Migration of saithe (*Pollachius virens*) in the Northeast Atlantic

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Saithe (*Pollachius virens*) stocks in the Northeast Atlantic intermingle as a result of migration among stock areas. The extent of migration has been poorly quantified. Here, we estimate measures of the migration based on existing tagging data from Icelandic, Faroese and Continental (Scotland, North Sea and Norway) waters. Saithe tagged in Icelandic waters were seldom caught outside Icelandic waters (<1% of tag returns), whereas 42% of adult saithe tagged in Faroese waters were recaptured outside Faroese waters. Of adult saithe tagged in Norwegian waters 6.6% were recaptured outside Continental waters. In broad terms, there was a net migration of saithe towards Icelandic waters. The distance between tagging and recapture increased with increasing size and age, with saithe tagged in Norwegian waters moving the longest distances. The results demonstrate significant, but variable, migration rates of adult saithe in the Northeast Atlantic. More detailed studies are needed to clarify the mechanisms behind the migration and what causes the differences among the areas.

Keywords: migration, Northeast Atlantic, *Pollachius virens*, Saithe, tagging.

Introduction

Saithe (*Pollachius virens*) are a commercially important species and are widespread in the Northeast Atlantic, from the Barents Sea in the north to the Bay of Biscay in south, also around Iceland and East Greenland. Saithe are regarded as a demersal fish, but they do exhibit pelagic behaviour as well (Bergstad, 1991; Stensholt et al., 2002; Neilson et al., 2003; Armannsson and Jónsson, 2012). The pelagic behaviour is also reflected in the diet, which is not directly associated with the seabed. The main prey items include pelagic crustaceans such as copepods, euphausiids, and amphipods (Nedreaas, 1987; Bergstad, 1991; Højgaard, 1999; Jaworski and Ragnarsson, 2006; Homrum et al., 2012), and fishes such as Norway pout (*Trisopterus esmarkii*), blue whiting (*Micromesistius poutassou*), herring (*Clupea harengus*), sandeel (Ammodytidae) and capelin (*Mallotus villosus*) (Pálsson, 1983; Du Buit, 1991; Bergstad, 1991; Jónsson, 1996; Jaworski and Ragnarsson, 2006; Olsen et al., 2010; Homrum et al., 2012).

Juvenile saithe reside in inshore waters the first 2–4 years (Bertelsen, 1942; Clay et al., 1989; Armannsson et al., 2007). As adults, saithe move to offshore waters (Jones and Jónsson, 1971; Homrum et al., 2012) and exhibit seasonal migrations between spawning and feeding areas (Jones and Jónsson 1971; Olsen et al. 2010).

Previous studies have demonstrated that saithe conduct migrations over long distances, but there are regional differences. Jakobsen and Olsen (1987) found that adult saithe, tagged in northern Norway, emigrated to Icelandic waters and, to a lesser degree, to Faroese waters. Also, significant changes in mean length-at-age from one year to another have been interpreted as immigration of saithe to Icelandic waters (Jónsson, 1996; ICES, 2000). Tagging in the Faroe area (Jones and Jónsson, 1971) showed that considerable proportions of saithe tagged on the Faroe Bank were recaptured in Icelandic waters, off North and West Scotland, and in the northern North Sea. In Icelandic

waters, juvenile saithe appear to have high affinity to the area of tagging, and there is no indication of mass emigration from Icelandic waters (Jones and Jónsson, 1971; Armannsson *et al.,* 2007).

Although studies have been made regionally, no integrated study of migration within the saithe complex in the Northeast Atlantic has been published, and some of the datasets have increased substantially since the earlier publications. Based on these updated datasets, we here attempt to estimate quantitative measures of the migration among the distinct stocks of saithe in the Northeast Atlantic. To do this, we have compiled the available updated information on recaptures of saithe tagged in Icelandic, Faroese and Norwegian waters. From this information, and other pertinent data on the stocks, we estimate the migration rates among stocks and to what extent they depend on individual fish length and time between tagging and recapture.

Material and methods

Within the advisory framework of ICES, saithe is treated as four separate stocks: Icelandic (Division Va) (ICES 2010a), Faroese (Division Vb) (ICES 2010a), Northeast Arctic (Subareas I and II) (ICES 2010b), and North Sea, Skagerrak and West of Scotland/Rockall (Subarea IV, Division IIIa and Subarea VI) (ICES 2010c). Saithe west of Scotland was earlier treated as a separate stock in the advice, and is still managed separately. These four stocks have in this study been allocated to three separate "stock areas", as defined in Figure 1. The Icelandic and Faroese stock areas roughly contain the respective ICES divisions, but are enlarged to include recaptures in the vicinity of the stock area. The Northeast Arctic and the North Sea and Skagerrak (North Sea) stocks are divided at 62°N in the ICES advisory framework. This division is not associated with any clear topographic, hydrographic or biological boundary, although the two stocks
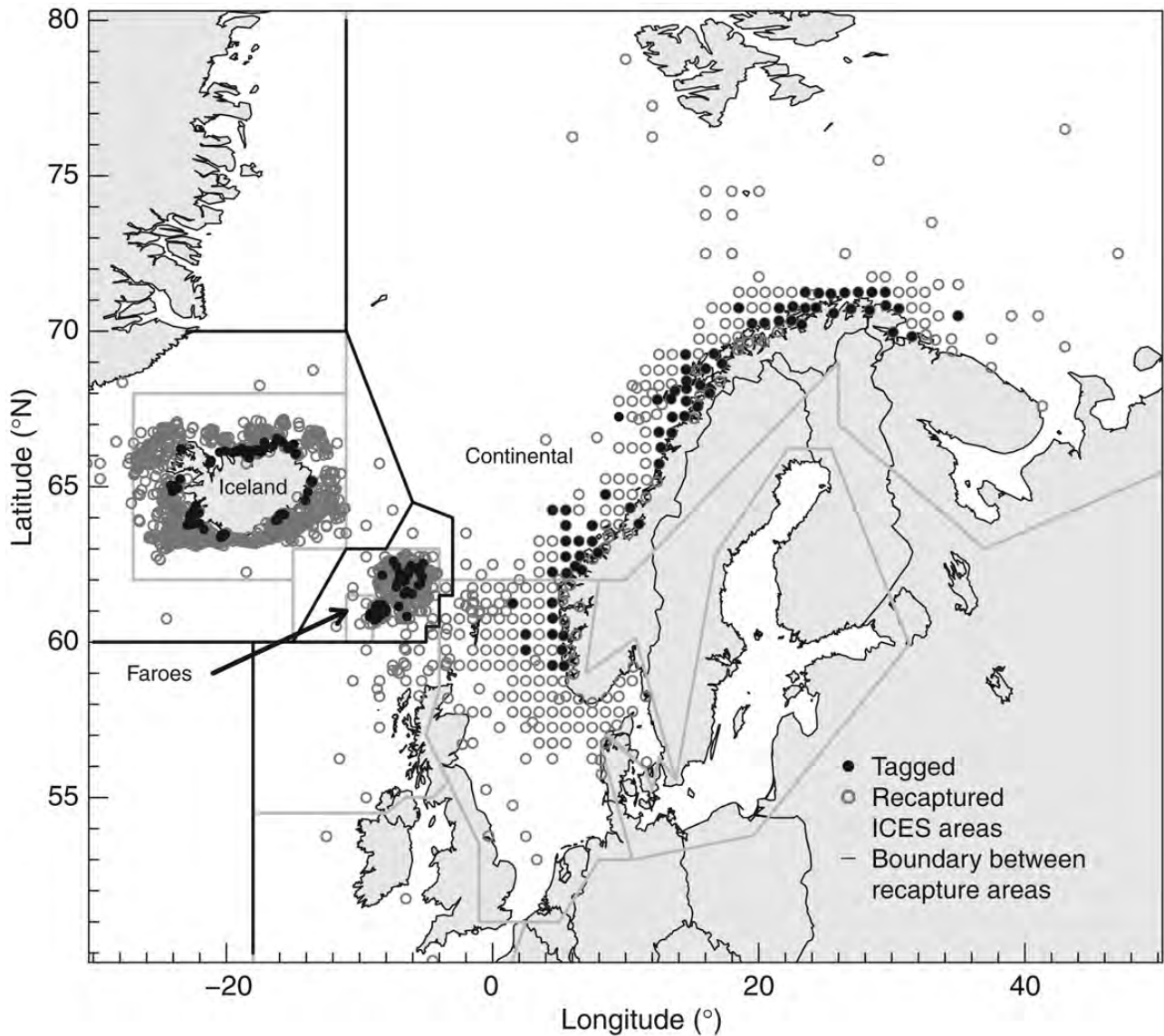

Figure 1. Study area. Stock areas (black lines), ICES areas (grey lines). Tagging localities (black closed circles) and recaptures (grey open circles) are shown as well, by statistical rectangle for Norwegian experiments.

Table 1. Number of saithe tagged in Faroese, Icelandic and Norwegian waters, and number and percentages recaptured.

	Iceland		Faroes		Norway	
Tagging country	**n**	**(%)**	**n**	**(%)**	**n**	**(%)**
Tagged	19919		13736		78264	
Recaptured						
all	1899	9.5	1513	11.0	15374	19.6
recapture length >60 cm	787	4.0	355	2.6		
3 years at liberty	406	2.0	214	1.6	901	1.2
length at tagging <50 cm	1278	6.4	1360	9.9	8916	11.4
Mean length	45 cm		39 cm		50 cm	
Main catch method when tagged	Jigging		Trawl, net, trolling		Purse seine	
Main tag type	T-bar anchor tags		Lea, anchor, Carlin		Lea	

Mean length, main catch method when tagged and tag type are also indicated.

have clearly distinct recruitment patterns. Migration between the two areas is extensive. Immature saithe tagged short distances north of 62°N were frequently recaptured south of this border and, less frequently, vice versa (Jakobsen, 1981). Furthermore, the southwards spawning migration from northern Norway often extends into the North Sea (e.g. ICES, 1965). Tagging experiments in the North Sea and West of Scotland (Newton, 1984; Fontaine, 1985) have been scarce, making it difficult to investigate or determine stock boundaries between the populations in the North Sea and the Northeast Arctic region. Therefore, we treat the Northeast Arctic and North Sea as one stock area, which we term "Continental".

Tagging

Tagging in all three stock areas focused on juvenile saithe. Most of the tagging was undertaken in the summer months, outside of the main spawning season in February–March (Homrum et al, 2012; Olsen et al, 2010). We are confident therefore that tagging was conducted on the dispersed stock, and that spawning aggregations were not tagged.

Icelandic waters

A total of 19 919 saithe were tagged in shallow coastal waters at different locations around Iceland from 2000–2010 (Table 1). Tagging intensity was highest in 2003 with 5400 saithe tagged, while no saithe were tagged in 2005 and 2006. Mean size at tagging varied from 43–50 cm between years. For detailed descriptions, see Armannsson et al., (2007), which is based on the same data (up to 2005), as used in this study.

Faroese waters

A total of 13 736 saithe were tagged in Faroese waters from 1959–1991 (Table 1). The tagging intensity varied over time, ranging from three fish tagged in 1967, to 3288 in 1962. The data originated from three Faroese tagging experiments in 1960–1965, 1975–1976, and 1991, and from an additional English experiment carried out between 1959 and 1967. The mean length of saithe in these experiments varied from 34–71 cm. The English experiments were conducted primarily on the Faroe Bank using trawls. This resulted in a larger mean size of fish tagged than from the Faroese experiments, which were concentrated in shallower waters where juvenile saithe resided (Bertelsen, 1942; Homrum et al., 2012).

Norwegian waters

The tagging experiments in Norwegian waters were the most comprehensive, covering varying parts of the Norwegian coast from 1954–1980 with 78 264 saithe tagged (Table 1). Tagging intensity varied considerably, as did the main areas of tagging and the mean size of the fish tagged. In the beginning of the project, emphasis was on the northern part of the coast and the fish were larger (mean size ~ 60 cm), but later in the project, there was a wider coverage along the coast, and the tagged saithe were smaller (mean size ~ 40 cm).

Recapture

Recaptures of tagged fish were mainly by the commercial fleet. Information on where to send information and tags was provided either directly (LEA-tags had a hollow cylinder containing information) or through advertisement (e.g. posters). Rewards were provided for recaptured tags, but it is hard to assess whether the values were comparable among stock areas or countries because e.g. the Icelandic experiments were conducted 20–50 years later than the Norwegian experiments and all three regions have different currencies. It was not possible to assess variability among stock areas in reporting rates from the data.

In this study, we based our analyses on the time, position, and fish length at tagging and at recapture. The "relative recapture percentage" (RRP) for one stock area was defined as the percentage of fish recaptured in that stock area, in relation to the total number of recaptured fish with reported location from that tagging. Thus, recaptures from several years are included in the RRP, since it is based on the year of tagging rather than the year of recapture. The "time at liberty" refers to the time in years elapsed between tagging and recapture. The "distance from tagging site" denotes the shortest distance over water (i.e. avoiding landmasses) between the position at tagging and the position at recapture. This distance was approximated using an implementation of Dijkstra's algorithm in the package "spatgraphs" (Rajala, 2012) and other packages in the R statistical environment (R Core Team, 2012). Shortest path searches were performed on a hexagonal grid out of which landmasses had been removed. Grid resolution was generally ~10% of the great circle distance between tag and return positions with a minimum of 1 km. A hexagonal grid provides a good representation of the space between tagging and recapture locations, because distances can theoretically be overestimated by a factor of $2/\sqrt{3}$ or by ~15% in the worst case.

Unfortunately, length at recapture was not available for saithe tagged in Norwegian waters, and therefore analyses regarding

recapture length apply only to the Icelandic and Faroese data. Based on tagging lengths, almost all the saithe tagged were estimated to be ≥ 2 years old. Fish that have spent ≥ 3 years at liberty would thus be ≥ 5 years old and be ~ 60 cm or more in length (Moguedet *et al.*, 1987; Homrum *et al.*, 2012; unpublished Icelandic data). Therefore, two criteria (>60 cm and >3 years at liberty) were used to distinguish between the migratory behaviour of young and adult saithe. This division into young and adult saithe is related to the sexual maturity of fish, since 50% of saithe have matured sexually around age 5–6 (ICES 2010a, 2010b, 2010c; Homrum *et al.* 2012).

Emigration and immigration rates

In this study, the observed *RRP* in a stock area, corresponding to saithe tagged in a different stock area, are considered representative for the emigration rate from the latter to the former. This interpretation may to some extent depend on the details of the migration behaviour and fishing mortalities in the different areas, but may be justified for some simple scenarios, e.g. the model presented in Appendix A, as long as fishing mortalities greatly exceed natural mortality. The model has been constructed based on general methods described in textbooks (e.g. Jennings *et al.*, 2001). With regards to migration behaviour the model assumes a permanent migration from one stock area to another, which may or may not be realistic. The emigration rate is calculated as a lifetime rate where average time- and area-specific fishing mortalities have been used (Appendix A). To quantify the effect of migration on the receiving stock, we define the immigration percentage (*IP*) as the *RRP* scaled by the ratio between stock sizes (in numbers, average for the period over which *RRP* was calculated) of adult fish in the donating and receiving stock areas (Appendix A). Stock sizes and fishing mortalities (Table 2 and Figure B1 in Appendix B) were obtained from the ICES assessments (ICES, 2010a, 2010b, 2010c). For the Icelandic saithe, the most recent reports contain data only back to 1980. To extend the Icelandic series back to 1960, assessment results from older reports were used (ICES 1978, 1987). Stock sizes were aggregated for adult fish (defined as ages 5–10), when the ratios between stock sizes among stock areas were calculated (Table 2).

To evaluate whether there were differences in emigration rates between stock areas, χ^2-tests were performed. Recaptures were defined as either inside or outside the stock area of tagging for

each tagging stock area, using data where saithe had been ≥ 3 years at sea or were ≥ 60 cm in length (Table 3). Similarly, temporal trends were tested for the Norwegian and Faroese tagging experiments, defining recaptures inside and outside the stock area of tagging by tagging period (Table 4).

Results

The migrated distance from tagging site increased with increasing recapture length and age of saithe (up to 80 cm and 5 years of liberty) in all areas. The relationship was more pronounced in some areas than in others (Figure 2a and b). For saithe in the Faroese and Icelandic stock areas the distance from tagging site levelled off around 200–300 km. Distances from tagging site of saithe, either <50 cm or during the first year at liberty, were shortest for saithe tagged in Faroese waters. The migrated distances were largest for saithe tagged in Norwegian waters, except during the first year at liberty, when the distance was comparable to that of saithe tagged in Icelandic waters. Distance from tagging site versus length at tagging is presented for the Norwegian data only (Figure 2c). The youngest saithe moved the shortest distances from the tagging site. For saithe >90 cm, there was a tendency towards shorter distances than for the 60–90 cm long saithe (Figure 2c). For adult saithe (>60 cm at tagging) in the Faroese ($n = 72$) and Icelandic ($n = 143$) stock areas, there was no apparent seasonal pattern in the distance from tagging site. For adult saithe in Norwegian waters ($n = 2806$) the distances were shortest in the summer months and longest in February–March (Figure 2d).

With respect to migration among stock areas, it was found that during the first one or two years at liberty, saithe were generally recaptured inside their stock area (Table 3). Adult saithe (>60 cm or at least 3 years at liberty) did, to some extent, migrate among the stock areas (Table 3), but the emigration (*RRP* outside the area of tagging) varied significantly among stock areas (χ^2-tests: for saithe >60 cm: $p < 0.001$, d.f. = 2; >3 years at liberty: $p < 0.001$, d.f. = 3). Adult saithe tagged in the Faroese stock area were frequently recaptured in foreign stock areas; >3 years at liberty, 42% were recaptured outside the Faroese stock area. Adult saithe tagged in Icelandic waters, on the other extreme, were seldom recaptured outside the Icelandic stock area (0.8%). The recaptures of Icelandic tags in the Faroese stock area derived exclusively from tagging locations on

Table 2. Summary of stock sizes and fishing mortalities per area and recapture period based on the respective ICES reports from stock assessments in 2010 (see text).

		Stock area of recapture								
		Mean			Standard deviation			Stock size ratio		
Tagging area	Periods of recapture	Iceland	Faroes	Cont[a]	Iceland	Faroes	Cont[a]	Iceland	Faroes	Cont[a]
Average stock size of ages 5–10 in recapture periods (million individuals)										
Iceland	2000–2010	51	71	418	18	28	82		0.71	0.17
Faroes	1959–1980, 1991–1997	63	28	232	32	11	108	0.45		0.12
Norway	1954–1983	68	27	221	30	12	103	3.26	8.15	
Average fishing mortality of ages 5–10 in recapture periods										
Iceland	2000–2010	0.38	0.60	0.35	0.11	0.23	0.13			
Faroes	1959–1980, 1991–1997	0.35	0.33	0.40	0.15	0.18	0.19			
Norway	1954–1983	0.32	0.27	0.38	0.13	0.12	0.18			

[a]Note that here, the Continental stock area is a combination of the Northeast Arctic and North Sea/Skagerrak.

Table 3. RRP (relative recapture percentage) in the Faroese, Icelandic and Continental stock areas in relation to the total number recaptured (with known position), by tagging area.

Tagging stock area:		Iceland				Faroes				Norway			
Recapture stock area:		Iceland	Faroes	Contin.	Recaptures (*n*)	Iceland	Faroes	Contin.	Recaptures (*n*)	Iceland	Faroes	Contin.	Recaptures (*n*)
Length at recapture (cm)	(26, 30)	–	–	–	0	0.0%	**100.0%**	0.0%	13				
	(30, 40)	**100.0%**	0.0%	0.0%	1	0.0%	**100.0%**	0.0%	224				
	(40, 50)	**100.0%**	0.0%	0.0%	91	1.0%	**98.5%**	0.5%	205				
	(50, 60)	**100.0%**	0.0%	0.0%	474	10.5%	**86.3%**	3.3%	153				
	(60, 70)	**99.3%**	0.7%	0.0%	422	24.1%	**71.3%**	4.6%	108				
	(70, 80)	**98.4%**	1.1%	0.5%	189	29.3%	**61.0%**	9.8%	82				
	(80, 90)	**100.0%**	0.0%	0.0%	74	27.5%	**60.8%**	11.8%	51				
	(90,100)	**100.0%**	0.0%	0.0%	21	11.1%	**77.8%**	11.1%	9				
	(100,120)	**100.0%**	0.0%	0.0%	9	50.0%	**50.0%**	0.0%	4				
All length groups	NA	**99.5%**	0.5%	0.0%	394	4.4%	**90.1%**	5.5%	365				
		99.5%	0.4%	0.1%	1675	8.3%	**87.9%**	3.8%	1214				
	>60 cm	**99.2%**	0.7%	0.1%	715	26.4%	**65.7%**	7.9%	254				
Years at liberty	0–1	**100.0%**	0.0%	0.0%	341	0.5%	**98.6%**	0.9%	651	0.3%	0.2%	**99.5%**	9650
	1–2	**99.6%**	0.4%	0.0%	460	9.6%	**86.4%**	4.0%	272	1.2%	1.2%	**97.6%**	3068
	2–3	**99.3%**	0.5%	0.2%	440	18.8%	**73.9%**	7.2%	138	2.8%	2.5%	**94.7%**	1171
	3–4	**99.1%**	0.9%	0.0%	223	27.7%	**61.5%**	10.8%	65	3.6%	1.4%	**95.0%**	443
	4–5	**98.8%**	1.2%	0.0%	86	40.0%	**52.5%**	7.5%	40	6.7%	1.7%	**91.6%**	179
	5–6	**100.0%**	0.0%	0.0%	46	37.5%	**45.8%**	16.7%	24	9.5%	3.6%	**86.9%**	84
	>6	**100.0%**	0.0%	0.0%	27	13.0%	**69.6%**	17.4%	23	4.7%	0.8%	**94.5%**	127
All years at liberty		**99.5%**	0.4%	0.1%	1623	8.3%	**88.0%**	3.7%	1213	1.0%	0.7%	**98.4%**	14 722
	>3	**99.2%**	0.8%	0.0%	382	30.3%	**57.9%**	11.8%	152	5.0%	1.6%	**93.4%**	833

The same variable is presented by length at recapture (upper part) and by time at liberty (lower part).

Table 4. Pattern in migration among tagging periods. *RRP* – percentage recaptured in the Faroese, Icelandic and Continental stock areas in relation to total number recaptured (with known position) where time at liberty exceeded 3 years. Presented for saithe tagged in Faroese (upper part) and Norwegian waters (lower part). The Faroese data are presented by period of tagging. The Norwegian data are presented by year of tagging aggregated into 5-year periods.

	Stock area of recapture			Recaptures (*n*)
Tagging period	**Faroes**	**Iceland**	**Continental**	
Saithe tagged in Faroese waters				
1959 – 1967 (British)	**50%**	23%	27%	22
1960 – 1965 (Faroese)	**61%**	28%	11%	109
1975 – 1976 (Faroese)	**50%**	50%	0%	2
1991 (Faroese)	**53%**	47%	0%	19
Total	**58%**	30%	12%	152
Saithe tagged in Norwegian waters				
<1956	2.3%	2.3%	**95.5%**	88
1956 – 1960	1.7%	4.7%	**93.5%**	232
1961 – 1965	1.1%	7.0%	**91.9%**	186
1966 – 1970	0%	6.4%	**93.6%**	94
1971 – 1975	2.0%	5.3%	**92.8%**	152
1976 – 1980	0%	2.5%	**95.1%**	81
Total	1.6%	5.0%	**93.4%**	833

the east coast of Iceland, while the tagging intensity was higher on the north coast. The *RRP* for adult saithe, tagged in Norwegian waters, outside the Continental stock area was intermediate at 6.6%.

The variation among periods of tagging in inter-area migration patterns was only investigated for saithe tagged in Faroese and Norwegian waters, where tagging experiments covered several decades. The emigration from Faroese to Icelandic waters varied between 23 and 50% among the four tagging projects, while the emigration from Faroese to Continental waters varied between 0 and 27% (time at liberty >3 years, Table 4). The emigration from Norwegian waters to Icelandic waters varied between 2.3 and 7%, and to Faroese waters between 0 and 2.3% among 5-year periods (Table 4). None of these variations were statistically significant (χ^2-tests: Norwegian experiments: $p = 0.94$, d.f. = 6, Faroese experiments: $p = 0.89$, d.f. = 4).

Emigration from one stock area implies immigration to another, but the relative influence depends on the stock sizes. The migration among stock areas is summarized in Figure 3. Emigration from a certain stock area was described by the observed *RRP* values (Table 3, where time at liberty >3 years). The largest *IP* values (immigration rates) were to Iceland (14% from the Faroese and 16% from the Continental stock area), and the lowest to the Continental stock area (0% from the Icelandic and 1% from the Faroese stock area). The immigration to the Faroese stock area was 1% from the Icelandic and 12% from the Continental stock area.

Discussion

Our findings suggest that the migration rates of saithe in the Northeast Atlantic vary considerably among stock areas, and this is in line with previous publications (Jones and Jónsson, 1971;

Jakobsen and Olsen, 1987; Armannsson *et al.*, 2007), which have partly used the same data as the present study. Young fish in all stock areas exhibited low emigration rates, as reflected by the short distances from tagging site. For adult fish, the distance from tagging site increased in all areas, but the emigration rates differed between areas, being lowest for the Icelandic (0.8%), intermediate for the Continental (6.6%), and highest for the Faroese stock area (42%).

Working with tagging data is associated with limitations. The observed migration patterns are affected by several factors. One factor is the differences in tag loss among different types of tags (Fowler and Stobo, 1991), which have varied considerably among the tagging experiments in this study. However, variations in tag loss will not affect our main conclusions if we assume that losses of specific tag types do not vary between areas of recapture. There are other factors, such as fishing patterns of the commercial fleet, e.g. gear used and multi-nation fleets, and varying and unknown reporting rates. For these factors, we have no estimates of the errors they may induce, and they are not discussed further, with the exception of seasonal variations in fishing effort.

Distances from tagging site in relation to size and stock area

Distances from tagging site were shortest for the youngest saithe, especially in the Faroese stock area. The most likely explanation for this is that young saithe prefer, or are restricted to, shallow habitat (Bertelsen, 1942; Jones and Jónsson, 1971; Nedreaas, 1987; Homrum *et al.*, 2012), which therefore limits the distance they can move away from the coast and their original tagging location. This would also explain why young Faroese saithe moved the shortest distances, because the shallow area available to saithe in Faroese waters is much smaller than in Icelandic and Norwegian waters. The shorter distances migrated by younger saithe appears to reflect a genuine behavioural characteristic, because the distance travelled by young saithe was similar whether they had been at liberty for just a short time, or were recaptured after one year or more at liberty (Figure 2c, shown for the Norwegian stock area only).

Adult saithe migrated longer distances than young saithe in all stock areas (Figure 2a, b and c), and moved farther in the Continental than in the Faroese or Icelandic stock area. For adult saithe tagged in Norwegian waters (length at tagging >60 cm) there was a seasonal pattern in the distance from tagging site, with the farthest distances observed in February–March and the shortest in the late summer months. Since most tagging experiments were conducted in the summer months it is likely that fish were mainly tagged on their feeding grounds. The shortest distances observed in the summer months indicate that saithe come back to the same feeding grounds. This impression is in accordance with these large saithe being primarily tagged along northern Norway and the spawning areas being located farther south along the Norwegian coast (Olsen *et al.*, 2010). The less obvious seasonal pattern in the Faroese and Icelandic data is probably mostly due to scarcer data, but could also partly be because the distance between feeding and spawning grounds is shorter in these smaller areas.

Migration among stock areas

As argued in Appendix A, the interpretation of the *RRP* values as emigration rates is a good approximation as long as fishing
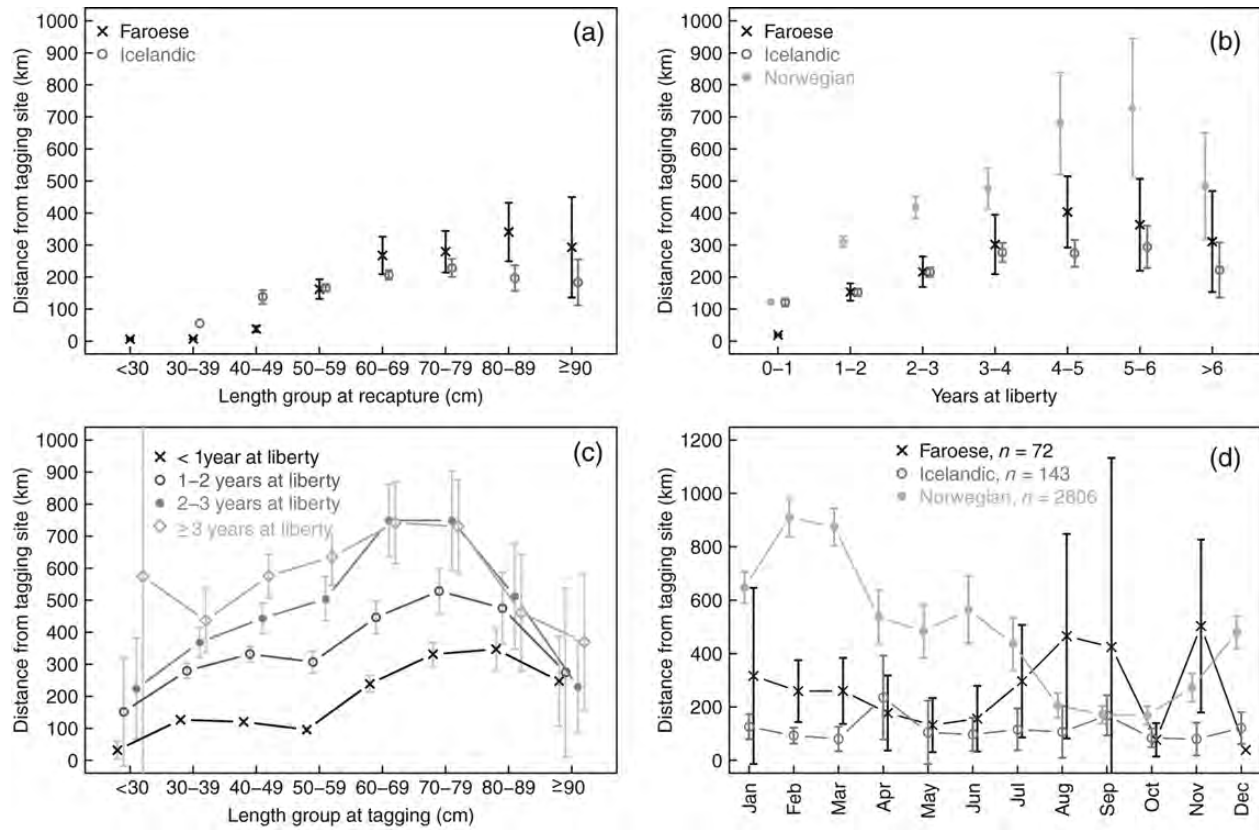
Figure 2. Distance between tagging site and site of recapture. (a) Mean distance from tagging site of saithe tagged in Faroese and Icelandic waters by length group at recapture. (b) Mean distance from tagging site versus time at liberty (for fish <50 cm at tagging). (c) Mean distance from tagging site of Norwegian saithe versus length at tagging (by years at liberty, as indicated in legend). (d) Mean distance from tagging site versus month of recapture based on fish >60 cm in length at tagging. Vertical bars represent 95% confidence intervals.

mortalities exceed natural mortality. The lowest average fishing mortality for ages 5–10 over the time-span of a tagging project was in the Faroese stock area in 1961–1983, where *F* was 0.27 compared with 0.38 in the Continental stock area (Table 3); for this change in *F* the *RRP* would decrease by only 12% (from 1.6–1.4%). We thus conclude that the observed *RRP*s are representative of the emigration rates.

The observed migration between stock areas was minor for young fish. Adult saithe (>60 cm, or time at liberty >3 years) exhibited migration between stock areas, but the migration rates varied significantly depending on the stock area of tagging.

Of the saithe tagged in Norwegian waters, after 3 years at liberty, 1.6% were recaptured in the Faroese and 5% in the Icelandic stock area. Norwegian survey and fisheries investigations have shown that saithe tend to follow the herring into the Norwegian Sea, as well as to the spawning areas of herring (Runde, 2005). This is supported by diet analyses of saithe (Bergstad, 1991; Olsen et al., 2010). The relatively high *RRP* in 1961–1970 in the Icelandic stock area of saithe tagged in Norwegian waters is likely to reflect a feeding migration following the herring. After the collapse of the Norwegian spring-spawning herring in 1968 (Hamilton et al., 2004), the recaptures of Norwegian tags in Icelandic waters decreased. The proportion of the saithe pursuing herring, and the extent of overlap between the two species in space and time is, however, not well known.

For adult saithe tagged in Faroese waters, a substantial fraction (26–30%) was recaptured in the Icelandic stock area (Table 3),

and 8% in the Continental stock area. One possibility is that the large emigration rates from Faroese waters to the Icelandic stock area reflect a feeding migration, e.g. pursuing blue whiting. In Faroese and Scottish waters, blue whiting has been an important prey to saithe, but Norway pout and euphausiids are also constituents of the diet (Du Buit, 1991; Homrum et al., 2012). In addition to diet studies, bycatch of saithe in the blue whiting fishery also indicate feeding migrations following blue whiting (Pálsson, 2005).

Adult saithe in Icelandic waters show negligible emigration (Table 3). This is consistent with previous studies, which have demonstrated <1% emigration from Icelandic waters (Jones and Jónsson, 1971; Armannsson et al., 2007). The material used in Armannsson et al. (2007) was used in the present study up until 2005, whereas the material used in Jones and Jónsson (1971) was not. The low emigration rate may perhaps be related to the distribution of the main prey species, especially capelin, which is the main constituent in the diet of saithe in Icelandic waters during part of the year (Pálsson, 1983; Jónsson, 1996; Jaworski and Ragnarsson, 2006). Capelin has a spawning migration to Icelandic waters, where most of the stock dies after spawning (Vilhjálmsson, 2002), and saithe will therefore not follow the capelin away from Icelandic waters.

The saithe is a capable swimmer (Videler and Hess, 1984) and is able to utilize the pelagic environment (Bergstad, 1991; Stensholt et al., 2002; Neilson et al., 2003; Armannsson and Jónsson, 2012). The pelagic behaviour is evidenced by the bycatch of saithe in the
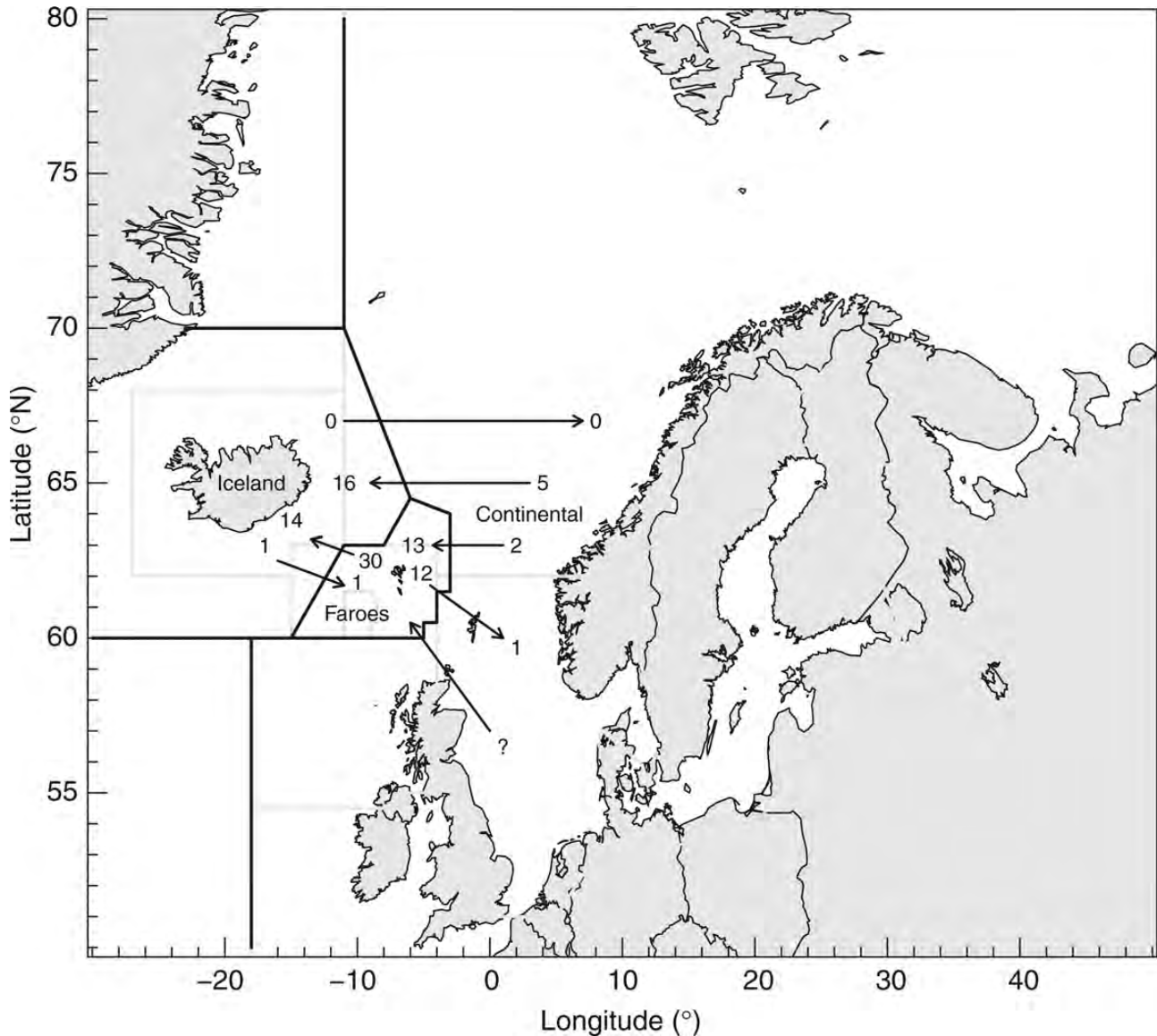
Figure 3. Map showing the estimated migration (in %) among the Faroese, Icelandic and Continental stock areas of saithe, where more than 3 years had elapsed between tagging and recapture. At the start of an arrow, the relative recapture percentages (RRP) (see text) are listed and at the end of an arrow the immigration percentage (IP) is shown.

blue whiting fishery (Pálsson 2005) and the connection between saithe and herring in Norwegian waters (Runde, 2005). The interplay between spawning and feeding migrations seems a plausible explanation for the observed migration rates among stock areas. Seasonal and interannual changes in distribution of prey species are likely drivers of saithe migration.

The overall trend is that there is a westward migration of adult saithe. There is a net import of saithe to Icelandic waters, and a net export of adult saithe from Faroese and Norwegian waters (Figure 3). The differences that we see in migration behaviour between stock areas have also been reported for the Northwest Atlantic (Neilson *et al.*, 2006). Saithe tagged in the western part of the Scotian Shelf were rarely captured in the eastern part (2%), whereas 22% of fish tagged in the eastern areas were recaptured in the west. Thus, migration patterns of the saithe complexes on both sides of the North Atlantic have some similar features.

There were seasonal variations in the number of reported tags, which probably reflected seasonal variations in the fishing effort. The Norwegian data differed from the Icelandic and Faroese, in that a pronounced proportion of the tags were reported by purse seiners in July–September. In more detailed studies the tag reports need to be standardized for variations in the fishing effort (Neilson *et al.*, 2006; Armannsson *et al.*, 2007). However, we do not believe seasonal variations in fishing effort impact our main conclusions radically, because the difference in the observed emigration rates between the stock areas was so pronounced.

Differences in *RRP* in individual periods (Table 4) could indicate differences in migration rates, but none of these differences were statistically significant. Therefore, we cannot identify any consistent interannual variations in migration rates. Due to the discontinuous nature of tagging between the three stock areas,

however, we cannot conclude that the migration rates have been constant over the six observed decades.

Implications for stock assessment

Substantial migration between saithe stocks, as shown here, implies that there are consequences for the management of saithe in the Northeast Atlantic. Quantitative implications for the assessments would require more detailed spatio-temporal information on migration behaviour than is presently available. Migration is, in a rudimentary manner, accounted for in the assessments of the Icelandic saithe, which incorporates interannual fluctuations in the length distributions and catches of immigrant year classes (Jónsson, 1996; ICES, 2000). In our study, the objective was to estimate migration rates between the main stock areas. Within these stock areas, there may be several subpopulations of saithe, and this is obviously the case with the Continental stock area, which consists of saithe stocks that are managed separately. It is equally important to document the spatial distribution of sub-populations as migration between stock areas, in order to ensure that fisheries are not exploiting vulnerable components and thus depleting genetic diversity (Stephenson, 1999; Hutchinson, 2008).

Conclusions and outlook

Young saithe move short distances and appear to be limited by the topography, such that saithe in Faroese waters move the shortest distances, and saithe in Norwegian waters move the farthest distances. Larger saithe migrate across boundaries set in the ICES advisory framework, but the different stocks appear to have different magnitudes of migration. Icelandic saithe are seldom recaptured outside domestic waters, whereas large Faroese saithe are often recaptured in foreign waters. Many questions on saithe migration in the Northeast Atlantic remain unanswered, however. In order to clarify the mechanisms behind the migration and what causes the differences between stock areas, the individual behaviour of saithe should be investigated much more intensively, e.g. by use of Data Storage Tags (Armannsson and Jónsson, 2012), *in situ* underwater tagging equipment (Sigurdsson *et al.* 2006), and fisheries independent tag types such as acoustic tags (Uglem *et al.*, 2009) and satellite pop-up tags. Also, simultaneous and coordinated tagging experiments of saithe in the entire Northeast Atlantic, conducted over several years, are needed to fill gaps in our knowledge.

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Appendix A

A detailed interpretation of tag recaptures in different areas would require detailed information about the migration behaviour, which is not generally available. To illustrate the relationships, we consider a somewhat idealized example.

Consider a certain stock component (e.g. an age group) of saithe in Area A. At time t_1, the number of fish in this stock component is N_1. At this time, a certain fraction, R, of these fish are tagged in Area A, where they remain until time t_2, i.e. for a period $t_a = t_2 - t_1$. The number of fish in the stock component still surviving in the sea (e.g. Jennings *et al.*, 2001) will be:

$$N_a = N_1 \cdot \exp(-Z_a \cdot t_a) \quad \text{with} \quad Z_a = F_a + M \qquad (1)$$

where we have assumed a constant total mortality Z_a, consisting of the area-dependent fishing mortality F_a and a natural mortality M. If the tagged fish behave as the rest of their stock component and have the same mortalities, the number of tagged fish still in the sea should be $R \cdot N_a$. Assume that a certain proportion P_m of the stock component and of the tagged fish then (at time t_2) emigrates instantaneously to Area B, where they remain (this may or may not be true, but it simplifies our model). The number of tagged fish that remain alive in Area A will then decrease with time, t, as:

$$N_A(t) = (1 - P_m) \cdot R \cdot N_a \cdot \exp[-Z_a \cdot (t - t_2)] \qquad (2)$$

During a short time interval, dt, the number of tagged fish that are caught in Area A will be given by $F_a\, N_A \cdot dt$ (e.g. Jennings *et al.*, 2001). The total number of tagged fish caught in the original area from time t_2, onwards, is then found by integrating this expression:

$$C_a = \int_{t_2}^{\infty} F_a \cdot N_A dt$$

$$= (1 - P_m) \cdot R \cdot N_a \cdot F_a \times t \int_{t_2}^{\infty} \exp[-Z_a \cdot (t - t_2)]dt$$

$$= (1 - P_m) \cdot R \cdot N_1 \times \exp(-Z_a \cdot t_a) \cdot \frac{F_a}{Z_a} \qquad (3)$$

In Area B, during the same period, we similarly expect a catch of tagged fish:

$$C_b = P_m \cdot R \cdot N_a \cdot F_b \cdot \int_{t_2}^{\infty} \exp[-Z_b \cdot (t - t_2)]dt$$

$$= P_m \times R \cdot N_1 \cdot \exp(-Z_a \cdot t_a) \cdot \frac{F_b}{Z_b} \qquad (4)$$

The relative proportion caught in the non-original Area B is then:

$$RRP = \frac{C_b}{C_a + C_b} = \frac{\alpha \cdot P_m}{1 - (1 - \alpha) \cdot P_m} \quad \text{with}$$

$$\alpha = \frac{Z_a \cdot F_b}{F_a \cdot Z_b} = \frac{1 + M/F_a}{1 + M/F_b} \qquad (5)$$

If fishing mortalities are the same in both areas, $\alpha = 1$ and the *RRP* that we measure will, under the given assumptions, equal the "true" proportion, P_m, for the whole stock component. Even with considerable differences in fishing mortality, α will remain close to 1 as long as fishing mortalities are substantially higher than the natural mortality. *RRP* is thus rather insensitive to differences in F between the areas. This is because we are observing the recaptures in the remaining lifetime of the tagged fish. With a high

F we take the fish over a shorter time period than if *F* is lower, but ultimately we catch the same number of fish, given that fishing mortalities are substantially higher than natural mortality.

With the approximation $\alpha \approx 1$, the effects of migration on the receiving stock may also be estimated quite simply. From the above, the total number of fish in this stock component migrating from A to B was $n_{ab} = P_m \cdot N_a$. Assume that the comparable stock component (e.g. age group) in Area B just before the time of migration has a total number N_b. The relative effect of the immigration on the receiving stock may then be defined as an immigration proportion:

$$IP = \frac{n_{ab}}{N_b} = \frac{P_m \cdot N_a}{N_b} \qquad (6)$$

Appendix B

The *RRP* and *IP* values are calculated using average time- and area-dependent fishing mortalities and stock sizes respectively.

The model described here assumes a cohort has lived out its life-span when *RRP* is calculated. This has implications for recent tagging experiments, where there are still tagged fish in the sea, which in this study is the case for the Icelandic data. But in practice this has little impact, since there were no fish tagged in 2005 and 2006, and fish tagged in 2008 and onwards have not yet been three years at sea, which is used as the criterion for adult fish. From the 2007 tagging experiment, only one saithe had been recaptured after three years at sea, so the *RRP* was actually calculated based on saithe up to six years at sea for the 2004 tagging experiment.
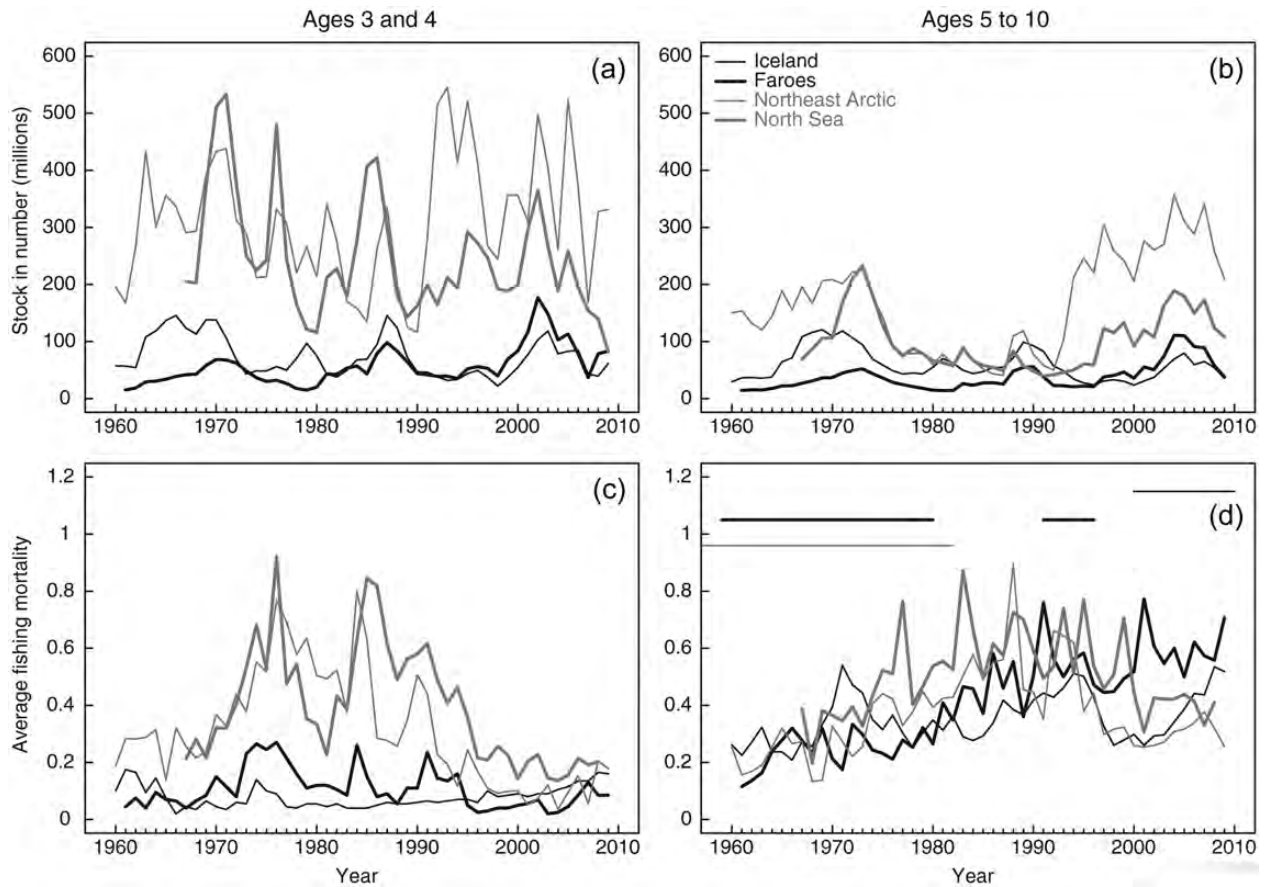

Figure B1. Stock in number and fishing mortality at age for saithe in the Northeast Atlantic (ICES 2010a, 2010b, 2010c). For Icelandic saithe results for 1960–1979 from older reports are used (ICES 1978, 1987). Stock in number has been summed for ages 3 and 4 (a), and ages 5–10 (b). Fishing mortality has been averaged for ages 3 and 4 (c), and 5–10 (d). The horizontal lines in (d) illustrate the periods when tagged fish have been recaptured for the three tagging areas (narrow black lines: Iceland; heavy black lines: Faroes; narrow grey lines: Norway)

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