UNIVERSITY OF TROMSØ UIT

FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS
DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

Anglerfish *Lophius piscatorius* L. in Faroese waters

Life history, ecological importance and stock status

Lise Helen Ofstad

A dissertation for the degree of
Philosophiae Doctor

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Lise Helen Ofstad

Abstract

Anglerfish *Lophius piscatorius* has during the last two decades become a highly exploited resource and is now one of the five most economically important demersal fish species in the Faroese fishery. Despite this, there is at present little information available on the population status of anglerfish in Faroese waters. The main aim of this study is to increase the biological knowledge of anglerfish and to perform an assessment of the stock in order to evaluate the sustainability of the anglerfish fishery and to investigate trophic interactions between anglerfish and other commercially important demersal fish species.

Anglerfish illicia, the first fin ray, were used for age reading. The age determinations were validated and concluded to be useful in an age-based assessment because the growth rates were consistent with length frequency and mark-recapture analyses. Anglerfish have a very high growth rate during their first year of life, compared with the older ages. Males mature at a lower length and younger age than females. The L_{50} for males and females was 58 cm and 84 cm, respectively, corresponding to an age of around four years for males and seven years for females. Observations of spawning males and females, egg-ribbons and pelagic anglerfish larvae revealed that anglerfish have a prolonged spawning season, which peaks from February to April. In addition, observations showed that there are at least two local spawning areas, one southwest of the Faroe Plateau and one in the Faroe Bank area.

Large anglerfish tagged with data storage tags and conventional tags showed a seasonal offshore-onshore migration. They migrated to shallow depths in summer to feed and to deeper waters in winter, presumably to spawn. Anglerfish performed vertical movements up into the water column, and were most active in these vertical movements during the winter time and during the nights, and light intensity seemed to trigger the migrations. Anglerfish distribution was temperature dependent, since anglerfish generally preferred temperatures warmer than 4ºC, usually between 6.5–11ºC. This may explain why anglerfish were distributed deeper west of the Faroe Bank area compared to the Faroe Plateau, which is surrounded by cold water deeper than approximately 500 m.

Anglerfish in Faroese waters preyed on a variety of food items. They were generally eating fish and the most important prey species in terms of numbers were Norway pout and blue whiting, whereas cod and haddock contributed most in weight. Annual consumption by anglerfish on commercially important demersal species, such as cod, haddock and saithe, was estimated to correspond to 33, 19 and 2% of the landings and to 75, 20 and 2% of biomass losses due to natural mortality, respectively. Even with this high cod consumption by anglerfish, cod cannibalism and fishing mortality still have greater impact on the cod stock dynamics than predation by anglerfish. The annual biomass loss of anglerfish due to cannibalism was estimated to nearly 15% of the annual loss due to natural mortality.

Anglerfish in Faroese waters may be regarded as a separate stock because all life stages are found in the area, local spawning area, seasonal offshore-onshore migration on the Faroe Plateau, together with insignificant emigration/immigration (< 5%). An age-based stock assessment of anglerfish in Faroese waters for the period 1999–2011 showed that the stock biomass ranged between 9000 and 19000 t with a peak in 2004–2005 and the fishing mortality for age 3–8 varied between 0.2 and 0.5 year^{-1}. The yield per recruit curve indicated that the stock was slightly growth overfished. Decreasing the fishing mortality could potentially increase the yield per recruit by around 10% leading to a 50% higher equilibrium biomass of anglerfish. No clear stock-recruitment relationship was found. On the other hand, anglerfish year-class strength was correlated with environmental variables, such as sandeel abundance. Hence, the rather short time series of anglerfish year-class strength provides little or no evidence of recruitment overfishing. It is recommended that stock assessments should be performed on an annual basis, allowing managers to react timely when there are signs of overfishing or recruitment failure due to natural or fishery causes.

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1 Papers

1.1 List of papers

I. Ofstad, L.H., Pedersen, T., Angus, C.H., and Steingrund, P. 2013. Age and growth of anglerfish (*Lophius piscatorius*) in Faroese waters. Fisheries Research, 139: 51–60. http://dx.doi.org/10.1016/j.fishres.2012.05.011.

II. Ofstad, L.H., Pedersen, T., and Steingrund, P. Maturation, reproduction and early life history of anglerfish *Lophius piscatorius* in Faroese waters. Submitted.

III. Ofstad, L.H., Steingrund, P., and Pedersen, T. Seasonal offshore-onshore migration and distribution of anglerfish *Lophius piscatorius* in Faroese waters. Manuscript.

IV. Ofstad, L.H., Steingrund, P., and Pedersen, T. Feeding ecology of anglerfish *Lophius piscatorius* in Faroese waters. Manuscript.

1.2 Main findings in the papers

Paper I: Age and growth of anglerfish (*Lophius piscatorius*) in Faroese waters

The main outcome of this study was the development and validation of an accurate method to age-determine anglerfish, e.g., a basis to perform an age-based stock assessment. Specifically, the illicia age determinations resulted in growth rates that were consistent with length frequency and with mark-recapture analyses in the same area. The study showed that anglerfish in Faroese waters had a very high growth rate during their first year of life (age 0–1, 18.5 cm year^{-1}). Small fish grew faster than larger fish. Growth rates of fish larger than 35 cm in length were similar to the fastest growth rates in other areas of the North Atlantic. The von Bertalanffy growth function fitted to male and female anglerfish showed that the length at age was similar for the sexes up to an age of five years, after which female anglerfish grew faster and lived longer than males.

The first two zones visible in the illicium, the benthic zone which is not a true age zone, and the first annual zone, had a horizontal diameter of 0.18 mm (age 0) and 0.32 mm (age 1), respectively. These zones could be identified in anglerfish of any length. Illicium width (total horizontal diameter) was strongly correlated with anglerfish length. An illicium edge analysis showed that the edge usually was dark in winter and light in summer (using transmitted light) and the transition between them took place in May–June. This information is crucial in the age-reading process.

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

This paper highlights that all stages in the life cycle of anglerfish occur in Faroese waters, from egg-ribbons, pelagic larvae, pre-settled juveniles, bottom-settled juveniles and all maturity stages of adult fish. This, together with the low degree of long-distance migration to and from Faroese waters (< 5%), indicates that the anglerfish population in Faroese waters may be considered as a separate stock, i.e., could represent an assessment and management unit.

Length at first maturity (L_{50}) differed between males and females. The L_{50} for males and females was 58 cm and 84 cm, respectively, corresponding to an age of about four years for males and seven years for females. Equal numbers of females and males were observed for fish smaller than 55 cm and less than 4 years, whereas males were significantly more frequently observed at medium lengths of 55–75 cm and 4–6 years. Thereafter females dominated among the larger and older specimens (> 85 cm, > 8 years). The main spawning season was from February to April, as indicated by the occurrence of spawning males and females, egg-ribbons and pelagic anglerfish larvae. The main spawning areas were probably located southwest of the Faroe Plateau and in the Faroe Bank area. A morphological transformation of the larvae to pelagic juveniles (metamorphosis) occurred when the fish were approximately 7–9 cm long, and the juveniles settled to the bottom when they were around 11 cm long. The occurrence of juvenile anglerfish (age 0 and 1) indicates that the Faroe Plateau serves as a nursery area.

Paper III: Seasonal offshore-onshore migration and distribution of anglerfish *Lophius piscatorius* in Faroese waters

The results of 10 data storage tags (DSTs) showed that anglerfish, larger than approximately 70 cm performed a seasonal offshore-onshore migration. They migrated between shallow depths (< 200 m, feeding area) in summer and deeper waters (> 300 m, spawning area) in winter. The DSTs revealed that these anglerfish preferred temperatures warmer than 4ºC, usually between 6.5–11ºC. Only around 5% of the total registrations showed more than 5 m of vertical movement between two consecutive DST registrations (one-hour intervals), and the fish were most vertically active during the winter time and during the night. Occasional incidents of extended vertical migrations, from the seabed (100–400 m) to near surface (< 50 m) for short time periods (few hours) were observed.

Conventional tagging was also performed during this study, and showed that 73% of the recaptured anglerfish moved less than 30 km from the tagging site in the summer season, indicating that anglerfish were fairly stationary during the summer. In addition, a spawning migration was evident from the fact that recaptures showed that large anglerfish moved to deep waters (> 300 m) in winter and were found in shallow waters (< 200 m) the following summer, i.e., a homing migration from spawning areas back to feeding grounds. Such a seasonal shift in the distribution of anglerfish is also consistent with data on commercial catch rates by depth as well as the spatial distribution of anglerfish caught in the winter and summer bottom trawl groundfish surveys, respectively. Light intensity, rather than temperature, might trigger the seasonal and daily migrations, since light intensity and individual vertical activity were strongly negatively correlated. It is hypothesised that anglerfish use the water currents as a transport medium when migrating between the spawning and feeding areas.

Paper IV: Feeding ecology of anglerfish *Lophius piscatorius* in Faroese waters

The stomach contents of 2772 anglerfish were investigated. The diet was dominated by fish, although some cephalopods and crustaceans were occasionally observed. Forty-two percent of the stomachs were empty. A total of 62 different prey types were identified. The pre-settled juveniles caught by pelagic trawl with lengths from 6 to 11 cm mostly predated on sandeels (*Ammodytidae*) and crustaceans. The main prey for anglerfish caught by dermersal trawl or gillnets (length 6 to 142 cm) were cod (29% by weight of the non-empty stomachs) and haddock (16%), whereas Norway pout (3%) and blue whiting (3%) were of less importance, but relatively important in terms of numbers. The anglerfish stock size, assessed by an age-based virtual population analysis, in the period from 1999–2011, varied between 9000 and 19000 t. The annual consumption by anglerfish of commercially important demersal fish species was most pronounced for cod (corresponding to 11% of the average stock biomass and 75% of the annual biomass loss due to assumed natural mortality), followed by haddock (3% of the average stock biomass corresponding to 20% of the annual biomass loss due to assumed natural mortality), whereas the consumption was less for saithe (2% of the annual biomass loss due to assumed natural mortality). Cannibalism amounted to 2% of the anglerfish stock size, corresponding to 15% of the assumed annual biomass loss due to natural mortality.

2 Introduction

The management of fisheries resources is a complex topic and consists of four general considerations: biological, social, recreational, and economic considerations (Hilborn and Walters, 1992). The primary considerations in fisheries management are, among others, to ensure that the resources are utilised in a sustainable and responsible way and to avoid overfishing (Hilborn and Walters, 1992). In this section, firstly some general issues regarding fisheries management are presented, then general information on anglerfish biology is outlined, and finally a description of the physical and biological environment and the fishery in Faroese waters is given.

2.1 General issues in fisheries management

The main goal in all fisheries management is to harvest fish populations in a sustainable way so that their growth potential and recruitment potential is fully utilised (Wootton, 1990; Hilborn and Walters, 1992). To achieve this, it is of crucial importance to have sufficient information on population (stock) structure, population dynamics and life history characteristics such as individual growth, natural mortality and age at first maturity (Wootton, 1990; Hilborn and Walters, 1992).

The concept of the 'stock' is fundamental to fisheries management, and can be defined in several ways (Begg *et al.*, 1999; Begg and Waldman, 1999). Here, the stock definition by Hilborn and Walters (1992) will be used which defines stocks as 'arbitrary groups of fish large enough to be essentially self-reproducing, with members of each group having similar life history characteristics'. There are several methods to identify a stock e.g., life history characteristics, mark-recapture by conventional and data storage tags, catch data from surveys and/or information from commercial fisheries, parasites, otolith microchemistry, morphology and genetics (Begg and Waldman, 1999; ICES a, 2012), and several of the same methods are used in investigations of migration.

Estimates of life history parameters and verifications of hypothetical migrations are important information when assessing the stock structure of a fish species. The life history of a fish population is often presented as a circuit, popularized as a migration triangle (Secor, 2002). The migration triangle demonstrates spatially separated adult feeding grounds, spawning grounds, and juvenile nursery areas among which fish must migrate during certain phases of their life cycle (Harden Jones, 1968).

To obtain an estimate of the biomass of a fish stock, stock dynamic models are frequently used in commercial fisheries management to perform age-based fish stock assessments. In short, the biomass of a fish stock is mainly dependent on four processes: recruitment (supply of young individuals), individual growth, natural mortality (mortality that is not caused by fishery) and fishing mortality (Wootton, 1990). Several fisheries suffer from overfishing (growth- and/or recruitment overfishing), where growth overfishing seems to be the more wide-spread form of overfishing and can be defined as 'depleting the young part of the stock before it has reached its full biological and economical potential' (Gulland, 1983; Hilborn and Walters, 1992). One other form of overfishing is recruitment overfishing, which has more disastrous consequences since it directly impedes the future viability of fish stocks. Recruitment overfishing is defined as 'depleting the reproductive part of the stock by so much that recruitment is impaired' (Gulland, 1983; Hilborn and Walters, 1992). Methods often used to investigate if stocks are overfished are comparisons of estimated fishing mortality rates with reference fishing mortality rates based on yield per recruit and spawning stock per recruit calculations and evaluation of spawning stock-recruitment relationships and current spawning stock size (Hilborn and Walters, 1992).

Although stock assessments, providing information on e.g., stock size, recruitment and fishing mortality, are certainly essential for sustainable stock management, it is indeed necessary to have a broader understanding of ecological and environmental influences on the fish stocks as well. Such environmental influences may be temperature, food availability, predation, amount of suitable habitats for the various life stages of the individuals, space competition and interactions with other species. As an example, the match-mismatch hypothesis between the fish larvae and its prey (Cushing, 1995) could be mentioned, which addresses the importance of the spatial and temporal overlap between the production of appropriate prey for fish larvae and the spawning activity and occurrence of first-feeding fish larvae. In modern fish stock management, relevant environmental influences should be added to traditional stock assessment information, providing more holistic advice, rather than the single-stock advice, that traditionally has been given in many regions (FAO, 2003; ICES, 2012 b).

2.2 Anglerfish biology

2.2.1 Classification and distribution of anglerfish species

Anglerfish (or monkfish) belong to the genus *Lophius*, family Lophiidae, suborder Lophioidei, order Lophiiformes, under teleost fishes (Caruso, 1983). There are eight species of the genus *Lophius* distributed in different geographical regions of the oceans: *L. litulon* in the western North Pacific off Japan, *L. gastrophysus* in the western Atlantic, south of Florida, *L. americanus* in the northwest Atlantic, North American coast, *L. vomerinus* at the South African coast, *L. upsicephalus* at the South African coast, re-described as a junior synonym of *L. vomerinus* (Leslie and Grant, 1991), *L. vaillanti* in the eastern Atlantic off the African coast, *L. budegassa* and *L. piscatorius* in the northeast Atlantic (Caruso, 1983). *L. americanus* and *L. piscatorius* are very similar in appearance, distribution depth and temperature and they were thought to be synonymous until Berrill (1929) established the validity of *L. americanus* as a separate species.

Of the two species distributed in the northeast Atlantic, *Lophius piscatorius* is the dominant species in Faroese waters, while *L. budegassa* is only occasionally observed (Thangstad *et al*., 2006). The common name "anglerfish" will hereafter be used as a synonym for *L. piscatorius* while the specific latin species name will be used for the other species of *Lophius*.

2.2.2 Ageing of anglerfish

For anglerfish it has proved difficult to age them accurately in almost all geographical areas of the northeast Atlantic, as the mean length at age have been very variable, even for small fish (0- and 1-group) (ICES, 2009; Landa *et al*., 2008). The main difficulty has been to locate the first annulus and the existence of false annuli (Fariña *et al*., 2008). So, it is also important to identify the benthic zone, which is a false annual zone deposited in the illicium during the period of settlement by juveniles from the pelagic environment to the bottom (Wright *et al*., 2002).

No age-based assessments of anglerfish are presently performed in ICES because of these unresolved problems (ICES, 2009). Several age-estimation workshops and exchange of illicia and otoliths between different age readers (Institutes) have dealt with the issue and attempted to standardize the age reading criteria (ICES, 1997; ICES, 1999; Landa *et al*., 2002; Duarte *et al*., 2005; Landa, 2012). However, despite these efforts there are still major unresolved challenges. In particular, validations of age determination methods are urgently needed (Fariña *et al*., 2008).

2.2.3 Life history

While the movement of anglerfish eggs and larvae from spawning areas to nursery areas may be considered a passive process (drift with the currents), the displacement between the other locations, e.g., of juveniles from the nursery areas to the feeding areas, involves an active swimming behaviour. A seasonal migration, probably between feeding and spawning areas, is hypothesized to exist among *Lophius* species such as *L. americanus* (Steimle *et al*., 1999), *L. budegassa* (Landa *et al.*, 2001) and *L. piscatorius* (Laurenson *et al*., 2005), although little is known about these migrations.

The spawning areas of anglerfish in the northeast Atlantic are poorly documented (Hislop *et al*., 2001; ICES, 2007; Fariña *et al*., 2008; ICES, 2009). The old hypothesis that anglerfish spawn in deep water west of Scotland (Fulton, 1903; Bowman, 1920), has yet to be confirmed by observations. Tåning (1943) suggested, based on findings of small pelagic larvae/juveniles, that the area west of the Faroe Islands and south to the Bay of Biscay, in depths of around 1000 m, could be important spawning areas for anglerfish. More recent work suggests spawning areas to be located in Icelandic waters (Solmundsson *et al*., 2010), in Norwegian waters (Bjelland and Asplin, 2007) and in Faroese waters (Ofstad and Laurenson, 2007), but closer investigations are needed.

Anglerfish are characterised by sexual dimorphism where males mature at a smaller length and age than females (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 is prolonged and extends from late winter to summer (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). Both sexual dimorphism and prolonged spawning season have also been documented for Faroese waters (Tåning, 1943; Ofstad and Laurenson, 2007).

The early life history of anglerfish is quite unique as the anglerfish eggs are spawned in a gelatinous and buoyant ribbon. These ribbons may be in excess of 10 m long and up to 1 m wide (Bowman, 1920), amounting to up to half of the female's total weight and containing more than one million eggs (Russell, 1976). It is assumed that the eggs of anglerfish are shed in a single batch and that the fertilization is external (Afonso-Dias and Hislop, 1996; Murua and Saborido-Rey, 2003). The spawning behaviour of anglerfish is poorly known (Fariña *et al*., 2008). The newly hatched larvae measure around 0.45 cm in length and are still found within the gelatinous ribbon (Russell, 1976). Morphological transformation (metamorphosis) from larvae to juveniles occurs when the fish are around 6–7 cm long (Joensen and Tåning, 1970), and this may last several weeks and even months (Bowman, 1920; Hislop *et al*., 2001). Fully mature females have occasionally been observed in Faroese waters, as well as yolk-sac larvae (0.7 cm in length) still located in the gelatinous ribbon, and pre-settled juveniles (Ofstad and Laurenson, 2007).

The 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 juvenile anglerfish (< 50 cm in length) are abundant in near-shore areas (0–50 m depth) in Shetland waters (Laurenson *et al*., 2008). Information on potential nursery areas of anglerfish in Faroese waters is very limited, but Tåning (1943) noted that some juveniles were present in the deeper part of Faroese fjords at depths around 80 m.

The population structure of anglerfish in the northeast Atlantic is poorly known, and it has been uncertain whether there is one (large) stock or many (small) stocks. No genetic differences have so far been detected among anglerfish in the northeast Atlantic (O'Sullivan *et al*., 2005), supporting the one-stock view. However, there could also be several stocks which are genetically similar. Anglerfish in Faroese waters are currently considered to be a separate fish stock by ICES (ICES, 2009).

2.3 The physical and biological environment in Faroese waters

The Faroe Islands are located in the northeast Atlantic at 62°N 7°W, between Iceland, Norway and Shetland. The surrounding physical environment is dominated by the warm North Atlantic Current in the upper layer, shallower than approximately 500 m depth and the cold overflow water from the Norwegian Sea flowing in the deep layer (Figure 1; Hansen *et al*., 1998; Hansen and Østerhus, 2000). Strong tidal currents maintain a clockwise current on the Faroe Shelf (Figure 2) and also around the Faroe Bank (Larsen *et al*., 2008).

The Faroe Shelf is defined here as the inner part of the Faroe Plateau (inner system), where a hydrographic front at approximately 120 m depth separates the shelf water from the oceanic water

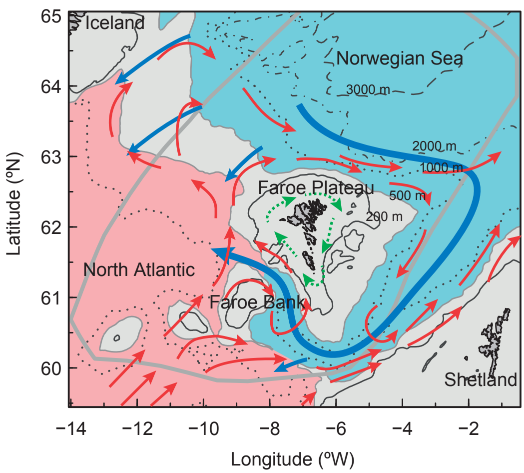

Figure 1. Topography and the main current system around the Faroe Islands. Thin red arrows: warm currents in upper layers, bold blue arrows: main cold (< 0°C) flow in deep layer, stippled green arrows: currents on Faroe Shelf. The grey areas are shallower than 500 m, the blue area deeper than 800 m in 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. Gray bold line: 200 nm exclusive economic zone.

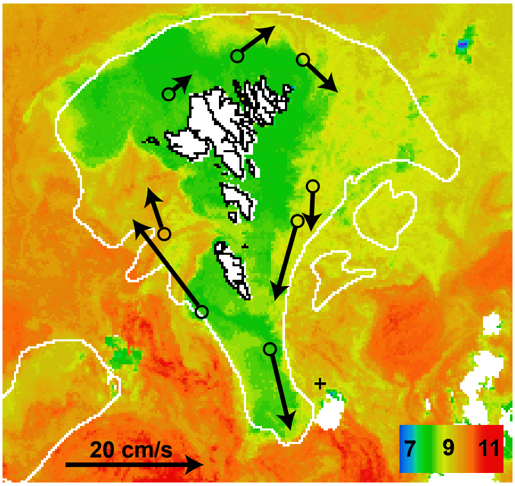

Figure 2. Sea surface temperature as recorded by a satellite on the cloudless day of 18th April 2003 and current velocity on the Faroe Plateau. The white line shows the 200 m bottom depth contours. The temperature is shown as colours (courtesy of P. Miller at Plymouth Marine Laboratory), the arrows show residual currents based on long-term current meter deployments at the site indicated by circles, based on Larsen et al. *(2008).*

(Larsen *et al.*, 2008). The Faroe Shelf functions as a retention area, that keeps fish eggs/larvae and other planktonic organisms on the shelf (Gaard and Steingrund, 2001). The productivity of fish on the Faroe Shelf is likely to be bottom-up controlled, since a positive relationship is found between a yearly index of primary production and recruitment and growth of cod and haddock (Gaard *et al.*, 2002; Steingrund and Gaard, 2005). Sandeels probably act as a major link between the primary production and the higher trophic levels since both cod and haddock feed on sandeels in Faroese waters (Eliasen *et al.*, 2011). However, the biomass of zooplankton on the Faroe Shelf (dry weight (g m^{-2}) in June–July), which by weight is dominated by the oceanic copepod *Calanus finmarchicus*, tends to be negatively correlated with the primary production on the Faroe Shelf (Gaard, 2003, Hansen *et al.*, 2005).

The water masses outside the Faroe Shelf, defined here as the outer system, are influenced by variations in the dynamics of the subpolar gyre, a strong and large gyre is preventing the northward flow of warm and salty eastern water from the Bay of Biscay region, and vice versa (Figure 3; Hátún *et al.*, 2005). A weak subpolar gyre leads to warmer and more productive conditions e.g., associated with a high abundance of blue whiting, and smaller amounts of *C. finmarchicus* in Faroese waters (Hátún *et al.*, 2009). Hence, the productivity of the outer areas on the Faroe Plateau has for at least two decades been negatively correlated with the primary production of the inner areas of the Faroe Shelf (Steingrund *et al.*, 2010).

Approximately 240 different fish species are registered in Faroese waters, many of them being quite rare (Mouritsen, 2007). Less than twenty species are important in terms of biomass, e.g., cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), Norway pout (*Trisopterus esmarki*), sandeel (*Ammodytes* sp.), red fish (*Sebastes* sp.), greater silver smelt (*Argentina silus*), ling (*Molva molva*), tusk (*Brosme brosme*) and Greenland halibut (*Reinhardtius*

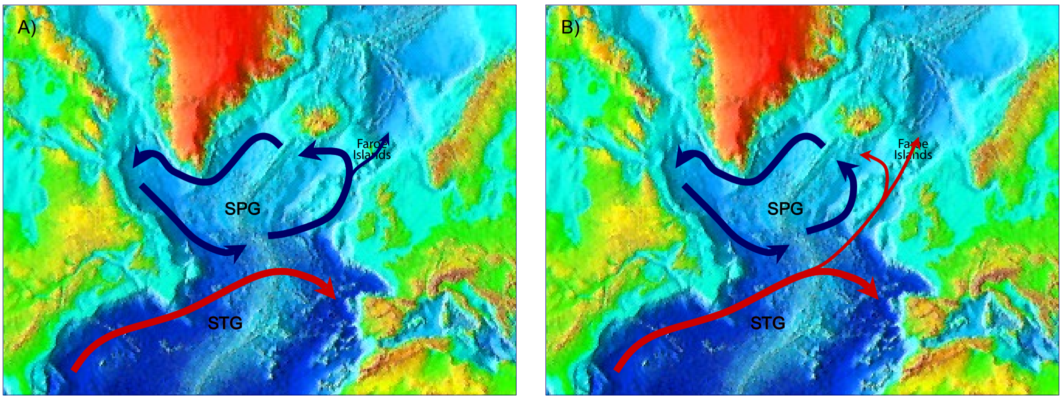

Figure 3. Examples of how the strength of the subpolar gyre (SPG) may influence the water masses around the Faroe Islands. A) A strong SPG (blue lines) leads to cool, subarctic waters around the Faroes, whereas B) a weak SPG allows more warm water masses from the subtropical gyre (STG, red lines) to enter the waters around the Faroes. Based on Hátún et al. *(2005).*

hippoglossoides). Also the migrating pelagic species blue whiting (*Micromesistius poutassou*), mackerel (*Scomber scombrus*) and herring (*Clupea harengus*) are dominant during part of the year (ICES, 2011). Anglerfish are found all over the Faroe Plateau, i.e., both in the Faroe Shelf area (the inner system) and in the deeper waters (the outer system).

2.4 Fisheries in Faroese waters

Fishery and fish processing are the most important contributors to the Faroese economy and employment (Statistic Faroe Islands, 2012). The two main fisheries in Faroese waters are the single-species pelagic fisheries and the mixed-species demersal fisheries (ICES b, 2012). The pelagic fisheries target mainly blue whiting, mackerel and herring and are mainly conducted by purse seiners and factory trawlers. The demersal fisheries target several species and are conducted by a variety of vessel types. Open boats and small vessels, using jigging and longlines, longliners (> 110 Gross Register Tonne (GRT)) and jiggers mainly target cod and haddock, while the longliners also fish for ling and tusk. The small otterboard trawlers (< 700 Horse Power (HP)) mainly target cod and haddock, but some are also licensed to fish for lemon sole, plaice and anglerfish within the 12 nm limit during the summer. The larger otterboard trawlers (> 700 HP) and the pair trawlers mainly fish for saithe, usually with a by-catch of e.g., cod and haddock. Some large pair trawlers have licenses to fish greater silver smelt during summer. The large trawlers, which seasonally fish in deep waters, catch mainly redfish, Greenland halibut, blue ling (*Molva dypterygia*), grenadiers (*Coryphaenoides* sp.) and black scabbardfish (*Aphanopus carbo*). The gillnet vessels mainly target anglerfish and Greenland halibut (ICES b, 2012).

Anglerfish in Faroese waters have become a highly exploited and valuable resource (top five in economical terms, due to high selling prices) together with cod, haddock, saithe and greater silver smelt. Traditionally, anglerfish were caught as by-catch in the demersal trawl fisheries for cod, haddock and saithe. A more direct fishery, including the introduction of a direct gillnet fishery, was developed in the early 1990s (Reinert, 1995). Annual catches of anglerfish varied between 500 and 1000 t in the period from the 1960s to 1990s, but in the period from 1996–2003 the catches increased twofold to around 2000 t. Catches subsequently increased to a peak of 5000 t in 2005–2006, but have since declined again to about 2000 t. The preliminary catch data for 2012 was nearly 1300 t, approximately half of the 2011 catch (Figure 4; Statistic Faroe Islands, 2013). During the last two decades, small trawlers (< 700 HP) and gillnetters have landed the majority (90%) of the total catch of anglerfish in Faroese waters. The rest is taken as a by-catch in the trawl (> 700 HP) and longline fisheries.

The Faroese anglerfish gillnet fishery is managed as a licensed fishery, without any total allowable catch (TAC) quota constraints. Five gillnet vessels are currently licensed to fish anglerfish. This fishery is restricted by area, depth (below 380 m), number of nets, soaking time, minimum mesh size (280 mm stretched), and by-catch rules. A few small trawlers, licensed to fish flatfish in specified areas inside the 12 nautical miles limit during June–August, also take relatively large catches of anglerfish. These small trawlers exert a direct fishery for anglerfish during the winter mainly in two areas on the Faroe Plateau outside the 12 nm limit. The trawler fleet is also regulated by numbers of fishing days, permanent and temporary area closures, and by-catch restrictions, without any TAC constraints (Thangstad *et al.*, 2006; ICES b, 2012).

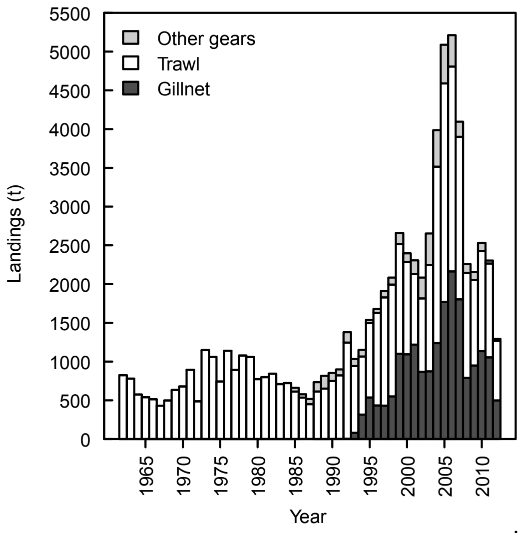

Figure 4. Annual landings of anglerfish in Faroese waters (ICES Division Vb) in the period from 1962 to 2012 by trawl, gillnet and other gears (mainly longliners and jiggers). The catch for 2012 is preliminary data from Statistic Faroe Islands (2013).

Despite the economical importance of the anglerfish fishery, there is little information on the biology, stock size and productivity of anglerfish in Faroese waters, and whether the fishery is sustainable. Also, there is no information on predation by anglerfish on other fish species. This PhD project was initiated to investigate and explore these questions.

3 Objectives

Despite the fact that anglerfish in Faroese waters represent a highly exploited resource and an economically important demersal fish species in the Faroese fishery, there is at present little information on the population status, in terms of stock identity (separation from other anglerfish populations), stock size and sustainability of the fishery. Furthermore, interactions with other fish species, e.g., predation on commercially important demersal species such as cod, haddock and saithe, are poorly known. Recent studies have provided new information about the anglerfish biology in Faroese waters (Thangstad *et al.*, 2006; Ofstad and Laurenson, 2007). The present study, building upon these past findings, provides new and valuable improvements to the biological knowledge of anglerfish in Faroese waters and relevant information is used for management purposes.

Specific objectives:

1) Investigate the life history of anglerfish in Faroese waters (Papers I, II, III, IV), with special attention to age determination and growth (Paper I), maturation and reproduction (Paper II) and migration (Paper III).
2) Investigate whether anglerfish in Faroese waters can be treated as a separate stock (Papers II, III).
3) Investigate the level of variations (Paper IV) and influence of recruitment, stock size, spawning stock size and fishing mortality and evaluate whether the anglerfish fishery in Faroese waters is sustainable.
4) Investigate trophic interactions between anglerfish and other commercially important demersal fish species, such as cod, haddock and saithe in Faroese waters (Paper IV).

4 Results and discussion

In this section, the main results of this study are presented and discussed. In addition, other relevant issues complementary to the papers regarding the ecology and management are shown and discussed.

4.1 The life history of anglerfish in Faroese waters

The life cycle of anglerfish is illustrated in Figure 5. The eggs, larvae and pre-settled juveniles drift with the currents before the juveniles settle in a nursery area, where they grow and mature. After that, the adults migrate between the feeding and spawning areas.

4.1.1 Age and growth

There have been difficulties in ageing anglerfish and the estimates of the mean length at age have shown a large variation already for 0- and 1-group fish, indicating that the first zones in the illicium were not interpreted correctly (Landa *et al.*, 2008; Landa, 2012). In this study we found that the benthic zone in the illicia on average was 0.18 mm wide (age 0) and the first true annual zone was 0.32 mm wide (age 1) for anglerfish in Faroese waters (Paper I), which is comparable with findings in other regions of the northeast Atlantic (Duarte *et al.*, 2002; Landa, 2012). The benthic zone in illicia often looked brighter and wider than the first annual zone. One reason for that could be that this zone

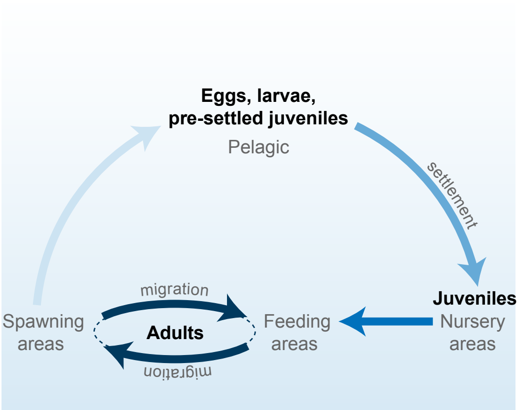

Figure 5. Overview of spatial movements between areas in the anglerfish life cycle.

is formed during both the period of metamorphosis and when they settle to the bottom as these events may occur over some months.

The illicia age determinations in this study resulted in growth rates that were consistent with length frequency and mark-recapture analyses from the same area (Paper I). The high growth rate of anglerfish in the Faroese area during their first year (18.5 cm year^{-1}, Paper I; Figure 6) is similar to results from other adjacent regions in the northeast Atlantic (Fulton, 1903; Tåning, 1943; Hislop *et al.*, 2001; Jónsson, 2007). The von Bertalanffy growth function (VBF) fitted to male and female anglerfish showed that the length at age were similar for both sexes up to an age of five years, after which female anglerfish grew faster and lived longer than males. Growth rates of fish larger than 35 cm in length were slightly less compared to the fastest growth rates in other areas of the northeast Atlantic (Dyb, 2003; Jónsson, 2007). Since around 2007, the perception of the growth rate of anglerfish has been revised thanks to new information from mark-recapture and length frequency analyses (Landa *et al.*, 2008; Landa, 2012). These results regarding age reading and growth of anglerfish in Faroese waters represent an important contribution to the ongoing issue of the accuracy in ageing anglerfish in the northeast Atlantic (Paper I).

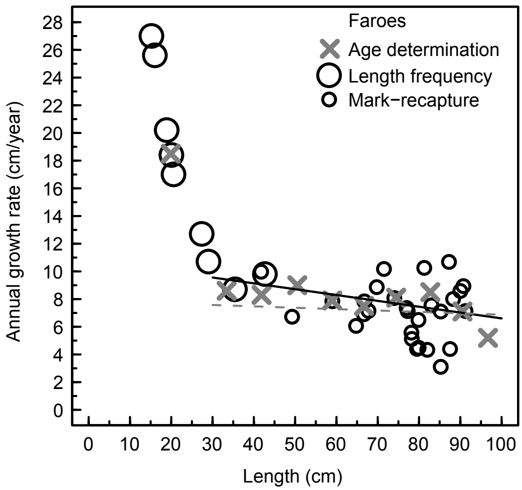

Figure 6. Annual growth rate as a function of anglerfish length from Faroese illicium-based age determination, length frequency data and mark-recapture data. The dots are plotted at average lengths (i.e., (recapture length + mark length)/2) and the line shows growth rates from a VBF-function based on Faroese length at age from illicium readings. The stippled grey line indicates annual growth rates from VBF-function based on Faroese mark-recapture data. The figure is from Paper I.

4.1.2 Eggs, larvae and pre-settled juveniles

Anglerfish egg-ribbons, larvae and pre-settled individuals were distributed pelagically over the Faroe Plateau and the Faroe Bank (Paper II; Figure 7A). These early life stages have also been caught pelagically in other regions of the northeast Atlantic (Tåning, 1943; Hislop *et al.*, 2000; Solmundsson *et al.*, 2010). Both anglerfish eggs and yolk-sac larvae have been found inside the gelatinous ribbons (Bowman, 1920; Russell, 1976; Paper II), and the gelatinous ribbon probably has two functions: firstly, it improves the buoyancy and thereby the ability to drift with the water currents and secondly, the ribbon probably protects the eggs and larvae from predation. This spawning tactic leads to a highly aggregated distribution of eggs and larvae, which could be one of the reasons for the few observations of these stages in the northeast Atlantic (Sundby, 1991; Thangstad *et al.*, 2006).

Anglerfish larvae are equipped with very large pectoral fins and threadlike ventral fins (Bowman, 1920), which may enhance their ability to be carried by water currents. The morphological transformation (metamorphosis) from larvae to juveniles in Faroese waters occurs when the larvae are between 7 and 9 cm long (Paper II), which is similar to findings in other regions in the northeast Atlantic (Bowman, 1920; Joensen and Tåning, 1970; Hislop *et al.*, 2001). The adult body-form is characterised by a dorso-ventrally flattened body and also a large mouth and teeth, which gives the fish an opportunity to feed on large prey (Sharf, 2000). In Faroese waters pre-settled juveniles (6–11 cm long) predate on fish, mostly sandeels and crustacea (Paper IV). The capability to feed on relatively large fish prey so early in life could be one of the reasons for the rapid growth of anglerfish in their first year of life (Paper I).

4.1.3 Juveniles

All sampled anglerfish juveniles that were longer than 11 cm had settled to the bottom (Paper II), and this is similar to findings in Scottish waters (Tåning, 1943). The Faroe Plateau probably acts as a nursery area for anglerfish younger than three

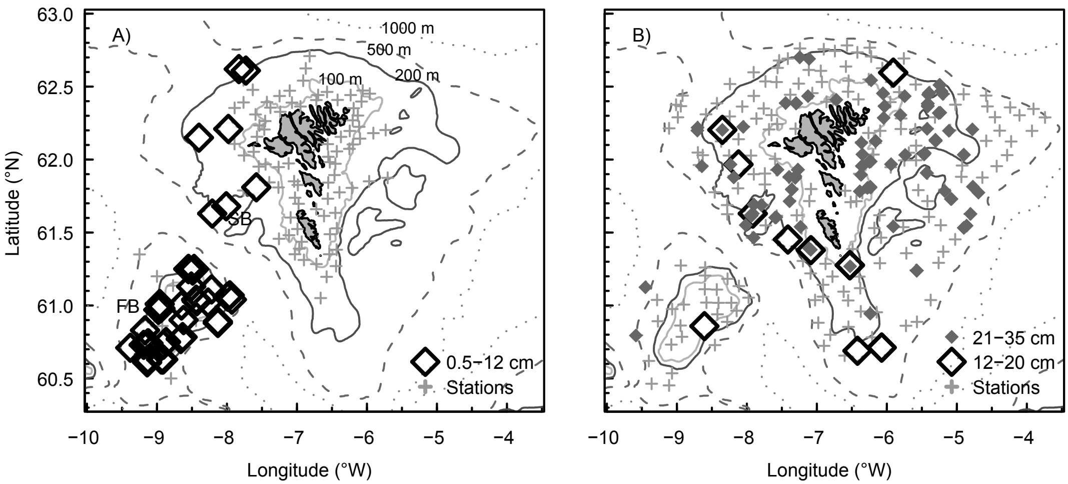

Figure 7. A) Anglerfish larvae/juveniles (N = 48) caught in the annual pelagic 0-group survey during June–July in Faroese waters (1997–2012). B) Small anglerfish, less than 35 cm (< 2 years old), caught in the Faroese annual summer groundfish survey using bottom trawl, during August/September (2000–2011). Crosses indicate the locations of the trawl stations without catch of anglerfish larvae or juveniles while diamonds show stations with catch of juveniles, FB is Faroe Bank and SB is Skeivibanki. Note that the Faroe Bank has not been surveyed every year. The figure is from Paper II.

years (Paper II and III). Tåning (1943) postulated that the deep parts of the Faroese fjords, which are between 70 and 90 m deep, could represent potential nursery areas. In Shetland waters juveniles are mainly distributed from the shore to 50 m depth (Laurenson *et al.*, 2008). One reason for the wide nursery area on the Faroe Plateau (Figure 7B) could be because anglerfish settle to the bottom wherever they are located at the time (size) of settling. If they settle to the bottom in an unfavourable habitat they would probably seek other areas in order to find more suitable habitats with e.g., prey, favourable temperature or bottom substrate. This could be the reason for the indications of movement to shallow waters for fish smaller than 50 cm (younger than age 4) (Paper III). These individuals are immature and the proportions of females and males are equal until a length of about 50 cm and age around three years (Paper II). The favourite prey of anglerfish with lengths of 12–50 cm is fish, dominated by Norway pout, juvenile blue whiting and haddock (Paper IV).

4.1.4 Adult fish

In Faroese waters, anglerfish males matured at lengths of 50–60 cm corresponding to around 4 years of age, while females matured at lengths of 75–85 cm corresponding to about 7–8 years of age (Figure 8; Paper II). The fact that males matured at a shorter length and younger age than females, is comparable to other studies 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), although the estimates of length at maturity were not always the same for the different regions. The length at maturity varied by about 10 cm for males and 35 cm for females and

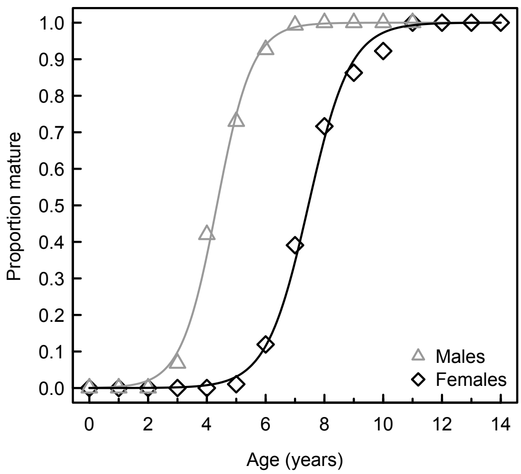

Figure 8. Proportion mature male and female anglerfish in Faroese waters by age. Sigmoid lines show logistic regression functions fitted to the data. Figure from Paper II.

the values in this study were similar to the largest values for males and more intermediate values for females reported in other studies (Afonso-Dias and Hislop, 1996; Quincoces *et al.*, 1998; Duarte *et al.*, 2001; Thangstad *et al.*, 2006; Laurenson *et al.*, 2008; ICES, 2009). The age of maturation for males corresponded very well with the age (of about 5 years) when the growth rate slowed down (Paper I, II) and when the proportion of males exceeded 0.5 (Paper II; Figure 9). The proportion of females became higher than 0.5 when the fish reached an age of 8 years. When the fish were more than 11 years old there were only females left in the population (Paper II). The von Bertalanffy's growth constants showed that females had a lower K value than males. K and the natural mortality rate are related, and a lower K value indicates a lower natural mortality rate, suggesting that males experience a higher natural mortality rate than females after sexual maturity (Paper I).

Male anglerfish mature at an earlier age, exhibit lower growth rates and experience higher mortality than females, but the reason for the higher mortality rates of males is unknown. The higher mortality rate for males could be due to a higher energy cost for males than for females to produce gonads. However, since the maximum gonadosomatic index (ratio of fish gonad weight to gutted body weight) of fish ready to spawn was 3 for males and 50 for females (Paper II), this explanation seems to be unlikely. A more likely explanation seems to be that when the females mature, the males have already migrated between spawning and feeding areas for several years, expending lots of energy and therefore being more vulnerable to predation and possibly to fishing. This, together with a prolonged spawning period, where the males probably devote much time and energy to spawning activity, could have a negative influence on the survival (Wootton, 1990). As the proportion of stored energy reserves spent on the migration increases, the proportion of fish surviving to spawn again is expected to decrease (Wootton, 1990).

Anglerfish in Faroese waters have a prolonged spawning season, with a peak in spawning between February and April (Paper II). This prolonged spawning season is comparable with other areas in the northeast Atlantic (Bowman, 1920; Joensen and Tåning, 1970; Afonso-Dias and Hislop, 1996; Woll *et al.*, 1996; Thangstad *et al.*, 2006; Laurenson *et al.*, 2008). There seems to be at least two local spawning areas in Faroese waters, one southwest of the Faroe Plateau and one in the Faroe Bank area (Paper II; Joensen and Tåning, 1970; Figure 10). The occurrence of larvae on the Faroe Plateau and on the Faroe Bank supports the view that there are spawning areas nearby (Paper II). The high catches of anglerfish between the banks southeast of the Faroes in November to March (Paper III) furthermore suggests that this area may be a spawning area (Figure 10). The bottom topography of these spawning areas on the Faroe Plateau are like small pockets (Figure 11), which seem to be favourable spawning sites for anglerfish (Paper II), but this is not the case in the Faroe Bank area. Other spawning areas of anglerfish in the northeast Atlantic have been documented in Icelandic waters (Solmundsson *et al.*, 2010), Norwegian waters (Bjelland and Asplin, 2007), and west of Scotland (Joensen and Tåning, 1970).

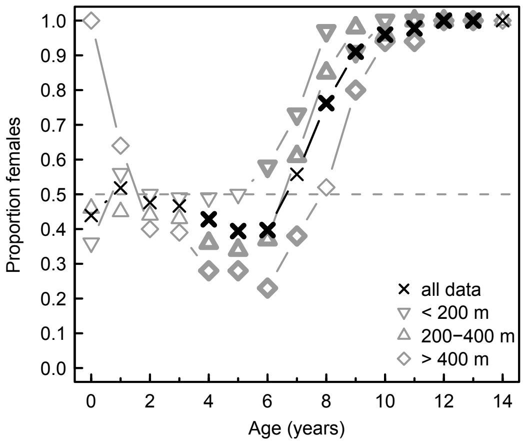

Figure 9. Proportion female anglerfish caught by research and commercial trawl in Faroese waters for all data (black) and depths; < 200 m, 200–400 m and > 400 m (grey) for age. Bold points represent proportions of females that are significantly different from 0.5 ($p < 0.05$) and the horizontal line shows equal proportions of males and females. Figure from Paper II.

Adult anglerfish were mostly located in relatively warm water of 6–11ºC and very seldom occurred in water colder than 4ºC (Paper III). Such a temperature dependent distribution is probably the main reason for the more shallow distribution on the Faroe Plateau, compared with the Faroe Bank. On the Faroe Plateau slope, anglerfish were very seldom caught deeper than 500 m. This could be due to the cold water, with temperatures less than 0ºC in the overflow water from the Norwegian Sea that surrounds the deep parts off the Faroe Plateau (Hansen *et al.*, 1998; Hansen and Østerhus, 2000;

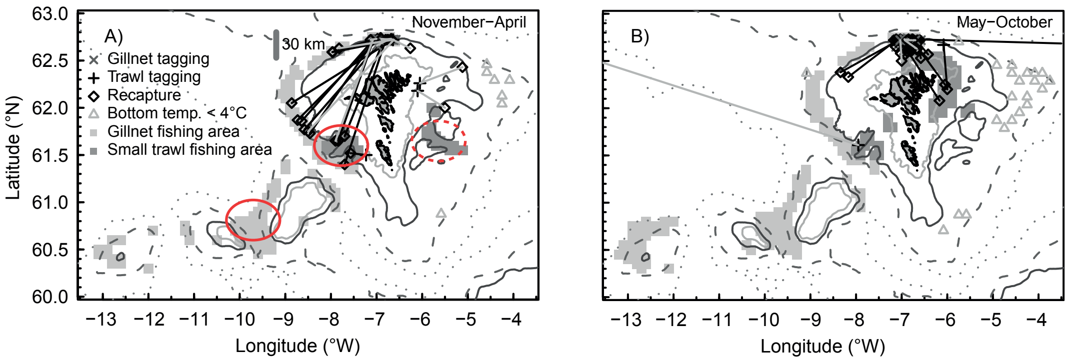

Figure 10. Horizontal movements of anglerfish tagged from gillnet and trawl and recaptured in A) November–February (black line) and March–April (grey line), B) May–August (black line) and September–October (grey line). Main anglerfish fishing areas on the Faroe Plateau are shown for gillnet (light grey squares) and trawl less than 700 HP (darker grey squares). The red circles indicate the locations of anglerfish spawning areas. Depth contours are shown for 100, 200, 500 and 1000 m. Modified from Paper III.

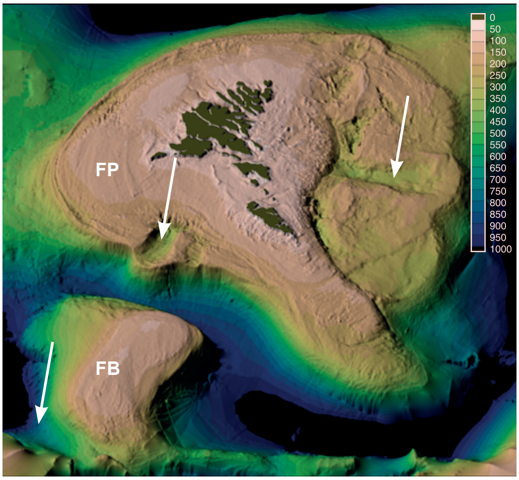

Figure 11. Seabed topography around the Faroe Islands. Faroe Bank is located to the southwest of the much larger Faroe Plateau. The arrows indicate the location of potential anglerfish spawning areas. Map courtesy Knud Simonsen, University of the Faroe Islands.

Figure 1). In the Faroe Bank area, the cold overflow water is located deeper, which may explain why anglerfish in this area have been caught at depths down to 950 m (Paper II).

The clockwise current systems on the Faroe Plateau and on the Faroe Bank, respectively, seem to retain the egg-ribbons and larvae in the area. The location and topography of the spawning areas on the southwest part of the Faroe Plateau (Figure 10 and 11) combined with information on the prevailing currents (Figure 1) suggests that there is a high probability that eggs/larvae be carried with the currents onto the Faroe Shelf. Nevertheless, very few larvae and pre-settled juveniles have been caught in the regular 0-group surveys on the Plateau in June–July. The reasons could be that the juveniles had already settled to the bottom on the Plateau, or that they were not located in the uppermost 10–40 m of the water column, surveyed by the pelagic 0-group trawl. A prolonged spawning period enhances the chances for a spatial and temporal overlap between the production of appropriate prey for the fish larvae and occurrence of first-feeding fish larvae, which is essential according to the match-mismatch hypothesis by Cushing (1995).

4.1.5 Migration

In Faroese waters, anglerfish longer than 70 cm perform a clear seasonal off-shelf migration in autumn to the spawning areas, which are located deeper than approximately 300 m, followed by an on-shelf migration in spring back to the feeding area in water shallower than 200 m (Paper III; Figures 12 and 13). The actuality behind this migration pattern fits well with the findings i) of a spawning area southwest of the Faroe Plateau at around 300–400 m depth (Paper II), ii) that large fish have higher feeding rates in summer in areas shallower than 200 m depth (Paper IV), and iii) that the recaptured anglerfish from conventional tagging showed longer migration distances from the tagging site in winter time than in summer time (Paper III).

Anglerfish exhibited a seasonal pattern in vertical activity that fits with the patterns of seasonal migration, as there was higher vertical activity during the winter time when the fish migrated to and from the spawning areas than during summer when the fish seemed to spend most of the time close to the bottom (Paper III; Figure 13). The diurnal pattern with much less vertical activity during the hours of daylight could be related to feeding activity. Because attraction of prey relies on the anglerfish using the illicia (fishing rod) as a visual stimulus to attract the prey, feeding activity should mostly occur during hours of daylight and hence it would be most beneficial for anglerfish to migrate during the night. This seasonal and diurnal migration pattern is probably triggered by the light intensity, rather than the sea temperature, since there was a very strong, negative correlation between the hours of high vertical activity during the day each month and the mean light intensity (Paper III). This fits well with the findings of Burchett (2000), who

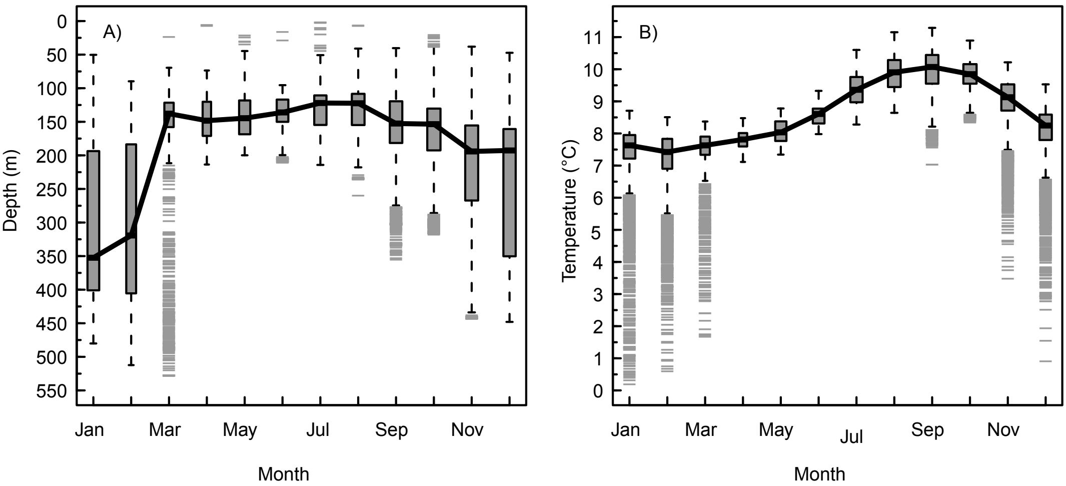

Figure 12. The distribution of A) depth and B) ambient temperature per month for all 10 of the recaptured anglerfish with data storage tags. The black line shows the median, the box represents the upper and lower quartile, the error bars show upper and lower extremes (excluding outliers) and the short grey horizontal lines show outliers. The outliers are defined as values 1.5 times larger than the inter-quartile range. The width of the box indicates the sample size. Modified from Paper III.

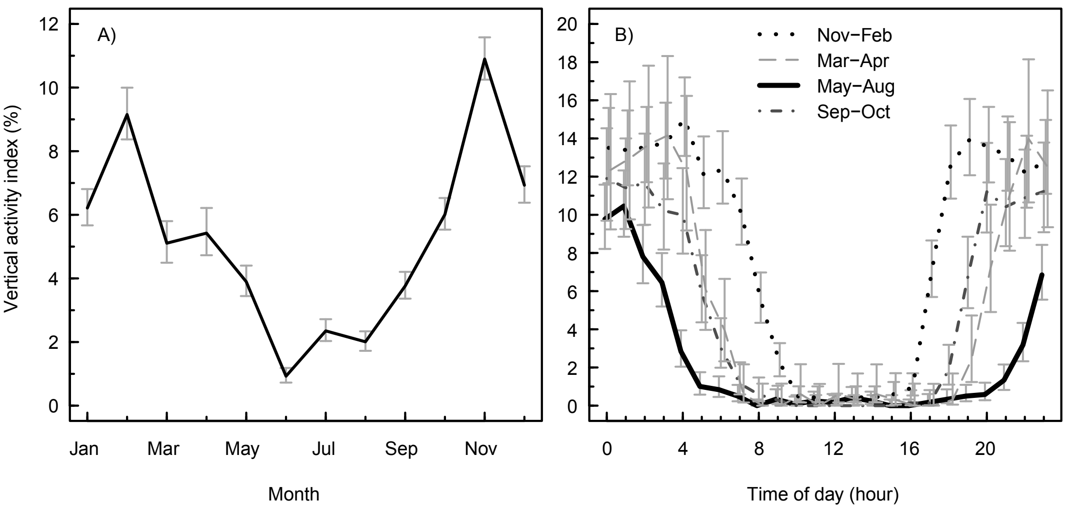

Figure 13. Average vertical activity index (%) plotted A) versus month and B) versus hour of the day for various seasons from pooled DST data of 10 anglerfish larger than 70 cm. The error bars show 95% confidence intervals. Figure from Paper III.

stated that the vision of many animals, including fish, is dependent on visible light, and the daylight may thus control certain behavioural and biological rhythms such as migration and breeding cycles.

Anglerfish in Faroese waters performed extensive vertical migrations, moving from depths of 100–400 m to near surface (0–50 m depth) during short time periods (few hours). The pelagic movement almost exclusively resulted in a different bottom depth after one vertical trip, and this movement occurred during all months in the year. This indicates that anglerfish in Faroese waters are not only restricted to stay close to the bottom, but may also occupy the pelagic environment (Paper III). Such pelagic movement behaviour of anglerfish is also documented in other areas in the northeast Atlantic, based on data from one DST tag (Thangstad *et al.* 2006) and from pelagic catches of anglerfish (Hislop *et al.*, 2000; Laurenson *et al.*, 2005; Thangstad *et al.*, 2006; Solmundsson *et al.,* 2010). Pelagic behaviour is also documented for one DST tagged *L. americanus* (Rountree *et al.*, 2008). Laurenson *et al.* (2005) hypothesized that anglerfish moved up in the water column to use the currents to migrate through an area and Solmundsson *et al.* (2010) hypothesized that one reason for vertical movement could be spawning or feeding migration through the area. The vertical activity of anglerfish in Faroese waters is low (approximately 5% of the registrations) (Paper III), so they can increase their movement efficiency and capacity by using currents as a transportation medium during migrations between spawning and feeding areas. Selective tidal migrations have been documented for Atlantic cod (Righton *et al.*, 2007).

The Faroese mark-recapture project of anglerfish using DSTs is the first in the northeast Atlantic to demonstrate the existence of a clear seasonal pattern in anglerfish migration/distribution (Paper III), and gives support to the hypothesis that anglerfish perform such migrations (Laurenson *et al.*, 2005). In addition, the importance of day length (i.e., light intensity) as a trigger of vertical migration/migration is indicated (Paper III).

4.2 Is there a Faroese anglerfish stock?

Both the investigations of life history parameters and mark-recapture analyses support the hypothesis that anglerfish in Faroese waters could be regarded as a separate stock. Firstly, all life history stages were found in this area, from eggs, larvae, juveniles, mature, ripe and spent males and females (Paper II). Secondly, feeding areas (Paper IV) as well as spawning and nursery areas (Paper II) were located in this area. Thirdly, the growth rate for sexes combined showed that anglerfish in Faroese waters grew slightly slower compared to anglerfish at Porcupine Bank (west of Ireland) (Landa *et al.*, 2013), in Icelandic (Jónsson, 2007) and Norwegian waters (Dyb, 2003). The difference in these results could be due to different stocks and/or due to difficulties in accurate ageing of anglerfish (Paper I and II; Landa *et al.*, 2008; Landa, 2012). Fourthly, mark-recapture data in Faroese waters, both conventional tagging and data storage tags showed an offshore-onshore migration on the Faroe Plateau, which is consistent with a spawning migration and a subsequent homing to the feeding areas (Paper III). Very few anglerfish migrated between neighbouring regions, e.g., between Iceland, Faroes and Norway (< 5%). All these informations strongly support the view that there is a separate anglerfish stock on the Faroe Plateau.

No anglerfish tagged on the Faroe Plateau were recaptured on the Faroe Bank and the presence of pelagic larvae on the bank could indicate an existence of a separate anglerfish stock on the Faroe Bank area, as is the case for cod (ICES b, 2012). However, the data is not sufficiently comprehensive to support this, and further studies are needed before any firm conclusions can be drawn. The existence of more than one anglerfish stock in Faroese waters as opposed to just one stock, is, however, not a major problem with regards to a stock assessment or management advice, since the assumption of limited exchange of individuals between Faroese anglerfish and other anglerfish populations in the northeast Atlantic is still fulfilled.

On the other hand, so far no genetic differences at microsatellite loci of anglerfish have been found in the northeast Atlantic (O'Sullivan *et al.*, 2005). Unfortunately no samples from Faroese waters were included in that work. Otolith microchemistry of the sagittal otoliths of juvenile anglerfish from the northeast Atlantic suggested limited exchange between locations during some period of the early life history (Swan *et al.*, 2004). Pelagic stages may intermix over wide areas, but in anglerfish there is evidence of transitory segregation (that individuals from different populations sometime mix), which probably leads to and explain the limited genetic and morphological differentiation between populations

(Swan *et al.*, 2004). An extensive drift of eggs and larvae throughout the region was considered to have limited the potential for genetic isolation, despite variation in environmental regimes that could have affected phenotypic features of larvae as they settle (Hislop *et al.*, 2001). This is, however, not a major problem for the performance of an assessment of the anglerfish stock in Faroese waters as long as all the exchange of eggs/larvae/juveniles has occurred before the recruitment to the fishery. However, the relationship between the size of the spawning stock and subsequent recruitment may in such cases be misleading or meaningless, depending on the degree of the exchange (import and export) of pre-recruit individuals.

An investigation of *L. vomerinus* is illustrated here as an example of a stock structure of a related species. Samples of *L. vomerinus* from different areas along the South African coast did not show any genetic differences, but the variation in meristic and morphometric characteristics was evident (Leslie and Grant, 1990). These differences in characteristics were thought to be environmentally driven and not related to segregation of specific genes (Leslie and Grant, 1990). The differences in life history characteristics of anglerfish in the northeast Atlantic could be environmentally driven as the different regions have different abiotic characteristics, e.g., temperature and current systems. Nevertheless, anglerfish in Faroese waters still fit in the stock definition by Hilborn and Walters (1992) who stated that 'stocks are arbitrary groups of fish large enough to be essentially self-reproducing, with members of each group having similar life history characteristics'.

4.3 Assessment, exploitation dynamics and sustainability of the anglerfish stock in Faroese waters

Here the results from the stock assessment of anglerfish in Faroese waters is used to investigate and explore how these results comply with the concept of sustainability in the fishery, or more specifically, whether there are signs of growth and/or recruitment overfishing.

4.3.1 Results from stock assessment

The demonstration of one (or two) separate Faroese stock unit(s) along with the development of a validated age determination (Paper I), estimates of proportion mature at age (Paper II) and weight at age (Paper IV) of anglerfish in Faroese waters, allowed the performance of an age-based assessment of anglerfish in this area. This is the first assessment of anglerfish in Faroese waters and the results were promising in terms of a good fit between catch at age and the age-disaggregated tuning series (Paper IV). The assessment provided quite reliable results (Paper IV), although there is certainly scope for improvement of the assessment in the future, such as further refinement of the tuning series and model settings.

The results from the stock assessment for the years 1999–2011 estimated that the recruitment at age 2 fluctuated between one and two million individuals, with high values in the period 2000–2003 with a maximum in 2003 of nearly 2 million individuals (the 2001 year class). Thereafter the recruitment decreased to between 1 million and 800 thousand individuals in the period from 2007 to 2011 (Figure 14A). The range in recruitment of about 1 million individuals of anglerfish is small (coefficient of variation = 0.29) compared to the range in recruitment of e.g., cod on the Faroe Plateau, which fluctuated with more than 100 million individuals (coefficient of variation = 0.65) (ICES b, 2012). Anglerfish stock size varied between 10 and 18 thousand tonnes, with a maximum in 2004 and 2005, and the spawning stock biomass varied between 4 and 8 thousand tonnes (Figure 14B). Fishing mortality (Fbar 3–8) was on average 0.32 $year^{-1}$ with a maximum in 2006 and 2007 of 0.50 $year^{-1}$ (Figure 14A). Comparing the fishing mortality of anglerfish in Faroese waters with the average F for the period 1999–2011 for other stocks in Faroese waters where there are assessments available e.g., Faroe haddock (Fbar 3–7 of 0.33 $year^{-1}$) gave comparable values, while they were lower compared with Faroe Plateau cod (Fbar 3–7 of 0.55 $year^{-1}$) and Faroe saithe (Fbar 4–8 of 0.43 $year^{-1}$) (ICES b, 2012).

4.3.2 Investigation of growth overfishing

'Growth overfishing occurs when (small) individuals are removed so rapidly from the population that their growth potential is not fully utilised' (Hilborn and Walters, 1992). Yield per recruit (Y/R) is one method to investigate if the stock is growth overfished (Hilborn and Walters, 1992). Y/R was

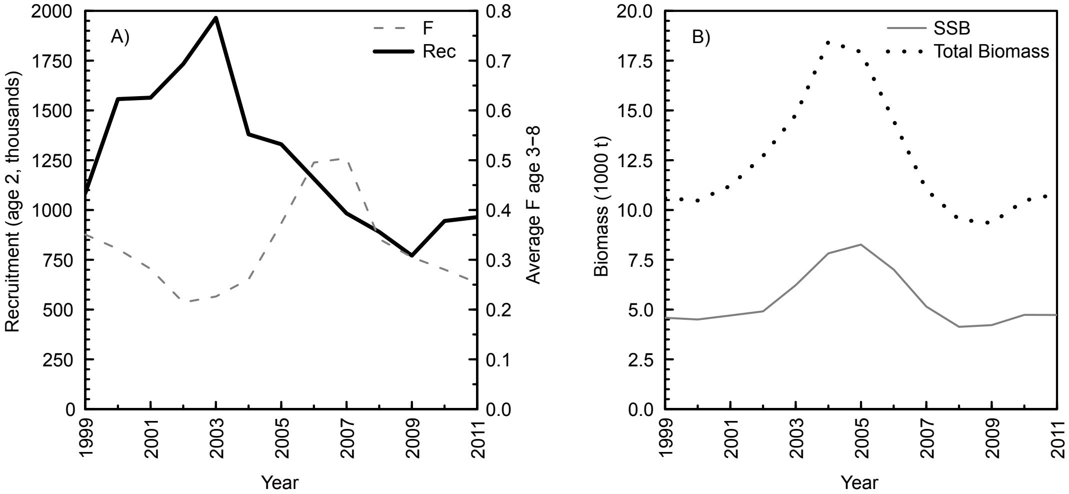

Figure 14. A) Recruitment (Rec, age 2, thousands) and annual fishing mortality rates (F, average for ages 3–8) and B) total biomass and spawning stock biomass (SSB) in tonnes as obtained in the age-based stock assessment of anglerfish in Faroese waters.

based on average weight at age and exploitation pattern obtained in the stock assessment (Paper IV). These calculations estimated a Fmax value of 0.15 year^{-1} and Y/R value of 2.7 kg (Figure 15). The Y/R curve had a rather well defined maximum, probably because the first catch age is lower than the age of biomass maximum and the natural mortality rate (M) is relatively low (Hilborn and Walters, 1992).

When comparing the average estimated fishing mortality (Fbar 3–8) of 0.32 year^{-1} for the period 1999–2011 with Fmax of 0.15 year^{-1} it is evident that there is some degree of growth overfishing. Therefore, the fishing mortality should be decreased to get the maximum yield per recruit. However, a fishing mortality of 0.3 year^{-1} leads to a Y/R of 2.5 kg, which is 90% of the maximum value of Y/R of 2.7 kg at Fmax. Still, a decrease in fishing mortality of 50% can give a potential increase of Y/R of about 10% and increase the stock biomass by around 50%. The expected yield was calculated by multiplying average recruitment of 1256 thousand individuals with Y/R for a specific F. The expected yield corresponding to an F of 0.3 year^{-1} is nearly 3100 t and for Fmax of 0.15 the expected yield becomes 3400 t, only 300 t higher.

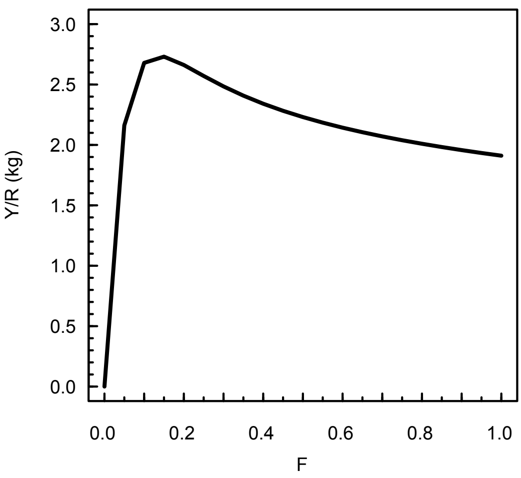

Figure 15. Yield per recruit (Y/R) as a function of fishing mortality (F ages 3–8). Fmax is 0.15 year^{-1} and maximum yield per recruit is then 2.7 kg.

4.3.3 Investigation of recruitment overfishing

'Recruitment overfishing occurs when the fishing pressure is so high that the spawning stock biomass (SSB) is severely reduced, causing a shortage of spawning products and subsequent reduced recruitment of young individuals to the fishable stock' (Hilborn and Walters, 1992). According to this, a positive relationship between the size of the spawning stock and subsequent recruitment should be expected, or at least a hampered recruitment at extremely low sizes of the spawning stock. For anglerfish in Faroese waters no such positive relationship is observed (Figure 16) (correlation between recruitment and SSB: $R = -0.33$, $df = 9$, $p = 0.32$). This indicates that other factors than size of

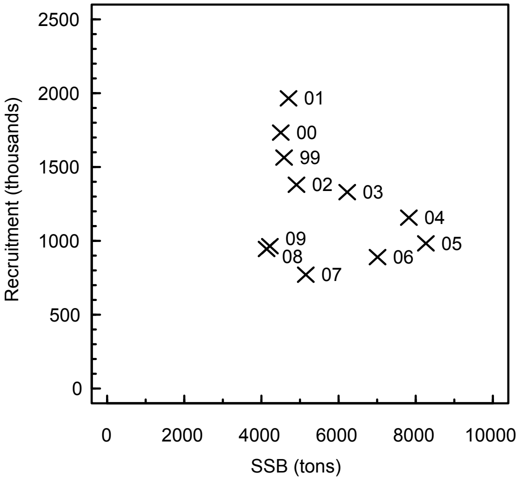

Figure 16. Recruitment versus spawning stock (SSB). The labels indicate the years when the recruits were 0 years old.

the spawning stock may have influenced anglerfish recruitment during the period 1999–2011.

It was explored whether the recruitment variability was correlated with environmental factors. The year class strength was assumed to be determined at the 0-group stage, and the best estimate of year class strength was assumed to be the number of individuals that recruited to the fishery two years later. The environmental factors included i) average annual sea temperature, ii) the extent of the subpolar gyre, iii) index of primary production on the Faroe Shelf, iv) zooplankton biomass in late June, and v) sandeel abundance as average number per stomach from cod, haddock and saithe stomachs (Figure 17). The results from a simple linear regression analysis between recruitment and each of these indices (one at a time as the independent variable) showed that only the sandeel index showed a significant positive relationship with anglerfish recruitment, whereas the zooplankton biomass showed a significant negative relationship (Figure 17).

It may be a difficult to link correlations to causal factors, but the strong correlation with sandeel abundance can be explained by the importance of sandeel as prey for pre-settled anglerfish juveniles and small bottom settled juveniles (Paper IV). If this relationship is causally linked, then it indicates that anglerfish recruitment is governed by the ecosystem dynamics in the shallow retention areas on the Faroe Plateau, as opposed by the deep areas where the anglerfish spawning occurs. The link to sandeels is further substantiated by the fact that sandeels are found to be an important link between primary production and higher trophic levels (Steingrund and Gaard, 2005; Eliasen *et al.*, 2011). The negative correlation with zooplankton biomass is more difficult to link causally, but one possibility is that the relationship is caused by a high predation pressure on copepods from various pelagic fish juveniles and sandeels or low advection of the oceanic copepod *C. finmarchicus* onto the shelf in years with good fish recruitment in general (Gaard *et al.*, 2002; Gaard, 2003; Hansen *et al.*, 2005).

As the anglerfish larvae and pelagic juveniles were only found in the "outer" areas on the Faroe Plateau (i.e., outside the shelf front), a correlation

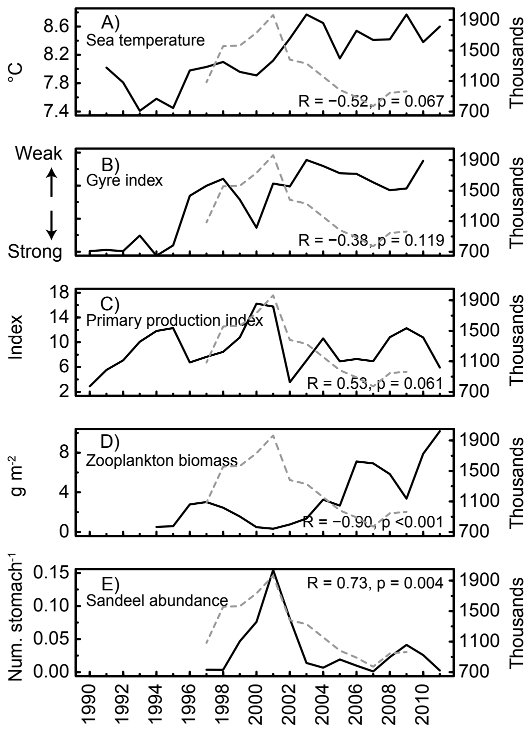

Figure 17. Comparison between anglerfish recruitment (age 2) for the period 1999–2011, moved two years back (age 0, grey dashed line, secondary axis) with A) annual average sea temperature, B) extent of the subpolar gyre (inverted), C) index of primary production, D) zooplankton biomass, and E) average of sandeel abundance in cod, haddock and saithe stomachs. Least square linear regressions between anglerfish recruitment and the indices (one at a time as independent variable) for the period 1997–2009 (13 years) are showed with R and significance probability (p). Note that the y-axis does not always start at zero.

between the gyre index and the year class strengths could be expected. This is, however, not the case. On the other hand there is a positive correlation with primary production in the inner area inside the shelf front. This further gives support to the finding that the shallow areas are more important for anglerfish recruitment than the deeper areas. It has to be noted that the 0-group survey indices for several species such as cod, haddock, saithe, Norway pout and sandeels showed a high index in 2001 (Faroe Marine Research Institute, unpublished data), so there seemed to be favourable conditions for many fish eggs and larvae that year, and not only anglerfish.

These medium ($R > 0.5$) and high ($R > 0.7$) correlations between anglerfish year class strength and environmental variables such as sea temperature, primary production, zooplankton biomass, and sandeel abundance could indicate that anglerfish recruitment depends much on what is happening during their first year of life (age 0). It should, however, be kept in mind that no firm conclusion can be drawn and further investigations are needed.

4.3.4 Is the anglerfish fishery in Faroese waters sustainable?

The stock assessment in this study showed that the anglerfish stock size and spawning stock size is at approximately the same level as before the large year classes spawned in 2000–2001 and in addition that maximum fishing mortality was approximately three times natural mortality (Paper IV). The yield per recruit analysis showed that the average fishing mortality of 0.3 $year^{-1}$ is indicative of a slight growth overfishing. A decrease of actual F to Fmax could potentially give rise to an increase in Y/R of about 10% and an increase in the equilibrium total stock biomass by as much as around 50%. The fact that the actual fishing mortality was higher than Fmax can be interpreted as growth overfishing. There was no clear relationship between the spawning stock size and recruitment indicating limited or no recruitment overfishing. In addition, the environmental factors, such as sandeel abundance and temperature, explain much of the variations in the recruitment. This suggests that the environmental factors have controlled the recruitment variability of anglerfish in Faroese waters whereas the size of the spawning stock has been of less importance.

It should, however, be borne in mind that the anglerfish assessment time period is short so the correlation between recruitment and environmental factors is based on a rather limited dataset (only 13 years), characterised by little variability and only one peak. Anglerfish have a large body size before they spawn so it is important to secure that the anglerfish are not overfished as this would affect not only the fish stock but in the end also have negative consequences for the profit of the anglerfish fishery. It is important to keep the stock so large that it is able to sustain both the fishing pressure and natural variations in the environment which could have negative effects on the anglerfish stock. If the relationship between anglerfish recruitment and environmental variables (e.g., sandeel abundance and zooplankton biomass) is real, then it is expected that the catch of anglerfish will be less in 2013–2015 than during the assessment period 1999–2011 where the catches were highest ever (between 2000 and 5200 t). The preliminary catch for 2012 of nearly 1300 t (Statistic Faroe Islands, 2013) supports this hypthesis. Stock assessments of anglerfish in Faroese waters should be performed on an annual basis, so managers can respond in time to unfavourable natural conditions and/or low stock sizes.

4.4 Interactions between anglerfish and cod, haddock and saithe

There was a clear predator prey interaction between anglerfish and cod. Annual consumption by anglerfish, for the period from 2001 to 2005, on cod is estimated at 11% of the stock biomass of cod, 33% of the annual landings and 75% of the estimated annual biomass loss due to natural mortality, respectively (Paper IV). There was a significant increase in the mean prey length of cod with anglerfish length (Paper IV), so anglerfish predated on all sizes of cod. Even though the annual loss of biomass due to natural mortality (mostly anglerfish predation) was so high for cod, the cod fishery itself had a greater impact on the stock dynamics of cod than anglerfish predation, since the fishing mortality was more than twice as high as the natural mortality losses due to predation by anglerfish (ICES b, 2012). It could be questioned whether the natural mortality value of 0.2 $year^{-1}$ for cod is set too low (P. Steingrund, pers. comm.). Anglerfish consumption of haddock and saithe corresponded to 3 and 0.3% of the stock biomass, 19 and 2% of the annual landings and 20 and 2% of estimated natural mortality biomass loss, respectively (Paper IV). Thus, assuming that the natural mortality estimates for these species were correct, anglerfish predation did not have any great impact on haddock and saithe compared with cod (Paper IV). An increase in anglerfish stock biomass will probably increase the predation on cod, haddock and saithe.

On the other hand, investigation of cod, haddock and saithe stomachs showed that only cod were found to predate on anglerfish. Eighteen cod stomachs (0.2%) contained anglerfish prey out of a total of 9048 cod stomachs from 1997–2010, and anglerfish was never found in the stomachs of haddock or saithe (Faroe Marine Research Institute, unpublished material). Cod larger than 70 cm in length (about 3 kg, age 5+) predated on juvenile anglerfish smaller than 25 cm (0 and 1 group fish). Comparing anglerfish year class strength with the biomass of predatory cod (age 5+ years) 1999–2011 gave significant positive relationship (linear regression, $R = 0.72$, $p = 0.006$, $N = 12$), indicating that the biomass of large cod did not have any large effect on anglerfish recruitment. Hence, anglerfish may affect cod more than cod affect anglerfish.

5 Conclusions and future perspectives

This study gave a vital contribution to the discussion of anglerfish growth in the northeast Atlantic, because the estimates of anglerfish growth rate in Faroese waters based on age determination fitted exceptionally well with growth estimates derived from the length frequency and mark-recapture analyses. Therefore the present results have provided an important basis with respect to potential future assessments of anglerfish in general.

Anglerfish in Faroese waters should be treated as a separate stock, because all anglerfish life stages, from egg-ribbons, larvae, juveniles, adults, nursery areas, spawning areas and feeding areas, have been observed and documented in the Faroese area and since the migration rate to and from this area is small. Both spawning and nursery areas have been indicated on the Faroe Plateau and on the Faroe Bank. It has been shown that anglerfish perform seasonal offshore migrations to spawning areas in deeper waters during the winter and onshore migrations to feeding grounds during the spring. This is the first study that proves seasonal migration for anglerfish with data from data storage tags.

An assessment of anglerfish in Faroese waters for the period 1999–2011 provided recruitment (age 2) estimates of between one and two million individuals and was highest during the period 2002–2003. The stock size (biomass) is estimated to have varied between 9000 and 19000 t while fishing mortality (Fbar 3–8) varied between 0.25 and 0.50 year^{-1}, with an average of 0.32 year^{-1}. The yield per recruit analysis indicated that an average F of 0.30 year^{-1} was indicative of a slight growth overfishing of anglerfish in Faroese waters, while a decrease of actual F to Fmax could potentially increase yield per recruit by about 10% and that the equilibrium biomass could increase by as much as around 50%. In addition, the environmental factors, such as sandeel abundance and zooplankton biomass, explained much of the variation in the recruitment. This could indicate that environmental factors were more important regulators of anglerfish year-class strength than the size of the spawning stock, and that recruitment overfishing was therefore of minor importance in Faroese waters for the time being.

The present study has revealed that there are still unsolved biological questions. There is no fecundity data for anglerfish in Faroese waters, so such data should also be obtained. The nursery areas of anglerfish shallower than around 80 m should be investigated more closely, because anglerfish recruitment seems to be closely linked to e.g., the sandeel abundance, which are present in the areas shallower than about 120 m on the Faroe Shelf. The data from ten data storage tags recaptured on the Faroe Plateau also needs to be investigated further. In order to investigate the possibility of more than one anglerfish stock in Faroese waters, a mark-recapture project, using both conventional and data storage tags should be introduced on the Faroe Bank area and perhaps also east of the Faroe Islands. In addition, the present stock assessment should be further analysed, and anglerfish stock assessments should be performed annually in order to monitor the sustainability of the anglerfish fishery.

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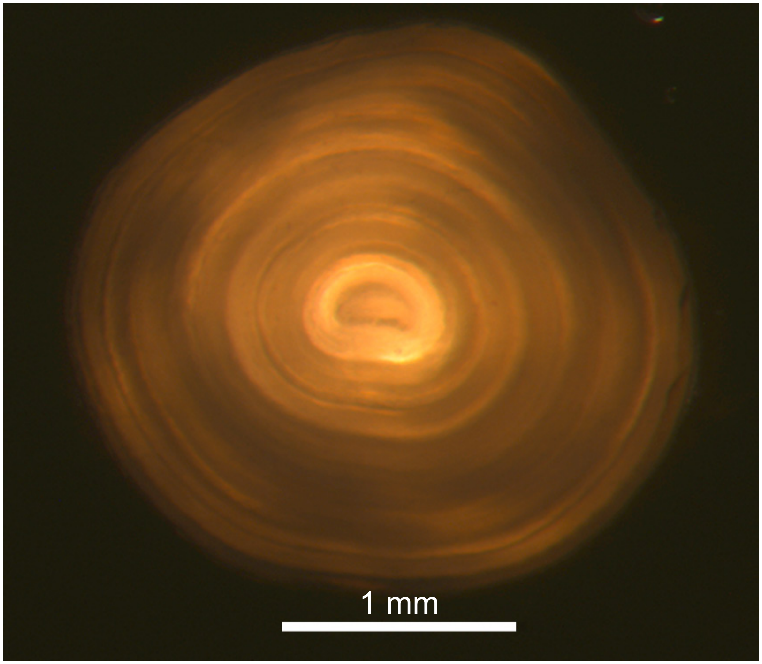
Paper I

Age and growth of anglerfish (*Lophius piscatorius*) in Faroese waters



Paper II

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

Paper III

Seasonal offshore-onshore migration and distribution of anglerfish *Lophius piscatorius* in Faroese waters

Paper IV

Feeding ecology of anglerfish *Lophius piscatorius* in Faroese waters

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