Ph.D. Thesis

Sandeel, *Ammodytes* spp., as a link between climate and higher trophic levels on the Faroe shelf

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Dedicated to the loving memory of my dear friend and cousin

Jákup Olsen

* 31. July 1984 † 4. April 2010

Preface and acknowledgements

As a young master student, and with my final report coming up, I contacted Eilif Gaard in 2003 to enquire whether there was any subject on whom researchers at the Faroe Marine Research Institute were especially interested in and wanted more knowledge of. The response came without hesitation and announced that there was a blank spot in the general understanding of the Faroe shelf ecosystem. Recent studies had shown a clear signal from primary production to higher trophic levels, however, the organism(s) responsible for this transport of energy was/were still unknown. The best qualified guess was that sandeel had an important role in this link. When the master thesis on the food choice of juvenile sandeel on the Faroe shelf was accomplished, I was encouraged to continue my work on sandeel in the shape of a Ph.D.-thesis, and here we are.

First and foremost I want to express my greatest gratitude to my two main supervisors, Peter Grønkjær (Aarhus University) and Bogi Hansen (Faroe Marine Research Institute), which have shown me tremendous support, guidance and humanity during the process of this work. Similarly, I want to thank my co-supervisors Jens Tang Christensen (AU), Eilif Gaard (FAMRI) and Jan Arge Jacobsen (FAMRI) for constructive support all the way. I want to thank the co-authors of the papers that accompany this thesis, Bergur Olsen, Høgni Debes, Jákup Reinert and Petur Steingrund, for exemplary involvement and cooperation. Also I would like to thank the former head of the Faroe Marine Research Institute, Hjalti í Jákupsstovu, for believing in me and for encouragement when the prospects of finding financial support for this study were poor. A special thanks to my colleague Eydna í Homrum for support and guidance on scientific as well as on personal matters. Thanks should also be extended to the staff at the Faroe Marine Research Institute and the crew of the R/V Magnus Heinason for friendliness and best interests in me and my work.

However, this work would under no circumstances have been accomplished without the unlimited support and patience of my loved ones. To my husband, children and parents, thank you for your patience, understanding and devotion, I am forever grateful.

This study was a part of the research programme ´Marine Climate and Ecosystem around the Faroes` and was financed by the Danish Agency for Science, Technology and Innovation and by the Fisheries Research Found of the Faroe Islands.

Kirstin Eliasen

Résumé

An almost instantaneous transfer of energy from primary producers to higher trophic levels, i.e. cod, haddock and guillemots, has been observed on the Faroe shelf as strong correlation between primary production and productivity of the highest trophic levels. This is believed only possible through a fast growing intermediate fish species, with the best qualified guess being sandeel.

Despite its inferred ecological importance, to date, no sandeel stock assessments have been conducted in Faroese waters. However, annual 0-group surveys, including juvenile sandeel, have been performed continuously for three decades. These surveys have shown large annual variations in sandeel recruitment potential and indicate that sandeel predators, such as seabirds and commercially important fish species, might be experiencing large annual variability in their prey availability.

The Faroe shelf (centered at 62°00´N, 06°47´W) contains a distinct neritic ecosystem surrounded by an oceanic environment. Due to warm ocean currents passing the shelf on their way north-eastwards, the shelf water temperature is relatively high, however, since the mid-1990´s, it has been observed to increase even further (by ~1°C).

The objectives of the current thesis were thus to investigate the ecological role of sandeel in the Faroe shelf ecosystem, and to estimate which influence changes in climate might have on sandeel.

In five consecutive years (2007-2011) sandeel (age 1+) surveys were conducted on the Faroe shelf in mid-April. Based on the results obtained on these surveys and on the available time-series on temperature, primary production, zooplankton, 0-group sandeel, cod and seabirds from the same area, analyses were performed to investigate the questions set.

To qualify as an intermediate link transporting energy from primary producers to higher trophic levels, sandeel must respond to changes in primary production in the same way as cod, haddock and guillemots. Indeed, up to 73% of the annual variation observed in the 0-group sandeel biomass index (defined as the number times length cubed) could be explained by the annual variation in primary production. Furthermore, moderate to strong positive correlations were found between the breeding success of seabirds (arctic tern, black-legged kittiwake, common guillemot and northern fulmar) and the local sandeel population, with the breeding success of black-legged kittiwakes showing the most pronounced dependency on sandeel. Additionally, when the breeding success of black-legged kittiwakes was used as a sandeel indicator, approximately 50% of the annual variability in cod recruitment and biomass could be explained.

In other areas, annual variation in the quality of sandeel as prey has been found to influence predators such as seabirds. On the Faroe shelf zooplankton biomass had a positive influence on sandeel growth during their foraging period, while sandeel condition (Fulton´s *K*) and fat content was negatively influenced by temperature during their overwintering phase. By extrapolating the relationship between sandeel condition and winter temperature, the sandeel condition could be simulated back to 1992, and thereby could approximately one third of the annual variation observed in the average weight of the local cod age 2 be explained.

This study has substantiated that sandeel has an important energy transferring role in the Faroe shelf ecosystem. Furthermore, it has shown how elevated temperatures influence sandeel negatively, as well as demonstrated how this further affects higher trophic levels. The climate induced lowered energetic value of sandeel as prey is most likely a phenomenon which can be applied onto most ecosystems where sandeel also is a key species. Further research on this topic is thus strongly encouraged.

Resume

I det marine økosystem rundt Færøerne er der observeret en næsten øjeblikkelig overførsel af variationer i primærproduktion til højere trofiske niveauer, såsom torsk, kuller og lomvie. Det ses som en stærk korrelation mellem primærproduktion og produktivitet i disse top-prædatorer. Denne tætte kobling vurderes til kun at være mulig med en hurtigt voksende og zooplankton spisende fisk som mellemled, hvor det bedste bud er tobis.

På trods af tobisens tilsyneladende store økologiske betydning, bliver der til dags dato ikke foretaget estimater af den færøske bestand. Årlige 0-gruppe togter, hvilke inkluderer tobisyngel, er dog blevet udført uafbrudt i de seneste tre årtier. Disse togter viser store årlige variationer i tobisens rekrutteringspotentiale og indikerer at prædatorer såsom havfugle og økonomisk betydningsfulde fiskearter oplever store årlige variationer i deres fødetilgængelighed.

Den Færøske sokkel (62°00´N, 06°47´W) har et distinkt neritiskt økosystem der er omringet af oceaniske omstændigheder. På grund af varme havstrømme der passerer soklen på deres nordøstlige vej er sokkelvandet relativt varmt. Dog er der observeret en yderligere øgning i temperaturen på ~1°C siden midten af 1990´erne.

Formålene med dette studie var derfor at undersøge tobisens økologiske funktion ved Færøerne og at vurdere hvilken effekt klimaændringer har på tobisen.

I fem følgende år (2007-2011) blev tobistogter (alder 1+) udført i midten af april på den færøske sokkel. Baseret på resultaterne fra disse, samt på tilgængelige tidsserier af temperatur, primærproduktion, zooplankton, 0-gruppe tobis, torsk og havfugle fra samme område blev dataanalyser udført med henblik på at redegøre for relevante problemstillinger.

Det første krav tobisen må opfylde for at kvalificere som bindeled mellem primærproduktion og højere trofiske niveauer i det færøske økosystem, er at den viser samme respons til variationer i primærproduktionen som torsk, kuller og lomvie. Dette gjorde tobisen blandt andet ved at 73% af de årlige variationer i dens 0-gruppe biomasse indeks (defineret som antal multipliceret med længde^3) kunne forklares af årlige variationer i primærproduktionen. Dertil blev moderate til stærke positive korrelationer fundet mellem yngelsuccesen hos havfugle (havterne, ride, lomvie og mallemuk) og den lokale tobisbestand, hvoraf ridens ynglesucces viste den stærkeste tobiseffekt. Ydermere, når ridens ynglesucces blev anvendt som tobisindikator, kunne cirka halvdelen af de årlige variationer i rekrutteringen og biomassen hos den lokale torskebestand forklares.

Årlige variationer i kvaliteten af tobis som føde er i andre områder observeret at påvirke prædatorer såsom havfugle. På den færøske sokkel påvirkes tobisvæksten positivt af zooplankton biomassen om sommeren, mens dens kondition (Fulton´s *K*) og fedtindhold forværres ved øgede temperaturer i dens overvintringsfase. Ved ekstrapolering af forholdet mellem tobisens kondition og vintertemperaturen, kunne tobisens kondition simuleres tilbage til 1992 og denne kunne forklare en tredjedel af de årlige variationer observeret i den lokale torsks gennemsnits vægt som 2-årig.

Dette studie har dokumenteret at tobisen har en vigtig rolle i transporten af energi i det færøske marine økosystem. Dertil, viser det hvorledes forhøjede temperaturer påvirker tobisen negativt, og hvordan dette sidenhen har en negativ indflydelse på de højere trofiske niveauer. Den klimainducerede reduktion af tobisens værdi som føde er højst sandsynligt et fænomen der kan overføres til de fleste økosystemer hvor tobisen også er en nøgleart. Fortsat forskning vedrørende dette emne bliver derfor stærkt anbefalet.

Contents

Papers

List of papers

I Eliasen K, Reinert J, Gaard E, Hansen B, Jacobsen JA, Grønkjær P, Christensen JT (2011) **Early life of sandeel in relation to primary production on the Faroe shelf**. Marine Ecology Progress Series 438:185-194.

II Eliasen K, Grønkjær P, Christensen JT, Hansen B, Gaard E, Jacobsen JA, Steingrund P, Debes H. **Biotic and abiotic effects on Faroese sandeel**. Marine Biology (*submitted on December 6th 2012*).

III Eliasen K, Olsen B, Reinert J, Steingrund P, Grønkjær P, Christensen JT, Hansen B, Gaard E, Jacobsen JA. **Sandeel dependent seabird breeding at the Faroes**. Seabirds (*submitted on November 28th 2012*).

Summary of papers

Paper I

Early life of sandeel in relation to primary production on the Faroe shelf

Eliasen Kirstin, Jákup Reinert, Eilif Gaard, Bogi Hansen, Jan Arge Jacobsen, Peter Grønkjær and Jens Tang Christensen

The paper establishes a positive correlation between primary production and juvenile sandeel length and abundance, as well as a highly significant and positive correlation between primary production and an index of juvenile sandeel biomass. With these results the Faroese sandeel qualifies as an intermediate species capable of transferring energy from primary producers to higher trophic levels within the same high productive period.

Paper II

Biotic and abiotic effects on Faroese sandeel

Kirstin Eliasen, Peter Grønkjær, Jens Tang Christensen, Bogi Hansen, Eilif Gaard, Jan Arge Jacobsen, Petur Steingrund and Høgni Debes

Results from sandeel surveys conducted in mid-April in five consecutive years show how sandeel growth is influenced positively by food availability in the foraging period, while high temperatures have negative effects on sandeel condition (Fulton´s K) and fat content during the overwintering phase. A model of sandeel condition based on temperature measurements dating back to 1992 could explain almost one third of the annual variation observed in cod weight-at-age 2 on the Faroe shelf.

Paper III

Sandeel dependent seabird breeding at the Faroes

Kirstin Eliasen, Bergur Olsen, Jákup Reinert, Petur Steingrund, Peter Grønkjær, Jens Tang Christensen, Bogi Hansen, Eilif Gaard and Jan Arge Jacobsen

The paper shows how ~55% of the annual variations observed in the breeding of arctic terns and black-legged kittiwakes and ~30% of the annual variations observed in the breeding of common guillemots and northern fulmars can be explained by annual variations in the local sandeel stock. By using the breeding success of kittiwakes as a proxy for the availability of sandeel as prey for cod, approximately 50% of the annual variations observed in cod recruitment and biomass in the area could be explained.

Introduction

The sandeel family (family *Ammodytidae*) consists of 18 species of zooplanktivorous fishes. Sandeel are valuable prey for many higher species, e.g. fish, seabirds and marine mammals, and thus often function as an ecological key species linking trophic levels. Until recently, sandeel supported the largest fishery in the North Sea, and can therefore also be of great economic importance.

Sandeel exhibit the rather unusual behaviour of alternating between swimming pelagically in well-formed schools and lying buried in the sediment. Their close affiliation with the seabed, of which they are highly specific in their choice, makes them less flexible and more vulnerable towards environmental changes.

The present thesis investigates the ecological role of sandeel on the Faroe shelf, as well as the impact climate has on them.

Life history

Based on the external pigmentation species identification of Macer (1967), a study in 2004 on juvenile sandeel on the Faroe shelf found 251 of the 258 sandeel larvae to be of the species *Ammodytes marinus* (Eliasen 2005). Similarly, but with species identification based on the number of vertebrae (Reay 1986), another study conducted on the Faroe shelf in 2007 found 81% of the 129 adult sandeel studied to be *A. marinus*, while the remaining 19% had a number of vertebrae in the range where *A. marinus* and *A. tobianus* are undistinguishable (Eliasen 2008). Thus, the sandeel on the Faroe shelf seem to be mainly *A. marinus*.

A. marinus (hereafter sandeel) have been most thoroughly studied in the North Sea, and unless otherwise noticed, the description of the biology of sandeel presented here will be from that area.

Sandeel are small, elongated, lipid-rich and schooling fish without swimbladder (Macer 1966). Sandeel are throughout their lives zooplanktivorous, with their chief food organisms being copepods (mainly *Calanus finmarchicus* and *Temora longicornis*), crustacean larvae and annelids (Macer 1966).

Sandeel stay buried within sandy sediment for up to ten months a year, only emerging to the water column to forage in daylight during the high-productive period in spring/summer and shortly in mid-winter to spawn (Macer 1966, Winslade 1974a). However, juvenile sandeel have been reported in the water column as late as December (Macer 1966, Kvist et al. 2001). This burying behaviour restricts the sandeel distribution to areas of suitable sediment and bottom depths allowing foraging in the upper water masses (Holland et al. 2005). Horizontal dispersal is thus mainly limited to their planktonic phase, i.e. as larvae (Wright and Bailey 1996).

To enable their overwintering behaviour, sandeel generate energetic reserves to support overwintering. Winslade (1974b) proposed that sandeel have to reach a certain minimum level of fat content before entering the overwintering state, but did not offer an approximate value. Experimentally, van Deurs et al. (2011) found the critical threshold length, below which the sandeel in the overwintering phase has to supplement with winter feeding and does not develop gonads, to be ~9.5 centimetres under temperature conditions representative for the North Sea. However, the same study also demonstrated the positive correlation between temperature and sandeel respiration, and that the critical threshold length increased by one centimetre for every 1°C increase in temperature (van Deurs et al. 2011).

Holland et al. (2005) found sandeel to avoid sediments containing too much silt and fine sand (particle sizes <250 µm) and preferring sediment with high coarse sand content (particle sizes ≥710 µm). Based on this, Greenstreet et al. (2010) defined seabed sediments into the categories unsuitable, suitable, sub-prime and prime for sandeel habitation (Figure 1).

Sandeel have a relatively short spawning period (Macer 1966). The eggs are demersal and attached to sand grains on the seabed (Reay 1970). Depending on the temperature and oxygen concentration, they hatch one to three months later, with 5-6.6 mm long planktonic larvae (Winslade 1971). The larvae are at hatching equipped with large yolk sacs, which, depending on the temperature, are absorbed within 12-15 days (Russel 1976). In contrast to many other marine fish larvae, the sandeel larvae are able to begin feeding prior to completed yolk sac resorption (Yamashita and Aoyama 1986).

Food availability is considered to be a crucial factor for growth and survival in the early life stage of sandeel (Arnott and Ruxton 2002, Frederiksen et al. 2006). Copepod eggs and nauplii are dominant prey items during the early development of most fish larvae, and, thus, the timing and magnitude of copepod production can be essential (McLaren and Avedano 1995, Michaud et al. 1996, Gaard and Steingrund 2001, Voss et al. 2003).

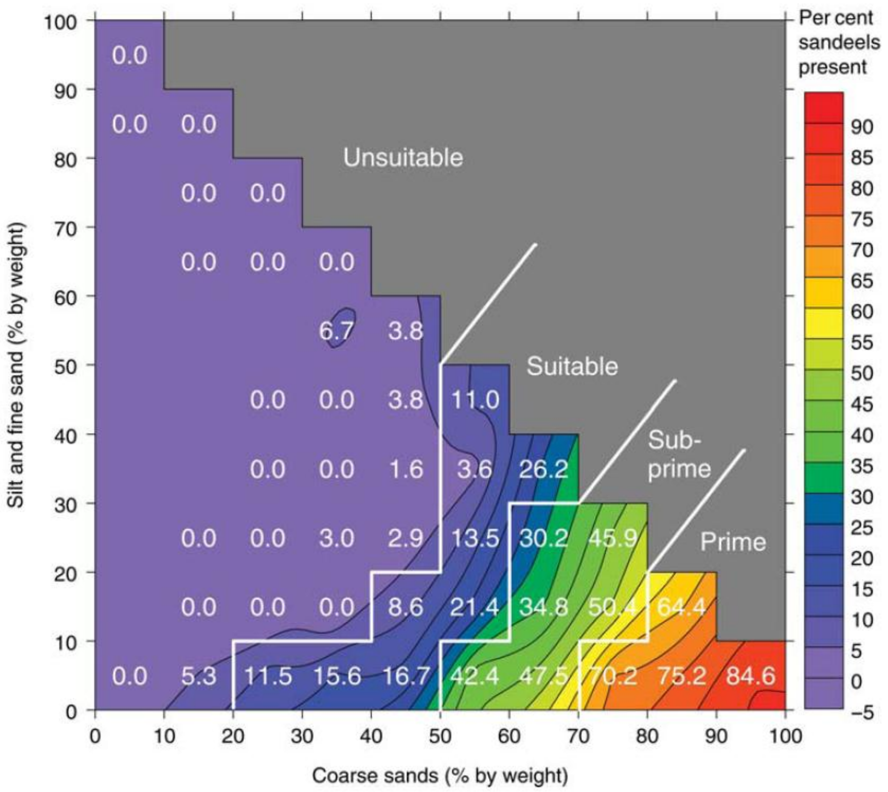

Figure 1 Categorisation of the seabed sediment into four sandeel sediment preference categories, depending on the relationship between the percentage of silt and fine sand and of coarse sand in the sediment and the proportion of samples with sandeels recorded present. From Greenstreet et al. (2010).

Many studies have shown a dependene of copepod reproduction on food availability (Diel and Tande 1992, Hirche 1996, Niehoff et al. 1999), predominantly phytoplankton (Irigoien 1998, Meyer-Harms et al. 1999), and seasonal variations in phytoplankton development can thus often be detected in subsequent copepod reproduction and growth (Gaard 1999, Durbin et al. 2003, Devreker et al. 2005). At high latitudes, e.g. the Faroe shelf, the seasonal variations in primary production are large, and the timing and magnitude of it significantly influence copepod reproduction, species composition, and abundance (Gislason and Astthorsson 1995, Gaard 1999, Debes et al. 2008a).

The timing of larval metamorphosis, i.e. transformation into the juvenile stage, is proposed to be influenced by food availability at a length of 40 to 55 mm (Wright and Bailey 1996). After metamorphosis, which typically occurs in late May/early June, the juvenile sandeel establish a diurnal rhythm similar to that of the adults (Wright and Bailey 1993, Frederiksen et al. 2007). In late summer-early autumn, the sandeel cease their diurnal vertical migration and begin their overwintering phase buried in the sediment (Winslade 1974b).

Sandeel have been observed to vary temporally in many of its life history traits, such as fecundity, hatching date, recruitment and growth (Wright and Bailey 1996, Bergstad et al. 2002, ICES 2010, Boulcott and Wright 2011). Among the variables suggested to influence sandeel recruitment are spawning stock biomass, sandeel density, food availability and temperature (Arnott and Ruxton 2002; van Deurs et al. 2009). The latter (defined as winter sea surface temperature) to such a degree, that it solely and in lack of actual sandeel stock assessments, has been used as a proxy for sandeel abundance in an attempt to estimate food availability for black-legged kittiwakes (Frederiksen et al. 2007).

Trophic position

In many of the highly productive ecosystems of the world there tends to be a crucial intermediate trophic level dominated by one, or at most a few, species (Cury 2000). These canalise the energy from primary and secondary producers to top-predators, such as piscivorous fish, seabirds and marine mammals. This functional role is often held by short-lived zooplanktivorous fish species such as capelin (*Mallotus villosus*), sprat (*Sprattus sprattus*) and sandeel (Vilhjálmsson 2002, Frederiksen et al. 2006, Østerblom et al. 2006) (Figure 2).

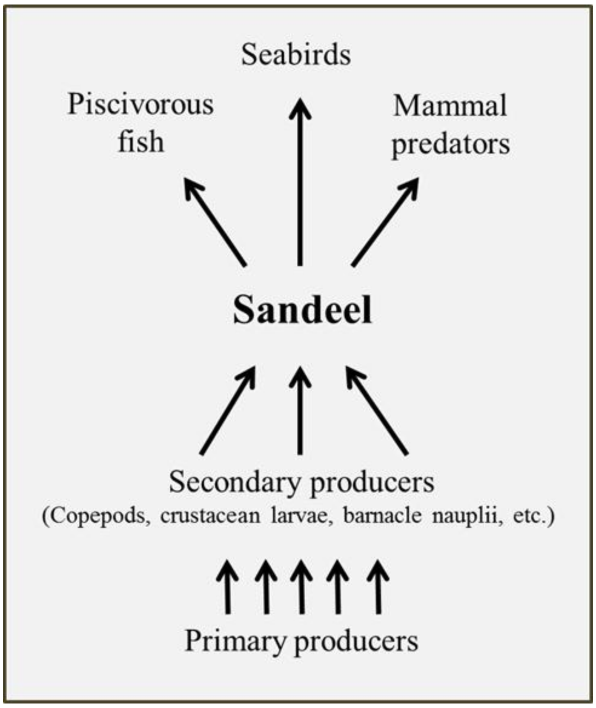

Figure 2 Example of a marine food web with sandeel as an intermediate species channelling energy from primary production via secondary producers to higher trophic levels.

On the Faroe shelf, interannual variations in the growth and recruitment of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), and in the number of attending guillemots (*Uria aalge*) have been found to correlate with the interannual variations in potential new primary production, i.e. the relative nitrate assimilation in the shelf water ecosystem during the high productive period (Gaard et al. 2002, Steingrund and Gaard 2005) (Figure 3). This implies an almost instantaneous transfer of energy from primary producers to higher trophic levels, and is believed only possible through a fast growing intermediate fish species such as sandeel (Steingrund and Gaard 2005).

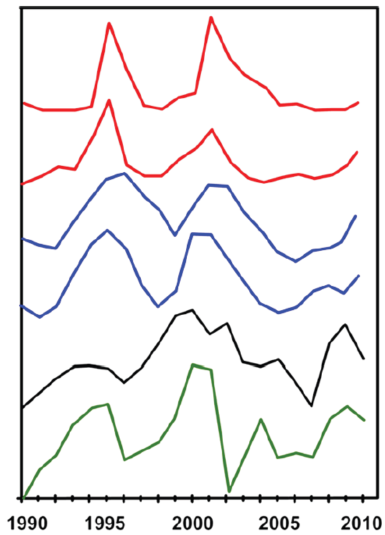

Figure 3 Relative variability in primary production, number of attending guillemots in a defined study area, recruitment of two year old cod and haddock and mean weight of 2-5 year old cod and haddock. Based on Gaard et al. (2002).

Sandeel are known to be an important prey for cod, haddock and seabirds on the Faroe shelf (Rae 1967, Du Buit 1982, Gaard et al. 2002). However, the effect of commercial fishery on fish stocks such as cod and haddock makes the bottom-up impact on stock size and productivity considerably harder to detect. However, both Yaragina and Marshall (2000) and Rose and O´Driscoll (2002) found the lipid condition index value, an indicator of physical condition of cod in the Barents Sea and off Newfoundland and Labrador, to be positively correlated to the biomass of capelin, another intermediate fish species.

Compared to most piscivorous fish and marine mammals, the response toward changes in food availability is relatively easy to detect in seabirds, especially when the breeding output of the seabird species is highly dependent on a certain prey. For example, Furness (2007) found 50% to 70% of the annual variation observed in the breeding success of black-legged kittiwakes (*Rissa tridactyla*), arctic terns (*Sterna paradisaea*) and arctic skuas (*Stercorarius parasiticus*) to be explained by the annual variation in estimated sandeel biomass in the Shetland area. However, other studies (Wanless et al. 2005) have indicated that high abundances of sandeel might not be sufficient to meet the energetic demand of breeding seabirds; the sandeel has to be of good nutritional quality as well.

Despite its inferred ecological importance, to date, no sandeel stock assessments have been conducted in Faroese waters. Nevertheless, annual 0-group surveys, including juvenile sandeel, have been performed continuously for three decades. These surveys have shown large annual variation in sandeel recruitment potential and indicate that sandeel predators, such as seabirds and commercially important fish species, e.g. cod and haddock, might be experiencing large annual variability in their prey availability. However, most sandeel predators do not solely prey on juvenile sandeel but on adults as well (Furness 1989, Lewis et al. 2001).

The Faroe shelf ecosystem

Despite its relatively small size (~10 000 km^2), the Faroe shelf (centered at 62°00´N, 06°47´W) contains a distinct neritic ecosystem surrounded by an oceanic environment (Figure 4). The shelf water is relatively well separated from the open ocean by a persistent front that surrounds the shelf, usually at a bottom depth of between 100 and 130 m (Gaard et al. 1998, Larsen et al. 2002, 2009), and due to warm ocean currents passing the shelf on their way north-eastwards, the shelf water temperature is relatively high (Larsen et al. 2008, Hughes et al. 2010).

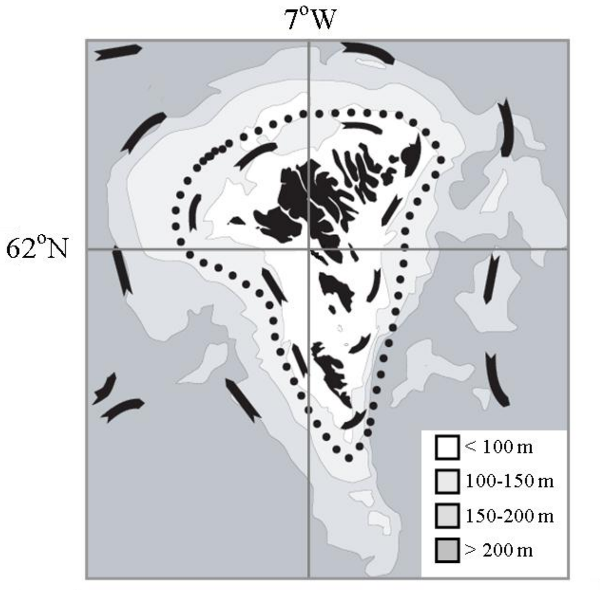

Figure 4 Topography and main features of the flow field around the Faroes. The dotted line enclosing the light grey area around the shelf indicates the typical position of the tidal front that separates the shelf water from the off-shelf water.

Tidal rectification and other effects drive a current system that circles the islands in a clockwise direction (Hansen 1992). Due to strong tidal currents, the water column in the shallow parts of the shelf is mixed from surface to bottom throughout the year and no summer stratification occurs (Gaard 1996, Gaard et al. 1998). The average residence time of the shelf water is estimated to be about two to three months, but it is highly variable and the monthly flushing rates might vary by a factor of six (Gaard and Hansen 2000, Gaard 2003).

The timing and intensity of the spring bloom on the Faroe shelf can vary considerably from one year to the next (Gaard et al. 2002, Debes et al. 2008b), and one hypothesis is that these variations are linked to the exchange rate between the on- and off-shelf water, where intensive exchange in spring leads to relatively large losses of phytoplankton from the shelf, retarding development of intensive spring blooms (Eliasen et al. 2005, Hansen et al. 2005).

Objectives

The rapid transfer of energy from primary producers to higher trophic levels observed on the Faroe shelf has left researchers wondering which organism(s) is/are responsible for this. It is likely a fast growing zooplanktivorous fish species, with the best qualified guess being sandeel.

The objectives of the current thesis are to investigate the ecological role of sandeel in the Faroe shelf ecosystem, and to estimate which influence changes in climate might have on it.

Data and methods

The data used in this study derive from several different sources:

- Water temperature on the Faroe shelf dating back to February 1992.
- Accumulated new primary production (PP-index) in the Faroe shelf ecosystem during spring and summer since 1990.
- Weekly measurements of chlorophyll *a* on the Faroe shelf from April to late June since 1997.
- Zooplankton biomass on the Faroe shelf in June 2006-2010.
- Juvenile sandeel from 0-group surveys conducted on the Faroe shelf in late June/early July since 1982.
- Age 1+ sandeel from sandeel surveys conducted on the Faroe shelf in mid-April 2007-2011.
- Recruitment (age 2), mean weight-at-age and total biomass of cod on the Faroe plateau since 1982.
- Breeding success of arctic terns, black-legged kittiwakes, common guillemots and northern fulmars at the Faroes.

Details on these data sources are to be found in Paper I-III.

This section further describes the data and methods for investigations not presented in Paper I-III.

Sediment analysis

The method was inspired by that presented by Holland et al. (2005). Using a Day grab, sampling an area of 0.096 m^2 (length 310 mm, width of both jaws 310 mm, depth 150 mm), 106 sediment samples were collected randomly along the route of the research vessel ´Magnus Heinason`. Generally, an adequate sample was obtained at each station with the first deployment of the grab. However, when empty grabs (indicating hard sediment) were recovered, an additional sample was attempted to verify that no sampling artefact had occurred.

In contrast to the procedure of Holland et al. (2005), the attempt of taking subsamples of the grab samples by corer failed. Subsamples, three per grab, were thus taken manually and stored frozen.

Onshore, the sediment samples were dried until no water was left, shaken in a sieve stack of 8, 2, 0.710, 0.250 and 0.063 mm sieves, and each component weighed in grams with a precision of two decimals.

None of the collected sediment samples contained sandeel.

Sandeel stomach and zooplankton analyses

The content of the non-empty sandeel stomachs, from oesophagus to the pyloric sphincter, was identified and counted. The copepods were identified to *C. finmarchicus*, *T. longicornis*, *Pseudocalanus* sp., and ´other copepod species`, while the remainders were identified to higher taxonomic level, e.g. fish egg/larvae, decapod larvae, barnacle nauplii, etc. In general, a specimen was only included in the count when it was in one piece. However, in the case of *C. finmarchicus*, the cephalosome, including its distinctive anterior antennas, was counted as a specimen, while the meta- and urosome alone were not. Due to the distinctive pear shape of the *T. longicornis*´ prosome, specimens lacking the urosome were accepted in the count. The decapod larvae were frequently observed to be more digested compared to the other species. However, their eyes did seem to be well preserved, and the presence of a pair of decapod larvae eyes was therefore accepted in the count, while a specimen lacking the eyes was not.

Immediately after sandeel sampling, zooplankton was sampled by vertical hauls from 50 meters depth to the surface using a WP-2 net with a mesh size of 200 µm and a hauling speed of 0.3-0.5 m sec^{-1}. The samples were preserved in 4% formaldehyde. With plankton splitters, subsamples were taken in the laboratory, where the zooplankton was identified and counted in the same manner as the sandeel stomach content.

Cod stomach content data

Cod were sampled during two annual groundfish surveys conducted in March and August on the Faroe plateau and dating back to 1997. Stomachs were sampled randomly from cod of all sizes. All sandeel found were registered, and when in one piece and not too much digested, they were length measured to the nearest whole millimetre as well.

Statistical significance

The statistical significance (p-values) of the relationships presented here has been corrected for serial correlation as suggested by Pyper and Peterman (1998).

Results and discussion

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

Sandeel habitat on the Faroe shelf

By grouping sediment samples from 106 different sites into the sediment categories of Greenstreet et al. (2010) (Figure 1), a preliminary attempt was made at identifying areas suitable for sandeel on the Faroe shelf and 70, 14, 20 and 2 of the sites studied could be defined as unsuitable, suitable, sub-prime and prime for sandeel habitation, respectively (Figure 5). Hard seabed was the most common reason for a site to be categorised as unsuitable for sandeel habitation, second were sediments with too high percentages of silt and fine sand (see Figure 1).

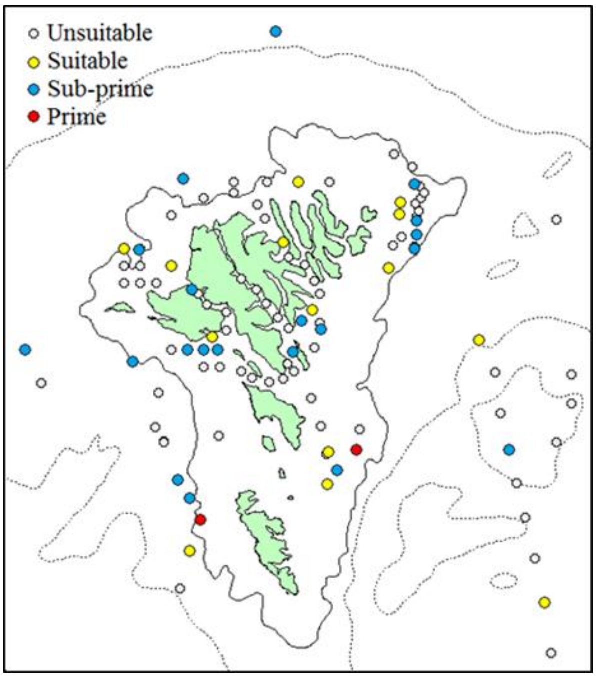

Figure 5 Location of the 106 sediment samples collected on the Faroe shelf and categorised as unsuitable (light grey), suitable (yellow), sub-prime (blue) and prime (red) for sandeel habitation according to Greenstreet et al. (2010).

Recruitment

Recruitment can be defined as the number of fish surviving to enter the fishery or some life history stage such as settlement or maturity.

Sandeel is not and has never been commercially exploited in Faroese waters, and thus no fisheries data are available. Nevertheless, annual 0-group surveys have been conducted on Faroe shelf for more than three decades, and although originally designed to obtain information on juvenile cod, the results of the 0-

group sandeel sampled on these surveys are of good quality, showing large annual variations in both average length and abundance (Figure 6).

In the North Sea, sandeel recruitment has been found to be negatively influenced by demographic density-dependent processes such as cannibalism and competition for food and suitable sediment, especially from 1-yr-old co-specimens (Arnott and Ruxton 2002). This was further substantiated by van Deurs et al. (2009) who showed how the otherwise positive correlation between spawning stock biomass and sandeel recruitment vanished in years with large stocks of 1-yr-old sandeel. However, based on the 0-group data from the Faroe shelf, an attempt at assessing the stock of 1-yr-old sandeel and the spawning stock according to Cook and Reeves (1993) and Cook (2004) showed no sign of negative demographic effects on sandeel recruitment defined as the abundance of juvenile sandeel in late June/early July (Paper I). Nevertheless, stomach analysis performed on cod in the period from 1949-1962 (Rae 1967) showed sandeel to be the dominant prey species, in contrast to in recent years (1997-2006), where sandeel only have ranked third (Steingrund 2009). This might imply that the sandeel stock was larger in the mid-twentieth century compared to recent years. In recent years, the sandeel stock might thus not have been at a maximum carrying capacity and thereby the likelihood of demographic effects is minimized.

Food availability, predation and temperature are generally considered to be the most influential factors affecting fish larval survival. However, in this study no significant relationship between the juvenile sandeel length and abundance and the temperature on the Faroe shelf were found (Paper I).

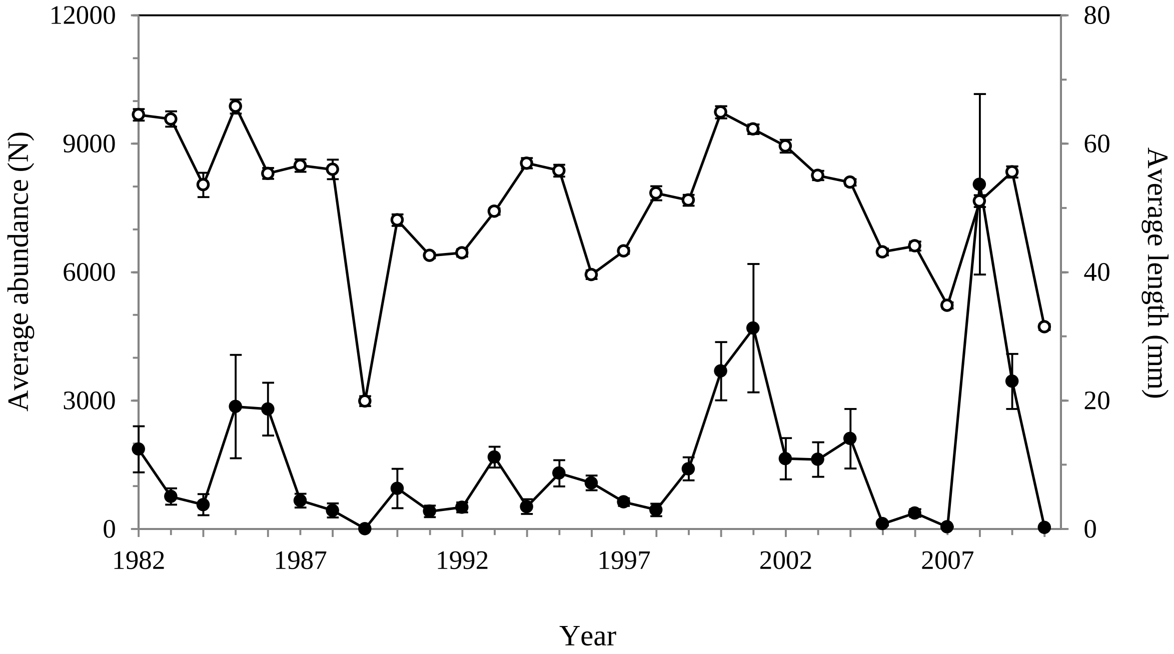

Figure 6 Annual variations in average length (mm, open circles) and abundance (average number caught per haul, filled circles) of juvenile sandeel sampled on the Faroe shelf in late June/early July 1982-2010.Vertical bars indicate standard error.

Sandeel are zooplanktivorous throughout their lives, but zooplankton data adequate for estimating food availability in the early life of sandeel are not available for the Faroe shelf area. However, continuous recordings of both potential new primary production (relative nitrate assimilation in the shelf water ecosystem from spring to mid-summer) and chlorophyll *a* concentrations have been performed on the Faroe shelf since 1990 and 1997, respectively. Many studies have shown the seasonal development in primary production to be followed by a subsequent and similar development in secondary producers, e.g. zooplankton (Niehoff et al. 1999), and this is also the case on the Faroe shelf (Gaard 1999, Debes and Eliasen 2006). Therefore, it was considered reasonable to use the new primary production (defined as an PP-index) and chlorophyll *a* data as proxies for food availability of juvenile sandeel, and 43% and 73% of the annual variation in the 0-group sandeel biomass index (defined as the number times length cubed) could be explained by the annual variations in the PP-index and chlorophyll *a* concentration, respectively (Figure 7 and Paper I).

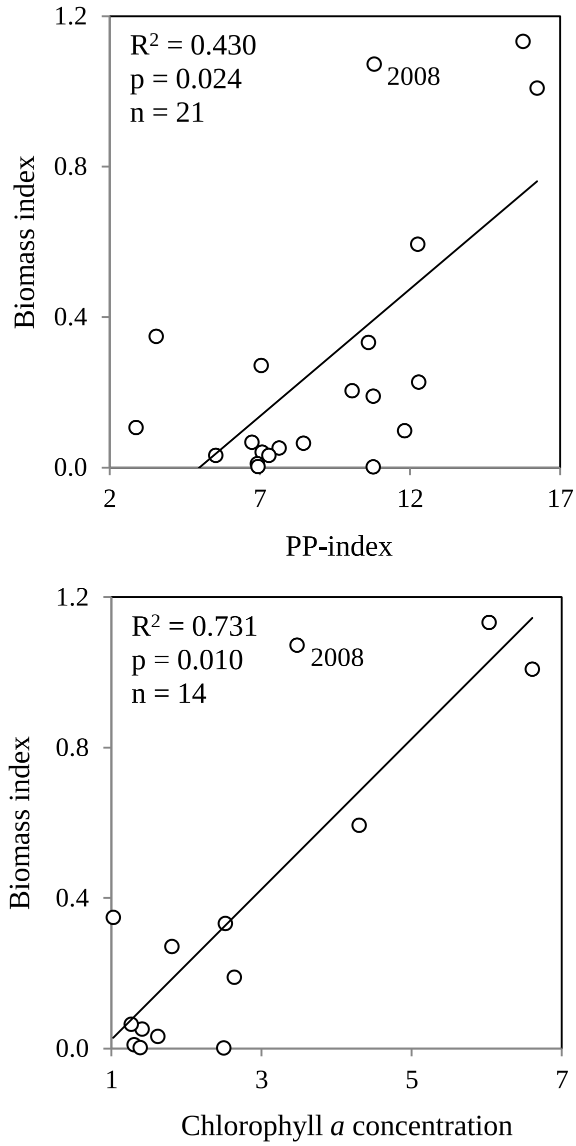

Figure 7 Relationships between the 0-group sandeel biomass index and the PP-index and chlorophyll a concentration on the Faroe shelf.

Insufficient food availability might also occur in years when fish larval production and the production of their food do not match temporally (Cushing 1974). The timing of the spring bloom on the Faroe shelf has been observed to vary greatly interannually (Gaard et al. 1998). However, no significant relationship between the abundance of juvenile sandeel and the timing of the onset of the spring bloom on the Faroe shelf were detected (Paper I).

The 0-group sandeel data also revealed another interesting relationship, where the abundance (N) was significantly correlated (R^2 = 0.191, p = 0.017, n = 29) with the average length (L) of juvenile sandeel. After metamorphosis, when juvenile sandeel adopt the burying behaviour characteristic of adults, predation mortality usually decreases substantially (Wright et al. 2000). Metamorphosis is often correlated with length, i.e. higher growth rates lead to shorter larval phases (Benoît et al. 2000). By this, high availabilities of food do not only reduce starvation mortality, but also lead to an earlier size-related exclusion of predators as proposed by van Deurs et al. (2009). The findings of high abundances in years with large average lengths thus seem reasonable. However, two models on juvenile sandeel mortality dominated by starvation and length-dependent predation, respectively, came up with exactly the same relationship, i.e.

$$\ln(N) = a - b \cdot \left(\frac{1}{L}\right) \qquad (1)$$

where a and b can be considered constants. To validate this model, ln(N) was plotted against 1/L, and it explained 72% of the variation in ln(N) (Figure 8 and Paper I).

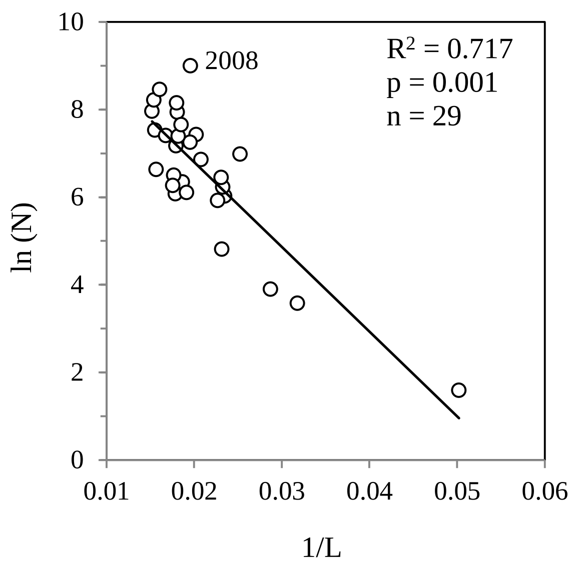

Figure 8 Relationships between the reciprocal value of the average length (L, mm) and the ln transformed average abundance (N, average number caught per haul) of sandeel juveniles on the Faroe shelf in the period from 1982 to 2010. From Paper I.

In Figure 6 the average abundance of 0-group sandeel was observed to be exceptionally high in year 2008 and 2008 is clearly seen as an outlier in Figure 7 and 8. However, year 2008 also appeared to be an outlying year when further data analyses were performed (Tables 1, 2 and 3). Thus, there are many indications that the very high 0-group abundance in 2008 was not representative, either due to sampling problems or for other reasons. Indeed, when year 2008 was excluded from the time-series, the relationship between the average number of juvenile sandeel in late June/early July and the proxies of food availability, i.e. the PP-index and Chlorophyll *a* concentration during the preceding spring bloom, went from being non-significant to significant (Table 1).

*Table 1. Squared correlation coefficient (R^2) between 0-group sandeel and proxies of food availability when year 2008 was included and excluded from the time-series, respectively. *, ** and *** indicate p-values of <0.05, <0.01 and <0.001, respectively. ns indicates non-significant relationships.*

		0-group sandeel	
Comment	**Food proxy**	Average abundance	
2008 included	PP-index	0.258	ns
	Chl. *a* conc.	0.430	ns
2008 excluded	PP-index	0.430	**
	Chl. *a* conc.	0.763	***

Since 1997, semi-annual (March and August) stock assessment surveys on cod have been conducted on the Faroe shelf. On these surveys, cod stomach content analyses have been performed as well, and have shown the sandeel preyed upon by cod to be mostly juveniles (5-7 cm) in August and young (12-13 cm) in March (pers. comm. Petur Steingrund). However, correlations between the occurrence of sandeel in cod stomachs and the average abundance of 0-group sandeel in the preceding late June/early July were only significant when year 2008 was excluded from the time-series (Table 2).

*Table 2 Squared correlation coefficient (R^2) between the average abundance of 0-group sandeel in late June/early July and the average number of sandeel in cod stomachs occurring in the subsequent August and March when year 2008 was included and excluded from the time-series, respectively. * and ** indicate p-values of <0.05 and <0.01, respectively. ns indicates non-significant relationships.*

Comment	Cod sampling	0-group sandeel Average abundance	
2008 included	August	0.229	ns
	March	0.189	ns
2008 excluded	August	0.491	**
	March	0.362	*

Food of adult sandeel

Sandeel are visual feeders, and some sort of consistency and selectivity were to be expected in their choice of prey on the Faroe shelf. Their favourite prey seemed to be medium to large sized copepod species (*C. finmarchicus*, *T. longicornis* and *Pseudocalanus* sp.), and polychaete, amphipod and decapod larvae (Figure 9).

Although medium to large sized copepods only represented ~50% of the total abundance of prey specimens in the environment, their contribution in the sandeel stomachs ranged from 50 to more than 90% of the total (Figure 9).

Variation in physical condition

As with the juvenile sandeel, interannual (2007-2011) variation was also observed in the physical condition of older sandeel. Generally, the sandeel with superior quality were found in the years 2008 and 2009 (Figure 10 and Paper II).

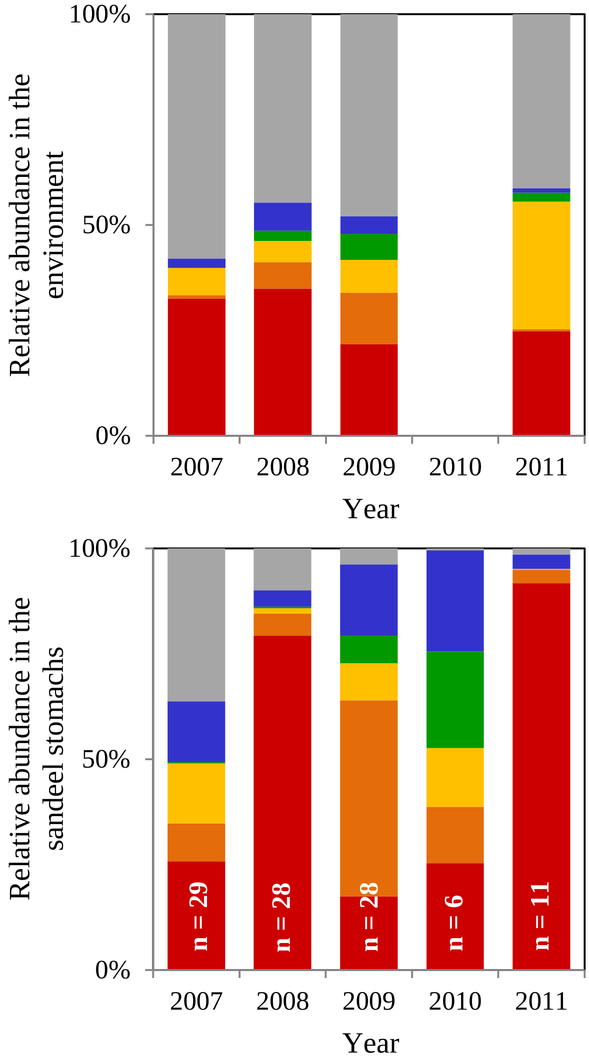

Figure 9 Relative abundance of prey in the environment (WP-2 sample, 0-50 m) and in the sandeel stomachs in mid-April 2007-2011. C. finmarchicus (red), T. longicornis (orange), Pseudocalanus sp. (yellow), polychaete larvae (green), deca- and amphipod larvae (blue), and ´other` (grey).

Since the sandeel were sampled in mid-April, they had most likely recently ended their overwintering phase. The onset of the spring bloom on the Faroe shelf is typically in late April/early May (Gaard et al. 2002, Debes et al.

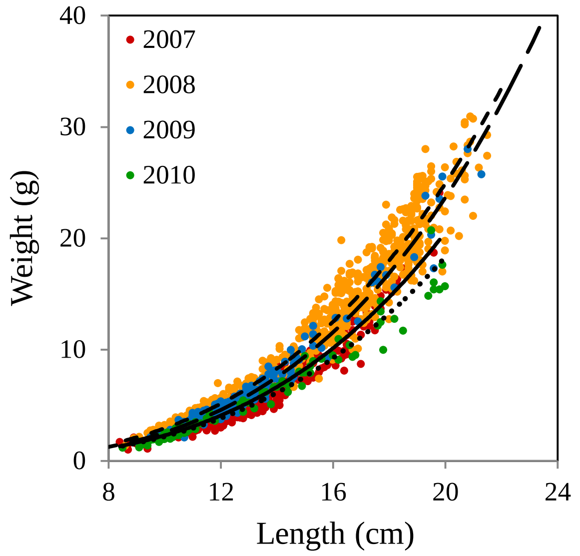

Figure 10 Length-weight relationship of sandeel sampled in mid-April 2007-2010. The relationships were best explained by power functions, where the continuous, dashed, long dashed and dotted lines represent year 2007, 2008, 2009 and 2010, respectively. Sampling of small (<11.4 cm) sandeel in 2011 failed, and the year 2011 was thus excluded from the length-weight relationships presented here.

2008b), co-occurring with the increase in copepod abundance and reproduction (Gaard 1999, Debes and Eliasen 2006). The recent foraging profit of the sandeel studied had thus most likely been at a very low level. It was thus assumed that the results represented the circumstances which influenced the sandeel in their newly ended overwintering phase and/or in their foraging period in the year before, rather than those of the same year. Macer (1966) showed that *A. marinus* in the North Sea did not grow in the overwintering phase, and the variations in length and length growth were thus presumed to be caused by variations in the foraging period of the previous year, while variations in weight, condition and fat content could be due to variations in the previous foraging period, as well as in the recently ended overwintering phase.

With the exception of 2007, the relative fat content seemed to be higher in the younger (age 1 and 2) than in the older sandeel (Figure 11). Since only a small fraction of sandeel age 1 and 2 are observed to be mature in other areas (Bergstad et al. 2001), this indicates low reproductive energetic expenditure of sandeel age 1 and 2 during the recently preceding spawning period on the Faroe shelf. To avoid bias due to reproductive expenditure, focus was set on these two age groups when causes for annual variation in physical condition were explored.

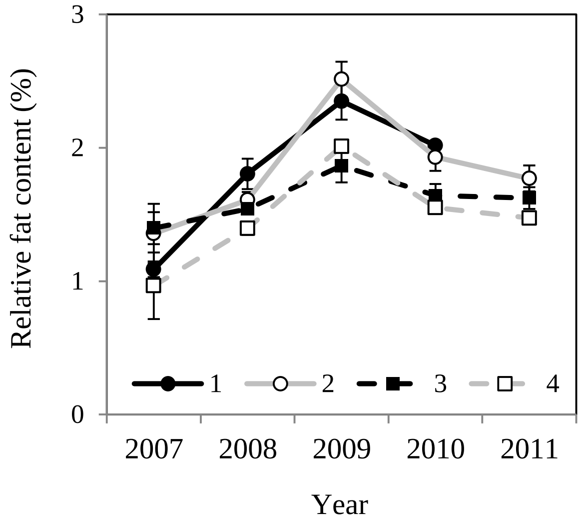

Figure 11 Relative fat content of age 1 to 4 sandeel sampled on the Faroe shelf in mid-April 2007-2011. Vertical bars indicate standard error. From Paper II.

Large interannual variation has been observed in the zooplankton biomass on the Faroe shelf. Sandeel growth in length was positively correlated with the zooplankton biomass in June of the intervening year (Figure 12), indicating sandeel growth to be food dependent. This is consistent with results from the North Sea and Shetland waters, where sandeel growth in the mid-1990´s was substantially poorer than that observed in the late 1970´s, where *C. finmarchicus* abundances also were considerably higher than in the mid-1990´s (Bergstad et al. 2002).

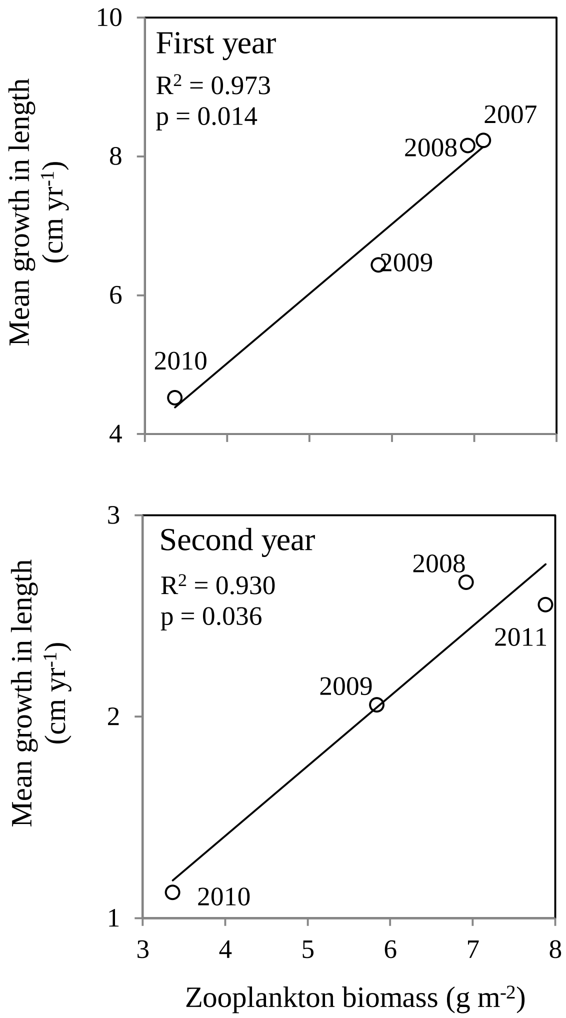

Figure 12 Growth in length in the first and second year of life of sandeel sampled in the period 2006-2011 in relation to the zooplankton biomass in June of the intervening year (2006-2010). From Paper II.

Although sandeel are zooplanktivorous (Macer 1966, Reay 1986), there were no examples of significant correlations between the somatic growth of sandeel and zooplankton biomass until this. Significant relationships have nonetheless been found between the somatic growth of other zooplanktivorous fish species, such as capelin, herring and sprat, and zooplankton biomass and abundance (Flinkman et al. 1998, Gjøsæter at al. 2002, Cardinale et al. 2002).

The temperature of the Faroese shelf water varies interannually, and in the years of the present study (2007-2011), the average winter (October-March) temperature varied by 0.5°C, with 2010 having the warmest (8.16°C) and 2008 (7.71°C) the coldest winter. By correlating the condition (Fulton´s *K*) of 1 and 2-yrs-old sandeel with the average winter temperature of the preceding winter, in which they had been buried passively in the sediment, a significant negative relationship was found between the two (Figure 13). To validate whether a temperature difference of ´only` 0.5°C could induce such a large effect on sandeel condition, a bioenergetic model, based on the findings of van Deurs et al. (2011), was produced and it showed the observed relationship between sandeel condition and average winter temperature to be reasonable (Paper II).

Ecological importance

Steingrund and Gaard (2005) found a positive and significant relationship between primary production (PP-index) during the spring bloom and cod recruitment on the Faroe shelf. The authors argued that this clear signal most likely was due to a cod diet consisting of food items younger than 1 year, for example 0-group sandeel. Feeding on older and longer lived prey such as crustaceans, which post-settlement cod on the Faroe shelf prey on in lack of sandeel (Rae 1967, Du Buit 1982), would not likely be able to transmit the phytoplankton signal this quickly.

This was further substantiated when sandeel (age 1) condition was simulated back to 1992, based on the relationship presented in Figure 13 (Paper II), and correlated with Faroe shelf cod mean weight-at-age 2. The annual variation in sandeel condition could explain almost one third (R^2 = 0.285, p = 0.007) of the annual variation observed in the mean weight-at-age of young cod on the Faroe shelf in the period 1992-2010 (Figure 14).

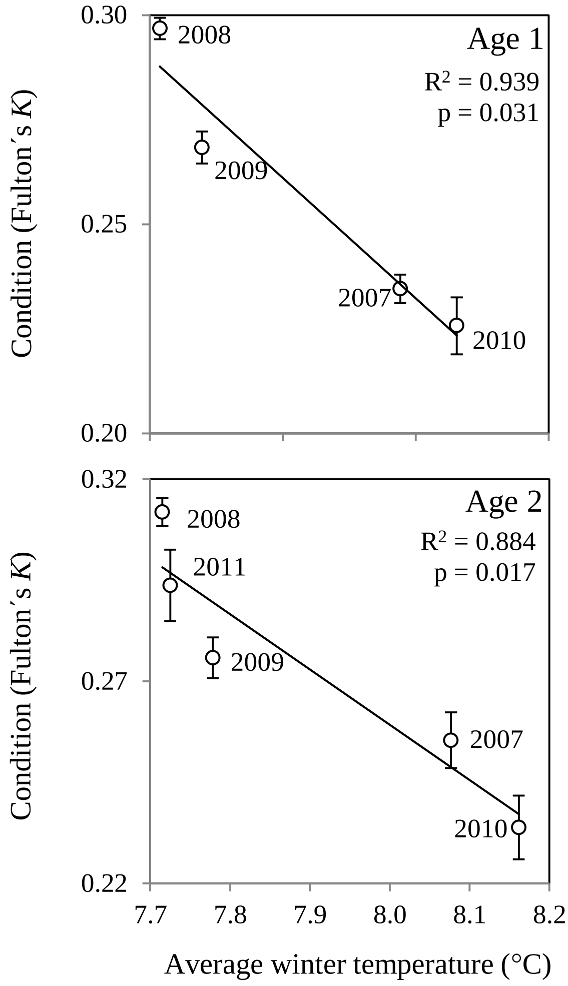

Figure 13 Condition of 1- and 2-yrs-old sandeel in mid-April in relation to the mean temperature of the preceding winter (October-March). Vertical bars indicate standard error. From Paper II.

Sandeel are important food for many breeding seabirds and for some species, they are essential for chick survival. Based on size, forage range and cost, time budget, physical abilities and the ability to switch to alternative prey, Furness and Tasker (2000) developed an index of the vulnerability of breeding success of 25 different seabird species to reduced sandeel abundance in the North Sea. The arctic tern (*Sterna paradisaea*) was ranked to be the most vulnerable, followed closely by the black-legged kittiwake (*Rissa tridactyla*), while seabird species such as common guillemot (*Uria aalge*) and northern fulmar (*Fulmarus glacialis*) were positioned at the lower end of the scale.

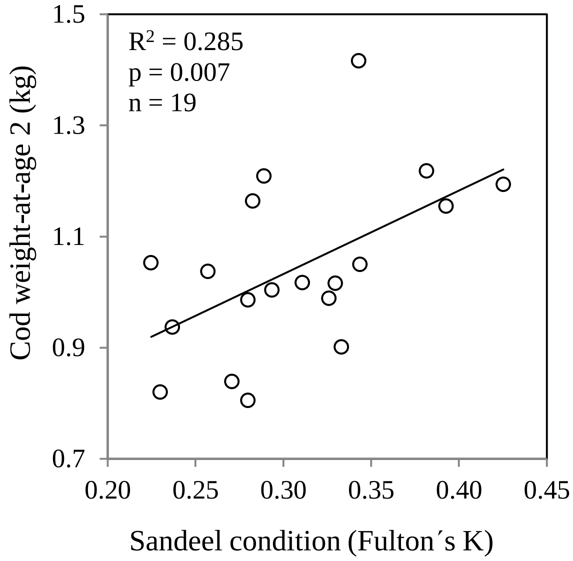

Figure 14 The relationship between the simulated condition (Fulton´s K) of 1-yr-old sandeel and the observed cod weight-at-age 2 (kg) on the Faroe shelf in the period 1992-2010. From paper II.

The time-series on seabird breeding at the Faroes are of variable lengths. However, consistent with the findings of Furness and Tasker (2000), the annual variation in the breeding of arctic terns and kittiwakes were best explained by variations in the juvenile sandeel stock (Table 3 and Paper III). However, the correlations between seabird breeding and 0-group sandeel abundance were only significant when 2008 had been excluded from the time-series or when an estimated abundance was derived from Eq. (1) (Table 3).

Seabirds have been suggested to make good status indicators of the local marine ecosystem and are used as both bio-monitors of ecosystem state with regard to e.g. pollution, and as quantitative indicators of specific ecosystem components such as the abundance of a prey species, e.g. sandeel (Piatt et al. 2007).

The results presented in Table 3 indicated that the breeding success of black-legged kittiwake is strongly correlated with 0-group sandeel, and by correlating its breeding success with cod recruitment and biomass in the same and following year, significant correlations were established in all instances (Figure 15).

Kittiwakes are widely acknowledged as sandeel monitors (Harris and Wanless 1997, Furness and Tasker 2000, Lewis et al. 2001, Frederiksen et al. 2005, Wanless et al. 2007, Parsons et al. 2008), and the annual variation in kittiwake breeding success could explain a larger and more significant proportion of the annual variation in cod recruitment and biomass compared to what the annual variation in the actual 0-group sandeel measurements could alone (Paper III).

This observation might have at least three different explanations. Firstly, the diet of kittiwakes, switching from 1+ sandeel to 0-group sandeel within the same year (Lewis et al. 2001), might be similar to that part of the sandeel population on which cod actually prey. Secondly, compared to the seabird breeding data, the 0-group sandeel data probably have a higher degree of noise, which might disturb the relationship between sandeel and cod. Thirdly, other prey species than sandeel may be involved. Thus, the thight relationship between kittiwake breeding success and cod could indicate that they depend on the same food items to a large extent. The relatively high correlation coefficients between sandeel and both kittiwake and cod suggests, however, that sandeel is an important component of this food.

*Table 3 Squared correlation coefficients (R^2) of the relationships between 0-group sandeel and the breeding success of four seabird species at the Faroes. The estimated abundance is derived from the average length using Eq. (1). * and ** indicate significance of $p < 0.05$ and $p < 0.01$, respectively. ns indicates non-significant relationships.*

		0-group sandeel			
Breeding success	**n**	Average length	Abundance 2008 incl.	Abundance 2008 excl.	Estimated abundance
Arctic tern	9	0.434 ns	0.194 ns	0.692 *	0.503 *
Black-legged kittiwake	26	0.409 **	0.054 ns	0.334 **	0.534 **
Common guillemot	25	0.251 *	0.193 ns	0.248 *	0.348 *
Northern fulmar	11	0.071 ns	0.019 ns	0.101 ns	0.116 ns

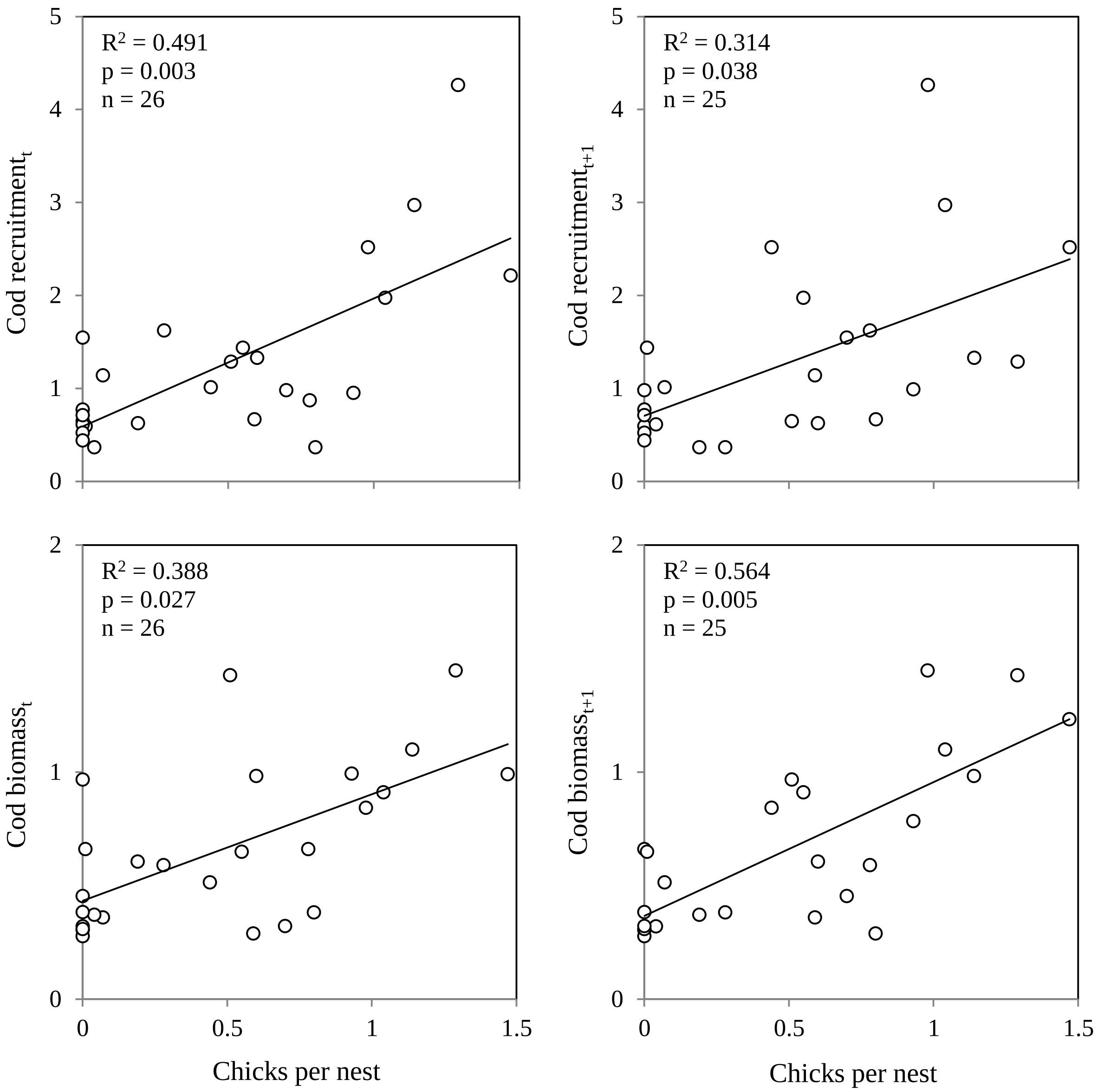

Figure 15 Correlations between the breeding success of black-legged kittiwakes at the Faroes and cod recruitment and biomass on the Faroe shelf in the same (t) and following year (t+1). From Paper III.

Of the four seabird species studied, the findings presented here strongly indicate that the black-legged kittiwake is the best qualified sandeel monitoring species. However, the sandeel monitoring potential of the arctic tern is believed not to be fully revealed due to the short period of time in which the arctic tern has been studied, and which, additionally, was a period characterised by breeding failure. The correlation between the breeding success of arctic terns and kittiwakes was very high ($R^2 = 0.943$, $p < 0.001$, Paper III). Furthermore, they were mutually well correlated with sandeel (Table 3) and had high correlations with the same principal component (Paper III), which again was the only principal component significantly correlated with sandeel. Altogether, this indicates very similar responses towards environmental changes.

It might be an advantage in the future to leave the possibility of the arctic tern as a sandeel monitoring species open, since the breeding success of the arctic tern was better correlated with the cod biomass in the following year, and although only close to being statistically significant ($p = 0.066$), its predictive power ($R^2 = 0.479$) regarding cod recruitment the following year was substantially higher than that of the kittiwake ($R^2 = 0.314$, Figure 15).

Climatic effects

Due to its life history, i.e. burying in sediment of specific characteristics within certain depth ranges (Holland et al. 2005, Wright et al. 2000), sandeel have, compared to more mobile fish species, limited opportunity for migrating to other areas in response to environmental changes (Behrens et al. 2009). This makes the sandeel more vulnerable to climate change.

In the North Sea, sandeel recruitment has been found to be negatively correlated with high winter sea temperatures during the egg/larval stages (Arnott and Ruxton 2002). Increasing temperature has also been suggested to be the main reason for the observed change in zooplankton abundance, which again is assumed to be the cause for the decreasing trend in the growth rate of sandeel in the north-western North Sea (Wanless et al. 2004), consequently leading to delayed maturation and decreased fecundity-at-age (Wanless et al. 2004, Boulcott et al. 2007, Boulcott and Wright 2008).

The results presented here indicate that the energy cost of overwintering increases substantially with increasing temperatures and temperature together with length determine the difference in lipid content of the sandeel in mid-April (Paper II).

In Figure 13 the sandeel condition in mid-April was observed to decrease with increasing winter temperature. Although only being close to statistically significant ($p = 0.086$), the same trend was also observed in the absolute fat content of 1-yr-old sandeel, where it decreased by a factor of ~2.5 with an increase in average winter temperature of 0.5°C (Figure 16).

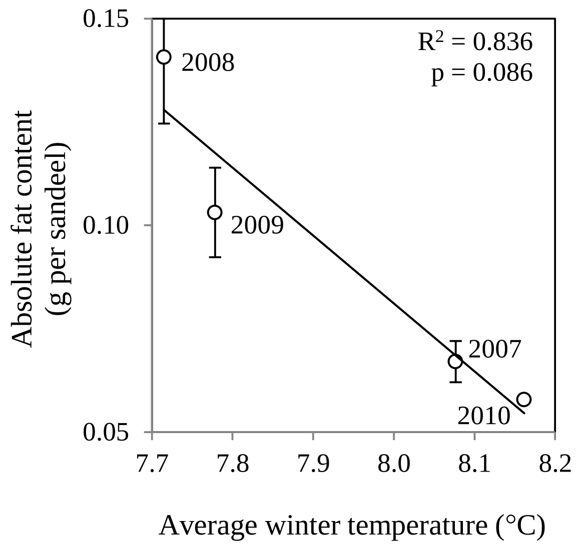

Figure 16 Absolute fat content of 1-yr-old sandeel in mid-April in relation to the average temperature of the preceding winter (October-March). From Paper II.

With an extrapolation of the regression between the winter temperature and the absolute fat content of the 1-yr-old sandeel (Figure 16), the absolute fat content hits zero when the mean winter temperature reaches 8.5°C. At temperature conditions comparable to those on the Faroe shelf, Boulcott and Wright (2008) found the critical period for reproductive allocation of energy in sandeel to be in August, i.e. prior to the overwintering phase. Boulcott and Wright (2008) further proposed that allocation to reproduction without sufficient energy stores might lead to increasing overwintering and pre-spawning mortality in sandeel. However, no significant relationship was found between the 0-group sandeel abundance in late June/early July and the temperature of the preceding winter on the Faroe shelf. This indicates that although elevated winter temperatures seems to have a negative influence on sandeel condition in the overwintering phase, which also includes the spawning period, it does not appear to have a negative effect on the reproductive output of sandeel.

Another possible response to energy shortage might be that sandeel short of energy, choose to shorten their overwintering phase and start foraging earlier on in the year. Van Deurs et al. (2010) made a modelling study, which showed the sandeel fitness (defined as a lifetime reproductive index) to be rapidly decreasing when foraging activity covered periods outside the zooplankton spring burst. The predation risk has also been observed to be highest when the sandeel leaves and buries into the seabed (Hobson 1986), thus a prolonged foraging period most likely will increase the predation mortality.

In 2004, unexpected breeding failures were recorded at many seabird colonies on the east coast of Britain. Wanless et al. (2005) found the parent guillemots, *Uria aalge*, which in the study area typically feed their young on adult (1+ group) sandeel, to be delivering substantially fewer sandeel to their chicks in 2004, compared to the average of 1981-2003. Additionally, the sandeel which were successfully delivered had less than 25% of the calorific value of the sandeel sampled in 1976 and 1986-1988, and later reported by Hislop et al. (1991). The temperature in the northern North Sea has been observed to vary annually, where the temperature in 1976 was exceptionally low, in 1986-88 at a medium level, and in 2004 exceptionally high (Hughes et al. 2010). It is thus proposed that the low abundance and low quality of adult sandeel observed in the North Sea in 2004 were the consequences of an unusually warm year where the adult sandeel either died buried in the seabed during the overwintering phase or re-entered the water column in an exceptionally poor state.

The Faroe shelf water temperature has been observed to increase about 1°C on average since the mid 1990´s (Paper II), and in recent years, severe seabird breeding failures have been observed in the area (Paper III), especially in seabird species considered to be vulnerable to fluctuations in the sandeel stock, i.e. black-legged kittiwakes and arctic terns (Furness and Tasker 2000). The black-legged kittiwake has already been found to be a good sandeel monitoring species, and by correlating its breeding success (average number of chicks per nest, Paper III) with the average winter temperature (October-March, Paper II), a significant and negative relationship emerged (Figure 17), further substantiating the negative influence of increasing temperatures on sandeel.

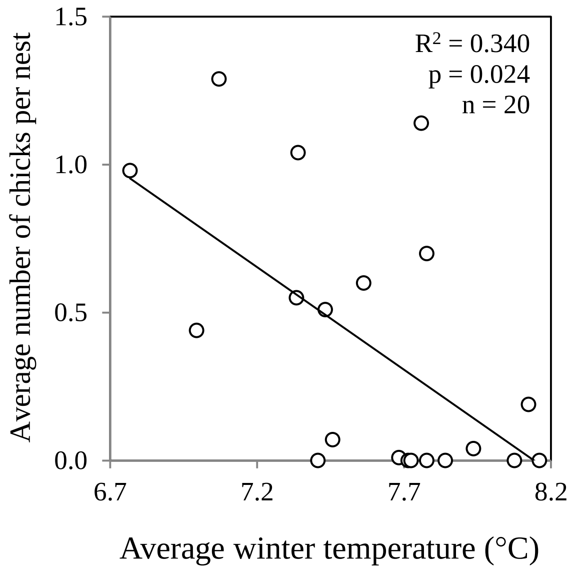

Figure 17 Breeding success of black-legged kittiwake at the Faroes in relation to average winter temperature of the Faroe shelf water in the period 1992-2011.

Additionally, the timing and intensity of the spring bloom on the Faroe shelf has been observed to vary considerably from one year to the next (Gaard et al. 2002, Debes et al. 2008b), and one hypothesis is that these variations are linked to the air temperature during the preceding months (Eliasen et al. 2005, Hansen et al. 2005). Thereby, and through food availability, sandeel might also be indirectly influenced by temperature.

Conclusions and perspectives

The present study provides new and important information to the knowledge of the structure of the Faroe shelf marine ecosystem, and hopefully, some pieces of the puzzle have been guided in their right direction.

This study has documented high correlations between sandeel recruitment and primary production on the Faroe shelf. The rapid transfer of energy from primary producers to higher trophic levels observed on the Faroe shelf might thus well be through sandeel. This was further supported by the sandeel dependent breeding success of four seabird species at the Faroes, in particular that of black-legged kittiwake. Additionally, when the breeding success of kittiwake was used as an indicator of sandeel availability, it could explain approximately half of the annual variations observed in cod recruitment and biomass on the Faroe shelf.

Annual variations were observed in some of the physical traits that determine the quality of sandeel as prey for higher trophic species such as seabirds and commercially important fish. The zooplankton biomass in the foraging period had the highest influence on sandeel length and sandeel growth in length, while temperature in the overwintering phase, where sandeel lie buried passive in the seabed, had large influence on their condition (Fulton´s *K*) and absolute fat content.

In the present study, the temperature, which the sandeel experienced during their overwintering phase, only varied by 0.5°C. However, this relatively small elevation in winter temperature managed to have severe effects on sandeel condition and fat content. The Faroe shelf is characterised by relatively high winter temperatures, which makes Faroese sandeel especially vulnerable to warming. The data material on which this is based is small and further study is needed but, if substantiated, this might indicate that sandeel in the north Atlantic before long will be facing a hard time surviving if climate change in the future leads to further elevations in temperature.

The results presented in current thesis call for further research, and an obvious study would be to experimentally validate the negative influence elevated temperatures seem to have on sandeel during their overwintering phase. On a more local scale, gaining more knowledge of areas suitable for sandeel habitation on the Faroe shelf should be of high priority in the future.

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