



Research papers

Faroe shelf bloom phenology – The importance of ocean-to-shelf silicate fluxes



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A B S T R A C T

The highly variable primary production on the spatially confined Faroe shelf has been comprehensively monitored since the early 1990s. Utilizing these data together with output from a realistic high-resolution numerical model, we here give a unique description of an interplay between bloom phenology in a productive temperate well mixed Central Shelf and the mixed layer dynamics in a surrounding seasonally stratified Outer Shelf. There is a shift to a persistently stratified Outer Shelf during late May – early June, which thereafter holds the highest phytoplankton biomass and becomes nutrient limited in the upper layer. The Central Shelf chlorophyll accumulation becomes impeded around this transition, which is coincident with strong silicate drawdown. Subsequently, a succession of blooms can occur, and these coincide with nutrient enriching erosion of the Outer Shelf stratification and become terminated by re-establishments of the stratification. We hypothesize that the mixed layer dynamics of the Outer Shelf regulates the lateral nutrient fluxes to the Central Shelf.

1. Introduction

The continuance of phytoplankton blooms is highly dependent on the availability of nutrients, and the seasonal development of a shallow upper mixed layer will drastically reduce the supply of nutrients to the photic layer. Classically, the upper layer on a continental shelf is resupplied with nutrients via the fortnightly strengthening and weakening of the tidal currents (Simpson and Sharples, 2012) or other mixing through the pycnocline (Chen and Beardsley, 1998; Franks and Chen, 1996). The refuelling of the tidally well-mixed shelf waters on the other hand relies on lateral exchanges with the surrounding waters and contributions from nutrient recycling and riverine inputs. Depending on the dynamics and nutrient concentrations of the surrounding deeper waters the lateral nutrient fluxes vary, both intra-seasonally as well as interannually, and this likely affects the phenology of the phytoplankton bloom.

The Faroe shelf (Fig. 1a) is embedded in the relatively warm Modified North Atlantic Water (MNAW) (Hansen and Østerhus, 2000), produced by the confluence of the hydrographically and biogeochemically contrasting Eastern and Western Atlantic water masses west of the British Isles (Holliday, 2003; Hátún et al., 2005; McGrath et al., 2012). Studies from the northwest European shelf highlight the importance of ocean-to-shelf nutrient fluxes to the on-shelf phytoplankton production (Holt et al., 2012). Both the European

(Holt et al., 2012) and the Faroe (Rasmussen et al., 2014) shelves are characterized by a net downwelling, with on-shelf flow in the upper layer, and a near-bottom off-shelf Ekman transport. Both studies suggest that the short term mixed layer dynamics and the upper layer primary production in the seasonally stratified outer shelves might impact the nutrient exchange rate between the shelf and the off-shelf water masses.

The Faroe shelf is characterized by strong tidal currents with a clockwise residual flow (Larsen et al., 2008). The Faroe Shelf Front separates the Faroe Shelf Water on the Central Shelf (CS, gray area in Fig. 1a) from the surrounding water mass (Larsen et al., 2009). Due to effective atmospheric cooling, both water masses are vertically well mixed during the winter. When the atmosphere adds heat to the ocean during spring and summer, the relatively quiescent Outer Shelf (OS) becomes stratified (Eliassen et al., 2017), whereas the tidal currents keep the shallower CS vertically well mixed out to about 100 m depths. The spring bloom onset is generally explained by the critical depth hypothesis (Sverdrup, 1953), where after the continued development of the bloom is regulated by the availability of nutrients (Chiswell et al., 2015) and the grazing pressure (Behrenfeld and Boss, 2014).

The conditions of commercial fish stocks and seabird populations on the Faroe Shelf have been linked to interannual variations in net new production of phytoplankton, proxied by a Primary Production Index (PPI, Fig. 2) (e.g. Eliassen et al., 2011; Gaard et al., 2002, 1998).

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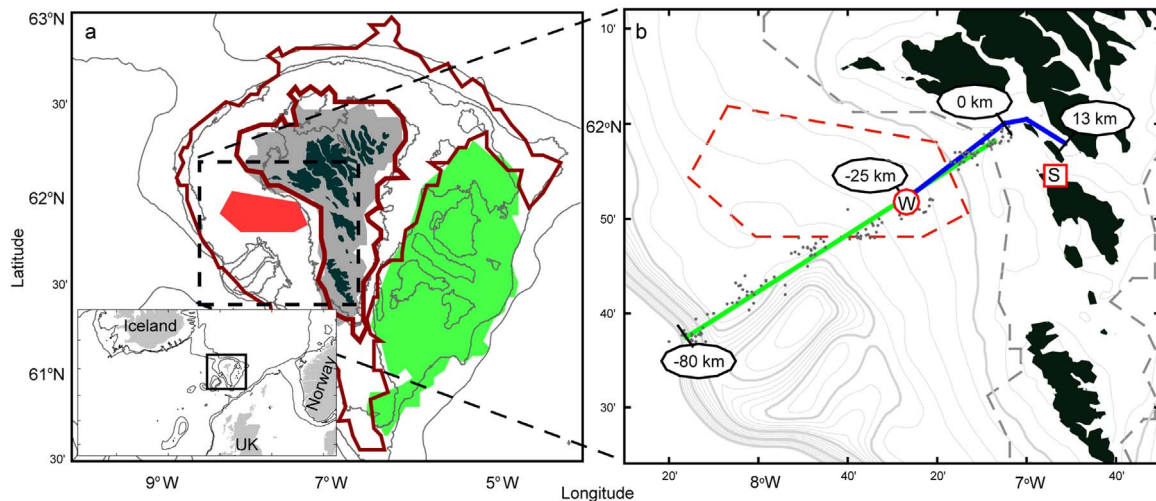


Fig. 1. The Faroe Shelf. a) Three domains on the Faroe shelf, with unique chl variability (Eliassen et al., 2017). The Central Shelf (CS, gray), the Eastern Banks (green) and the core of the Western Region (WR, red) are shown. The Outer Shelf is demarked by the dark red lines. The 100 m, 200 m, 300 m and 500 m isobaths are shown. A geographical overview is given in the inset. The study region is highlighted by the dashed rectangle. b) Map of the sampling area. Section I (green line) and Section II (blue line) are shown with encircled numbers indicating section distances. Gray dots show the sampling stations along the sections. The dashed gray and red lines encircle the CS and the core of the WR, respectively. Isobaths in the range 60 m to 500 m are plotted with 20 m intervals with every 100 m in thicker lines. S and W indicate coastal Station S and wave-buoy mooring W, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

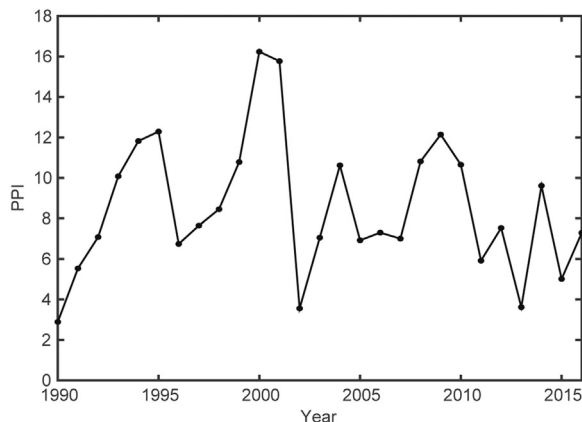


Fig. 2. Primary Production Index (PPI) 1990–2016. The index is based on the nitrate drawdown from winter to late June at two stations on the shelf and an estimate of net inflow of nitrate. Updated from Gaard et al. (2002) and described in Gaard et al. (2002) and Steingrund and Gaard (2005). The index is commonly used together with other ecosystem indicators.

Being an acknowledged primary production indicator, this time series is invoked below when interpreting multiannual plots.

Since 1997, phytoplankton abundance has been monitored weekly at coastal Station S (Fig. 1b) during April – August by measurements of chlorophyll *a* (chl) concentrations. This time series displays large seasonal and interannual variations – the annual maximum at Station S varies by a factor of 10 (Gaard, 2003), and the date of onset of the bloom by at least a month (Gaard et al., 1998). Although photosynthetically active radiation (PAR) is necessary for phytoplankton growth, variations in light are not found to be a controlling factor in the observed seasonal pattern (Debes et al., 2008b; Eliassen et al., 2016; Gaard et al., 1998). A study from 2004 estimates the copepod grazing impact to never exceed 3% of the total phytoplankton biomass (Debes et al., 2008a), however, grazing by other zooplankton groups has hitherto not been investigated on the shelf.

Attempts to explain the interannual variation in phytoplankton abundances at Station S have led to an *exchange-hypothesis*, which suggests that variable cross-shelf exchange dilutes the phytoplankton biomass inside the tidal front, and thus induces variations in the phytoplankton accumulation (Hansen et al., 2005; Eliassen et al., 2005,

2016). This mechanism seems to explain some of the variability prior to June (Eliassen et al., 2016), after which nutrient depletion and grazing possibly become more important limiting factors (Debes et al., 2008a, 2008b; Djurhuus et al., 2015).

With regards to intra-seasonal chl variability, Hansen et al. (2010) found that the 2008–2009 blooms co-varied with air-sea heat exchanges and they propose a coupling between the northern and southern parts of the CS, where the CS normally behaves as a coherent water mass, but where the southern part occasionally disconnects from the north. Shifts between these two states are suggested to induce irregular phytoplankton variability. Further, a model study (Rasmussen et al., 2014) suggests that an early establishment of a shallow mixed layer on the seasonally stratified OS can result in high production by generating blooms along the frontal area, which then seed the CS primary production.

Four independent studies from the shallowest part of the Faroe Shelf (Debes et al., 2008b; Djurhuus et al., 2015; Gaard et al., 1998; Jacobsen, 2015) show that diatoms dominate phytoplankton biomass throughout the spring and summer. Occasionally the flagellate abundance is high ($> 10^5$ cells L^{-1}), but the resulting chl concentration is always < 2 mg chl m^{-3} and chl levels > 2 mg chl m^{-3} are always associated with elevated diatom abundance. Diatoms need silicate to build their frustules. Winter concentrations of nitrate and silicate on the Faroe Shelf are ~ 12 μM and ~ 5 – 7 μM , respectively (i.e. a Si:N ratio of $\sim 1:2$) (Gaard et al., 1998; Djurhuus et al., 2015). The diatom Si:N ratio (Brzezinski, 1985) implies that silicate and nitrate are consumed at roughly equal rates, and silicate limitation should therefore be reached before nitrate depletion. In 2004, 2005 (Debes et al., 2008b) and 2010 (Djurhuus et al., 2015), there was a community shift from dominance of large fast-growing diatoms, to smaller diatoms and/or flagellates and other smaller species, when the silicate concentration reached 2 μM , which often is considered as growth inhibiting for diatoms as a group in the subpolar Atlantic (Egge and Aksnes, 1992; Allen et al., 2005; Brown et al., 2003). Also, the main community shift on the CS is observed to be followed by a drop in chl (Djurhuus et al., 2015). The most productive years (1995, 2000, 2001) were, however, characterized by nitrate dropping to almost zero (Steingrund and Gaard, 2005). Thus, nitrate and silicate are considered the most important nutrients on the Faroe Shelf. Phosphate is not found to control or inhibit the phytoplankton biomass accumulation on the

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