Contribution of different spawning components to the mixed stock fishery for cod in Icelandic waters

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Jónsdóttir, I. G., Marteinsdottir, G., and Campana, S. E. 2007. Contribution of different spawning components to the mixed stock fishery for cod in Icelandic waters. – ICES Journal of Marine Science, 64: 1749–1759.

Otolith chemistry and length-at-age were used to estimate the contribution of different spawning components to the harvested stock of cod (*Gadus morhua*) at two of their main feeding grounds northwest and east of Iceland. Spawning cod were sampled at different spawning locations around Iceland in spring of 2002 and 2003. Significant differences were detected between cod from the different spawning locations. Cod of unknown stock origin were also sampled at two of the main feeding grounds in October of the same years. Analyses based on maximum likelihood were used to estimate the proportion of each spawning group in the mixed stock catches using otolith chemistry and fish length-at-age. Attempts to use otolith shape to estimate the contribution of the spawning groups to the mixed harvested stock were, however, unsuccessful. The results indicated that spawning locations northwest and north of Iceland, as well as in water deeper than 125 m south of Iceland, contributed the most to the harvested stock. Cod spawning shallower than 125 m south of Iceland did not contribute to the feeding grounds in October of 2002 and 2003. Therefore, exploitation of the feeding stock mixtures seems to be based on spawning components that have previously been considered to be of minor importance to the Icelandic cod stock.

Keywords: cod, *Gadus morhua*, migration, mixed stock analysis, otolith chemistry.

Received 31 January 2007; accepted 29 September 2007; advance access publication 2 November 2007.

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Introduction

Exploited fish stocks commonly originate from several spawning components (Begg *et al.*, 1999), and the contribution of each component to the harvested stock varies with their productivity and their availability to the fishery. Less productive populations may be more vulnerable to heavy fishing pressure than more productive ones (Jennings *et al.*, 1998), potentially resulting in overexploitation of the less productive populations and loss of genetic variation (Stephenson, 1999). To improve stock assessment accuracy, the relative contribution of each population is needed for estimation of exploitation, mortality, and harvest rate. Recruitment, production, and growth need to be estimated for each population individually to avoid incorrect estimates of stock size and productivity (Hilborn, 1985). Therefore, a major concern for successful fisheries management is to distinguish the different populations contributing to mixed stock fisheries.

The main spawning grounds of cod (*Gadus morhua*) at Iceland are along the south and southwest coasts. Tagging studies from the mid-20th century indicated that most Icelandic cod migrated to these areas to spawn (Jónsson, 1954, 1982). Recent studies indicate that Icelandic cod originate from several spawning areas around Iceland, and that local reproduction outside the main southern spawning areas south and southwest of Iceland can be of significance (Begg and Marteinsdottir, 2000, 2002; Marteinsdottir *et al.*, 2000). Comparisons of otolith shape, otolith chemistry, and genetics indicate the presence of three major groups of Icelandic cod: one north of Iceland and two south of Iceland (shallower and deeper than 125 m) (Jónsdóttir *et al.*, 2006a, b; Pampoulie *et al.*, 2006; Petursdottir *et al.*, 2006). Tagging studies have indicated that, after spawning, Icelandic cod disperse from the spawning locations in search of food at two main feeding and fishing grounds, northwest and east of Iceland (Jónsson, 1996). However, tagging studies have shown that cod feed in both shallow and deep areas at other locations around Iceland (Pálsson and Thorsteinsson, 2003).

Mixed stock analysis has been used to estimate the contribution of different cod populations to mixed stock fisheries off Canada using both vertebral number (Swain *et al.*, 2001) and genetics (Ruzzante *et al.*, 2000). The elemental composition of otoliths has also been used successfully to estimate the contribution of different populations in mixed stock fisheries of cod (Campana *et al.*, 1999, 2000) and redfish (Campana *et al.*, 2007). The advantage of otolith elemental composition as a natural tag of groups of fish is that otoliths grow continuously throughout life and are metabolically inert, i.e. otolith material is neither resorbed nor metabolically reworked after deposition (Campana and Neilson, 1985). Therefore, if cod spend at least some part of their life in different chemical or physical environments, differences may result in otolith elemental compositions that can be used to discriminate among groups (Campana *et al.*, 2000). As otolith chemistry discriminates between the three major groups of Icelandic cod (Jónsdóttir *et al.*, 2006b), this method appears to be ideal

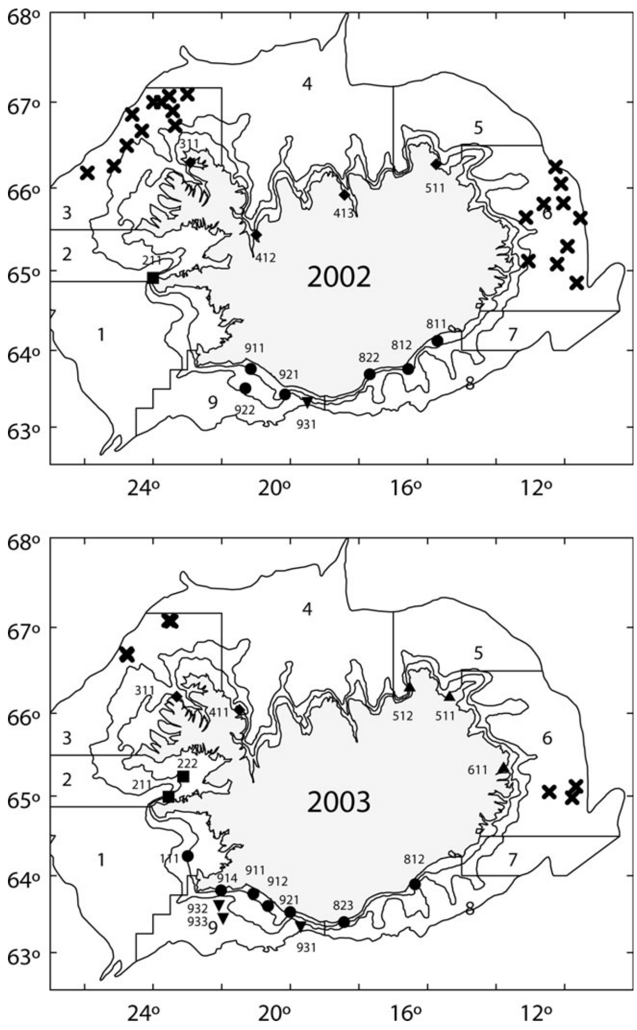

Figure 1. Sampling locations in spring (filled symbols) and autumn (crosses) of 2002 and 2003. Each spawning location was identified by a three digit number: the first digit represents one of the nine areas around Iceland, the second the depth interval (1, <75 m; 2, 75–125 m; 3, >125 m), and the last the station number. Spawning groups were divided into four and five groups in 2002 and 2003, respectively: G1 (shallow south, dots), G2 (north, squares), G3 (northwest, diamonds), G4 (northeast and east, triangles) and G5 (deep-water south, inverted triangles). Depth contours shown are 75, 125, and 500 m.

for studying the stock composition of mixed stock fisheries of the population. Life history parameters (such as length-at-age) and otolith shape, which are commonly used to discriminate between spawning groups and vary greatly between cod around Iceland (Jónsdóttir *et al.*, 2006a), may also be useful in mixed stock analysis. These methods have, however, not been applied for that purpose.

The otolith elemental composition characterizing the spawning stocks of Icelandic cod was determined in an earlier study (Jónsdóttir *et al.*, 2006b). Cod otoliths were sampled from the main feeding grounds in autumn of 2002 and 2003 (the same years as the spawning stocks were characterized; Jónsdóttir *et al.*, 2006b). The aim of this study was to use the otolith elemental composition specific to each spawning group to estimate the proportion of the different spawning groups in the mixed fisheries at the main feeding grounds.

Methods

Sampling

Mature and spawning cod were sampled at spawning locations around Iceland in spring of 2002 ($n = 12$ locations) and 2003 ($n = 17$ locations) (Figure 1; see Jónsdóttir *et al.*, 2006a, b, for the sampling protocol). On the basis of the discrimination of spawning groups using otolith shape (Jónsdóttir *et al.*, 2006a) and otolith chemistry (Jónsdóttir *et al.*, 2006b), spawning groups were pooled into four groups in 2002 and into five groups in 2003 (Table 1). Cod spawning in the same geographical area were pooled; shallow southern spawning locations (G1), west of Iceland (G2), northwest and north of Iceland (G3), north and east of Iceland (G4), and deep southern locations (G5). The main cod feeding and fishery grounds in autumn are northwest (A-NW) and east (A-E) of Iceland (Figure 2). Sampling of cod at the main feeding grounds northwest and east of Iceland was carried out in October of 2002 and 2003 using a bottom trawl (Figures 1 and 2). In 2002, samples were collected during the annual autumn survey of the Marine Research Institute, Iceland. In all, 263 samples were collected northwest of Iceland and 265 east of Iceland. Only 75 and 93 of these fish were in the age range 5–8 years (which was the age range of cod common to all spawning and feeding locations) northwest and east of Iceland, respectively (Table 2). In 2003, samples from the feeding grounds were collected from commercial fishing trawlers. Fewer locations were sampled in 2003 than in 2002 because the commercial trawlers did not cover as large a geographical area as the research vessel did in 2002. That year, 600 samples (300 from each feeding ground) were collected northwest and east of Iceland. However, just 179 and 260 of them were in the age range 5–8 years, northwest and east of Iceland, respectively (Table 2). While at sea, total length, weight, sex, and maturity (except for maturity in autumn 2003) were recorded for each cod. Sagittal otoliths were removed from each fish with non-

Table 1. Spawning locations sampled in spring 2002 ($n = 12$ locations) and 2003 ($n = 17$ locations), grouped into four groups in 2002 and five in 2003.

Group	Area	2002	2003
G1	South	811, 812, 822, 911, 912, 922	111, 812, 823, 911, 912, 914, 921
G2	West	211	211, 222
G3	Northwest and north	311, 412, 413, 511	311, 411
G4	North and east	–	511, 512, 611
G5	Deep-water south	931	931, 932, 933

Each spawning location was identified by a three-digit number: the first digit represents one of the nine areas around Iceland, the second the depth interval (1, <75 m; 2, 75–125 m; 3, >125 m), and the last the station number. Grouping was based on the otolith elemental analysis of Jónsdóttir *et al.* (2006b). For locations see Figure 1.

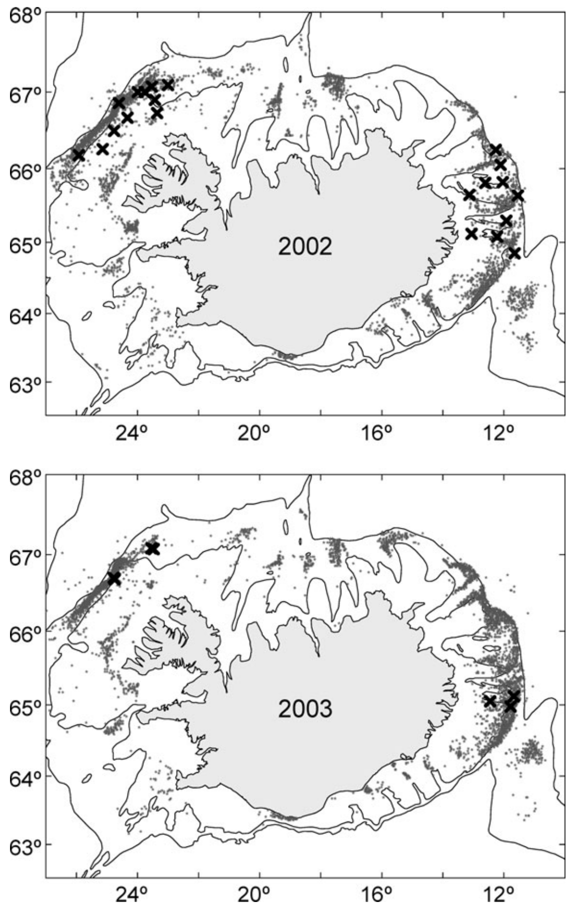

Figure 2. Fishing locations of cod trawlers in September, October, and November of 2002 and 2003 (one grey point for each tow). The percentage of cod in each tow was >50%. Crosses indicate sampling sites in the present study.

metallic forceps, cleansed of adhering tissue, and stored dry in paper envelopes until further analysis. The left otolith from each pair was used for the shape and elemental analysis, and the right otolith was sectioned for age estimation.

Shape analysis

The otolith contours from the left side of the fish were digitized using a microscope attached to an image analyser. Otoliths were orientated in a consistent manner, with the sulcus side up (magnification $\times$3.6–4.8, depending on the size of the otolith). The area, length, width, perimeter, circularity, rectangularity, and 64 Fourier coefficients (based on an angle of 5.625°) of each otolith were measured using Optimas version 6.51. Circularity was defined as the perimeter of the otolith squared, divided by its area. Rectangularity was defined as the otolith area divided by the area of its minimum enclosing rectangle. All otoliths were weighed to the nearest 0.1 mg.

Elemental analysis

Otoliths were decontaminated with a 5 min sonification in an acid-washed vial and Milli-Q water, followed by a 1 min scrubbing of the otolith, a triple-rinse in Milli-Q water, two 5-min sonifications, and a final triple-rinse in Milli-Q water. The otoliths were then dried under a laminar flow hood and weighed to the nearest 0.1 mg. The decontaminated otoliths were stored dry in sealed, acid-washed polypropylene vials until analysis. The otoliths were exposed only to acid-washed plastic materials during decontamination, and all steps other than sonification, brushing, and weighing were carried out under a laminar flow hood.

The decontaminated otoliths were dissolved in 0.6 ml of 70% (v v^{-1}) high purity nitric acid (TraceSelect, Fluka) per 0.1 g of otolith. All otoliths were dissolved in an acid volume proportional to the otolith weight, to ensure that the solutions were of similar concentration, to minimize possible instrument drift. The acid–otolith solution was heated in a microwave oven for 5 min until it reached 120°C, then kept at that temperature for 25 min to complete digestion. When the solution had cooled, the volume was brought up to 50 ml with Milli-Q water. Solutions were further diluted before analysis, $\times$5000 compared with otolith dry weight. Internal standards (Ga, In, and Ce) were then added to the samples. Five trace elements were measured (Ba, Mg, Li, Mn, and Sr) using inductively coupled plasma mass spectrometry (ICP–MS; LECO Renaissance mass spectrometer). A standard was run every four samples, and a blank and a laboratory reference sample were run every eight samples. The laboratory reference sample, consisting of a batch solution of digested otolith material, was used to monitor measurement precision across sample batches, and was subsequently used to normalize sample batches to a constant reference value. Detection limits for each element (in $\mu g\ g^{-1}$ for all elements except Sr, which was mg g^{-1}) were calculated as 3 $\times$ the standard deviation (s.d.) of the blank: Ba 0.1, Li 0.3, Mg 1.4, Mn 0.2, and Sr 0.01. The relative s.d. of the laboratory

Table 2. Depth range (m), total number (*n*), and number of cod aged 5, 6, 7, and 8 years sampled in spring and autumn of 2002 and 2003.

Group	2002						2003					
	Depth range (m)	*n*	Age				Depth range (m)	*n*	Age			
			5	6	7	8			5	6	7	8
G1	58–97	577	38	48	99	101	36–88	584	37	109	68	78
G2	64	100	17	25	29	13	46–108	200	10	43	22	25
G3	12–37	401	43	110	142	33	34–41	200	7	40	12	41
G4	–	–	–	–	–	–	16	321	25	48	41	35
G5	395	100	17	19	30	12	131–454	271	10	86	45	8
A-NW	113–274	263	45	21	5	4	238–347	300	103	59	15	2
A-E	146–323	265	56	29	5	3	152–297	300	89	110	48	13

The remaining individuals of the total *n* were ≤4 years old or ≥9 years. See Table 1 for spawning locations within each group. A-NW, autumn samples northwest of Iceland; A-E, autumn samples east of Iceland.

reference sample concentrations (five in each run) was used as a measure of precision. The precision was good for Ba (3%), Mg (3%), Mn (4%), and Sr (1%), but was lower for Li (13%).

Data analysis

All otolith variables from the spawning samples were tested for normality and homogeneity of variance, and transformed if necessary. Otolith weight and Li were transformed by natural-log transformation. Substantial size differences were detected between spawning groups, so to ensure that size differences were not influencing the analysis, the effect of fish length or otolith weight was removed statistically from those variables that showed a significant size effect. Analysis of covariance (ANCOVA) was used to determine the effect of fish length and otolith weight on the magnitude of the otolith shape and elemental variables, respectively. ANCOVA assumes a linear relationship between the dependent and the covariate. If the relationship was not linear, one or both of the variables were natural-log-transformed to establish a linear relationship. Fish length (for shape variables) or otolith weight (for otolith elements) was used as the covariate, and spawning location as the main factor. Where the effect of fish length or otolith weight was significant, the product of fish length or otolith weight and the common within-group slope (b) from the ANCOVA for a given variable was subtracted from the variables to create a standardized variable. The standardized variables were natural-log-transformed weight ($b = 1.518$), length ($b = 7.311$), natural-log-transformed area ($b = 0.936$), perimeter ($b = 23.937$), and natural-log-transformed Li ($b = -0.122$). Length-at-age was also standardized with a common within-group slope from an ANCOVA ($b = 4.178$), where age was used as the covariate and spawning location as the main factor. The same transformations and slopes were used to standardize the autumn mixture samples. Mean differences among locations for individual variables were tested with one-way analysis of variance (ANOVA). A Tukey HSD was then used to examine individual variables to explain any significant differences detected by the ANOVAs. Forward stepwise canonical discriminant analysis of the standardized data was used to discriminate between the different spawning groups. The functions from the discriminant analysis were then used to calculate discriminant scores for the mixed cod at the feeding grounds, to determine if any baseline spawning groups were missing from the mixtures.

Mixed stock analysis

The spawning stock composition of the autumn mixtures was estimated with a refined version of the maximum-likelihood-based integrated stock mixture analysis (ISMA) (Campana *et al.*, 1999, 2000). The reference (known stock) data were the spring spawning groups sampled in spring, and the unknown samples were the mixed stock samples from autumn of the same years. In addition to analysis of the whole mixed stock sample from each feeding ground, separate analyses were also made for immature and mature individuals in 2002. The product of each analysis was the proportion of each reference (spawning) group in the mixed harvested group. In 2002, six otolith shape variables contributed significantly to the discrimination of the spawning stocks: otolith weight, otolith length, otolith area, and amplitudes 1, 4, and 6. Additionally, otolith perimeter contributed in 2003. The standardized amplitudes showed some residual trend with fish length and were therefore eliminated from the mixed stock analyses. Three elements contributed to the discrimination of the spawning stocks based on otolith chemistry (Sr, Li, and Ba) and were therefore used for the mixed stock analyses. Additionally, fish length-at-age was introduced as a factor into the mixed stock analyses. Li and length-at-age were standardized as described earlier to remove the effect of otolith weight or age.

Simulation test

To evaluate the relative accuracy of otolith shape and otolith chemistry as stock discriminators of the mixtures, each spawning location from the baseline samples was treated in turn as an unknown mixture and classified in terms of baseline composition. The simulation tests were done separately for 2002 and 2003. In each year, every spawning location was used as a mixed unknown sample as well as one of the baselines. As baselines, 12 locations, 4 groups, or 9 areas were identified in 2002, and 17 locations, 5 groups, or 9 areas in 2003. A perfect classification would be 100% of the fish to their own location, group (Table 1), or area (Figure 1). Simulation tests such as these invariably give an elevated estimate of overall classification accuracy, but are usually reasonably close to unbiased estimators.

Results

Length-at-age

The mean length-at-age of cod sampled at the feeding grounds in 2002 and 2003 was in general less than that of cod spawning south and southwest of Iceland (Figure 3). At all ages, the mean length-at-age of cod sampled at the feeding grounds in 2002 and 2003 was significantly smaller than those from G1 (south and southwest) (Tukey HSD, $p < 0.05$; Figure 3), but was never significantly different from G3 (Tukey HSD, $p > 0.05$). In 2002, the younger cod (5 and 6 years old) at the feeding grounds were significantly smaller than those of the same age from all other spawning groups except G3. The lengths-at-age of older cod (7 and 8 years old) were not significantly different from G2 or G5 (Tukey HSD, $p > 0.05$).

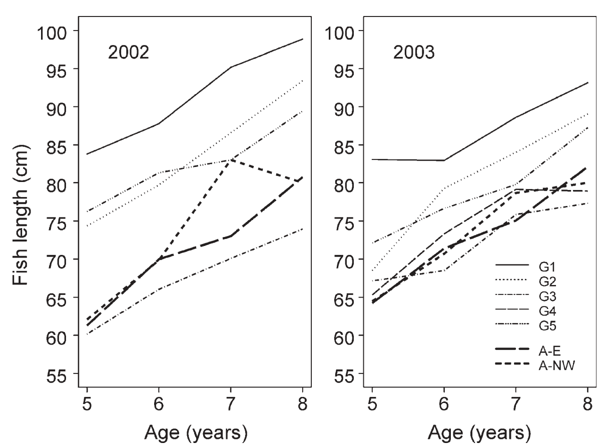

Figure 3. Mean length-at-age of cod at different locations in spring and autumn of 2002 and 2003. G1, shallow southern locations; G2, west of Iceland; G3, northwest and north of Iceland; G4, north and east of Iceland; G5, deep-water southern locations; A-E, feeding ground east of Iceland; A-NW, feeding ground northwest of Iceland.

Elemental concentration

The mean otolith elemental concentration of Ba, ln Li, and Sr varied significantly among spawning groups (Figure 4; ANOVA, $p < 0.001$). Some of the elements varied significantly among years for each spawning group; G1 (Ba, ANOVA, $p = 0.002$), G2 (Sr, ANOVA, $p = 0.009$), G3 (Ba, ANOVA, $p = 0.003$; Sr, $p < 0.001$), G4 (Sr, ANOVA, $p < 0.001$), and G5 (Sr, ANOVA, $p = 0.029$; ln Li, $p = 0.03$). The mean otolith elemental concentration (Ba, ln Li, and Sr) also varied significantly between A-NW and A-E in 2003 (ANOVA, $p < 0.05$), but not in 2002 (ANOVA, $p > 0.05$). However, no significant differences were found for any of the elements between years at A-NW or A-E.

In 2002 and 2003, the mean Ba, ln Li, and Sr concentrations at both feeding grounds were significantly different from G1 (shallow south) (Tukey HSD, $p < 0.001$; Table 3). Moreover, all elements were significantly different between A-E and G3 in 2002, and A-NW and G4 (northeast) in 2003 (Tukey HSD, $p < 0.001$; Table 3). Mean Li concentration was significantly different between feeding grounds and all spawning groups in both years, except for A-NW and G5 in 2002 and G2 in 2003 (Tukey HSD, $p < 0.05$; Table 3). In addition, Sr was significantly different between A-NW and G3 in 2002 and also between both feeding grounds in 2003 and G5 (Tukey HSD, $p < 0.05$; Table 3). The mean elemental concentrations therefore imply that it would be unlikely to find cod originating from G1 (shallow southern spawning locations) in the autumn mixed samples.

Simulation tests

The simulation tests indicated that otolith chemistry and fish length-at-age provided the most accurate classifications of unknown samples. In 2002, the highest classification accuracy was gained by using a combination of otolith chemistry and fish length-at-age (Figure 5). The greatest classification accuracy was also gained by grouping the spawning locations into five groups (Table 2; Figure 5). In 2003, there was not much difference in classification accuracy between otolith chemistry and otolith shape (both including fish length-at-age). However, when otolith shape was used without fish length-at-age, the classification success was low. In 2002, using otolith shape, only one location was classified correctly to its own location, group, or area, whereas the other 11 locations did not give any result. However, in 2003, 11 spawning locations were classified correctly to their own location, group, or area, and six locations did not give any result (not shown). On the basis of these results, otolith chemistry would be much more likely to recognize fish in the mixed group successfully. Therefore, otolith shape was not used for the mixed stock analysis.

Table 3. Results of a Tukey HSD of elemental analyses showing which spawning groups (G1, shallow water southern locations; G2, west of Iceland; G3, northwest and north of Iceland; G4, north and east of Iceland; G5, deep-water southern locations) differed significantly from each of the feeding grounds (A-NW, feeding ground northwest of Iceland; A-E, feeding ground east of Iceland) in 2002 and 2003.

Year and area	Ba	ln Li	Sr
2002			
A-NW	G1	G1, G2, G3, G4	G1, G3
A-E	G1, G3	G1, G2, G3, G4, G5	G1, G3
2003			
A-NW	G1, G4	G1, G3, G4, G5	G1, G4, G5
A-E	G1	G1, G2, G3, G4, G5	G1, G5

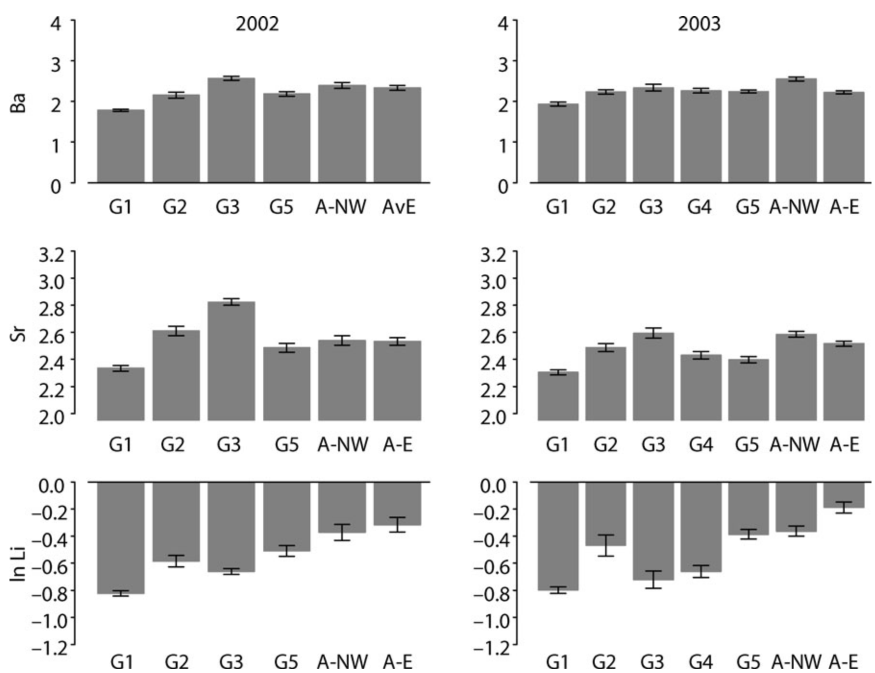

Figure 4. Mean ($\pm$ s.e.) concentration of Ba (µg element g^{-1} otolith), Sr (mg element g^{-1} otolith) and natural-log-transformed Li (ln Li; µg element g^{-1} otolith) in otoliths sampled at different locations in spring and autumn of 2002 and 2003. G1, shallow southern locations; G2, west of Iceland; G3, northwest and north of Iceland; G4, north and east of Iceland; G5, deep-water southern locations; A-E, feeding ground east of Iceland; A-NW, feeding ground northwest of Iceland.

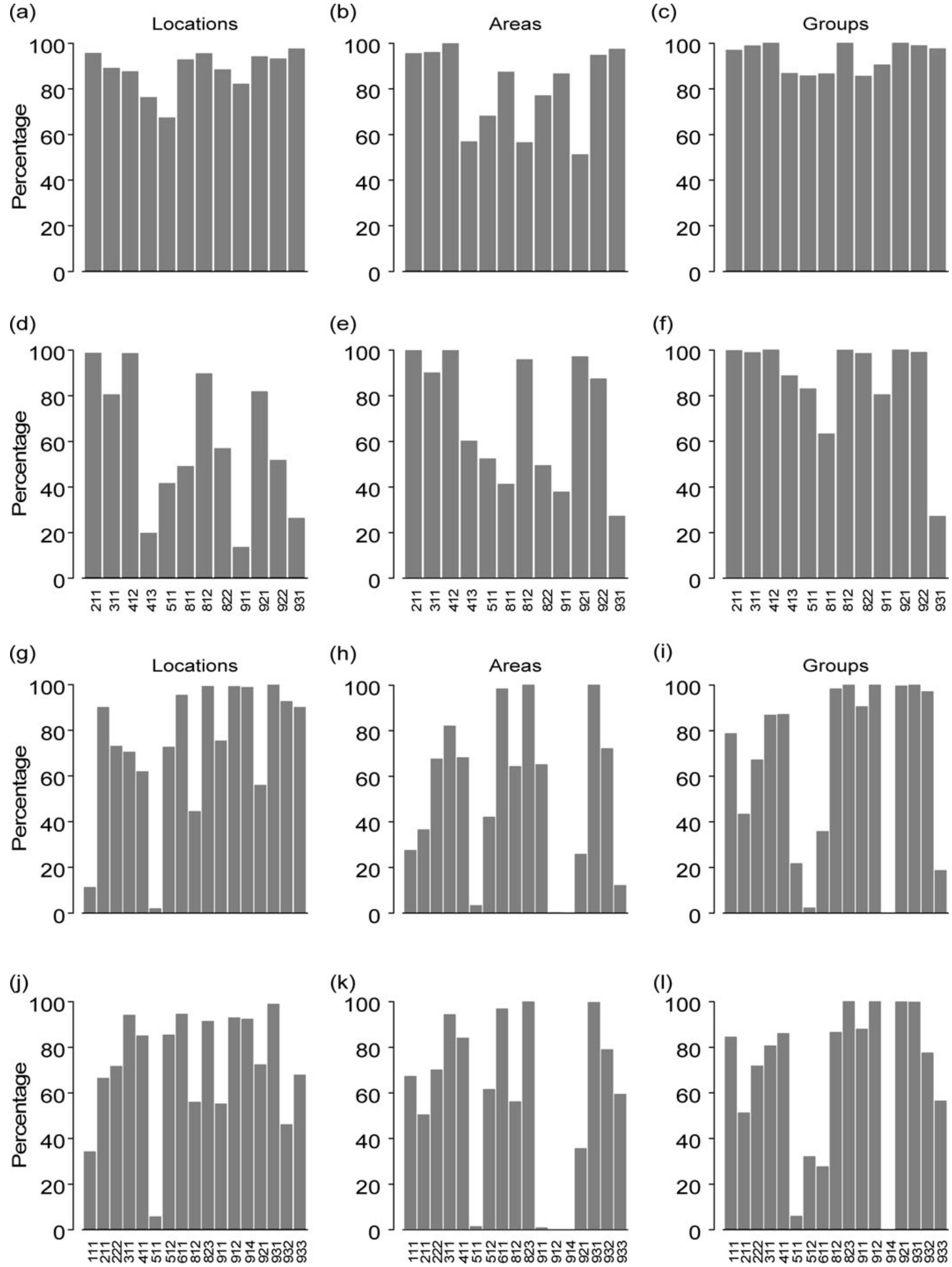

Figure 5. Percentage (%) of individuals from each spawning location correctly classified to its own spawning location, area (one of nine areas 1–9; Figure 1) or group (one of four or five groups; Table 1) in a test of relative accuracy. (a)–(c) based on otolith chemistry in 2002, (d)–(f) based on otolith shape in 2002, (g)–(i) based on otolith chemistry in 2003, (j)–(l) based on otolith shape in 2003. Fish length-at-age was included in all analyses. For locations see Figure 1 and Table 1.

Discriminant analysis

To infer whether cod sampled at the feeding grounds might have originated from a spawning group that had not been sampled and characterized (e.g. a baseline reference group was missing from the analysis), discriminant analysis was used to calculate discriminant scores for autumn feeding samples based on the discriminant functions calculated for the spawning groups. The discriminant scores of cod from the feeding grounds appeared to fit well in the discriminant space defined by the spawning groups, suggesting that the baseline sampling of spawning groups contained all the reference groups of importance for the mixed stock analyses (Figure 6).

Mixed stock analysis

Mixed stock analysis based on otolith chemistry without length-at-age suggested that most cod from both feeding

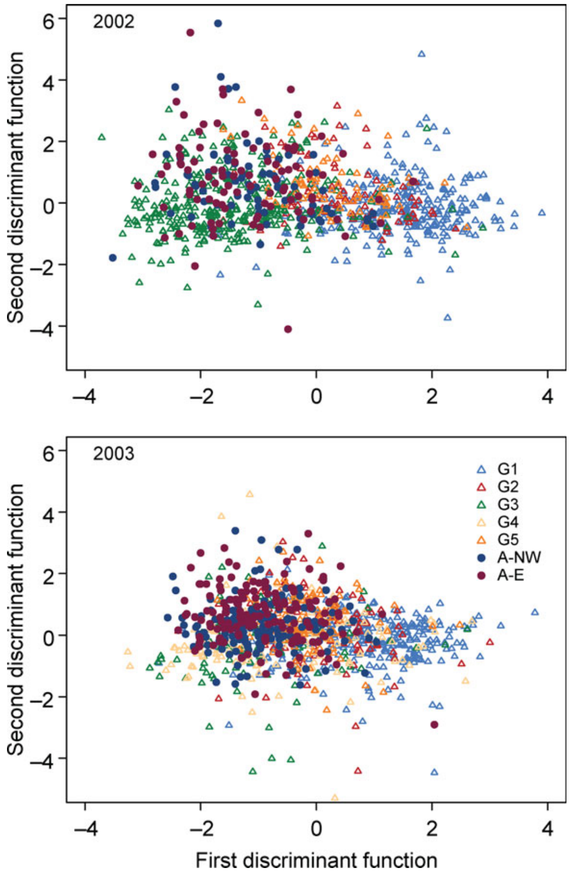

Figure 6. Discriminant scores based on otolith chemistry and length-at-age using 2002 and 2003 spawning groups (open symbols) as reference groups. Discriminant scores of fish from feeding grounds (filled symbols) were calculated from the spawning group discriminant functions.

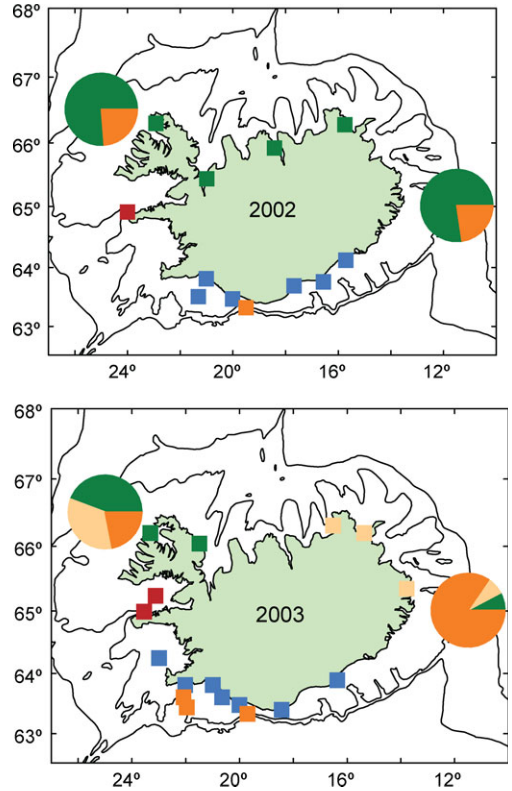

Figure 7. Estimated proportional spawning stock origin of cod sampled at the main feeding grounds northwest and east of Iceland in 2002 and 2003. Stock composition was estimated with a four- or five-group baseline of spawning samples (Table 1), based on otolith chemistry and length-at-age.

grounds originated from G2 and G5. Small proportions of cod from both feeding grounds were also estimated to have originated from G3 and G4 (north and northeast). However, no cod were determined to have originated from G1 (shallow south). These analyses were carried out to see the effect of otolith chemistry alone, but the simulations described earlier indicated that the combination of otolith chemistry and length-at-age was necessary to provide optimum classification accuracy.

Using a combination of otolith chemistry and length-at-age in 2002, cod at both feeding grounds were determined to have originated from G3 and G5 (Figure 7). In 2003, most cod at A-NW were determined to have originated from G3 and G4, and G5 contributed to the A-NW mixture. However, most cod from A-E were determined to have originated from G5, G3, and G4 (Figure 7). No cod from the main spawning area southwest (G1) of Iceland were identified at the feeding grounds in either 2002 or 2003 (Figure 7).

After restricting the stock mixture analysis to mature fish, the estimates of G3 origin were high in 2002 at A-NW. G2 also contributed to A-NW. G3 and G5 spawners contributed almost equally to the A-E. However, all immature cod were estimated as having originated from areas northwest and north of Iceland (Figure 8).

Discussion

Our mixed stock analyses indicate that in Icelandic waters, the contribution of different spawning components of cod to the harvested stock varies both spatially and temporally. Because of the migratory ability and mixing potential of marine fish, it is often difficult to estimate the contribution of marine fish populations to a mixed stock fishery. Mixed stock analysis has been applied successfully to a variety of anadromous fish species where the spawning stock origin has been readily identified, e.g. brown trout (*Salmo trutta*: Ruzzante *et al*., 2004), sockeye salmon (*Oncorhynchus nerka*: Wood *et al*., 1987, 1989), and steelhead trout (*Oncorhynchus mykiss*: Beacham *et al*., 2004). The mixing of different spawning components among cod assemblages off Canada has been identified using several methods (Campana *et al*., 1999, 2000; Ruzzante *et al*., 2000; Swain *et al*., 2001; Méthot *et al*., 2005). In addition, otolith chemistry has been used for mixed stock analysis of redfish (*Sebastes* spp: Campana *et al*., 2007), and genetics has been used for mixed stock analysis of Atlantic herring (*Clupea harengus*) in the North Sea (Ruzzante *et al*., 2006). Although considerable information on the movements and distribution of Icelandic cod has been gathered through tagging, there are still many questions unanswered concerning the migration and mixing of the different spawning groups during winter and on the main feeding grounds. Tagging studies have indicated that post-spawning cod migrate to the two main feeding grounds northwest and east of Iceland

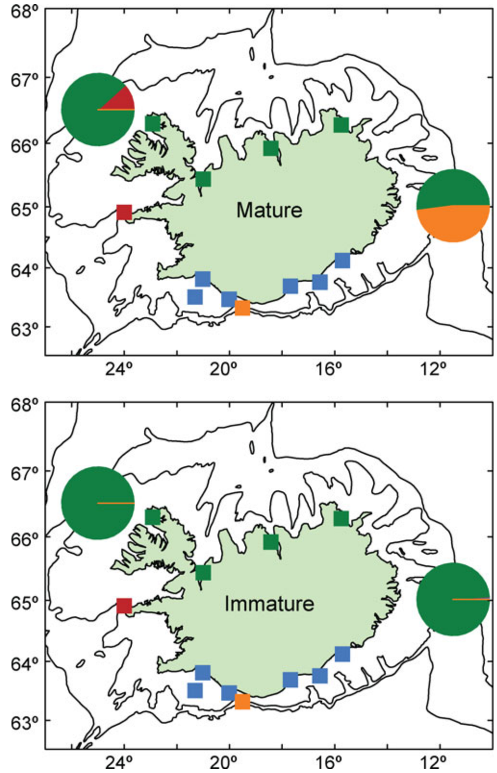

Figure 8. Estimated proportional spawning stock origin of mature and immature cod sampled at the main feeding grounds northwest and east of Iceland in 2002. Stock composition was estimated with a four-group baseline of spawning samples (Table 1), based on otolith chemistry and length-at-age.

(Jónsson, 1996). However, the results of this study strongly suggest that inshore cod spawning at the main spawning area south of Iceland did not contribute to the two main feeding grounds in October of the years 2002–2003.

Off Iceland the main cod fishing grounds in autumn (September–November) are northwest and east of Iceland, and appear to be well represented by the sites sampled for this study (Figure 2). As noted earlier, inshore cod from the main spawning area south of Iceland did not contribute to the major cod fisheries at two of the main feeding grounds in October 2002 and 2003. In contrast, most cod at the feeding grounds were estimated to have originated from spawning locations northwest and north of Iceland, as well as from deep offshore cod-spawning areas south of Iceland. Differences in individual otolith elemental concentrations between fish from feeding and spawning locations also indicated little or no contribution of the inshore southern cod to the feeding grounds. Length-at-age differed greatly between cod spawning south and north of Iceland (see also Jónsdóttir *et al.*, 2006a), so cod south of Iceland were larger than those north of Iceland. On the basis of length-at-age alone, it was likely that in 2002 the cod 5 and 6 years old on the feeding grounds came from the northern areas, but older cod probably also originated from other spawning areas. The difference in length-at-age between cod at the spawning and feeding grounds was less in 2003 than in 2002, but nevertheless differed significantly between cod at the feeding grounds and the inshore cod at the main spawning area. Finally, the discriminant analysis and the mixed stock analysis, combining the otolith elemental concentration and length-at-age, supported these findings. Spawning outside the main southern inshore spawning area has previously been considered limited and of little significance (Jónsson, 1954, 1982). However, agreeing with more recent studies on the origin of juvenile cod (Marteinsdottir *et al.*, 2000; Begg and Marteinsdottir, 2000, 2002), the results of this study suggest that the smaller local spawning areas west, north, and east of Iceland make an important contribution to the harvested population.

Tagging studies have shown that at least some cod from the main spawning area in the south migrate to the main feeding grounds (Jónsson, 1996). Pálsson and Thorsteinsson (2003) indicated that cod from this spawning area migrated along either shallow- or deep-water routes. Recent studies on stock structure of Icelandic cod have also discriminated between cod spawning shallower and deeper than 125 m south of Iceland (Jónsdóttir *et al.*, 2006a, b; Pampoulie *et al.*, 2006; Petursdottir *et al.*, 2006). In other areas, extensive offshore cod populations have been observed to migrate longer distances than cod closer to land or in fjords that are more localized (Robichaud and Rose, 2004). Cod sampled at the feeding grounds in the present study were all collected in the depth range 113–347 m. Therefore, it is possible that the shallower migrating fish were not collected at the feeding grounds in the present study. Cod from the main spawning area have been found along the south and southwest coast as well as on the Reykjanes Ridge southwest of Iceland (V. Thorsteinsson, unpublished data). Moreover, the length distribution of cod in the annual research programme of the Marine Research Institute, Iceland, in October indicates that larger cod are found both west and east of the main spawning area (Figure 9). Therefore, it appears that the sampling sites in this study, although located at the main fishing grounds, did not include the main overwintering grounds for the southern cod, which may be farther south.

About 45% of the cod 5–8 years old sampled at the feeding grounds were immature (90% of immature cod were 5 or 6 years old). A central assumption of mixed stock analysis is that all contributing groups are included in the baseline reference groups (Wood *et al.*, 1987, 1989; Campana *et al.*, 2000). Therefore, mixed stock analysis with immature fish as the unknown group would require samples of immature cod from the main nursery grounds north of Iceland for the baselines. Otolith chemistry is influenced by the environment and does not necessarily indicate genetic differences (Begg and Waldman, 1999). Differences in otolith chemistry between northern and southern areas have been established already (Jónsdóttir *et al.*, 2006b). However, the differences between the adjacent spawning locations north or south of Iceland were less pronounced (Jónsdóttir *et al.*, 2006b). Owing to the similarity of the environments, we assume that otolith chemistry of cod from the spawning locations north of Iceland and cod from the northern nursery grounds (Astthorsson *et al.*, 1994; Saemundsson, 2005) are similar. In 2002, the immature cod were estimated to originate from the northern areas. These cod were likely to have migrated from the main nursery areas of cod, but not from the northern spawning locations.

With the simulation tests, it was possible to evaluate the relative accuracy of the techniques and the adequacy of the baselines used to estimate the origin of the mixed stock. The simulation tests indicated that the best results were obtained by combining samples from similar (geographically adjacent) spawning locations, a practice that reduces the statistical variance (Millar,

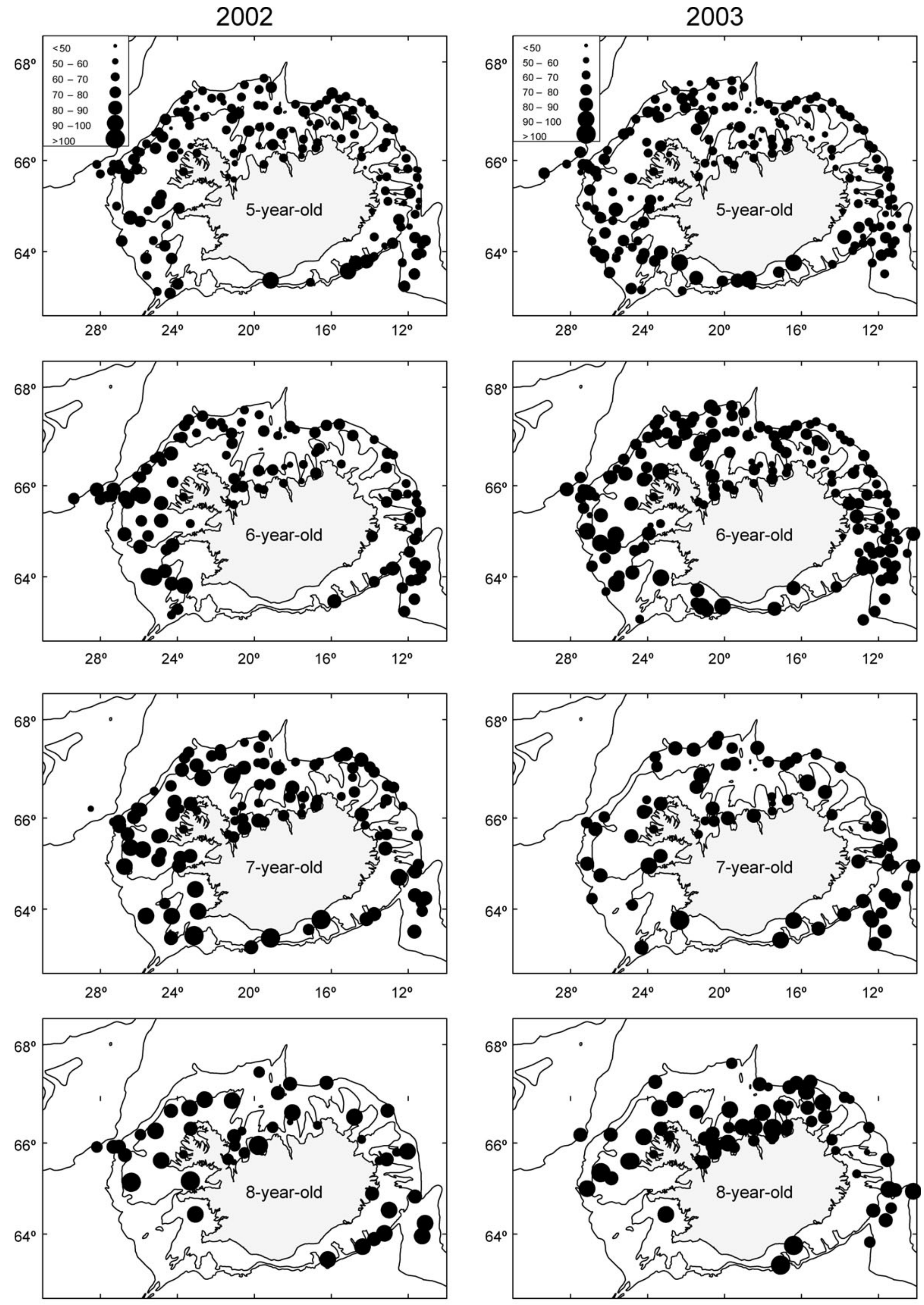

Figure 9. Mean length of cod aged 5, 6, 7, and 8 years in the annual survey of the Marine Research Institute, Iceland, in October of 2002 and 2003.

1987). Although the simulation tests indicated reasonable accuracy, residual error in the estimates of the mixed stock composition undoubtedly remains. Inaccurate estimates could arise if some component of the mixed stock was derived from an unsampled spawning region (e.g. a missing baseline group), or a portion of the mixed stock had not started spawning and therefore was not represented by any of the baseline spawning samples (Campana *et al*., 1999; Beacham *et al*., 2005). However, the discriminant scores of cod from the feeding grounds fitted well into the discriminant space defined by the spawning groups, suggesting that all baselines were included. Not all recorded spawning locations (Marteinsdottir *et al*., 2000) were sampled, however, and it is possible that a spawning location within the five groups was missing from this study. However, based on the similar elemental composition of adjacent spawning locations (Jónsdóttir *et al*., 2006b), it is unlikely that an additional spawning location would change the results of this study.

Otolith chemistry has been used earlier, with success, to estimate proportions of different spawning stocks in a mixed harvested stock (Campana *et al*., 1999, 2007). However, otolith shape has not to our knowledge been used for this purpose. Given that otolith shape measurements are relatively inexpensive to produce and because it is possible to analyse large numbers of samples in a short time, it is, at least in principle, a good technique to use before more complex and expensive methods are applied. Otolith shape has been used successfully to discriminate among spawning stocks of cod off Iceland (Jónsdóttir *et al*., 2006a), Canada (Campana and Casselman, 1993), and the Faroe Islands (Cardinale *et al*., 2004). However, our attempts to use otolith shape to estimate the stock origin of a known mixture (the simulation tests) were not very successful, indicating that otolith shape was not a good discriminator of mixed stock composition in the waters around Iceland.

The Icelandic cod stock is currently managed as a single management unit, for which most fish are assumed to originate from the main spawning area southwest of Iceland. The results of this study indicated that most cod on the main autumn fishing ground did not spawn at the main spawning area, but at smaller spawning areas northwest and north of Iceland. Although these northern spawning components were previously considered to be of minor importance to the stock, our results indicate that these components are of greater importance than previously realized.

Acknowledgements

We thank the captains and crews of the vessels used for sampling, and the chief scientists and researchers working aboard for assistance with sampling. Thanks are also due to A. Jónsdóttir for assistance with the decontamination of the otoliths, S. Jóhannsdóttir for age reading, S. R. Ólafsdóttir and J. Ólafsson for assistance in the chemistry laboratory, and H. Þórðarson and G. H. Sveinsson for the elemental analysis. We also thank R. Kean of the Research Productivity Council in New Brunswick, Canada, for helping in the development of the otolith assays. Finally, we thank Steve Cadrin, editor Audrey Geffen, and an anonymous reviewer for valuable comments on an early version of the manuscript. The project was funded by EU (METACOD - project number Q5RS-2001-00 953), the Icelandic Research Council, the Icelandic Ministry of Fisheries, and the memorial fund of H. Jónsdóttir and S. Kristjánsson.

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doi:10.1093/icesjms/fsm157