**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 (L50) 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 (L50) 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 (55­70 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 Føroya­ banka. Landgrunnurin er helst uppvakstrarøki fyri havtaskuyngul. Umskapanin frá yngli til ungfisk hendir tá havtaskan er 7­9 cm long, og hon tekur botn, tá hon er um 11 cm. Saman­

umtikið hevur man í føroyskum sjógvi øll

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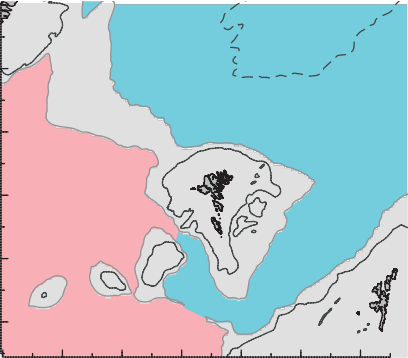
menningarstigini hjá havtasku, umframt at man hevur funnið uppvakstrarøki, gýtingarøki og føðiøki; hetta bendir á, at havtaskan í før­ oyskum sjógvi er ein egin fiskastovnur.

**Introduction**

Two anglerfish species, *Lophius piscatorius* and *Lophius budegassa*, are distributed in the Northeast Atlantic (Caruso, 1983), al­ though 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 en­ vironment is productive with the warm North Atlantic Current in the upper layer (< 500 m depth) and the cold overflow

65



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 reten­ tion area, that keeps fish eggs/larvae on the shelf (Gaard and Steingrund, 2001).

Anglerfish in Faroese waters have during the last decade become a highly exploited and economically important re­ source 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 cur­ rently regarded as a separate stock by ICES (ICES, 2009), although the stock structure of anglerfish in the Northeast Atlantic is

Iceland

64

63

Latitude (ºN)

62

North Atlantic

61

60

Norwegian Sea

3000 m

2000 m

1000 m

Faroe Plateau 500 m

200 m

Faroe Bank

Shetland

poorly known. Reproduction and recruit­

ment 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 propor­ tion females are key parameters needed for the understanding of the population

−14 −12 −10 −8 −6 −4 −2

Longitude (ºW)

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 (< 0ºC) 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 0ºC, while the red area deeper than 800 m in the North Atlantic is usually warmer than 6ºC, except the areas where there is a cold overflow from the Norwegian Sea. Grey bold line: 200 nm exclusive economic zone.

dynamics (ICES, 2007; Hilborn and Wal­ ters, 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; Afonso­Dias 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 ef­ fects. In the northern part of the distribu­ tion 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), al­ though spatial and temporal variation ex­ ists (Laurenson *et al.*, 2008; ICES, 2009).

The spawning season of anglerfish seems to extend from late winter to sum­ mer in the Northeastern Atlantic (Bow­ man, 1920; Joensen and Tåning, 1970; Afonso­Dias 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 (Tån­ ing, 1943; Ofstad and Laurenson, 2007). Little is known about potential spawn­ ing sites (Hislop *et al.*, 2001; ICES, 2007; Fariña *et al.*, 2008). The old hypothesis that anglerfish spawn in deep water (Ful­ ton, 1903; Bowman, 1920) has not been confirmed by observations. Tåning (1943) suggested, based on findings of small pe­ lagic 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 im­ portant spawning area for the anglerfish in Northern Atlantic. A particle­tracking 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 an­

glerfish are spawning in Faroese waters (Ofstad and Laurenson, 2007) in addition to local spawning sites in Icelandic waters (Solmundsson *et al.*, 2010) and Norwe­ gian waters (Bjelland and Asplin, 2007).

Whereas the eggs of most other marine fish are dispersed individually, angler­ fish eggs are spawned in a gelatinous and buoyant ribbon, which may be in excess of 10 m long and up to 1 m wide (Bow­ man, 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 (Afonso­Dias and Hislop, 1996; Murua and Saborido­ Rey, 2003), which may lead to highly ag­ gregated distribution of the eggs/larvae. Females with very large gelatinous go­ nads, 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 tem­ perature (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 oto­ liths suggested that those were between

21 and 124 days old (Hislop *et al.*, 2001). Most larvae live pelagically at depths be­ tween 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 (metamor­ phosis) 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 sea­ bed during late summer/autumn (Joensen and Tåning, 1970; Hislop *et al.*, 2001). No particular nursery areas have been report­ ed 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 near­shore areas (0–50 m depth) in Shetland waters (Laurenson *et al.*, 2008).

Several theories for how fish popu­ lations are maintained and structured have been put forward. The member­vagrant concept predicts that successful individu­ als of a population are retained in an area by current patterns and vagrants are trans­ ported out of the retention area (Iles and Sinclair, 1982). The retention area should contain spawning, nursery and feeding are­ as. In contrast, an alternative stock concept states that marine populations could be highly connected with large flows of indi­ viduals and genes between sub­populations 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 angler­ fish 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 metamor­ phosis from larvae to juveniles and length at bottom settling, v) area distribution of pelagic larvae, pre­settled 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 pre­settled *L. piscatorius* juveniles were obtained from the regu­ lar Faroese 0­group surveys (1983–2012) using pelagic trawl at depths between 20 and 40 m. The stations are above bot­ tom depths shallower than 100 m, with a few deeper stations (Gaard and Reinert,

2002). The majority of the information about bottom­settled anglerfish originates from two dedicated anglerfish surveys in February 2002 and 2003, conducted with

Source Year Month Depth (m) Mesh size

(mm)

Fish N

length

(cm)

0­group 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 ad­ dition, 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. An­ glerfish 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). Age­ ing *illicia* was done according to Ofstad *et al.* (2013a). Sex and maturity stage was de­ termined 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 ma­ turity stage I and II were classified as im­ mature and stage III, IV and V as mature.

***Data analysis***

Length, age, round and gutted weight at

50% maturity (L50, A50, W50, GW50) 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, posi­ tions of records of pre­settled anglerfish juveniles from the 0­group 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 de­ fined 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 (5­cm length intervals) or by age (1­year intervals). Po­ tential differences in the proportion mature between males and females were investigat­ ed with the χ2­test (working with all length/ age intervals simultaneously). Potential differences in the proportion females were investigated by using the binomial distri­ bution (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 t­test (as­ suming equal variances) was used. The level of significance for all statistical tests (all two­tailed) was 5%.

**Results**

***Maturation***

Males matured at smaller length (L50 =

57.8 versus 83.6 cm, Fig. 2A) (χ2 = 1488.5;

df = 15; p < 0.001), round weight (W50 =

2.7 versus 8.5 kg) and younger age (A50 =

4.3 versus 7.3 years, Fig. 2B) (χ2 = 904.2;

df = 11; p < 0.001) than females (Table 2). The gutted weight at first maturity (GW50) for females was almost three times higher

than for males, 6.8 kg and 2.3 kg, respec­ tively (Table 2). L50 and A50 for sexes com­ bined 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* for males (4.91). Females with *I* values larger than 10 had a large, gelatinous go­ nad and the gonad widths were between

G G

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, indi­

cating pre­spawning 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

1.0

0.9

A) B)

0.8

0.7

Proportion mature

0.6

0.5

0.4

0.3

0.2

0.1

0.0

Males

Females

0 20 40 60 80 100 120 140

Length (cm)

0 2 4 6 8 10 12 14

Age (years)

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

L50 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

A50 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

W50 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

GW50 2.29 6.80 4.21

N 1876 2017 3893

Table 2. Estimated logistic regression coefficients (a and b) and length (L50), age (A50), round weight (W50) and gutted weight (GW50) at 50% maturity of anglerfish in Faroese waters. N – Number of fish examined.

50 A) B)

20

10

5

Gonadosomatic index

(log scale)

1

Males

Females

0 2 4 6 8 10 12 14

<25

30−34

40−44

50−54

60−64

70−74

80−84

90−94

>100

Length interval (cm)

Age (years)

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.

1.0

0.9

0.8

0.7

Proportion females

0.6

0.5

0.4

0.3

0.2

0.1

0.0

A) B)

all data

< 200 m

200−400 m

> 400 m

0 2 4 6 8 10 12 14

<40

45−49

55−59

65−69

75−79

85−89

95−99

105−109

115−120

Length interval (cm)

Age (years)

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.

Length

All data Depth < 200 m

Depth 200–400

m Depth > 400 m Season May–Oct Season Nov–Apr

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.

To tal 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 domi­ nated among the larger and older speci­ mens (> 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

medium­sized fish whereas females re­

quired 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

Age

All data Depth < 200 m

Depth 200–400

m Depth > 400 m

Season May–

Oct Season Nov–Apr

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.

To tal 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 gonadoso­ matic index in January–April, two po­ tential spawning sites were identified, one area southwest of the Faroe Pla­ teau, „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 gill­

net (300 mm mesh size).

***Early life history***

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

50 Fig. 5. Gonadosomatic index for each month for mature anglerfish in Faroese waters for males

20 and females. The black line is the median, the box

10 represents the upper and lower quartile, the error

5 bars are upper and lower extremes (excluding outliers) and the triangles/diamonds are outliers. The

Gonadosomatic index

(log scale)

2 outliers are defined as values 1.5 times larger than the

1 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.

Males

Females

Jan Mar May Jul Sep Nov

Month

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 0­group 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 ground­ fish 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 egg­ribbon, pelagic larvae, juveniles, ma­

ture, ripe and spent fish, nursery areas and spawning areas in these waters.

In Faroese waters male anglerfish ma­ ture 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; Afonso­Dias 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; Afonso­Dias and Hislop, 1996; Quincoces *et al.*, 1998; Duarte *et al.*, 2001; Thangstad *et al.*, 2006; Laurenson *et al.*, 2008; ICES,

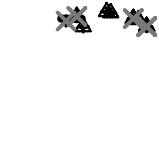
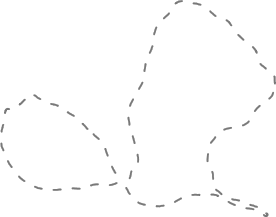
2009).

Based on maturity stages, male angler­ fish 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 go­

nads are weighted and not only inspected

visually. For males the transition from im­ mature to mature individuals occurred at a length (L50) of around 58 cm whereas the

63.0



A)

1000 m

500 m

Males

62.5

200 m

100 m

62.0

61.5

Latitude (°N)

61.0

IG > 3.5

60.5

60.0

IG > 2.5

length > 65 cm

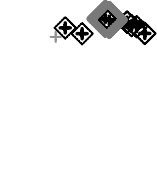
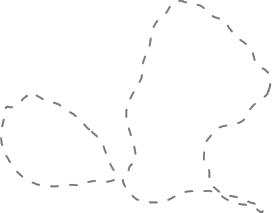
ripe

mature

all

−13.5 −12.5 −11.5 −10.5 −9.5 −8.5 −7.5 −6.5 −5.5 −4.5 −3.5

Longitude (°W)



63.0

B)

1000 m

500 m

Females

62.5

200 m

100 m

62.0

61.5

Latitude (°N)

61.0

60.5

60.0

IG > 20

IG > 5

length > 95 cm

ripe

mature

all

−13.5 −12.5 −11.5 −10.5 −9.5 −8.5 −7.5 −6.5 −5.5 −4.5 −3.5

Longitude (°W)

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.

18

Juveniles

16 Unknown

Larvae

14

12

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.

10

Number

8

6

4

2

0

<1

1−2

2−3

3−4

4−5

5−6

6−7

7−8

8−9

9−10

10−11

11−12

Length interval (cm)

G started to increase at comparable lengths of 50–55 cm. For females, however, the L50 of 84 cm was shorter than the length of

*I*

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

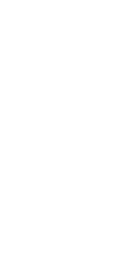
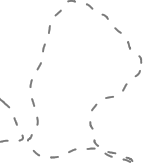
classified, i.e., the inclusion of numerous early stage maturing females into the ma­ turity stage III. Maturity stage III is includ­ ing individuals having gonads with barely visible oocyte clusters as well as individu­ als with large gonads and egg clusters em­ bedded in a gelatinous matrix (Thangstad *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) (Afonso­Dias and Hislop,

1996; Quincoces *et al.*, 1998; Duarte *et al.*,

2001; Laurenson *et al.*, 2008). The larger range in maturity ogive values for females

63.0

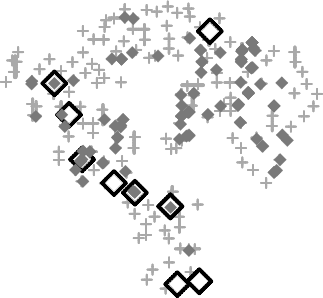
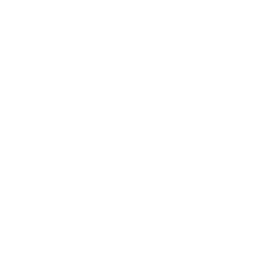
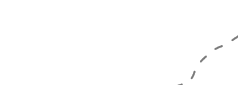
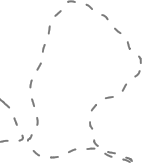


A)

62.5

100 m

1000 m B)



500 m

200 m

62.0

Latitude (°N)

SB

61.5

61.0 FB

60.5

0.5−12 cm

Stations

21−35 cm

12−20 cm

Stations

−10 −9 −8 −7 −6 −5 −4

Longitude (°W)

−10 −9 −8 −7 −6 −5 −4

Longitude (°W)

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 us­ ing 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 A50 values

found in these studies (Woll *et al.*, 1995;

Afonso­Dias and Hislop, 1996; Quincoces *et al.*, 1998; Duarte *et al.*, 2001; Lauren­ son *et al.*, 2008; ICES, 2009). The defini­ tions of immature and mature anglerfish (Thangstad *et al.*, 2006) used in this study resemble those used in Afonso­Dias and Hislop (1996) and in ICES (2007), so the results should be directly comparable. For assessment purposes, it should be consid­ ered 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 matura­ tion is reached, causing an accumulation of males in these length groups before fe­ males 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 sex­specific 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 prob­ ably migrate deeper at a smaller length and age than females. The very low pro­ portion of males among old fish also sug­ gests 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 At­ lantic and the timing is mainly from Janu­ ary 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. egg­ribbons at the surface in July 2001 on the Faroe Bank area (B. Mikkelsen, pers. comm., Faroese Museum of Natural His­ tory) as well as in March 2002 (R. Mour­ itsen pers.comm., Faroe Marine Research Institute) combined with the findings of pre­settled anglerfish larvae and juveniles on the Faroe Bank and the Faroe Plateau in June and July suggest that these individ­ uals 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 Brit­ ish Isles in March–June (Tåning, 1943). Egg­ribbons have been observed later in April–June in Norwegian coast waters be­ tween 59oN and 65oN (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 sup­ ported 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 south­ west and south of the Faroes and along the European coasts around the 1000 m contour line, as well as oceanic. The shal­ lower 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 undis­ covered spawning areas in Faroese waters. Only a small number of near spawning fe­ males 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 ap­

parent rarity of ripe females in the mate­ rial 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 sug­ gest either that spawning is non­synchro­ nous or that gonad development in stage III (maturing) females lasts for a long time (Thangstad *et al.*, 2006) and that the pe­ riod 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 be­ tween 7 and 9 cm, and this is similar to ob­ servations from other areas in the North­ east 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 pre­settled juvenile caught pelagic (11.6 cm, mesh size 5 mm) indi­ cate that juveniles are settled to the bot­ tom at a fish length about 11–12 cm, and this is similar to the findings in Scottish (Tåning, 1943) and Icelandic waters (Sol­ mundsson *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 indi­ cations of a gyre just east of the supposed spawning area on the plateau (H. Hátun, pers. comm., Faroe Marine Research In­ stitute) that could function as a retention area. That few pelagic larvae have been found in this area is probably due to lit­ tle coverage in the 0­group survey for that particular area or, perhaps, earlier spawn­ ing time so the individuals have already settled. The larval­retention / 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 geographi­ cal 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 had­ dock 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 poten­ tial spawning areas (Hislop *et al.*, 2001). A potential, although very limited, immigra­ tion of larvae and pelagic juveniles to Far­ oese waters is not a major problem with regards to (an age­disaggregated) stock as­ sessment, 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 scu­ ba­divers in depths shallower than twenty meters in summer and autumn (pers. obs.; B. Mikkelsen pers. comm., Faroese Mu­ seum 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 find­ ings 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 spawn­ ing area, nursery area (this study) and a migration between spawning and feed­ ing 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 member­vagrant concept. Thus, anglerfish in Faroese wa­ ters may be regarded as a separate stock. Recent tagging studies have demonstrated some migration between Shetland, Faroe Islands, Iceland and Norway of both im­ mature and mature anglerfish (Laurenson *et al.*, 2005; Thangstad *et al.*, 2006; Lau­ renson *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 materi­ al between anglerfish in the Northeast At­ lantic. In the future, more knowledge on the exchange rates of early life stages of an­ glerfish 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 ac­ quired.

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