Distribution and migration of saithe (Pollachius virens) around Iceland inferred from mark-recapture studies

Hlynur Armannsson, Sigurdur Th. Jonsson, John D. Neilson, and Gudrun Marteinsdottir

Knowledge of the distribution and migration of populations is necessary to identify and conserve stock components and therefore genetic variability. Compared with other gadoid species, little is known about the life history of saithe (Pollachius virens) (known as pollock in the Northwest Atlantic) or its stock components. About 15,800 saithe were tagged near Iceland from 2000 to 2004 to estimate population parameters, to describe saithe dynamics on the Icelandic shelf, and to monitor long-distance migrations, should they occur. A multiplicative model was used to standardize fishing effort to describe the distribution of the tagged population, based on tag returns from the fishery. Saithe have a high affinity to their tagging area, but move considerably within that area. Because of variability in fishing effort among areas, tagged fish exhibit different area-specific catchabilities. The results also indicate seasonal offshore–inshore migrations during summer and variability in migratory routes among different tagging areas related to affinities to different feeding grounds. This could indicate a more complex stock structure than previously thought. Finally, results to date do not indicate large-scale emigration of saithe from Icelandic fishing grounds.

Keywords: distribution, effort, mark-recapture, migration, multiplicative model, Pollachius virens, saithe.

Introduction

Knowledge of the spatial distribution of commercial fish stocks is important for understanding their population dynamics and, hence, for fisheries management (Polacheck and Valstad, 1993). Moreover, understanding dispersal and movement patterns of juvenile fish and their subsequent distribution is necessary for understanding the processes underlying population structure (Hanson, 1996). Failure to recognize or to account for complex population structure could result in a loss of biological diversity with unknown ecological consequences (Stephenson, 1999). Little information is available on migration and distribution of juvenile saithe or their affinity to putative nursery areas. The life history of saithe in the Northeast Atlantic involves an offshore spawning and larval phase, recruitment to the coastal environment, and tracking studies by Smith et al. (1993) and Sarno et al. (1994) demonstrated an affinity of juvenile saithe to an underwater reef, with diurnal foraging excursions in its vicinity. Seasonal changes in depth distribution have also been reported where juvenile fish migrate to deep water during winter and return to shallow water during summer (Olsen, 1959a, 1961; Jones and Jonsson, 1971; Bergstad et al., 1987; Bergstad, 1990, 1991). This pattern is similar to the pattern reported for other juvenile gadoids, such as cod (Gadus morhua) (Bergstad et al., 1987; Nakken and Raknes, 1987; Pihl and Ulmestrand 1993; Anderson and Gregory, 2000; Saemundsson, 2005) and haddock (Melanogrammus aeglefinus) (Bergstad et al., 1987; Albert, 1994; Jonsson, 1996a).

Although the saithe is a common and commercially important species on both sides of the Atlantic, little is known about its biology. Saithe are considered to be strong facultative schoolers, fish of about the same size tending to school together (Schmidt, 1955; Steele, 1963; Partridge et al., 1980; Bergstad, 1991; Neilson et al., 2003). It is also known that saithe spend more time moving freely through the water column and less time on the bottom than other gadoid species (Scott and Scott, 1988), and that these movements up and down the water column are variable with regard to season and time of day (Schmidt, 1955; Bergstad, 1991; Neilson et al., 2002, 2003). Around Iceland, saithe are found from the surface to depths of at least 450 m (Jonsson, 1992; Gunnarsson et al., 1998), but based on logbook data from Icelandic vessels, they are most common at depths <250 m (STH based on the Icelandic logbook database).

The spawning of saithe around Iceland begins in late January, peaks in February, and ends around the middle of March (Jonsson, 1992; Gunnarsson et al., 1998). Spawning saithe are generally observed in waters off the southeast to northwest coasts, but are rarely seen off the north or east coasts (Figure 1). The main spawning sites, however, are thought to be off the southwest Icelandic shelf, with spawning aggregations of about 500 000–2 million fish, the largest in the North Atlantic (Jonsson and Saemundsson, 1987).
coast on Selvogsbanki and Eldeyjarbanki (Saemundsson, 1924; Jones and Jonsson, 1971; Jonsson, 1992; Gunnarsson et al., 1998) (Figure 1). The main fishing grounds for saithe around Iceland are off the southeast, south, southwest, and west coasts (Anon., 2006). Saithe are taken as bycatch in fisheries targeted at other groundfish species as well as in a directed fishery. During the period 2000–2005, some 75–85% of the annual landings of saithe in Icelandic waters were reported from bottom trawls and the other 15–25% mainly divided among jigging, longline, gillnet, and Danish seine (Anon., 2006).

In Northeast Atlantic waters, saithe are divided into several management units, including the Northeast Arctic, North Sea and West of Scotland, and Iceland and Faroe Islands, although tagging studies have shown considerable migrations among these units (Olsen, 1959a, b, 1961; Jones and Jonsson, 1971; Reinsch, 1976; Jakobsen, 1978; Jakobsen and Olsen, 1987). Olsen (1959b, 1961) and Jakobsen and Olsen (1987) reported the results of tagging off northern Norway, and a large proportion of the recaptures came from waters around Iceland and Faroe Islands. Results from tagging experiments around the Faroe Islands also revealed some migration from Faroese waters to Icelandic waters (Jones and Jonsson, 1971).

Before the current study, the only large-scale tagging experiment around Iceland was conducted in 1964 and 1965, when 6000 juvenile saithe (mostly 3–5 years old) were tagged off northern Iceland (Jones and Jonsson, 1971). The recapture rate from that tagging experiment was high, ~53%, with a large proportion taken near the release sites soon after tagging in a seasonal purse-seine fishery off the north coast of Iceland. The results also showed that the tagged population was relatively stationary during its first year at liberty in the inshore area off the north coast. In subsequent years, as the fish grew larger and an increasing proportion matured, an annual migration pattern evolved where the fish moved in a counterclockwise direction around Iceland in autumn and winter to the west and southwest coast of Iceland, then back into northern waters during early summer. With increasing size of tagged fish, recapture locations were farther offshore and the fish did not return to the north coast. Fewer than 1% of recaptures were reported outside Icelandic fishing grounds, thus providing no evidence for large-scale emigration (Jones and Jonsson, 1971).

Here, our objective was to analyse migration patterns of saithe around Iceland inferred from tagging experiments performed from 2000 to 2004. Where migration patterns among tagging areas were obviously different, potential underlying factors responsible for the differences were explored. In particular, we considered whether varying patterns reflected affinities to different feeding and/or spawning areas. We also investigated whether juvenile saithe showed affinities to their nursery areas during the first years after tagging. Finally, we evaluated whether there was any indication of large-scale emigration from Icelandic fishing grounds and if such mass migration events were related to changes in the migration of other fish stocks known as important prey for saithe. This information is critical for improved understanding of the behaviour and structure of the saithe stock around Iceland and will lead to more informed fishery management in future.

Material and methods
Tagging
In all, 15 840 saithe were tagged during the months of June–September 2000–2004, at different locations around Iceland.

![Figure 1](https://academic.oup.com/icesjms/article-abstract/64/5/1006/642916/10869629816) by guest on 26 December 2018

Figure 1. Location of tagging (dots), areas (1–10), and the numbers of saithe tagged in each area. Spawning areas of saithe around Iceland are shaded light grey and the main spawning areas are shaded dark grey. Eld is Eldeyjarbanki, and Sel is Selvogsbanki. Important feeding grounds located on the frontal zones (northeast and southwest off Iceland), and on the Reykjanes Ridge are shown hatched. The inset shows reference points used to calculate migration distance.
(Figure 1; Table 1). The saithe ranged in length from 20 to 110 cm, although some 90% of the tagged individuals were 33–59 cm and ~65% were 37–49 cm, the mean length being 45 cm (Figure 2). Fish age ranged from 1 to 10 years, but ~82% were 2 and 3 years old (Figure 3). The time of tagging was selected so as to permit capture of saithe in shallow water to enhance survival. Palsson et al. (2003) reported significantly increased mortality of undersized cod with increasing depth, and Schmidt (1959) and Clay et al. (1989) demonstrated that attempts to tag adult saithe offshore were unsuccessful. Research has shown that young saithe tend to aggregate in shallow water during summer and early autumn (Jones and Jonson, 1971; Clay et al., 1989). The fish were captured with jigs from small boats owned by Iceland’s Marine Research Institute (MRI) or rented small commercial fishing boats. Commonly, No. 7 J-hooks with artificial rubber baits were employed, with crushed barbs to minimize wounding. Once aboard, the fish were kept in 400-l plastic tanks with flowing seawater until tagging, 1–15 min later.

Fish to be tagged were removed from holding tanks by hand with dipnets and placed on a measuring board, where the total length was measured to the nearest centimetre. Only saithe in good condition (with minimal or no visible wounds and no

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Na, not available.
swimming abnormality) were tagged. The tags were inserted in the dorsolateral region, at the base of the first dorsal fin. Tags were conventional T-Bar anchor type, with a total length of 8 cm. Floy tags (Floy Manufacturing, Seattle, WA, USA) were used from 2000 to 2004, and Hallprint tags (Hallprint Ltd, Victor Harbour, South Australia) were introduced in 2004. Each tag was imprinted with a unique identification number and an Icelandic return address on the vinyl sleeve, printed in Icelandic. During the period 2000–2003, 519 saithe were double-tagged with T-bar tags posterior to the second dorsal fin. In 2004, 1453 saithe were double-tagged with 6 cm long Hallprint body cavity anchor tags imprinted in the same manner as the traditional T-bar tags. The anchor of body cavity tags was inserted through a puncture in the body wall slightly (~2 cm) dorsal and posterior to the anal opening. Double tagging was done along with single tagging, in equal proportions in each area, and should therefore not have biased the recapture rate. It was done for future research on assessing tag loss and is not evaluated in this study. At each tagging site, information about position, date and time, depth, and weather were gathered, and a sample of saithe was taken which represented the body wall slightly (~2 cm) dorsal and posterior to the anal opening. Double tagging was done along with single tagging, in equal proportions in each area, and should therefore not have biased the recapture rate. It was done for future research on assessing tag loss and is not evaluated in this study. At each tagging site, information about position, date and time, depth, and weather were gathered, and a sample of saithe was taken which represented

Areas and seasons

The waters around Iceland were divided into eight areas inside the 500-m isobath, based on hydrographical and ecological considerations, as set forth in the BORMICON model (Stefansson and Palsson, 1997) (Figure 1). Areas 3.4 and 6.7 represent combined areas from the original model. These areas were combined because of the low prevalence of catches by certain gear types, which made calculation difficult. We decided to exclude returns from areas farther offshore in the main analyses, because of lack of precise effort data, and instead provide a brief summary of total recaptures in those areas.

We divided the year into four seasons: winter (January–March), spring (April–June), summer (July–September), and autumn (October–December), to determine whether migration patterns were seasonal, which in turn could be related to life history traits such as spawning and feeding migrations. This division was also necessary to evaluate whether fishing effort differed significantly among seasons. We combined seasons and years into one factor to simplify our model. This meant that instead of having separate factors of 5 years and four seasons, we had 20 factors of combined year–seasons. This simplification is important because the main area analysis was done with those from landings (SThJ based on the Icelandic logbook database). Therefore, scaling of the logbook database with respect to landings was deemed unnecessary. Nominal fishing effort was measured in hours trawled for bottom trawls, number of sets for

Recaptures

All recaptures (with a few exceptions) came from the commercial fishery around Iceland. Fishers were asked to return tags and otoliths to the MRI along with information about location and depth of recapture, date of recapture, length, sex, and sexual maturity of the fish. For each tag returned, a reward of 1000 ISK (equivalent to some €11) was offered. In addition to the reward, the finder was provided with a summary of release and recapture information for each tag returned. By the end of 2005, recaptures totalled 1279, i.e. 8.1% of releases. In the spatial analysis, we only included fish where location of recapture was known and fish had been at liberty for at least 30 d (n = 1179). Most unusable returns originated from fish processing plants or fish markets that had no knowledge of the exact location of recapture.

Standardization of fishing effort

As mentioned earlier, some 75–85% of annual catches of saithe were taken by bottom trawl in the period 2000–2005 (Anon., 2006), and recaptures by fishing gear reflect that proportion. Although exclusion of fishing gear other than bottom trawl was considered, we decided to include all major fishing gears in our analyses because in some areas and seasons, a large proportion of catches and recaptures came from fishing gears other than bottom trawl. Such gear was mainly Danish seine, gillnets, longlines, and jigging gear. We used data from obligatory commercial fishing logbooks to estimate the spatial distribution and the magnitude of effort in each area, but only used effort where saithe was reported as part of the catch, to filter out fisheries targeting other species. Recently, information from logbooks has been in accord with those from landings (SThJ) based on the Icelandic logbook database). Therefore, scaling of the logbook database with respect to landings was deemed unnecessary. Nominal fishing effort was measured in hours trawled for bottom trawls, number of sets for
Danish seines, number of hooks for longlines, number of nets for gillnets, and hours of jigging reels in use for jiggers.

To standardize fishing effort for saithe over the period analysed, we used a multiplicative model, as outlined by Gavaris (1980). Under the assumption that catch rate is a lognormally distributed variable, this method gives a minimum variance unbiased estimator of catch rates, from which unbiased estimators of effort can be computed (Gavaris, 1980). The multiplicative model allowed us to examine the relationship between saithe catch rate and factors such as year–season, area, and fishing gear.

An expression for the model, assuming that catch rate is a lognormally distributed variable, is

$$U_{ijk} = U_R \prod_{ijk} (P_{ijk}X_{ijk}) \exp(e_{ijk}),$$

where $U_{ijk}$ is the catch rate (kg per unit of nominal effort) of factor $i$ (fishing gear) in factor type $j$ (year–season), and factor type $k$ (area); $U_R$ the catch rate in the bottom trawl in the first season in area 1, used as a reference value; $P_{ijk}$ the relative "power" of factor $i$ in factor type $j$ and factor type $k$; $X_{ijk} = 1$ when category $ijk$ occurs, otherwise 0; and $e_{ijk} = N(0, \sigma^2)$ and assumed identically and independently distributed for all $ijk$ combinations.

The corresponding model,

$$\ln \hat{U}_{ijk} = \ln U_R + \sum_{ijk} (\ln P_{ijk})X_{ijk} + e_{ijk},$$

may be solved using ordinary least squares. Further mathematical details for the model are given by Gavaris (1980). The results can be used to obtain an estimate of total standard effort with the equation

$$\hat{E}_{jk} = \frac{C_{jk}}{\hat{U}_{jk}},$$

where $\hat{E}_{jk}$ is the effort that would have been expected by the standard (hours of bottom trawling) to obtain the total catch in an area and year–season, $C_{jk}$ the total catch in an area and year–season, and $\hat{U}_{jk}$ the prediction from Equation (2) using hours of bottom trawling as standard.

The number of recaptured saithe in each area and year–season was calibrated with the model estimate of total fishing effort and the size of each area. For the purpose, we used an equation modified from Bayliff (1979) where the proportional recaptures of tagged fish ($P_k$) in an area $k$ and year–season $j$ is estimated from the number of recaptures ($R_k$) within area $k$ and year–season $j$, weighted by the total effort ($\hat{E}_{jk}$) within area $k$ and year–season $j$ and the size of that area ($A_k$):

$$P_k = \frac{R_k/\hat{E}_{jk}/A_k}{\sum_k R_k/\hat{E}_{jk}/A_k}.$$ 

This method assumes that the probability of tag recapture is related linearly to fishing effort. Tag reporting rate, catchability, and patchiness of fishing effort in a season are assumed to be equal between areas, and tag-reporting rates from different gear types are assumed to be equal (Solmundsson et al., 2005). To obtain proportional recaptures of tagged fish in each area over the whole period, we summed proportional recaptures for all year–season combinations in each area and divided by the number of year–season combinations.

Migration distance

To calculate the distance between tagging and recapture locations, we used the method of Saemundsson (2005). The distance was calculated as the smallest possible vector distance between the two locations (km). If the vector intersected the coast, an additional vector was added, passing through a fixed reference point (Figure 1), resulting in two composed vectors that followed the coast. If the vector from that reference point and the recapture locations intersected the coast, a third vector was established, and so on.

Results

Spatial and temporal distribution of catches in relation to recaptures

The monthly difference in the numbers of recaptures in relation to total landings of saithe (Figure 4) was striking. In the period 2000–2005, recaptures in January were high if looked at in terms of total landings of saithe. In the months following, recaptures declined rapidly and were comparatively low from April to July, despite monthly landings being similar to those in the earlier months. In accord with the seasonal changes, the proportion of recaptures in fishing gear other than bottom trawls reached nearly 40% in June, although the total landings from such gear types were only 23% of the total landings that month (results not shown). The proportion of total recaptures increased linearly with both length and age at tagging (Figures 2 and 3).

Recapture rates and time at liberty varied among tagging areas (Table 1). In area 6.7, most saithe were recaptured within a year of tagging, whereas in area 3.4, most saithe were recaptured during the third year after tagging. In areas 1, 2, and 9, most were recaptured within the first or second year of tagging, and in areas 5 and 10, most were recaptured during the second year after tagging. The total percentage recaptures reflected these differences, the greatest percentage recapture being generally from area 6.7 and the least from area 3.4.

![Figure 4. Monthly landings of saithe by all main fishing gears over the study period (bars), and the number recaptured (line) per month.](https://academic.oup.com/icesjms/article-abstract/64/5/1006/642916/1010)
Model building

Significant interactions in catch rates were detected between year–season and fishing gear as well as between area and fishing gear, but not between year–season and area ($p = 0.13$). Therefore, interactions between year–season and area were excluded from the model. To determine whether the other interactions were necessary for the model, we used the Akaike information criterion (AIC), which explicitly penalizes any superfluous parameters in the model and prevents overfitting. In comparing models, the smaller the AIC, the better the fit (Crawley, 2002). The AIC was lowest for the model with the main effects (year–season, area, and fishing gear) and the interaction between area and fishing gear. The ANOVA results for the model applied are listed in Table 2. When calibrating effort, we used catch per unit effort (cpue) in terms of hours bottom trawling as the benchmark and calculated the effort in each area as hours of trawling using Equation (3). Analyses of variances of the multiplicative model gave us a high $r^2 (0.96)$, suggesting that a high fraction of the variation in catch rates was explained by the model (Table 2).

Spatial and temporal distribution of standardized effort

Through the study period, there were general trends of increasing standardized fishing effort and catch rate in all areas, seasons, and years, although there was some variability (results not shown). The highest catch rate and standardized effort were in areas 8, 9, and 10 (southeast and south Iceland), whereas the lowest catch rate and standardized effort were in areas 3.4, 5, and 6.7 (north, northeast, and east Iceland, respectively; Figure 5).

Spatial and temporal distribution of recaptures

When corrected for fishing effort, most recaptures were in the corresponding tagging area (Figure 6). The percentage recaptures within tagging areas ranged from 38.1% in area 6.7 (east Iceland) to 83.2% in area 9 (south Iceland). If tagging and adjacent areas are pooled, the percentage recaptures ranged from 80.4% for area 6.7 to 98.4% for area 1 (west Iceland).

Most saithe were recaptured around the 200-m depth contour (Figure 6). The median depth of saithe at recapture, by month of recapture, changed significantly through the year (Figure 7). During the period August through March, the median depth of saithe at recapture was around 200 m. Then from April, the median depth decreased gradually to its shallowest in June (110 m), then began to increase again in July. Migration distance was positively correlated with time at liberty and the distance to the nearest feeding ground (Figure 8). However, the migration distance was not correlated with length at recapture ($p = 0.92, r^2 = 0.00001$). The proportions of recaptured fish on the three main feeding grounds (scaled to represent recaptures from 2000 tagged fish in each release area) varied in terms of tagging area (Figure 9). On the feeding grounds northwest of Iceland, the recaptures originated mainly from area 2 (50.2%), 1 (25.7%), 3.4 (13.8%), and 5 (6.9%). On the feeding grounds southeast of Iceland, the recaptured fish came almost exclusively from areas 6.7 (76.9%), 5 (11.4%), and 9 (11.2%). On the feeding grounds on the Reykjanes Ridge most recaptured fish had been tagged in areas 10 (61.3%) with 1 (27.6%), with the balance divided randomly among the other tagging areas.

For tagged saithe recaptured outside their tagging areas, there was a notable difference in standardized recaptures between areas in a clockwise or a counterclockwise direction from the tagging area (Figure 6). Saithe from areas 2 and 3.4 tended to migrate in counterclockwise around Iceland, whereas saithe from areas 6.7 and 1 migrated more frequently in a clockwise direction. Saithe from area 5, 9, and 10 seemed to migrate roughly equally in both directions. Saithe recaptured outside their tagging area were caught on average significantly deeper and had spent more time at liberty than those recaptured within their own tagging areas. However, there was no notable difference in length or age at recapture (Table 3).

Of the 1179 usable recaptures, only 12 fish were recaptured outside the areas shown in Figure 1, and of those 12, nine were caught just outside the areas shown. A small part of the catch is always taken outside the areas shown. The other three saithe undertook relatively long migrations. One was recaptured southeast of the Faroe Islands, another west of the Shetlands, and the third west of Iceland on Greenland’s continental shelf.

Table 2. Analyses of variance of factors which influence saithe catch rates around Iceland in the applied multiplicative model.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>d.f.</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>$F$</th>
<th>$p$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1</td>
<td>2 160.0</td>
<td>2 160.0</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Regression</td>
<td>62</td>
<td>1 200.0</td>
<td>194.00</td>
<td>70.91</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Year–season</td>
<td>23</td>
<td>31.9</td>
<td>1.39</td>
<td>2.53</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Area</td>
<td>7</td>
<td>205.0</td>
<td>29.30</td>
<td>53.32</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Fishing gear</td>
<td>4</td>
<td>1 400.0</td>
<td>2 850.0</td>
<td>5 186.27</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Area × fishing gear</td>
<td>28</td>
<td>119.0</td>
<td>4.26</td>
<td>7.52</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Residual error</td>
<td>764</td>
<td>479.0</td>
<td>0.63</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Total</td>
<td>827</td>
<td>14 700.0</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

Multiple $r^2 = 0.962$.

 Combined year and season.

Discussion

The results indicate a great fidelity of juvenile saithe to their tagging area during the first years after tagging. However, despite...
this fidelity, some saithe did migrate relatively long distances. Most saithe migrated out of shallow water towards the continental slope where they were recaptured ~200 m deep. Such fidelity to tagging areas partially supports the results of Jones and Jonsson (1971), who recorded juvenile saithe to have high fidelity to their nursery grounds off the north coast of Iceland during the first year after tagging. Olsen (1959a) also reported that saithe stayed near their nursery grounds off Norway. Fidelity to tagging areas has also been found in other juvenile gadoids around Iceland. For instance, Jonsson (1954, 1996a) and Saemundsson (2005) reported high fidelity of juvenile cod to their nursery grounds during the first years after tagging, and Jonsson (1996a) reported fidelity of juvenile haddock to their nursery grounds. Further, tagging studies in Norway, Greenland, Sweden, and Canada have shown that juvenile cod often remain close to the tagging site during the first 2–3 years of life (Templeman, 1979; Godø et al., 1986; Jakobsen, 1987; Hovgård and Christensen, 1990; Pihl and Ulmestrand, 1993; Anderson and Gregory, 2000; Lawson and Rose, 2000). Offshore migrations of tagged juvenile saithe with increasing age have been reported around Iceland (Jones and Jonsson, 1971), Norway (Olsen, 1959a, 1961; Jakobsen, 1978), and Canada (Neilson et al., 2006).

Saithe from different tagging locations seemed to choose different migration routes, some counterclockwise and some clockwise around Iceland. Saithe tagged in areas 2 and 3.4 tended to migrate in a counterclockwise direction, consistent with the conclusions of Jones and Jonsson (1971). However, the predominant migration direction was clockwise from areas 1 and 6.7. Saithe from areas 5, 9, and 10 migrated roughly equally in both directions. The most probable causes for the differences in migratory routes are

![Figure 6. Mean percentage recaptures in tagging areas (a) 1, (b) 2, (c) 3.4, (d) 5, (e) 6.7, (f) 9, and (g) 10, 2000–2005, standardized by fishing effort and size of area.](https://academic.oup.com/icesjms/article-abstract/64/5/1006/642916)

![Figure 7. Depth-distribution of saithe recaptured per month: broad black line (median), grey area (95% confidence intervals), box (interquartile range, IQR), whiskers (1.5 × IQR), narrow black lines (outliers).](https://academic.oup.com/icesjms/article-abstract/64/5/1006/642916)
likely to be related to the presence of important feeding grounds on the Reykjanes Ridge and off northwest and southeast Iceland (Figure 1). As a consequence, saithe recaptured on the three main feeding grounds originated from different tagging areas. Most saithe recaptured on the feeding ground northwest of Iceland originated from areas 2 and 1 and a lesser proportion from areas 3.4 and 5. Saithe on the feeding grounds southeast of Iceland originated almost exclusively from three tagging areas, 6.7, 5, and 9. Almost 90% of the saithe recaptured on the feeding grounds on the Reykjanes Ridge originated from areas 10 and 1, with the rest divided among the other areas. These results clearly indicate preferences for different feeding grounds by saithe tagged at different locations. In comparison, cod and haddock tagged around Iceland seem to choose different feeding grounds around their location of tagging (Jonsson, 1996a). Saithe tagged in areas 1 and 5 seemed to prefer the feeding grounds of northwest Iceland and the Reykjanes Ridge, and northwest and southeast Iceland, respectively. For many of the saithe tagged in those areas, the distance to the two feeding grounds is roughly similar. As migratory distance was correlated with distance to the nearest feeding ground, those areas therefore probably represent areas where the direction of migration may vary.

As saithe around Iceland mature relatively late in life (50% maturity at age 6; Anon., 2006) compared with those in Canadian waters (50% mature at age 3; Trippel et al., 1997), there are insufficient data to determine whether the differences in migratory routes are related to different spawning locations. However, fish tagged in areas 5, 6.7, and 9 and recaptured as potential spawners (>70 cm) during the spawning season of January–March were more likely to be caught off the southeast coast, whereas fish tagged in other areas were more likely to be caught on the main spawning grounds off the southwest coast of Iceland. Given these observations, the stock structure of saithe around Iceland may consist of a number of subpopulations, as found for cod off Iceland (Marteinsdottir et al., 2000; Jonsdottir et al., 2006; Pampoulie et al., 2006). Already, the dispersal pattern of juvenile cod tagged at different sites around Iceland has indicated that there may be isolated subpopulations that demonstrate great fidelity to their tagging sites (Saemundsson, 2005).

Seasonal changes in depth preferences were apparent from the depth distribution of recaptured saithe. Saithe moved from deep to shallow water during summer, then back to deep water in autumn. These changes were reflected by the decrease in recaptures in bottom trawls during summer and an increase in recaptures in other fishing gears that operate more in shallow water. Part of the change in the depth distribution of recaptured saithe may therefore be a reflection of seasonal changes in the depth distribution of fishing effort. Recapture rates varied considerably by month. In January, recapture rates were very high, perhaps related to spawning activity or other behaviour of the tagged population. Data from DST tags (data storage tags recording depth and temperature) showed that the depth distribution of at least part of the tagged population increased during the period December–February (SThJ pers. obs.). The low recapture rate during summer could be caused by lesser catchability attributable to the migration of the tagged population into shallow water. Later in the year, the total recaptures rose as catches increased, but this finding could also reflect distributional changes in the tagged population, fish returning to deeper water and/or including a new influx of tagged fish. Bergstad (1990, 1991) showed that juvenile saithe appear in greater numbers in deeper water of the

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Recapture area</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Inside tagging area</td>
<td>Outside tagging area</td>
</tr>
<tr>
<td>Depth at recapture (m)</td>
<td>168</td>
<td>211</td>
</tr>
<tr>
<td>Days at liberty</td>
<td>550</td>
<td>612</td>
</tr>
<tr>
<td>Length at recapture (cm)</td>
<td>61</td>
<td>60</td>
</tr>
<tr>
<td>Age at recapture (years)</td>
<td>4.8</td>
<td>4.8</td>
</tr>
</tbody>
</table>

The test results are for differences between recapture areas. ¹Results from two-sample t-test. ²Result from two-sample Wilcoxon test.
Icelandic waters could be related to prey preference and abundance. Unfortunately, such research effort has been lacking in recent years. (Ofstad, 2005; Anon., 2006) tagging experiments because of the similarity in growth and (Palsson, 2005; Anon., 2006). However, the only way to detect whiting are often continuous from the Faroe Islands to Iceland Icelandic blue whiting fishery and found that the most abundant which use the area between the Faroe Islands and Iceland as a feeding migrations of blue whiting (Clupea harengus) in the same direction. The Norwegian spring-spawning herring stock collapsed in the late 1960s and its feeding migrations to Icelandic waters ceased (Dragesund and Ulltang, 1978; Jakobson and Østvedt, 1999; Kvaamme et al., 2003; Holst et al., 2004). Runde (2005) found the size and distribution of commercial catches of saithe off western Norway to be closely related to the migration of herring into spawning grounds close inshore, indicating that saithe may well follow migrating schools of herring. Jakobsen (1978), Huse and Ona (1996), Bjelland and Holst (2004), and Holst et al. (2004) all described saithe as one of the main predators of Norwegian spring-spawning herring in northern Norwegian waters, and several studies have shown herring to be an important constituent of the diet of saithe >60 cm (e.g. Bergstad, 1991; Høines and Bergstad, 1999; Runde, 2005).

The results of saithe tagging experiments around the Faroe Islands have shown substantial migration into Icelandic waters (Jones and Jonsson, 1971). These migrations could be related to feeding migrations of blue whiting (Micromesistius poutassou), which use the area between the Faroe Islands and Iceland as a feeding ground (Jonsson, 1992; Palsson, 2005). Blue whiting are an important prey of saithe around the Faroe Islands (Høeggaard, 1999). Palsson (2005) analysed the bycatch in the Icelandic blue whiting fishery and found that the most abundant bycatch species was saithe. The main fishing areas for blue whiting are often continuous from the Faroe Islands to Iceland (Palsson, 2005; Anon., 2006). However, the only way to detect immigration from the Faroe Islands to Iceland is through tagging experiments because of the similarity in growth and dynamics of the two stocks (Oftstad, 2005; Anon., 2006). Unfortunately, such research effort has been lacking in recent years.

Another reason saithe do not migrate in great abundance from Icelandic waters could be related to prey preference and abundance. The dominant fish prey of saithe around Iceland are adult capelin (Mallotus villosus), preyed on during its spawning migrations, and sandeels (Ammodytes tobianus) (Jonsson, 1996b; Jaworski and Ragnarsson, 2006). Neither of these species migrates away from Icelandic fishing grounds after they become available as prey for saithe (Jonsson, 1992), so they do not trigger emigration of the saithe population away from Icelandic fishing grounds. Jakobsen and Olsen (1987) suggested that the Icelandic stock of saithe could be less vulnerable to overexploitation because of a net gain of immigrants. It should be noted, however, that the possibility of emigration from Icelandic waters to the Faroe Islands was proposed by Schmidt (1957, 1959) and Reinsch (1976), based on reciprocal variations in year-class strength in landings around the Faroe Islands and Iceland.

Recaptures increased linearly with both length and age at tagging (Figures 2 and 3). This is not surprising, because larger and older fish would likely come under greater fishing pressure earlier than younger, smaller saithe. However, the result is in accord also with that of Fowler and Stobo (1999), who analysed tag returns of saithe in Canadian waters, and found larger fish to be relatively better represented in recapture data than younger ones. The difference in recapture rates and time at liberty among areas is probably a consequence of the difference in effort among areas, but possibly also in differences in size at tagging (Table 1).

To obtain an unbiased picture of the spatial distribution of a population from mark-recapture experiments, it is necessary to standardize effort to evaluate its relationship to recapture rates. This is widely accepted as scientific procedure, but only a few studies of fish populations have followed it. Solmundsson et al. (2005) used standardization in their mark-recapture studies on the fidelity of Icelandic plaice (Pleuronectes platessa) to spawning and feeding grounds. Saemundsson (2005) used the same method to evaluate the dispersal of juvenile cod in Icelandic waters, and Wright et al. (2006) used a similar method to evaluate the fidelity of adult cod to spawning grounds in Scottish waters. To our knowledge, the only study that has used a multiplicative model to standardize effort in a mark-recapture study was that of Neilson et al. (2006), who used the approach to standardize the effort of mobile gears (side and stern otter trawl) when evaluating stock structure of saithe in the Canadian Maritimes. In our analysis, we use a novel method that treats fishing gear as a different factor in a multiplicative model. Again to our knowledge, this is the first time that such an approach has been used to standardize effort in a mark-recapture experiment. Integration of gear type into our multiplicative model permitted a more comprehensive analysis than previously, because gears other than bottom trawls were used in different areas and seasons during the study period.

Our research has demonstrated that saithe around Iceland have great fidelity for their tagging areas, although long movements do take place within some areas (seasonally and vertically). Saithe from different tagging locations migrate along different routes, counterclockwise and clockwise around Iceland, probably as a result of fidelity to different feeding grounds. However, there is no indication of large-scale emigration of saithe away from Iceland.

Acknowledgements
We thank Stratis Gavris, Kristinn Haftor Sæmundsson, and Hóskuldur Bjornsson for their advice in statistical and spatial analyses, and two anonymous referees and the editor for useful comments on the submitted version. We are also grateful to those within Iceland’s Marine Research Institute who conducted the tagging work and gathered and recorded the recapture data, and all the fishers who returned tags and the requested information.
Finally, the first author thanks those at the Biological Station in St Andrews who supported him while he worked there on the publication. The project was funded by Iceland’s Marine Research Institute (MRI), the Federation of Icelandic Fishing Vessels Owners (LIU), and the Icelandic Centre for Research (RANNIS).

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doi:10.1093/icewms/5sm076