distributions from the main spawning grounds in region 1. According to the otolith microstructure analysis, hatching occurred mostly from early April to mid May in regions 1 and 2 and from mid April to early June in regions 4 and 5 (Fig. 9). It has been shown that the plaice larva settle in water deeper than 5 m and moves into shallow water following metamorphosis (Lockwood, 1974). When the fish grows to more than 40-50 mm they tend to gradually migrate again into deeper water (Lockwood, 1974; Gibson et al. 2002). In regions 4 and 5, it is likely that newly settled juveniles were still entering the shallow coastal zones from deeper waters when the samples were collected. At the same time it is possible that juveniles, at least in region 1 and 6, had started to move out again into deeper waters. This would lead to even more pronounced differences in size and consequently age between the juveniles on the south coast and the north and east coasts respectively.

The present study shows that juvenile plaice is found on sandy beaches on the west, north and east coasts of Iceland, confirming Tåning's (1929) findings from the first decades of the 20th century. Additionally, we found that juvenile plaice are also found along the south coast. The highest densities were found in region 6 (1034 ind. 100 m⁻²) on the southeast coast and in region 3 (1022 ind. 100 m⁻²) on the northwest coast (Fig. 5). Sampling with 1 m beam trawl on the west coast of Iceland in 1999 (Hjörleifsson and Palsson, 2001) indicated peak densities up to 10 ind. 100 m⁻² while this study measured order of magnitude higher densities on the west coast. The magnitude of the highest estimates in this study are higher than those obtained in the nursery areas of the Scottish coasts (Poxton and Nasir, 1985) and considerably higher compared with the Wadden Sea (Berghahn, 1986). However, more detailed observations are required for further evaluation (comparison) of the abundance. Plaice has spatially restricted nursery grounds located in shallow soft bottom areas, where the nursery areas only make up a small fraction of the species distribution range (Gibson, 1999). The importance of different coastal areas for recruitment is expected to depend on the quality and size of the nursery grounds. An important element in moving toward sustainable fisheries is the identification and conservation of essential fish habitats (Wennhage et al. 2006). For these purposes, information is needed to identify and evaluate how habitat quality and quantity may influence habitat use and recruitment success of plaice in Icelandic. Such information is valuable for describing

essential fish habitats and to determine the importance of different coastal areas for fish.

Solmundsson et al. (2005) suggested the occurrence of geographically distinct spawning locations maintained by site fidelity and connected by straying, indicating a complex structure in Icelandic plaice. The present study supports this theory and provides evidence for the existence of a local population structure within the Icelandic plaice stock. This may have important implications for improving the management of the Icelandic plaice stock in the future. Future studies should collect evidence of spawning times, locations and genetic research around the country in order to identify local spawning and nursery grounds. Furthermore, application of a high-resolution circulation model developed for Icelandic waters (Logeman and Harms, 2006; Brickman et al., 2006) would facilitate understanding of the observed abundance and the age distributions of the juveniles, contributions from the various spawning grounds and the extent of mixing in nursery areas.

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Tables

Table 1. Summary of sampling, length, hatch date, growth rate and length of larval period (\pm SD) from the July survey 2006.

Region number	1	2	3	4	5	6
Number of stations	3	5	4	8	7	3
Number of plaice collected	437	1063	3336	818	484	1725
Number of plaice aged	91	74	76	108	87	98
Mean length - survey (mm) *	32.1 \pm 7.8	27.4 \pm 4.5	21.4 \pm 4.3	20.7 \pm 4.8	18.8 \pm 4.8	30.1 \pm 6.3
Mean length - aged (mm) *	33.5 \pm 7.9	28.8 \pm 4.5	23.4 \pm 4.9	22.7 \pm 8.3	20.8 \pm 5.2	32.0 \pm 7.5
Mean growth rate (mm d ⁻¹)	0.51 \pm 0.10	0.43 \pm 0.10	0.36 \pm 0.06	0.40 \pm 0.13	0.35 \pm 0.12	0.52 \pm 0.14
Mean hatch date (day of year)	105 \pm 11	108 \pm 9	112 \pm 11	122 \pm 9	130 \pm 12	114 \pm 11
Mean larval period (days)	53 \pm 6	58 \pm 5	61 \pm 6	58 \pm 7	59 \pm 7	52 \pm 5

*Length not adjusted to mean cruise date.

Table 2. Table of Kolmogorov-Smirnov two sample test probability levels. Above the diagonal is the comparison of SL between regions (Fig. 6), and below the diagonal is the comparison of hatch date between regions (Fig. 9).

	Region 1	Region 2	Region 3	Region 4	Region 5	Region 6
Region 1	-	<0.001	<0.001	<0.001	<0.001	<0.001
Region 2	>0.10	-	<0.001	<0.001	<0.001	<0.001
Region 3	<0.05	>0.10	-	<0.001	<0.001	<0.001
Region 4	<0.001	<0.001	<0.001	-	<0.001	<0.001
Region 5	<0.001	<0.001	<0.001	<0.001	-	<0.001
Region 6	<0.001	<0.001	>0.10	<0.001	<0.001	-

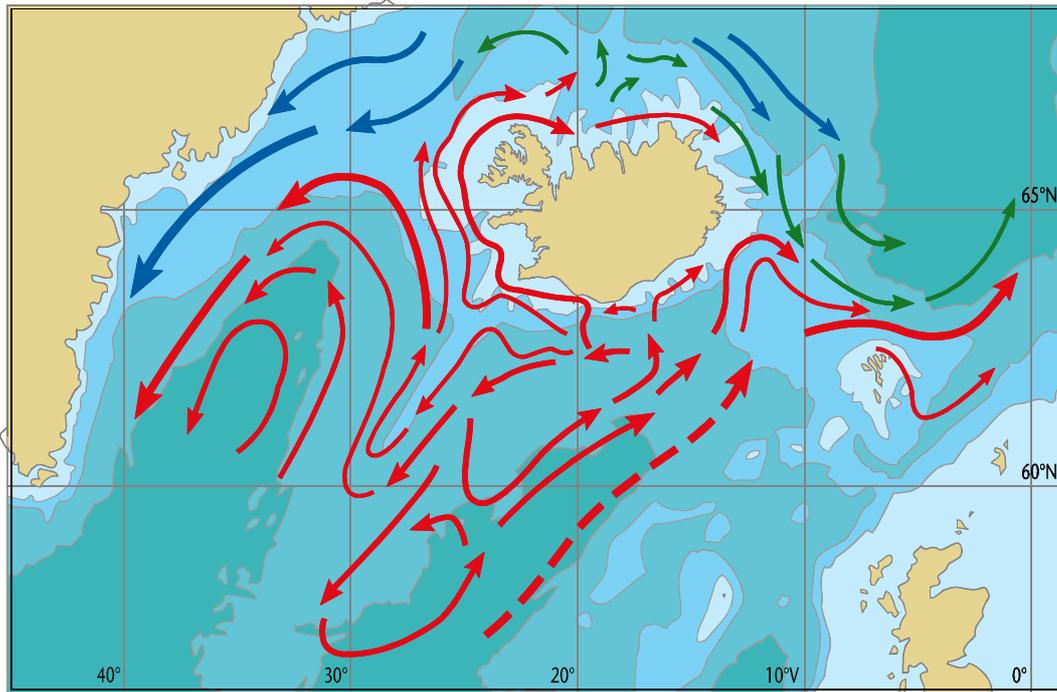


Fig. 1. Schematic presentation of the surface circulation around Iceland. Red arrows: relatively warm and saline Atlantic water; Blue arrows: Polar water; Green arrows: Mixed water (Adapted from Valdimarsson & Malmberg, 1999).

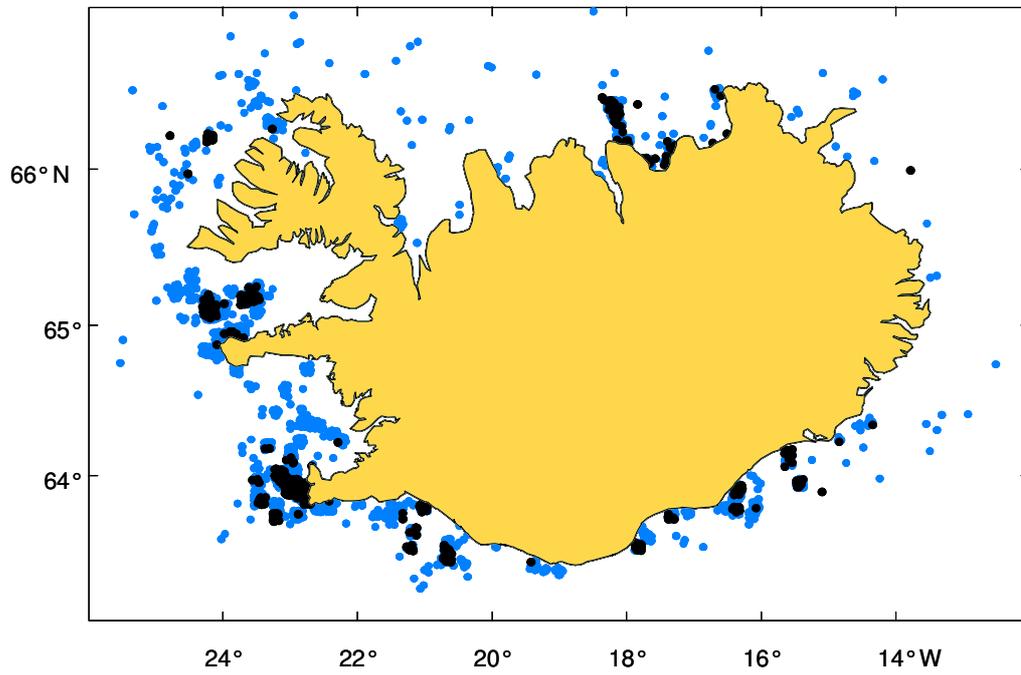


Fig. 2. Plaice spawning grounds as revealed by the distribution of actively spawning (running) female (in black) and male (blue) plaice registered in the fish database of the Marine Research Institute from 1987 -2004 (Solmundsson et al. 2005).

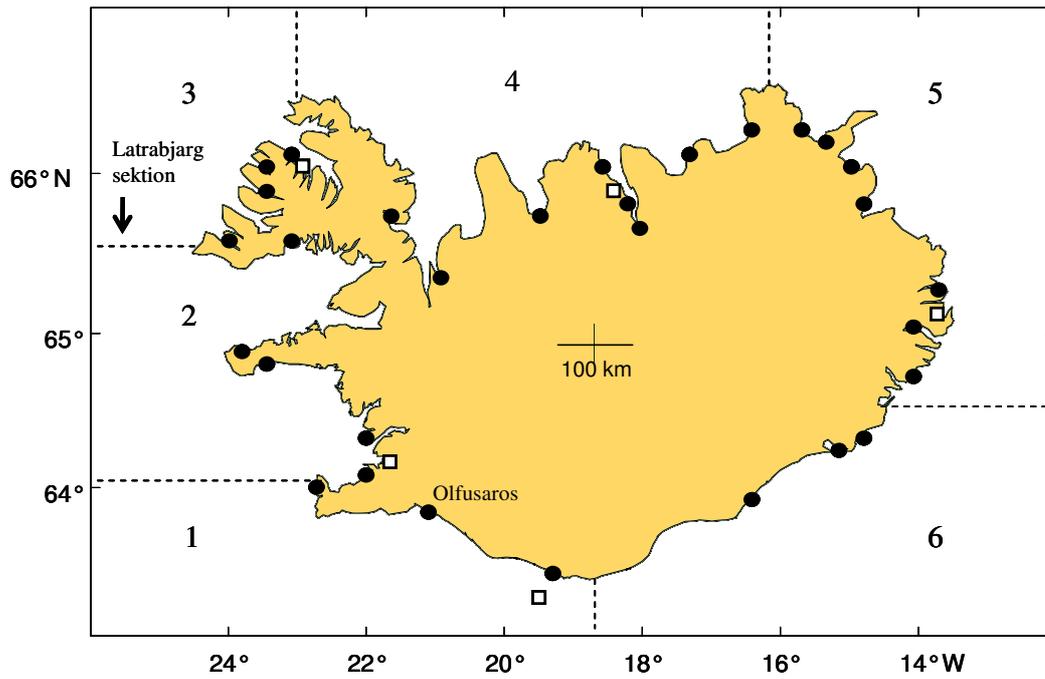


Fig. 3. Location of the six regions and the 30 stations sampled for juvenile plaice in July 2006 (black circles). Temperatures were obtained at locations shown by the open boxes.

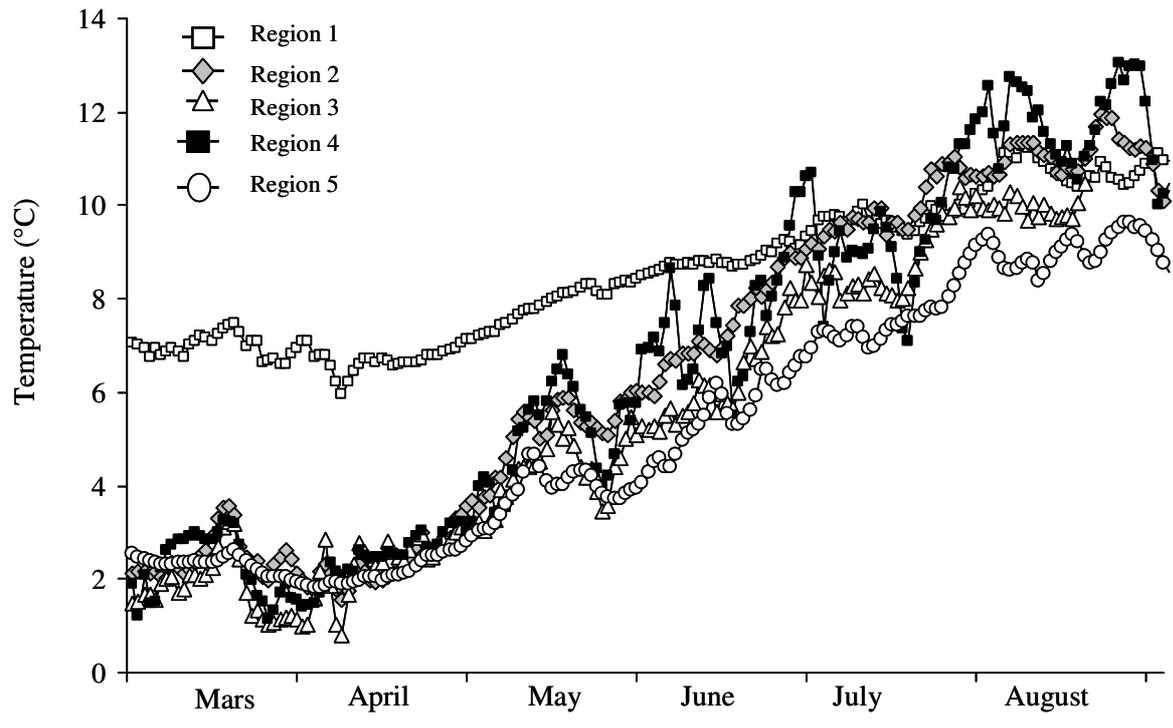


Fig. 4. Average daily temperature in regions 1-5 during late winter and summer 2006.

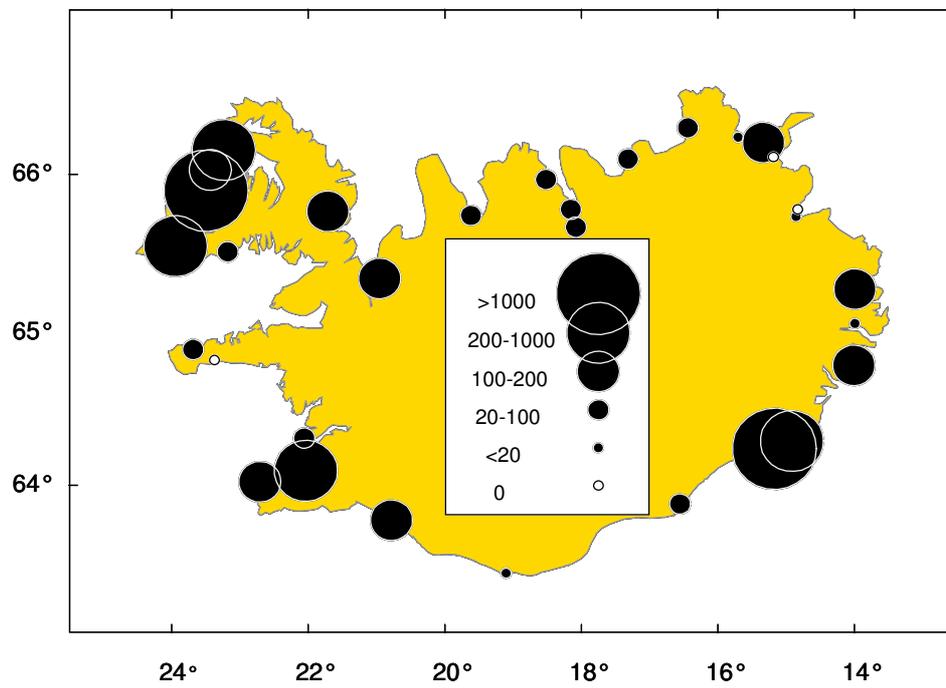


Fig. 5. Expanding symbol plot of juvenile plaice density (No. 100 m²) during sampling in July 2006.

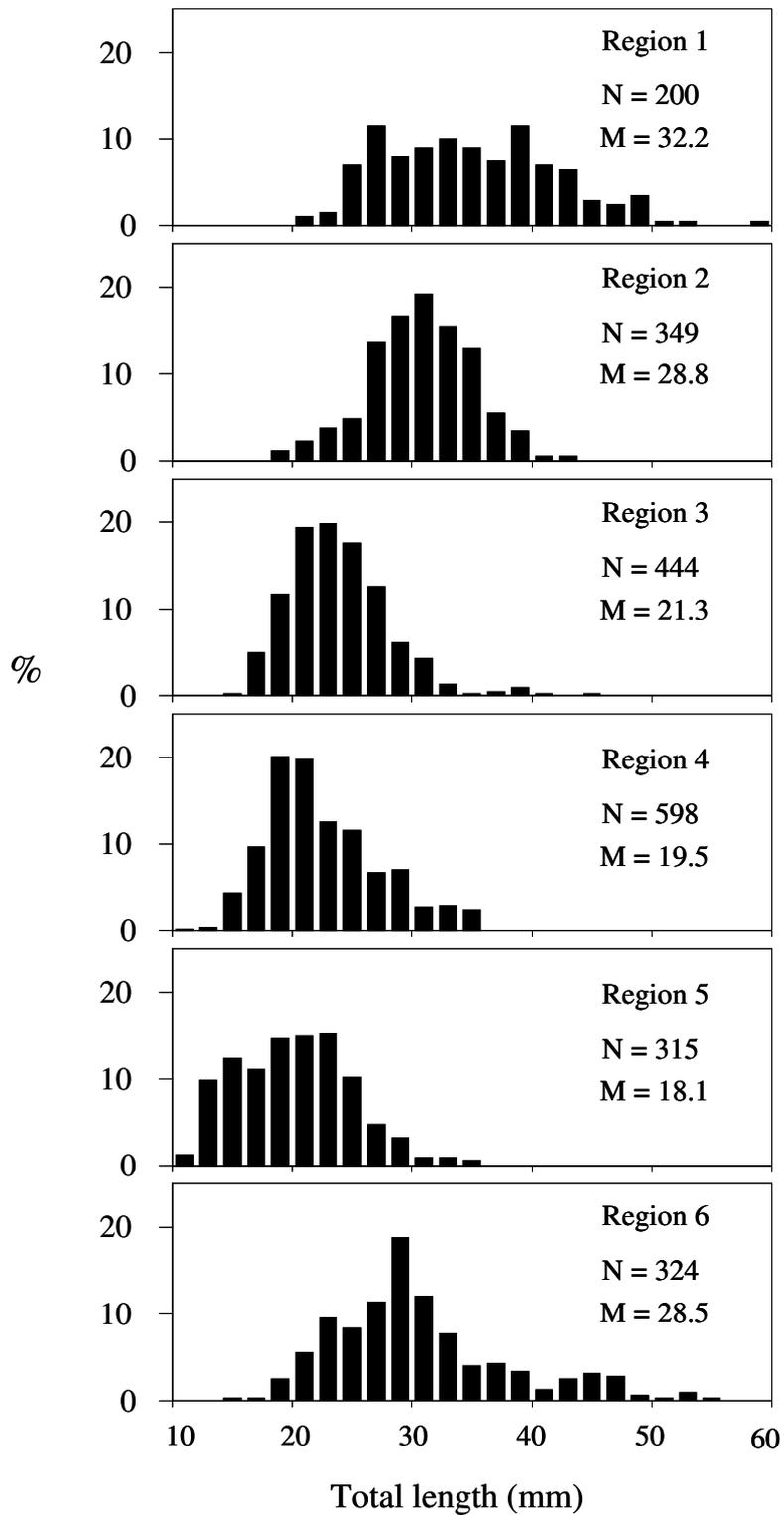


Fig. 6. Adjusted total length frequency distribution of juvenile plaice in July 2006. Total lengths were adjusted by mean daily growth in every region to the mid-cruise date on 22 July (N: Number of individuals; M: Median length).

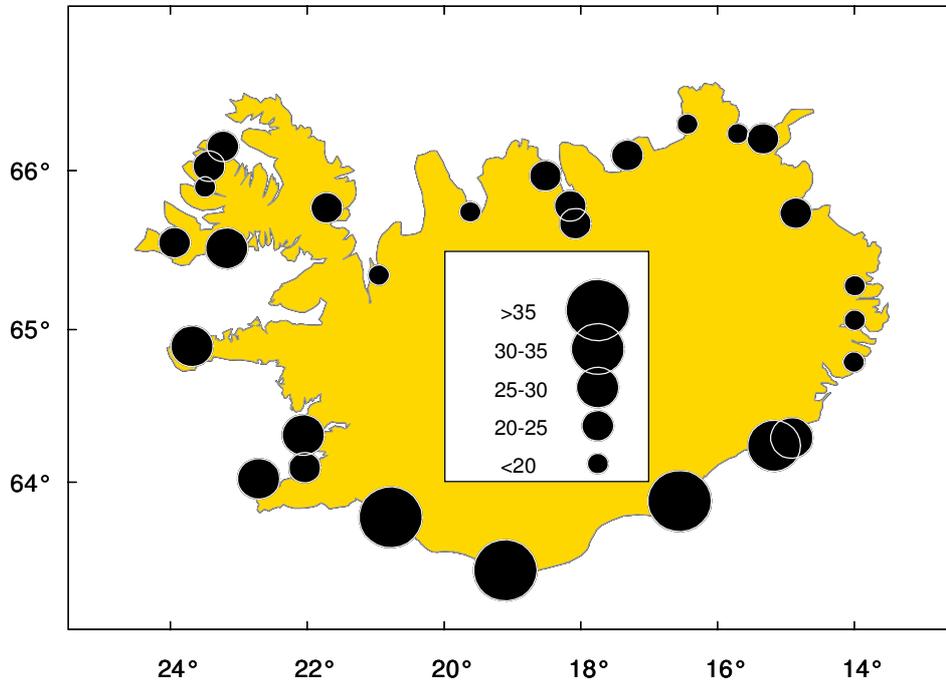


Fig. 7. Expanding symbol plot of juvenile plaice adjusted median length (mm) during sampling in July 2006.

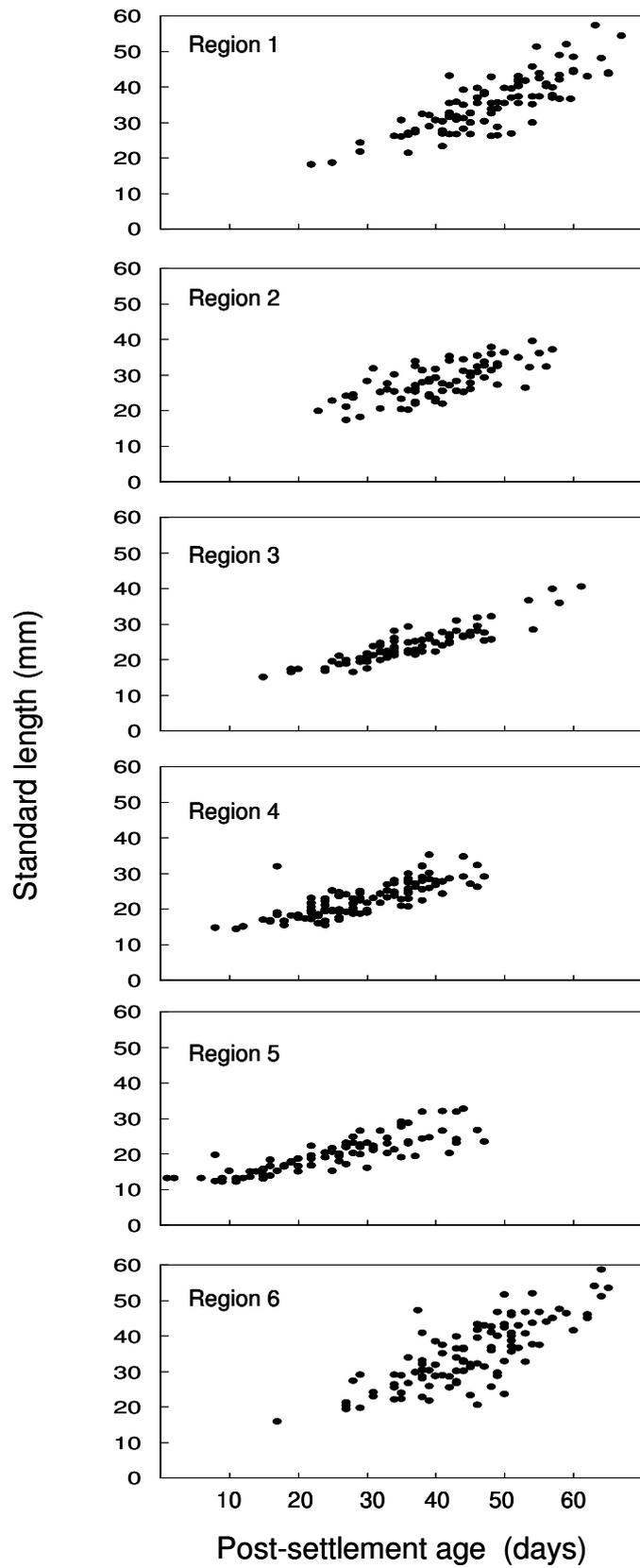


Fig. 8. Scatter plot of standard length on age for all regions.

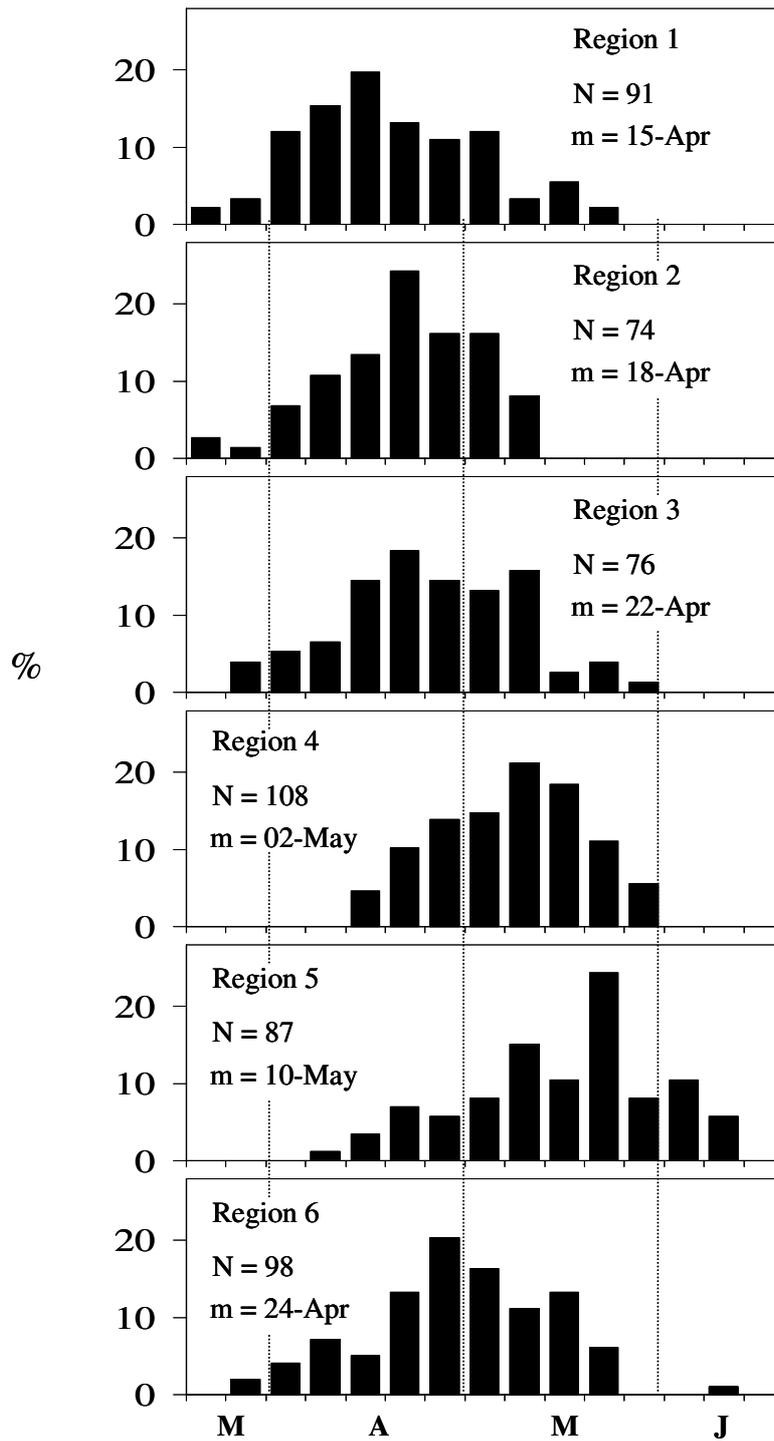


Fig. 9. Hatch date frequency distribution of juvenile plaice sampled around Iceland in July 2006. N: number of individuals; m: mean hatch date.