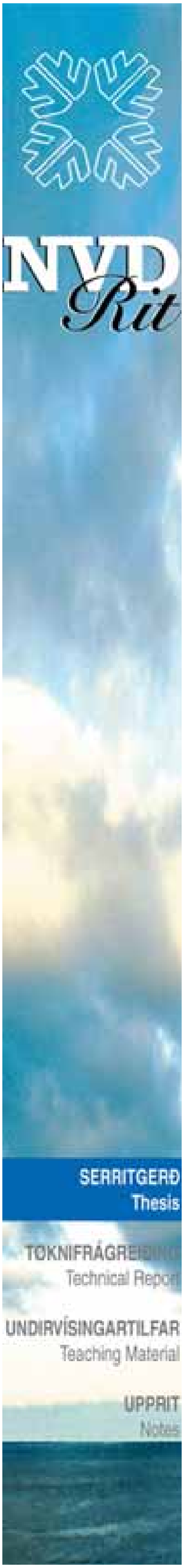

Ph.D. Thesis

The Effects of Climate and Ocean Currents on Faroe Saithe

Eydna í Homrum

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NÁTTÚRUVÍSINDADEILDIN FRÓÐSKAPARSETUR FØROYA
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The Effects of Climate and Ocean Currents on Faroe Saithe

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Preface

This work has been done at Faroe Marine Research Institute in Tórshavn, Faroe Islands and is the basis for the dissertation for the degree of philosophiae doctor (Ph.D.) in marine biology at the University of the Faroe Islands, where also the majority of the Ph.D. courses have been taken.

The first part of this thesis, is a list of the papers with a short summary. Paper I is published in a peer-reviewed journal. Paper II and III are submitted to peer-reviewed journals and the remaining three papers are manuscripts. Paper V was originally presented at an ICES conference during the first year of the project, and is included because the conclusions were more like questions, which have driven the work ahead since.

In the next part an introduction is given to provide a background consisting of existing knowledge on saithe, in Faroese waters and also more generally, and a brief overview over the Faroese marine ecosystem and to explain the objectives of the study. After that follows a short presentation of the datasets, on which the results of the project are based. The results and discussion have been merged. To some extent they follow distinct papers, but where themes overlap they are discussed. In the end of the discussion there is a section that discusses some of the findings in relation to management of saithe. Finally, there are two sections with the main findings of the Ph.D.-project and proposed future research.

After that Papers I-VI follow.

Acknowledgements

First and foremost I wish to thank my main supervisor, Prof. Bogi Hansen. With patience, enthusiasm and thorough guiding he has helped me tremendously during this project. My co-supervisors Dr. Petur Steingrund and Dr. Hjálmar Hátún have also contributed much to my understanding of being a scientist and have readily commented on drafts of various kinds.

Part of the project was done in collaboration with scientists abroad, and this has been an experience that I know I will value a lot in the future. Especially, I wish to thank Kathrine Michalsen, Norway, and Sigurður Þór Jónsson, Iceland, for their hospitality when I visited their institutes.

To my fellow Ph.D-students at Faroe Marine Research Institute: Dr. Gunnvør á Norði, Lise Helen Ofstad and Kirstin Eliasen – thanks to all of you. Discussions on both scientific and personal issues have helped me very well.

Also the staff at Faroe Marine Research Institute and the director, Dr. Eilif Gaard, have supported me well. This they have done with their interest in my work, and also by providing a joyful working environment. Thanks to Dagunn Clementsen for taking time to prepare the layout of the thesis.

The scientific material available to me during the Ph.D.-project has been sampled over many years. The effort many people have put into this work is greatly acknowledged.

I also wish to thank relatives who have offered to help us at home, with keeping daily routines during the past months.

At last I wish to thank my family. Sometime during the first year of the project, my son Sigurd (10 at the time) said: “I know why it is called Ph. D. It means People Have much to Do.” Yes, there have been late hours, and at times the fuse has been short. You have all been very patient and understanding. Thank you for standing by me.

This research was a part of the research programme “Marine Climate and Ecosystem around the Faroes” and was funded by the Danish Agency for Science, Technology and Innovation.

Tórshavn, April 2012
Eydna í Homrum

Føroyskur samandráttur (Faroese summary)

Upsi verður fiskaður víða um í Norðuratlantshavinum, og her við Føroyar hevur upsin seinnu árini landsbúskaparliga havt minst líka stóran týdning sum toskurin, sum annars søguliga hevur verið tann botnfiskurin, sum hevur havt størst týdning fyri føroyingar. Árligu landingarnar av upsa hava ligið millum 20 og 60 túsund tons síðstu hálvu øldina, og sveiggini í landingum spegla í stóran mun, at upsastovnsstøddin er skiftandi. Síðan sekstiárini hevur Havstovan gjørt stovnsmetingar av upsa, og í hesum tíðarskeiði er stovnsstøddin vaksin og minkað í trimum tíðarskeiðum, sum vara eini 20 ár hvørt. Seinnu árini hevur nógv verið granskað í sambandinum millum umhvørvi og fiskastovnar, og til dømis hevur verið ávíst, at gróðurin á innaru økjunum á Landgrunninum stýrir bæði tilgongd og vøkstri hjá toski og hýsu. Eisini er funnið út av, at svartkjaftastovnurin í stóran mun verður ávirkaður av fysiskum broytingum í havstreymunum kring okkum – tann sonevndi subpolari meldurin.

Upsastovnsstøddin vísir eitt tíðarmynstur, sum líkist nógv gongdini í subpolara meldrinum, og henda verkætlan varð sett í gongd til tess at kanna, um vit kunnu finna nøkur sambond millum fysiska umhvørvið og lívfrøðina hjá upsa undir Føroyum.

Høvuðsúrslit

Upsi gýtir í februar-marts mánaði eystanfyri. Vøksturin fyri kvenn- og kallfiskar líkist nógv, men kvennfiskar kynsbúnast eitt ár seinni enn kallfiskar. Helvtin av kvennfiskunum er kynsbúgvin, tá upsin er um 6 ára aldur. Tá eru kvennfiskarnar um 60 cm til longdar. Høvuðsføðin hjá føroyskum upsa er svartkjaftur, hvítingsbróðir, krill og nebbasild. Fyri ungan upsa eru hvítingsbróðir, nebbasild og krill týdningarmest, meðan svartkjafturin fær størri týdning, sum upsin veksur og flytur longri út á Landgrunnin.

Tilgongdin av trý ára gomlum upsa til stovnin er knýtt at gróðrinum inni á Landgrunninum, men sterkari samband varð funnið millum upsatilgongd og nøgdina av nebbasilda- og hvítingsbróðuryngli í junimánaði í árunum undan tilgongdini, tvs tá seiðurin var 1-2 ára gamal. Hinvegin var eisini eitt veikt samband funnið millum tilgongd og heitari umstøður í ytru økjunum á Landgrunninum, tá subpolari meldurin er lítil. Ábendingar eru um, at ein javnvág á føroyska landgrunninum er broytt síðan mitt í farnu øld. Áðrenn 1970 vóru toska- og hýsustovnarnir lutfalsliga nógv størri samanborið við upsastovnin, og nebbasild var tá týðandi partur av føðini hjá toski øll árini. Seinnu árini er upsastovnurin vorðin væl størri, og nebbasild er nú einans vanlig toskaføði fá ár á rað. Samlaða náttúrliga framleiðslan av toski, hýsu og upsa tykist tó fylgja væl gróðrinum, sum er á teimum innaru økjunum á Landgrunninum. Hetta bendir á, at sambandið millum tilgongd hjá upsa og subpolara meldurin (umstøður á ytru leiðum á Landgrunninum) ikki er veruligt, og at gróðurin í innaru økjunum á Landgrunninum hevur størri týdning fyri tilgongdina hjá upsa.

Samstundis sum upsastovnurin er skiftandi í stødd, so vera einstøku fiskarnir smærri, tá upsastovnurin er stórur. Greiðar ábendingar eru um, at talan er um tættleikatengdan vøkstur, serliga fyri 3-6 ára gamlan upsa, soleiðis at talið av upsa er avgerandi fyri, hvussu stórir einstøku fiskarnir verða. Fyri elsta fiskin var vøksturin tó óávirkaður av stovnsstødd.

Upsi er ferðandi fiskur, men merkingarroyndir av upsa í eystara parti av Norðuratlantshavi vísa, at munur er á ferðingini hjá upsa í kanningarøkjunum. T.d. verður sera lítil útferðing funnin úr íslendskum øki (minni enn 1%), meðan eini 40% av vaksna føroyska upsanum verða fingin aftur uttan fyri føroyskt øki – størri parturin í íslendskum sjógvi. Vaksin upsi, merktur í Noregi, varð afturfingin uttan fyri europeiska landgrunnin í 7% av førunum. Upsi ferðast longri, jú størri hann er, upp til eina stødd á umleið 60 cm; tá upsin er størri enn 60 cm heldur ferðingin sær á sama støði.

Tá upsi er 5-7 ára gamal, byrja størstu upsarnir í hvørjum aldursbólki eitt árligt ferðingarmynstur. Í gýtingartíðini finnast allir støddarbólkar saman, men móti sumri fækkast størstu fiskarnir í hesum aldursbólkum. Longdin, har henda fráferðing byrjar at síggjast, svarar til longdina, tá upsin byrjar at verða kynsbúgvin, og tí kann hugsast, at her er talan um eina árliga ferðing millum gýtingarøki um veturin og føðiøki um summarið. Hesar niðurstøðurnar um árliga ferðing, sum eru grundaðar á broytingar í longdarbýtunum, verða stuðlaðar av gomlum merkingarroyndum. Merkingarroyndirnar vísa, at upsi, sum er merktur á Landgrunninum, ofta verður afturfingin í Íslandi um summarið, meðan bara fáir fiskar verða afturfingnir í Íslandi í gýtingartíðini.

Eitt modell var roynt, til at gera eina stovnsmeting av upsa, sum tók atlit til ferðing (vanligar stovnsmetingar taka ikki atlit til ferðing). Stovnsmetingin vísti, at gongdin í stovnsstøddini og fiskideyðanum frá vanligu stovnsmetingunum neyvan ávirkast nógv av ferðing, men at nøgdirnar og fiskitrýstið tó verða undirmett nakað.

Niðurstøður

Betraðu umstøðurnar, sum eru í okkara øki, tá subpolari meldurin viknar, vóru upprunaliga væntaðar at vera atvoldin til, at upsastovnurin økist júst tá. Sum verkætlanin er liðin, hava vit ikki funnið nógvan stuðul til hesa hypotesu – tó so, øktu nøgdirnar av svartkjafti, tá meldurin er veikur, eru vaksna upsanum til gagns. Tað er heldur gróðurin í innaru økjunum á Landgrunninum, sum hevur størstu ávirkan á føroyska upsan. Tá gróðurin er góður, økist tilgongdin til upsastovnin. Tá stovnurin so økist, vaksa einstøku fiskarnir seinni, og hetta ávirkar aftur ferðingarmynstrið. Tó at vit enn ikki kenna smálutirnar, týðir nógv soleiðis á, at skiftandi veðurlag gjøgnum gróður hevur stóra ávirkan á føroyska upsan.

Eisini er staðfest ein munandi ferðing hjá stórum upsa úr føroyskum øki. Henda ferðing kollveltir tó ikki niðurstøðurnar frá vanligu stovnsmetingunum, har tað ikki verður roknað við nakrari ferðing.

Contents

1 Papers

1.1 List of papers

I Homrum, E. í, Hansen, B., Steingrund, P. and Hátún, H. (2012): Growth, maturation, diet and distribution of saithe (*Pollachius virens*) in Faroese waters (NE Atlantic), Marine Biology Research, 8:3, 246-254.

II Homrum, E. í, Hansen, B., Jónsson, S. Þ., Michalsen, K., Righton, D., Steingrund, P., Jakobsen, T., Mouritsen, R., Hátún, H., Armannsson, H. and Joensen, J. S. (submitted): Migration of saithe (*Pollachius virens*) in the Northeast Atlantic: submitted for publication in ICES Journal of Marine Science.

III Homrum, E. í, Eliasen, K., Hansen, B., Hátún, H., Gaard, E., Reinert, J. and Steingrund, P. (submitted): Recruitment and growth of saithe (*Pollachius virens*) in Faroese waters. Submitted for publication in Marine Biology Research.

IV Homrum, E. í, Hansen, B., Steingrund, P. and Hátún, H. (manuscript): Seasonal migration of Faroe saithe (*Pollachius virens*).

V Homrum, E. í, Hansen, B., Steingrund, P., Ofstad, L. H. and Hátún, H. (manuscript): Is the growth of Faroese saithe density dependent or climate dependent.

VI Steingrund, P., Gaard, E., Reinert, J., Olsen, B., Homrum, E. í and Eliasen, K. (manuscript): Trophic relationships on the Faroe Shelf ecosystem and potential ecosystem states.

1.2 Summary of papers

I The paper describes life-history parameters of saithe in Faroese waters based on annual research cruises on the Faroe Plateau and Faroe Bank. The results are discussed in relation to the Faroese marine ecosystem and to knowledge on other saithe stocks in the Northeast Atlantic. Growth and maturity of Faroe saithe resembles that of other stocks, but the diet varies more among the regions in the Northeast Atlantic, although there is overlap.

II Migration among regions in the Northeast Atlantic is explored with the aim to obtain quantitative measures of migration rates. The paper demonstrates that the migration among regions in the Northeast Atlantic is considerable. It is found that migration between regions starts when saithe are approximately 50 cm in length and that beyond 60 cm the migratory behaviour is of substantial magnitude – but less so for Icelandic saithe than for Faroese and Norwegian saithe.

III This paper describes the negative correlation between stock size and individual size of saithe, and shows how the recruitment may be linked to the availability of 0-group sandeel and Norway pout to juvenile saithe on the Faroe shelf.

IV Seasonal variability in the length distributions in samples from the commercial catches is analysed. In periods, when individual saithe length is high, the length tends to decrease from January to August. This pattern seems to originate from seasonal migration from the main fishing grounds, with the largest fish in an age-group leaving the area in the summer months, i.e. probably after spawning. The seasonal variation in CPUE and in recapture of tagged fish outside the Faroe area supports this interpretation and indicates that the migratory behaviour of Faroe saithe may be seen as emigration in search of food combined with return spawning migration.

V Growth in weight of saithe from one year to the next is related to the amount of stomach contents in the year of growth. The results indicate that there is no correlation between growth and stomach contents. Some explanations to these contradictory results are discussed.

VI Trophic pathways from phytoplankton to seabirds are investigated for the Faroe Plateau. Two states are proposed, where zooplankton, Norway pout, and saithe dominate in one state and herring, sandeel, cod, and seabirds in the other.

2 Introduction

To manage a living resource well, in this case a fish stock, good understanding of the biology is of vital importance. The exploited resource is closely linked to other living organisms, as competitors, prey or predators. A physical change may thus affect the resource directly, e.g. in terms of salinity or temperature preferences. Perhaps more importantly, though, physical changes impact the lowest trophical levels – the primary production – and thereby the livelihood of entire ecosystems.

In a historical perspective, saithe have been an important part of the Faroese nation's food when large shoals came near to the coast and thus formed the basis for fisheries in fjords and sounds (Joensen and Tåning, 1970). Saithe are, nowadays, exploited commercially widely in the Northeast Atlantic. In Faroese waters, annual catches have varied between 20,000 and 60,000 tonnes per year during recent decades, which makes them one of the most important commercial species on the Faroe Plateau. From 2005-2010, when the landings were at the highest, the export value of saithe was around 500 million DKK (Statistics Faroe Islands, 2012). In some years, this exceeded the export value of cod, which traditionally has had the highest export value of the demersal stocks.

In addition to the scientific outcome of this work, it is hoped, that the acquired knowledge will be valuable to the assessment and management of the saithe stock in Faroese waters.

To prepare for the discussions of the main findings of the Ph.D.-project, we start out by presenting existing knowledge on the biology of saithe, prior to this project, and give a brief overview over the ecosystem on the Faroe Plateau. Data from stock assessments are also presented and strengths and weaknesses of these data are discussed.

2.1 Biology of saithe

2.1.1 General biology

Saithe (*Pollachius virens*) are a gadoid species, i.e. belonging to the same taxonomical family as e.g. cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), Norway pout (*Trisopterus esmarkii*) and blue whiting (*Micromesistius poutassou*). The first four are classified as demersal species, that is, they are closely associated with the sea-floor environment. Blue whiting, on the other hand, are a pelagic species. Saithe are generally described as being demersal, and in Faroese waters they are most often fished with bottom-trawl (e.g. ICES 2011a). But they do also exhibit pelagic behaviour (Neilson et al., 2003; Stensholt et al., 2002; Armannsson and Jónsson, submitted) and they are further distinguished from e.g. cod and haddock by forming schools (Partridge et al., 1980) to a greater degree.

Saithe are living on both sides of the North Atlantic Ocean – on the eastern side from the Barents Sea in north as far south as to the Bay of Biscay and across the Iceland-Scotland Ridge covering both Faroese and Icelandic waters. On the western side, saithe is found at the border between Canada and USA.

Spawning takes place primarily at bottom depths between 100 and 200 m (Olsen et al., 2010; Anon, 1998) in winter (Clay et al., 1989; Olsen et al., 2010). Juvenile saithe reside in inshore waters the first 2-4 years (Bertelsen, 1942; Clay et al., 1989; Armannsson et al., 2007). As adults, saithe move to offshore waters (Jones and Jónsson, 1971) and exhibit seasonal migrations between spawning and feeding areas (Jones and Jónsson 1971; Olsen et al. 2010).

The pelagic behaviour is also reflected in the diet, which is not directly associated with the sea-floor, e.g. pelagic crustaceans such as copepods, euphausiids, and amphipods (Nedreaas, 1987; Bergstad, 1991; Højgaard, 1999; Jaworski and Ragnarsson, 2006), and fishes such as Norway pout, blue whiting, herring (*Clupea harengus*), sandeel (Ammodytidae), and capelin (*Mallotus villosus)* (Pálsson, 1983; Du Buit, 1991; Bergstad, 1991; Jónsson, 1996; Jaworski and Ragnarsson, 2006; Olsen et al., 2010). Du Buit (1982) showed that the main diet of adult saithe in Faroese waters was the euphausiid *Meganyctiphanes norvegica* and fishes – especially Norway pout and sandeel.

2.1.2 Juvenile biology of saithe in Faroese waters

Questionnaires to fishermen (J. Reinert, pers. comm.) have indicated that the main spawning areas in Faroese waters are in the eastern part of the Faroe Plateau and in a narrow band north and west of the Faroe Islands (Anon, 1998).

Danish research vessels conducted marine biological studies in Faroese waters from 1903 to

1939. Results regarding saithe were presented by Bertelsen (1942) with a main focus on shallow water where juveniles reside.

Bertelsen (1942) found that the spawning of saithe in Faroese waters peaks around 1 April, inferred from the size of fry. Settlement of the juveniles was found to be in June – July in the littoral region and this is where they are found during the subsequent two years. Migration from the shallow coastal areas was suggested to start in the second summer as 1-year-olds, but all individuals within an age group did not necessarily leave at the same time.

The diet of the 0-group saithe (0-group implies that it is in the year of "birth") was dominated by copepods, chironomids, and amphipods. For 1-group saithe, small 0-group saithe were found in the diet in addition to copepods, and amphipods. In a more recent study, Højgaard (1999) found that the main diet of juvenile saithe (age group 1 and 2) consisted of pelagic crustaceans (hyperiid amphipods and euphausiids), polychaetes, and sandeel.

2.1.3 Migration

Faroe saithe are situated between three other saithe stocks: in Icelandic waters, in the Barents Sea and off the Norwegian coast north of 62°N and in the North Sea, Skagerrak and west of Scotland. Compared to these neighbouring stocks, the Faroe saithe is, historically, the smallest in terms of biomass (ICES, 2010a, 2010b, 2011a).

Jakobsen and Olsen (1987) found that adult saithe, tagged in northern Norway, emigrated to Icelandic waters and, to a lesser degree, to Faroese waters. Also, significant changes in length-at-age and catch-at-age from one year to another have been interpreted as immigration of saithe to Icelandic waters (Jonsson, 1996; ICES, 2000). Tagging in the Faroe area (Jones and Jónsson, 1971) showed that considerable proportions of saithe tagged on the Faroe Bank were recaptured in Icelandic waters, at North and West Scotland, and in the northern North Sea. In Icelandic waters, juvenile saithe appear to have high affinity to the area of tagging, and there is no indication of mass emigration from Icelandic waters (Jones and Jónsson, 1971; Armannsson et al., 2007). In Canada, migration of saithe has also been studied by means of tagging studies and also there, significant migration has been documented; 22% of recoveries of fish tagged in the eastern component of the stock were recaptured in the western study area, whereas only 2% of saithe tagged in the western component were recaptured in the eastern study area.

The saithe fisheries in the Northeast Atlantic have been monitored for a long time, and since the 1960s working groups addressing saithe have assembled at the International Council for the Exploration of the Seas (ICES). The migratory behaviour of saithe should encourage scientists to co-operate, as has been emphasized, e.g. in the Coalfish working group (1965). And the Saithe Study Group (1995) recommended that future tagging experiments should be internationally coordinated, provided that ICES managed to create the framework for designing tagging experiments and implementing migration in stock assessment. So far, there have, however, been only limited attempts to integrate the multinational information on migrations between the saithe stocks in the Northeast Atlantic.

2.2 The marine ecosystem in Faroese waters

The Faroe Islands are located on the Faroe Plateau between Iceland and Shetland on a ridge system

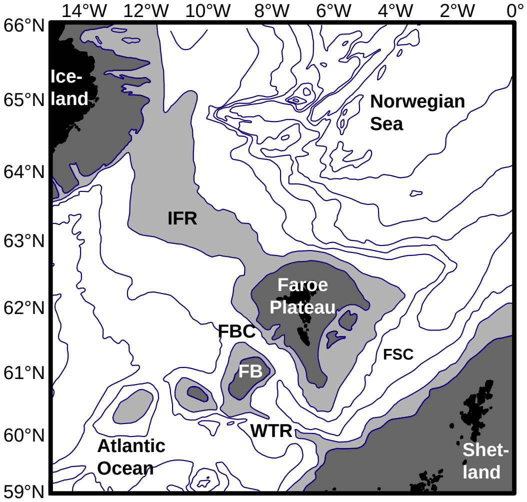

Figure 1. Bottom topography around the Faroe Plateau. Light gray areas are shallower than 500 m. Dark gray areas are shallower than 200 m. Topographic features: The Iceland-Faroe Ridge (IFR), the Wyville-Thomson Ridge (WTR), the Faroe-Shetland Channel (FSC), the Faroe Bank (FB), and the Faroe Bank Channel (FBC).

separating the Norwegian Sea from the Atlantic Ocean (Hansen and Østerhus, 2000). The Faroe Plateau is separated from shallow areas in all directions by deep waters (Figure 1). The shallowest connections to other areas are to Iceland following the Iceland-Faroe Ridge with sill depth slightly less than 500 m and to the European continental shelf via the Wyville-Thompson Ridge with sill depths around 600 m.

2.2.1 Inner system

The Faroe Shelf water is partially isolated from the oceanic water masses surrounding it, by clockwise residual currents generated by the strong tidal currents, which also keep the water column homogeneously mixed vertically (Larsen et al., 2008) (Figure 2). The vertical mixing combined with the shallow depths on the shelf also imply that winter cooling is more efficient than in the deeper surrounding areas (green area in Figure 2). Therefore the shelf water is denser in the early months of the year and this further inhibits exchange between the shelf water and oceanic water masses. This retention of the shelf water has important consequences for the ecosystem on the shelf, because it helps keep the primary and secondary production within the shelf, where they support an array of higher organisms, several of which are of commercial importance e.g. saithe, cod and haddock. Mean weight-at-age for cod and haddock, recruitment of cod and haddock and number of guillemots (*Uria aalge*) in a monitored area exhibit high correlation to an index of primary production (PP-index) (Gaard et al., 2002) (Figure 3). The primary production on the shelf has been monitored since 1990. Sandeel are a key species acting as a link between the primary production and higher trophic levels (Eliasen et al., 2011). Saithe, cod and haddock all feed on sandeel in Faroese waters.

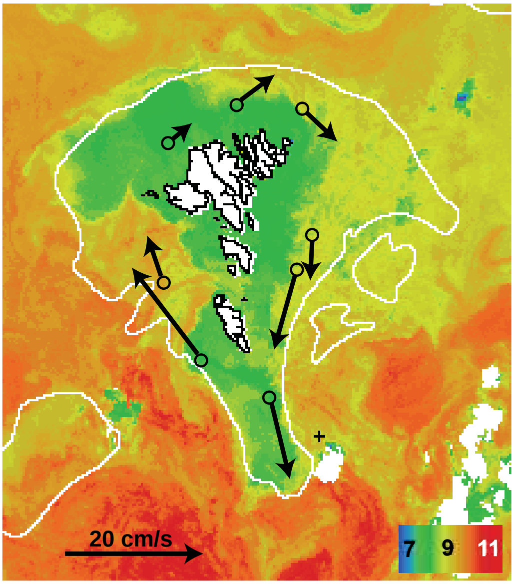

Figure 2. Background colours show surface temperature on 18, April 2003, measured from satellite (courtesy of P. Miller at Plymouth Marine Laboratory). Arrows show residual currents based on long-term current meter deployments at the sites indicated by circles, based on Larsen et al. (2008). Temperature and current velocity scales are shown in the bottom of the figure.

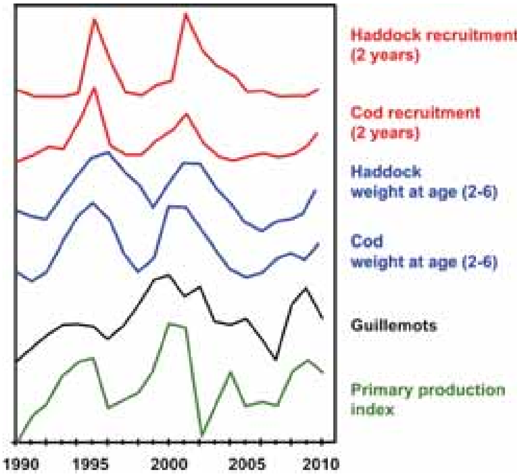

Figure 3. Relative variability in primary production, number of guillemots in a defined study area, recruitment of 2 year old cod and haddock and mean weight of 2-5 year old cod and haddock. Based on Gaard et al. (2002).

2.2.2 Outer system

The primary production outside the shelf on the Faroe Plateau is not monitored in the same manner as on the shelf. But several trophical levels (zooplankton, blue whiting and pilot whale (*Globicephala melas*), present in the deeper areas in the Faroese marine ecosystem, are linked to variability in the Atlantic subtropical and subpolar gyre system (Hátún et al., 2009a). Subpolar and subtropical water masses meet in an area south

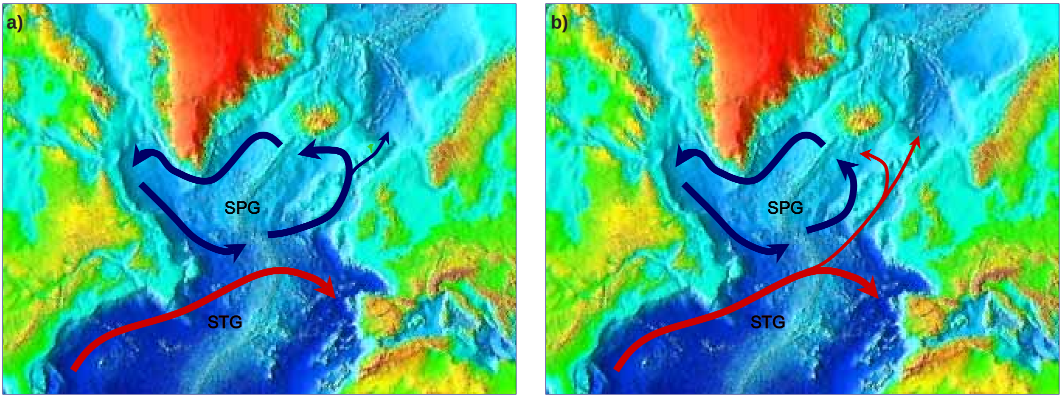

Figure 4. (a) A strong subpolar gyre results in strong influence of cold, subarctic water near the Faroes and Iceland. (b) A weak gyre results in a higher influence of warm, subtropical water masses. Based on Hátún et al. (2005).

of the Greenland-Scotland ridge, after which they flow into the Arctic Mediterranean (Hátún et al., 2005) (Figure 4). The warmer and more saline water of the subtropical gyre is associated with higher productivity. A weak subpolar gyre leads to increased inflow of warmer water masses, and increased productivity in the region. The denser water of the subpolar gyre has a lower sea level anomaly relative to the geoid than the subtropical water, and therefore a subpolar gyre index (GI) (Figure 5) was calculated based on sea surface height measurements (Hátún et al., 2005; Häkkinen and Rhines, 2004).

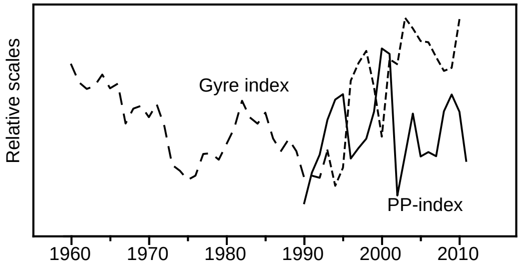

Figure 5. The inverted gyre index GI (dashed) and the PP-index (full). The GI from 1960 to 1993 is based on simulations (long dashed) (Hátún et al., 2005) and from 1993 to 2010, it is based on mapped satellite altimetry data (http://www.aviso.oceanobs.com) (short-dashed). From Paper III.

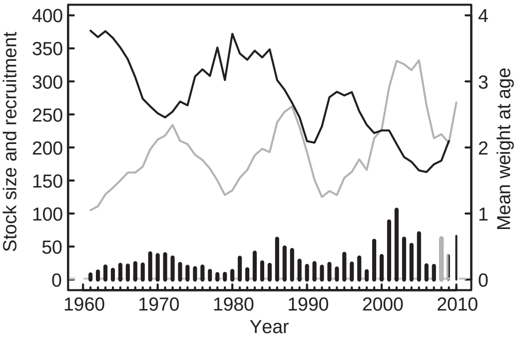

Figure 6. Recruitment in millions (bars), average weight of ages 4 to 7 in kg (black curve) and total stock biomass in thousand tonnes (grey curve). The grey bars indicate the 3 latest years, in which the recruitment estimates are generally rather uncertain.

This index serves as a proxy for productivity in the outer parts of the marine ecosystem on the Faroe Plateau. The distribution of blue whiting is linked to the GI, such that when the GI is negative (and productivity high), recruitment of blue whiting increases and it becomes much more abundant in the region between the Faroes and Iceland than in periods when the GI is positive (Hátún et al., 2009a; Hátún et al., 2009b).

Juvenile saithe live in the near shore areas, but as they grow, they move farther from land and become part of the outer system on the Faroe Plateau, in the reign of the GI. One of the main objectives of this Ph.D.-project was to investigate whether biology of saithe could be linked to this driver of productivity.

2.3 Stock assessments

The saithe stocks in the Northeast Atlantic are monitored to allow good management of the stocks. Every year scientists meet in ICES expert groups to present and discuss the stock-assessments, and ultimately ICES accepts or rejects the work and advices on the fisheries, based on the expert group reports. The assessment of saithe is based on virtual population analysis (VPA), an age based analysis where the stock sizes are calculated as seen in hindsight based on the catches of distinct year classes. This implies that a lot of biological data have to be sampled. Age, length and weight are required, in order to obtain estimates of catches-at-age. Age and sexual maturation are needed to estimate the spawning stock-biomass. In Figure 6, mean weight-at-age is presented together with the total stock biomass and recruitment for the Faroe saithe stock. For Faroe saithe, total stock refers to ages 3 and older. There is a cyclical pattern with saithe weighing least when recruitment/stock sizes are large.

The output from the stock-assessment consists of numbers in the stock of each age group. This coupled to mean weight-at-age and maturity data allows estimating the biomass in either the total stock or the spawning stock. Another output is the fishing mortality (F) – that is, the proportion taken from the stock by fishery.

There are strengths and weaknesses associated with assessment data. Strengths include that they provide long series (back to 1961 for the Faroe saithe) of both input and output data. The input data are originally based on other databases, but e.g. the original weight-at-age data for Faroe saithe are no longer available for the earliest years in the series. Weaknesses, tied to output data of the VPA, are that these are modelled values, assuming several things, e.g. constant natural mortality, and no migration.

In this Ph.D.-project, the assessment data have been used, knowing that there are uncertainties associated with them. In many cases they are used, because they cover 50 years, and therefore the main variability is believed to be consistent. In other cases, the uncertainties are discussed in relation to the obtained results.

2.4 Objective

The main objective of the Ph.D.-project was to investigate the role of climate and oceanographic factors in the biology of Faroe saithe. The objectives, as originally phrased, were:

- To explore migration patterns of saithe in the North Atlantic in relation to ocean currents.
- To explore how feeding, prey selection, growth, and condition of Faroe saithe depend on climate and ocean currents.
- To determine the effects of climate and ocean currents on fluctuations in the biomass of Faroe saithe.

It became clear that a paper describing the general biology of saithe was needed, and more detailed tasks were initiated:

- Analysis of survey data to acquire information on general biology of saithe in Faroese waters, i.e. spawning, distribution, growth, maturation and diet (Paper I).
- Analysis of density dependent growth of Faroe saithe, and how variable productivity in the ecosystem may explain the variability in recruitment of saithe to the adult stock (Paper III).
- Analysis of saithe migration based on tagging experiments. This work was done in collaboration with scientists in Iceland, Norway and England, thus obtaining an extra dimension (immigration to Faroese waters) to the research (Paper II).
- Analysis of seasonal migration of saithe based on individual length data from the commercial landings of saithe, logbooks from commercial trawlers and tagging data (Paper IV).
- Initially, an analysis of growth and food availability was done (Paper V), to investigate whether stomach contents could explain an observed decrease in mean weight-at-age. This paper opened the way for many of the hypotheses worked on later in the project, but did not come to clear conclusions regarding the fluctuations over time in mean weight-at-age, perhaps partly because some of the underlying assumptions turned out to be wrong, e.g. in how growth was calculated.
- Analysis of trophic pathways on the Faroe Plateau, which describes two possible regimes in the Faroese marine ecosystem (Paper VI).

3 Material

To achieve these objectives, a series of available data-sets were used:

Groundfish surveys in spring (1994-2011) and summer (1996-2011): These surveys are primarily designed for abundance indices of cod and haddock on the Faroe Plateau and Faroe Bank. In addition, biological parameters such as total length, round weight, sex, sexual maturity and age are sampled for an array of species. Also, stomach content analyses on cod, haddock and saithe have been conducted on these cruises since 1997.

Tagging studies: Saithe in Faroese waters were tagged from 1959-1967 and again in 1975-76 and 1991. Data from both tagging and recapture are available such as date, position and length. Also tagging data from Icelandic and Norwegian tagging studies were generously made available.

Biological data from samples of the commercial landings (~1985-2011): This database contains length, gutted weight and age for several species (including saithe), several gears and throughout the year.

Logbook data from the commercial fleet 1994-2009: Logbook data provide catch per unit effort series (CPUE) throughout the year for pair trawlers with directed fishery for saithe (defined as having at least 50% saithe in each haul).

Stock data 1961-2010: The stock assessments of Faroese fish stocks are quality checked under the ICES framework. Reports from these working groups contain valuable information on saithe in the Northeast Atlantic. From these reports, both input data and output data have been used. In principle the input data originate from other databases, e.g. survey data and samples from commercial catches, but these data are no longer available for the earliest years. Output data are the estimated stock-sizes in both numbers and biomass.

Index of primary production on the Faroe shelf 1990-2011: The PP-index is based on nutrient-depletion of the shelf water in June.

Gyre Index 1960-2011: The subpolar gyre index (GI) describes the strength of the subpolar gyre and is based on measurements of sea surface height (1993-2011). A simulated series is available for the period 1960-2003.

0-group survey 1983-2010: Abundance (mean number per haul) and mean length of fry of sandeel, Norway pout and saithe are obtained from the annual 0-group survey in June-July.

4 Results and Discussion

This section describes and discusses the main results gained during the Ph.D. project.

4.1 General biology

Saithe have been monitored for more than 50 years in Faroese waters (ICES, 2011a) and during this time, a lot of scientific material has been gathered. The knowledge acquired from these investigations has been important to the stock assessments, and in addition, several reports have been written. Unfortunately, little was available in the published literature. Paper I describes the general biology of saithe based on groundfish surveys conducted in February-March (since 1994) and August (since 1996).

4.1.1 Spawning time and main spawning area

Main spawning of saithe in Faroese waters has ceased by mid-March, which is earlier than concluded by Bertelsen (1942). Earlier spawning period in recent years has also been observed for cod (Steingrund et al., 2005). The discrepancy may, however, be caused by the different study methods. In our study, spawning time was determined by how the percentage of ripe, spawning and spent saithe changed over time, although a rigid determination of the peak spawning was not possible based on our data. Along the Norwegian coast, peak spawning occurs during February (Olsen et al., 2010) and in the North Sea, from January to March-April (Reinsch, 1976). In Canadian waters, saithe are found to spawn from November to March with peak spawning in December to February (Clay et al., 1989). In addition to the difference in timing of the spawning in the eastern and western North Atlantic, there is also difference in the lowest temperature and salinity tolerated by saithe, with western saithe spawning at temperatures down to 3°C and salinities as low as 32 whereas the limits for the eastern saithe are 5.5°C and 35 (references in Reinsch, 1976).

The main spawning area seems to be on the eastern parts of the Faroe Plateau based on the distribution of ripe and spawning saithe, even though spawning fish are not conclusive evidence of spawning area. It is, however, supported by the fact

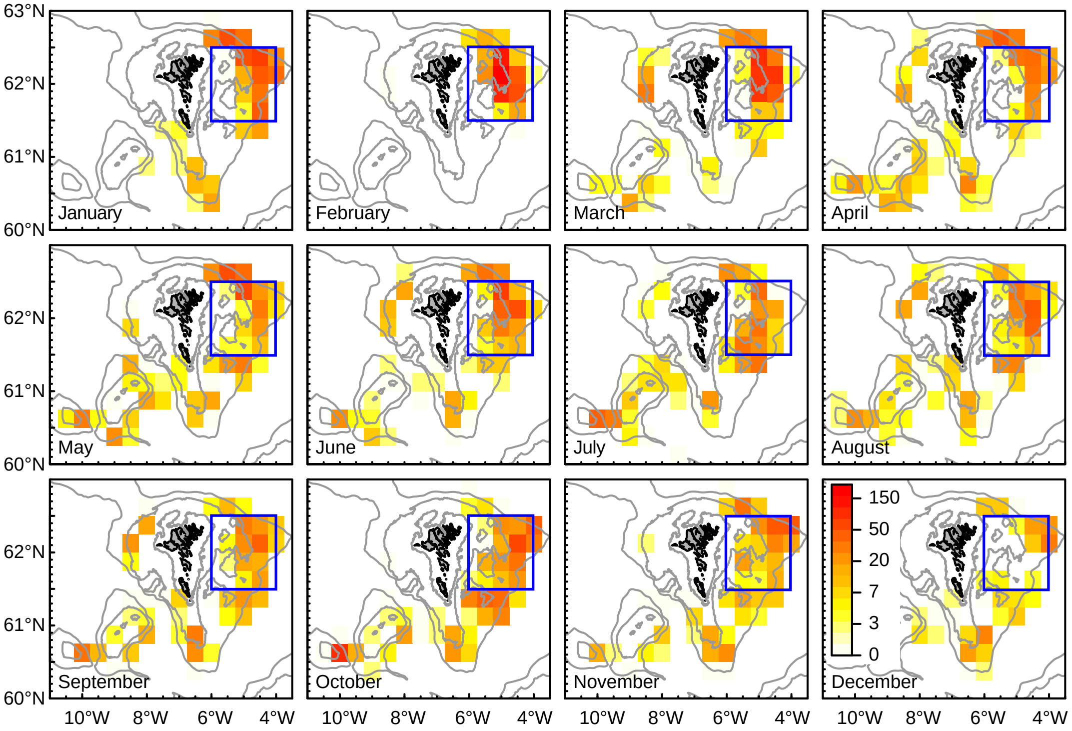

Figure 7. The number of trawl hauls in various months from 2007 to 2009 in the scale shown on the December plot. The blue box indicates the main sampling area. From Paper IV.

that this is the main fishing area for the commercial fleet during the spawning period (Figure 7). The spawning area, previously suggested to be on the western Faroe Plateau (Anon, 1998), was not evident in our study.

4.1.2 Growth, condition factor and maturation

The growth curve of saithe does not follow the von Bertalanffy growth curve very precisely (Figure 8). It showed a distinct change at an age of around four, after which the growth rate decreases and becomes more or less constant. Growth did not differ between the sexes. The decision to use the von Bertalanffy model, despite the poor fit, was to allow comparison with saithe from other regions. Using the von Bertalanffy equation gave asymptotic length L_∞ = 117 cm for males and 112 cm for females, and growth rate k = 0.14 for males and 0.15 for females. This is comparable to available data on growth of saithe in other regions (Magnussen, 2007), but according to Bertelsen (1942), the adult Faroe saithe was intermediate in growth rate between Norwegian and Icelandic saithe. Bertelsen's conclusions are consistent with input data for stock assessment, where the weight-at-age of adult Faroe saithe is lower than Icelandic and larger than Norwegian and North Sea saithe (ICES, 2010a, 2010b, 2011a).

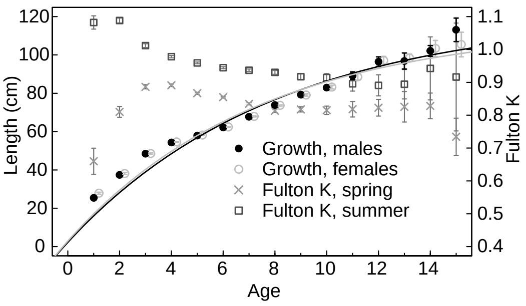

Figure 8. Growth and Fulton condition factor of saithe in Faroese waters. Heavy lines are fitted von Bertalanffy curves to growth data. Vertical bars represent 95% confidence intervals. From Paper I.

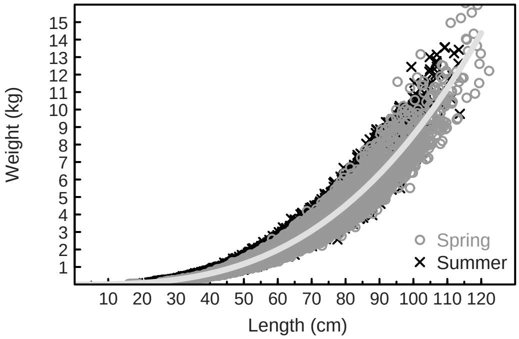

Figure 9. Length weight relationship of saithe in Faroese waters based on ungutted weights. Spring and summer samples have been combined.

The length-weight relationship of saithe in Faroese waters is described by the power function $weight = 1.64 \cdot 10^{-5} \ x \ length^{2.86}$ where spring and summer samples have been combined (Figure 9). This relationship is for ungutted weights in kg and lengths in cm.

In spring, the youngest saithe have the lowest condition factor (*Fulton K*), whereas in summer they have the highest. The low *Fulton K* of young saithe in spring indicates that this period is hard for them to survive. After age 3, the *Fulton K* curves in spring and summer are parallel but with higher values in summer, indicating better feeding circumstances during summer. In this study, ungutted weights were used to calculate *Fulton K*. Data from commercial samplings of gutted saithe did not show as large a difference between spring and summer, and part of the difference seen in Figure 8 is therefore due to seasonal changes in gonad-, liver-, and stomach weights. The shift in the growth curve and the condition factor occurs at an age when the saithe are maturing sexually, and where part of the energy is channelled into developing the reproductive organs.

The maturity ogives of saithe in Faroese waters showed that females mature approximately one year later than males (Figure 10). 50% sexual maturation was attained at age 5.2 (or 55 cm) for males and 6.1 (or 61 cm) for females, which is after the fish have moved into deeper waters. In Norwegian waters, the age at maturity has been estimated at about 5.5 years (Fotland and Mehl, 2008) and in Icelandic waters at about 6.1 years (Armannsson, 2007), for sexes combined. Females also seem to mature later than males in Icelandic waters (Armannsson, 2007). In the western component of the Canadian saithe stock, a distinct decrease has been observed in the length when 50% have matured sexually from 60 cm in the 1960s to nearly 45 cm at the turn of the century (Armannsson, 2007). Such a decrease does not seem to be the case for neither Faroese (unpublished data), nor Icelandic saithe (Armannsson, 2007).

4.1.3 Distribution

According to Bertelsen (1942), the transition from the shallow habitat of young saithe to the deeper areas of adult specimens is not an abrupt event at age three, but rather a successive emigration at age one, two and three. This suggestion was supported by survey data, as the smallest size groups of saithe were found closest to land, and successively moving farther from land with increasing size (Figure 11). Beyond 50 cm, the age groups overlapped extensively and the spatial distributions approached the 500 m depth contour. The apparent boundary at 500 m depth is, however, provided by

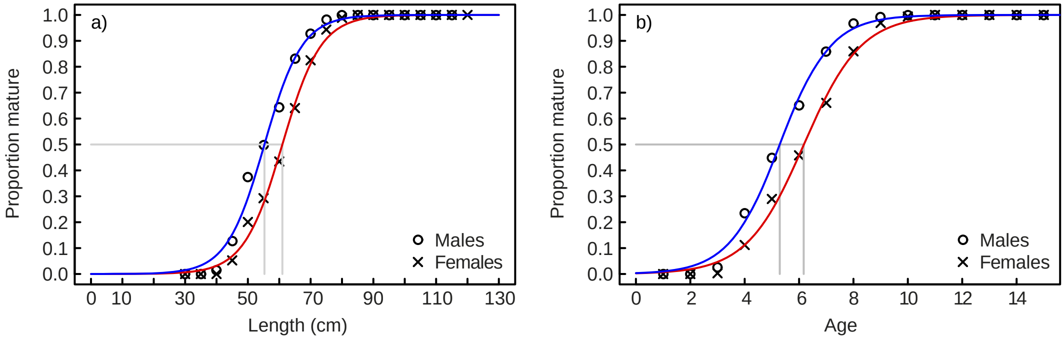

Figure 10. Maturity ogives of saithe in Faroese waters, with grey vertical lines indicating the length (a) and age (b) when 50% of saithe have matured sexually.

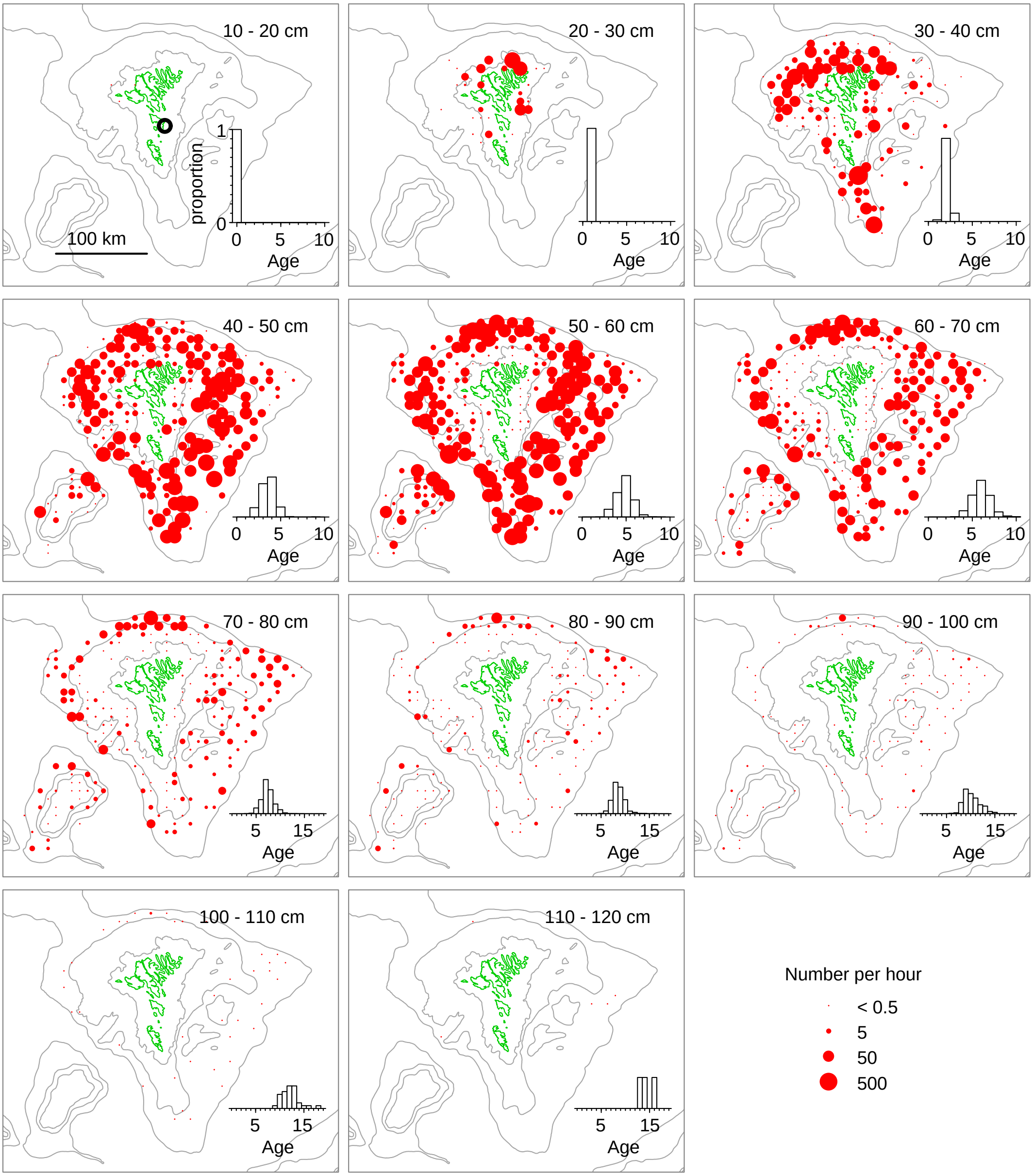

Figure 11. Distributions of saithe of different sizes on the Faroe Plateau and Faroe Bank. Grey lines indicate the 100, 200 and 500 m depth contours. Histograms indicate the age distribution in the length groups (y-axis is indicated on the first map). The maps are based on average values from the summer surveys. From Paper I.

the area covered by the surveys – not necessarily the inhabitable boundary of saithe. On the Faroe Bank, the smallest saithe were between 40 and 50 cm (Figure 11) indicating that the bank is not a nursery area, which is consistent with Bertelsen (1942).

The movement of saithe to deeper waters with age has also been observed in other regions such as in the Norwegian Deep where some, but not very pronounced, segregation of sizes by depth may occur (Bergstad, 1991). Also in Canadian waters, Clay et al. (1989) observed that there was a successive replacement of older (second year) fish by the younger year class in their inshore study area. By November, many of the second year fish left the area not to return.

The distribution of saithe is varying seasonally (Neilson et al., 2002; Olsen et al., 2010), as was also found for Faroe saithe, where the mean distance from the centre of distribution was longer in spring than in summer (Paper I). This is further supported by the varying catches in the commercial fishery, where there are generally larger catches in the spawning period than later in the summer (see later).

4.1.4 Diet

As stated in the introduction, the diet of saithe reflects the pelagic behaviour. This was also confirmed by the survey data. The main prey species of saithe in Faroese waters were found to be blue whiting, Norway pout, euphausiids, and sandeel (Paper I). There is geographical, seasonal, interannual, as well as size dependent variability in the relative importance of the prey species to saithe. Overall, blue whiting appears to be the most important prey species to adult saithe, but this is mostly in the outer areas on the Faroe Plateau in summer (Paper I). In spring, the stomach fullness was considerably lower than in summer (Figure 12). For sexually mature saithe, this may in part reflect that the samples are taken in the spawning period, but the low fullness indices probably also reflect the deprivation and outgrowing of suitable prey since the last bloom of primary production – and subsequent cascade into higher trophic levels (Gaard et al., 2002; Hátún et al., 2009a; Steingrund and Gaard, 2005). It is the 0-group that are the bulk of the blue whiting found in the stomachs, as is also the case with sandeel (Figure 13). With regards to Norway pout, which grows slower than e.g. blue whiting (Monstad, 1990; ICES, 2012), probably several age groups are taken as prey by saithe (Figure 13).

Based on the groundfish surveys, there is a shift in the diet with age, with the juveniles relying most on Norway pout, and blue whiting constituting increasingly larger proportion of the diet with increasing age (Figure 12). This difference between younger and older saithe is linked to where on the Faroe Plateau they are distributed. The older saithe are in the deeper waters of the Plateau, where blue whiting are more abundant, but distributed farther out than Norway pout. Euphausiids and sandeel are taken more uniformly by all ages of saithe. The shift in the growth curve (Figure 8) occurs at an age when the saithe are maturing sexually, and where part of the energy is channelled into developing the reproductive organs. This is also a period, however, after the young saithe have moved from inshore to offshore waters, and the shift in both growth and *Fulton K* could be a consequence of this habitat shift, as is also indicated by the shift in diet.

There is an apparent discrepancy between our juvenile diet study based on survey data and those of Bertelsen (1942) and Højgaard (1999), since we found Norway pout to be most abundant, whereas Højgaard found sandeel, and Bertelsen amphipods and copepods to dominate the diet. But, whereas the surveys are by bottom trawl, and therefore not very near the shoreline, both (Bertelsen, 1942) and (Højgaard, 1999) sampled near land, and this may very well induce the observed differences in the diet of juveniles. When survey data are divided in

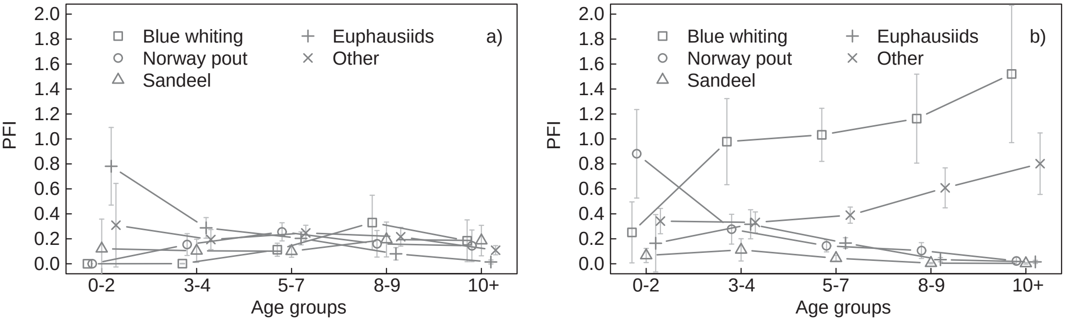

Figure 12. The diet of different age-groups in a) spring and b) summer. Vertical bars are 95 % confidence intervals. The unit on the y-axis is Partial Fullness Index (see Paper I). From Paper I.

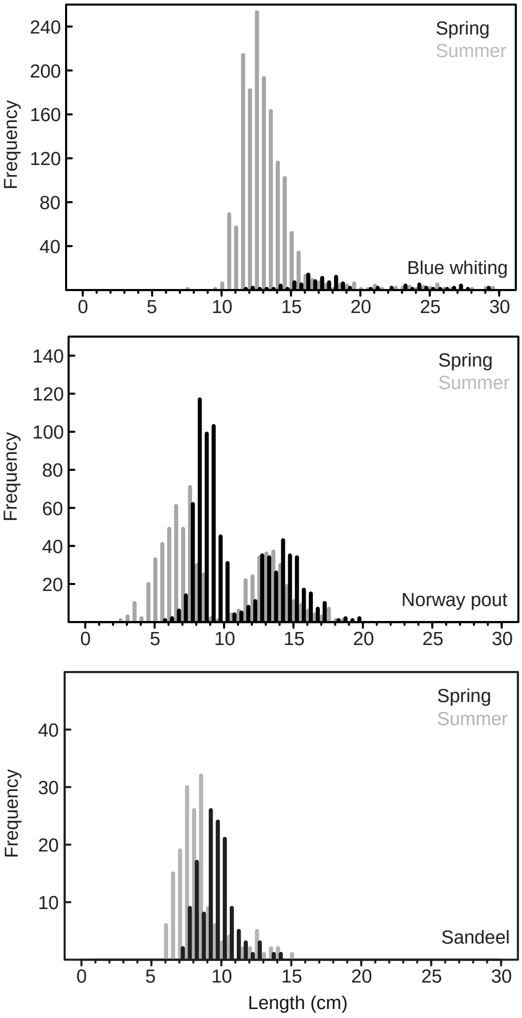

Figure 13. Length distribution of blue whiting, Norway pout and sandeel in the stomach contents of saithe.

depth intervals (Paper VI), there are indications that sandeel are important to saithe in waters shallower than 150 m in March.

It could be argued that the diet analyses based on March and August data are not sufficient to describe diet throughout the year. With regards to quantities this may be true. Sandeel on average comprise 4% of the diet (by weight) in summer on the Plateau, but the abundance of sandeel may have been higher earlier in the summer. Studies have shown that the optimal behavioural response of sandeel to increased predation mortality is to reduce foraging activity, given that foraging activity is proportional to the mortality and a critical minimum energy uptake is not compromised (van Deurs et al., 2010 and references therein). Similar ecological explanations for seasonal variability probably exist for other prey species as well. But with regards to the combination of prey species, it is not very likely that other species outrange the four specified prey groups in not covered periods, since the same four groups are most abundant in both spring and summer.

The main diet of saithe in the Northeast Atlantic varies regionally (Paper I), but the diet overlaps. For instance, in Scottish waters, blue whiting has been found to be most important in the western parts, but euphausiids and Norway pout were most important in the eastern parts (du Buit, 1991). On the other hand, several prey species important to other saithe stocks do not amount to much in the diet of Faroe saithe, e.g. capelin and herring (Paper I, Jónsson, 1996; Jaworski and Ragnarsson, 2006; Olsen et al., 2010).

The results in Paper I indicate that the most important prey for adult saithe is blue whiting,

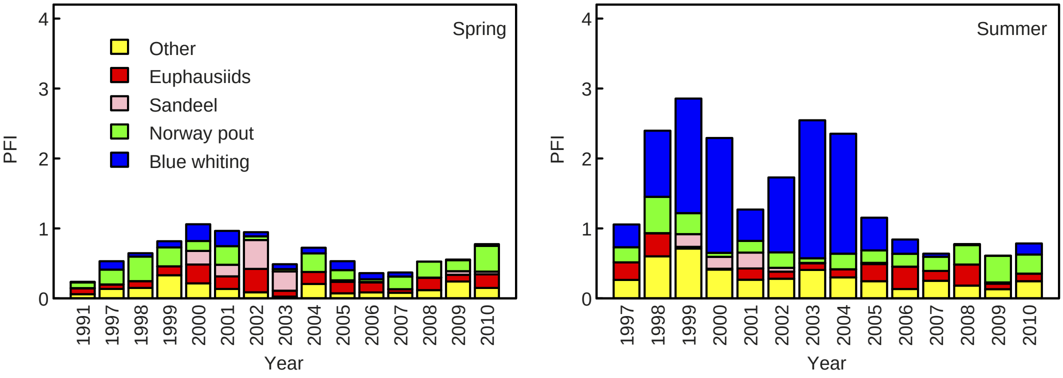

Figure 14. Temporal variation in stomach contents of saithe in Faroese waters. The unit on the y-axis is Partial Fullness Index (see Paper I).

which is present in Faroese waters throughout most of the year (unpublished data). The blue whiting stock was historically large during the period our diet study covers, and the abundance of small blue whiting, suitable as prey to saithe, was also high in Faroese waters in this period (ICES, 2011b). This may influence the impression that blue whiting is by far the most dominant prey of adult saithe in Faroese waters. The interannual variability in stomach fullness in Faroese waters in summer is mainly driven by the amounts of blue whiting in the stomach contents (Figure 14). This is in accordance with the recruitment to the blue whiting stock (ICES, 2011b), which decreased drastically in 2005.

4.2 Recruitment

The recruitment of Faroe saithe to the fishable stock is positively correlated to the amount of sandeel and Norway pout fry in June (Figure 15, Paper III). Sandeel, in turn, is tightly linked to the primary production on the shelf (Eliasen et al., 2011). Indeed, a positive correlation, albeit weak, is seen between recruitment of saithe at age three and the primary production on the Faroe shelf averaged over the three years preceding recruitment. This is in accordance with the shallow habitat of juvenile saithe (Paper I). Recruitment shows the highest correlation with the availability of sandeel to saithe at age 2, but also Norway pout as prey to saithe at age 1 gives good correlations (Paper III). Paper III provides support to the findings of Paper I and previous studies on diet of juvenile saithe in Faroese waters (Bertelsen, 1942; Højgaard, 1999), which find that these are both important prey fish-species

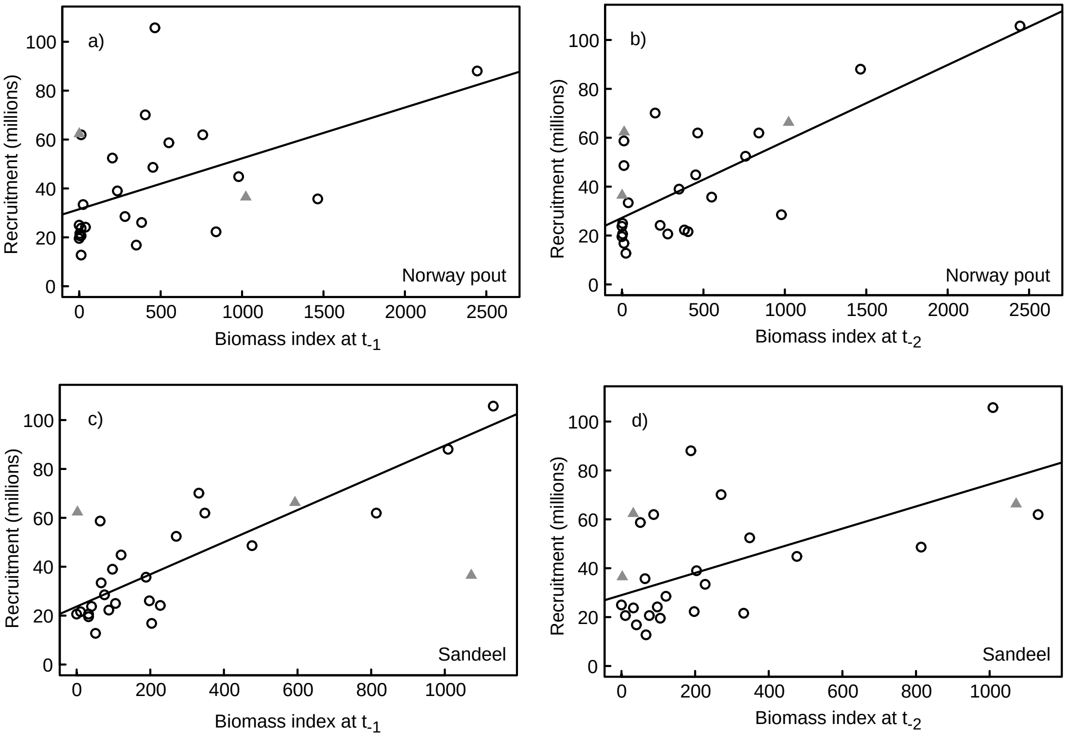

Figure 15. Recruitment of saithe at age 3 in relation to the biomass index of Norway pout (a) and (b) and sandeel (c) and (d). Figures (a) and (c) show the relationships between recruitemnt at age 3 and the prey biomass the year before (t_{-1}), while (b) and (d) show the relationships between recruitment at age 3 and the prey biomass two years before (t_{-2}), representing the food-availability of the one- and two-year-old saithe, respectively. The grey triangles indicate the three last years in the series, in which the recruitment estimates are generally rather uncertain. The lines are the regression lines when the three last years have been excluded. From paper III.

to juvenile saithe in addition to e.g. copepods, amphipods, saithe larvae and euphausiids.

For more than ten years we have known that the recruitment of cod and haddock are linked to the PP-index. Our finding that saithe recruitment also is driven by productivity on the shelf implies that all three major demersal stocks (saithe, cod and haddock) in Faroese waters are depending on the same resources. Whereas the response in cod and haddock can be seen very directly from the primary production (Figure 3) (Gaard et al., 2002), for saithe, the response is more obvious in relation to trophic levels higher than the primary production itself (Paper III). There are indications of two different trophic pathways on the Faroe Plateau (Paper VI), where sandeel and Norway pout are important links between lower and higher trophic levels. Sandeel were found to be dominating in the diet of cod in the 1950's (Rae, 1967) whereas they are a more variable diet of cod in recent years (Paper VI). Over the last decades, saithe have comprised an increasingly larger part of the total biomass of saithe, cod and haddock. In Paper VI, this was linked to the amounts of Norway pout and sandeel in the stomach contents from survey data (same as presented in Paper I). The two proposed ecosystem regimes include a stable regime, which was acting up until the 1960s and an unstable regime during the past decades. The stable regime is characterized by a stable state, where herring, sandeel, cod, and seabirds are dominating. The unstable regime is characterized by states shifting between a Norway pout-state, where zooplankton, Norway pout, and saithe dominate, and a sandeel-state, where sandeel, cod and haddock are boosted, although this has not led to a recovery of seabirds.

In addition to being correlated with the PP-index, saithe recruitment is also weakly negatively correlated to the GI (Paper III). The highest correlation coefficients are observed for lags 0-4. Zero lag would imply effects around the time when saithe enter the outer system of the Plateau, whereas a lag of 4 years represents conditions at the time of spawning, since it takes approximately 1 year until the marine climate in the Faroe area responds to the subpolar gyre (Hátún et.al, 2005).

Saithe recruitment is also weakly correlated with the abundance of the same cohort at the 0-group stage, and this may support an effect of the GI on saithe recruitment through processes occurring around the time of spawning or hatching. The 0-group survey provides the only estimate we have on abundance of saithe before they enter the fishery at age 3-5, but caution is needed when using the 0-group survey data for saithe, because saithe are found in the littoral zone as early as in May (Bertelsen, 1942), whereas the survey starts in the second half of June. The abundance of saithe fry in the 0-group survey, in comparison to sandeel and Norway pout, is 1 to 2 orders of magnitude lower.

4.3 Density dependent growth

Both cod and haddock exhibit increased individual growth as well as good recruitment, when productivity is high (Gaard et al., 2002; Steingrund and Gaard, 2005), but saithe are generally small when recruitment is good (ICES, 2011a). There seems to be an element of density dependent growth in Faroe saithe (Figure 6), and this topic was explored further in paper III. Growth was found to be inversely correlated to the total stock size, either in number or biomass, especially until age 6, after which the density effect of the total stock ceased (Table 1). Again, the changing spatial distribution with size can explain much: there is little overlap between the oldest and the youngest saithe, which are much more numerous than the old saithe. Generally, 3 and 4 year old saithe comprise

Table 1. Correlation coefficients between the 3-year running mean growth in weight of individual age groups and the inverse of three different limiting parameters representing stock size: Number, basic metabolism, or biomass, summed either over all ages (3-13), over the young component (3-6), or over the old component (7-12).

Lim. Param.	Ages	3-4	4-5	5-6	6-7	7-8	8-9	9-10
Number:	3-13	0.85	0.78	0.72	0.44	0.19	0.15	0.14
Metabolism:	3-13	0.83	0.71	0.68	0.39	0.28	0.23	0.19
Biomass:	3-13	0.79	0.62	0.62	0.34	0.31	0.27	0.23
Number:	3-6	0.78	0.78	0.69	0.44	0.08	0.12	0.12
Number:	7-12	0.46	0.17	0.28	0.24	0.57	0.09	0.14

Table 2. Correlation between actual and simulated weight-at-age for the period 1971 to 2007 where the weight-at-age 3 (w_3) is either fixed, equal to its average, (top row) or the actual weight (bottom row).

Age:	4	5	6	7	8	9	10	11	12	13
Fixed w_3:	0.67	0.83	0.83	0.79	0.79	0.84	0.68	0.69	0.63	0.28
Actual w_3:	0.75	0.81	0.78	0.74	0.73	0.84	0.70	0.68	0.63	0.26

40% of the total stock in number (age 3 and older) (ICES, 2011a).

Weight-at-age was simulated from weight-at-age 3 based on the inverted stock number, assuming the density effect to apply to saithe age 3-6 and using the average growth for ages 7 and older. These simulations supported the conclusions regarding density dependent growth, with high correlations between actual and simulated weight-at-age (Table 2). In addition, the total stock biomass was fairly well estimated (Paper III) when based on the simulated weights. The model, assuming total stock number being the limiting factor, had the best fit with the highest deviations in a given year being a 15% underestimate and a 17% overestimate.

The correlation between the mean growth for age 3-7 year old saithe and the GI was positive, i.e. saithe grow least when the conditions are best. Perhaps the most plausible mechanism would be that the good conditions from the GI lead to good recruitment, which in turn reduces the growth due to density dependence. With regards to the older saithe there tended to be a negative correlation to the GI – and therefore the GI may be an indicator of food availability to the largest saithe. This is supported by the temporal variability in the stomach contents (Figure 14), which corresponds well with largest fullness index in the period when the subpolar gyre has been weak. Blue whiting seems to be an important link. The higher recruitment of blue whiting from 1996 - 2004, when the subpolar gyre was weak, can be seen in the stomach contents of Faroe saithe, because it is blue whiting that induces the largest variability in the stomach contents (Figure 14), and it is the 0-group blue whiting that are important to saithe as prey on the Faroe Plateau (Figure 13). That blue whiting is important as prey to saithe is further supported by the bycatch of saithe in the blue whiting fishery (Pálsson, 2005).

In a preliminary study, there were no clear conclusions regarding the relationship between stomach contents in summer and the weight gain in the subsequent months (Paper V). This may, however, in part be because some of the underlying assumptions in that study turned out to be violated, e.g. in how growth was calculated.

4.4 Migration

Migration of saithe was studied in two ways. Probably the most certain, and usual, way to describe migration is by tagging and recapture. This was done, using existing datasets (Paper II, Paper IV).

In addition, seasonal migration was studied as inferred from CPUE series and changes in length distributions within an age group throughout the year from commercial catches of saithe in Faroese waters (Paper IV).

4.4.1 Inter-regional migration of saithe in the Northeast Atlantic

The tagging studies were conducted in Icelandic, Faroese and Norwegian waters. Thus a large proportion of the Northeast Atlantic was covered, although not simultaneously. But the North Sea is not covered in our study. We are aware of Scottish tagging experiments conducted from 1973-1979, but these data were not available to us. Preliminary results from these experiments will be discussed later on.

The study area was divided into three stock-areas, where the Icelandic and Faroese stock areas were roughly equal to the ICES-divisions for Iceland and Faroes, respectively. The Northeast Arctic, North Sea and Skagerrak and waters west of Scotland were treated as a unit, based on the less obvious boundaries between the stocks, and it was named the Continental stock area.

Young fish in all areas exhibited low emigration rates (Paper II), corresponding well to the short distances these fish were recaptured from the site of tagging. With increasing size, the distance from tagging site increased in all areas (Figure 16), which corresponds well with the findings in Paper

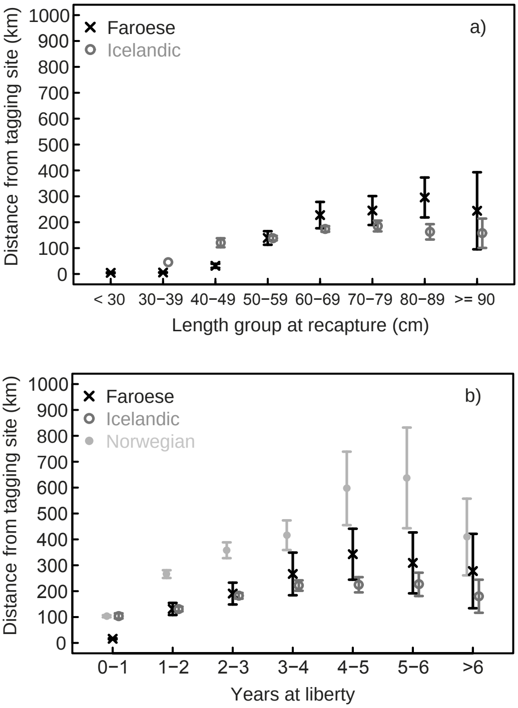

Figure 16. Distance between tagging site and site of recapture. a) Mean distance from tagging site of saithe tagged in Faroese and Icelandic waters by length group at recapture. b) Mean distance from tagging site versus time at liberty (for fish shorter than 50 cm at tagging). Vertical bars represent 95% confidence intervals. From Paper I.

I that saithe are distributed progressively farther from land with increasing length in Faroese waters (Figure 11).

The smallest Faroese saithe were recaptured shorter distances from the tagging site than Icelandic and Norwegian saithe, which can be interpreted as a limitation caused by the much smaller shelf in the Faroe area. There were also indications of the oldest saithe exhibiting shorter distance from tagging site (Paper II). This could perhaps be explained by a combination of spawning site fidelity and larger saithe being more prone to capture in the spawning season than the rest of the year, when they may reside outside fishing areas.

From the Faroese and Icelandic data, it was seen that the migrated distances increased after saithe had reached lengths of 50 cm, and beyond 60 cm, 33% of Faroese saithe were recaptured outside the Faroese stock area (Table 3). Unfortunately, length at recapture was not available for the Norwegian data, so instead time at liberty was used as an approximation of age, assuming that all saithe recaptured after 3 years at liberty were adults. The emigration rates of adult saithe differed among areas, being lowest for the Icelandic (0.8%), intermediate for the Continental (6.6%), and highest for the Faroese area (42%).

To compare the proportion of recaptures (termed relative recapture percentage (RRP)) among the stock-areas, an idealized scenario was assumed (Appendix A in Paper II) where saithe tagged in area A were assumed to migrate all at once at a specified time after tagging to area B, where they remained. RRP was then found to be a good approximation for the emigration rate, given that the fishing mortality was higher than the natural mortality. The immigration rate was calculated as the RRP multiplied by the ratio between the average stock sizes in area A and B in the period of recapture.

The overall impression from the tagging studies is that there was a westward migration of the adult saithe, because there was net immigration to

Table 3. RRP (relative recapture percentage) in the Faroese, Icelandic and Continental stock areas in relation to the total number recaptured (with known position), by tagging area. The same variable is presented by all sizes, length at recapture and by time at liberty. Modified from Paper II.

		Stock-area of recapture			
	Stock-area of tagging	Faroes	Iceland	Continental	Recaptures (n)
All sizes	Faroes	87.9%	8.3%	3.8%	1214
	Iceland	0.4%	99.5%	0.1%	1675
	Norway	0.7%	1.0%	98.3%	14733
> 60 cm	Faroes	65.7%	26.4%	7.9%	254
	Iceland	0.7%	99.2%	0.1%	715
> 3 years at liberty	Faroes	57.9%	30.3%	11.8%	152
	Iceland	0.8%	99.2%	0.0%	382
	Norway	1.6%	5.0%	93.4%	833

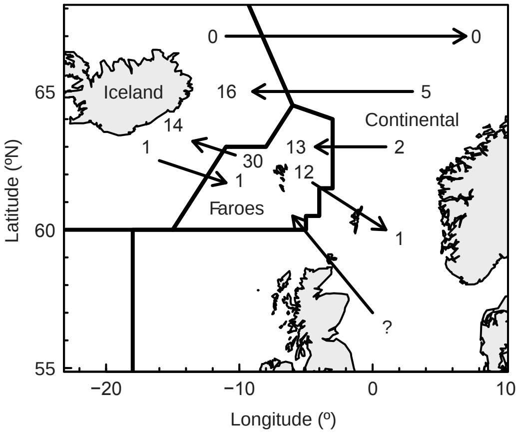

Figure 17. Map showing the estimated migration (in %) among the Faroese, Icelandic and Continental stock areas of saithe, where more than 3 years had elapsed between tagging and recapture. At the start of an arrow, the relative recapture percentage (RRP) is listed and at the end of an arrow the immigration percentage is shown. From Paper II.

Icelandic waters and net emigration from Faroese and Norwegian waters (Figure 17). Clearly, information from the western North Sea is missing in this picture. From Scottish tagging studies 1973-1979, the preliminary results indicated that saithe tagged near the Scottish coast tended to stay close to the coast, but after age 3, fish tagged near Aberdeen were recaptured more widely in the North Sea, but none outside the North Sea. Of 257 saithe tagged east of Shetland, 63 were returned and of those, 3 were recaptured outside the North Sea (Newton, 1984). That would mean a RRP outside the North Sea of 4%, but allocating these among the three stock areas is not possible, and we must await future tagging studies to obtain emigration rates from the North Sea.

There were indications of temporal variability in emigration rates from Faroese and Norwegian waters (Paper II), but they were not statistically significant. Due to the broken time-line of tagging among the three stock-areas, however, we cannot safely conclude that the migration rates have been constant over the six observed decades. In addition, the emigration rates from Norwegian tagging experiments were based on tagging along the entire Norwegian coast line. Jakobsen (1981, 1982), however, has noted that there is variability in the migration patterns of saithe along the Norwegian coast, with some components tending to migrate more northwards and others more southwards. It is possible that reanalysis would show that some of these components also exhibited higher westward migration rates – and clearer temporal variations could be detected.

The found extent of migration – and the variability among regions – may well be related to feeding conditions of saithe and the distribution of the prey species. Saithe in Norwegian waters is known to follow the Norwegian spring spawning herring (Runde, 2005; Olsen et al., 2010), and a main prey of Faroe saithe, the blue whiting, are also distributed near Iceland (Hátún et al., 2009a). Capelin are a main constituent in the diet of Icelandic saithe in part of the year, and capelin in Icelandic waters have a migration pattern that do not take them near the Faroese or Continental stock areas (Vilhjálmsson, 2002).

4.4.2 Seasonal migration trends – as inferred from length distributions throughout the year

The seasonal pattern in the fishing area of the standard commercial fleet (Figure 7) is indication of seasonal migration in saithe. Mean weight-at-month varied very differently in periods when saithe generally were small as compared to when they were larger (Paper V). This pattern remained when length-at-month was considered, and could therefore not be attributed to investment in gonads or condition factor. In Paper IV, this decrease in mean length was investigated in a defined sampling area, which is also one of the main fishing areas (Figure 7) – and where the main spawning area is (Paper I). Generally, when all available years were pooled, lengths of the sampled fish decreased from January to August (Figure 18, Paper IV).

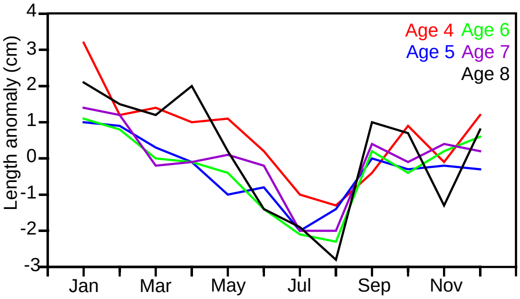

Figure 18. The length anomaly (defined in Paper IV) in the main sampling area through the year for age groups 4 to 8 on average for cohorts 1986 - 2008. From Paper IV.

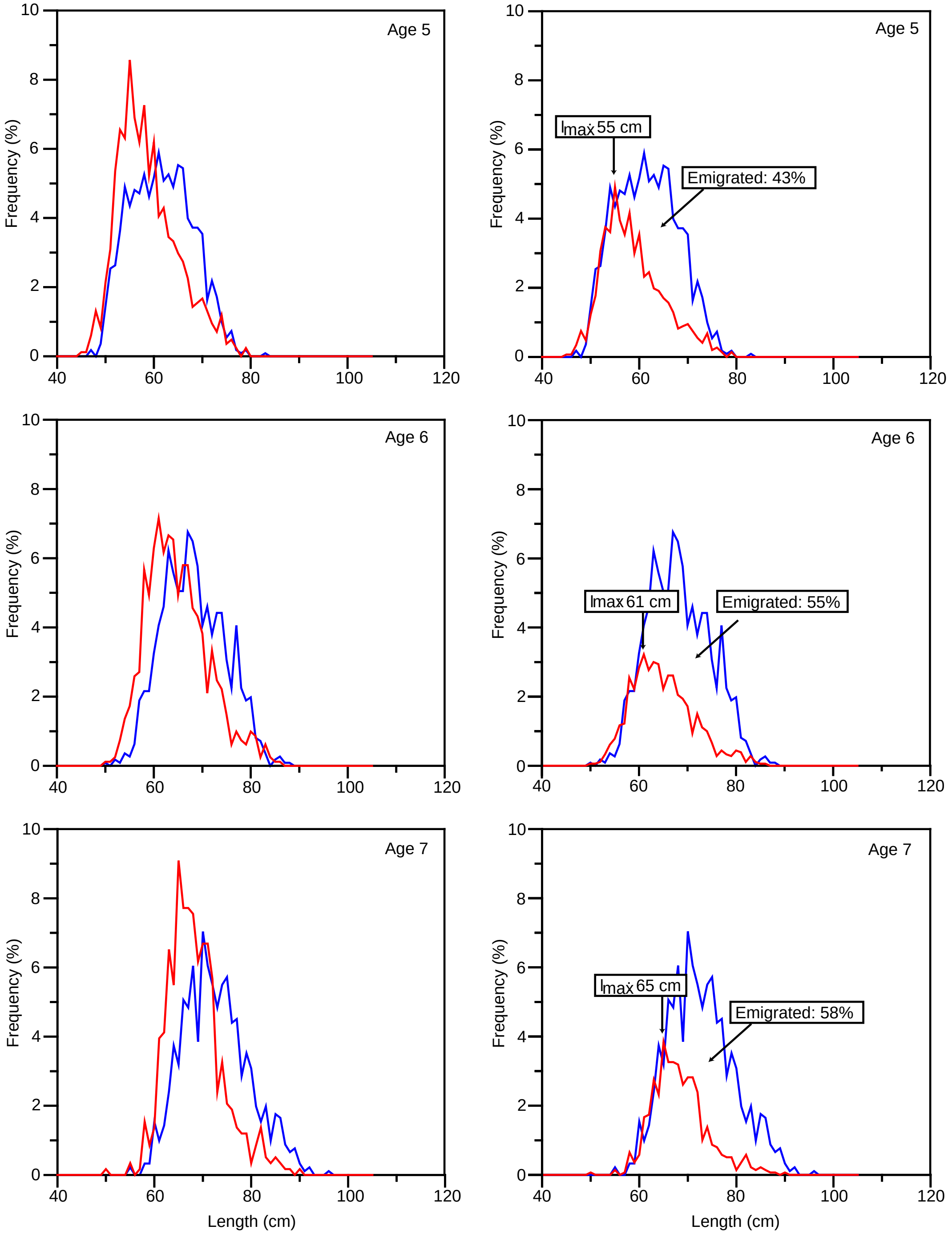

Figure 19. Length distribution of saithe in the main sampling area in January - March (blue) and June - August (red) for individual age groups averaged over those cohorts for which the mean length for that age group decreased by at least 2 cm from January to August. The graphs on the left hand side are unadjusted. On the right hand side the distributions for June-August are adjusted so that the area up to the maxima (indicated) equaled the area of the January - March distribution for the same length interval. The fractions of fish that have emigrated from each age group are indicated. From Paper IV.

Table 4. Correlation coefficients between the "Jan-Aug lengthening" (ΔL_{JA}), the average spawning length, L_{sp} (Jan-March), and the average length for the whole year L_{An} for age groups 4 to 9 in the main sampling area. The number of years for each calculation are shown in brackets. From Paper IV.

	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9
$\Delta L_{JA}/L_{sp}$:	-0.44 (17)	-0.74 (17)	-0.83 (17)	-0.87 (17)	-0.18 (15)	0.08 (16)
$\Delta L_{JA}/L_{An}$:	0.07 (17)	-0.64 (17)	-0.78 (17)	-0.83 (17)	-0.08 (15)	0.21 (16)

From September to December, lengths increased following the average growth (Paper IV).

In years, when lengths decreased at least 2 cm from January to August, the length distributions were shifted towards shorter lengths during June-August as compared with January-March (the spawning period) (Figure 19). This pattern was pronounced for saithe from age 5 to 7. Since it could not be interpreted as actual shortening of fish, emigration from the sampling area was believed to be a plausible explanation. The change in shape of the distribution from January to August was consistent with an interpretation, in which maximum frequency length in summer was the length beneath which no fish emigrated.

5 year old saithe started to emigrate at shorter lengths than age 6 and 7. For ages 8 and 9 there was no apparent difference in the length distribution in summer as compared with the spawning period. The conclusion based on these results is that the emigration is probably length dependent, with the longest fish in an age group emigrating from the Faroe Plateau early in the year. The critical lengths observed (55, 61, and 65 cm for age 5, 6, and 7, respectively) are around the time when saithe mature sexually and therefore a combination of feeding and spawning migration is plausible, as is also seen Norwegian waters (Olsen et al., 2010). The continuous increase in length from September to December (Figure 18) indicates return migration during the autumn and winter months.

The shortening from January to August was correlated with the length of the saithe for the age groups 5 to 7 (Table 4). This result shows that the longer saithe are at e.g. age 6, the more the length distribution is shifted towards shorter sizes in summer, i.e. the larger the proportion of saithe in that age group that are emigrating from the area in summer. This is consistent with the findings in Paper V, that in year classes with poorer growth the fluctuations were smaller than in year classes with better growth.

When looking at data representing all areas except the spawning area, a very similar pattern was revealed (Paper IV), and therefore, it is not plausible that all saithe had remained in other areas on the Faroe Plateau. How far saithe emigrate from the sampling area is impossible to manifest, based on these data. They may have moved to deeper waters on the Faroe Plateau, they may have resided predominantly in the pelagic environment, or they may have followed a prey species to other regions in the Northeast Atlantic.

The observed lengths, after which emigration seems to occur, are between 55 and 65 cm, i.e. in the range where tagged Faroe saithe are recaptured in other stock areas (section 4.4.1 and Paper II). This supports the conclusion that the shifted length distribution may be a result of emigration from the Faroe Plateau.

The Faroese tagging data further support that the observed migration is a combination of spawning and feeding migration (Paper IV, Figure 20). Of fish tagged on the Faroe Plateau, the majority of the saithe recaptured in Icelandic waters were recaptured there in the summer months. The recaptures in Faroese waters were most frequent in the spawning period. With regards to fish tagged on the Faroe Bank, most recaptures in Continental waters (as defined in Paper II) were in the spawning period. Recaptures on the Faroe Bank, on the other hand, were most numerous in the summer months. The numbers are low, but rather convincing and a possible interpretation is that these are predominantly Continental saithe feeding on the Faroe Bank. The Wyville-Thompson Ridge (Figure 1) is actually a shallower passage to the Faroe Bank than crossing the Faroe Bank Channel, and the tagging experiments were primarily conducted in the summer months, which makes this hypothesis plausible.

4.4.3 Virtual Population Analysis (VPA) including emigration from Faroese waters

Throughout this thesis, the total size of the saithe stock has been used in various analyses. A weakness,

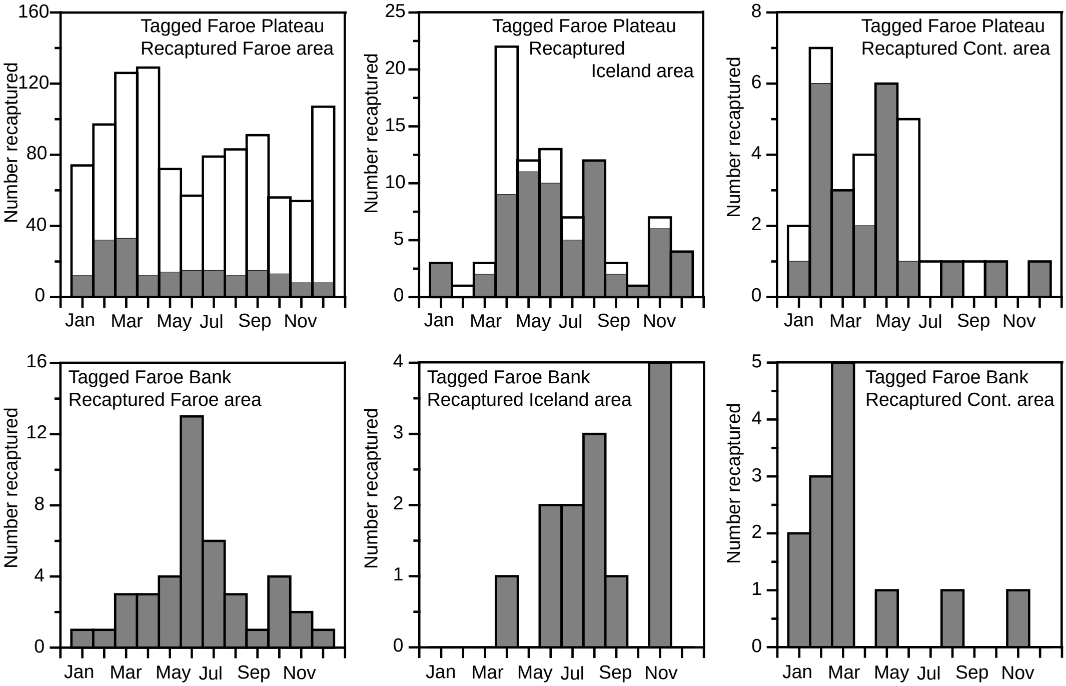

Figure 20. Number of tagged saithe recaptured in the Faroe area, the Iceland area, and the Continental area from taggings on the Faroe Plateau (top row) and on the Faroe Bank (bottom row). Grey bars indicate saithe longer than 60 cm when recaptured. From Paper IV.

in using these data, is that the stock estimates based on VPA do not include migration, but we have demonstrated that a significant proportion of the recaptures of saithe tagged in Faroese waters were from outside Faroese waters (Paper II).

In VPA-analyses, the effects of migration on the stock estimates were tested (Paper IV). One case (red curve in Figure 21) assumed constant migration of 30% for ages 5 and older. These numbers are taken from Paper II, where more than 30% of Faroe saithe were recaptured outside Faroese waters when saithe were longer than 60 cm or older than 5 years. This case resulted in stock variations very similar to the variations in the case with no migration, but with a higher biomass. Assuming length dependent migration of ages 5 to 7 (Paper IV) also led to similar variations (blue curve in Figure 21), but smaller stock sizes, as compared with constant migration, in periods when stock size is large (and individual saithe smaller).

In these simplified cases of estimating the effect of migration on stock size, one assumption is that there is no immigration to Faroese waters. Another assumption is that when saithe are outside Faroese waters the total mortality is the same as within Faroese waters, which is not necessarily the case. Additionally, differences over years in distribution of prey species, e.g. blue whiting and herring, may induce variable migration rates. We believe, though, that the high correlation

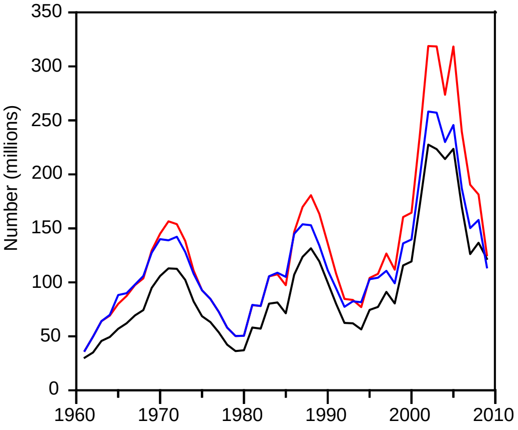

Figure 21. The total number in the stock as computed by VPA in three different cases. The black curve assumes no migration, whereas the two coloured curves represent two different types of migration behaviour described in the text. From Paper IV.

between the migration-modified stock estimates as compared to the official stock estimates (R = 0.976) (Paper IV), indicate that temporal variability in the official stock estimates probably reflect "the reality" well, in a relative sense, although not in absolute numbers. This furthermore implies that relationships that have been deduced by correlating with the official stock numbers from ICES may still be valid even if migration changes the absolute stock numbers. Examples of such relationships are relations between saithe recruitment and food in the juvenile phase and density dependent growth (Paper III).

4.5 The effects of climate and ocean currents on Faroe saithe

In the beginning of the project (paper V), there was much focus on the high correlation between total stock biomass of Faroe saithe (age 3 and older) and the GI (Figure 22), where the saithe biomass was lagged 4 years behind (Figures 5 and 6). The line of reasoning for this lag was, that it takes time for the weakened subpolar gyre to affect the higher trophic levels in the region, e.g. blue whiting (Hátún et al., 2009a; Hátún et al., 2009b)), which saithe prey upon. But it is not plausible that it is merely food availability in the outer areas of the Faroe Plateau, e.g. increased abundance of small blue whiting, because the stock biomass is dominated by young saithe (ICES, 2011), which to a greater degree reside in the shallower areas, where blue whiting is not a big part of the diet (Paper I).

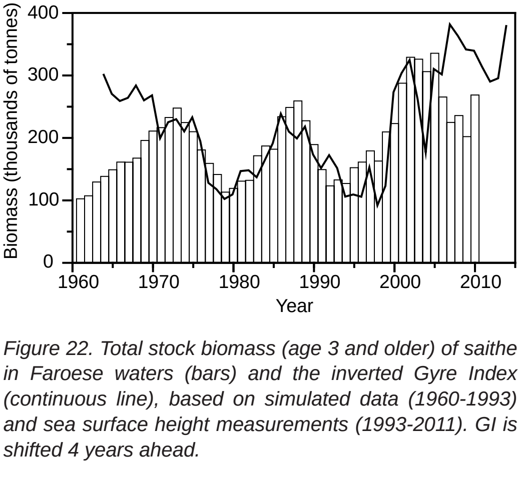

Figure 22. Total stock biomass (age 3 and older) of saithe in Faroese waters (bars) and the inverted Gyre Index (continuous line), based on simulated data (1960-1993) and sea surface height measurements (1993-2011). GI is shifted 4 years ahead.

The effect on saithe by climate is rather a mixed effect of both the primary production on the Faroe shelf and the subpolar gyre. Recruitment of saithe at age 3 to the fishable stock may increase by i) the enhancing effects on recruitment by a weak subtropical gyre at time of hatching or recruitment at age 3 and ii) good feeding conditions when 0-group biomasses of sandeel and Norway pout are large, which in turn, is linked to the primary production on the Faroe shelf. Adult saithe seem to experience increased food availability in the deeper waters of the Faroe Plateau when the subpolar gyre is weak.

Although our original hypothesis of dominant control from the subpolar gyre on Faroe saithe has been weakened by the results of the project, climate variations may still be very important for several aspect of the Faroe saithe stock. Through the effect on the primary production in the shallow waters, climate variations may control the amount of food available to juvenile saithe, which seems to control recruitment. Recruitment then controls growth through density dependence, which affects migration through length dependence. Added to this, are the effects from the subpolar gyre variations. Indirectly, climate variations thus may have strong effects on recruitment, growth and migration of Faroe saithe.

4.6 Outcome of the Ph.D.-project in relation to management

The scientific outcome of this Ph.D. project is not ready to use in assessment at present, but it is hoped that the presented knowledge will pave the way for implementing important biological findings in the management of the Faroe saithe.

The migrating behaviour of saithe is found to affect the stocks in the Northeast Atlantic differently (Paper II). At this stage, it is not possible to implement the increased knowledge directly in the assessment because the available data are not detailed enough neither spatially nor temporally. The found emigration rates for the adult Faroese saithe are of such magnitude (33-42%) that migration is believed to impact the stock (Paper II). The VPA-analysis including simple scenarios for migration, on the other hand, gives the impression that the temporal variability in stock size of Faroe saithe may not be much altered by migration (Paper IV).

The discovered links between recruitment and both food-availability to juvenile saithe and drivers of the ecosystems (Paper III) provides potential for predicting the recruitment a couple of years in advance. Further analyses are needed, though, to decide the predictive strength of these links.

5 Main findings

Faroe saithe spawns in February on the eastern side of the Faroe Plateau. The growth of Faroe saithe is similar for females and males, and the females mature a year later (6.1 years) than males. The main diet of Faroe saithe consists of blue whiting, Norway pout, sandeel and euphausiids, where blue whiting becomes increasingly important with age, reflecting deeper distribution of both adult saithe and blue whiting on the Faroe Plateau.

Recruitment of Faroe saithe is linked to primary production on the Faroe shelf, mainly via the availability of sandeel and Norway pout in the juvenile phase of saithe. Perhaps recruitment is also improved by enhanced conditions in the deeper waters of the Faroe Plateau, induced by a weakened subpolar gyre, at either the time of hatching or when saithe enter the deeper waters.

The growth of Faroe saithe is density dependent for at least ages 3 to 6, and the number of saithe in the stock seemed to be the limiting factor, although biomass also gave high correlations. For the oldest ages no such density effect on growth was detectable.

Emigration rate of saithe from Faroese waters was found to be 33% when they were 60 cm or longer. After 3 years at liberty, 42% were recaptured elsewhere. The corresponding figures for Norwegian and Icelandic saithe were 6.6% and less than 1% respectively. The immigration rates to Faroese waters were lower than the emigration rates, although missing data for North Sea saithe may explain some of this.

When saithe are 5 to 7 years old, part of them has reached some critical length and a seasonal migration pattern becomes apparent. The observed pattern includes emigration from the Faroe Plateau in the summer months and return in the winter months. The migration is seen as a shift in the length distributions. The critical lengths observed are around the length, when saithe mature sexually, and therefore a combination of feeding and spawning migration is a plausible explanation. Feeding migrations in summer are further supported by tagging data, showing many saithe tagged on the Faroe Plateau were recaptured in Icelandic waters in the summer months, but only few in the spawning period.

A modified VPA including simple migration behaviour indicates that the relative stock variation and fishing mortality from the official stock assessments appear not to be much modified by migration, although the absolute numbers may be underestimated.

6 Outlook

In this study, correlations were found between the recruitment of saithe and the availability of 0-group sandeel and Norway pout. The actual sampling of juvenile saithe, however, is scarce in the catch method (bottom trawl) used in the primary source for biological information on saithe. The work presented in Bertelsen (1942) provides good information on juvenile saithe, but the design of those studies does not allow for comparison over years, since often the sampling area and timing varied among years. Future research should focus on shallow waters to obtain better estimates of e.g. diet of juvenile demersal fish. Given the trophic pathways presented in Paper VI, such studies should not be limited to e.g. saithe and cod, but should aim at mapping shallow water ecosystems in a wider sense.

The results obtained regarding migration (Paper II, Paper IV) have led to several new questions. Is the migration among regions in the Northeast Atlantic a permanent migration, or is it recurring migration between spawning and feeding areas? There are indications of migration between spawning and feeding areas (Paper IV, Olsen et al., 2010), but these questions are best addressed by tagging saithe with Data Storage Tags (DST-tags), as has already been done in Icelandic waters (Armannsson and Jónsson, submitted).

With regards to migration among the regions in the Northeast Atlantic, internationally coordinated tagging studies using traditional tags (e.g. T-bar tags) are needed to describe migration behaviour of saithe sufficiently, where saithe in all areas need to be tagged simultaneously and for a number of years. This is very labour consuming, since it requires joint efforts over several years. In addition, other research needs to be done, e.g. studies on reporting rates, and fishing patterns in the different areas.

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Paper I

Growth, maturation, diet and distribution of saithe (*Pollachius virens*) in Faroese waters (NE Atlantic)

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Paper II

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

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

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Abstract

Saithe (*Pollachius virens*) stocks in the Northeast Atlantic intermingle as a result of migration between stock areas. The extent of migration has been poorly quantified. Here, we estimate measures of the migration based on existing tagging data from Icelandic, Faroese and Continental (Scotland, North Sea and Norway) waters. Icelandic saithe were seldom caught outside Icelandic waters (less than 1% of tag returns), whereas 42% of adult saithe tagged in Faroese waters were recaptured outside Faroese waters. Only 6.6% of adult saithe tagged in Norwegian waters were recaptured outside Continental waters. In broad terms, there was a net migration of saithe towards Icelandic waters. The distance between tagging and recapture increased with increasing size/age, with the Norwegian saithe moving the longest distances. The observed migration rates indicate that simultaneous tagging experiments in the entire Northeast Atlantic should be conducted to improve the accuracy of stock assessments of saithe in this region.

Key words: Saithe, *Pollachius virens*, migration, Northeast Atlantic, tagging.

Introduction

Saithe (*Pollachius virens*) is a commercially important species and is widespread in the Northeast Atlantic (from the Barents Sea in the north to the Bay of Biscay in south, also around Iceland and East Greenland). Saithe is regarded as a demersal fish, but it does exhibit pelagic behaviour as well (Bergstad, 1991; Stensholt *et al.*, 2002; Neilson *et al.*, 2003; Armannsson and Jónsson, submitted). The pelagic behaviour is also reflected in the diet, which is not directly associated with the sea-floor, e.g. pelagic crustaceans such as copepods, euphausiids, and amphipods (Nedreaas, 1987; Bergstad, 1991; Højgaard, 1999; Jaworski and Ragnarsson, 2006; Homrum *et al.*, 2012), and fishes such as Norway pout (*Trisopterus esmarkii*), blue whiting (*Micromesistius poutassou*), herring (*Clupea harengus*), sandeel (Ammodytidae) and capelin (*Mallotus villosus*) (Pálsson, 1983; Du Buit, 1991; Bergstad, 1991; Jónsson, 1996; Jaworski and Ragnarsson, 2006; Olsen *et al.*, 2010; Homrum *et al.*, 2012). Juvenile saithe reside in inshore waters the first 2-4 years (Bertelsen, 1942; Clay *et al.*, 1989; Armannsson *et al.*, 2007). As adults, saithe move to offshore waters (Jones and Jónsson, 1971; Homrum *et al.*, 2012) and exhibit seasonal migrations between spawning and feeding areas (Jones and Jónsson 1971; Olsen *et al.*, 2010).

An interesting question is, to what extent such seasonal migrations may extend into foreign waters. Jakobsen and Olsen (1987) found that adult saithe, tagged in northern Norway, emigrated to Icelandic waters and, to a lesser degree, to Faroese waters. Also, significant changes in length at age from one year to another have been interpreted as immigration of saithe to Icelandic waters (Jonsson, 1996; ICES, 2000). Tagging in the Faroe area (Jones and Jónsson, 1971) showed that considerable proportions of saithe tagged on the Faroe Bank were recaptured in Icelandic waters, at North and West Scotland, and in the northern North Sea. In Icelandic waters, juvenile saithe appear to have high affinity to the area of tagging, and there is no indication of mass emigration from Icelandic waters (Jones and Jónsson, 1971; Armannsson *et al.*, 2007).

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

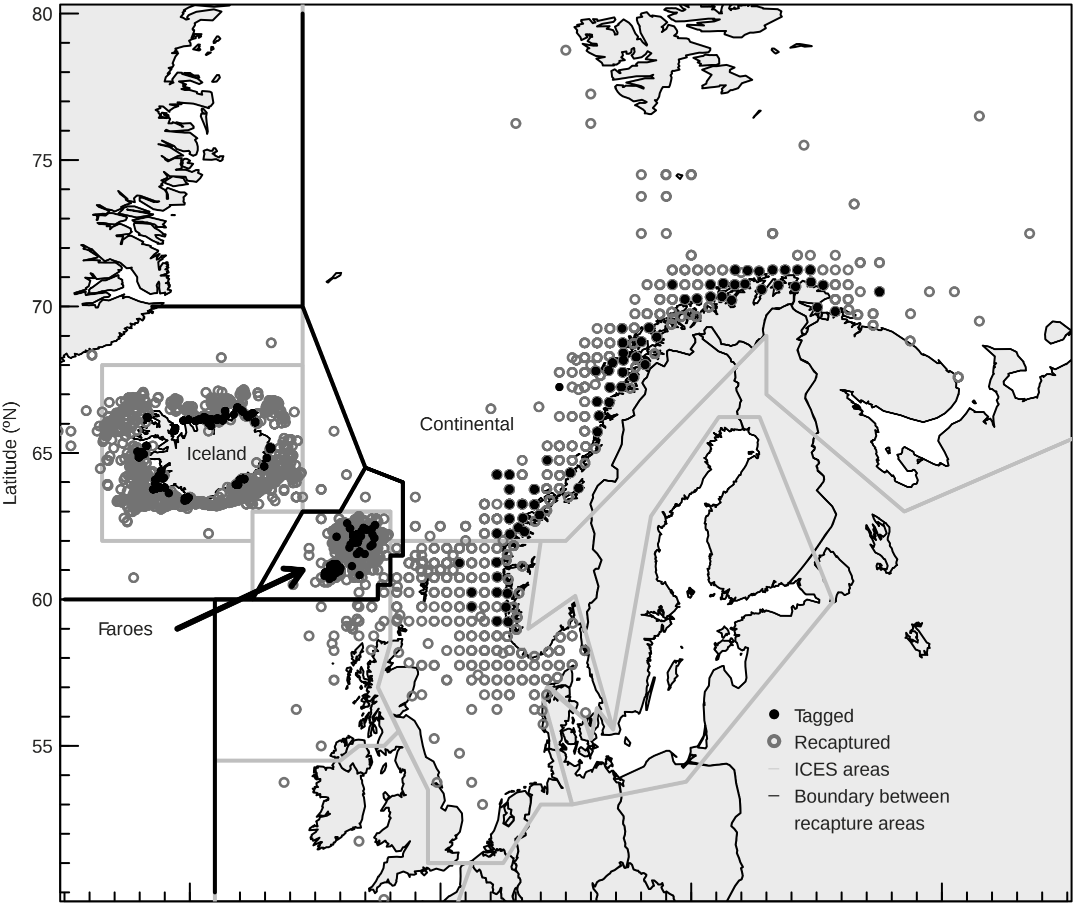

Figure 1. Study area. Stock areas (black lines), ICES areas (gray lines). Tagging localities (black points) and recaptures (grey circles) are shown as well, by statistical rectangle for Norwegian experiments.

stocks and to what extent they depend on individual fish length and time between tagging and recapture.

Material and methods

Within the advisory framework of ICES, saithe is treated as four separate stocks: Icelandic (Division Va) (ICES 2010a), Faroese (Division Vb) (ICES 2010a), Northeast Arctic (Subareas I and II) (ICES 2010b) and North Sea, Skagerrak and West of Scotland/Rockall (Subarea IV, Division IIIa and Subarea VI) (ICES 2010c), (Figure 1). Saithe west of Scotland was earlier treated as a separate stock in the advice, and is still managed separately. These four stocks have in this study been allocated to three separate "stock areas", which are defined in Figure 1. The Icelandic and Faroese stock areas roughly contain the respective ICES divisions, but are enlarged to include recaptures in the vicinity of the stock area. The Northeast Arctic and the North Sea and Skagerrak (North Sea) stocks are divided at 62°N in the ICES advisory framework. This division is not associated with any clear topographic, hydrographic or biological boundary, although the two stocks have clearly distinct recruitment patterns. Saithe tagged short distances north of 62°N were frequently recaptured south of this border and, less frequently, vice versa (Jakobsen, 1981). In this study, we therefore treat Northeast Arctic and North Sea as one stock area, which we term the "Continental" (Figure 1).

Tagging

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

Faroese waters: A total of 13 736 saithe were tagged in Faroese waters from 1959 to 1991 (Table 1). The tagging intensity varied over time, ranging from 3 tagged fish in 1967 to 3288 in 1962. The mean length of saithe in these experiments varied from 34 to 71 cm. The data originated from four tagging experiments. British experiments in 1959-1967 were primarily on the Faroe Bank (using trawl). This resulted in larger mean size of the tagged fish, than from the Faroese experiments, which were concentrated in shallower waters where juvenile saithe resided (Bertelsen, 1942; Homrum *et al.*, 2012). The Faroese taggings were conducted in 1959-1967, 1975-1976, and 1991.

Norwegian waters: The tagging experiments in Norwegian waters were the most comprehensive, covering varying parts of the Norwegian coast from 1954 to 1980 with 78 264 saithe tagged (Table 1). The tagging intensity varied considerably as did the main areas of tagging and the mean size of the tagged fish. In the beginning of the project, emphasis was on the northern part of the coastline

Table 1. Number of saithe tagged in Icelandic, Faroese and Norwegian waters, number and percentages recaptured. Mean length, main catch method when tagged and tag type are also indicated.

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

and the fish were larger (mean size ≈ 60 cm); later in the project, there was a wider coverage along the coastline, and the tagged saithe were smaller (mean size ≈ 40 cm).

Recapture

In this study, we based our analyses on the time, position, and fish length at tagging and recapture. The "relative recapture percentage" (RRP) for one stock area was defined as the percentage of fish recaptured in that stock area in relation to the total number of recaptured fish with reported location from that tagging. The "distance from tagging site" denoted the straight-line distance (sometimes crossing land) between the position at tagging and the position at recapture. The "time at liberty" denoted the time in years elapsed between tagging and recapture.

Unfortunately, length at recapture was not available for saithe tagged in Norwegian waters, and therefore, analyses regarding recapture length apply only to the Icelandic and Faroese data. Based on tagging lengths, almost all the saithe tagged were estimated to be at least 2 years old. Fish that have spent at least 3 years at liberty would thus be at least 5 years old and be roughly 60 cm or more in length (Moguedet *et al.*, 1987; Homrum *et al.*, 2012; S. Þ. Jónsson, unpublished data). Therefore, two criteria (larger than 60 cm and more than 3 years at liberty) were used to distinguish between the migratory behaviour of young and adult saithe. This division into young and adult saithe is related to the sexual maturity of fish, since 50% of saithe have matured sexually around age 5-6 (ICES 2010a; ICES 2010b; ICES 2010c; Homrum *et al.*, 2012).

Emigration and immigration rates

In this study, the observed RRP in a stock area, of saithe tagged in another stock area, are considered representative for the emigration rate from the latter to the former. This interpretation may to some extent depend on the detailed migrating behaviour and fishing mortalities in the different areas, but may be justified for some simple scenarios, e.g., the model presented in Appendix A, as long as fishing mortalities exceed natural mortality. To quantify the effect of migration on the receiving stock, we define the immigration percentage, IP, as the RRP scaled by the ratio between stock sizes (in numbers) of adult fish in the donating and receiving stock areas (Appendix A). Stock sizes and fishing mortalities (Figure B1 in Appendix B) were acquired from the ICES assessments (ICES, 2010a; 2010b; 2010c). For the Icelandic saithe, the most recent reports contain data only back to 1980. To extend the Icelandic series back to 1960, assessment results from older reports were used (ICES 1978; 1987). These stock data were aggregated for adult fish (defined as ages 5 to 10), to acquire the ratios between stock sizes among stock areas.

Results

The migrated distance from tagging site increased with increasing recapture length and age of saithe (up to 80 cm and 5 years of liberty) in all areas. The relationship was more pronounced in some areas than in others (Figures 2a and b). For saithe in the Faroese and Icelandic stock areas the distance from tagging site levelled off around 200-300 km. Distances from tagging site of saithe, either smaller than 50 cm or during the first year at liberty, were shortest for Faroese saithe. The migrated distances were largest for Norwegian saithe, except during the first year at liberty, when the distance was comparable to that of Icelandic saithe. Distance from tagging site versus length at tagging by time at liberty is provided for the Norwegian data only (Figure 2c). The youngest saithe moved the shortest distances from the tagging site. For saithe larger than 90 cm, there was a tendency towards shorter distances than for the 60-90 cm long saithe.

With respect to migration among stock areas, it was found that during the first one or two years at liberty, saithe were generally not recaptured outside their stock area (Table 2). Adult saithe (> 60 cm or at least 3 years at liberty) did, to some extent, migrate among the stock areas (Table 2), but the RRP varied significantly among stock areas ($\chi 2$-tests: for saithe larger than 60 cm: $p<0.001$, df = 2; more than 3 years at liberty: $p<0.001$, df = 3). Adult saithe tagged in the Faroese stock area were frequently recaptured in foreign stock areas – beyond 3 years at liberty, 42% were recaptured outside the Faroese stock area. Adult Icelandic saithe, on the other extreme, were seldom recaptured outside the Icelandic stock area (0.8%) (Table 2). The recaptures of Icelandic tags in the Faroese stock area derived exclusively

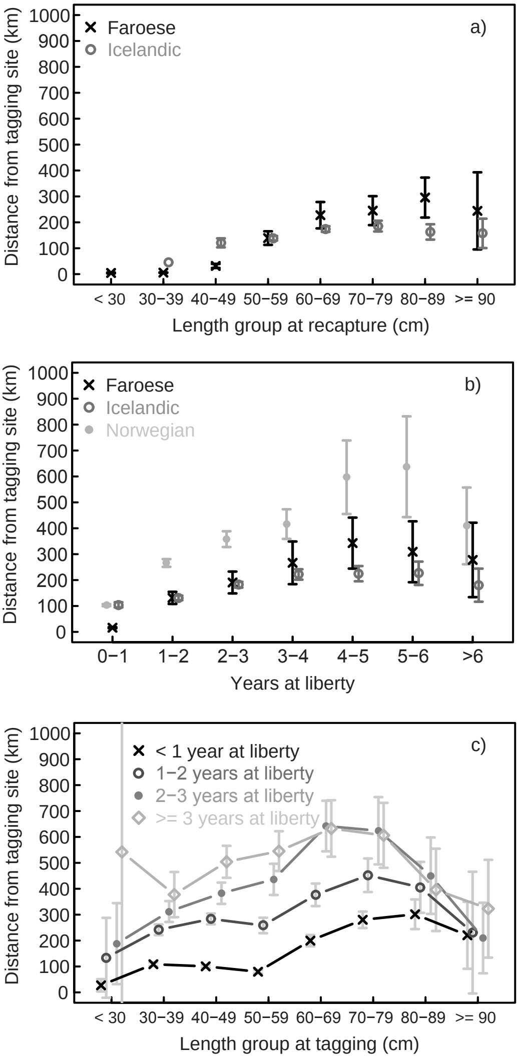

Figure 2. Distance between tagging site and site of recapture. a) Mean distance from tagging site of saithe tagged in Faroese and Icelandic waters by length group at recapture. b) Mean distance from tagging site versus time at liberty (for fish smaller than 50 cm at tagging). c) Mean distance from tagging site of Norwegian saithe versus length at tagging – by years at liberty as indicated in legend. Vertical bars represent 95% confidence intervals.

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

The temporal variation in the inter-area migration pattern was only investigated for Faroese and Norwegian saithe, where the tagging experiments covered several decades. The emigration from Faroese to Icelandic waters varied inter-annually between 23 and 47% and the emigration from Faroese to Continental waters varied between 0 and 27% (time at liberty > 3 years, Table 3). The emigration from Norwegian waters to Icelandic waters varied inter-annually between 2.3 and 7%, and to Faroese waters between 0 and 2.3% (Table 3). None of these variations were statistically significant ($\chi 2$-tests: Norwegian experiments: p = 0.94, df = 6, Faroese experiments: p = 0.89, df = 4).

Emigration from one stock area implies immigration to another, but the relative influence depends on the stock sizes. The migration among stock areas is summarized in Figure 3. Emigration from a certain stock area was described by the observed RRP (Table 2, where time at liberty exceeds 3 years). The largest IP values (immigration rates) were to Iceland (14% from the Faroese and 16% from the Continental stock area) and the lowest to the Continental stock area (0% from the Icelandic and 1% from the Faroese stock area). The immigration to the Faroese stock area was 1% from the Icelandic and 12% from the Continental stock area.

Discussion

Our findings suggest that the migration rates of saithe in the Northeast Atlantic vary considerably among stock areas, and this is in line with previous publications (Jones and Jónsson, 1971; Jakobsen and Olsen, 1987; Armannsson *et al.*, 2007). Young fish in all stock areas exhibited low emigration rates, corresponding well to the short distances from tagging site. For adult fish, the distance from tagging site increased in all areas, and the emigration rates differed among areas, being lowest for the Icelandic (0.8%), intermediate for the Continental (6.6%), and highest for the Faroese stock area (42%).

Working with tagging data is associated with limitations. The observed migration patterns are affected by several factors. One factor is differences in tag-loss among tag-types (Fowler and Stobo, 1991), which have varied considerably among the tagging experiments in this study. Variations in tag-loss will not affect our main conclusions, however, if we assume that losses of specific tag types do not vary between areas of recapture. There are other

Table 2. RRP (relative recapture percentage) in the Faroese, Icelandic and Continental stock areas in relation to the total number recaptured (with known position), by tagging area. The same variable is presented by length at recapture (upper part) and by time at liberty (lower part).

Tagging stock area		Iceland				Faroes				Norway			
Recapture stock area		Iceland	Faroes	Contin.	Recaptures (n)	Iceland	Faroes	Contin.	Recaptures (n)	Iceland	Faroes	Contin.	Recaptures (n)
Length at recapture (cm)	[26, 30)	-	-	-	0	0.0%	100.0%	0.0%	13				
	[30, 40)	100.0%	0.0%	0.0%	1	0.0%	100.0%	0.0%	224				
	[40, 50)	100.0%	0.0%	0.0%	91	1.0%	98.5%	0.5%	205				
	[50, 60)	100.0%	0.0%	0.0%	474	10.5%	86.3%	3.3%	153				
	[60, 70)	99.3%	0.7%	0.0%	422	24.1%	71.3%	4.6%	108				
	[70, 80)	98.4%	1.1%	0.5%	189	29.3%	61.0%	9.8%	82				
	[80, 90)	100.0%	0.0%	0.0%	74	27.5%	60.8%	11.8%	51				
	[90,100)	100.0%	0.0%	0.0%	21	11.1%	77.8%	11.1%	9				
	[100,120]	100.0%	0.0%	0.0%	9	50.0%	50.0%	0.0%	4				
	NA	99.5%	0.5%	0.0%	394	4.4%	90.1%	5.5%	365				
All length groups		99.5%	0.4%	0.1%	1675	8.3%	87.9%	3.8%	1214				
	> 60 cm	99.2%	0.7%	0.1%	715	26.4%	65.7%	7.9%	254				
Years at liberty	0-1	100.0%	0.0%	0.0%	341	0.5%	98.6%	0.9%	651	0.3%	0.2%	99.5%	9650
	1-2	99.6%	0.4%	0.0%	460	9.6%	86.4%	4.0%	272	1.2%	1.2%	97.6%	3068
	2-3	99.3%	0.5%	0.2%	440	18.8%	73.9%	7.2%	138	2.8%	2.5%	94.7%	1171
	3-4	99.1%	0.9%	0.0%	223	27.7%	61.5%	10.8%	65	3.6%	1.4%	95.0%	443
	4-5	98.8%	1.2%	0.0%	86	40.0%	52.5%	7.5%	40	6.7%	1.7%	91.6%	179
	5-6	100.0%	0.0%	0.0%	46	37.5%	45.8%	16.7%	24	9.5%	3.6%	86.9%	84
	> 6	100.0%	0.0%	0.0%	27	13.0%	69.6%	17.4%	23	4.7%	0.8%	94.5%	127
	Total	99.5%	0.4%	0.1%	1623	8.3%	88.0%	3.7%	1213	1.0%	0.7%	98.4%	14722
	> 3	99.2%	0.8%	0.0%	382	30.3%	57.9%	11.8%	152	5.0%	1.6%	93.4%	833

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

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

factors, such as fishing patterns of the commercial fleet, e.g. gear used and multi nation fleets, and varying and unknown reporting rates. For these factors, we have no estimates of the errors they may induce, and they are not discussed further.

Distances from tagging site in relation to size and stock area

Distances from tagging site were shortest for the youngest saithe – especially in the Faroese stock area. One explanation could be that the younger saithe had a shorter time to move from their tagging sites. But considering only fish that had been recaptured during the first year after tagging (shown for the Norwegian stock area only) the same pattern was revealed (Figure 2c). Therefore, the shorter distance migrated by smaller saithe appears to reflect a genuine behavioural characteristic. The most likely explanation for this is that young saithe prefer shallow habitat (Bertelsen, 1942; Jones and Jónsson, 1971; Nedreaas, 1987; Homrum *et al.*, 2012), which therefore limits the distance they can move away from the coast and their original tagging location. This would also explain why young Faroese saithe moved the shortest distances, because the shallow area available to the Faroese saithe is much smaller than the shallow waters available to the Icelandic and Norwegian saithe.

Adult saithe migrated longer distances than young saithe in all stock areas (Figures 2a, b, c), and moved farther in the Continental than in the Faroese and Icelandic stock area. The distance from tagging site decreased for the largest sizes at tagging (Figure 2c). This is interesting and could perhaps be explained by a combination of spawning site fidelity and larger saithe being more prone to capture in the spawning season than the rest of the year, when they may reside outside fishable areas.

Migration among stock areas

As argued in appendix A, the interpretation of the RRP values as emigration rates is a good approximation as long as fishing mortalities exceed natural mortality. The lowest average fishing mortality for ages 5 to 10 over the time-span of a tagging project is in the Faroese stock area in 1961-1983, where F is 0.27 compared with 0.38 in the Continental stock area (Table 4), and for this change in F the RPP would decrease by only 12% (from 1.6% to 1.4%). We thus conclude that the observed RPPs are representative for the emigration rates.

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

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

For adult saithe tagged in Faroese waters, a substantial fraction (26-30%) was recaptured in the Icelandic stock area (Table 2), and 8% in the Continental stock area. In Faroese and Scottish waters, blue whiting has been an important prey to saithe, but Norway pout and euphausiids are also constituents of the diet (Du Buit, 1991; Homrum *et al.*, 2012). In addition to diet studies, by-catch of saithe in the blue whiting fishery also indicates feeding migrations following blue whiting (Pálsson, 2005).

Adult saithe in Icelandic waters show negligible emigration (Table 2). This is consistent with previous studies, which have demonstrated less than 1% emigration from Icelandic waters (Jones and Jónsson, 1971; Armannsson *et al.*, 2007). This may perhaps be related to the distribution of the main prey species, especially capelin, which is the main constituent in the diet of saithe in Icelandic waters part of the year (Pálsson, 1983; Jonsson, 1996; Jaworski and Ragnarsson, 2006).

The saithe is a capable swimmer (Videler and Hess, 1984) and is able to utilize the pelagic environment (Bergstad, 1991; Stensholt *et al.*, 2002; Neilson *et al.*, 2003; Jonsson Armannsson, submitted). The pelagic behaviour is evidenced by saithe by-catch in the blue whiting fishery (Pálsson 2005) and the connection between saithe and herring in Norwegian waters (Runde, 2005). The interplay between spawning and feeding migrations seem a plausible explanation for the observed migration rates among stock areas and seasonal and inter-annual changes in distribution of prey species are likely drivers of saithe migration.

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

*Table 4. Summary of stock sizes and fishing mortalities per area and recapture period based on the respective ICES reports from stock assessments in 2010 (see text). *Note that here, the Continental stock area is a combination of the Northeast Arctic and North Sea/Skagerrak.*

		Stock-area of recapture								
Tagging area	Periods of recapture	Ice	Far	Cont*	Ice	Far	Cont*	Ice	Far	Cont*
		Mean			Standard deviation			Stock size ratio		
Average stock size of ages 5-10 in recapture periods (x106)										
Iceland	2000-2010	51	71	418	18	28	82		0.71	0.17
Faroes	1959-1980, 1991-1997	63	28	232	32	11	108	0.45		0.12
Norway	1954-1983	68	27	221	30	12	103	3.26	8.15	
Average fishing mortality of ages 5-10 in recapture periods										
Iceland	2000-2010	0.38	0.60	0.35	0.11	0.23	0.13			
Faroes	1959-1980, 1991-1997	0.35	0.33	0.40	0.15	0.18	0.19			
Norway	1954-1983	0.32	0.27	0.38	0.13	0.12	0.18			

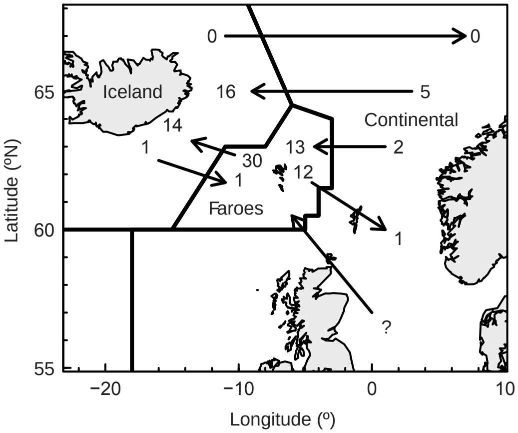

Figure 3. Map showing the estimated migration (in %) among the Faroese, Icelandic and Continental stock areas of saithe, where more than 3 years had elapsed between tagging and recapture. At the start of an arrow, the relative recapture percentages (RRP) (see text) are listed and at the end of an arrow the immigration percentage (IP) is shown.

Differences in RPP in individual periods (Table 3) could indicate differences in migration rates, but none of these were statistically significant. Therefore, we cannot identify any consistent temporal variations in migration rates. Due to the broken time-line of tagging among the three stock areas, however, we cannot safely conclude that the migration rates have been constant over the six observed decades.

Implications for stock assessment

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

Conclusions and outlook

Young saithe move short distances and appear to be limited by the topography, such that saithe in Faroese waters move the shortest distances and saithe in Norwegian waters move the farthest distances. Larger saithe migrate across boundaries set in the ICES advisory framework, but the different stocks appear to have different magnitudes of migration. Icelandic saithe are seldom recaptured outside domestic waters whereas large Faroese saithe often are recaptured in foreign waters. Many questions on saithe migration in the Northeast Atlantic remain unanswered, however. In order to clarify the mechanisms behind the migration and what causes the difference among stock areas, the individual behaviour of saithe should be investigated much more intensively, e.g. by use of Data Storage Tags (Armannsson and Jónsson, *submitted*). Also, simultaneous tagging experiments of saithe in the entire Northeast Atlantic, maintained for several years, are needed to fill gaps in our knowledge.

Acknowledgement

Here three large and partially old data-sets have been used. The immense effort that many people have put into acquiring all this information is greatly acknowledged. With respect to this specific study, we wish to thank Ove Djupevåg for quality checking the Norwegian data and Lise H. Ofstad for commenting on earlier drafts. We would also like to thank Steinar Olsen for constructive comments and suggestions during this study.

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Appendix A

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

Consider a certain stock component (e.g. an age group) of saithe in area A with the number of fish equal to N_0. Assume that a certain fraction, R, of these fish are tagged at time t_1 in area A where they remain until time t_2, i.e. for a period $ta=t_2 - t_1$. The number of fish in the stock component still surviving in the sea will be:

$$N_a = N_0 \cdot \exp(-Z_a \cdot t_a) \qquad \textit{with} \qquad Z_a = F_a + M \qquad (1)$$

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

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

During a short time interval, dt, the number of tagged fish that are caught in area A will be given by $F_a \cdot N_A(t) \cdot dt$ and the total number caught in the original area from time t_2, onwards, is then given as:

$$C_a = (1-P_m) \cdot R \cdot N_a \cdot F_a \cdot \int_{t_2}^{\infty} \exp\left[-Z_a \cdot (t-t_2)\right] dt = (1-P_m) \cdot R \cdot N_0 \cdot \exp(-Z_a \cdot t_a) \cdot \frac{F_a}{Z_a} \qquad (3)$$

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

$$C_b = P_m \cdot R \cdot N_a \cdot F_b \cdot \int_{t_2}^{\infty} \exp\left[-Z_b \cdot (t-t_2)\right] dt = P_m \cdot R \cdot N_0 \cdot \exp(-Z_a \cdot t_a) \cdot \frac{F_b}{Z_b} \qquad (4)$$

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

$$RRP \equiv \frac{C_b}{C_a + C_b} = \frac{\alpha \cdot P_m}{1-(1-\alpha) \cdot P_m} \qquad with \qquad \alpha \equiv \frac{Z_a \cdot F_b}{F_a \cdot Z_b} = \frac{1+M/F_a}{1+M/F_b} \qquad (5)$$

If fishing mortalities are the same in both areas, α=1 and the RPP that we measure will, under the given assumptions, equal the “true” proportion, P_m, for the whole stock component. Even with considerable differences in fishing mortality, α will remain close to 1 as long as fishing mortalities are substantially higher than the natural mortality. RRP is thus rather insensitive to differences in F between the areas. This is because we are observing the recaptures in the remaining lifetime of the tagged fish. With a high F we take the fish over at shorter time period than if F is lower, but ultimately we catch the same number of fish (still given that fishing mortalities are substantially higher than natural mortality).

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

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

Appendix B

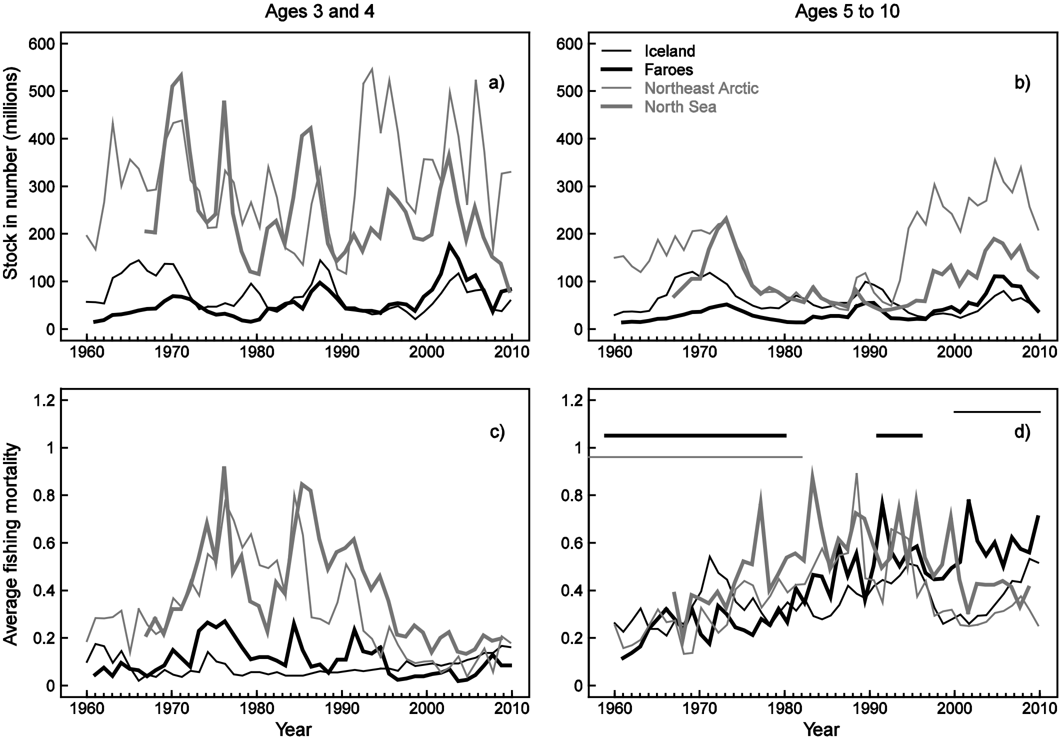

Figure B1. Stock in number and fishing mortality at age for saithe in the Northeast Atlantic (ICES 2010a; 2010b; 2010c). For Icelandic saithe results for 1960-1979 from older reports are used (ICES 1979; 1987). Stock in number has been summed for ages 3 and 4 (a), and ages 5 to 10 (b). Fishing mortality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

Paper III

Recruitment and growth of saithe (*Pollachius virens*) in Faroese waters

Recruitment and growth of saithe (*Pollachius virens*) in Faroese waters

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Abstract

Saithe is one of the dominant and most exploited fish stocks on the Faroe Plateau. Data on recruitment and weight-at-age have been obtained through annual stock assessments and show large variations. However, the mechanisms generating these variations have not been documented. Here we show that a large part of the variation in recruitment at age 3 can be explained by food availability in earlier life stages (age 1 and 2) in form of 0-group sandeel and Norway pout. Since juvenile sandeel have been shown to depend on primary production, saithe recruitment might be indirectly dependent on the spring bloom, which has been suggested to be controlled by regional climate variations, e.g. air-sea heat loss. Variations in the intensity of the subpolar gyre circulation also seem to affect saithe recruitment, however less strongly. In contrast to recruitment, we find no environmental influence on saithe growth. Instead, the growth of young saithe (ages 3 to 6) is inversely proportional to the total number of saithe in the stock. For the growth variations of older saithe (age 7+), we find no convincing explanation, however, these age groups have been shown to migrate extensively, and this might confound potential relationships.

Key words: Climate, density dependence, food availability, primary production, subpolar gyre.

Introduction

Faroese waters (Figure 1) comprise the relatively shallow area over the Faroe Plateau and surrounding banks as well as a wide deep-water region (Hansen and Østerhus 2000). Although exhibiting pelagic behaviour (Stensholt et al. 2002), saithe (*Pollachius virens*) is generally considered a demersal fish and is grouped with cod and haddock as one of the dominating demersal species on the Faroe Plateau. After spawning, saithe larvae and juveniles are concentrated in the shallow regime of the Faroe Shelf from which they move to deeper waters as 2-3 years old and progressively with size (Bertelsen 1942; Homrum et al. 2012), as is also observed in e.g. Norwegian and Canadian waters (Clay et al. 1989; Bergstad 1991).

Faroe saithe is initially recruited to the commercial fisheries at age 3 and stock assessments have provided data on number- and weight-at-age for the period 1961-2010 (ICES 2011). These data show that recruitment, defined as the number of 3 year old saithe each year, may vary by more than an order of magnitude, while the mean weight of the ages 4 to 7 may vary by more than a factor of two. Although both cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) on the Faroe Plateau exhibit positive correlations between individual growth and recruitment, no such pattern is evident for saithe. On the contrary, weight-at-age is generally small when recruitment is high (ICES 2011). Recruitment and growth of cod and haddock has been linked to primary production on the Faroe Shelf (Gaard et al. 2002; Steingrund and Gaard 2005), but little is known about the processes that control these features in the Faroese saithe stock.

The aim of this study is to investigate these processes. To do so, we compare time series of saithe recruitment with several causal variables that might influence the early life stages of saithe. These include an index for primary production on the Faroe Shelf and indices from the annual 0-group survey on the Faroe Plateau. Based on stomach content analysis, 0-group sandeel (Ammodytidae) (Højgaard 1999) and Norway pout (*Trisopterus esmarkii*) (Homrum et al. 2012) are important constituents in the diet of juvenile saithe in Faroese waters, and special attention is thus paid on these two species. Since the subpolar gyre has been shown to affect several trophic levels in the deep-water region of Faroese waters (Hátún et al. 2009a), we also consider the 'gyre index', which reflects the strength of the subpolar gyre in the North Atlantic.

To study individual growth, we use the weight-at-age data to compute growth as the weight increase of a cohort from one year to another. These values are compared to indices for the living conditions, such as the gyre index, and to various stock parameters. We try to clarify whether the generally inverse relationship between weight-at-age and stock size (ICES 2011) can be explained by some density dependent process, governed by e.g. abundance or biomass.

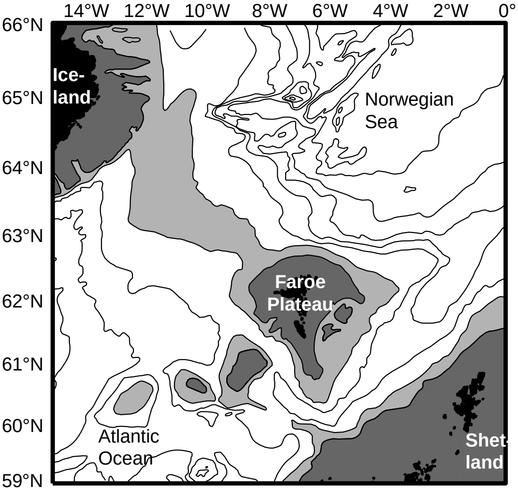

Figure 1. The Faroe Islands are located on the Faroe Plateau between Iceland and Shetland. Light gray areas are shallower than 500 m. Dark gray areas are shallower than 200 m. Black areas are land.

Material and methods

The primary data set used in this study is based on stock assessments of Faroe saithe, which includes time series of number- and weight-at-age. To investigate saithe recruitment, we also examine data on primary production and 0-group fish species that can serve as food for juvenile saithe on the Faroe shelf, as well as the gyre index.

Stock data

The number N_i of saithe at age i from 3 to 14 (number-at-age) was obtained from the 2011 stock-assessment for the years 1961 to 2010 (ICES, 2011), which is based on a virtual population analysis (VPA). From these data, we obtain the recruitment as the number of 3 year old fish entering the fishery, as seen in hindsight. Unless otherwise noted, this definition of recruitment is maintained throughout the paper, i.e. the time of recruitment is the year that a certain cohort reaches age 3. Since a specific year class has to have been fished for some years before the VPA converges, the last three years in the number-at-age and recruitment series are rather uncertain.

Because the input-series to the stock assessment of saithe in Faroese waters extends furthest back in time, data on mean weight-at-age (ages 3 to 14 from 1961 to 2010) were taken from this series. These data are based on samples of the commercial catches of saithe in Faroese waters.

From the weight-at-age data, we have computed time series of growth by subtracting the mean weight of a cohort for one year from that of the following year. These series were, however, fairly noisy and 3-year running means of the growth (averaged over 3 years; not following year classes) were therefore computed and used in the analyses.

Density dependent growth

Density dependent growth occurs when the growth of individuals is inhibited by its own or coexisting stocks. Several different attributes of a stock might inhibit individual growth, e.g. the total number of the stock or certain age groups within it, the total biomass, and the required basic metabolism of the total stock, which generally is found to increase with weight to the power 0.75 (Schmidt-Nielsen

1983). The three possibilities, mentioned here, may be investigated by testing how well the smoothed weight growth values $\Gamma_{i,i+1}(t)$ for growth from age i to i+1 fit a linear relationship:

$$\Gamma_{i,i+1}(t) = G_i + g_i \cdot \frac{1}{\sum_k N_k(t) \cdot W_k(t)^v} \qquad (1)$$

where $N_i(t)$ and $W_i(t)$ are number and weight of age group i, whereas G_i and g_i are constants for each age group. The exponent, v, may be set to 0, 1, or 0.75, depending on whether the growth is assumed to be limited by the total number, the total biomass, or the required basic metabolism. The success of these fits for each age group may be measured by the correlation coefficient between the growth values and the last term in Eq. (1).

By regression analysis, we can for each age group determine the coefficients G_i and g_i in Eq. (1). This allows us to generate simulated values of weight-at-age. The simulation is initialized by specifying actual values for ages 4 to 13 to the first year in our records (1961). Thereafter, we assume the weight of 3-year old saithe either to be constant (equal to its average) or given by the actual weight at age 3, whereas the weights of the older fish are calculated by Eq. (1).

Primary production

The primary production index (hereafter PP-index), a measure of the accumulated new primary production in the Faroe shelf water ecosystem during the spring bloom from 1990 to 2010, was calculated based on the reduction in nitrate concentration from winter levels until a fixed date (June 26 each year) at fixed stations plus estimated net influx of nitrate from the surrounding off-shelf water during the same period of time. For further details see Gaard et al. (2002) and Steingrund and Gaard (2005).

0-group survey

Data on abundance and length of the fry of saithe, sandeel and Norway pout were obtained from the annual 0-group survey on the Faroe Plateau (1983 - 2010). The survey was primarily designed to investigate juvenile biology of cod, but other species were adequately sampled as well. Up to 72 stations on the Plateau with bottom depths between 45 and 150 m were sampled each year. The gear used was a capelin trawl (5 mm mesh size in the cod end) towed at 3 knots at between 25 and 45 meters depth (the exact trawling depth was decided based on writings on the echo sounder) for 30 minutes during daytime. In case of large samples, a subsample, approximately 0.2 liters of fry, was sorted to species and 150-200 individuals of each species were measured to the nearest lower mm, the rest was counted.

The abundance of fry from each species was calculated as the mean number per haul. Mean length was calculated for all specimens caught. A biomass index was obtained assuming a constant condition factor, i.e. the biomass is proportional to abundance multiplied by mean length cubed.

Gyre index

The gyre index originates from a Principal Component Analysis of the sea surface height field in the northern North Atlantic (Häkkinen and Rhines 2004; Hátún et al. 2005). The gyre index is the first principal component (time series) from this analysis. Dominance of cold and fresh subarctic water in the Iceland Basin is associated with a high index value (implying a strong gyre circulation) and dominance of warmer and more saline water is associated with a low index (implying a weak gyre circulation). Here, we use a more regional version of the index, which has been extended back to 1960, using an ocean model forced with air-sea fluxes from reanalyses (Hátún et al. 2009b).

Results

In this section, we present the main features of the saithe stock variations and compare the recruitment values to the PP-index and the amount of food that might have been available to the juvenile saithe. To investigate whether growth might be density dependent, we also compare growth values of saithe with various causal inhibiting variables.

Stock variations

The recruitment of saithe, as obtained from the annual stock assessment (ICES, 2011), varied from 7 to 105 million individuals. There was a cyclical pattern (Figure 2a) with maxima around 1970, 1986 and 2002. Although not in phase, a similar pattern was observed in the mean weight of 4-7 year old saithe.

Recruitment and primary production

Since the recruitment of saithe as 3 year old may be assumed to depend on preceding living conditions, the number of 3-year old saithe each year was correlated to the PP-index (Figure 2b) averaged over the three preceding years. When all values in the time series were included, the averaged PP-index explained 31% of the total variance (R = 0.56, N = 20). However, if the last three uncertain years were excluded, the correlation increased (R = 0.60).

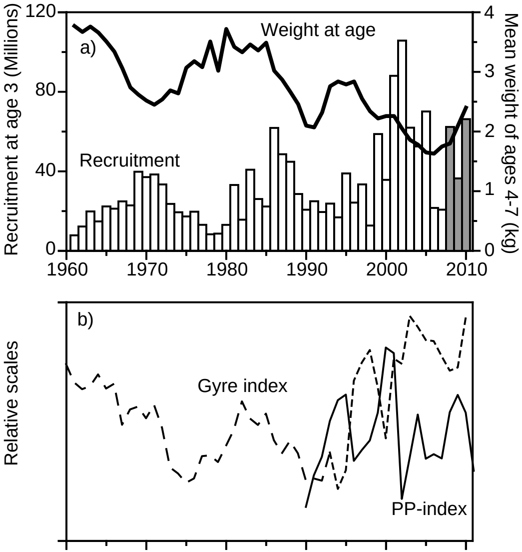

Figure 2. (a) Recruitment (bars) and average weight of ages 4 to 7 (full curve). The grey bars indicate the 3 latest years, in which the recruitment estimates are generally rather uncertain. (b) The inverted gyre index (dashed) and the PP-index (full). The gyre index from 1960 to 1993 is based on simulations (long dashed) (Hátún et al., 2005) and from 1993 to 2010, it is based on mapped satellite altimetry data (http://www.aviso.oceanobs.com) (short-dashed).

Food availability for juvenile saithe

To investigate the importance of food availability in the earlier stages (age 1 and 2) of saithe, the recruitment of saithe (age 3) was correlated to the biomass, abundance and mean length of sandeel and Norway pout fry one (t_{-1}) and two (t_{-2}) years before (Table 1).

Generally, biomass was the prey parameter showing the highest correlations with recruitment (Table 1, Figure 3) and the relationships were stronger, especially regarding sandeel, when the last three years of the recruitment series were excluded. The recruitment of saithe had the best correlation with the sandeel fry biomass of the previous year (t_{-1}) (R = 0.85 for the period 1984 - 2007). However, the Norway pout fry biomass (t_{-2}), representing the food availability of the age 1 saithe two years before, was stronger than that of the sandeel fry biomass. Although weaker, the recruitment was also correlated with the abundance and mean length of the prey species (the two parameters used to calculate the index of biomass) (Table 1). It is worth noting that all the correlation coefficients were positive, which gives some statistical support to their validity.

The effect of the gyre index on recruitment

The marine climate in the Faroe region has been found to respond to the gyre index with a one year lag (Hátún et al. 2005). To illustrate the similar temporal variations of the gyre index (inverted) and the saithe recruitment, they are both presented in Figure 2. Table 2 shows that the correlation coefficient is highest (negatively) when a lag of four years is applied, corresponding with one year lag + three years of growth. However, the annual differences are not that large, and zero lag gives almost the same correlation coefficient as a four year lag (Table 2).

Density dependence of growth

Smoothed growth values, indicating the average individual weight increase from one age to the next in a cohort and averaged over three years, are shown in Table 3. The sample sizes, from which the weight-at-age values each year are computed, decrease with age, which might be one reason for

Table 1. The correlation coefficients between the recruitment of saithe (age 3) and the availability (index of biomass, abundance and length) of sandeel and Norway pout fry one (t_{-1}) and two years (t_{-2}) prior to recruitment of saithe in the period 1984-2007, N = 24. Numbers in brackets show the correlations when the period was extended to cover 1984 - 2010, N = 27.

	Norway pout						Sandeel					
	Biomass		Abundance		Mean length		Biomass		Abundance		Mean length	
	t_{-1}	t_{-2}	t_{-1}	t_{-2}	t_{-1}	t_{-2}	t_{-1}	t_{-2}	t_{-1}	t_{-2}	t_{-1}	t_{-2}
Saithe	0.50	0.74	0.45	0.72	0.56	0.41	0.85	0.59	0.83	0.57	0.59	0.40
Recruitment	(0.45)	(0.71)	(0.42)	(0.69)	(0.45)	(0.32)	(0.69)	(0.56)	(0.49)	(0.49)	(0.50)	(0.35)

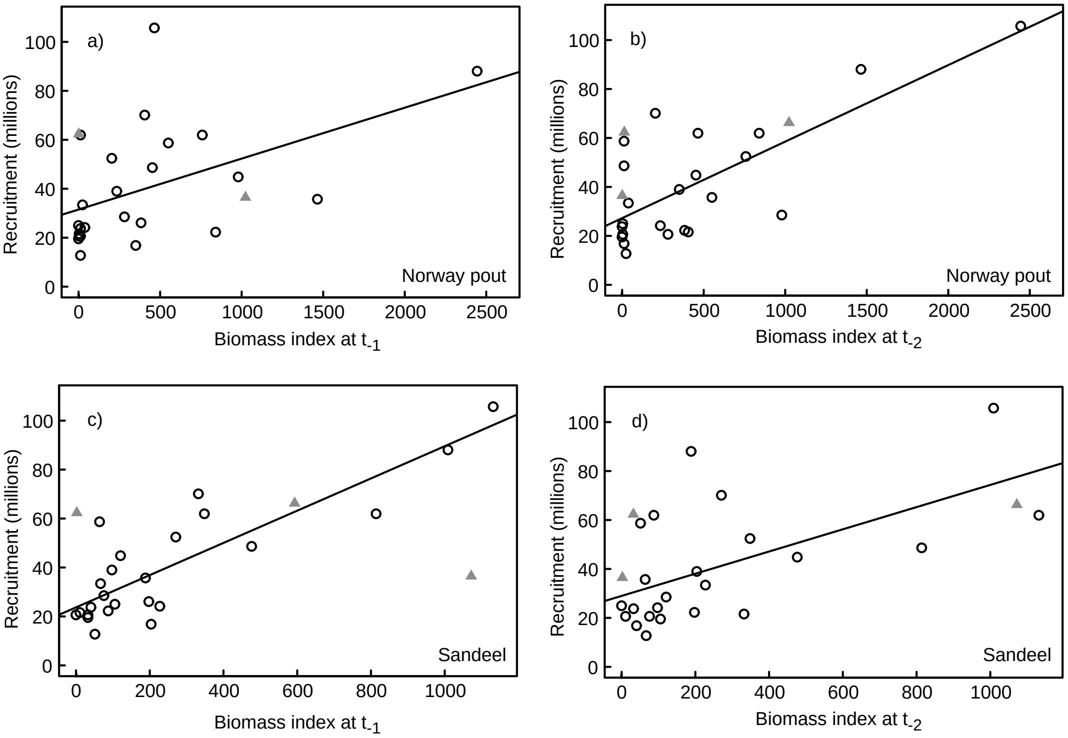

Figure 3. Recruitment of saithe at age 3 in relation to the biomass index of Norway pout (a) and (b) and sandeel (c) and (d). Figures (a) and (c) show the relationships between recruitment at age 3 and the prey biomass the year before (t-1), while (b) and (d) show the relationships between recruitment at age 3 and the prey biomass two years before (t-2), representing the food-availability of the one- and two-year-old saithe, respectively. The grey triangles indicate the three recentmost years, in which the recruitment estimates are generally rather uncertain. The lines are the regression lines when the three last years have been excluded.

Table 2. Correlation coefficients between recruitment of saithe and the gyre index with different lags (1961 to 2007, N = 47). Positive lag indicates that recruitment lags after the gyre index. Numbers in brackets show correlations when the period is extended to include 2008 - 2010, N = 50.

Lag:	0	1	2	3	4	5	6	7
Correlation:	-0.38 (-0.44)	-0.32 (-0.37)	-0.27 (-0.33)	-0.36 (-0.41)	-0.39 (-0.45)	-0.29 (-0.37)	-0.21 (-0.29)	+0.09 (-0.06)

Table 3. Average, standard deviation, and the ratio between the two (std. dev./average) of the 3-year running mean (weight) growth of individual age groups.

Age:	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	13-14
Average:	0.45	0.54	0.64	0.77	0.84	0.75	0.69	0.82	0.54	0.45	1.37
Std. dev.:	0.05	0.11	0.06	0.06	0.07	0.11	0.07	0.22	0.20	0.54	1.09
Ratio:	0.10	0.20	0.09	0.07	0.08	0.15	0.11	0.27	0.37	1.21	0.80

Table 4. Correlation coefficients between the 3 year running mean (weight) growth of individual age groups and the number of saithe in that age group on 1 January of the third year (top row) as well as the inverted number. Period 1961-2007, N = 47.

Age:	3-4	4-5	5-6	6-7	7-8	8-9	9-10
Number at age:	-0.62	-0.59	-0.70	-0.38	-0.35	-0.04	-0.26
Inverted number:	0.59	0.65	0.67	0.31	0.31	0.18	0.25

the increased standard deviations for the older saithe. In the following, we neglect data for saithe older than 10 years.

From age 3 to 10, we compared the smoothed growth values with the number of saithe of that age (Table 4) and with more integrated indicators of the stock, as defined by Eq. (1). Since the smoothed growth values were based on average weight values for 4 years, we used stock values dated at 1 January of the third year for comparison.

The top row of Table 4 lists correlation coefficients between the smoothed growth values for each age group and the number of saithe in that age group. For the 3 younger age groups of saithe, we see fairly strong negative correlations. This is reflected in positive correlation coefficients for the same age groups when we correlate the growth with the inverted number of number-at-age (bottom row). The growth of one age group might not, however, necessarily depend on the number of individuals in that age group and higher correlation coefficients are seen when the growth is compared to more integrated measures of the stock (Table 5).

From Table 5, it appears that from 50% to more than 70% of the variations in growth from age 3 to 6 can be explained by density dependence on the total stock. The most inhibiting factor seems to be the total number ($v = 0$), rather than biomass ($v = 1$) or basic metabolism ($v = 0.75$), although we cannot in a statistically meaningful way determine, which form of inhibiting factor is most likely. The simplest interpretation, supported by the first row in Table 5, is that from ages 3 to 6 or 7, the growth is inversely related to the total number of saithe in the stock. For the older saithe, the total stock does not seem to affect the growth substantially and neither does the older component of the stock (last row in Table 5).

Using Eq. (1) with $v = 0$, we have generated series of simulated weight-at-age. For growth from age 3 to 7, where the correlation coefficients in Table 6, first row, are relatively high, we used the values for G_i and g_i as determined in the regression analyses. For ages above 7 years, we assumed constant growth, equal to the average ($g_i = 0$). In spite of these simplifications, the simulated weight-

Table 5. Correlation coefficients between the 3 year running mean weight growth of individual age groups and stock size as described by different versions of the last term in Eq. (1). The first column shows the exponent, v, and the second column shows the ages over which the denominator in the last term of Eq. (1) is summed.

Exp.	Ages	3-4	4-5	5-6	6-7	7-8	8-9	9-10
0	3-13	0.85	0.78	0.72	0.44	0.19	0.15	0.14
0.75	3-13	0.83	0.71	0.68	0.39	0.28	0.23	0.19
1	3-13	0.79	0.62	0.62	0.34	0.31	0.27	0.23
0	3-6	0.78	0.78	0.69	0.44	0.08	0.12	0.12
0	7-12	0.46	0.17	0.28	0.24	0.57	0.09	0.14

Table 6. Correlation between actual and simulated weight-at-age for the period 1971 to 2007 (N = 37) where the weight at age 3 (w_3) is either fixed to equal its average (top row) or the actual weight (bottom row).

Age:	4	5	6	7	8	9	10	11	12	13
Fixed w_3:	0.67	0.83	0.83	0.79	0.79	0.84	0.68	0.69	0.63	0.28
Actual w_3:	0.75	0.81	0.78	0.74	0.73	0.84	0.70	0.68	0.63	0.26

at-age remains fairly well correlated with the actual values up to age 12, even when we neglect the first 10 years after initialization (Table 6).

For the weight at 4 years of age, Table 6 indicates that a correct weight-at-age 3 is important, but for the older fish, assuming a fixed weight-at-age 3 gives a just as good or even better weight estimate. The simulated weights-at-age may be combined with the number of fish in each age group to calculate the total biomass of the stock (ages 3 to 13) and the best fit is obtained if the actual weight-at-age 3 is used (Figure 4). However, since the 3 and 4 year old saithe on the average contribute more than 40% of the total biomass, this could be expected.

It thus appears that the simulated weight-at-age values allow us to calculate the total biomass fairly well. Using the actual weight-at-age 3 in the simulation (red curve in Figure 4), the largest relative deviations from the actual values (black curve) are an underestimate by 15% in 1985 and an overestimate by 17% in 1990-91 and 1998. If we had used average values for weight-at-age instead of the simulated values (not shown in Figure 4), the total biomass would have been underestimated by 22% in 1961 and overestimated by 61% in 2006.

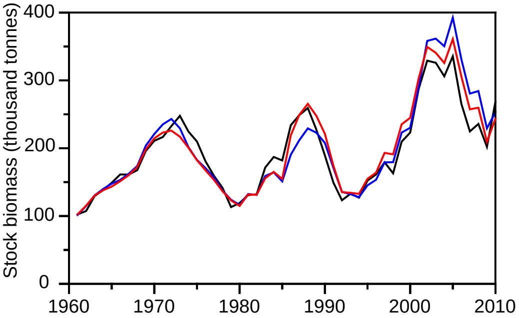

Figure 4. The total biomass of the saithe stock calculated from actual weight-at-age (black) and from simulated weight-at-age using Eq. (1) with v = 0 and the weight at age 3 either fixed (blue) or given by the actual value (red).

The effect of the subpolar gyre on growth

Comparing the smoothed growth values to the gyre index (Table 7), we find positive correlations for the young age groups and some indication of negative correlations with growth from ages 8 to 10, when the gyre index is lagged 1-2 years. This signal is weak, however.

Discussion

The results of our study point towards some clear conclusions regarding both recruitment and growth. Migration and statistics are, however two general limitations of this study which must be recognized.

Throughout the study, we have used values from the stock assessment for recruitment, which are based on a VPA that assumes no migration, while we know from tagging experiments that about 33% of Faroese saithe with lengths above 60 cm are recaptured outside Faroese waters (Homrum et al. submitted). The migration seems also to be

Table 7. Correlation between the 3 year running mean weight growth of individual age groups and the gyre index, where growth lags from 0 to 2 years after the gyre index.

Lag (years)	3-4	4-5	5-6	6-7	7-8	8-9	9-10
0	0.33	0.36	0.47	0.67	0.35	0.10	0.09
1	0.39	0.54	0.35	0.14	-0.02	-0.11	-0.43
2	0.30	0.48	0.35	0.20	0.00	-0.22	-0.44

length dependent (Homrum et al. in prep), which thus might bias weight-at-age and hence growth data.

Unfortunately, we are not at present able to determine the temporal variations in migration rates and thus to modify the VPA to account for migration. The fact that we do find consistent relationships between data derived from the stock assessment argues that the effect of migration is not sufficient to disrupt the main features of the recruitment and growth time series.

The second main limitation of our study is in terms of statistics. We have presented a series of correlation coefficients, but without statistical significance (*p*-values). This was done deliberately and is due to the large serial (auto) correlation of most of the time series. A number of more or less empirical methods which account for serial correlation are found in the literature, but we have found it hard to identify a method that rigorously excludes both type I and type II errors in our results. We argue, instead, that persistent patterns in correlation coefficients, e.g. consistent variations with age, are indications of rigorous results.

Recruitment

The recruitment of saithe is positively correlated with the primary production on the Faroese shelf. Given the trophical distance between the primary production and saithe, it is not surprising that the correlation is relatively weak. However, primary production has been shown to drive both recruitment and individual growth of both cod and haddock on the Faroe Plateau (Gaard et al. 2002; Steingrund and Gaard 2005).

Primarily, we found relatively high and positive correlations between recruitment of saithe and biomass index, abundance and length of sandeel and Norway pout fry from the 0-group surveys, which both are saithe prey resources (du Buit 1982; Bergstad 1991; du Buit 1991; Jónsson 1996; Jaworski and Ragnarsson 2006; Homrum et al. 2012). The fact that biomass exhibits the strongest correlation with recruitment (Table 1) is intuitively easy to understand, since abundance by itself may not be a suitable indicator of food availability if the individual fish vary in length.

The closer connection between sandeel as prey for two year old, rather than for one year old, saithe is in accordance with Højgaard (1999), who found that sandeel constituted 30% by weight in the diet of 2 year old saithe as compared to 6% in the diet of one year old saithe. The studies of Højgaard (1999) were conducted in a Faroese fjord (in 1996), as opposed to the ground-fish surveys (Homrum et al. 2012), in which the main diet of the youngest saithe (0-2 years of age) was found to be Norway pout. The apparent discrepancy between these two cited studies might have several possible explanations – e.g. the surveyed areas do not overlap, and thus sandeel might be of higher importance in near-shore areas than farther from land. Another explanation of the difference might be that the fjord studies were performed within a single year (before the stomach programme on the ground-fish surveys started in 1997), and interannual variability is large. However, our study seems to support that both sandeel and Norway pout are important prey species to juvenile saithe.

In Figure 3 there are many incidents of both low fry biomass and low recruitment, some incidents of both high fry biomass and high recruitment, and other points are positioned farther from the regression line. This indicates that sandeel and Norway pout generally are of great importance to the juvenile saithe, but in some years other factors might be critical as well.

The large differences in some of the correlation coefficients in Table 1 between the full period (1983 - 2010) and the reduced period (1983 - 2007) are troubling. One motivation for neglecting the last three years in the series was non-convergence of the VPA used to estimate recruitment. There are, however, also reasons to question some of the 0-group data during this period. The main discrepancy is for the recruitment value (as 3 years) in 2009, which was not exceptionally high even though the abundance of sandeel fry in the 0-group survey in 2008 was by far the highest on record. The sandeel abundance in 2008 also appears as an outlier when correlated to the PP-index (Eliasen et al. 2011). Moreover observations of puffin (*Fratercula arctica*) nesting success, which depends on sandeel fry, also indicate that 2008, as a whole, was not a good sandeel year (Olsen 2009). This supports our decision to rely on the reduced 1983-2007 period in Table 1.

From Table 2, it may appear that a weak gyre index might act positively on recruitment both around age 3, as the saithe moves from shallow to deeper domains (lags 0-1 years), and at the time of spawning (lags around 4 years). This latter effect would require that year-class strength to some extent is determined by processes already at or before the 0-group stage. Indeed, the correlation coefficient between saithe abundance during the 0-group surveys and recruitment three years later is 0.59 for the period (1983 to 2007) and 0.53 for the period (1983 to 2010).

Growth

For young saithe, ages 3 to 6, the growth in weight of a cohort from one year to another seems mainly to be controlled by the magnitude of the total stock of Faroe saithe (Table 5). Whether the inhibiting factor is total number, total biomass, total basic metabolism, or some other factor, remains unclear. If food limitation were the reason for the density dependent growth observed, we would expect the total biomass or total basic metabolism to be most important, but they do not exhibit the highest correlations although it is hard to distinguish in a statistically acceptable manner.

Saithe is a schooling species (Partridge et al. 1980) and there may be limitations to the number of individuals in a school for it to be successful. This could perhaps lead to the total number in the stock being the most severe inhibitor of growth, but this must remain pure speculation, as long as our knowledge on the behaviour of Faroe saithe, and saithe in general, is on the sketchy stage of today.

For saithe older than 7 years, the total stock magnitude seems to have little impact on the growth, whatever inhibiting factor is considered (Table 5). The mean individual weight of these age groups is, however, to a large extent determined at a younger age. Thus the mean weight-at-age can be fairly well estimated from the total stock size up to at least age 12 (Table 6) and this allows us to estimate the total stock biomass from the total stock number solely (Figure 4).

When correlating growth to the gyre index, we found positive correlation coefficients for ages 3 to 7 (Table 7). Since a positive gyre index indicates unfavourable conditions (Hátún et al. 2009a), this is confusing, but might perhaps be due to the effect of the gyre index on recruitment. A positive gyre index will tend to reduce recruitment and therefore the total number of saithe in the stock, which is dominated by the young age groups. With density dependent growth, this should lead to increased growth as observed in Table 7.

Here we have demonstrated density dependent growth of young saithe as a result of increased recruitment when the productivity on the shelf is favourable. This might seem counterintuitive as the increased productivity also would be expected to ensure food availability to the adult saithe. The adult saithe have, however, moved out off the shelf area into deeper waters, where the PP-index not is equally important. Instead, a negative gyre index might be a better indicator of food availability to the adult saithe after a lag of 1 to 2 years and Table 7 gives some support to that. An obvious next step would be to study temporal variability in the diet to see if the density effects are in terms of amount of food per capita – or whether the physiological mechanisms are to be sought elsewhere.

Climatic regulation

Since several parameters of the saithe stock are correlated to both the PP-index for the Faroe Shelf and to the gyre index, it is difficult to distinguish between these two as driving agents for the saithe stock dynamics.

It has been suggested that the controlling mechanism for the spring bloom is the horizontal exchange rate between the waters on the shelf and off-shelf (Eliasen et al. 2005) and this seems further to be affected by the air-sea heat transfer during spring (Hansen et al. 2005), providing a potential link between atmospheric variation and saithe recruitment.

The circulation strength of the subpolar gyre is also regulated by air-sea heat loss, not around the Faroes, but over the Labrador-Irminger Seas (Häkkinen and Rhines 2004). Weak heat loss leads to a weakening subpolar gyre (negative gyre index), which in turn, after about one year, results in an increase inflow of relatively warm water masses in the pelagic domain of the Faroe region. This affects the whole pelagic ecosystem from phytoplankton to whales and leads to good living conditions for species such as blue whiting (Hátún et al. 2009a, Hátún et al. 2009b). We might therefore expect some effect of the gyre on saithe recruitment, which also is indicated in Table 2, although the correlation coefficients are small.

Since air-sea heat flux is an important driving mechanism for both the gyre strength (gyre index) and the on-shelf primary production (PP-Index) (Häkkinen and Rhines 2004; Hansen et al. 2005) it remains uncertain which process is most important for the Faroe saithe; direct atmospheric influence on the Faroe Shelf or remote integration of atmospheric signals in the oceans, and subsequent horizontal advection of physical and biological anomalies by the ocean currents.

Conclusions

We find, that recruitment of saithe at age 3 to the fishable stock is linked to the prey availability of sandeel and Norway pout during the two preceding years prior to recruitment. Sandeel has been shown to be linked to the primary production on the Faroe shelf (Eliasen et al. 2011) and we do find a positive correlation between recruitment of saithe and the primary production (PP-index) on the shelf, although this relationship is weak. Recruitment of saithe was also found to be weakly negatively correlated to the subpolar gyre index, for which a negative index is associated with the productivity in oceanic waters around the Faroe Plateau (Hátún et al. 2009a). Finally, we demonstrate that increased recruitment of Faroe saithe results in reduced growth, where the total stock number appears to inhibit growth especially from age 3 to age 6. For the oldest saithe (8 and 9 years of age) no such density effects were observed. Indices of productivity and food availability are known between 1 and 4 years in advance of the recruitment of saithe as 3 year olds, and therefore there might be a potential for predicting both recruitment and weight-at-age.

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Paper IV

Seasonal migration of Faroe saithe (*Pollachius virens*)

Seasonal migration of Faroe saithe (*Pollachius virens*)

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Abstract

Saithe in Faroese waters have been shown to migrate to other regions in the Northeast Atlantic. Whether this is a permanent change of region, or whether they return each year has not been clear. Here, we analysed monthly samples from the commercial landings to investigate seasonal variations in individual length. The results indicate a length dependent seasonal emigration from the sampling area after the spawning period in January-March, with return migration during autumn. Tagging data from the Faroe Plateau support this view, whereas taggings on the Faroe Bank indicate that the Faroe Bank may be a feeding area to Saithe in the North Sea and West of Scotland. Finally, the effects of migration on stock variability is estimated by running Virtual Population Analyses for three simplified cases of emigration: 0%, constant at 30% for saithe older than 5 years, and length dependent emigration increasing to 30% at 8 year of age. The results from this analysis indicate that although the traditional VPA may underestimate absolute stock size of Faroe saithe, the relative stock variations and fishing mortalities are very similar.

Key words: Seasonal migration, length distribution, VPA.

1 Introduction

The Faroe Islands are located on the Faroe Plateau between Iceland and Shetland on a ridge system separating the Norwegian Sea from the Atlantic Ocean (Hansen and Østerhus, 2000). The Plateau is linked to the Icelandic shelf through the Iceland-Faroe Ridge with sill depth slightly less than 500 m. Towards the European continental shelf, the link goes over Faroe Bank and the Wyville-Thomson Ridge with sill depth around 600 m. This link is, however, interrupted by the channel system consisting of the Faroe-Shetland Channel and its continuation in the Faroe Bank Channel (Figure 1).

Within the Faroese economical zone, saithe is mainly fished on the Faroe Plateau and Faroe Bank (Figure 2) and most years, saithe dominates the catches of demersal fish in Faroese waters. Thus, it is an important economic resource and reliable stock-assessment is a prerequisite for rational management of the Faroese saithe stock. Annual stock-assessment efforts have provided data on stock size from 1961 onwards (ICES, 2011), based on virtual population analyses (VPA). For lack of

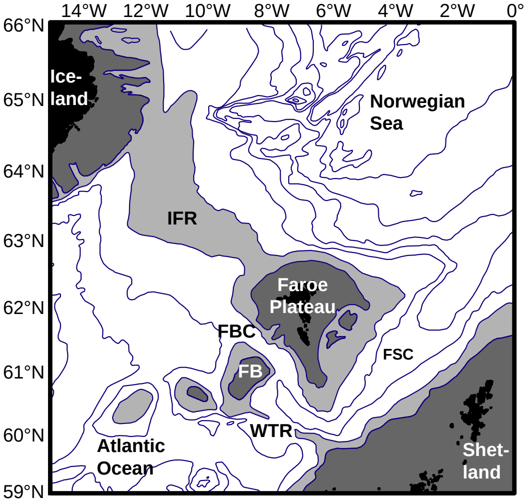

Figure 1. Bottom topography around the Faroe Plateau. Light gray areas are shallower than 500 m. Dark gray areas are shallower than 200 m. Topographic names: The Iceland-Faroe Ridge (IFR), the Wyville-Thomson Ridge (WTR), the Faroe-Shetland Channel (FSC), the Faroe Bank (FB), and the Faroe Bank Channel (FBC).

detailed quantitative information on migration, these analyses have assumed the stock to be a relatively isolated unit.

It has, however, been clear for some time that Faroe saithe does have significant migratory behaviour. Tagging in the Faroe area 1959-1966 (Jones and Jónsson, 1971) showed that considerable proportions of saithe tagged on the Faroe Bank were recaptured in Icelandic waters, at North and West Scotland, and in the northern North Sea. Also saithe tagged on the Faroe Plateau during this experiment were recaptured outside of the Faroese area.

Recently, Homrum et al. (submitted) have analysed all available data from tagging experiments in the Northeast Atlantic and saithe tagged in Faroese waters exhibited by far the highest rates of recapture outside the stock-area of tagging. For saithe exceeding 60 cm in length at recapture, about one third of the total number of fish tagged in Faroese waters were recaptured in other areas, especially in Icelandic waters.

Thus, the saithe in Faroese waters do not form a very isolated stock; but the details of migratory behaviour are not well known. Apparently, Faroe saithe have to reach a certain length (~ 50 cm) before emigrating from the Faroe area (Homrum et al., submitted); but do the stay abroad once they have emigrated? Or do they return, e.g. for spawning? Are there seasonal and/or inter-annual variations in the rate of emigration? And, if so, are these variations induced by physiological or environmental signals.

Some clues to these questions may be found in the seasonal signals in data collected from the commercial fleet fishing for saithe. Seasonal variability in behaviour of saithe, e.g. spawning and feeding periods, as well as in food-availability implies that growth and condition factor vary throughout the year. Often, a decrease in the average length of a saithe cohort is, however, also observed during the spring and early summer. This is more readily interpreted in terms of migration, rather than by physiological processes.

In this study, we analyse data from the commercial fleet to study these processes and combine this with data from tagging experiments to identify the mechanisms that control migration of Faroe saithe. From this, we try to estimate the

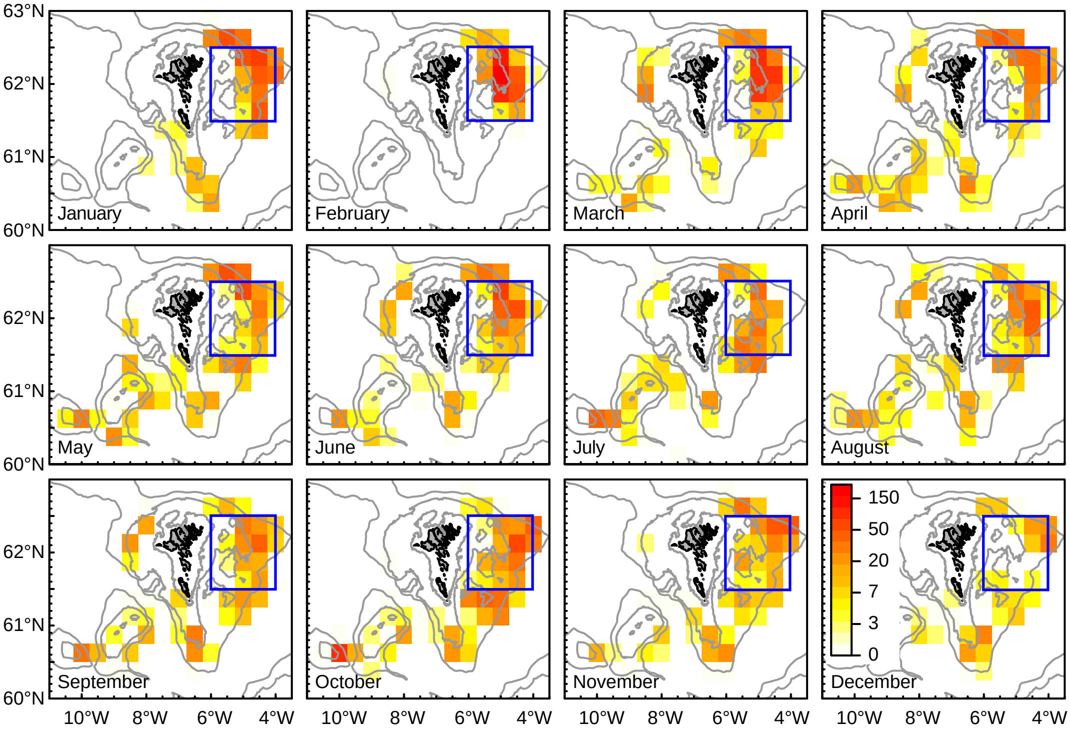

Figure 2. The number of trawl hauls in various months from 2007 to 2009 in the scale shown on the December plot. The blue box indicates the main sampling area.

effects of migration on stock assessment. We are not able to generate quantitative time series of migration rate that can be used to make more accurate stock estimates, but with an estimate of the magnitude of the migration rate, we can run some examples of alternative VPA analyses. These are modified to include migration with different sets of parameters consistent with our (limited) knowledge of migratory behaviour in order to explore the magnitude of uncertainties in stock parameters that neglecting migration in VPA may induce.

2 Material

The material in this study includes data on catches and samples from the commercial fleet as well as data from tagging experiments. We also use data on the stock size from the annual stock assessments.

2.1 Stock data

The stock-assessments of Faroese fish stocks are quality checked under the ICES framework. Reports from the ICES working groups contain both input data and output data for the assessment. Here, we use the estimated stock-sizes of saithe at ages 3 to 14 (number at age) and the average weight at age for the years 1961 to 2010 (ICES, 2011). For ages 3 years and older, Homrum et al. (2012) find a relatively constant Fulton condition factor for Faroese saithe, which implies that the average weight at age i, w_i, should be proportional to the average length, L_i, to the third power. A more accurate fit, based on the same data, gives $w_i = 1.64 \cdot 10^{-5} L_i^{2.86}$, where w_i is in kg and L_i in cm. Using this relationship, we have generated time series of average length at age for ages 3 to 14 from 1961 to 2010.

2.2 Data from the commercial fleet

Saithe is fished throughout the year in Faroese waters and over fairly wide areas (Figure 2), but most concentrated east of the islands in an area that we define as our "main sampling area" (61°30'-62°30'N, 4-6°W), which is also the main spawning area (Homrum et al., 2012). The Faroe Marine Research Institute regularly gathers samples from the commercial landings, from which age, length and gutted weight of each fish are recorded. For old saithe, the number sampled becomes too small to be statistically meaningful and we only use the length and age data up to age 9 from these samples.

To study the seasonal variation in length, we compute the "length anomaly", defined as the deviation of the length from linear growth. Due to monthly gaps in the series, we determine linear growth by linear regression over three years. To calculate the length anomaly for age 4 of a specified cohort, as an example, we regress the average length for each month through ages 3 to 5 on time and this is subtracted from the average length each month in age 4. Only months, for which the average is based on at least 10 fish, are included and the length anomaly values are accepted only if at least 24 monthly values were included in the regression and the regression coefficient exceeded 0.5.

An often recurring seasonal pattern is a decrease in average length during the first 7 to 8 months of the year. To quantify this, we define the "Jan-Aug lengthening" (ΔL_{JA}) by regressing monthly averaged length each year on time from January to August and use this to calculate the average length change in this period. We only include months, for which the average is based on at least 10 fish and ΔL_{JA} is only calculated for years with at least 6 months of observations in the Jan-Aug period.

The commercial fleet includes vessels of different types, using different gears. We focus especially on the "standard fleet", which is a group of pair trawlers (> 1000 HP), using stock assessments (ICES, 2011).

The cpue values include all age groups, but they can be converted into number of saithe in each age group by combining them with the sample data. Let cpue(t) be the catch per unit effort in tonnes per hour at time t and let w_i be the average weight at age i that year. If the total number of saithe at age i that were sampled during the month t was n_i and we assume that the sample was representative, then we can estimate the number of saithe of age i, caught per hour, $npue_i(t)$:

$$npue_i(t) = \frac{cpue(t) \cdot n_i}{\sum_k n_k \cdot w_k} \qquad (1)$$

where the sum is over all ages, k, in the sample (3-9). This number should vary with the stock size, but we can define an index, rnpue$_i$(t), representing the relative number saithe at age i, caught per unit time in relation to the total number N$_i$(t) of this age group in the stock, which is available from the stock assessments:

$$rnpue_i(t) = \frac{npue(t)\cdot 24\cdot 365}{N_i(t)} = \frac{cpue(t)\cdot n_i\cdot 24\cdot 365}{N_i(t)\cdot \sum_k n_k\cdot w_k} \qquad (2)$$

where we have multiplied by (24·365) so that the index represents the relative number caught per year, rather than hour. The index is only calculated for months with at least 100 saithe sampled, but from 1996 to 2009, data coverage is sufficient to allow calculation of this index for most months.

2.3 Tagging studies

Saithe was tagged in Faroese waters (Faroe Plateau and Faroe Bank) from 1959-1966 and again in 1975-76 and in 1991. Data from both tagging and recapture are available such as date, position and length. The fish length at recapture was not always reported. If length at tagging and days at liberty were available, the length at recapture was in these cases estimated by assuming the von Bertalanffy growth curve with parameters determined by Homrum et al. (2012).

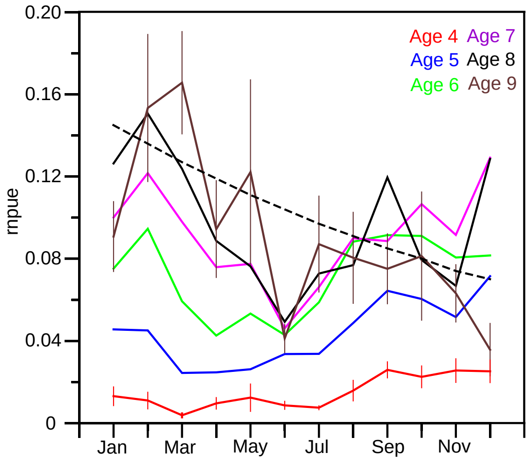

Figure 3. The relative number of saithe of different age groups caught per year by the standard fleet (rnpue$_i$ in Eq. (2)) in the main sampling area averaged over 1996-2009. Vertical lines for ages 4 and 9 indicate plus/minus one standard error. The dashed line represents the expected decrease of rnpue$_i$ for age 8 saithe due to mortality (see text).

In a more comprehensive study, including most of the saithe stocks in the Northeast Atlantic, Homrum et al. (submitted) divided the area where saithe are found into three stock areas: the Icelandic, the Faroese, and the Continental stock areas, where the last one includes both Northeast Arctic saithe and North Sea saithe.

3 Results

3.1 Catch per unit effort

In Figure 3 is shown the seasonal variation of the index, rnpue$_i$(t), that represents the relative number of saithe at age i, caught per unit time, in relation to the total number of this age group in the stock, Eq. (2). The youngest saithe, age 4 and to some extent age 5, are caught relatively more frequently towards the end of the year. To some extent, this may reflect increasing recruitment to the fisheries as they grow in length. The older saithe are caught most frequently during the time of spawning in February-March (Homrum et al., 2012) with a pronounced decrease until June and then again more frequently.

The values used for N$_i$(t) in Eq. (2) are the number at age at the beginning of the year. At this time, rnpuei can therefore be interpreted as the fishing mortality (F-value) of the standard fleet. As the number of fish in an age group decreases through the year due to mortality, the values for rnpuei should decrease similarly. As an example, the average fishing mortality of age 8 (black curve in Figure 3) for the 1996-2009 period was 0.6, giving a total mortality of 0.8. If the total mortality were constant through the year and the rnpue$_i$ value started out at 0.15, it would be expected to decrease as the dashed line in Figure 3 as long as the same fraction of age 8 saithe remained available to the standard fleet. The lower rnpue$_i$ values for autumn, compared to spring for age 7 and older may thus be misleading.

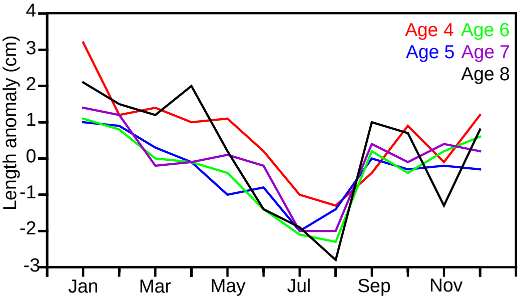

Figure 4. The length anomaly (defined in section 2.2) in the main sampling area through the year for age groups 4 to 8 on average for cohorts 1986 - 2007.

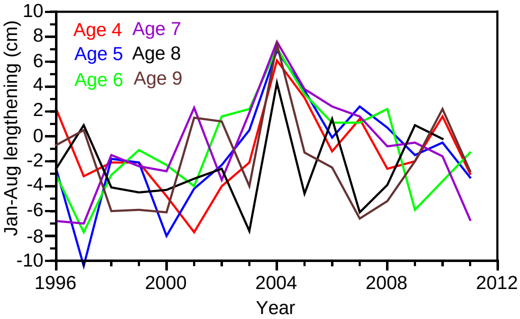

Figure 5. The change in average length from January to August (ΔL_{JA}) in the main sampling area for age groups 4 to 9 in different years.

3.2 Seasonal length changes of cohorts

The average seasonal variation in the “length anomaly”, defined as the deviation of the length from linear growth, shows a regular pattern with decreasing values from January until July or August for all age groups 4 to 8 (Figure 4). In spite of this regular behaviour, there is considerable variation between years, as documented by the variation in the “Jan-Aug lengthening” (ΔL_{JA}), defined in section 2.2 and shown in Figure 5.

In general, we do not expect individual fish to consistently shorten during a season and Figure 3 indicates that a large fraction of the older fish, at least, migrate away from the main sampling area after the spawning period. It seems likely that these two observations are related, so that the decrease in average length during spring and early summer is due to emigration away from the main sampling area of those fish in each age group that are especially long.

To test this, we have compared the length distributions during the spawning period (January-March) and during summer (June-August) for the years when there was pronounced shortening ($\Delta L_{JA} < -2$ cm). For ages 5 to 7, the distributions do change shape consistent with this hypothesis. To illustrate this, Figure 6 shows both the original averaged length distribution for each of these age groups and the “adjusted” distribution where it is assumed that all the fish shorter than the most frequent length in summer (l_{max}) have remained, whereas a large fraction of the longer ones have left the area as explained in more detail in Appendix B.

For ages 5 to 7, the Faroe saithe seems to have critical lengths (55, 61, and 65 cm for ages 5, 6, and 7, respectively) below which they remain in the main sampling area. Above this limit, a large fraction of the cohort leaves the main sampling area in those years when the average length decreases by more than 2 cm from January to August ($\Delta L_{JA} < -2$ cm). The fraction of fish from each age group leaving the area may be estimated by a simple model (Appendix B) and the numbers are indicated on Figure 6.

Neither age group 4, nor saithe older than 7, exhibit this characteristic change in the shape of the length distribution. At age 4, saithe are still not fully recruited to the fisheries, which may mask a change. For ages above 7, the number of fish in the samples is small and the length distributions noisy. Thus, there may be a similar change in the shape of the distributions for these older fish, masked by noise. In any case, Figure 4 clearly shows average shortening for all age group from 4 to 8 (age 9 had too few samples to fulfill the criteria for the analysis, section 2.2).

In the years when the average length increases, the shape of the length distribution does not change in the same characteristic manner, but rather seems to be shifted, consistent with no migration and individual growth.

For ages 5 to 7, Figure 6, thus, supports the interpretation that the decrease in average length in some years is associated with a migration away from the main sampling area of the largest fish in each cohort in some years. We also find that these three age groups have similar temporal variations of ΔL_{JA}, as indicated by the correlation coefficients in Table 1. Age 4 seems to follow this “young fish group”, although not as closely. In a similar manner, ages 8 and 9 are positively correlated with one another, but this “old fish group” is not correlated with the “young fish group” when all years are

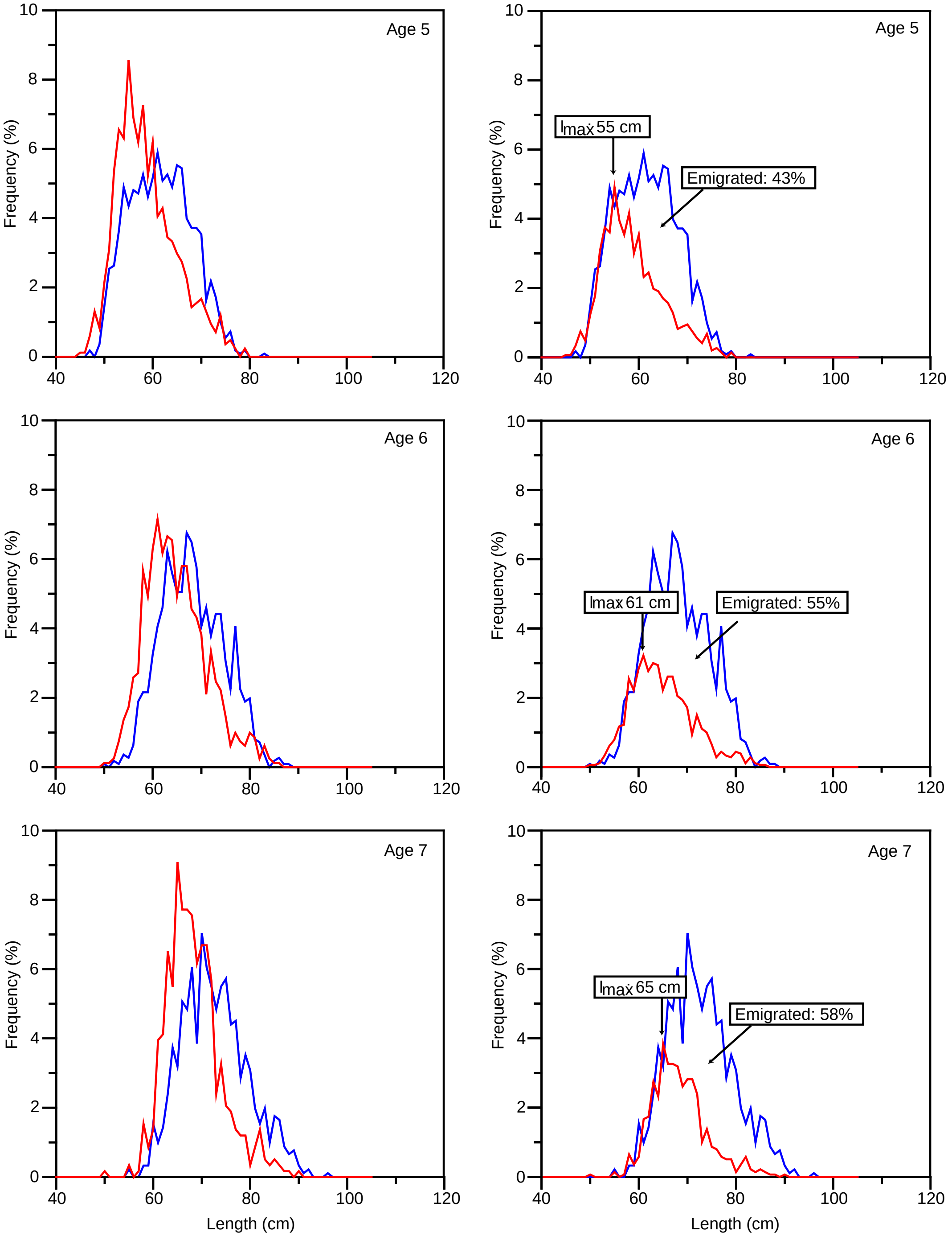

Figure 6. Length distribution of saithe in the main sampling area in January - March (blue) and June - August (red) for individual age groups averaged over those cohorts for which the mean length for that age group decreased by at least 2 cm from January to August. The graphs on the left hand side are unadjusted. On the right hand side the distributions for June-August are adjusted (Appendix B) so that the area up to the maxima (indicated) equaled the area of the January - March distribution for the same length interval. The fractions of fish that have emigrated from each age group are indicated.

Table 1. Numbers above the diagonal show correlation coefficients between "Jan-Aug lengthening" of different age groups, based on all the years. Numbers below the diagonal are correlation coefficients when the year 2004 is excluded. Numbers in brackets indicate number of years included in each calculation.

	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9
Age 4		0.61 (17)	0.37 (17)	0.15 (17)	0.32 (15)	0.35 (16)
Age 5	0.47 (16)		0.80 (17)	0.73 (17)	0.06 (15)	0.22 (16)
Age 6	0.13 (16)	0.72 (16)		0.67 (17)	-0.06 (15)	0.15 (16)
Age 7	-0.14 (16)	0.62 (16)	0.53 (16)		0.12 (15)	0.26 (16)
Age 8	-0.02 (14)	-0.35 (14)	-0.57 (14)	-0.31 (14)		0.71 (15)
Age 9	-0.03 (15)	-0.19 (15)	-0.33 (15)	-0.15 (15)	0.55 (14)	

considered. The year 2004 is clearly exceptional in Figure 5. If this year is excluded, the correlation coefficients within each of these groups remain positive, but now the two groups seem negatively correlated, although weakly.

To investigate, what might characterize the years with pronounced emigration from the main sampling area as compared with other years, we have correlated ΔL_{JA} to the average fish length in the spawning period, L_{sp}, (Table 2). For the young saithe, especially ages 5 to 7, ΔL_{JA} is negatively correlated with L_{sp}, (Table 2, top row). The two parameters are not independent, but the second row in Table 2 shows that ΔL_{JA} for the 5-7 year old saithe is also negatively correlated with fish length averaged over the whole year, L_{an}, which argues against a statistical artefact.

Thus, the decrease in average length from January to August of 5-7 year old saithe is especially pronounced in years when they are relatively long. The correlation coefficients in Table 2 and hence this conclusion are not substantially affected by omitting the exceptional year 2004 from the analysis. For ages 8 and 9, we do not see this relationship.

The main sampling area only covers a limited part of the Faroe Plateau (Figure 2) and the migration indicated by our results might only be away from this limited area, but still within the Faroe Plateau. This may be tested by doing the same analysis on all the available samples outside the main sampling area. The number of those samples is somewhat less, but the patterns in the correlation coefficients are very similar (Table 3), except for age 9 where the number of samples, however, is very small. This implies that the seasonal emigration is away from all our sampling area and hence away from the area covered by the main fishing fleet.

3.3 Tagging experiments

For all saithe tagged in Faroese waters, we have counted all recaptures with well defined location and determined the stock area (section 2.3), in which they were recaptured. When these numbers

Table 2. Correlation coefficients between the "Jan-Aug lengthening" (ΔL_{JA}), the average spawning length, L_{sp} (Jan-March), and the average length for the whole year L_{An} for age groups 4 to 9 in the main sampling area. The number of years for each calculation are shown in brackets.

	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9
$\Delta L_{JA}/L_{sp}$:	-0.44 (17)	-0.74 (17)	-0.83 (17)	-0.87 (17)	-0.18 (15)	0.08 (16)
$\Delta L_{JA}/L_{An}$:	0.07 (17)	-0.64 (17)	-0.78 (17)	-0.83 (17)	-0.08 (15)	0.21 (16)

Table 3. As Table 2, but based only on samples outside the main sampling area.

	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9
$\Delta L_{JA}/L_{sp}$:	-0.88 (8)	-0.91 (9)	-0.73 (10)	-0.77 (9)	-0.07 (8)	-0.97 (4)
$\Delta L_{JA}/L_{An}$:	-0.66 (8)	-0.85 (9)	-0.68 (10)	-0.70 (9)	0.27 (8)	-0.94 (4)

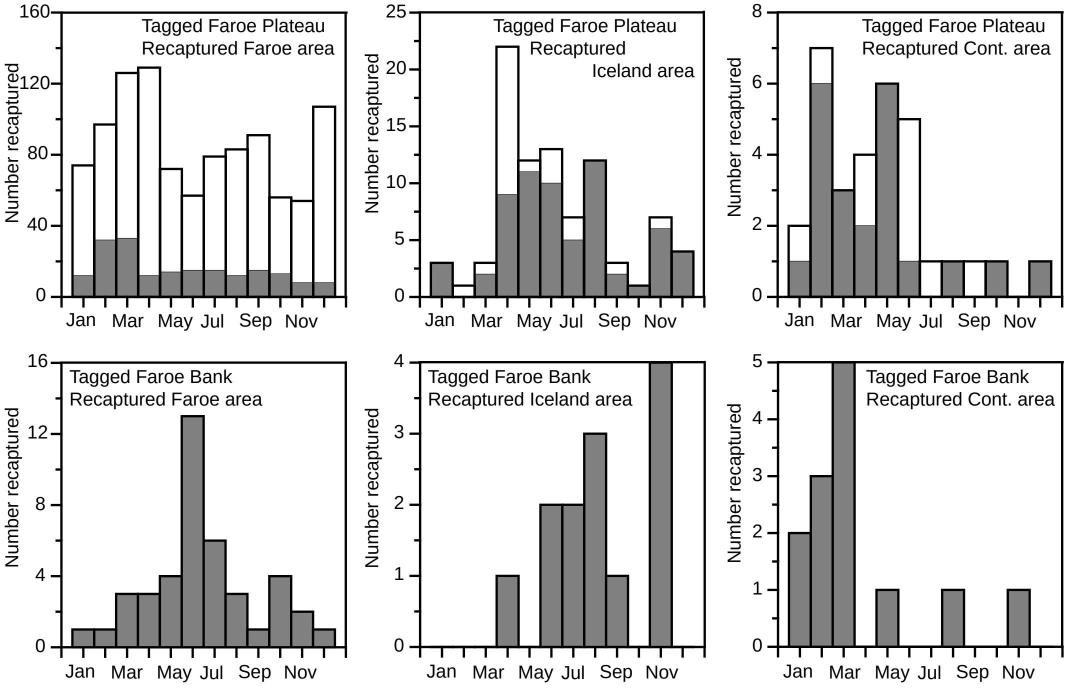

Figure 7. Number of tagged saithe recaptured in the Faroe area, the Iceland area, and the Continental area from taggings on the Faroe Plateau (top row) and on the Faroe Bank (bottom row). Grey bars indicate saithe longer than 60 cm when recaptured.

are sorted into months, they exhibit characteristic features (Figure 7).

For saithe that were tagged on the Faroe Plateau (top row in Figure 7), the most frequent recaptures in the Faroe stock area were in Feb-April, i.e. during and just after spawning, whereas very few of these fish were recaptured in the Iceland stock area during spawning. This pattern becomes even more pronounced, if we count only fish that exceeded 60 cm in length at recapture (gray bars in Figure 7). This may indicate that fish tagged on the Faroe Plateau, which migrate to Iceland, will return "home" to spawn. This picture is not as clear for fish recaptured in the Continental stock area, although the numbers are so small that it is hard to conclude anything definitely.

For saithe tagged on the Faroe Bank (bottom row of Figure 7), recaptures in the Faroe stock area and the Iceland stock area were most frequent outside the spawning period, whereas recaptures in the Continental stock area peaked during the spawning period.

4 Discussion

4.1 Seasonal migration

Length distributions of 5 to 7 year old saithe were found to shift towards shorter lengths in summer (June-August) as compared to January-March (Figure 6) and more so during years when the mean length throughout the year was large (Table 2 and 3). This pattern is consistent with emigration from the sampling area of the longest fish in the age groups. The shortening from January to August was correlated with the length of the saithe for the age groups 5 to 7 (Table 4). This result shows that the longer saithe are at e.g. age 6, the more the length distribution is shifted towards shorter sizes in summer, i.e. the larger the proportion of saithe in that age group that are emigrating from the area in summer.

The observed shortening of 8 year old saithe (when most saithe have matured sexually) from January to August (Figure 4), indicates that smaller saithe of an age group remain in the area regardless of spawning.

The sampling area (Figure 2) is also where the main spawning area is found to be (Homrum et al. 2012). A plausible explanation for the observed shifts in length distributions is a combination of spawning and feeding migrations, where the largest fish in an age group are more prone to seek into deeper waters after the spawning period. Seasonal migration in saithe have been described in Icelandic waters (Jones and Jónsson 1971) and in Norwegian waters, where saithe is found to follow the Norwegian spring spawning herring (Olsen 1959) and is also feeding on herring spawning grounds (Høines and Bergstad 2005). Jakobsen and Olsen (1987) also described significant emigration from Northern Norwegian to Icelandic waters, and to a lesser extent, to Faroese waters. They found the migration rates to cease after the collapse of the Norwegian spring spawning herring in the late 1960s (Hamilton et al. 2004).

For 5 year old saithe, the lengths, after which the emigration is found to occur (l_{max}), are shorter as compared with the 6 and 7 year old (Figure 6). This indicates that it is not the length *per se* that induces seasonal migration. 50% of Faroe saithe have matured sexually at age around 5-6 (Homrum et al. 2012) and at lengths around 58 cm (unpublished data), which is in the range of the observed l_{max} values for 5 to 7 year old saithe, further supporting a connection to spawning behaviour. The lower rnpue's found in the summer months (Figure 3) give support to the conclusion that it is emigration that is observed. The consistent pattern found between samples in the sampling area and samples outside it (Table 3), implies that the emigration is from the Faroe Plateau and not only the spawning area. Whether this is a migration to deeper waters of the Faroe Plateau, to a more pelagic phase or to other regions in the Northeast Atlantic can not be deduced from these data, but tagging studies help clarify this.

Homrum et al., (submitted) have shown that saithe tagged in Faroese waters were frequently recaptured outside Faroese waters when saithe were larger than 60 cm, and less frequently when they were between 50 and 60 cm. Below 50 cm there were virtully never caught outside Faroese waters. Those findings are consistent with what is found in the present study.

The Faroese tagging data presented by month (Figure 7) support that the observed migration is a combination of spawning and feeding migration, and that it is often to other areas. The fish tagged on the Faroe Plateau, the majority of which were juveniles at tagging, were more often recaptured in Icelandic waters during the summer months, than during the winter. This would be consistent with these fish being of Faroese origin and returning to Faroese waters after a feeding migration in summer. With regards to fish tagged on the Faroe Bank, most recaptures in Continental waters were in the spawning period.

Recaptures on the Faroe Bank, on the other hand, were most numerous in the summer months. The numbers are low, but rather convincing and a possible interpretation is that these were predominantly Continental saithe feeding on the Faroe Bank. The Wyville-Thompson Ridge (Figure 1) is actually a shallower passage to the Faroe Bank than crossing the Faroe Bank Channel. Also, the depths of the Faroe Bank Channel are continuously filled with very cold (<0°C) water, whereas the Wyville-Thomson Ridge (and the Iceland-Faroe Ridge) only intermittently have very cold water at the bottom. The tagging experiments on the Faroe Bank were primarily conducted in the summer months, which makes the hypothesis of a Continental origin for many of its saithe plausible.

In conclusion, our results indicate that the migration behaviour of Faroe saithe involves length dependent feeding migrations after the spawning period with a return later in the year. These proposed hypotheses would be clarified better, if a tagging program using Data Storage Tags was initiated.

4.2 The effect of migration on VPA

The stock-assessment of Faroe saithe is, as for other similar stocks, based on a virtual population analysis (VPA), where the main input is the catch of each age group every year. This analysis assumes the stock to be an isolated system without substantial immigration or emigration. For Faroe saithe, this is clearly not the case, so we have to ask, how reliable the stock data are. To answer that question fully, we would need detailed and quantitative information on both immigration and emigration rates of various age groups and how they have changed throughout the assessment period. That is not possible on the basis of the available data, but the order of magnitude changes may be estimated by some simplified case studies.

In these cases, we assume no immigration and assume that the emigration for each age group

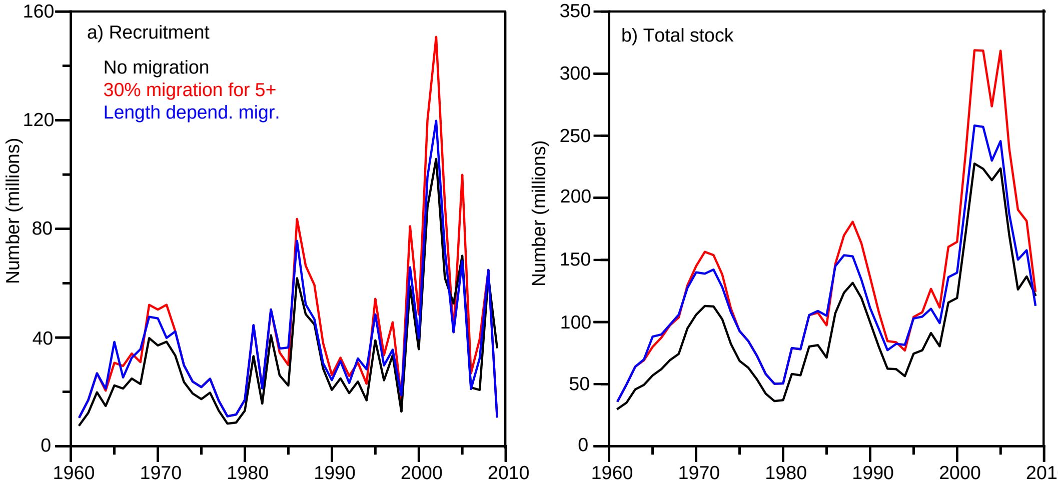

Figure 8. Number of saithe recruited at age 3 (a) and total number in stock (b) as computed by VPA in three different cases described in the text.

can be described by a number, α, defined as the fraction of that age group that has emigrated from the Faroese fishing grounds on average over a year. As detailed in Appendix A, the basic equations of the VPA can under some further assumptions be modified to include this, and we have implemented a computer program that does this.

The program was run for three different cases (Figure 8). The first case, 'No migr.', had α=0 for all age groups. This should be similar to the standard VPA and it gave almost exactly the same result for number at age as the official series from the ICES reports (ICES, 2011) with correlation coefficients of 0.997 or higher for all ages 3 - 13.

In the second case, 'Const. α', the emigrated fraction, α, was 0.3 for age 5 and older and zero for ages 3 and 4. The computed number of 3-year old and total number in the stock for this case is shown by the red curves in Figure 8, which may be compared to the black curves that represent no migration (α = 0).

In the third case, 'L-dep. α', ages 3 and 4 were again assumed to have no migration (α = 0) and ages 8 and higher to have α = 0.3. For ages 5 - 7, we assumed length dependent migration, so that the value for α each year depended on the average length. When the average length was below the values for l_{max} in Figure 6, α for that age group was set to zero. For average length above l_{max}, α was set to increase linearly up to a value of 0.3 when the average length was l_{max} +10 cm or higher. This gave the blue curves in Figure 8

As might have been expected, the cases with migration have higher recruitment and higher total stock numbers than without migration. For the old saithe, the fishing mortalities remain unchanged, however (Table 4). This follows from the simplifying assumption in Appendix A that remote and local fishing mortalities should always be the same. When that is so and α is constant, the total (local + remote) catch as well as the total number of an age group are both multiplied by 1/(1-α). Thus the ratio between them, which gives F (Appendix A), is unchanged. For the younger fish, where we have assumed less or no migration, fishing mortalities are reduced compared with the no migration case.

For saithe tagged in Faroese waters, more than 30% of recaptures longer than 60 cm have occurred

Table 4. Fishing mortalities for the three cases shown in Figure 8 averaged over the 1961-2006 period, for which the VPA should have converged.

Age:	3	4	5	6	7	8	9	10	11	12	13
No migr.:	0.050	0.164	0.296	0.387	0.412	0.425	0.435	0.449	0.437	0.586	0.477
Const. α:	0.038	0.119	0.296	0.387	0.412	0.425	0.435	0.449	0.437	0.586	0.477
L-dep. α:	0.039	0.125	0.284	0.357	0.379	0.425	0.435	0.449	0.437	0.586	0.477

in remote stock areas (Homrum et al., submitted). Thus, the cases considered here are not extreme. They indicate that the Faroe saithe stock may be considerably larger than estimated by a standard VPA method, but that fishing mortalities may be realistic or somewhat overestimated for the younger saithe.

This does presuppose, however, that immigration onto Faroese fishing grounds of saithe from other stocks is limited. If there is substantial immigration from the Continental stock area (Homrum et al., submitted) and if these saithe remain sufficiently long to contribute significantly to the Faroese catches, then Figure 8 and Table 4 have to be modified.

From Figure 8 it appears that both recruitment and total stock number have quite similar temporal variations for the three cases, although the amplitudes are different. This may be verified by correlation analysis. Comparing the 'No migr.' case with the 'Const. α' case, the correlation coefficient exceeded 0.986 for all ages. Comparing the 'No migr.' case with the 'L-dep. α' case, the correlation coefficient exceeded 0.976 for all ages.

Stronger length dependence or other temporal variations, induced e.g. by food availability, may well give more variable values for α, but these high correlation coefficients still indicate that the 'real' stock variations may well be quite similar to those generated by the traditional VPA in a relative, although not absolute, sense. Although the stock numbers that we used in Figure 3 may be changed by including migration in the VPA, this robustness of relative variations implies that the general look of that figure and the conclusions based on it are not affected.

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Appendix A

Virtual population analysis with migration

In a traditional VPA, it is assumed that the number of fish of a certain cohort remaining alive in the stock at time t is given by:

$$N(t) = N_0 \cdot e^{-Z \cdot t} \qquad (A1)$$

Where the total mortality, Z, is the sum of natural mortality, M, usually assumed constant equal to 0.2, and fishing mortality, F (Z=M+F). Since the catch is assumed to be proportional to N(t), this leads to the two basic equations of the VPA (Virtual Population Analysis) method. The first of these allows us to calculate the number $N_{i,k}$ of fish in age group k at 1st January of year i from the total catch $C_{i,k}$ of that age group throughout that year, if we know the mortalities M and $F_{i,k}$ which are assumed constant during each year:

$$N_{i,k} = \frac{M + F_{i,k}}{F_{i,k}} \frac{C_{i,k}}{1 - e^{-(M + F_{i,k})}} \qquad (A2)$$

The second equation is:

$$\frac{C_{i-1,k-1}}{N_{i,k}} = \frac{F_{i-1,k-1}}{M + F_{i-1,k-1}} \left(e^{M + F_{i-1,k-1}} - 1 \right) \qquad (A3)$$

If we have run the VPA backwards through time to the year i, and know the catches in year i-1, the left hand side of this equation is known, which allows $F_{i-1,k-1}$ to be calculated, e.g. by the Newton-Raphson method.

When a fraction, α(t), of the stock emigrates out of the area covered by the local fishing fleet, the catch will no longer be proportional to N(t), but rather to [1-α(t)]·N(t) and equations (A2) and (A3) have to be modified. Since we only aim to estimate the order of magnitude effect of migration on the VPA, we can make some simplifying assumptions. First, we assume that the total mortality is the same in the remote areas, to which saithe has emigrated, as in the local area. Then the local catch of an age group over a year may be written:

$$C = \int F \cdot [1 - \alpha(t)] \cdot N(t) dt = N_0 \cdot F \cdot \int [1 - \alpha(t)] \cdot e^{-Z \cdot t} dt \approx [1 - < \alpha >] \cdot \frac{F}{Z} N_0 \cdot \left(1 - e^{-Z}\right) \qquad (A4)$$

where the integral is over that year and <α> is the average value of α through the year. To check the last approximation in Eq. (A4) with seasonal migration, assume that α(t) is equal to 2·<α> from March to August and zero and zero for the rest of the year, making <α> the annual average. With F=0.4, i.e. Z=0.6, an exact calculation of Eq. (A4) would result in replacement of the bracket [1-<α>] in the last term of (A4) by [1-1.04·<α>]. Thus, the approximation gives an error of 4% in this example. Accepting the approximation, leads to the replacement of equations (A2) and (A3) by:

$$N_{i,k} = \frac{M + F_{i,k}}{F_{i,k}} \frac{C_{i,k}}{1 - e^{-(M + F_{i,k})}} \frac{1}{1 - \alpha_{i,k}} \qquad (A5)$$

and

$$\frac{1}{1-\alpha_{i-1,k-1}}\frac{C_{i-1,k-1}}{N_{i,k}}=\frac{F_{i-1,k-1}}{M+F_{i-1,k-1}}\left(e^{M+F_{i-1,k-1}}-1\right) \qquad (A6)$$

where $\alpha_{i,k}$ is the average value of α for age group k in year i. If the values for $\alpha_{i,k}$ can be estimated, a modified version of the VPA is easily implemented and run.

Appendix B

Adjustment of length distributions

The change of shape of length distributions from the spawning period to summer in some years may be interpreted in terms of seasonal emigration through a simple model where we assume that all the fish that are shorter than the peak length (l_{max}) in the summer distribution (red curves in Figure 6) are those that did not migrate away. Let N_{sp} be the number of fish of a certain age group of a cohort in the main sampling area at spawning (January-March) and let $f_{sp}(l)$ be the length (l) distribution (normalized to one). Similarly, N_{su} and $f_{su}(l)$ represent number and distribution in the main sampling area of the same age group and cohort during summer (June-August) whereas N_{mi} and $f_{mi}(l)$ represent those fish of this age group and cohort that migrated away. If we can ignore mortality and individual growth during the intervening months, this requires:

$$N_{sp}=N_{su}+N_{mi} \quad \textit{and} \quad N_{sp}\cdot f_{sp}(l)=N_{su}\cdot f_{su}(l)+N_{mi}\cdot f_{mi}(l) \quad \textit{for all } l \qquad (B1)$$

In the suggested model, $f_{mi}(l)$ would be zero for all $l \leq l_{max}$. This implies:

$$N_{sp}\sum_{l=0}^{l_{max}} f_{sp}(l)=N_{su}\sum_{l=0}^{l_{max}} f_{su}(l) \quad \Rightarrow \quad N_{su}=\alpha\cdot N_{sp} \quad \textit{and} \quad N_{mi}=(1-\alpha)\cdot N_{sp} \qquad (B2)$$

where α is the fraction of fish that remain within the main sampling area, given by:

$$\alpha=\frac{\sum_{l=0}^{l_{max}} f_{sp}(l)}{\sum_{l=0}^{l_{max}} f_{su}(l)} \qquad (B3)$$

which can be calculated from the observed distributions for each age group and cohort. From this, we can define a new summer distribution function $g_{su}(l) = \alpha\cdot f_{su}(l)$, which is normalized with respect to the original number of fish in the spawning season rather than the number during summer. This is the distribution function used to plot the red curves in Figure 6 and the fractions in that figure listed as “Emigrated” are α.

Paper V

Is the growth of Faroe saithe density dependent or climate dependent?

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Is the growth of Faroe saithe density dependent or climate dependent?

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Abstract

Since 1961, mean weight at age of Faroe saithe has fluctuated by a factor of two, the lowest mean weights at age coinciding with large stock sizes. One causal mechanism could be density dependence, where limited local food resources are being shared by the total stock. Another possibility is immigration of individuals from other areas that have experienced a different growth during their life. This may be related to the fact that the stock size of Faroe saithe fluctuates in much the same way as the combined stock size of saithe in Icelandic and Norwegian waters. At the same time, it is found that the stock size variations of Faroe saithe are very well correlated with the Subpolar gyre index, which is associated with food availability in the area. The Subpolar gyre index is controlled by climatic variations, which probably also affect migration of saithe. Stomach content analyses have been conducted twice annually on the Faroe Plateau since 1997, and here we use these and other data on saithe, to clarify whether density dependence explains the observed variations in mean weight at age.

Keywords: Density dependence, growth, saithe, stomach content analysis, Subpolar gyre index

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Introduction

Saithe (*Pollachius virens*) is an important actor in the Faroese marine ecosystem, and its fishery is economically important. The biology of saithe in Faroese waters is well known and the main spawning is in February on the eastern slope, at 150-350 m depths. The nursery grounds are close to land during the first two-three years. The saithe subsequently moves to the deeper areas of the Faroe Plateau, the banks to the west of the Faroes and the Iceland-Faroe ridge. Faroe saithe reaches sexual maturity at approximately age 5. Main prey of saithe on the Faroe Plateau are blue whiting (*Micromesistius poutassou*), krill (*Euphasiacea*) and Norway pout (*Trisopterus esmarkii*) (Højgaard, 1999; í Homrum et al., 2009).

Stock assessments of Faroe saithe have been conducted since 1961, and so there are time series available of e.g. stock size, maturity-at-age and size-at-age (Anon. NWWG report, 2009). Mean weight at age has fluctuated by a factor of two in this period and is fluctuating inversely to the total stock biomass (Figure 1). What causes these fluctuations is still not clear. One feasible explanation could be density dependent growth, where a (roughly) constant food supply is shared by a variable number of fish. But there are other possible explanations as well, some of which do not assume, that the Faroe Plateau is a closed system in terms of either horizontal or vertical distribution.

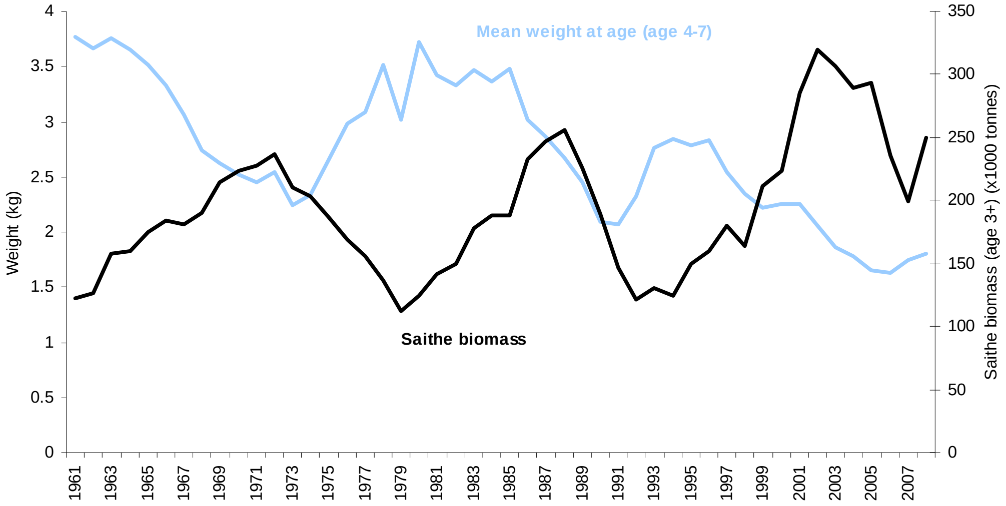

Figure 1. Mean weight at age of saithe on the Faroe Plateau is highest when stock size is low. Stock size and mean weight at age are acquired from the stock assessment.

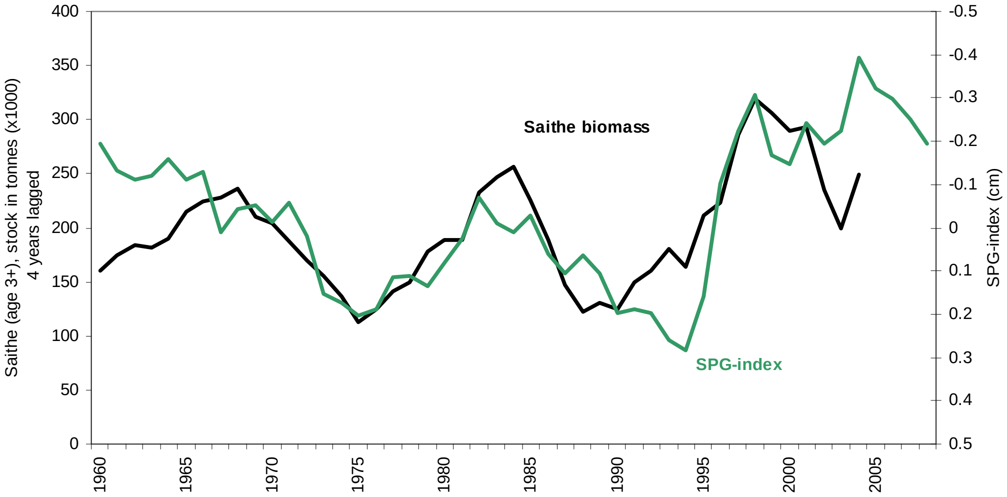

Figure 2. Total stock biomass (age 3+) of saithe on the Faroe Plateau is negatively correlated to the SPG-index (note secondary y-axis is inverse), when the saithe biomass is lagged 4 years behind. A negative SPG-index implies increased productivity in the area west of the Faroe Islands.

The total stock biomass of saithe on the Faroe Plateau seems to be linked to open ocean productivity. Primary production over the deeper regions of the Faroe Plateau is not well documented, but there are other indicators. The varying surface current system of the Subtropical gyre (STG) and the Subpolar gyre (SPG) in the north Atlantic has great impact on the productivity in this area. Warm and saline water from the STG and cold, less saline water from the SPG mix in the area south of Iceland and west of the Faroes (Hatun et al., 2005). The STG is associated with higher productivity. The relative influence of the STG and SPG to the water masses west of the Faroes is described by the SPG-index (Hatun et al. 2005). A low gyre index is equivalent to a weak sub-polar gyre and therefore the conditions near the Faroes become warmer and more saline. The relative contribution of these two water masses therefore impact higher trophic levels in Faroese waters, which has been shown for zooplankton, fish and marine mammals (Hatun et al., 2009a; 2009b).

The oscillating SPG alters productivity – and thereby food availability – as well as the physical environment of saithe on the Faroe Plateau. A strong relationship has been found between the total stock biomass of saithe in Faroese waters and the SPG-index, with large stock sizes occurring 4 years after the SPG has been weak (Steingrund and Hatun, 2008) (Figure 2).

We are left with the contradiction that increased productivity in the area is associated with an increased stock, but the individual fish decrease in size. Since 1997 stomach content analyses have been conducted, and these quantify the food-intake of saithe. In this paper we attempt to clarify whether the negative correlation between stock size and mean weight at age can be linked to density dependent mechanisms, i.e. reduced growth as a consequence of reduced food intake.

Material and methods

Stomach contents: Stomach content analyses of saithe have been conducted twice annually (March and August) on the Faroe Plateau since 1997. Stomachs have been sampled and sorted onboard the research vessel “Magnus Heinason”. Fish weight and length, sex, maturity and age are available for all stomach samples as well as fishing depth and position. For this study total weight of stomach contents has been used to quantify the food-intake of saithe. Only the August survey has been used, since it is possible that spawning behaviour might alter feeding behaviour in March.

Growth: To assess changes in mean weight at age, growth has been calculated. In this case sampling of the commercial landings of large pair trawlers was chosen, as this is a large material available throughout the year; the fish weights available from the commercial landings are from gutted fish. Most weight is gained from august to December, and mean weight was calculated for this period. Growth was then calculated as the difference between one year and the previous.

The correlation between stomach contents and growth was assessed using regression analysis. Growth was the dependent factor and stomach contents the independent factor.

Because both growth and stomach content data are noisy, the regression analysis was evaluated, by inspecting the relative contribution of measurement errors to the variance. This was done assuming, that the standard error (SE) of growth and stomach contents are proxies for the measurement errors, and computing the relative contribution of measurement errors, *C*.

$$C = \frac{\frac{1}{n}\sum_{i=1}^{n} {g_i}^2 + \alpha^2 \cdot \frac{1}{n}\sum_{i=1}^{n} {m_i}^2}{(1-R^2)\cdot S^2}$$

where
C is the relative contribution of measurement errors
g_i is the SE associated with growth measurements in distinct years i
m_i is the SE associated with stomach content measurements in distinct years i
n is the sample size of g and m
α is the slope of the regression between growth and stomach contents
R is the correlation coefficient of the regression
S^2 is the total variance of the growth

If this fraction is small ($C << 1$), then measurement errors contribute little to the total error and we conclude that a linear relationship between *G* and *M* is not well supported. If, however, *C* approaches 1, then the lack of correlation may well be due to the measurement errors, and we cannot conclude whether a linear relationship is a reasonable hypothesis, or not. For details, see appendix 1.

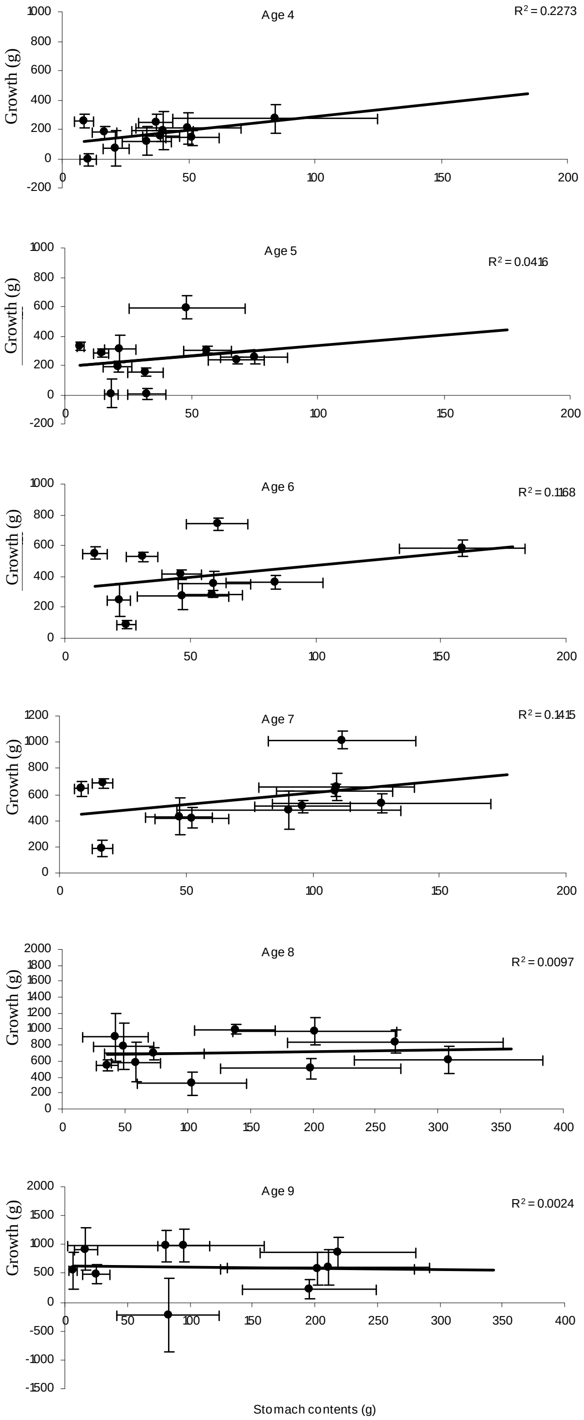

Figure 3. Regression of growth onto food-availability described by stomach contents shows, that there is no correlation between stomach contents in august, and growth from the previous autumn.

Results

There is no correlation between stomach contents and growth in weight of saithe in age-groups 4-9 on the Faroe Plateau (Figure 3 and Table 1). The R^2 values are low in all cases, and the correlations not significant. In addition the slope α of the regression, in no case is significantly different from zero.

The *C*-values in table 1 show that for age 5, 6 and 7 the relative contribution of measurement errors are low ($C<<1$), and therefore the lack of correlation between stomach contents and growth in weight can not be attributed to noisy data. For age 4, 8 and 9, the measurements errors are high ($C\approx1$) and the lack of correlation might be due to noisy data.

Table 1. Summary of regression-analysis between stomach contents and growth of saithe on the Faroe Plateau. The *C*-value is elaborated to evaluate whether the lack of correlation may be due to noisy data.

	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9
Regression:						
R^2	0.23	0.04	0.12	0.14	0.01	0.00
p-value	0.14	0.55	0.30	0.25	0.77	0.89
Intercept	100	191	315	436	675	621
slope	1.84	1.45	1.57	1.77	0.22	-0.22
Lower 95%	-0.72	-3.80	-1.68	-1.52	-1.45	-3.83
Upper 95%	4.39	6.71	4.82	5.05	1.88	3.40
C-value	1.56	0.14	0.13	0.28	0.83	1.07

Discussion

Our purpose was to investigate whether the negative correlation between stock size and mean weight at age was due to density dependent mechanisms - that is less food per capita, when stock size is large and subsequent poor growth.

Growth of all observed age-groups (4-9) exhibited no correlation to food quantity. For ages 4, 8 and 9 this may well have been due to large variation in the data-sets (Figure 3 and Table 1). For ages 5, 6 and 7 the lack of correlation between stomach contents and growth cannot be attributed to noisy data, because the relative contribution of measurement errors was small ($C<<1$ (Table 1)). For these age-classes, this result would imply that the growth is not controlled by food intake. This conclusion, of course, presupposes that both growth and stomach content have been adequately sampled, and that may be questioned. Our stomach content data are sampled during four weeks in August each year, and it could be argued that this is not representative for the whole period.

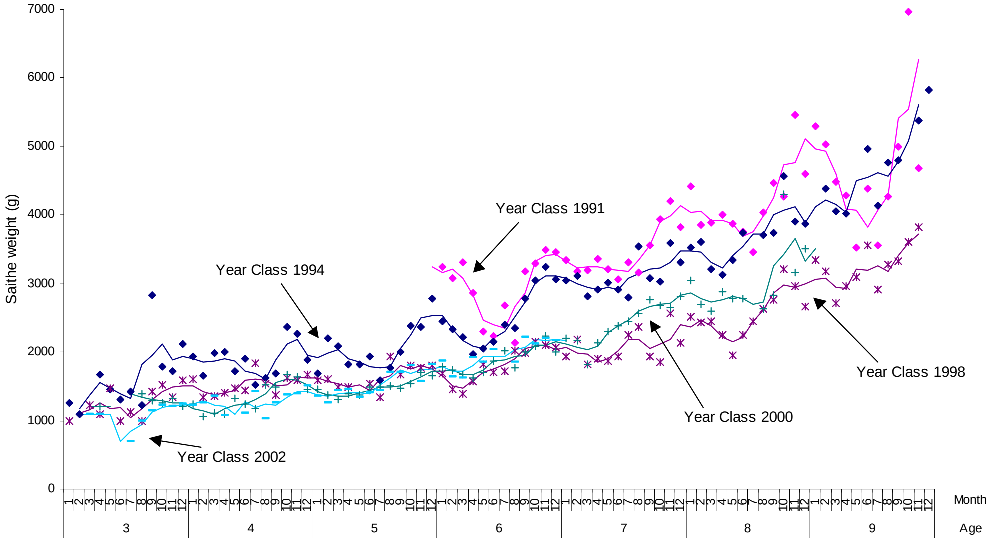

Figure 4. Growth progress from age 3 to 9 of saithe in Faroese waters is oscillating with maximum weight in winter. There are significant interannual fluctuations, here exemplified with five years. The lines are 3 month running average of weight.

There is, however, another line of evidence that supports our result. This is illustrated in Figure 4, which shows how the weight changed with age for five different cohorts. This figure clearly shows that in some cases the growth from one year to another depended as much on the weight decrease during part of the year as on the increase during the rest of the year.

For some cohorts or in some periods, Figure 4 explains why a relationship between food intake and growth is not to be expected, but what is the reason for this behaviour? A priory, at least three different mechanisms may be considered:

- Reproductive biology. The increased weight loss in spring after a large weight gain the previous winter might be linked to spawning. In these periods, larger reserves could conceivably be translocated to spawning products than when the weight gain has been moderate.

- Exchange with neighbouring stocks. Immigration from an area with slower growth in some periods would result in reduced mean weight at age in the stock. Stock sizes of saithe in the North Atlantic are to some extent co-fluctuating, indicating either connectivity between the stocks, or that all stocks are being governed by similar conditions. Migration between the Norwegian, Icelandic and Faroese saithe stocks has been shown (Jakobsen and Olsen, 1987; Jones and Jónsson 1971), but the fluctuations in the Faroese mean weights at age seem to exceed variations that could be caused by migration alone.

- Habitat changes in relation to fishing fleets. The basic data behind the mean weight at age values and the growth curves in Figure 4 are sampled by bottom trawls. The fraction of the stock that is sampled, therefore, depends on the vertical and horizontal distribution of saithe. And whether this distribution varies throughout the year. The fluctuations could then originate from differences in growth of a pelagic population compared to a demersal population. There is some by-catch of saithe in the blue whiting fishery (Lamhauge, 2004; Ofstad 2007), illustrating that blue whiting is the main prey. A consequence of this might be, that saithe predominantly in the pelagic might experience increased growth compared to those living mainly demersally.

At present, we do not know, which of these – or alternative – mechanisms dominates, but they open the possibility that the generally accepted values for mean weight at age (Figure 1) may not necessarily be representative for the total stock. If this is borne out by future research, the apparent contradiction between Figures 1 and 2 may be removed and the question posed in the title answered.

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Appendix 1

Assume that there is a linear relationship between the growth of saithe, G, and their stomach content, M, in an intermediate period, but that this relationship is also disturbed by other processes:

$$G_i = G_0 + \alpha \cdot M_i + E_i \qquad (1)$$

Here, G_i is the growth from one age to the next (e.g. from age 5 to age 6) for the year i and M_i is similarly the stomach content, whereas E_i is an error term, representing other disturbing processes.

In order to analyze this, we regress measured growth against measured stomach contents. The measured values are, however, degraded by uncertainty. If G_i' and M_i' are the measured parameters, they will be related to the ”real” values by:

$$G_i' = G_i + g_i \qquad and \qquad M_i' = M_i + m_i \qquad (2)$$

where g_i and m_i are measurement errors. Combining these equations, we get:

$$G_i' = G_0 + \alpha \cdot M_i' + (E_i + g_i - \alpha \cdot m_i) \qquad (3)$$

The term in brackets is the error term in the regression, which degrades it and reduces the correlation coefficient. It is composed of the measurement errors in the two parameters (g_i and m_i) and the deviation (E_i) from a linear relationship. We now assume, that the measurements are unbiased and that a constant value in E_i can be included in G_0. This implies that all the error terms have zero average values:

$$\langle g_i \rangle = \langle m_i \rangle = \langle E_i \rangle = 0 \qquad (4)$$

If, furthermore, we assume that the various error terms are uncorrelated, the variance, S^2 of G_i' can be expressed as:

$$S^2 = \frac{1}{n}\sum_{i=1}^{n}(G_i' - \langle G \rangle)^2 = \alpha^2 \cdot \frac{1}{n}\sum_{i=1}^{n}(M_i' - \langle M \rangle)^2 + \frac{1}{n}\sum_{i=1}^{n} E_i{}^2 + \frac{1}{n}\sum_{i=1}^{n} g_i{}^2 + \alpha^2 \cdot \frac{1}{n}\sum_{i=1}^{n} m_i{}^2 \qquad (5)$$

The first term on the right hand side is the part ”explained” by the assumed linear relationship and is equal to $R^2 \cdot S^2$ where R is the correlation coefficient. The rest is the ”unexplained” part:

$$\frac{1}{n}\sum_{i=1}^{n} E_i{}^2 + \frac{1}{n}\sum_{i=1}^{n} g_i{}^2 + \alpha^2 \cdot \frac{1}{n}\sum_{i=1}^{n} m_i{}^2 = (1 - R^2) \cdot S^2 \qquad (6)$$

If the correlation is low ($R^2 << 1$), it may be because the assumed linear relationship in (1) is swamped by other processes, which are represented by E_i, but it may also be due to the measurement errors (g_i and m_i). To assess this, we define the relative contribution of measurement errors by:

$$C = \frac{\frac{1}{n}\sum_{i=1}^{n} g_i^{\,2} + \alpha^2 \cdot \frac{1}{n}\sum_{i=1}^{n} m_i^{\,2}}{(1-R^2)\cdot S^2} \qquad (7)$$

If this fraction is small ($C << 1$), then measurement errors contribute little to the total error and we conclude that a linear relationship between G and M is not well supported. If, however, C approaches 1, then the lack of correlation may well be due to the measurement errors and we cannot conclude whether a linear relationship is a reasonable hypothesis, or not.

In order to employ this relation, we need to be able to compute the terms in the numerator of (7). For α, we use the coefficient from the regression analysis. To estimate the magnitudes of the m_i^2, we note that the stomach content for each year is derived as an average over a number of individual fish stomachs:

$$M_i' = \frac{1}{N_i}\sum_{k=1}^{N_i} M_{i,k} \qquad (8)$$

The uncertainty of this value is the standard error and we therefore use the standard error associated with (8) as a measure of m_i. A measure for g_i can be derived in a similar way, but with a small difference, since the growth from one year to another is determined as a difference between between the mean weight $W_{i,a}$ of a year class one year minus the mean weight $W_{i-1,a-1}$ of the one year younger yearclass, the year before. We, therefore, use:

$$g_i^{\,2} = SE(W_{i,a})^2 + SE(W_{i-1,a-1})^2 \qquad (9)$$

where SE denotes standard error.

Paper VI

Trophic relationships on the Faroe Shelf ecosystem and potential ecosystem states

Trophic relationships on the Faroe Shelf ecosystem and potential ecosystem states

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Abstract

Trophic pathways from phytoplankton to fish and seabirds are investigated for the Faroe Shelf ecosystem. While the sum of cod, haddock and saithe production correlated highly with phytoplankton production, the amount of sandeels seemed to determine whether the energy should flow to cod, haddock and seabirds or to saithe. Zooplankton density seemed to affect sandeels negatively, probably via the interaction with Norway pout. It is proposed that abundant zooplankton predators, such as herring, may keep the ecosystem in a steady state dominated by sandeels, cod, haddock and seabirds whereas a low abundance of zooplankton-consuming fish may lead the ecosystem to fluctuate between the former state and a state dominated by Norway pout and saithe.

1 Introduction

The Faroe Shelf ecosystem (Figure 1) may be regarded as a distinct neritic ecosystem where the water masses circulate in a clockwise manner around the Faroe Islands (Larsen et al., 2008) and retain fish eggs and larvae within the system (Gaard and Steingrund, 2001; Steingrund and Gaard, 2005). An index of primary production has been developed that shows large variations between years (a factor of 5), which are propagated through the food web from zooplankton via forage fish (sandeels), to demersal fishes (cod, haddock) and seabirds (Gaard et al., 2002).

A close relationship has been observed between primary production and cod production, i.e., numbers times growth summed up for all age groups, and both variations in recruitment and individual growth contributed to the relationship (Steingrund and Gaard, 2005). Steingrund et al., (2010) further elaborated the factors behind the variability in cod recruitment, which was explained by cannibalism and the presence (biomass) of the non-recruiting part of the cod population, although no mechanism was obvious for the latter factor. The relationship between the primary production and cod production seemed to explain that large cod catches were observed in 1996 after three years of above-average primary production (1993-1995). The same happened again in 2002 after three preceding years of high primary production (1999-2001). However, the third time this happened, i.e., in 2011 after above-average primary production in 2008-2010, the expected large catches of cod were not observed, and the groundfish survey in March

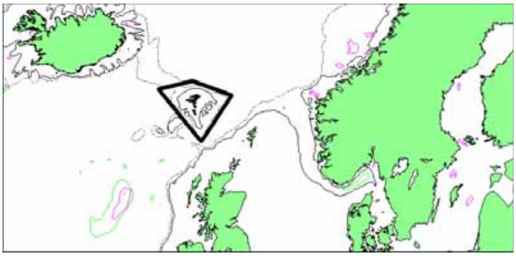

Figure 1. The study area covering the Faroe Plateau, which is located between Iceland, Scotland and Norway.

2012 did, in fact, indicate a fairly low size of the cod stock on the Faroe Plateau.

Such observations beg for further research, and the goal of the present paper is to investigate the trophic relationships on the Faroe Plateau in more detail. Specifically it is investigated whether the trophic energy flows to alternative fish species than cod, and the link between phytoplankton and fish, i.e., zooplankton and forage fish, is included into the research.

2 Materials and methods

2.1 Primary production

A measure of the annual accumulated new primary production (PP-index) in the Faroe shelf water during spring and summer was calculated based on the reduction in nitrate concentration from winter levels until a fixed date (June 26) + estimated net influx of nitrate from the surrounding off-shelf water during the same period (Gaard 2003, Debes et al., 2008).

2.2 Zooplankton biomass

Zooplankton samples were collected annually between 18 and 30 June 1991-2011 on 90 fixed stations that were dispersed over the shelf and slope. The samples were collected by vertical hauls from 50 meters depth to the surface, using a WP-2. The net had a mesh size of 200 µm and a towing speed of 0.3-0.5 m sec-1. The samples were dried at 60-65°C until they reached constant weight.

2.3 Fish stomach content

Direct density estimates of the forage fish Norway pout (*Trisopterus esmarkii*) were obtained from the annual spring groundfish survey, which occupies 100 fixed stations of one-hour duration (3 nautical miles towed) during daytime from late February and four weeks onward on depths between ~70 and 520 meters. The research vessel 'Magnus Heinason' has been used for the purpose since 1983. The doors are of the Steinham type, using either bridles of 60 m length (bottom depth < ~140 m) or 120 m length (bottom depth > ~140 m). The trawl is a box trawl with length between the wing tips of approximately 18 meters. The mesh size in the cod-end is 40 mm. Prior to 1992 a random design was used and in 1992 a mixture of random and fixed stations. A survey in August was initiated in 1996 covering 200 fixed stations during day and night, and half of them were the same as in the March survey.

The survey catch (most often weighed but occasionally estimated) was sorted into species, and subsamples were analysed in case of large catches, where sample weight (2 to 100 g resolution) and length in millimeters were recorded. Subsamples of those were analysed in more detail: length (mm), weight (g), sex, maturity status and age (otoliths).

Catch of Norway pout in kilo per hour was calculated for each tow and log-transformed, i.e., log(kg/hour + 1). The tows were assigned to three depth strata (70-150 m, 151-250 m and 251-520 m) and the average was taken of the log-transformed catch-per-unit-effort (CPUE) values for each stratum. Then the average of the three strata was calculated. This procedure reduced the influence of exceptionally large catches and seemed to perform better for cod (when compared with the age-based assessed biomass) than the untransformed values. It also performed well for saithe.

Density estimates for the other main forage fish species, sandeel (most likely *Ammodytes marinus* and referred to as "sandeels") were obtained from stomach samples of cod, haddock and saithe in the spring and summer groundfish surveys on the Faroe Plateau 1997-2010. The stomachs were sampled randomly from age-determined fish. The stomach content was assorted by taxonomic groups and digestion level (1: not digested at all – often eaten in the trawl, 2: little digested, 3: moderately digested, 4: much digested and often in fragments, and 5: totally digested and not possible to assign to any taxonomic group). The balance had a precision of whole grams and values less than 1 were treated as zero. Specimens eaten in the trawl were excluded from the analysis and empty stomachs were included. Since the number of stomachs usually was large (> 100), an arithmetic mean was used to quantify the amount of sandeels in the stomachs. The stomach content was standardized to predator length, i.e., divided by the length (mm) in the third power and multiplied by 10^8, so the index corresponded closely to the percentage of predator weight. Hence, an index of 2 indicated that the weight of sandeels in the stomach corresponded to 2 % of the (ungutted) predator weight. A number of other prey taxa were also quantified in the same way as sandeels.

We compiled charts of the spatial distribution of sandeels, Norway pout and benthic Crustacea. Sandeels seemed to be the preferred prey of all the three predator species (cod, haddock and saithe), since the fullness in the stomachs was positively correlated for these species, although haddock preyed seldom on sandeels. Hence, all three predator species were used with regards to sandeels. With regards to Norway pout, we chose to use only the saithe stomachs, because saithe did seldom prey on benthic invertebrates. With regards to benthic Crustacea, we choose to use the results from haddock stomachs, because haddock preyed little on sandeels. More specifically, the results from March at depths less than 150 were used, since they correlated best with other data (for depths greater than 150 meters in March as well as to the data for August at depths less than 150 m). The charts showed results for three 3-year periods: 1999-2002 (sandeels abundant, high primary production), 2003-2006 (sandeels scarce, below-average primary production) and 2007-2010 (sandeels scarce, but above-average primary production).

The stomach estimates of sandeels (and other prey taxa) during 1997-2010 were compared with the stomach investigations on the Faroe Plateau in the period from 1949 to 1962 (Rae, 1967). Rae investigated only cod and did not have balances available, and the abundance of prey taxa was, therefore, expressed as frequency of occurrence, i.e., the percentage of cod having eaten the specified prey taxa. The results for all years were pooled and grouped into ten areas on the Faroe Plateau. These areas covered, in average, the depth range from 102 to 165 meters. Cod sizes were grouped into two categories (up to 50 cm and above 51 cm length). In the present paper, we first calculate absolute abundances of prey taxa for the ten areas in Rae's material, add them together, and divide them by the total number of stomachs (empty and non-empty), i.e., we get frequency of occurrence estimates for the various prey taxa on the Faroe Plateau for the period 1949-1962. For comparison, the same procedure (cod $\geq$ 51 cm length and depths between 102 to 165 meters) is used for the stomach material 1997-2010, as well as during the "sandeel years" 2000-2002.

2.4 Fish

The abundance, growth and biomass of cod, haddock and saithe was obtained from the age-based assessment found in ICES (2011), covering the period from 1961 to 2010 (haddock from 1957). For cod, there were catch-per-unit-effort (CPUE) estimates (in tonnes per million tonne-hours, Jones, 1966; Jákupsstovu and Reinert, 1994; Steingrund et al., 2010) available from 1924 to 1972. In addition, there were CPUE-data for the period 1906 to 1925 in cwts per day the vessels were absent from port (1 cwt = 112 lb = 50.8 kg according to http://en.wikipedia.org/wiki/Hundredweight). These two series had two points in common (1924 and 1925), and the latter was raised to the level of the former series in order to cover the whole period from 1906 to 1972. A regression was made between the CPUE-series and the age 2+ biomass (from the age-based assessment) for the overlapping period 1961 to 1972, and biomasses extended back to 1906 (with gaps during the two world wars).

The biomasses of cod, haddock and saithe were also extended back in time by using the earliest biomass estimates as starting points and then using the surplus production per capita (average value for the years covered by the age-based assessment) combined with catch data to estimate biomasses stepwise back in time (Eero and MacKenzie, 2011). The surplus production per capita (SPR) of saithe prior to the stock assessment period was set to the average value for 1961 to 1977, because Eero and MacKenzie (2011) detected significant changes in SPR for Faroe saithe during the assessment period. It might be expected that a low directed fishery for saithe prior to 1939 could have underestimated saithe biomasses further back in time, but Eero and MacKenzie (2011) present material showing that variations in fishing mortality had little effect on their biomass estimates back in time. For cod, a comparison was made with the biomass estimates obtained from the CPUE-data, which led to the exclusion of the period around the Second World War (1937-1947) due to a marked discrepancy.

The production of fish by age (see Steingrund and Gaard, 2005) was calculated as the number of individuals in the beginning of the year *y* (taken directly from the stock number-at-age table in the age-based assessment) multiplied by the individual cohort growth from mid year *y*-1 to mid year *y*, e.g. the number of 5-year-old cod in January 1975 multiplied by the weight increase of 4-year-old cod in 1974 to 5-year-old cod in 1975. All age classes were then summed up. The weights of 1-year-old cod and haddock, as well as 1-2 year-old saithe, were not available in the weight-at-age matrix and were thus based on survey weights in August averaged for the 1996-2011 period, i.e., a constant value for all years. The number of 2-year-old saithe was not available in the number-at-age matrix, and was thus calculated as the number of 3-year-old saithe the next year multiplied by exp(0.2), where 0.2 denoted the natural mortality rate. Hence, the last year of saithe production was for the year 2008, since 2009 (providing age 3 saithe) was considered to be the last year of reliable stock estimates (2010 omitted). Hence, production estimates were available for age 2+ cod and saithe from 1961 to 2008, and for haddock from 1957 to 2008. The production figures (from mid year *y* to mid year *y*+1) were compared with the primary production in May-June year *y*. A moving 3-year average of primary production was also compared with production estimates.

2.5 Seabirds

The attending guillemots *Uria aalge* have been monitored on a breeding cliff "Høvdin", which is the largest guillemot colony on the Faroe Islands (Olsen 1992). The first census was made in 1961 (Joensen 1963, Joensen in litt.) and repeated in 1972 (Dyck and Meltofte 1973, 1975). Since 1973 the attending birds have been counted individually

Table 1. Stomach content (corresponding to per mille of body weight) of cod, haddock and saithe on the Faroe Plateau 1997-2010. Bold figures indicate values greater than the 75% percentile (=1.51) and '-' indicates strict zero values. Crustacea comprised almost entirely benthic Crustacea for cod and haddock, whereas krill represented the vast majority for saithe.

Depth	Month	Cod	Haddock	Saithe	Cod	Haddock	Saithe	Cod	Haddock	Saithe
			Total content			Fish			Number of stomachs	
60-150 m	March	6.88	4.27	7.20	3.02	0.27	4.34	2864	2204	354
	August	11.84	6.58	16.71	5.86	0.86	14.50	1874	1762	527
151-300 m	March	12.93	3.33	6.19	10.51	1.05	4.39	1449	2074	2080
	August	15.57	5.79	15.12	10.99	0.89	11.87	1560	1384	2009
301-520 m	March	21.50	5.51	9.16	18.33	0.52	6.85	132	181	472
	August	24.67	6.30	18.73	20.68	0.00	16.49	258	52	511
			Polychaeta			Echinodermata			Crustacea	
60-150 m	March	0.14	1.30	0.00	0.55	0.96	0.00	1.98	0.77	2.53
	August	0.12	2.10	-	0.37	0.98	0.00	3.24	0.93	1.18
151-300 m	March	0.02	0.45	0.01	0.01	0.46	0.00	1.20	0.57	1.50
	August	0.10	1.22	0.00	0.04	0.91	0.00	2.55	1.15	2.47
301-520 m	March	0.00	0.17	0.02	0.00	2.19	0.00	1.19	1.72	1.63
	August	0.03	0.49	-	0.00	2.07	0.00	1.56	1.86	0.88
			Mollusca			Other			Haddock	
60-150 m	March	0.28	0.16	0.04	0.50	0.46	0.23	0.06	-	-
	August	0.47	0.21	0.03	1.28	1.01	0.81	0.04	0.00	0.02
151-300 m	March	0.42	0.13	0.01	0.61	0.44	0.23	0.08	0.00	0.00
	August	0.40	0.09	0.02	1.32	1.23	0.64	0.03	0.00	0.01
301-520 m	March	0.04	0.11	0.16	1.82	0.61	0.49	0.14	-	-
	August	0.09	0.03	0.05	2.14	1.23	1.16	0.00	-	0.01
			Sandeels			Norway pout			Blue whiting	
60-150 m	March	0.84	0.18	1.69	0.29	0.00	0.87	0.03	-	-
	August	0.88	0.48	0.87	1.88	0.20	7.92	0.49	0.03	3.20
151-300 m	March	0.08	0.01	0.08	6.84	0.79	2.76	0.22	0.00	0.49
	August	0.15	0.39	0.14	3.81	0.22	2.04	3.43	0.14	7.23
301-520 m	March	-	-	-	1.27	0.16	1.13	12.67	0.15	3.90
	August	-	-	-	0.18	-	0.42	14.27	-	12.78

once a year except in 1975. A map was drawn in 1973 with all the 302 guillemot breeding ledges, and the number of birds on each ledge has been collated. The census has occurred late in the incubation period and in the early chick rearing period (late June and early July) when the number of birds is most stable.

2.6 Statistics

Regressions with one y- and one x-variable, where the x-variable represented years in a time series, were tested with the modified Chelton method, proposed by Pyper and Peterman (1998), which takes autocorrelation into account. Regressions with one y-variable and two x-variables (where the number of data points exceeded 13) were tested with the regression function in MS Excel, i.e., where autocorrelation is not taken into account.

3 Results

Cod, haddock and saithe fed more intensively in August than in March, and cod also tended to feed more intensively with increasing depth (Table 1), although there were large individual differences (not shown). Fish comprised the majority of food for cod and saithe, and the importance of sandeels and Norway pout in shallow waters (< 300 m), as well as blue whiting in deep waters, is clear.

Sandeels tended to be distributed more westerly, and shallower, than Norway pout, and there were great differences between periods in sandeel density, the period 2000-2002 characterised by high sandeel densities down to around 200 meter depth (Figure 2). The benthic Crustacea were more evenly distributed with regards to the amount found in haddock stomachs, although the species composition changed with depth (mostly Munida spp. deeper than 150 meters, not shown).

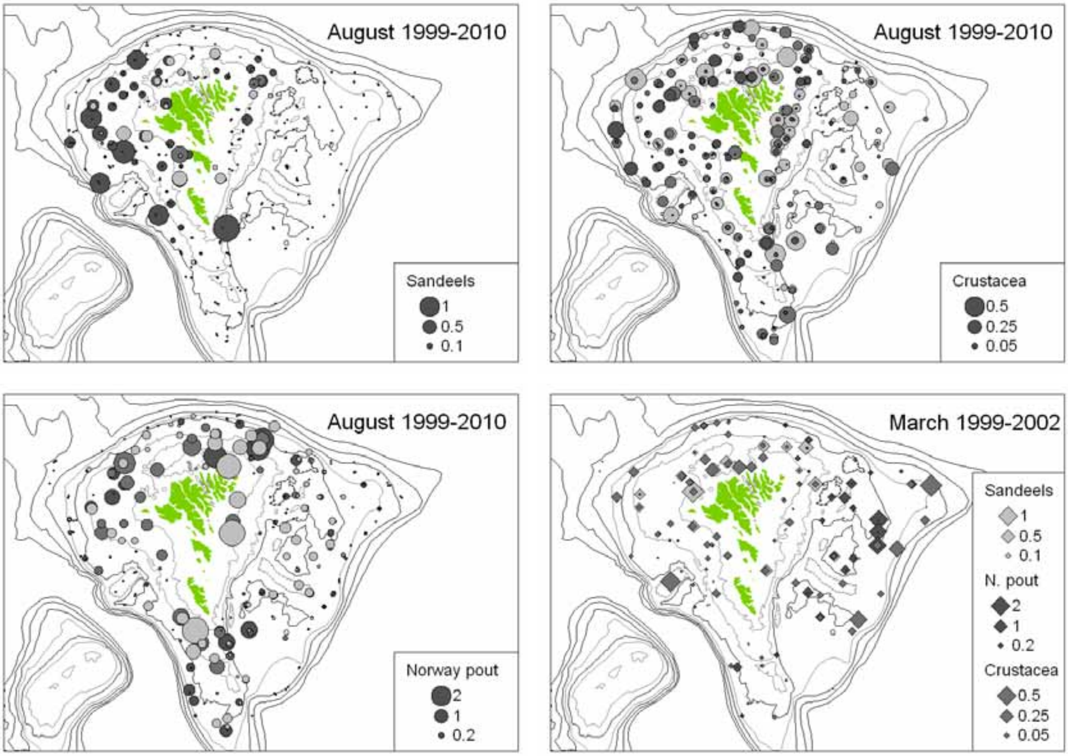

Figure 2. Stomach content in August 1999-2010 of cod (in per mille of predator weight) feeding on sandeels (upper left), haddock feeding on Crustacea (upper right) and saithe feeding on Norway pout (lower left). Dark gray symbols indicate 1999-2002, gray: 2003-2006, and light gray 2007-2010. The panel on the lower right corner shows the corresponding figures for March 1999-2002 with regards to Norway pout (dark gray), Crustacea (gray) and sandeels (light gray).

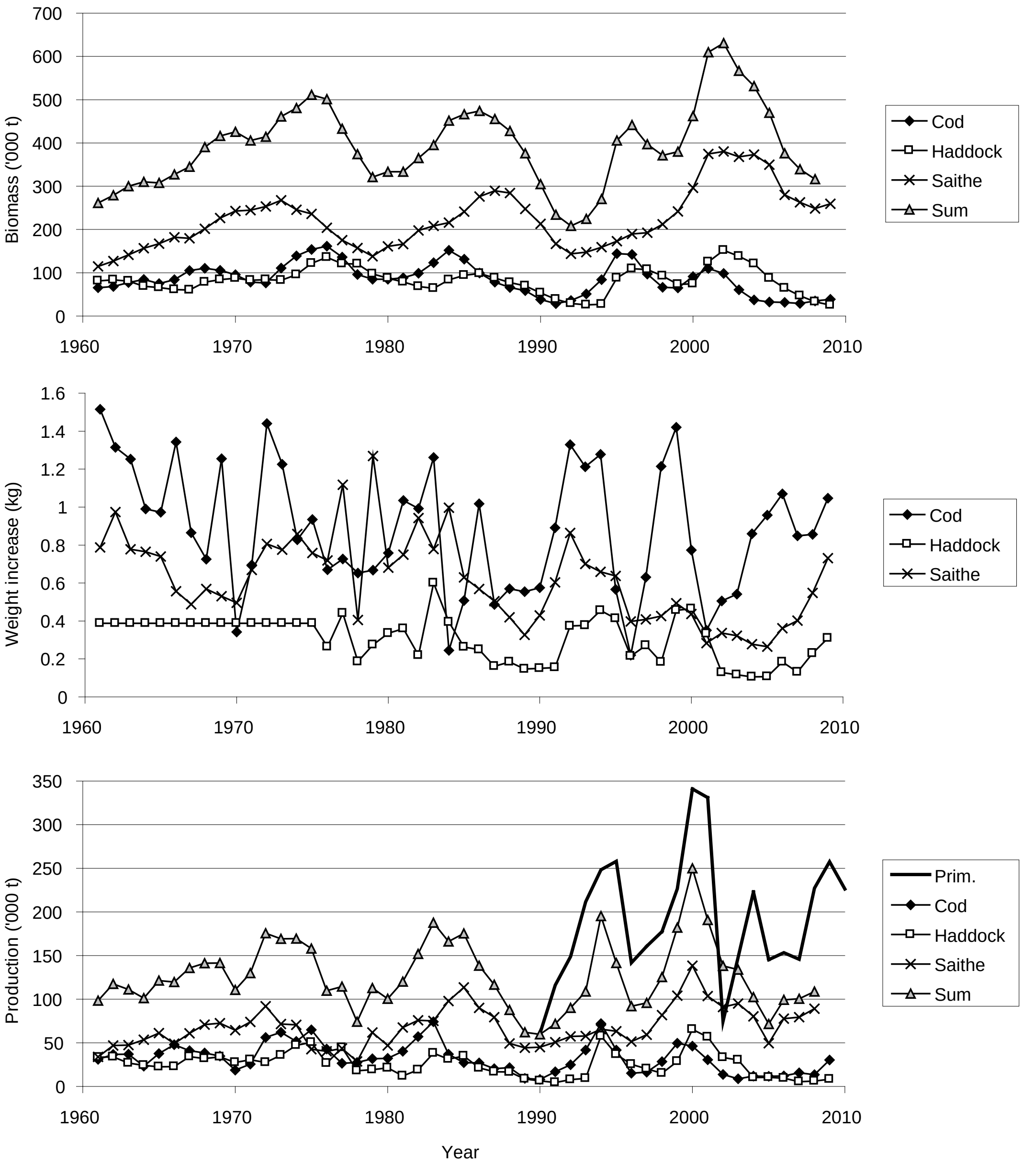

Figure 3. Biomass and production of cod, haddock and saithe in Faroese waters, as well as their sum. The index of primary production (x 21) is also shown in the lowest panel.

The biomasses of cod and haddock, as observed in the age-based assessments since ~1960, were of comparable sizes, and decreased over time, although great fluctuations were observed (Figure 3). Saithe (age 2+), starting on the same level as cod and haddock in 1961, increased, however, steadily over time and reached almost 400 thousand tonnes just after year 2000. Although saithe grew more slowly than cod, the stock production was markedly higher than for cod and haddock, except during the early sixties. The cod and haddock production in relation to the total production of cod, haddock and saithe decreased over time. This tendency was also observed for the number of attending guillemots (Figure 4).

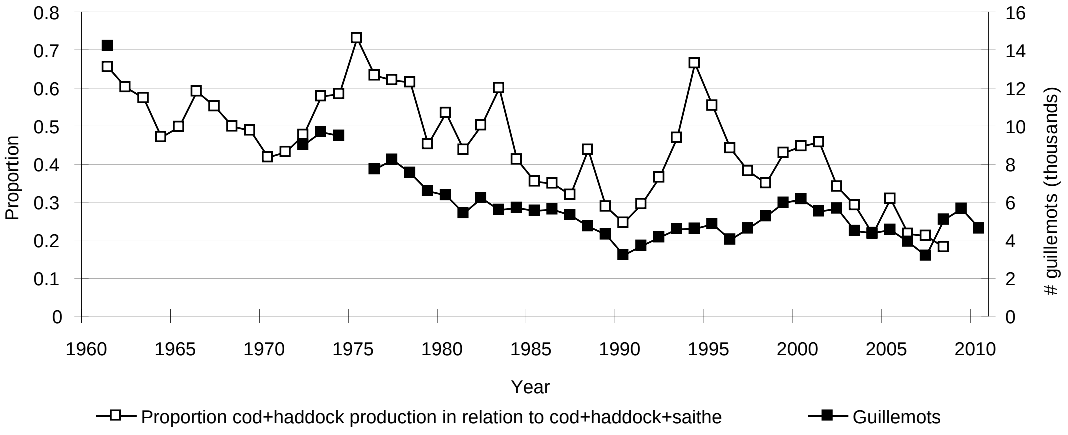

Figure 4. Proportion of cod+haddock production on the Faroe Plateau in relation to cod+haddock+saithe. The number of guillemots observed on the breeding cliff "Høvdin" is also shown.

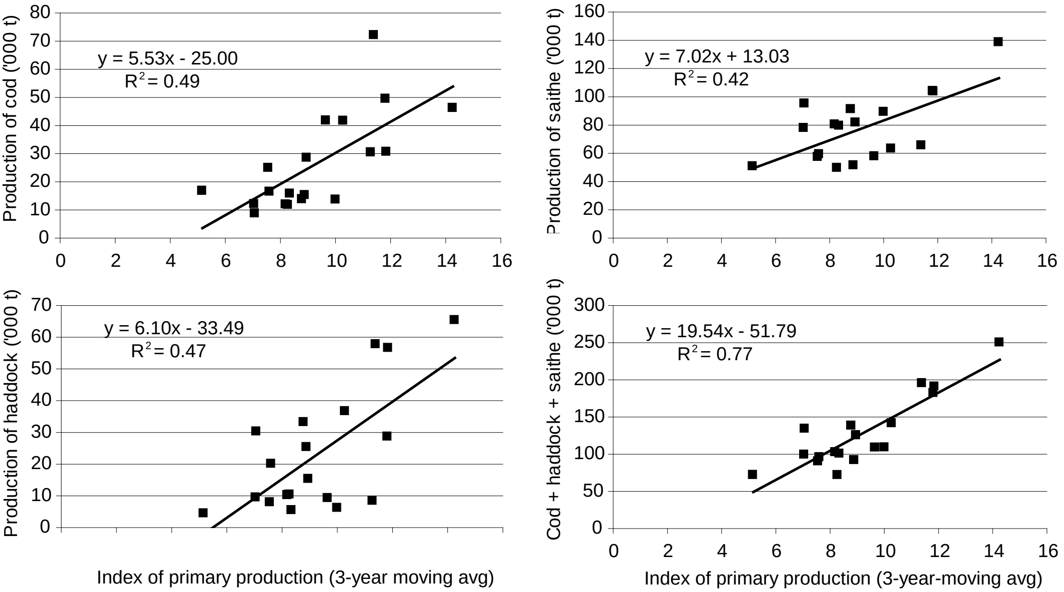

Figure 5. Correlations between primary production (3-year moving average) and the production of cod, haddock and saithe in Faroese waters.

There was a moderate correlation between primary production (3-year moving average) and the production of the individual species cod, haddock and saithe, respectively. However, when combining all three fish species, a considerably higher correlation is observed ($p < 0.01$, Table 2, Figure 5). The model of fish production was further improved (adjusted $R^2 = 0.82$, $p < 0.001$) by including Norway pout as an independent variable ($p = 0.02$) in addition to the smoothed primary production ($p < 0.001$) (Figure 6).

In search for mechanisms explaining the features observed in Figure 4, where the proportion of saithe production increased steadily over time,

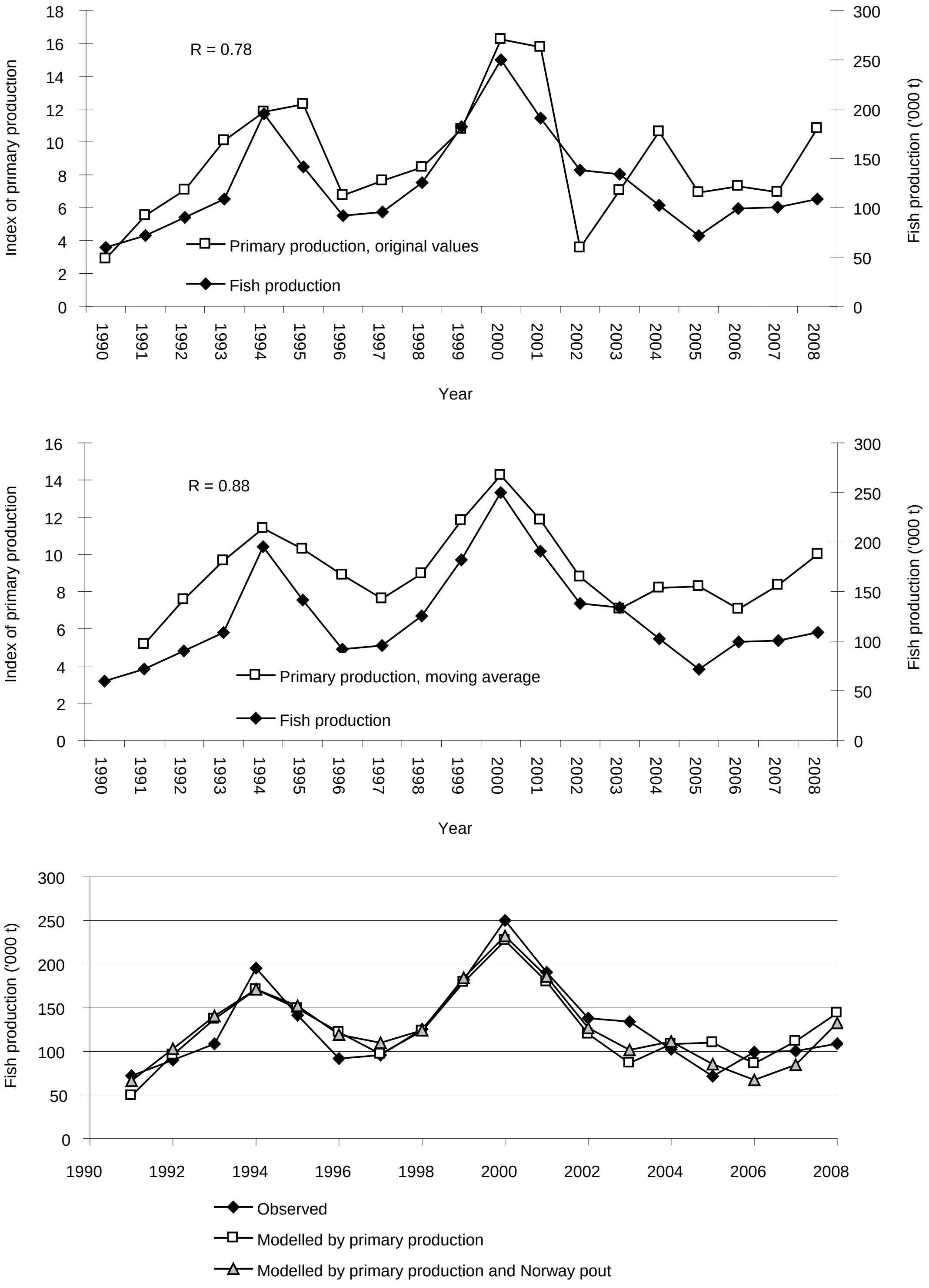

Figure 6. Relationship between primary production (original values and 3-year moving average) and fish (cod + haddock + saithe) production in Faroese waters. The lowest panel shows fish production modeled by either primary production (3-year moving average) alone or together with the catch-per-unit-effort of Norway pout in March.

Table 2. Correlation analysis and associated statistics with regards to primary production, zooplankton biomass and forage fish abundance on the Faroe Plateau. Upper part of the table shows correlation coefficients whereas the lower part shows the number of data points. Stars indicate significant p-values < 0.05 when autocorrelation is not taken into account, whereas bold figures indicate significant values when autocorrelation is taken into account. The score denotes the average R^2 for the column or row. Abbreviations: C2: recruitment of cod at age 2 years, H2: recruitment of haddock at age 2 years, C2H2: the sum of them, C2H2y-1: the sum of cod at age 2 the current year and haddock at age 2 the following year, SumProd: production of cod+haddock+saithe, PP: index of primary production, PP3: 3-year moving average of primary production, Zoo: zooplankton, N.pout: Norway pout.

Variables	Sandeels	N.pout	C2	H2	C2H2	C2H2y+1	SumProd	Score
PP	0.53*	-0.06	0.62*	0.28	0.39	0.65*	0.78*	0.28
PP3	0.65*	-0.04	0.57*	0.23	0.33	0.71*	0.88*	0.31
ZooOnshelf	-0.57*	0.67*	-0.43	-0.52*	-0.53*	-0.70*	-0.63*	0.34
ZooOffshelf	-0.51	0.76*	-0.34	-0.52*	-0.51*	-0.47*	-0.29	0.26
N.pout	-0.35		-0.14	-0.28	-0.26	-0.35	-0.30	0.08
Sandeels		-0.35	0.89*	0.83*	0.90*	0.80*	0.69*	0.59
Guillemots	0.62*	-0.17	0.27	0.23	0.27	0.27	0.31	0.11
PP/ZooOnshelf	0.87*	-0.40	0.72*	0.62*	0.68*	0.85*	0.80*	0.52
PP3/ZooOnshelf	0.90*	-0.43	0.72*	0.62*	0.68*	0.92*	0.85*	0.56
PP/ZooOffshelf	0.82*	-0.35	0.61*	0.71*	0.73*	0.56*	0.50*	0.39
PP3/ZooOffshelf	0.86*	-0.38	0.63*	0.74*	0.76*	0.60*	0.53*	0.43
PP/N.pout	0.60*		0.47*	0.41	0.45*	0.71*	0.82*	0.35
PP3/N.pout	0.58*		0.38	0.38	0.40	0.70*	0.85*	0.33
Score	0.46	0.18	0.31	0.28	0.32	0.44	0.45	0.13
PP	14	22	21	21	21	20	19	
PP3	14	20	20	20	20	19	18	
ZooOnshelf	14	21	20	20	20	19	18	
ZooOffshelf	14	21	20	20	20	19	18	
N.pout	14		28	28	28	27	26	
Sandeels		14	14	14	14	13	12	
Guillemots	14	28	35	35	35	34	33	
PP/ZooOnshelf	14	21	20	20	20	19	18	
PP3/ZooOnshelf	14	20	20	20	20	19	18	
PP/ZooOffshelf	14	21	20	20	20	19	18	
PP3/ZooOffshelf	14	20	20	20	20	19	18	
PP/N.pout	14		21	21	21	20	19	
PP3/N.pout	14		20	20	20	19	18	

the primary production and zooplankton densities were scrutinized (Figure 7). There was, at least for some periods, a negative relationship between the primary production and zooplankton densities on the Faroe Shelf (on-shelf, water depth < ~130 m), whereas there was no correlation with the zooplankton densities off-shelf (Figure 7). However, there was a positive correlation between the zooplankton densities off-shelf and the catch-per-unit-effort of Norway pout (Table 2, Figure 7).

Sandeels in fish stomachs correlated weakly with the primary production (Table 2), but strongly with the ratio of primary production to zooplankton density, both on-shelf and off-shelf (Table 2, Figure 8). The sum of cod recruitment (age 2) and haddock recruitment (age 2 the following year) correlated strongly with both sandeels in fish stomachs and the ratio between primary production and zooplankton on-shelf (Table 2) and the same feature was observed for guillemots (Figure 8). The ratio between primary production and Norway pout, indicating the positive effect of food and the negative effect of Norway pout on sandeels, performed less well than the ratio between primary production and zooplankton on-shelf (Table 2).

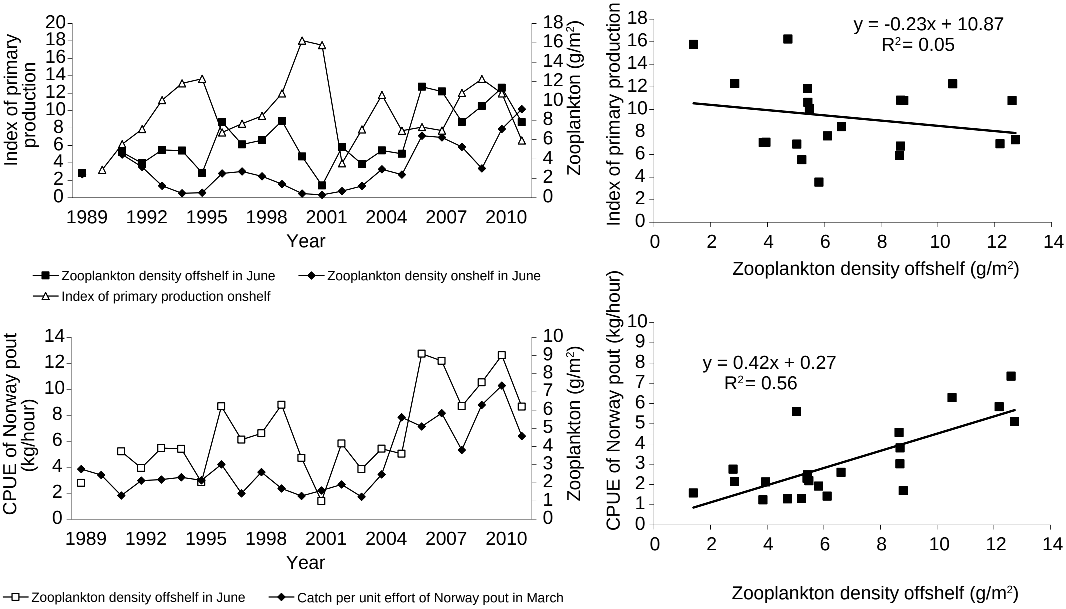

Figure 7. Relationship between primary production and zooplankton density (on-shelf and off-shelf) on the Faroe Plateau, as well as the relationship between the off-shelf zooplankton density and the catch-per-unit-effort of Norway pout in March.

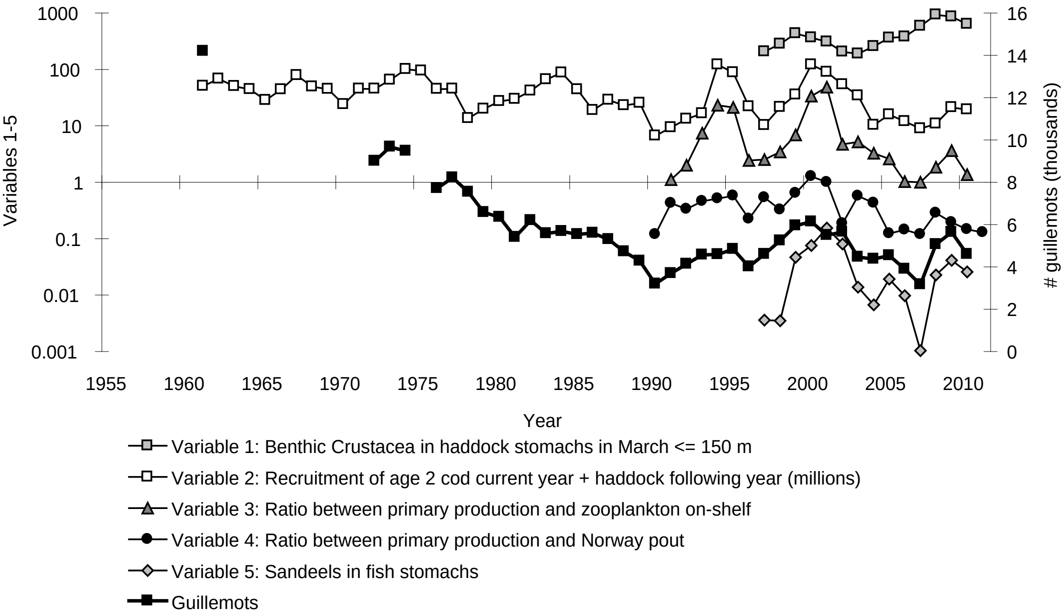

Figure 8. Relationship between six variables on the Faroe Plateau. 1: Benthic Crustacea (per mille of predator weight x 5000) in haddock stomachs in March shallower than 150 m. 2: the recruitment of cod the current year + haddock the following year, which indicates sandeel abundance. 3: The ratio between the primary production (May-June) and zooplankton (June), which indicates the condition for sandeels. 4: The ratio between the primary production and the catch-per-unit-effort of Norway pout in March, where Norway pout indicates the extent of the competition with sandeels. 5: The stomach content of sandeels in fish (cod, haddock and saithe averaged) stomachs (per mille of predator weight), where March and August each calendar year were pooled. 6: Number of guillemots observed on the breeding cliff "Høvdin".

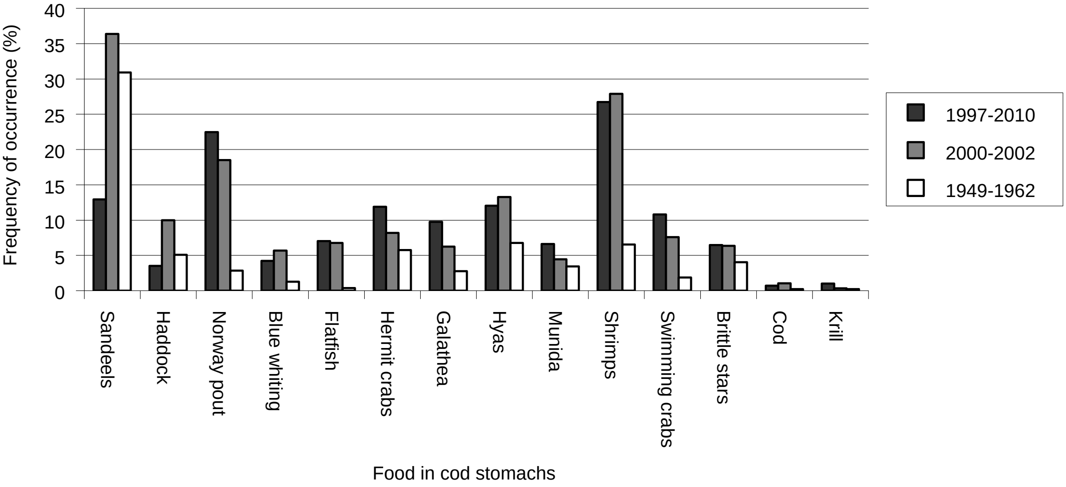

Figure 9. Comparison of the food content of cod on the Faroe Plateau in the period 1949-1962 (N = 1909) and 1997-2010 (N = 2911), as well as during "sandeel years" 2000-2002 (N = 573).

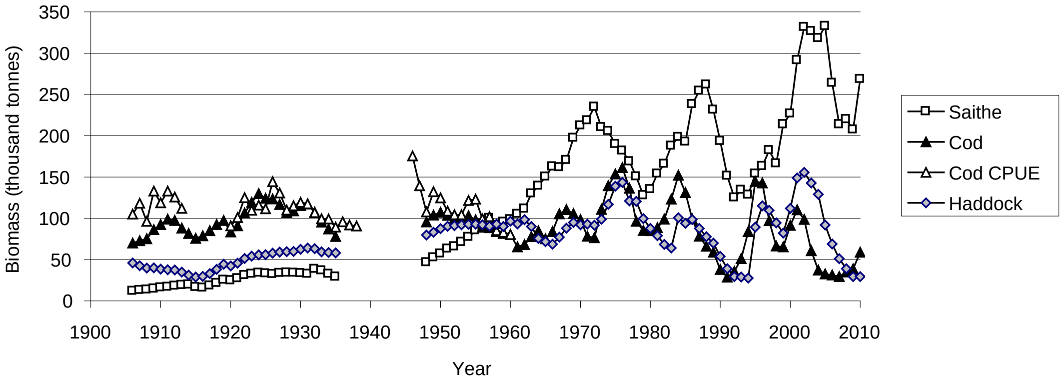

Figure 10. Biomasses according to age-based stock assessments of cod (since 1961), haddock (since 1957) and saithe (since 1961) in Faroese waters, as well as biomasses estimated back in time by the use of surplus production per capita and annual catch. The estimated biomass of cod 1906 to 1960, based on simultaneous catch-per-unit-effort (CPUE) data combined with the age-based stock assessment is also shown. The surplus-based biomasses are not shown for the period 1936-1947, since they were regarded to be unreliable.

Figure 8 also indicates that the abundance of sandeels was higher in former times (1960s or before) than recent years, and stomach analyses during 1949-62 confirm this (Figure 9). On the other hand, cod preyed less on benthic Crustacea, flatfish and Norway pout. This seems not only to be caused by prey choice, preferring sandeels over other prey items, since the same is observed for the "sandeel years" 2000-2002.

Extending fish biomass estimates back in time shows a shift in the relative amounts of cod, haddock and saithe around 1960 (Figure 10), where especially the amount of saithe was considerably less than during the recent years.

4 Discussion

The fact that there was a very strong correlation between the primary production and fish (cod+haddock+saithe) production (Table 2, Figure 5, Figure 6) strongly suggests that there is a bottom-up control of fish production in the Faroe Shelf ecosystem. It also suggests that a fairly constant proportion of produced phytoplankton is available for these three fish species. However, when Norway pout are very abundant some production seems to be lost to these three fish species. The reason may be that cod and saithe are not able to consume more than a certain amount of Norway pout and that the excess of Norway pout, therefore, is not reflected in the stomachs. The fact that the smoothed version of the primary production performed better than the yearly values suggests that there is some elasticity in the predator-prey interactions, i.e., that some food may be left over from previous years.

Even though a nearly fixed proportion of the primary production became transferred to fish production, the amount allocated to each of the three fish species was highly variable. The proportion allocated to cod and haddock ranged between 20 and 70 % and was highest when the amount of sandeels was highest (Figure 4). A short answer to the question posed in the Introduction why so little cod was present in 2011 after three years of above-average production is that most of the energy went to saithe.

This indicates the crucial role of sandeels vs. Norway pout as intermediate links of the energy from plankton to predatory fish. When sandeels are abundant (Eliasen et al., 2011), a high proportion of the energy is transferred to cod and haddock whereas the energy flow to saithe is more pronounced when sandeels are scarce. The reason seems to be that the youngest age groups (recruitment) of cod and haddock, which dominate the production, are most abundant when sandeels are abundant (Table 2), i.e., that sandeels positively affect survival of young cod and haddock.

The mechanisms controlling sandeel abundance are less clear. Here we have set up two tentative examples, although there might exist other alternatives. Example 1: Sandeels crop down the zooplankton biomass, i.e., exert a bottom-up effect on its predators and a top-down effect on its prey, a so called “wasp-waist ecosystem” (Fauchald et al., 2011). However, sandeels may not be particularly abundant on the Faroe Plateau compared with other zooplanktivorous fish species such as Norway pout (Table 1), which actually tended to be negatively correlated with sandeels (Table 2). Also, the fact that the zooplankton density on-shelf and off-shelf were highly correlated (R = 0.70, see also Figure 7), indicating advection of the oceanic copepod *Calanus finmarchicus* onto the shelf (Gaard, 2003), does not support a down-cropping of zooplankton (on-shelf) by sandeels.

Example 2: Sandeel abundance is a result of food availability in shallow regions (as measured by the index of primary production) and the interaction with Norway pout. However, when replacing the variable “PP/Zooplankton onshelf” with “PP/Norway pout”, a less clear relationship was observed with sandeels (Table 2, Figure 8), which indicates that zooplankton density better captured the negative effect on sandeels than Norway pout. The competition between sandeels and Norway pout, as well as the predation pressure on zooplankton, certainly merits further investigation.

Looking back in time into the 1950s and 1960s gives the impression of a very different ecosystem than today: cod and probably also haddock were more abundant than during recent years, whereas saithe were much less abundant (Figure 10), especially when looking into the 1930s. The abundance of sandeels and seabirds was substantially higher and probably more constant than today accompanied by a low abundance of Norway pout, benthic Crustacea and flatfish. The Norwegian spring spawning herring was abundant in the 1950s, but decreased considerably during the 1950s, and went to a very low level in the late 1960s (Holst et al., 2004).

Unfortunately, no zooplankton studies were conducted around the Faroes prior to 1990 and therefore no information is available on the zooplankton community at the times when sandeels and cod were at a high and constant level prior to the 1970s. However, a regime shift has undoubtedly happened, from high abundance of sandeels, cod, probably haddock, and seabirds, towards Norway pout, crustaceans and saithe.

At present, no final explanation exists why there seems to be a negative relationship between zooplankton abundance and sandeels. Earlier studies have shown that in years with low zooplankton biomass the abundance of small neritic copepods is high, especially in spring, indicating low advection of *C. finmarchicus* and high (local) production of (smaller-sized) neritic species and *vice versa* (Gaard, 1999, 2003). On the other hand, it should not be ignored that substantial predation pressure by planktivorous fish, such as sandeels may affect zooplankton abundance. This needs to be studied further.

It is also interesting to find out whether the increased density of benthic Crustacea, accompanying the decreased recruitment of benthos-eating cod and haddock (Bundy, 2005), may influence negatively on herring and sandeel eggs while lying on the seabed. Benthic amphipods predate on benthic capelin eggs off eastern Canada (DeBlois and Leggett, 1993). Finally, it would be necessary to look at the interaction between haddock (a pronounced egg-predator) and herring, as is done off Nova Scotia (Richardson et al., 2011).

5 Conclusion

Analysis of historical and recent data from the Faroe shelf ecosystem indicate that there has been a regime shift from a stable regime, which was acting up until the 1960s to an unstable regime during the past decades. The former regime was characterized by a stable state, where herring, sandeels, cod, and seabirds were dominating. The latter regime is unstable and is characterized by states shifting between a Norway pout-state, where higher proportion of the energy is transferred to benthic Crustacea, Norway pout, and saithe, and a sandeel-state, where sandeels, cod and haddock are boosted. The short duration of this state has not led to a recovery of seabirds.

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