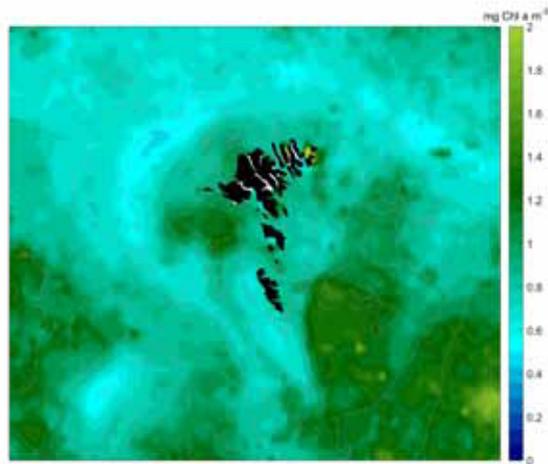




Ph.D. Thesis

**Primary production on the Faroe Shelf -
Spatial and temporal variations with links to
hydrography**

Sólvá Káradóttir Eliassen



NVDRit

2017:05

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Faculty of Science and Technology

FRÓDSKAPARSETUR FØROYA
University of the Faroe Islands

**Primary production on the Faroe Shelf -
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Føroyskur samandráttur

(Faroese summary)

Føroyski landgrunnurin hevur stóran týðning fyri føroysku fiskivinnuna, og ynskiligt er at skilja samansettu vistskipanina á Landgrunninum væl. Gróðurin í sjónum er grundarlagið undir allari føðiketuni, og leingi hevur verið greitt, at munir í gróðri frá ári til annað síggjast aftur í t.d. tilgongd av fiski og sjófugli.

Endamálið við hesi verkætlan var at fáa betri kunneleika um gróðurin á Landgrunninum. Mátingar, sum Havstovan hevur gjørt seinastu 20 árin, eru gagnýttar saman við dátum frá háuppløysiligum havmodellum av føroyska landgrunninum, altjóða veðurlagsmodellum og mátingum frá fylgisveinum. Úrslitini frá verkætlanini geva eina betri heildarfatan av, hvussu broytingar í havi og atmosferu ávirka gróðurin, og hvussu gróðurin á Landgrunninum er tengdur at árstíð, staði, útskipting og tøðvnum. Úrslitini siga eisini nakað um útbreiðsluna av djóraæti, og tiskil eisini hvar ymisk fiskasløg gýta og halda til.

Høvuðsúrslit

Árstíðargongdin hjá gróðrinum er í høvuðsheitum henda: Í mars-apríl, (Mynd 5a-b á síðu 18) er lítið av gróðri; tó er mest gróður á innaru leiðunum og næstan ongin gróður longri útiá. Útskipting og avmarkað ljós tálma gróðrinum inni við land um hetta mundið. Gróðurin á ytru leiðunum er treytaður av lagbýti, sum ikemur, tá atmosferan byrjar at hita sjógvin um várið. Vanliga gerast økir, har botndýpi er størri enn umleið 100 m, lagbýtt í mai, og um somu tíð kemur gongd á gróðurin inni við land (Mynd 5c á síðu 18). Eftir at rættulig gongd er komin á gróðurin á innaru leiðunum, er skjótt at tøðvnistrot, serliga trot av silikati, gerst avmarkandi fyri gróðurin. Hetta hendir ofta í juni og varir restina av sumrinum (Mynd 5d-f á síðu 18). Um hesa tíðina er mesti gróðurin longri úti, og blanding við niðaru lögini longri úti tilfórir tá nýggj tøðvni bæði uppeftir og inneftir.

Út frá fylgisveinamátinum ber til at býta Landgrunnin upp í trý økir við sereyðkennum hvat gróðri viðvíkur:

Gróðurin á Innara Landgrunninum (grátt á Mynd 6 á síðu 19) fylgir í stóran mun gongdini í Skopunarfirði, sum verður mátað við Lívískastøðina í Skopun. Í miðal tekur gróðurin her veruliga dik á seg í mai, men gerst ofta tøðvnisavmarkaður út á summarið.

Ytri Landgrunnurin (ljósareytt á Mynd 6 á síðu 19) gerst í miðal lagbýttur í mai, og gongd kemur á gróðurin eftir hetta. Gjøgnum alt summarið eru nøgdin av plantuæti í ovaru lögnum á Ytra Landgrunninum høgur. Nógv blanding gjøgnum sjóvarfalsfrontin førir nýggj tøðvni upp til vatnsorpuna, soleiðis at gróðurin kann halda á alt summarið. Økið millum Vágoynna og Skeiva Banka er serliga ríkt í plantuæti (reytt á Mynd 6 á síðu 19). Ikki er heilt greitt, hví hetta økið hevur nógvan gróður, men møguliga er tað eitt gagnligt býti millum blanding og lagbýti, sum skapar eitt tøðvnisríkt og harvið gróðraríkt umhvørvi.

Eystaru Bankarnir (grønt á Mynd 6 á síðu 19) blóma ofta tíðliga um várið, men hava lítið av plantuæti gjøgnum summarið. Økið er nakað djypri enn restin av Landgrunninum og kann tí lagbýttast og harvið blóma tíðliga. Sama lagbýti gerst sera sterkt um summarið og tiskil avmarkast uppblending av tøðvnum um hetta mundið.

Gróðurin og hægri lið í føðiketuni

Kanningarnar vísa, at nøgdin av smáum djóraæti er tengd at gróðrinum á Innara Landgrunninum, meðan sama samband ikki varð funnið fyri størri djóraæti.

Greiningin av økjum hevur týðning, tá ferðing og gýting hjá fiski verður kannað. T.d. vísa kanningar av upsamagum, at upsi fiskaður um summarið á Innara Landgrunninum inniheldur mest hvitingsbróður, meðan upsi fiskaður um summarið á Ytra Landgrunninum og á Eystaru Bankunum í størri mun hevur etið svartkjaft. Eisini er væl kent, at upsi gýtir, og at norðhavssildin í trýssunum plagdi at gýta á Eystaru Bankunum. Hesi bæði fiskasløgini gýta ein til tveir mánaðir fyrr enn toskur og hýsa, sum gýta nærri landi. Hetta, at gróður byrjar tíðliga í eystara økinum, er ivaleyst ein av orsökunum til, at upsi gýtir og norðhavssild gýtti har.

Preface

This work is the basis for the dissertation for the degree of philosophiae doctor (Ph.D.) in biological oceanography at the University of the Faroe Islands (Fróðskaparsetrið) and has been carried out at the Faroe Marine Research Institute (Havstovan) in Tórshavn, Faroe Islands. The Ph.D. thesis was submitted in April 2017, defended in August 2017 and printed in December 2017.

Section 1 of this synthesis provides a state-of-the-art description of existing knowledge, introduces the study area and outlines the main objectives of the thesis. A brief description of the materials used in the study is presented in Section 2. The main results and discussion from the six manuscripts comprising this thesis are summarised in Section 3, and the major findings and some future perspectives are given in Section 4. The structure of Section 3 is not organised in the chronological order the papers were produced, but rather seeks to adopt a synthetic approach that places the collective findings in a wider context. Results and/or discussion points in Section 3 that have not been presented in any of the papers have been marked with an asterisk (*).

The latter part of this thesis contains six papers. At the time of submission, two papers were still in review and were subsequently accepted and printed.

In this printed version of the Ph.D. thesis, the final versions of these papers are included and references in the synthesis have been updated accordingly. Also a few minor errors in the text have been corrected and a Faroese summary and a list of abbreviations has been added to the thesis.

List of papers

- Paper I Eliassen, S.K., Hansen, B., Larsen, K.M.H., Hátún, H., 2016. The exchange of water between the Faroe Shelf and the surrounding waters and its effect on the primary production. *J. Mar. Syst.* 153, 1–9. doi:10.1016/j.jmarsys.2015.08.004
- Paper II Eliassen, S.K., Hátún, H., Larsen, K.M.H., Hansen, B., Rasmussen, T.A.S., 2017: Phenologically distinct phytoplankton regions on the Faroe Shelf - identified by satellite data, *in-situ* observations and model, *J. Mar. Syst.* 169, pp. 99–110. doi: 10.1016/j.jmarsys.2017.01.015.
- Paper III Eliassen, S.K., Hátún, H., Larsen, K.M.H., Jacobsen, S., 2017. Faroe shelf bloom phenology – the importance of ocean-to-shelf silicate fluxes. *Cont. Shelf Res.* 143, 43–53. doi:10.1016/j.csr.2017.06.004.
- Paper IV Eliassen, S.K., Hátún, H., Larsen, K.M.H., 2017: The Faroe Shelf spring bloom linked to change in frontal character. Draft.
- Paper V Jacobsen, S., Gaard, E., Larsen, K.M.H., Eliassen, S.K., Hátún, H., 2018. Temporal and spatial variability of zooplankton on the Faroe shelf in spring 1997–2016. *J. Mar. Syst.* 177, 28–38. doi:10.1016/j.jmarsys.2017.08.004.
- Paper VI Pacariz, S. V., Hátún, H., Jacobsen, J.A., Johnson, C., Eliassen, S.K., Rey, F., 2016. Nutrient-driven poleward expansion of the Northeast Atlantic mackerel (*Scomber scombrus*) stock: A new hypothesis. *Elem. Sci. Anthr.* 4, 105. doi:10.12952/journal.elementa.000105

Acknowledgements

During these past three years I have had the privilege to dig into the topic of phytoplankton on the Faroe Shelf, and I am grateful to the Faroe Marine Research Institute that entrusted me to do this work. The scope of the research object, which encompasses phytoplankton cells in the about 11 magnitudes larger dynamic marine environment of the Faroe Shelf ($\sim 1 \mu\text{m}$ vs $\sim 100 \text{ km}$) has often felt like a daunting task, and without help this project would never have been completed.

First and foremost I wish to thank my supervisors, Dr. Karin Margretha Húsgarð Larsen, Prof. Bogi Hansen, Dr. Hjalmar Hátún and Dr. Till Andreas Soya Rasmussen who with patience and enthusiasm have helped and guided me through this project. They, and other colleagues at the Faroe Marine Research Institute, have supported, helped, inspired and taught me about topics previously foreign to me – thank you very much.

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 appreciated.

I would also like to extend my gratitude to the Danish Government, which has funded the work through the research program “Marine Climate in the North Atlantic and Its Effects on Plankton and Fish”.

Tórshavn, April 2017
Sólvá Káradóttir Eliassen

Abbreviations

CDH	Critical Depth Hypothesis
Chl	Chlorophyll
CS	Central Shelf
CTD	Conductivity, Temperature, Depth
CTH	Critical Turbulence Hypothesis
DRH	Disturbance-Recovery Hypothesis
EB	Eastern Banks
EIC	East Icelandic Current
ENAW	East North Atlantic Water
FAMRI	Faroe Marine Research Institute
FSF	Faroe Shelf Front
FSW	Faroe Shelf Water
G_p	Average net phytoplankton growth rate [d^{-1}]
HF_{lat}	Lateral heat flux across the FSF
HYCOM	Hybrid Coordinated Ocean Model
IB	Iceland Basin
k	Exchange rate [$m d^{-1}$]
MNAW	Modified North Atlantic Water
NB	Norwegian Basin
OS	Outer Shelf
PAR	Photosynthetically Active Radiation
PPI	Primary Production Index
Q	Air-sea heat flux
SST	Sea Surface Temperature
WNAW	West North Atlantic Water
WR	Western Region

1 Introduction

Fisheries and aquaculture are the main source of income to the Faroese economy. Phytoplankton forms the basis of the marine food chain and ultimately sustains higher trophic level production through food web links via zooplankton. On the Faroe Shelf (Fig. 1) calanoid copepods are consumed by forage fish such as sandeel, norway pout and blue whiting, that in turn serve as prey items for commercially important fish stocks, including cod and saithe (Steingrund and Ofstad, 2010; Homrum *et al.*, 2012). Since 1990 the new primary production on the Faroe Shelf has been estimated based on the winter-to-end-of-June nitrate draw-down (Gaard *et al.*, 2002). In addition, weekly variations in phytoplankton biomass have been documented since 1997 by measuring chlorophyll *a* (hereafter chl) concentrations at a coastal station (Gaard *et al.*, 1998). Interannual variations in fish and bird stocks do to some extent co-vary with variations in the primary production (Eliassen *et al.*, 2011; Hansen *et al.*, 2005; Steingrund *et al.*, 2010; Steingrund and Gaard, 2005; Gaard *et al.*,

2002), however, the dynamics of the phytoplankton growth on the shelf and its physical drivers is still not fully understood.

1.1 Marine primary production

Net phytoplankton growth occurs in the oceans given sufficient light and nutrients and if not inhibited by grazing. Main hypotheses to explain spring bloom initiation in the open ocean are the *Critical Depth Hypothesis* (CDH), *Critical Turbulence Hypothesis* (CTH) and *Disturbance-Recovery Hypothesis* (DRH).

The CDH (Sverdrup, 1953) states that spring phytoplankton blooms occur when surface mixing shoals to a depth shallower than a critical depth horizon defining the point where phytoplankton growth exceeds losses. Sverdrup himself noted that this scenario might not apply to situations where grazers are present in significant numbers and he noted that phytoplankton abundances may increase independently of mixed layer depth under conditions of moderate turbulence. The CTH

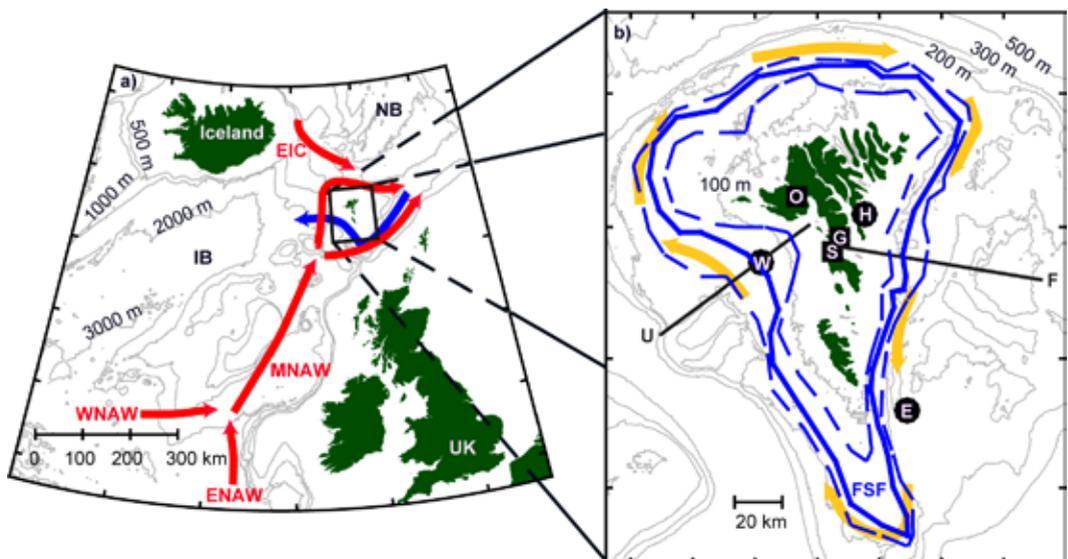


Fig. 1 Regional overview (adapted from Larsen *et al.*, 2008, 2012) (a) and the Faroe Shelf (b). The letters in panel a) indicate the Iceland Basin (IB), the Norwegian Basin (NB), Western North Atlantic Water (WNAW), Eastern North Atlantic Water (ENAW), Modified North Atlantic Water (MNAW) and East Icelandic Current (EIC). Red and blue arrows indicate the main currents in the upper layers and bottom layers of the region, respectively. In panel b) letters indicate sections (black lines), coastal stations (squares) and oceanic stations (circles), to which there are references in the text. The yellow arrows indicate the average circulation on the shelf and the blue line indicates the average position of the Faroe Shelf Front (FSF, dashed lines indicates ± 1 standard deviation, Larsen *et al.*, 2009).

(Huisman *et al.*, 1999; Taylor and Ferrari, 2011) offers a framework linking phytoplankton growth and winter convection. Explicitly it states that net growth will occur when phytoplankton cells remain in the euphotic zone for sufficiently long periods. According to the DRH (Behrenfeld, 2010; Behrenfeld *et al.*, 2013) a phytoplankton bloom begins when physical processes disrupt the balance between phytoplankton cell division and grazer consumption, explaining how blooms can start in mid winter. Feedbacks between predator and prey populations subsequently lead to a recoupling of the ecosystem, but may only occur following a period of significant phytoplankton accumulation.

In high latitude shelf environments (Fig. 2), where bottom depth exceeds the critical depth and light limitation can occur, the mechanisms described above may control bloom dynamics. Atmospheric heat flux is considered to regulate the onset of stratification although other factors including riverine input, eddy slumping, waves, winds, tides and cross-shelf exchange may also play a role (Behrenfeld and Boss, 2014; Brandt and

Wirtz, 2010; Chiswell *et al.*, 2015; Huthnance *et al.*, 2009; Mahadevan *et al.*, 2012; Saba *et al.*, 2015; Sharples, 2008; Smyth *et al.*, 2014). Moreover, biotic factors including benthic-pelagic coupling, grazing and virally-induced mortality may influence the phytoplankton population (Behrenfeld and Boss, 2014; Cottrell *et al.*, 1995; Friedland *et al.*, 2016; Marcus and Boero, 1998). At the termination of winter (Fig. 2a) heat fluxes are negative, but increasing light expands the zone on the shallowest part of the shelf in which the critical depth exceeds the bottom depth and net water column primary production is positive. As spring progresses, a shoaling upper mixed layer develops on the deeper parts of the shelf in response to a weakening in wind mixing, cessation of winter convection and/or stratification due to air-sea heat exchange (Chiswell *et al.*, 2015). The system gradually shifts to a situation characterised by sufficient light for phytoplankton growth in the upper stratified layer and in the shallower well mixed region (Fig. 2b). However, during times of good growth conditions, nutrients are rapidly depleted and sustained growth becomes dependent on nutrient resupply.

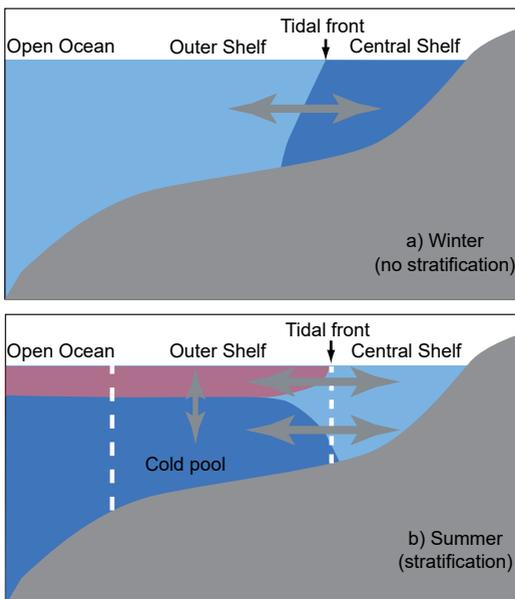


Fig. 2 An idealized cross-shelf section. The gray arrows indicate diapycnal transports and colours symbolize different temperatures, red is warmest and dark blue is coldest. a) Winter, when stratification is absent, and b) Summer, after stratification is established in the deeper parts of the shelf. The white, dashed lines in panel b) delimit the 'Outer Shelf' region.

1.2 Regional perspective

The subpolar Atlantic, which is one of the most productive marine regions in the world, is to a large degree modulated by the anticlockwise rotating subpolar gyre (Hátún *et al.*, 2005). Major flows in the uppermost 500 m of the Northeast Atlantic are summarised in Fig. 1a. The Western North Atlantic Water (WNAW), a relatively cold and fresh mixture of subtropical and subpolar water masses, flows towards the Rockall region where it mixes with the relatively warm and saline Eastern North Atlantic Water (ENAW) (Hansen *et al.*, 2008; Holliday, 2003). These source water masses mix to produce Modified North Atlantic Water (MNAW), which continues towards the Faroe Shelf from the southwest (Larsen *et al.*, 2012) and is transported across the Iceland-Scotland Ridge both south and north of the Faroe Shelf – the latter branch as the Faroe Current. On the northern and eastern side of the Faroe Shelf the poleward flowing MNAW meets the colder and fresher East Icelandic Current (EIC) that flows southeast from Iceland. The near bottom flows in the area are characterized by the deep and cold overflows from the Norwegian Basin

to the Iceland Basin (blue arrow in Fig. 1a, Hansen and Østerhus, 2000).

Since the upper layer poleward flow reaching the Faroe Shelf is downstream from the Iceland Basin and the Rockall region, it is likely that the biochemical properties in these water masses influence the water mass properties of Faroe Shelf water. Historically shelf ecosystems have been studied individually, although potential interaction between shelves and the adjacent open-ocean is increasingly acknowledged (e.g. Gröger *et al.*, 2013; Painter *et al.*, 2016). Thus, it is possible that studies conducted in the regions upstream of the Faroe Shelf and on the shelves that surround the subpolar gyre contain results that apply to the Faroe Shelf. Below follows a brief overview of results from these areas.

The interaction between the relatively warm upper layer water masses and cold winds during the subpolar Atlantic winter induces winter cooling and convection. This resets the water column with regard to nutrients by mixing nutrient rich deep water masses up to the surface (Backhaus *et al.*, 2003; Bonnin and Van Raaphorst, 2004; Hátún *et al.*, 2016). Numerous studies in the northeast Atlantic have revealed much about the timing, intensity and carbon absorption in phytoplankton blooms in this highly productive region (e.g. Brody *et al.*, 2013; Ferreira *et al.*, 2015; Friedland *et al.*, 2016; Henson *et al.*, 2009, 2006a, 2006b; Sathyendranath *et al.*, 1995; Tilstone *et al.*, 2014; Zhai *et al.*, 2012). In early spring diatoms typically prevail in the well mixed Iceland Basin whereas flagellates are more common in the Norwegian Basin, largely attributed to the differences in stratification between the two regions (Daniels *et al.*, 2015). On the Northwest European Continental Shelf, several studies have focused on ocean-shelf fluxes of nutrients and carbon, which both are important components in the biological pump (Holt *et al.*, 2012; Huthnance *et al.*, 2009; Painter *et al.*, 2016; Sharples, 2008; Wakelin *et al.*, 2012). Modelling studies (Wakelin *et al.*, 2012) and observations (Painter *et al.*, 2016), estimate that there is a net downslope carbon flux from the lower layer on the outer shelf to the deep ocean. Previous studies from the Nova Scotian Shelf, Gulf of Maine, Middle Atlantic Bight and Georges Bank on the western side of the subpolar Atlantic have shed light on processes applicable to the Faroe Shelf. In particular Georges Bank is surrounded by a tidal front with a persistently well mixed water mass on the shallowest portion of the

bank. It is remote from land and terrestrial nutrient sources are unimportant (Ji *et al.*, 2008). Primary production is high, especially in the frontal zone, possibly due to significant nutrient fluxes across the front (Franks and Chen, 1996). On Georges Bank, nutrient fluxes are shown to be spatially variable and there are certain key areas for the influx of nutrients (Hu *et al.*, 2008). Diatoms dominate the spring bloom on Georges Bank and in the Gulf of Maine and in both environments silicate reaches limiting concentrations prior to the onset of nitrate limitation (Saba *et al.*, 2015). A cold pool, which is shown to affect phytoplankton productivity, develops on the deeper part of the Middle Atlantic Bight during spring and there is an export of phytoplankton biomass from shallow to deeper areas (Malone *et al.*, 1983).

1.3 The Faroe Shelf

The Faroe Shelf is located on the Greenland-Scotland Ridge and is bordered by the Norwegian Basin on the northeastern side and the Iceland Basin on the western side (Fig. 1). The area falling inside the 200 m isobath encompasses approximately 20.000 km² and the adjacent area with bottom depths between 200 m and 300 m, mostly found on the eastern side of the shelf, represents further 10.000 km².

1.3.1 Oceanographic overview

The Faroe Shelf (Fig. 1b) is characterized by strong tidal currents with a clockwise residual circulation around the islands (Larsen *et al.*, 2008). The Faroe Shelf Front (FSF) separates the Faroe Shelf Water (FSW) on the shallowest part of the shelf from the surrounding MNAW (Larsen *et al.*, 2009). The average residence time of the shelf water is estimated to be about 2–3 months, but is highly variable and the flushing rates may vary by about a factor of six (Gaard *et al.*, 2002; Gaard and Hansen, 2000). Inside the FSF the water is generally considered to be quite homogeneous with regard to temperature and salinity (Fig. 2). It is almost always vertically well mixed and simultaneous observations on different locations indicate only minor horizontal differences (on the order of ± 0.2 °C) (Larsen *et al.*, 2008). Due to effective winter cooling of the shallow waters and excess precipitation over land, the temperature and salinity during spring in the

FSW are ~ 1 °C and ~ 0.1 psu lower, respectively, than in deeper waters (Larsen *et al.*, 2009).

1.3.2 Biological overview

Total primary production on the Faroe Shelf is estimated to be around $200 \text{ g C m}^{-2} \text{ year}^{-1}$, with $77 \text{ g C m}^{-2} \text{ year}^{-1}$ based on nitrate as nitrogen source, corresponding to an f-ratio of 0.4 (Debes *et al.* 2008b). Seasonal nitrate draw-down (winter-to-end-of-June) forms the basis of deriving an annual Primary Production Index (PPI, Gaard *et al.*, 2002), which has exhibited significant interannual variability during the period 1990–2016 (Fig. 3a).

Phytoplankton growth on the Faroe Shelf has been monitored at a coastal station (Station S, Fig. 1b) since 1997 and the phytoplankton bloom has generally been considered to occur when chl concentrations exceed a threshold value. The seasonally averaged (April–June) chl concentrations at Station S co-vary with the PPI (Eliassen *et al.*, 2011) and furthermore exhibit notable intra-seasonal fluctuations (Fig. 3b). The interannual variations in phytoplankton dynamics could be explained by top-

down control since there is an inverse relationship between the PPI and zooplankton biomass on the Faroe Shelf in late June (Gaard *et al.*, 1998; Larsen, 2009). However, direct measurements during the 2004 growth season suggest that grazing pressure by copepods never accounted for more than 3% of phytoplankton biomass (Debes *et al.*, 2008a). A modelling study (Eliassen *et al.*, 2005) demonstrated how variable exchange can modulate bloom dynamics through a dilution-effect that keeps phytoplankton abundances low, a so-called ‘horizontal Sverdrup mechanism’. Such a mechanism has also been suggested to explain the observed inverse relationship between PPI and the zooplankton biomass, which is dominated by the abundance of the relatively large and ecologically important oceanic copepod *Calanus finmarchicus*. High PPI is suggested to coincide with weaker ocean-shelf exchange resulting in less influx of *C. finmarchicus* onto the shelf.

Hansen *et al.* (2005) further identified a link between winter temperatures and primary production and suggested that cold winters would strengthen the FSF, thus reducing physical losses

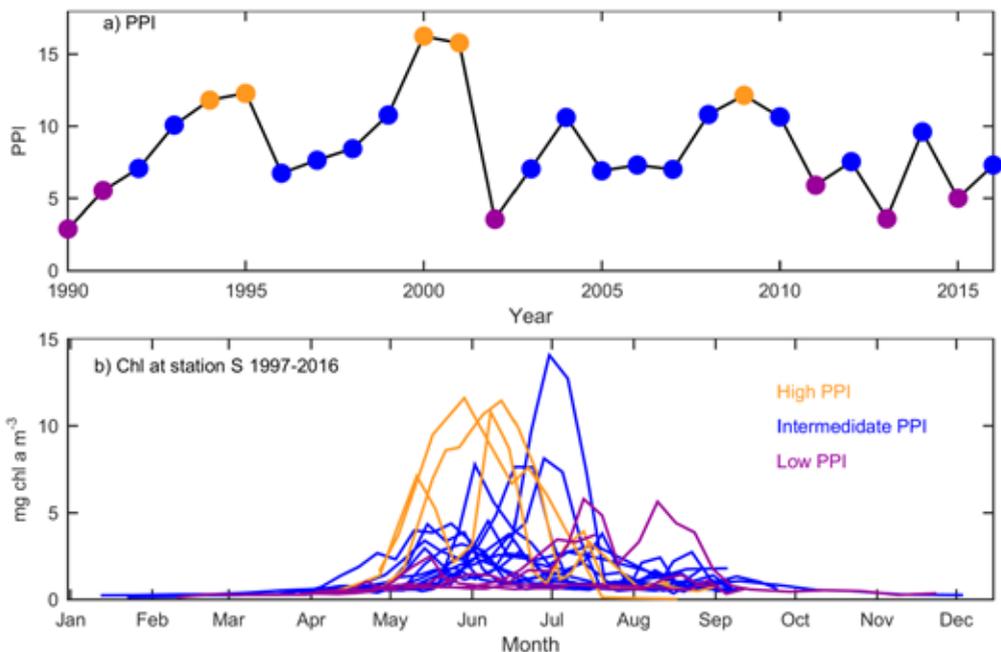


Fig. 3 Annual Primary Production Index (PPI) 1990–2016 (Updated from Gaard *et al.*, 2002) (a) and chl sampled at Station S, 1997–2016 (b). Low, intermediate and high PPI years are colour coded in red, blue and green, respectively, in both panels.

of shelf production across the front. With regard to phytoplankton growth, Debes *et al.* (2008b) found that there was sufficient light on the shallowest part of the shelf for growth to occur already by the end of March and that the specific growth rates were maximal in April–May. Despite these high growth rates, low chl concentrations ($< 2 \text{ mg chl m}^{-3}$) were typically observed during the April–May period further suggesting that large ocean-shelf exchange can be a major loss term.

To date there have been four independent studies (location H, G and S, Fig. 1b) from the shallowest part of the Faroe Shelf focussing on phytoplankton dynamics (Gaard *et al.*, 1998; Debes *et al.*, 2008b; Djurhuus *et al.*, 2015; Jacobsen, 2015). These studies consistently show that diatoms dominate phytoplankton biomass throughout the spring and summer, and that chl levels $> 2 \text{ mg chl m}^{-3}$ are always associated with elevated diatom abundance. During the summer there is typically a community shift from larger to smaller diatom species and non-siliceous taxa, such as flagellates and cryptophyta. Flagellate abundances occasionally exceed $10^6 \text{ cells L}^{-1}$, corresponding to up to 2 mg chl m^{-3} . Diatoms require silicon to precipitate their opaline frustules and thus orthosilicate concentrations are an important control to the spring diatom blooms. Silicate concentrations below $2 \text{ }\mu\text{M}$ are often considered limiting for diatom growth (Allen *et al.*, 2005; Brown *et al.*, 2003; Egge and Aksnes, 1992) and indications of a similar threshold has been observed on the Faroe Shelf (Djurhuus *et al.*, 2015). Nitrate systematically decreases every spring, but is only totally depleted during the most productive years. Variations in phosphate are small and it seems that there is always sufficient of phosphate on the shelf (Djurhuus *et al.*, 2015).

Common to the above mentioned biological studies is that focus has been on the shallowest part of the shelf environment. To date there has been less emphasis on the deeper parts of the shelf and the interaction between the shallow and the deeper parts. The chl time series from Station S is a valuable record, but the areal extent to which these observations can be considered representative remains poorly characterised. Although it has been common to distinguish between the shallower and deeper areas, ambiguity remains concerning the geographical extent of these definitions. In particular, the seasonal variability in the position of the FSF, and thus the size and spatial structure of the shallowest region, has received little attention.

Furthermore there is limited knowledge concerning the part of the Faroe Plateau outside of the FSF with regards to hydrography, seasonal stratification and nutrient dynamics. Variable horizontal exchange has been suggested to influence phytoplankton growth on the shallow part of the shelf, but spatial and temporal variations in the rate of exchange and emergent properties (e.g. heat, nutrients, phytoplankton, zooplankton, etc.) transported to the shallowest part of the shelf are yet to be addressed. With the exception of studies on the shallowest part of the shelf the spatial distribution of phytoplankton blooms, intra-seasonal variability, community dynamics, and total primary production on the shelf remain uncharacterised.

Since the first indications of a relationship between physical processes and phytoplankton ecology (Gaard *et al.*, 2002), observational data sets are substantially expanded both by local *in-situ* data acquisition and the large amount of reanalysis and satellite data now available. In addition, a high-resolution 3-D numerical model has been developed for the Faroe Shelf, facilitating a much more detailed investigation of the variations linking physical forcing and biology over multi-annual timescales (Fig. 4). These recent advances motivated the initiation of the present study.

1.4 Objective of the study

The objective of this study was to describe spatial distribution, seasonal and interannual variations of phytoplankton and physical mechanisms controlling primary production in both the shallow and deeper parts of the Faroe Shelf. Particular emphasis was placed on the effect of the seasonal vertical stratification, the variable position of the tidal front, the spatial extent of the shallow and surrounding regions and horizontal exchange between these regions.

The study area is approximately within the 300 m isobath, but does not include fjords and sounds between the Islands. Chl concentrations have been utilized as a general indicator of phytoplankton biomass without much attention to size spectra or species composition of the individual phytoplankton types, for which spatio-temporal observations are not available.

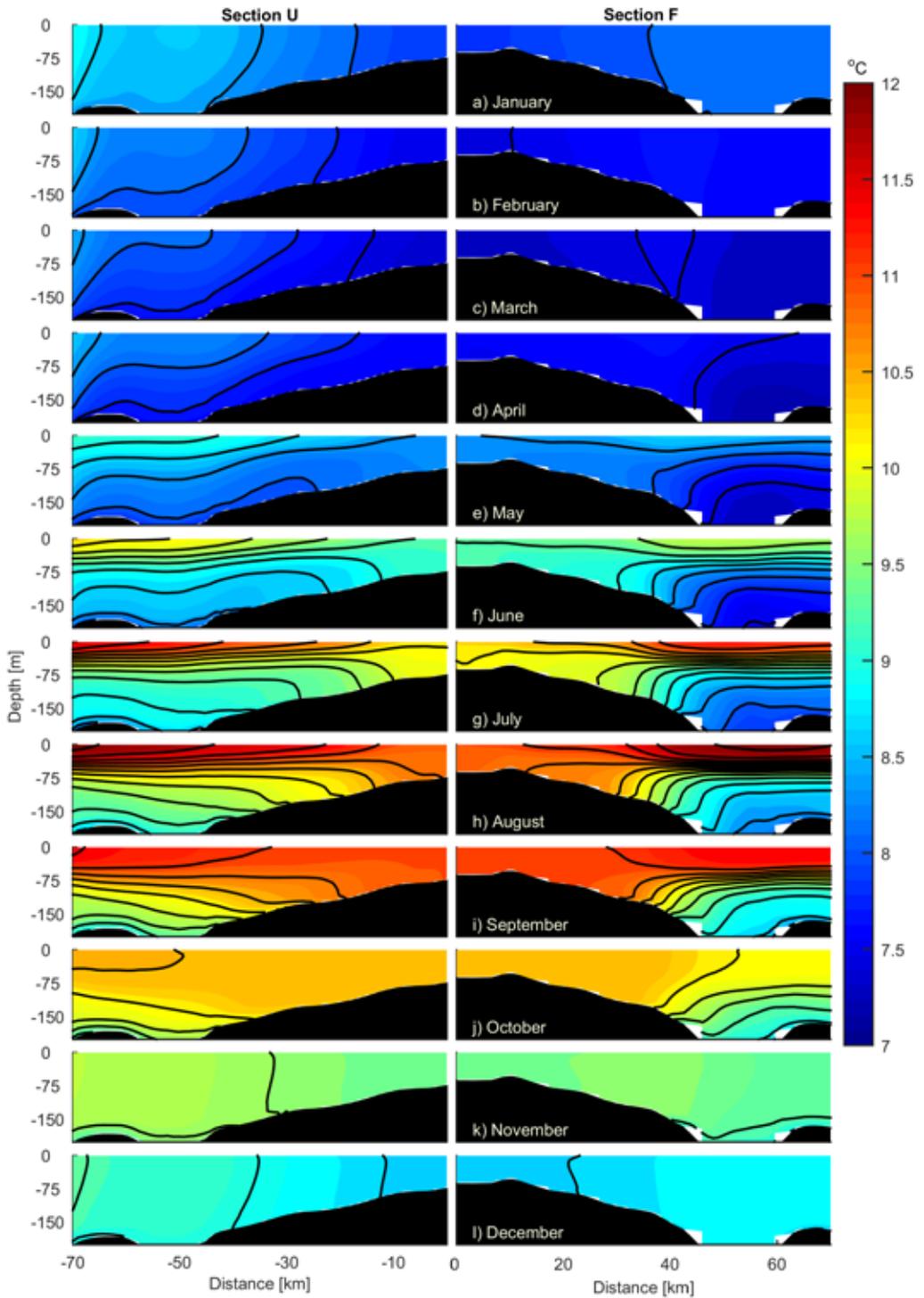


Fig. 4 Average seasonal temperature development along Section U and F, (Fig. 1b). Based on the HYCOM model, 2000–2009. Black isotherms are plotted for every 0.3 °C.

2 Materials

A broad suite of data collected since the 1990s have been compiled and analysed as part of the present study. Repeated observations on the Faroe Shelf obtained at the same time of year and/or at the same locations have been supplemented by meteorological reanalysis data, remote sensing data and output from a numerical model. The different types of data are briefly summarised below and further details may be found in the individual manuscripts. The data used in Paper V and VI are not included here.

The Faroe Marine Research Institute (FAMRI) maintains two coastal stations, Station S and Station O (Fig. 1b). The temperature of FSW has been measured routinely at Station O since 1991 and tidally well mixed water is pumped from 18 metres depth and sampled on a weekly basis during the spring and summer at Station S. The water samples are analysed for nitrate and silicate (since 1995) and chl (since 1997). In addition, temperature is recorded five meters below the surface and close to the seafloor at two mooring locations (Fig. 1b, W: 130 m depth, since 2011, and E: 260 m depth, since 2013).

CTD (Conductivity, Temperature, Depth) data, collected by R/V Magnus Heinason on the Faroe Shelf from the period 1990–2016 have also been utilized. In particular, data from Section U (Fig. 1b), sampled in connection with the annual 0-group survey, conducted every year since 1994 in late June, have been analysed in Paper III. In 2013, the innermost part of section U was sampled 12 times from April to June and water samples were collected for phytoplankton cell counts. Parallel with CTD-data, fluorescence is also recorded, and at selected stations water samples collected for nutrient and chl measurements. The chl measurements were used to calibrate the fluorescence sensor.

In order to investigate the effects of tidal currents, tidal constituents were estimated based on current meter deployments on the Faroe Shelf over a period of several months (Larsen *et al.*, 2008) and were used to derive current velocities at hourly resolution.

A high-resolution Hybrid Coordinate Ocean Model (HYCOM) was applied to the Faroe Shelf for the period 2000–2009 (Rasmussen *et al.*, 2014). Numerous model outputs, including current velocities and tracer distributions, have been compared with direct observations generally

revealing a good fit. In this thesis and the corresponding manuscripts, temperature data from the model have been utilized.

Meteorological reanalysis data from <http://www.ecmwf.int/> (Dee *et al.*, 2011) and <https://www.esrl.noaa.gov/psd> (Kalnay *et al.*, 1996) are available for the full period corresponding to *in-situ* observations from Faroe Shelf. Heat fluxes (shortwave, longwave, latent and sensible) and Photosynthetically Active Radiation (PAR) data have been used. Satellite sea surface temperature (SST) and chl data (CHL1) from <http://marine.copernicus.eu/> and <http://globcolour.info/> (The GlobColour Project, distributed by ACRI-ST) are available from September 1997 onwards with a growing palette of various products during later years. Both remote-sensing and reanalysis data have been cross validated against *in-situ* observations yielding encouraging results, although satellite-derived chl values appear slightly lower than those obtained *in-situ* (Paper II). Similar discrepancies have been observed in the Iceland Basin, the Norwegian Basin and in Icelandic waters (Daniels *et al.*, 2015 and Kristin Agustsdottir, pers. comm.) and seem to indicate that the remote sensing algorithms for satellite-derived chl are sub-optimal in the subpolar Atlantic. Nevertheless, satellite chl adequately documents temporal variations in chl when compared to *in-situ* observations.

3 Results

3.1 Spatial phytoplankton variation and phenology on the Faroe Shelf

Analysis of 18 years of satellite chl data reveals the general scheme of phytoplankton bloom phenology on the shelf (Fig. 5 and paper II). In early spring phytoplankton biomass first starts to increase near shore and on the eastern side of the shelf, but from June onwards the highest surface concentrations are observed in areas with bottom depths of 100 – 200 m, approximately in the region where the FSF moves in and out (Larsen *et al.*, 2009).

Based on a statistical analysis of the satellite data (Paper II), the shelf was divided into three distinct regions with regard to phytoplankton phenology: the Eastern Banks (EB), the Outer Shelf

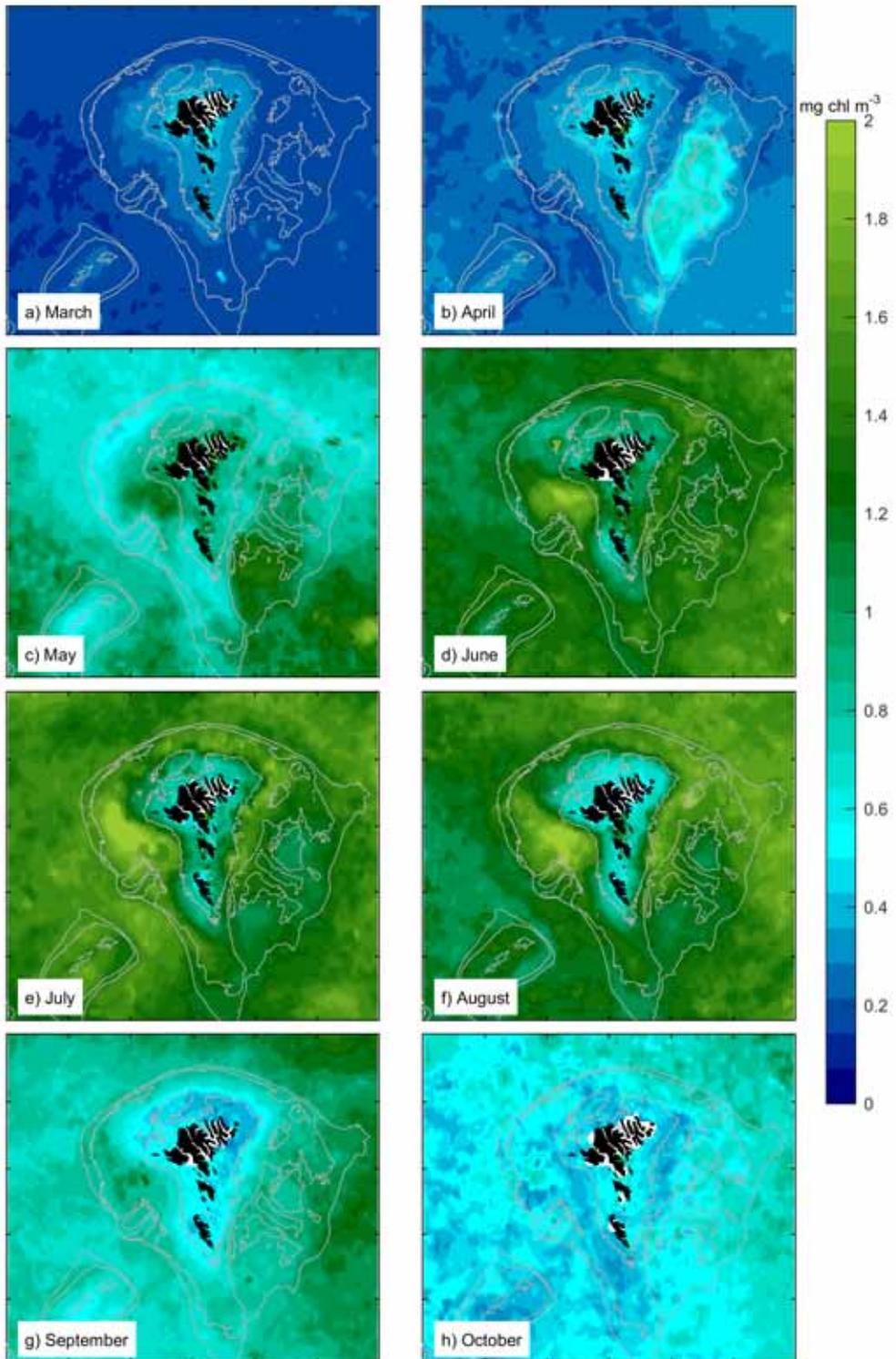


Fig. 5 Monthly surface chl climatology on the Faroe Shelf, averaged over 1998–2016. The 100 m, 200 m and 300 m isobaths are shown in gray. (Updated and adjusted from Fig. 5 in Paper II).

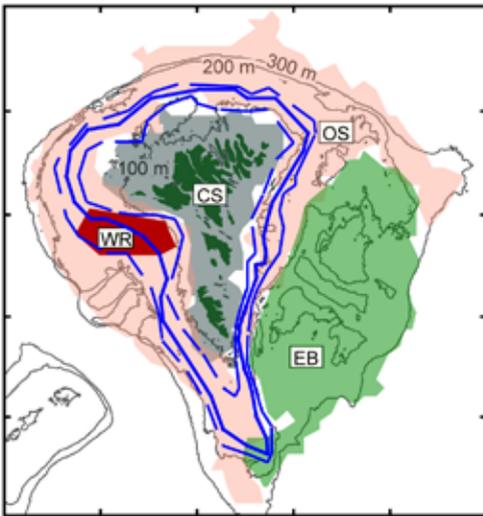


Fig. 6 Three regions: the Central Shelf (CS, gray), the Eastern Banks (EB, green) and the Outer Shelf (OS, reddish). The Western Region (WR), which is a part of the OS, is dark red. The average position of the FSF is outlined in blue (dashed lines indicate ± 1 standard deviation). (Fig. 6d in Paper II, colours slightly adjusted).

(OS) and the Central Shelf (CS) (Fig. 6). These empirically defined regions were also characterised by distinct seasonal evolution of water column structure, demonstrated by observed and simulated seasonal development of temperature (Paper II and Fig. 4). In all three regions the water column is vertically homogeneous in the winter, but during the summer it is only the CS region that remains vertically well mixed. It is worth noting that the boundaries delineating these regions are identified based on satellite chl data, which has the best coverage and strongest signal in the summer, and thus the boundaries outlined in Fig. 6 are probably best considered to represent the summer situation. Furthermore, the boundaries of these regions are very dynamic and likely incorporate both seasonal (c.f. Fig. 4) and interannual variability.

The EB region, which is 200 – 300 m deep, is characterized by relatively early bloom initiation and only moderate growth during the summer. Strong stratification is likely to limit nutrient supply to the relatively thick (> 50 m) upper layer during summer and could explain the moderate levels of biomass measured at this time of year. The small impact of tidal mixing forces in the deeper areas, characteristic of the EB region, implies that a relatively low positive air-sea heat flux induces

stratification here and growth occurs early in the season according to the CDH.

The seasonally stratified OS generally overlaps with the average position of the FSF, as estimated from data during all seasons (Larsen *et al.*, 2009). The bloom occurs considerably later than the other two regions, but elevated surface chl values persist during June–August. The high chl concentrations are probably only found in a shallow upper layer and it is probable that diapycnal mixing sustains growth over the summer period where nutrient limitation would otherwise terminate the bloom (Paper III). The highest surface chl values are almost exclusively observed in an area on the western side of the shelf (the Western Region (WR), red hexagonal in Fig. 6), where the upper stratified layer with high chl values is on average less than 50 m thick. Although the exact mechanisms sustaining growth in the WR are not fully understood it is likely attributable to a favourable interaction between mixing and stratification that is a unique characteristic of this region compared to the rest of the OS.

3.1.1 Species distribution on the Faroe Shelf*

It is well documented that diatoms dominate the phytoplankton community during summer on the CS (Gaard *et al.*, 1998; Debes *et al.*, 2008b; Djurhuus *et al.*, 2015; Jacobsen, 2015), but it is possible that the species composition is different in the stratified environment. Phytoplankton in stratified waters generally have a higher fluorescence:chl ratio compared to those found in well mixed environments (Fig. 7). In June 2013 a few samples for phytoplankton counts were taken in stratified waters from the innermost part of Section U, close to mooring W (Fig. 1b), and revealed high abundances of flagellates as well as cryptophyta and diatoms (Fig. 6 and S5, Paper III). Flagellates are typically more abundant in these stratified environments than on the CS (Daniels *et al.*, 2015; Siemering *et al.*, 2016).

3.2 Phytoplankton on the Central Shelf

Previous studies concerning phytoplankton dynamics have primarily focused on understanding primary production on the shallowest part of the shelf. For this purpose the chl time series from

*This has not been presented in any of the papers

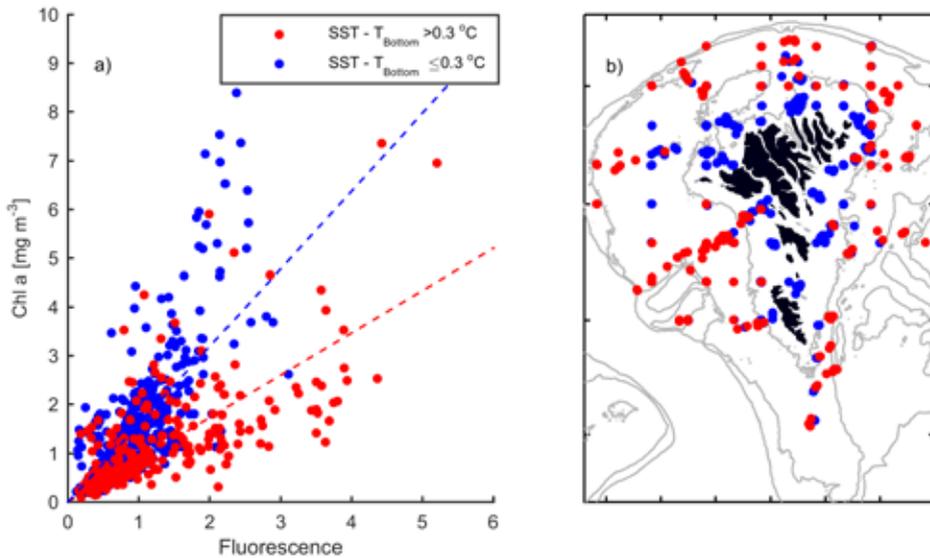


Fig. 7 Fluorescence:chl ratio (a) and spatial distribution of stations (b), sorted according to water column structure in the corresponding CTD-profile. Data are sampled between April and mid-July, 2002–2015. The red and blue dashed lines in panel a) indicate a zero offset data regression. The 100 m, 200 m and 300 m isobaths are shown in gray in panel b).

Station S, together with the PPI (Gaard *et al.*, 2002) have been used as indicators for the entire shelf. However, the representativeness of chl measurements at Station S for the wider shelf environment has remained largely uncharacterised. In the present study this issue was addressed by performing a correlation analysis between Station S samples and satellite-derived chl data to define the spatial footprint of the observations at the time series station i.e. the CS (Fig. 6 and Paper II). Generally strong tidal mixing on the CS results in vertically well mixed environment such that satellite observations of surface chl can be considered representative of the entire water column. A seasonal description of hydrography and phytoplankton bloom dynamics on the CS is presented in Sections 3.2.1 – 3.2.3.

3.2.1 The effect of exchange

A simple two-box model of the Faroe Shelf was applied to describe the interaction between the water masses inside and outside the 120 m isobath (paper I). Both water masses were assumed to be spatially homogeneous and separated by a front through which water, nutrients and phytoplankton were exchanged (Fig. 2a). An exchange rate (k) was defined, which had the dimensions of a velocity (m

d⁻¹). Based on temperature data from coastal Station O and the deeper parts of the shelf together with air-sea heat flux data, time series of the exchange rate were determined and were found to increase with tidal current speed and decrease with the cross-frontal temperature difference.

The method is based on the assumption that the lateral heat exchange between deeper areas and the shallow part of the shelf is proportional to the exchange of volume between these compartments. Crucially, theoretical constraints regarding diffusion across a front are consistent with the values obtained by this approach. Temperature changes in the well mixed shelf water are driven by air-sea heat fluxes and lateral mixing with the deeper shelf water masses. The lateral heat transport represents

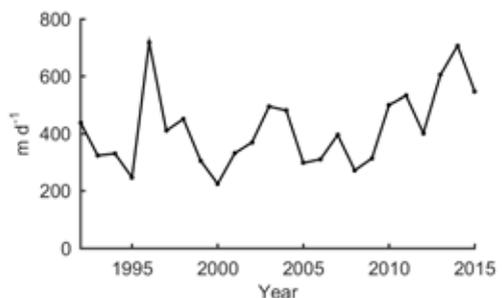


Fig. 8 Average exchange rate, k , for January–April, 1992–2015. (Updated from Fig. 8 in Paper I).

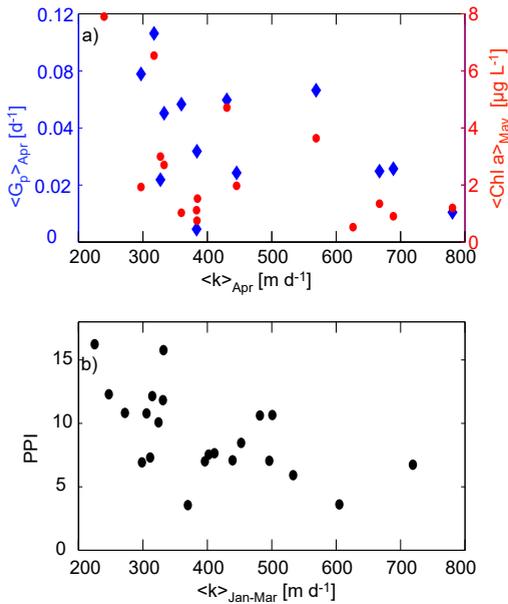


Fig. 9 Average net growth rate in April, average chl in May and PPI against the rate of exchange, k . a) $\langle G_p \rangle_{Apr}$ (blue, diamonds) and $\langle Chl \rangle_{May}$ (red, circles), plotted against $\langle k \rangle_{Apr}$. Based on observations from Station S, 1997–2001 and 2004–2013. b) The PPI plotted against the average exchange rate during the winter, $\langle k \rangle$. (Fig. 10 in Paper I).

the difference between the air-sea heat flux and the rate of heating of the shelf water mass and this in turn is proportional to the rate of exchange, k .

This approach only allows an estimation of the exchange rate during the winter (January to April). During this period the average rate of exchange between the shallow and the deeper parts of the shelf was found to vary between years by a factor 3 (Fig. 8). The results indicate an inverse relationship between exchange rate and the average net chl growth, G_p ($G_p = \ln(chl_{t1}/chl_{t2})/\Delta t$), in April, the average chl in May and the PPI (Fig. 9a-b). These results support the earlier hypothesis that significant exchange in early spring can hinder accumulation of phytoplankton biomass (Eliassen *et al.*, 2005).

Paper I deals specifically with exchange across the FSF, but it is also possible that horizontal mixing inside the FSF, i.e. within FSW, can slow down accumulation of phytoplankton biomass*. The volume of the homogeneous FSW is greater early in the spring, prior to the onset of stratification on the OS, than in June (Fig. 4 and Paper IV). Although the FSW is generally well mixed ($SST - T_{bottom} < 0.3$ °C) inside the 140 m isobath in April (Paper IV), satellite chl data demonstrate that there is a horizontal chl-gradient in the area identified as the CS, with decreasing chl concentrations coinciding with an increase in bottom depth (Fig. 10). Consequently, despite the fact that phytoplankton biomass is vertically well mixed, there exists significant horizontal variability. These data suggest that there must be a dilution of phytoplankton within the FSW in early spring,

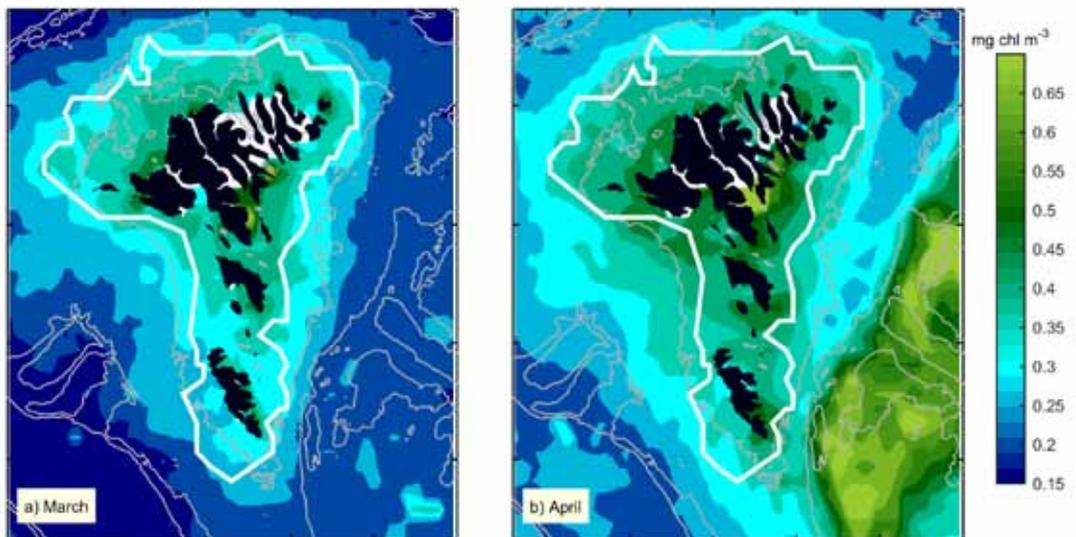


Fig. 10 Average surface chl concentrations in March (a) and April (b). The white line indicates the average summer position of the CS region and the gray lines indicate the 100 m, 200 m and 300 m bottom contours. (Updated and adjusted from Fig. 5 in Paper II).

when nutrients are sufficient and growth depends primarily on light availability.

During January–April, chl concentrations at Station S remain low, increasing from 0.1–0.2 mg chl m⁻³ in January/February to 0.4–0.5 mg chl m⁻³ in April (Fig. 3b). A similar trend is observed in satellite data between March and April (Fig. 10). Debes *et al.* (2008b) found that phytoplankton doubling rates were highest in April–May, (during 2004–2005), despite total chl values always falling below 2 mg chl m⁻³. Changes in chlorophyll biomass also imply that average net growth at Station S is positive throughout the spring, with highest values occurring before mid-May (Fig. 11)*. Therefore, it is clear that active phytoplankton growth occurs during the period January–April, although chlorophyll concentrations typically remain low. The suppression of significant biomass accumulation could be partly explained by dilution within FSW and subsequently exchange across the FSF.

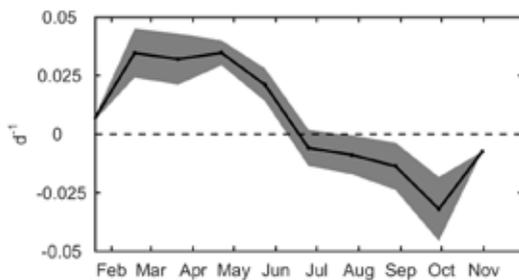


Fig. 11 Average net growth rate, G_p , at Station S. $G_p = \ln(chl_{t_1}/chl_{t_2})/\Delta t$, computed from chl observations sampled less than 13 days apart in the period 1997–2016 (Fig. 2b) and subsequently grouped into monthly bins and averaged. The shaded areas indicate ± 1 standard error.

A transition in hydrography occurs around May as stratification takes place on the outer shelf (see section 3.2.2). Following this transition, the effect of shelf exchange on bloom dynamics remains ambiguous. Although exchange can still potentially dilute phytoplankton biomass on the shallowest part of the shelf, it may also import phytoplankton from the upper stratified layer of the OS and deliver nutrients from the lower layer, stimulating further production (Fig. 2b).

3.2.2 The effect of the Faroe Shelf Front and interaction with the Outer Shelf

Heat induced stratification typically occurs on the OS during May (Figs. 2, 4 and 12 and Paper III and IV) and the onset of the spring bloom on the CS occurs during this transition (Paper IV). The hydrographical transition occurring over the months April–June is forced by atmospheric heating of the ocean. During winter, air-sea heat fluxes are negative and convective mixing is strong (Fig. 2a). At some stage during spring there is a shift that results in positive air-sea heat fluxes and the onset of stratification (Fig. 2b). Exceptions occur in areas where the action of tidal currents, wind and waves continue to mix the entire water column. As the FSF encroaches shoreward in April–June, stratification on the OS is accompanied by a reduction in the total volume of CS waters (Fig. 12). Assuming that the mixing across the FSF is less than horizontal mixing within the CS, a reduction of CS volume will result in a decrease in the average depth of CS waters. This would result in a more favourable light climate in CS waters by increased average amount of PAR received by individual cells, exerting a net positive effect on phytoplankton growth. The CS volume was estimated based on temperature data from the HYCOM model. Lateral heat transport, i.e. the heat exchange between the shallowest and the deeper part of the shelf, was estimated based on temperature observations at coastal Station O and air-sea heat flux reanalysis data (Paper IV).

The seasonal progression of PAR, air-sea heat flux, lateral heat flux, CS volume and chlorophyll are presented in Fig. 13. As expected, PAR increases smoothly throughout the spring, although it is difficult to identify a specific threshold that corresponds to bloom onset, even when investigating the individual years. In contrast, bloom initiation (threshold of 1 mg chl m⁻³ (Paper IV)) always occurs after the shift of air-sea heat fluxes to a positive state and the development of negative lateral heat fluxes. The volume of the CS water mass also decreases and follows closely the lateral heat flux. A negative lateral heat flux implies that cold water is imported onto the CS, presumably from a newly established cold pool (Fig. 2b). These data suggest that a decreasing volume of well mixed water which coincides with the establishment of a cold pool promotes bloom development on the CS. Study of the individual years shows that increasing chl concentrations often co-occur with

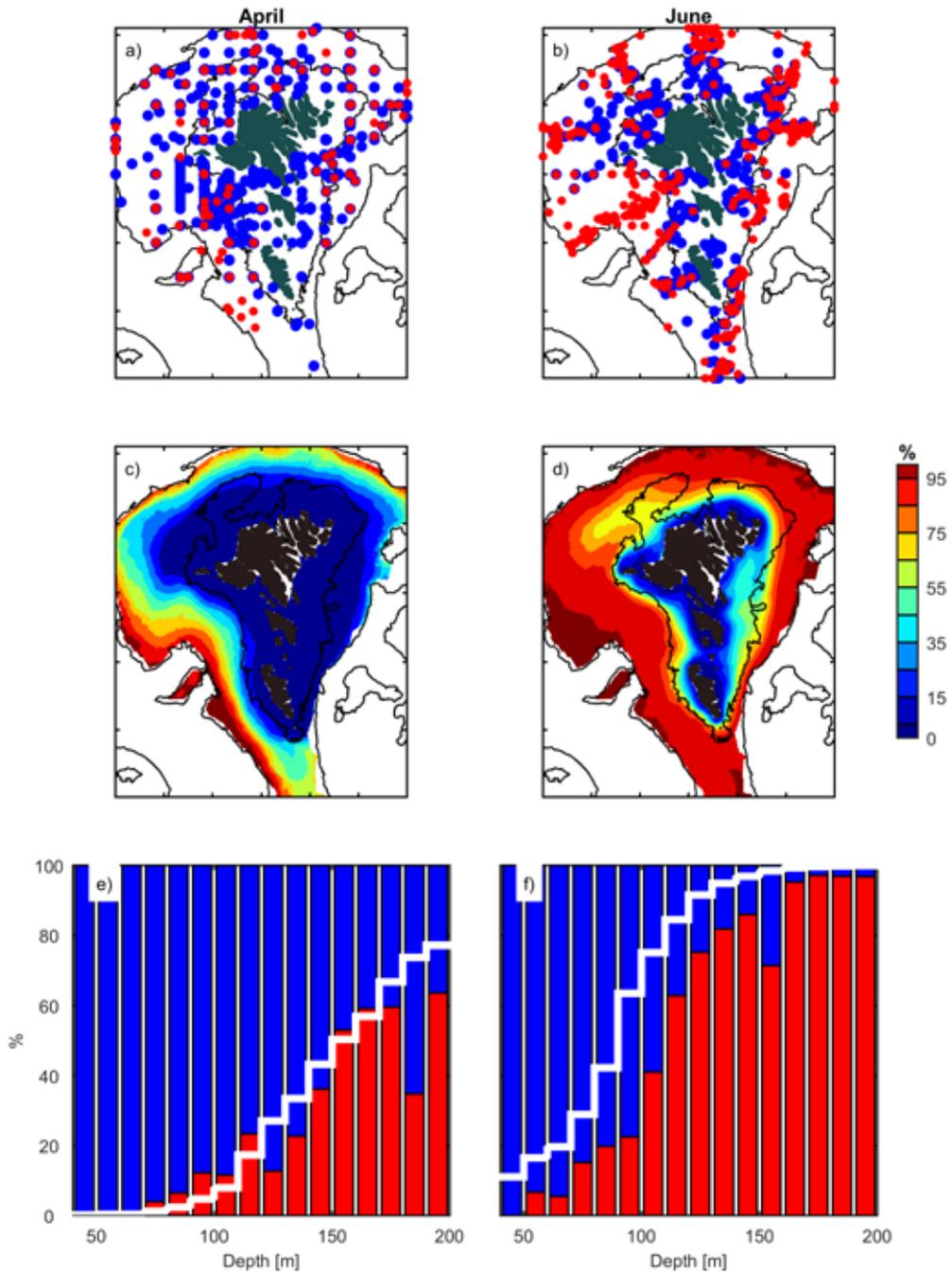


Fig. 12 CTD-profiles (1990–2016) and simulations (2000–2009) in April (left panels) and June (right panels) sorted according to whether they were stratified (red) or unstratified (blue). a-b CTD-profiles, c-d) relative distribution of all modelled profiles, e-f) Relative distribution of stratified and unstratified CTD-profiles as a function of depth. The corresponding distribution in the model is indicated by the jagged white line. The 100 m and 200 m isobaths are shown in panels a-d. (Fig. 3 in Paper IV).

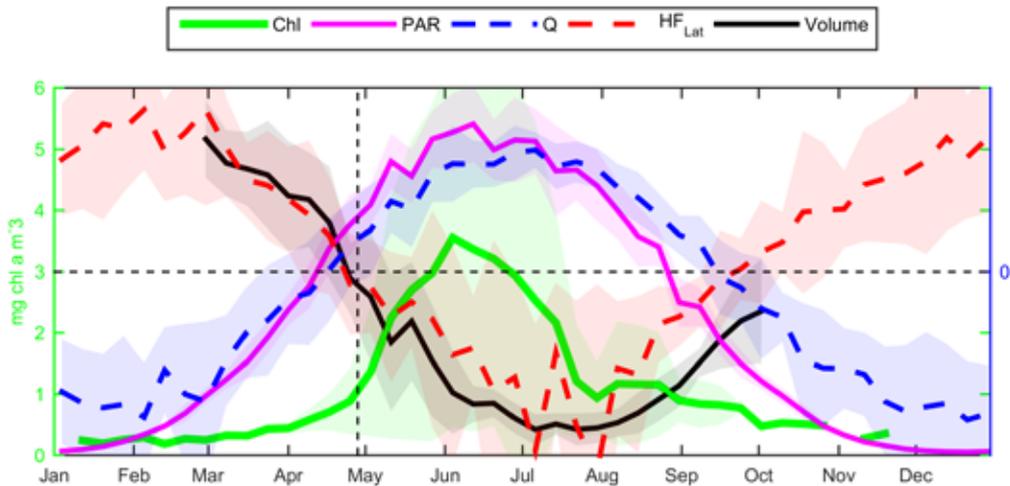


Fig. 13 Chl at Station S, averaged over 1997–2016 and averages of PAR, air-sea heat flux (Q), lateral heat flux, (HF_{lat}) (averaged over 1997–2016) and estimated volume of the CS water mass, (based on the HYCOM model 2000–2009). Only chl is to scale and the parameters that fluctuate around zero are plotted with dashed lines (right axis). The vertical black dashed line indicates the shift from positive to negative lateral heat flux, which also coincides with chl increasing above 1 mg chl m^{-3} . Shades indicate ± 1 standard deviation. (Average of Fig. S1 in Paper IV).

a dramatic decrease in volume (Fig. 8 in Paper IV). Also it seems that a rapid and/or early transition results in larger and more rapid increase in net chl biomass than a slow and/or late transition (Paper IV, figs 5 and S1). Despite this general picture the exact dynamics of these processes remain poorly constrained and it represents an intriguing avenue for future research.

To further illustrate the spatial structure of summer phytoplankton blooms on the Faroe Shelf, a snapshot of the hydrographic conditions following the bloom peak of 2007 is shown in Fig. 14*. With the exception of Section h), which is stratified at 75 m depth, the CS water mass is generally constrained within the 80 m isobath. The cold pool is seen as the water mass with temperatures $< 8.6 \text{ }^\circ\text{C}$. CS water is low in chl, whereas high concentrations are observed in the upper, generally less than 50 m thick, stratified layer on the OS.

Tidal currents in the vicinity of Station S are on average 1 m s^{-1} and it therefore remains possible that strong turbulence can affect phytoplankton biomass accumulation. However, this only occurs on rare occasions when tidal current speeds are at their most extreme (i.e. U^3 averaged over two days $> 4.3 \text{ m}^3 \text{ s}^{-3}$, Paper IV). In general the onset of the spring bloom occurs when tidal current speeds are not extreme and although strong tidal currents can

disturb bloom development, moderate and meek currents appear to have no effect.

3.2.3 The effect of silicate limitation

A relationship between short term increases in phytoplankton growth at Station S and the degree of stratification on the OS after the hydrographical transition (Section 3.2.2) is described in Paper III. Nitrate and silicate concentrations at Station S often reach low concentrations during the growth season. Silicate, a micronutrient essential for diatom growth, typically falls below $2.0 \text{ } \mu\text{M}$ between late May and early June (Fig. 9 in Paper III). Nitrate concentrations reach their lowest values later in the year and rarely decrease beyond $4 \text{ } \mu\text{M}$. At Station S, silicate concentrations associated with chl peaks in late May – June are always around the $2.0 \text{ } \mu\text{M}$ mark (Fig. 15 and Paper III). At this time diatom blooms are terminated by silicate limitation and there is probably a shift to smaller, non-blooming diatom species and/or non siliceous phytoplankton.

In May–June, a nutrient rich cold pool develops on the OS (Figs. 4 and 14) and exchange between the OS and CS results in cooler CS waters, represented as a negative lateral heat flux (Fig. 13). During this time nutrient concentrations are at their lowest values. However, model and *in-situ*

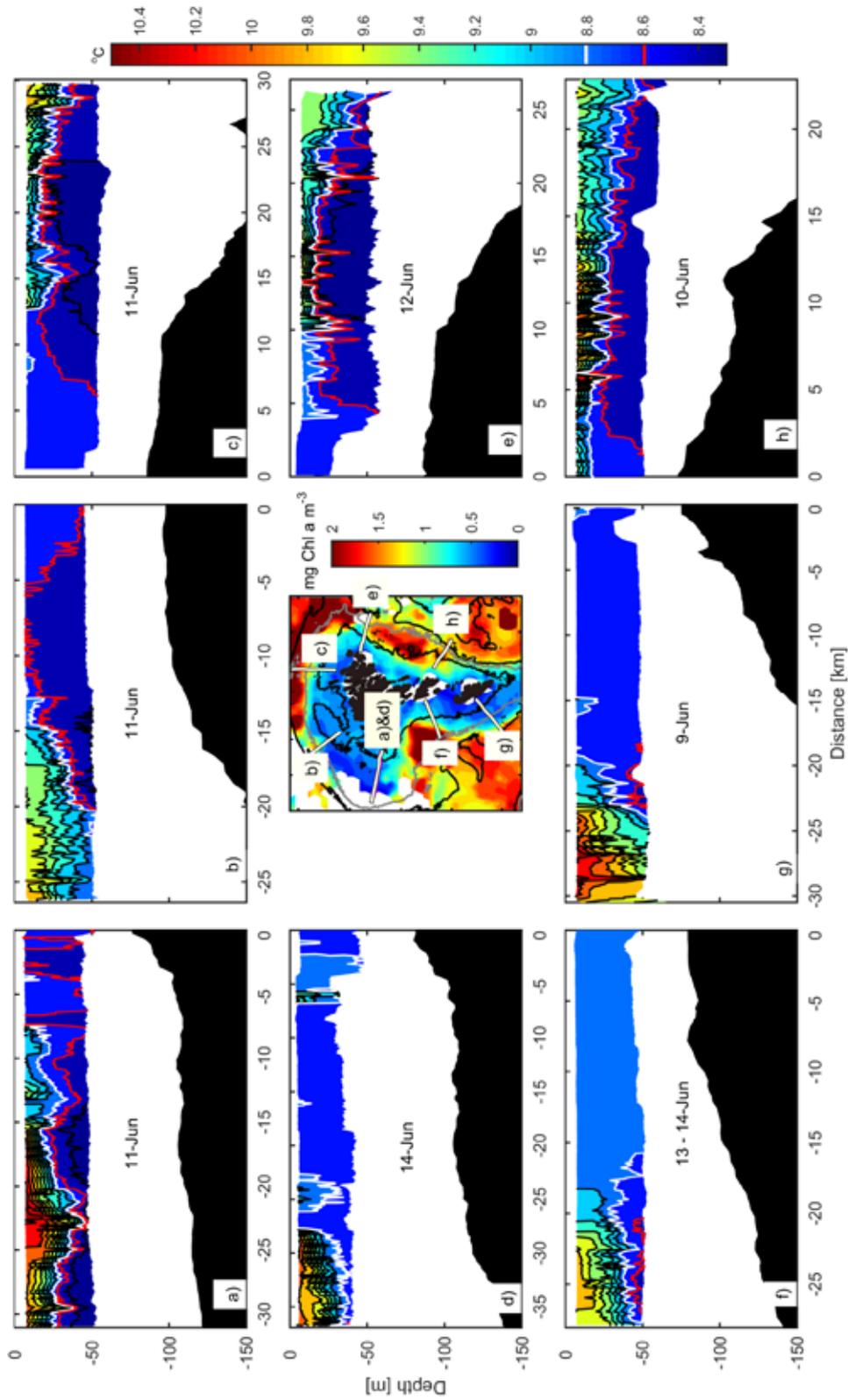


Fig. 14 Snapshot of surface chl 10–17 June, 2007 (centre) and vertical temperature sections 9–14 June, 2007 (a–h). On sections a–h, black isotherms are plotted for every 0.2 °C, with a red and white isotherm indicating 8.6 °C and 8.8 °C, respectively. Temperature data are obtained by a Towed Temperature Wire (TTW) and were collected by RV Magnus Heinason (Larsen et al., 2009).

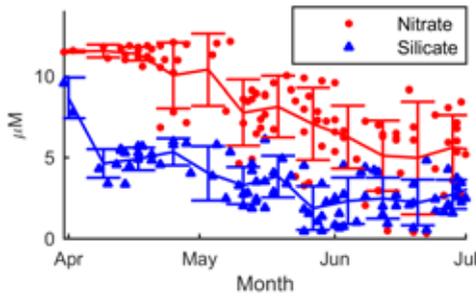


Fig. 15 Nitrate and silicate concentrations associated with chl peaks at Station S. The averages are computed for 8-days periods and the error bars indicate ± 1 standard deviation. The samples are from the years 1995–2015 (no silicate observations were available for 2006 and 2008). (Fig. S6 in Paper III).

data both show that heat losses out of the ocean and weakening stratification correspond to a feature of increasing chl concentrations at Station S. These short term increases in chl at Station S may be explained by nutrient supply from the cold pool (Fig. 2b) as frontal erosion admixes high nutrient water to the CS (Paper III).

3.3 Ecological implications

The present study has delineated several biogeographical zones on the Faroe shelf. Correct consideration of this zonation is critical when addressing the dynamics of several fish stocks on the shelf. For example, a study on the diet of saithe (*Pollachius virens*) on the Faroe Shelf in summer (Homrum *et al.*, 2012) found the forage fish blue whiting (*Micromesistius poutassou*), in stomachs of specimens caught on the OS and Norway pout (*Trisopterus esmarkii*) in those caught inside the CS area. The EB is a spawning ground for saithe (Homrum *et al.*, 2012) and used to be a spawning ground for the now-absent Atlanto-scandian herring (*Clupea harengus*) (Joensen, 1966). Both of these fish species spawn in February, 1–2 months earlier than cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). Cod spawns at the interface between the WR and the CS and north of the Islands, peaking in the second half of March (Steingrund and Gaard, 2005), whilst haddock spawns more widely on both sides of the southern half of the shelf from March to May (Gaard and Reinert, 2002). Thus, the early increase in phytoplankton concentrations on the EB could

explain why this region is a preferred area for the saithe and herring juveniles. These examples demonstrate that the three regions identified in this study are not only distinct when it comes to phytoplankton bloom phenology, but also for commercially important fish stocks – the two clearly linked through trophic dynamics.

3.3.1 Spatial and temporal variations in zooplankton on the Faroe Shelf in April

Spatial and temporal variations in zooplankton on the Faroe Shelf in late April (1997–2016) were investigated in Paper V. Seven major groups were enumerated (Neritic species, Meroplankton, Copepod egg, Copepod nauplii, *C. finmarchicus* CI-CIII (Recruits), *C. finmarchicus* CIV-CVI (adults) and everything else grouped as Other), and of those groups Neritic species, Meroplankton and Copepod eggs were most abundant on the CS (Fig. 16 a,f,g). The abundance of neritic species displays a tight correlation with chl concentration on the CS (Fig. 17).

The *C. finmarchicus*, Copepod nauplii, Copepod egg and Other were found in high abundances in areas with bottom depths greater than ~200 m, and in particular on the outskirts of the western side of the OS (Fig. 16 a-e). *C. finmarchicus*, which is often considered an important species in marine ecosystems due to its relatively large size and high lipid content, hibernates during the winter in the deep oceanic gyres west and northeast of the Faroe Shelf. They ascend in spring and can reach the Faroe Shelf either from the subpolar gyre in the west or from the Norwegian Sea through the deep overflow through the Faroe-Shetland Channel and Faroe Bank Channel. The highest abundances found in the surface layers of the Faroe Bank channel are therefore consistent with the known life history of *C. finmarchicus* as it is an area where individuals both ascend from the deep overflow and are advected by the surface currents.

The ratio between the numbers of adults and recruits of *C. finmarchicus* highlights a phenology shift around 2007, after which, spawning and thus probably also ascension from the diapause occurs earlier. Unfortunately the factors responsible for this shift remain elusive. However, it is of note that a similar shift in the phenology of *C. finmarchicus* has been reported north of the Faroe Islands in the southwest Norwegian Sea in 2003 (Kristiansen *et al.*, 2015). This shift was proposed to be caused by

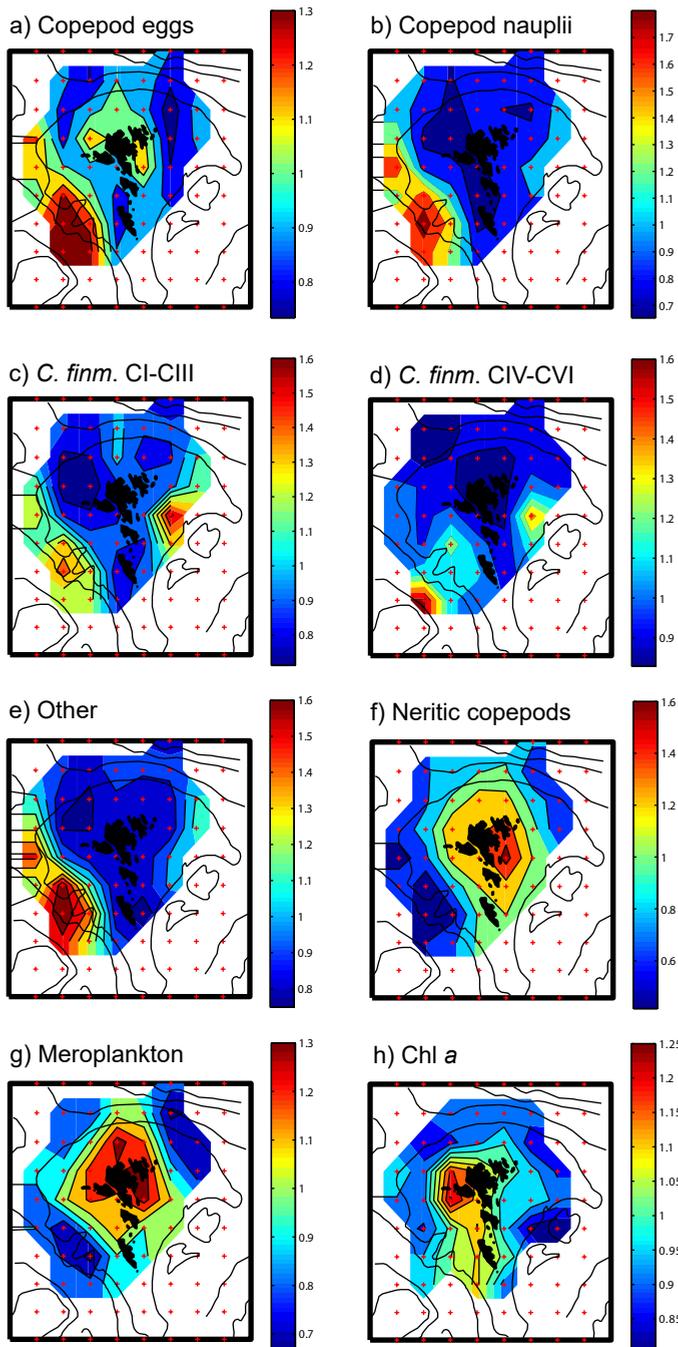


Fig. 16 Average late April distributions (1997–2016) of zooplankton species groups (a-g) and chl (h) in the uppermost 50 m. The data have been normalized and are thus without units. (Fig. 5 in Paper V).

a westward retraction of the zooplankton rich cold and low-saline East Icelandic Water. It is intriguing that phenology shifts in *C. finmarchicus* have not

been observed in the CS area (Paper V) and the exact mechanisms behind these dynamics represent an important area for future studies.

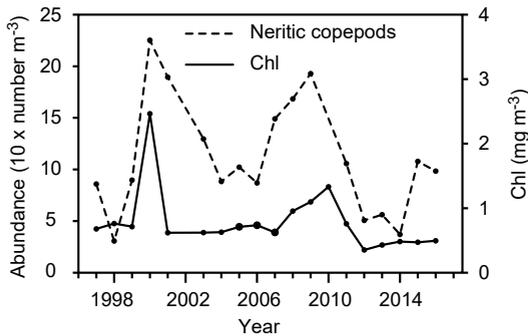


Fig. 17 Average (0–50 m) abundance of Neritic copepods and chl concentration in the CS in late April 1997–2016. (Fig. 10 in Paper V).

3.3.2 The Outer Shelf and similarities with the European margin

Annual means of chl concentrations in the WR correlate with the annual mean chl on the Northwest Scottish shelf (Fig. 18). Since variations in primary production along the European margin have been linked to variations in oceanic nutrient influxes (Holt *et al.* 2012), it is likely that large-

scale oceanic variability also impacts the adjacent Faroe Shelf. The relative contribution of WNAW and ENAW determines the properties of MNAW, which flows past both shelves (Fig. 1a). Therefore a better understanding of the Northeastern Atlantic climate is an important prerequisite to fully describe dynamics of the Faroe Shelf ecosystem. Common atmospheric forcing of both neighbouring shelves can furthermore contribute to the similar chl variability.

3.3.3 *Calanus finmarchicus* and mackerel in the Northeast Atlantic

Mackerel (*Scorpaenidae*) has significantly expanded its feeding area in the Northeast Atlantic since 2006 (Nøttestad *et al.*, 2016; Olafsdottir *et al.*, 2015). Two main reasons have been evoked previously to explain this expansion: increased temperatures and high densities of fish in the steadily growing stock. As a contribution to this discussion, the larger scale implications of changes in nutrient concentrations with respect to spatial and temporal variations in mackerel distribution were investigated in Paper VI.

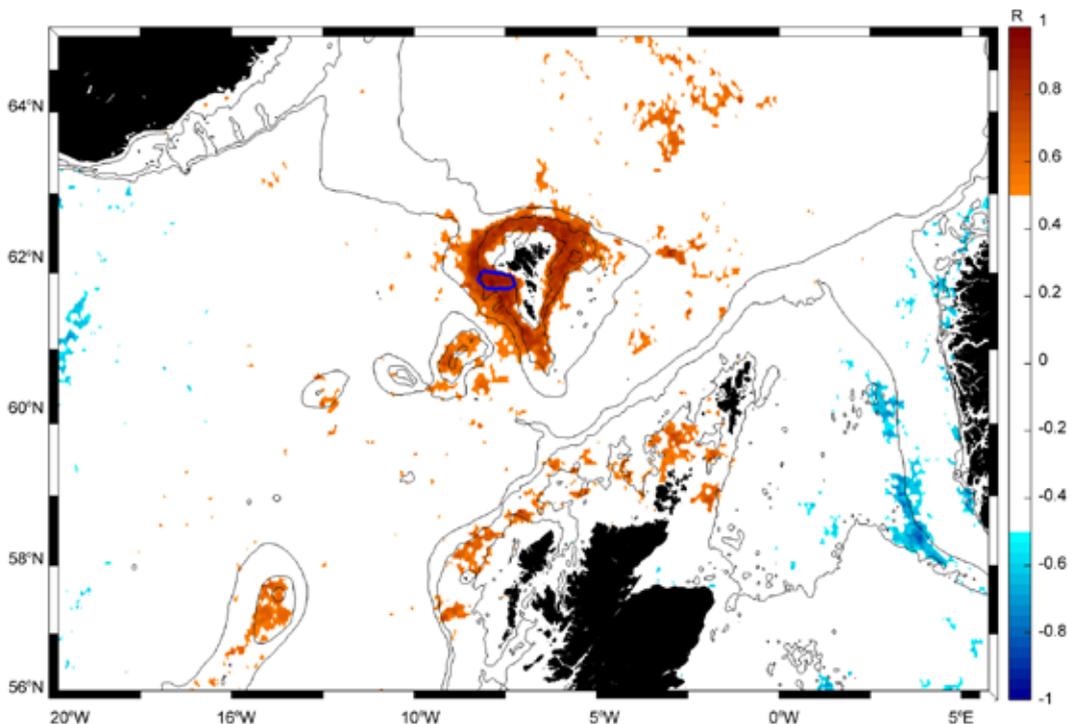


Fig. 18 Correlations between annual chl concentrations in the WR and in the Northeast Atlantic. Only $|R| > 0.5$ is shown. (Fig. 8 in Paper II).

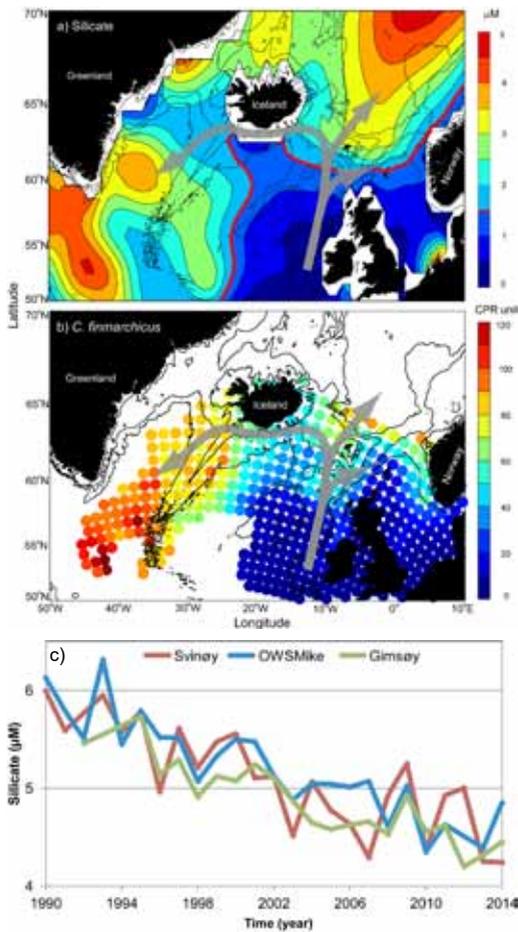


Fig. 19 Average silicate concentration at 50 m depths in June, (1960–2013) (a), average near-surface *C. finmarchicus* abundances (1958–2005) (b), and winter silicate concentrations at three stations along the Norwegian Slope (c). The general mackerel feeding migration is illustrated with gray arrows in panel a) and b). Fig. 2 and 7 in Paper VI.

There is a coarse spatial overlap between average silicate concentrations $> 2 \mu\text{M}$ in June and the high average abundance of *C. finmarchicus* in the Northeast Atlantic (Fig. 19a-b). The reason for this positive relationship is attributed to the fact that *C. finmarchicus*' preferred food item, diatoms, are dependent on silicate to build their frustules. Three time series along the Norwegian slope all display a trend of decreasing winter silicate concentrations from $\sim 6 \mu\text{M}$ in 1990 to $\sim 4.5 \mu\text{M}$ in 2014 (Fig. 19c). It is likely that this decrease is propagated through the food chain and may explain why mackerel, which prefers to feed on *C. finmarchicus*, are migrating

further westwards. Although mackerel has expanded its feeding area, it remains largely absent from the Iceland Basin, where both silicate concentrations and zooplankton abundances are on average low, but rather migrates along the southern Iceland Shelf to the area west of Iceland. These patterns suggest that basin scale shifts in nutrient inventories can influence upper trophic level dynamics. It is also probable that changes in nutrient composition will impact phytoplankton growth on both the Faroe and European Shelves, with important ramifications for other commercially important fish stocks.

4 Summary and outlook

4.1 Summary

Below follows a short list of the main findings in this study.

Three distinct regions on the Faroe Shelf have been identified with regard to phytoplankton bloom dynamics:

- The Central Shelf (CS): characterised by a vertically well mixed water column and phytoplankton blooms that on average occur in May.
- The seasonally stratified Outer Shelf (OS): blooms later than the CS, but exhibits persistently high surface chl values from June to August. The strong and persistent growth observed during summer is likely attributed to a shallow upper layer and/or continuous nutrient resupply in the frontal mixing zone. In particular the Western Region (WR) stands out as a highly productive area within the OS.
- The seasonally stratified Eastern Banks (EB): blooms early in the season with moderate chlorophyll values throughout the summer. The extent of biomass accumulation is controlled by a thick upper mixed layer and strong stratification, which limits nutrient renewal.

The average exchange rate between the shallow and the deeper parts of the shelf has been constrained

and variations in exchange were found to impact the phytoplankton growth on the Faroe Shelf prior to the onset of spring bloom.

A marked hydrographical transition occurs on the Faroe Shelf every spring (typically in May) when the OS becomes persistently stratified, causing the volume of the well mixed CS water mass to decrease.

The hydrographical transition has been linked to the onset of the CS spring bloom. The reduction in volume of the CS water mass is hypothesized to induce a more favourable light climate for phytoplankton growth. A rapid, and possibly early, transition appears to favour significant biomass development on the CS.

The diatom-dominated phytoplankton bloom on the CS usually becomes silicate limited in late May – early June, following the hydrographical transition, and continued growth depends on nutrient resupply from the OS cold pool.

In the period following the hydrographical transition a link was identified between intermittent short term increases in phytoplankton biomass on the CS and heat loss out of the ocean. It is hypothesized that heat loss causes erosion of the innermost part of the OS stratification, and thereby nutrients from the lower OS layer are admixed to the CS, and bloom development further promoted.

Persistent phytoplankton growth on the OS following stratification is hypothesized to result from favourable diapycnal mixing conditions that delays the onset of nutrient limitation.

Similar large scale patterns in phytoplankton biomass on the OS and European Margin suggest basin-scale forcing is an important factor in explaining the dynamics of adjacent shelf systems in the Subpolar Atlantic.

4.2 Outlook

In order to further develop our understanding on the interaction between oceanic waters, the OS and the CS, the following questions should be addressed:

- How significant are short term variations in the exchange rate?

- Are there certain main passages through which water is imported and exported?
- What is the relative importance of the upper and lower OS layer for exchanges between the OS and CS?
- How does frontal mixing supply nutrients to the CS and the upper layer of the OS?
- Why is the Western Region the most productive area on the OS during summer?
- Investigation of the hydrographical transition: Is a rapid and early transition more beneficial for the bloom development than a slow/late transition?

With regards to biology, further knowledge of ecosystems dynamics is required and the following questions should be addressed:

- What is the grazing impact of zooplankton groups other than copepods on the phytoplankton community?
- What is the significance of benthic-pelagic coupling for Faroe Shelf ecosystem dynamics?
- The transfer of photosynthetically-fixed carbon to higher trophic levels and the bathypelagic ocean is crucial for a complete understanding of the climate system and ecosystem dynamics. How important is phytoplankton species composition for regulating nutrient:carbon and carbon:chl ratios?

The present study has identified bio-geographical zones on the Faroe Shelf, detailed the importance of stratification, nutrient limitation and described the interaction of shelf waters with surrounding oceanic waters. This has allowed a more complete understanding of the factors regulating the Faroe Shelf bloom dynamics. However, a complete explanation for the strong interannual variability of the Faroe Shelf primary production and trophic dynamics remains somewhat elusive. Further resources should be allocated to pursue these questions that are of critical importance for the understanding of the Faroe Shelf marine environment.

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