Maturation, reproduction and early life history of anglerfish *Lophius piscatorius* in Faroese waters

Búning, nøring og yngullívssøga hjá havtasku í føroyskum sjógvi

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Abstract

Maturation, reproduction and early life history of *Lophius piscatorius* was investigated in Faroese waters. Length at first maturity (L_{50}) was 58 cm for males and 84 cm for females, corresponding to an age of about four years for males and seven years for females. The proportions of females and males were similar in fish less than 55 cm long, and were skewed towards more males in medium sized fish (55–75 cm). Females were predominant in the larger fish (> 85 cm). Observations of spawning males and females, egg ribbons and pelagic anglerfish larvae, suggest that the main spawning season is from February to April and the spawning area seems to be southwest of the Faroe Plateau and in the Faroe Bank area. The Faroe Plateau probably serves as a nursery ground for juvenile anglerfish. Morphological transformation from larvae to juveniles occurred when the fish were about 7–9 cm long and they settled to the bottom when they were about 11 cm long. Thus, all life stages, as well as nursery areas, spawning areas and feeding areas of anglerfish are found in Faroese waters, indicating a separate stock in the area.

Úrtak

Búning, nøring og yngullívssøgan hjá havtasku (*Lophius piscatorius)* í føroyskum sjógvi er kannað. Longd við búning (L_{50}) var 58 cm fyri kallfisk og 84 cm fyri kvennfisk, svarandi til umleið 4 ára aldur fyri kallfisk og 7 ára aldur fyri kvennfisk. Lutfallið millum kynini var javnt, tá fiskarnir vóru minni enn 55 cm; fyri miðal fiskastøddir (55-70 cm) vóru lutfalsliga fleiri kallfiskar, meðan kvennfiskarnir vóru ráðandi í lutfallinum hjá stóra fiskinum (> 85 cm). Við støði í eygleiðingum av gýtandi kallfiski og kvennfiski, rognabondum og uppsjóvaryngli hjá havtasku letur til, at høvuðsgýtingartíðin er frá februar til apríl, og at gýtingarøkini eru í ein útsynning úr Landgrunninum og við Føroyabanka. Landgrunnurin er helst uppvakstrarøki fyri havtaskuyngul. Umskapanin frá yngli til ungfisk hendir tá havtaskan er 7-9 cm long, og hon tekur botn, tá hon er um 11 cm. Samanumtikið hevur man í føroyskum sjógvi øll

menningarstigini hjá havtasku, umframt at man hevur funnið uppvakstrarøki, gýtingarøki og føðiøki; hetta bendir á, at havtaskan í føroyskum sjógvi er ein egin fiskastovnur.

Introduction

Two anglerfish species, *Lophius piscatorius* and *Lophius budegassa*, are distributed in the Northeast Atlantic (Caruso, 1983), although the latter is only rarely observed in the northernmost part of the distribution (Thangstad *et al.*, 2006). The Faroe Islands are located in the Northeastern Atlantic at 62°N 7°W, between Iceland, Norway and Shetland. The surrounding marine environment is productive with the warm North Atlantic Current in the upper layer (< 500 m depth) and the cold overflow water from the Norwegian Sea flowing in the deep layer (Fig. 1; Hansen *et al.*, 1998). Strong tidal currents maintain a clockwise current (front) on the Faroe Shelf (about 120 m depth), which functions as a retention area, that keeps fish eggs/larvae on the shelf (Gaard and Steingrund, 2001).

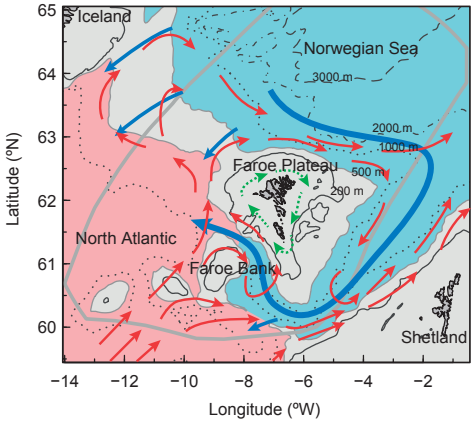

Fig. 1. Topography and the main current system around the Faroe Islands. Thin red arrows: warm currents in upper layers, bold blue arrow: main cold (< 0°C) flow in deep layer, stippled green arrows: currents on Faroe Shelf. The grey areas are shallower than 500 m, the blue area deeper than 800 m in Norwegian Sea is colder than 0°C, while the red area deeper than 800 m in the North Atlantic is usually warmer than 6°C, except the areas where there is a cold overflow from the Norwegian Sea. Grey bold line: 200 nm exclusive economic zone.

Anglerfish in Faroese waters have during the last decade become a highly exploited and economically important resource in the Faroese fisheries (Thangstad *et al.*, 2006), just as in Iceland (Sigurðsson and Magnússon, 2012), Norway (ICES, 2009; Thangstad *et al.*, 2006) and Scotland (e.g. Laurenson *et al.*, 2008). Anglerfish in Faroese waters (Division Vb) are currently regarded as a separate stock by ICES (ICES, 2009), although the stock structure of anglerfish in the Northeast Atlantic is poorly known. Reproduction and recruitment processes are important elements in the life cycle of fish populations and have major influence on how fish stocks react to environmental and fishery exploitation (Cowan and Shaw, 2002).

Estimates of length and age at sexual maturity and information on proportion females are key parameters needed for the understanding of the population dynamics (ICES, 2007; Hilborn and Walters, 1992) as well as in the assessment of the anglerfish spawning stock size (ICES, 2009). Generally, males mature at a smaller length and age than females in the Northeast Atlantic (Woll *et al.*, 1995; Afonso-Dias and Hislop, 1996; Quincoces *et al.*, 1998; Duarte *et al.*, 2001; Thangstad *et al.*, 2006; Laurenson *et al.*, 2008; ICES, 2009), including Faroese waters (Ofstad and Laurenson, 2007). Any segregation of

the sexes by depth or area can also have important implications for exploitation effects. In the northern part of the distribution area, the sex ratio is equal for small fish (< 50 cm), males dominate in the length range from 60 to 70 cm, after which females take over and totally dominate at lengths greater than 100 cm (Thangstad *et al.*, 2006; Ofstad and Laurenson, 2007; Laurenson *et al.*, 2008; ICES, 2009), although spatial and temporal variation exists (Laurenson *et al.*, 2008; ICES, 2009).

The spawning season of anglerfish seems to extend from late winter to summer in the Northeastern Atlantic (Bowman, 1920; Joensen and Tåning, 1970; Afonso-Dias and Hislop, 1996; Quincoces *et al.*, 1998; Duarte *et al.*, 2001; Thangstad *et al.*, 2006; Laurenson *et al.*, 2008) and this is also the case in Faroese waters (Tåning, 1943; Ofstad and Laurenson, 2007). Little is known about potential spawning sites (Hislop *et al.*, 2001; ICES, 2007; Fariña *et al.*, 2008). The old hypothesis that anglerfish spawn in deep water (Fulton, 1903; Bowman, 1920) has not been confirmed by observations. Tåning (1943) suggested, based on findings of small pelagic larvae/juveniles, that the area west of the Faroes and south to the Bay of Biscay, in depths of about 1000 m, may be an important spawning area for the anglerfish in Northern Atlantic. A particle-tracking model presented by Hislop *et al.* (2001) indicated that offspring of anglerfish spawning west of Scotland and Rockall (about 57°N 14°W), could be transported to Faroese waters as well as towards the northern North Sea, Norway and Iceland. More recent work also suggests that anglerfish are spawning in Faroese waters (Ofstad and Laurenson, 2007) in addition to local spawning sites in Icelandic waters (Solmundsson *et al.*, 2010) and Norwegian waters (Bjelland and Asplin, 2007).

Whereas the eggs of most other marine fish are dispersed individually, anglerfish eggs are spawned in a gelatinous and buoyant ribbon, which may be in excess of 10 m long and up to 1 m wide (Bowman, 1920). Such a ribbon may amount to up to half of the females" total weight and contain more than 1 million eggs (Russell, 1976). Fertilization is probably external and the eggs of *L. piscatorius* are supposed to be shed in a single batch (Afonso-Dias and Hislop, 1996; Murua and Saborido-Rey, 2003), which may lead to highly aggregated distribution of the eggs/larvae. Females with very large gelatinous gonads, which were close to spawning, have been observed in Faroese waters (Ofstad and Laurenson, 2007).

The newly hatched larvae measure about 0.45 cm in length and are still found within the gelatinous ribbon (Russell, 1976), and such larvae (length 0.7 cm) have also been observed in Faroese waters (Ofstad and Laurenson, 2007). The yolk is absorbed and the larvae begin feeding at lengths between 0.65–0.8 cm 8–15 days after hatching, depending on the temperature (Bowman 1920; Lebour, 1925). Individuals measuring between 0.6 and 11.2 cm in length have been recorded in Scottish waters and ageing of lapillus otoliths suggested that those were between 21 and 124 days old (Hislop *et al.*, 2001). Most larvae live pelagically at depths between 30–150 m (Tåning, 1943), and the

length of pelagic period could last up to 9 months (Bowen, 1920; Hislop *et al.*, 2001). Morphological transformation (metamorphosis) from larvae to juveniles occurs at 6–7 cm fish length when the elongate fins and body gradually assume the adult form (Joensen and Tåning, 1970), and this may last several weeks and even months (Bowen, 1920; Hislop *et al.*, 2001). The main changes during the transition to the adult form are increased breadth of the head, decreased size of the pelvic fins and increased length of the first fin ray (Bowen, 1920). Juveniles settle to the seabed during late summer/autumn (Joensen and Tåning, 1970; Hislop *et al.*, 2001). No particular nursery areas have been reported in the Northeast Atlantic, but Tåning (1943) noted that some juveniles grew up in the deeper part of Faroese fjords (< 80 m depth). More recent work suggests that juvenile anglerfish (< 50 cm in length) are abundant in near-shore areas (0–50 m depth) in Shetland waters (Laurenson *et al.*, 2008).

Several theories for how fish populations are maintained and structured have been put forward. The member-vagrant concept predicts that successful individuals of a population are retained in an area by current patterns and vagrants are transported out of the retention area (Iles and Sinclair, 1982). The retention area should contain spawning, nursery and feeding areas. In contrast, an alternative stock concept states that marine populations could be highly connected with large flows of individuals and genes between sub-populations of a larger population complex (Cowen *et al.,* 2000; Stephenson *et al.,* 2009).

Since knowledge about the life cycle of *L. piscatorius* in the Northeast Atlantic is rather scarce, new life history knowledge from Faroese waters represents a valuable input with regards to life history of anglerfish in the Northeast Atlantic. The aims of this study are to investigate: i) whether the length, weight and age at first maturity of males and females differ, ii) whether the proportion females changes with fish length, age or depth, iii) the season and area of spawning, iv) length at metamorphosis from larvae to juveniles and length at bottom settling, v) area distribution of pelagic larvae, pre-settled juveniles, and bottom settled juveniles 0 and 1 years old (nursery areas). It will be discussed whether these characteristics differ from other areas of the Northeast Atlantic and whether the assumptions of the member-vagrant theory hold true for anglerfish in Faroese water.

Material and methods

Data sources and recordings

Individual anglerfish were collected from several sources/surveys in Faroese waters (Table 1). Data on pre-settled *L. piscatorius* juveniles were obtained from the regular Faroese 0-group surveys (1983–2012) using pelagic trawl at depths between 20 and 40 m. The stations are above bottom depths shallower than 100 m, with a few deeper stations (Gaard and Reinert, 2002). The majority of the information about bottom-settled anglerfish originates from two dedicated anglerfish surveys in February 2002 and 2003, conducted with

Source	Year	Month	Depth (m)	Mesh size (mm)	Fish length (cm)	N
0-group survey	1983–2012	Jun, Jul	pelagic	5	0.7–12.5	82
Anglerfish survey	2002–2003	Feb	90–800	135	18–116	1321
Spring survey	2002–2011	Feb, Mar	80–650	40	18–122	303
Summer survey	2001–2011	Aug, Sep	60–650	40	11–133	1298
Blue ling survey	2002–2003	Apr	550–1000	100	33–142	445
Greenland halibut survey	2001–2011	May, Jun	180–550	135	28–129	91
Redfish survey	2002–2011	Sep, Oct	230–750	135	14–118	404
Other surveys	2001–2005	Jan, Apr, Oct, Nov	80–530	80, 135	14–119	219
Commercial trawl	2001–2002	Jan, Mar, Apr, Jun, Nov, Dec	120–380	120, 145	22–123	411
Commercial gillnet	2001–2006	Jun, Jul, Aug, Sep	180–210	300, 320	64–142	460

Table 1. Summary of sources of anglerfish samples in Faroese waters.
N – Number of fish examined.

a demersal trawl using a „tickler" chain, and covering the main fishing grounds on the Faroe Plateau and Faroe Bank. In addition, the two annual spring and summer groundfish surveys, targeting mainly cod, haddock and saithe in February/March and August/September cover the Faroe Plateau (Steingrund and Ofstad, 2010) and the Faroe Bank (Magnussen, 2002) and target some anglerfish, as well. Anglerfish caught in other surveys and from observation trips on commercial trawlers and gillnetters are also used (Table 1).

The following data were recorded for individual anglerfish: total fish length (cm), round and gutted weight (g), age, sex, maturity and gonad weight (g). Ageing *illicia* was done according to Ofstad *et al.* (2013a). Sex and maturity stage was determined by macroscopic examination of the gonad (Thangstad *et al.*, 2006). A five-stage maturity scale was used; (I) virgin/immature, (II) developing, (III) maturing, (IV) ripe or spawning and (V) spent or resting (Thangstad *et al.*, 2006) and maturity stage I and II were classified as immature and stage III, IV and V as mature.

Data analysis

Length, age, round and gutted weight at 50% maturity (L_{50}, A_{50}, W_{50}, GW_{50}) were estimated by fitting a sigmoid curve to the proportion of mature fish (maturity stages III, IV and V) by using logistic regression (Crawely, 2005; ICES, 2008). The logistic curve is given by the equation: $p(x) = \exp^{(a + bx)}/(1 + \exp^{(a + bx)})$

where p is the proportion of mature fish, x is length, age or body weight of the fish and a and b are the parameters of the model. Length, age, round and gutted weight at 50% maturity are estimated from

the two regression parameters by dividing them (-a/b).

The gonadosomatic index (I_G) was calculated as weight of gonad mass (g) divided with the gutted fish weight (g), multiplied with 100. The gonad width was measured as a cross section (mm) on the middle of the gonad and the gonad length was measured when the gonad was stretched (cm).

To investigate potential spawning and nursery area(s) in Faroese waters, positions of records of pre-settled anglerfish juveniles from the 0-group survey in June/July, and catches of juveniles < 40 cm length, mature females and males from bottom trawl surveys and commercial data were used. The nursery areas, as defined here, are those areas where bottom settled juveniles were distributed during their first and second year of life (0 and 1 group fish, < 40 cm in length).

Data on the sex distribution by size were either grouped by length (5-cm length intervals) or by age (1-year intervals). Potential differences in the proportion mature between males and females were investigated with the χ^2-test (working with all length/age intervals simultaneously). Potential differences in the proportion females were investigated by using the binomial distribution (comparing the number of males with females for each length/age interval separately, setting the expected probability for each to 0.5). To investigate whether the gonadosomatic indices differed between females and males the Student t-test (assuming equal variances) was used. The level of significance for all statistical tests (all two-tailed) was 5%.

Results

Maturation

Males matured at smaller length (L_{50} = 57.8 versus 83.6 cm, Fig. 2A) (χ^2 = 1488.5; df = 15; $p < 0.001$), round weight (W_{50} = 2.7 versus 8.5 kg) and younger age (A_{50} = 4.3 versus 7.3 years, Fig. 2B) (χ^2 = 904.2; df = 11; $p < 0.001$) than females (Table 2). The gutted weight at first maturity (GW_{50}) for females was almost three times higher than for males, 6.8 kg and 2.3 kg, respectively (Table 2). L_{50} and A_{50} for sexes combined were 68.8 cm and 5.9 years (Table 2).

As a measure of sexual maturity, the gonadosomatic index (I_G) increased at smaller lengths (50 versus 90 cm) and age (3 versus 9 years) for males than for females (Fig. 3). A similar pattern was shown for round- (2 versus 11 kg) and gutted (1.5 versus 8.5 kg) weight also. The maximum I_G for females (45.95) was more than nine times higher than the maximum I_G for males (4.91). Females with I_G values larger than 10 had a large, gelatinous gonad and the gonad widths were between 10–45 cm and gonad lengths between 5–11 m. During the spawning season in January–April, 8% (14 out of 181) of the mature females had I_G larger than 10, indicating pre-spawning individuals, whereas only 0.02% (four out of 250) were ripe, indicating spawning individuals, and 23% (41 out of 181) were spent.

Proportion females

Equal numbers of females and males were observed for fish smaller than about 55 cm (less than about 4 years), whereas

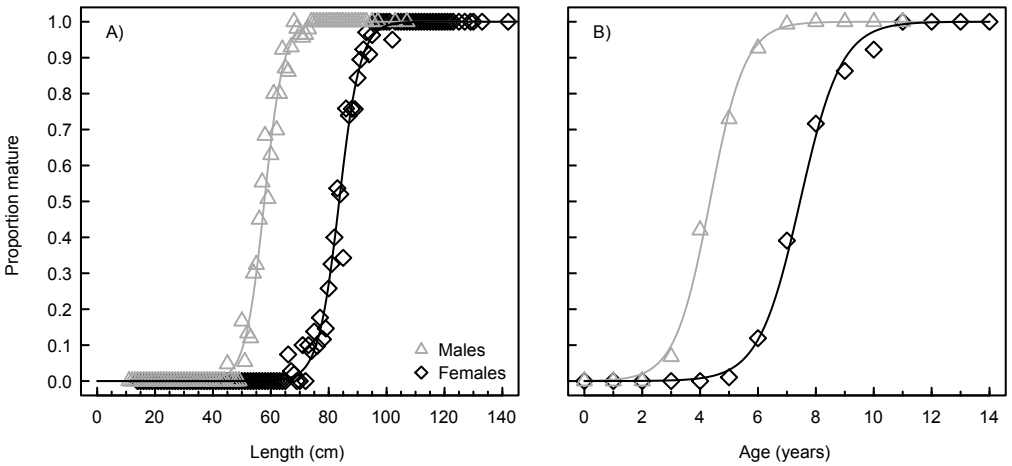

Fig. 2. Proportion mature for male and female anglerfish in Faroese waters by A) length and B) age. Sigmoid lines are the predictions of a logistic regression fitted to the data.

	Males		Females		Combined sexes	
Coefficient	Value	s.e.	Value	s.e.	Value	s.e.
a	-17.48	0.857	-22.96	1.159	-6.66	0.202
b	0.30	0.014	0.27	0.014	0.10	0.003
L_{50}	57.77		83.61		68.78	
N	2187		2479		4666	
a	-7.16	0.357	-10.45	0.492	-4.25	0.142
b	1.65	0.079	1.40	0.068	0.72	0.025
A_{50}	4.34		7.45		5.87	
N	1787		2074		3861	
a	-5.50	0.260	-7.41	0.339	-2.21	0.070
b	2.00	0.089	0.87	0.041	0.42	0.014
W_{50}	2.75		8.52		5.23	
N	2185		2475		4660	
a	-5.89	0.300	-8.19	0.435	-2.39	0.080
b	2.57	0.124	1.20	0.066	0.57	0.021
GW_{50}	2.29		6.80		4.21	
N	1876		2017		3893	

Table 2. Estimated logistic regression coefficients (a and b) and length (L_{50}), age (A_{50}), round weight (W_{50}) and gutted weight (GW_{50}) at 50% maturity of anglerfish in Faroese waters. N – Number of fish examined.

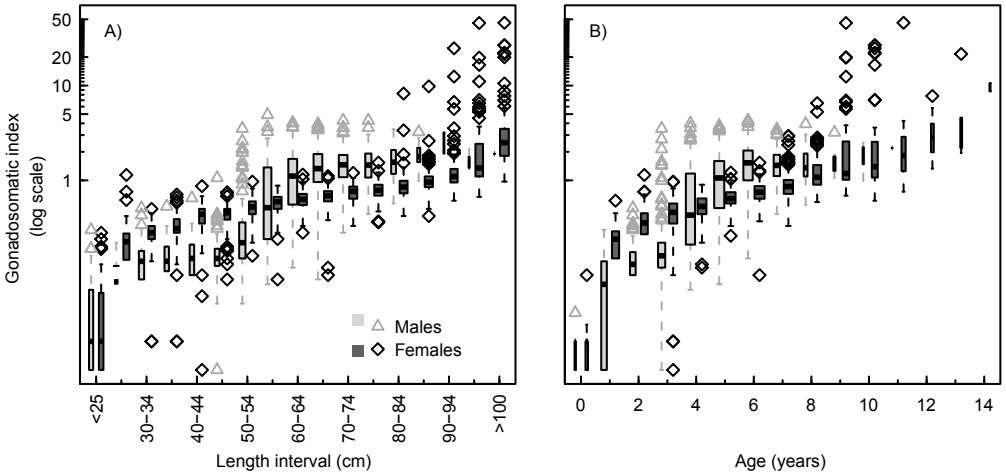

Fig. 3. Gonadosomatic index for male and female anglerfish in Faroese waters for A) length interval and B) age. The black line is the median, the box represents the upper and lower quartile, the error bars are upper and lower extremes (excluding outliers) and the triangle/diamonds are outliers. The outliers are defined as values 1.5 times larger than the inter-quartile range. The width of the box indicates the size sample (broader box indicate larger sample size). Note that the y-axis values are presented on a log scale.

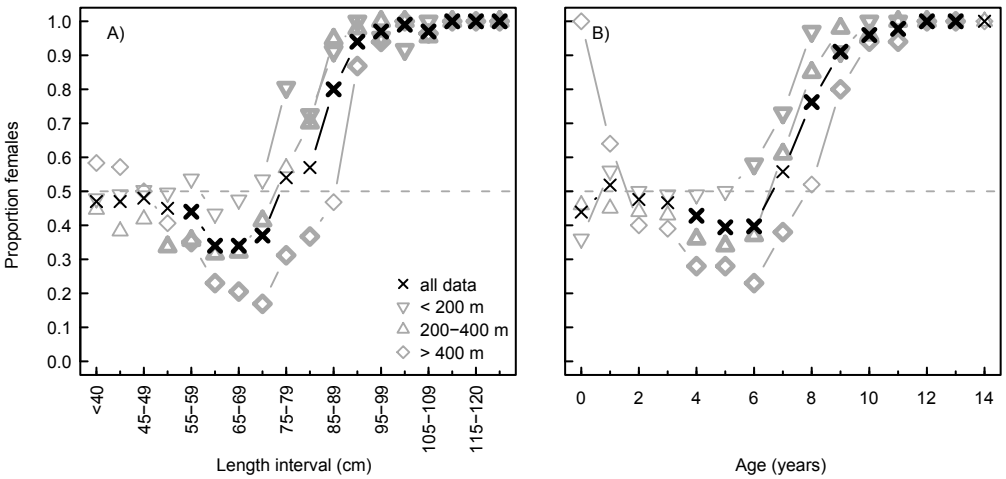

Fig. 4. Proportion female anglerfish caught by research and commercial trawl in Faroese waters for all data (black) and depths < 200 m, 200–400 m and > 400 m (grey) for A) length interval and B) age. Bold points represent proportions of females that are significantly different from 0.5 ($p < 0.05$) and the horizontal line show equal proportions of males and females.

	All data			Depth < 200 m			Depth 200–400 m			Depth > 400 m			Season May–Oct			Season Nov–Apr		
Length int.	F	M	*p*	F	M	*p*	F	M	*p*	F	M	*p*	F	M	*p*	F	M	*p*
<40	274	307	n.s.	144	157	n.s.	109	135	n.s.	21	15	n.s.	118	123	n.s.	156	184	n.s.
40–44	98	111	n.s.	76	79	n.s.	18	29	n.s.	4	3	n.s.	45	47	n.s.	53	64	n.s.
45–49	117	125	n.s.	89	88	n.s.	23	32	n.s.	5	5	n.s.	52	65	n.s.	65	60	n.s.
50–54	148	184	n.s.	106	108	n.s.	29	57	**	13	19	n.s.	76	82	n.s.	72	102	*
55–59	210	263	*	125	108	n.s.	58	105	***	27	50	*	98	101	n.s.	112	162	**
60–64	175	334	***	88	115	n.s.	61	132	***	26	87	***	76	140	***	99	194	***
65–69	171	328	***	75	83	n.s.	72	152	***	24	93	***	83	115	*	88	213	***
70–74	157	273	***	55	48	n.s.	79	112	*	23	113	***	74	103	*	83	170	***
75–79	162	140	n.s.	62	15	***	66	50	n.s.	34	75	***	68	43	*	94	97	n.s.
80–84	112	84	n.s.	29	11	**	54	23	***	29	50	*	47	38	n.s.	65	46	n.s.
85–89	126	32	***	31	3	***	73	4	***	22	25	n.s.	57	9	***	69	23	***
90–94	103	6	***	25	0	***	45	1	***	33	5	***	49	0	***	54	6	***
95–99	106	3	***	20	1	***	55	0	***	31	2	***	49	1	***	57	2	***
100–104	76	1	***	11	1	**	39	0	***	26	0	***	42	1	***	34	0	***
105–109	58	2	***	10	0	**	21	1	***	27	1	***	37	1	***	21	1	***
110–114	34	0	***	5	0	n.s.	17	0	***	12	0	***	17	0	***	17	0	***
115–120	19	0	***	2	0	n.s.	4	0	n.s.	13	0	***	6	0	*	13	0	***
>120	13	0	***	1	0	n.s.	6	0	*	6	0	*	8	0	**	5	0	n.s.
Total	2159	2193	n.s.	954	817	**	829	833	n.s.	376	543	***	1002	869	**	1157	1324	***

Table 3. Number of females (F) and males (M) of anglerfish in Faroese waters as well as ***p***-values associated with equal numbers of females and males (binominal distribution, two-tailed test) in each length interval. n.s. – $p > 0.05$ (non-significant), * – $p < 0.05$, ** – $p < 0.01$, *** – $p < 0.001$.

males were significantly more frequently observed at medium lengths (55–75 cm, 4–6 years) and thereafter females dominated among the larger and older specimens (> 85 cm, > 8 years) (Fig. 4, Table 3). Using round- or gutted weight gave the same impression. No males longer than 107 cm and females longer than 142 cm were recorded (Table 3). Males were found in the deep water (200–400 m, and > 400 m, during November to April) already as medium-sized fish whereas females required a much larger size (Table 3, 4).

Spawning season and spawning area

Males with large gonads, i.e., presumed to be close to spawning ($I_G > 3$), were most frequently observed during December–April (Fig. 5), although some ripe and spawning individuals were observed year round. Females close to spawning ($I_G > 10$) were confined to a slightly shorter season

	All data			Depth < 200 m			Depth 200–400 m			Depth > 400 m			Season May–Oct			Season Nov–Apr		
Age groups	F	M	*p*	F	M	*p*	F	M	*p*	F	M	*p*	F	M	*p*	F	M	*p*
0	13	8	n.s.	6	5	n.s.	4	3	n.s.	3	0	n.s.	8	7	n.s.	5	1	n.s.
1	104	107	n.s.	51	49	n.s.	39	50	n.s.	14	8	n.s.	60	64	n.s.	44	43	n.s.
2	119	131	n.s.	76	76	n.s.	39	49	n.s.	4	6	n.s.	64	65	n.s.	55	66	n.s.
3	195	223	n.s.	145	153	n.s.	38	51	n.s.	12	19	n.s.	104	101	n.s.	91	122	*
4	280	374	***	193	199	n.s.	61	108	***	26	67	***	123	167	*	157	207	*
5	268	412	***	145	147	n.s.	88	173	***	35	92	***	125	169	*	143	243	***
6	222	336	***	97	70	*	91	153	***	34	113	***	102	115	n.s.	120	221	***
7	177	143	n.s.	57	21	***	80	51	*	40	71	**	74	41	**	103	102	n.s.
8	139	43	***	35	1	***	72	13	***	32	29	n.s.	57	4	***	82	39	***
9	108	11	***	21	2	***	58	1	***	29	8	***	52	1	***	56	10	***
10	97	4	***	15	0	***	49	2	***	33	2	***	39	0	***	58	4	***
11	44	1	***	6	0	*	21	0	***	17	1	***	13	0	***	31	1	***
12	24	0	***	3	0	n.s.	10	0	**	11	0	***	6	0	*	18	0	***
13	10	0	**	2	0	n.s.	2	0	n.s.	6	0	*	3	0	n.s.	7	0	*
14	2	0	n.s.	0	0		1	0	n.s.	1	0	n.s.	0	0		2	0	n.s.
Total	1802	1793	n.s.	852	723	**	653	654	n.s.	297	416	***	830	734	*	972	1059	n.s.

Table 4. Number of females (F) and males (M) of anglerfish in Faroese waters as well as ***p***-values associated with equal numbers of females and males (binominal distribution, two-tailed test) in each age group. n.s. – $p > 0.05$ (non-significant), * – $p < 0.05$, ** – $p < 0.01$, *** – $p < 0.001$.

during January–April, although little data was available for May and July.

Based on geographical distributions of mature fish (males > 65 cm, females > 95 cm) and fish with high gonadosomatic index in January–April, two potential spawning sites were identified, one area southwest of the Faroe Plateau, „Skeivibanki" with bottom depth of about 200–400 m, and another area on the western slope of the Faroe bank (depth about 200–800 m) (Fig. 6). Only one spawning female was caught in an area north of the Faroes (Fig. 6B), but no males because the samples was from gillnet (300 mm mesh size).

Early life history

In the Faroese 0-group survey conducted annually in June and July, covering the Faroe Plateau and occasionally the Faroe Bank with pelagic hauls at 20–45 m water depth, one gelatinous ribbon has been caught on the Faroe Bank area in 2003 and it contained more than 2000 yolk-sack larvae with lengths of about 0.7 cm. In the same survey, other 82 pre-settled pelagic anglerfish larvae and juveniles, 3 to 12 cm

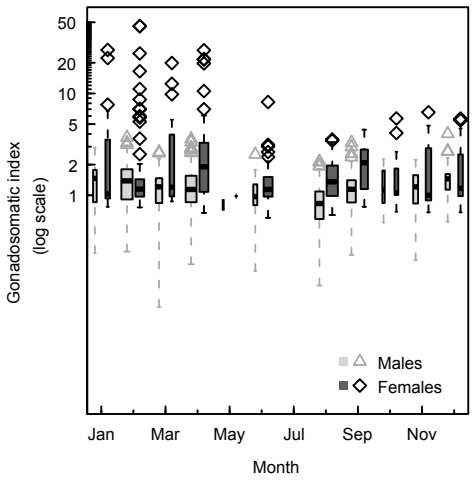

Fig. 5. Gonadosomatic index for each month for mature anglerfish in Faroese waters for males and females. The black line is the median, the box represents the upper and lower quartile, the error bars are upper and lower extremes (excluding outliers) and the triangles/diamonds are outliers. The outliers are defined as values 1.5 times larger than the inter-quartile range. The width of the box indicates the size sample (broader box indicate larger sample size). Note that the y-axis values are presented on a log scale.

long (Fig. 7), were mainly caught on the Faroe Bank and only 7 were caught in the area west of the Faroe Islands. The bottom depth was between 94 and 500 m (Fig. 8A). The morphological transformation from larvae to juveniles occurs at lengths between 7 and 9 cm (Fig. 7). The largest anglerfish caught in the pelagic 0-group survey (mesh size 5 mm) was 11.6 cm long while the smallest juvenile caught in the annual bottom trawl groundfish survey (mesh size 40 mm) was 11.4 cm in length, indicating that anglerfish juveniles in Faroese waters have settled to the bottom when they are about 11 cm long. Juvenile anglerfish, with lengths less than 35 cm (< 2 years old), caught in the annual groundfish surveys in August were distributed scattered on the Faroe Plateau, but were quite rare on the Faroe Bank (Fig. 8B).

Discussion

Anglerfish seem to have a closed life cycle in Faroese waters as there are findings of egg-ribbon, pelagic larvae, juveniles, mature, ripe and spent fish, nursery areas and spawning areas in these waters.

In Faroese waters male anglerfish mature at a smaller size than females and there was also a skewed sex ratio where males dominated at intermediate size and females dominated at larger size, which corresponds well to reports from other areas of the Northeast Atlantic (Woll *et al.*, 1995; Afonso-Dias and Hislop, 1996; Quincoces *et al.*, 1998; Duarte *et al.*, 2001; Thangstad *et al.*, 2006; Laurenson *et al.*, 2008; ICES, 2009). The spawning season in Faroese waters lasts for several months with a peak in February to April, which is also found in other areas (Woll *et al.*, 1995; Afonso-Dias and Hislop, 1996; Quincoces *et al.*, 1998; Duarte *et al.*, 2001; Thangstad *et al.*, 2006; Laurenson *et al.*, 2008; ICES, 2009).

Based on maturity stages, male anglerfish matured at shorter length, earlier age and lesser weight than females in Faroese waters, and this finding is supported by the gonadosomatic index (I_G), where the gonads are weighted and not only inspected visually. For males the transition from immature to mature individuals occurred at a length (L_{50}) of around 58 cm whereas the

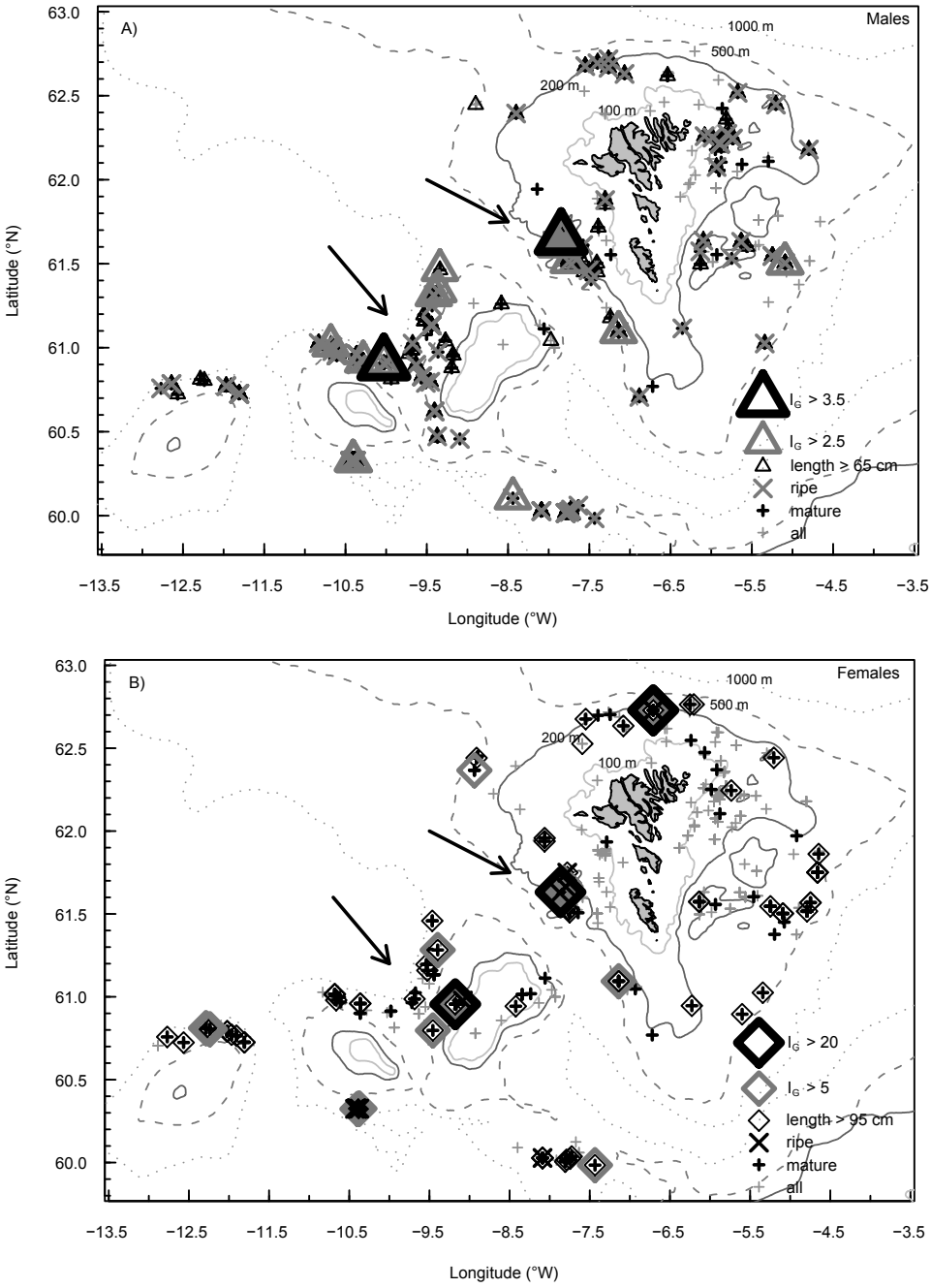

Fig. 6. Possible spawning areas (indicated with an arrow) of anglerfish in Faroese waters from data on gonadosomatic index (I_G), length and maturity stage in January to April for A) males and B) females.

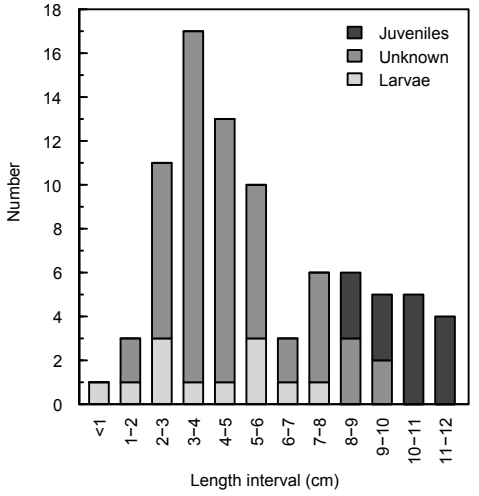

Fig. 7. Length distribution of pre-settled anglerfish larvae/juveniles caught in the Faroese 0-group survey, using pelagic trawl, in June/July 1983–2012 (N = 84). The data indicate at which length the larvae transform to juveniles.

I_G started to increase at comparable lengths of 50–55 cm. For females, however, the L_{50} of 84 cm was shorter than the length of 90–95 cm, at which the I_G increased and the large gonad widths were observed. This discrepancy could be caused by the method by which the maturity stages were classified, i.e., the inclusion of numerous early stage maturing females into the maturity stage III. Maturity stage III is including individuals having gonads with barely visible oocyte clusters as well as individuals with large gonads and egg clusters embedded in a gelatinous matrix (Thangstad *et al.*, 2006). The maturity ogive values in this study (58 cm, 4 years for males and 84 cm, 7 years for females) are within the range observed in other areas in the Northeastern Atlantic (49–58 cm, 4–6 years for males and 73–98 cm, 7–14 years for females) (Afonso-Dias and Hislop, 1996; Quincoces *et al.*, 1998; Duarte *et al.*, 2001; Laurenson *et al.*, 2008). The larger range in maturity ogive values for females

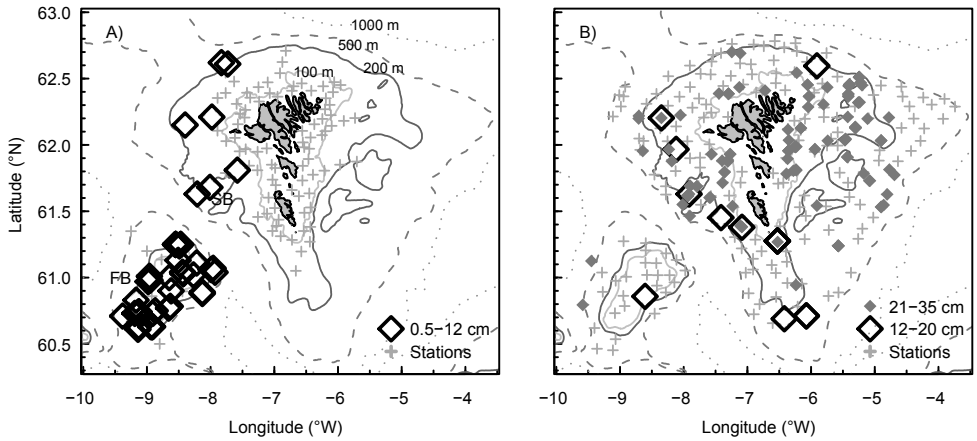

Fig. 8. A) Anglerfish larvae/juveniles (N=48) caught in the pelagic annual 0-group survey in Faroese waters (1997–2012). B) Small anglerfish (< 2 years old) caught in the Faroese annual summer groundfish survey (2000–2011). Crosses indicate the standard trawl stations, FB- Faroe Bank and SB- Skeivibanki. It has to be noted that the Faroe Bank is not surveyed each year.

can partly be due to the low numbers of mature females recorded in some of these studies (Duarte *et al.*, 2001; Laurenson *et al.*, 2008) or because of subjectivities in using the maturity scales (Thangstad *et al.*, 2006; ICES, 2007) or, thirdly, that there are differences between populations (Iles and Sinclair, 1982). Problems in the anglerfish ageing (Landa *et al.*, 2008) can account for some of the differences in A_{50} values found in these studies (Woll *et al.*, 1995; Afonso-Dias and Hislop, 1996; Quincoces *et al.*, 1998; Duarte *et al.*, 2001; Laurenson *et al.*, 2008; ICES, 2009). The definitions of immature and mature anglerfish (Thangstad *et al.*, 2006) used in this study resemble those used in Afonso-Dias and Hislop (1996) and in ICES (2007), so the results should be directly comparable. For assessment purposes, it should be considered to use the proportion of maturity of females at age (ICES, 2009) as the females mature at an older age than males and a use of combined maturation ogive could possibly give a too high spawning stock.

One reason for the skewed sex ratio for lengths above 55 cm could be that male growth slows down after maturation is reached, causing an accumulation of males in these length groups before females outnumber them at the largest sizes as they outgrow and outlive males (Duarte *et al.*, 2001; Ofstad *et al.*, 2013a). Another reason could be behavioural differences such as sex-specific movement pattern as suggested for *L. americanus* (Richards *et al.*, 2008). Since males mature at a smaller size than females and there probably is a spawning migration to deeper waters in winter (Laurenson *et al.*, 2005; Ofstad *et al., 2013, in prep.*), the mature males probably migrate deeper at a smaller length and age than females. The very low proportion of males among old fish also suggests a higher mortality among males after maturation.

This study indicates that anglerfish in Faroese waters have a prolonged spawning season that lasts from January to July, with a main season from February to April. There is also a prolonged spawning period in the other areas of the Northeastern Atlantic and the timing is mainly from January to June (Bowman, 1920; Joensen and Tåning, 1970; Woll *et al.*, 1995; Afonso-Dias and Hislop, 1996; Quincoces *et al.*, 1998; Duarte *et al.*, 2001; Laurenson, 2003; Thangstad *et al.*, 2006; Laurenson *et al.*, 2008). Observations of floating *Lophius* sp. egg-ribbons at the surface in July 2001 on the Faroe Bank area (B. Mikkelsen, pers. comm., Faroese Museum of Natural History) as well as in March 2002 (R. Mouritsen pers.comm., Faroe Marine Research Institute) combined with the findings of pre-settled anglerfish larvae and juveniles on the Faroe Bank and the Faroe Plateau in June and July suggest that these individuals could probably have been spawned in Faroese waters a week to four months before, according to the daily growth rates suggested by Hislop *et al.*, 2001. There are also findings of egg ribbons in Scottish waters in February–June (Bowman, 1920) and to the west and southwest of the British Isles in March–June (Tåning, 1943). Egg-ribbons have been observed later in April–June in Norwegian coast waters between 59°N and 65°N (Thangstad *et al.*, 2006) and as late as in August–Septem-

ber in Icelandic waters (Thangstad *et al.*, 2006).

There are strong indications of at least two local spawning areas in Faroese waters where one is located in an area southwest on the Faroe Plateau at about 300–400 m depth and another one in the bank areas further southwest from the Faroe Islands at 300 m depth and deeper. The function of the first area as a spawning site is supported by results from data storage tags that showed that fish longer than 70 cm performed a winter migration to mainly depths between 300–400 m (Ofstad *et al., 2013, in prep.*). The latter is supported by the findings of Joensen and Tåning (1970), which suggested that the main spawning ground of anglerfish is located southwest and south of the Faroes and along the European coasts around the 1000 m contour line, as well as oceanic. The shallower spawning area on the Faroe Plateau (300–400 m) compared to the Faroe Bank (300–900 m) and the areas further south (about 1000 m) can be explained by that anglerfish seem to have a temperature preference of water masses warmer than 4oC (Solmundsson *et al.* 2010; Ofstad *et al., 2013, in prep.*). The cold overflow water from the Nordic Seas is shallower around the Faroe Plateau than in the Bank area and further south (Hansen *et al.*, 1998; Fig. 1).

It is possible that there exist undiscovered spawning areas in Faroese waters. Only a small number of near spawning females were recorded, and this is similar to results from other studies in Northeastern Atlantic (Duarte *et al.*, 2001; Laurenson, 2003; Thangstad *et al.*, 2006). This apparent rarity of ripe females in the material may suggest that anglerfish perform spawning migrations to areas or depths not sampled in the present study (e.g., oceanic spawning as suggested by Joensen and Tåning, 1970) or alternatively, that the period of very high I_G in anglerfish females is very short or that females do not spawn every year (Staalesen, 1995). Conversely, spawning males have been observed year round (Laurenson *et al.*, 2008, this study), and these broad periods of gestation suggest either that spawning is non-synchronous or that gonad development in stage III (maturing) females lasts for a long time (Thangstad *et al.*, 2006) and that the period of very high I_G in anglerfish females is very short.

Anglerfish larvae in Faroese waters have a morphological transformation from larvae to juveniles in lengths between 7 and 9 cm, and this is similar to observations from other areas in the Northeast Atlantic (Bowman, 1920; Joensen and Tåning, 1970; Hislop *et al.*, 2001). The lengths of the shortest juvenile caught in bottom trawl (11.4 cm, mesh size 35 mm) and the longest pre-settled juvenile caught pelagic (11.6 cm, mesh size 5 mm) indicate that juveniles are settled to the bottom at a fish length about 11–12 cm, and this is similar to the findings in Scottish (Tåning, 1943) and Icelandic waters (Solmundsson *et al.*, 2010). The larvae were caught pelagic at depths between 20 and 45 m over bottom depths from about 100 m to > 2000 m in Icelandic, Faroese and International waters (Solmundsson *et al.*, 2010).

Findings of anglerfish larvae and pre-

settled juveniles on the Faroe Bank could be an example of larval retention area as the currents make a gyre around the bank (Hansen *et al.*, 1998). There are also indications of a gyre just east of the supposed spawning area on the plateau (H. Hátun, pers. comm., Faroe Marine Research Institute) that could function as a retention area. That few pelagic larvae have been found in this area is probably due to little coverage in the 0-group survey for that particular area or, perhaps, earlier spawning time so the individuals have already settled. The larval-retention / member-vagrant hypothesis states that specimens in a stock tend to spawn at specific times and places within predictable and distinct circulation features which enhances the retention time by limiting dispersal of passive eggs and weakly swimming larvae until they are able to control their own distribution, thus defining the geographical limits of the breeding grounds of the stock (Iles and Sinclair, 1982). Gyres are not impermeable and do not have 100% retention of fish larvae as shown for haddock larvae hatched on Brown's Bank, off Nova Scotia (Campana *et al.*, 1989). So, some larvae spawned in Faroese waters (vagrants) could drift to Iceland, North Sea and Norway. Also, some larvae may drift to Faroese waters from other potential spawning areas (Hislop *et al.*, 2001). A potential, although very limited, immigration of larvae and pelagic juveniles to Faroese waters is not a major problem with regards to (an age-disaggregated) stock assessment, as it occurs before the fish enter the fishery.

The distribution of juveniles smaller than 35 cm, as observed in the groundfish surveys, could indicate a nursery area on the Faroe Plateau, on depths from 80–400 m. The shallow water from shore to about 100 m may also function as a nursery area in Faroese waters, as for cod (*Gadus morhua*) and saithe (*Pollachius virens*) (Steingrund *et al.*, 2010; Homrum *et al.*, 2012), but there are no direct surveys of fish in those areas to explore this. Small anglerfish are frequently observed by scuba-divers in depths shallower than twenty meters in summer and autumn (pers. obs.; B. Mikkelsen pers. comm., Faroese Museum of Natural History; B. Geyti pers. comm., Faroese Aquarium), which shows that these shallow areas are inhabited by small anglerfish. In Shetland the length frequency distribution in depths 0–50 m indicate an aggregation of juvenile anglerfish smaller than 50 cm in length (Laurenson *et al.*, 2008), and that could possibly be the case on the Faroe Plateau as well. In Tåning (1943) it is stated that juveniles grow up in the deeper part of Faroese fjords, which are about 75–85 m in depth. The reason for infrequent findings of juveniles on the Faroe Bank could be because they are outside the sampled area. There are *Lophelia* reefs in deeper waters at the Faroe Bank slope where the juveniles could seek protection and food (Thomsen, 2005).

The findings of larvae retention areas, spawning areas and all stages in the life cycle on the Faroe Plateau area and in the Faroe Bank area indicate the possibility of two distinct anglerfish stocks in Faroese waters, as for cod (ICES, 2012). However, there is far from enough data to draw any

conclusion of this and further studies are needed. Although, the fact that all stages in the life cycle of anglerfish are found in Faroese waters, the area contain spawning area, nursery area (this study) and a migration between spawning and feeding area on the Faroe Plateau (Ofstad *et al., 2013b, in prep.*) indicates that there is a Faroese population of anglerfish and that the life cycle seems to be in agreement with predictions made by the member-vagrant concept. Thus, anglerfish in Faroese waters may be regarded as a separate stock. Recent tagging studies have demonstrated some migration between Shetland, Faroe Islands, Iceland and Norway of both immature and mature anglerfish (Laurenson *et al.*, 2005; Thangstad *et al.*, 2006; Laurenson *unpub. data*; Bjelland *unpub. data*; Ofstad *et al., 2013b, in prep.*), but probably less than 5 % of the recaptures are taken in other regions. No genetic differences have so far been detected between anglerfish in the Nordic areas (O'Sullivan *et al.*, 2005), which could be taken as an indication of a high degree of exchange of genetic material between anglerfish in the Northeast Atlantic. In the future, more knowledge on the exchange rates of early life stages of anglerfish between regions in the Northeast Atlantic should be acquired. Also a closer investigation of anglerfish in the area from shore to about 100 m depth should be acquired.

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