Phytoplankton community structure on the Faroe Shelf

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Úrtak

Kanningar vórðu gjørdar í 1995 av plantuplankton, og ymiskum viðurskiftum í sjónum, ið ávirkaðu gróðurin á Landgrunninum. Sjógvurin í innara parti av Landgrunninum er rættiliga væl avbyrgdur frá sjónum uttanfyri og tí hevur innari parturin av Landgrunninum eina vistskipan av plankton, ið fyri stóran part er skild frá teirri, ið er á opnum havi. Stórur munur er á plantuplanktoninum á Landgrunninum og uttanfyri og bæði sløgini og nøgdirnar av plantuplankton og umstøðurnar fyri gróður eru heilt øðrvísi á Landgruninum enn uttanfyri. Várgróðurin í 1995 kom á Landgrunninum seinast í apríl-fyrst í mai. Hetta var umleið ein mánaða áðrenn gróðurin kom úti á opnum havi. Várgróðurin kom fyrst í norðara parti av Landgrunninum og síðan í syðra parti. Nøgdin av sjógvi – og tí eisini av tøðevnum – á Landgrunninum er rættiliga avmarkað, og tíðliga í juli 1995 var alt nitratið í mið- og norðara parti av Landgrunninum brúkt upp. Tað ið eftir var av sumrinum var tann nýggi gróðurin tí avmarkaður til tey tøðevnini, ið róku inn á Landgrunnin uttaneftir. Í várgróðrinum var mest gjørt av kiselalguni, *Thalassoisira nordenskioeldii* og nakað minni av øðrum sløgum, m.a. *Rhizosolenia sp.*, men í seinnu helvt av mai mánaða tók *Phaeocystis pouchetii* (Prymnesiophyceae) yvir. Hetta vardi til umleið tíðliga í august mánað, tá nøgdirnar av planktonalgum minkaðu nógv, samstundis sum nøgdirnar av tøðsøltum aftur hækkaðu á Landgrunninum.

Abstract

The phytoplankton distribution, biomass and species composition were investigated in relation to the hydrographical and chemical environment for the algae on the Faroe Shelf during 1995. The water on the Faroe Shelf is relatively well isolated from the surrounding waters by a tidal front, which surrounds the islands at about 100-130 m bottom depth. It has its own plankton ecosystem, which is separated and is quite different from that in the surrounding oceanic environment. The phytoplankton spring bloom developed in late April-early May in the shelf water which was about one month earlier than outside the tidal front. The spring bloom started in the central and the northern part of the shelf. The limited water mass on the shelf – and, hence, also the limited amount of nutrients – affected the potential new primary production and around mid July 1995, all the nitrate on the central and northern shelf had been assimilated. From mid July and throughout the rest of the summer, the potential new production was low and was dependent on advection of nutrients from outside the tidal front.

Introduction

The tidal currents on the Faroe Shelf are strong and the water column in the shallow parts is, therefore, fairly homogeneous from surface to bottom. This well-mixed water mass is termed the shelf water and is separated from the outer waters by a tidal front that usually is located at about 100-130 m bottom depth. The size of the shelf is about 60x80 NM and the area of the shelf water is about 8000-10000 km^2. There is an anticyclonic residual circulation of the shelf water with a typical speed of about 10-15 cm sec^{-1} (Hansen, 1992). The water outside the tidal front is traditionally ter-

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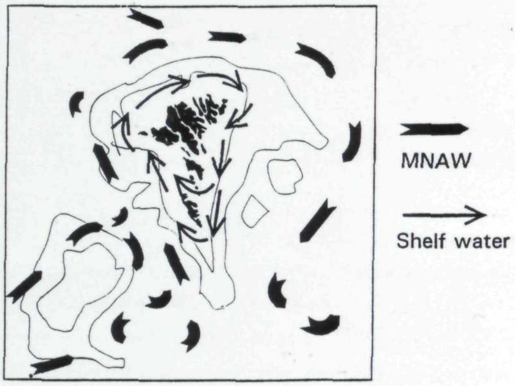


Fig. 1. *Bottom topography and main features of the flow field in the upper layers around the Faroes and on the Faroe Shelf. (Based on Hansen, 1992 and Hansen et al., 1994)*

med the Modified North Atlantic Water (MNAW) (Fig. 1).

These hydrographical circumstances cause quite different environmental conditions for the phytoplankton on the shelf compared to the outer areas. Inside the tidal front, the phytoplankton is relatively well isolated from the outer area with the water column well-mixed throughout the summer. Outside the tidal front, the hydrograpical conditions are typically oceanic with stratification of the water column during summer due to the development of a thermocline.

The Faroe Shelf water, therefore, has its own plankton ecosystem, separated from the surrounding area. It has its own phytoplankton community which is affected by quite different hydrographical, chemical and light conditions than the phytoplankton in the area outside the tidal front.

While the hydrography on the Faroe Shelf is relatively well described (Hansen, 1992; Hansen *et al*., 1994), no description of the phytoplankton community has been given. The aim of this paper is to describe the community on the Faroe Shelf in 1995 and to relate it to its hydrographical and chemical environment.

Material and methods

The study was conducted on 5 cruises from April to November 1995, with the Faroese Research vessel „Magnus Heinason". Sample collection and measurements were carried out of hydrography, nutrients, fluorescence, chlorophyll *a* and phytoplankton. In addition, samples for nutrient analysis and phytoplankton were collected from a monitoring station marked »S« on Fig. 5. This water was pumped through an underwater tunnel (0.8 m in diameter) from about 18 meters depth in an area with strong tidal currents and the samples were collected with 3 or 4 days intervals during the period May-December 1995.

On the research vessel the temperature and salinity (and hence the density) was in April 1995 measured with a EG&G Mark III CTD and from May 1995 and the rest of 1995 they were measured with a Seabird Electronics SBE911 + CTD. Both instruments were equipped with a rosette sampler.

Water samples were collected with Niskin bottles from the CTD rosette. The samples for analysis of nitrate and silicate were preserved with 3 drops of chloroform per 25 ml of sample immediately after sampling. Normally, they were stored in a refrigerator and analysed in the laboratory 3-15 days after sampling. However, in

June-July 1995, the nitrate samples were analysed on board the research vessel. On the monitoring station S the samples from May and June were frozen immediately after sampling. The other samples were preserved in chloroform, stored in a refrigerator and analysed 5-30 days after sampling. Nitrate and nitrite were measured automatically and silicate was analysed manually using the methods described by Grasshoff *et al*. (1983).

In situ fluorescence was measured with a Sea Tech fluorometer interfaced to the CTD and fluorescence was calibrated from selected samples which were analysed for chlorophyll *a*. The chlorophyll *a* measurements were carried out using the methods described by Baltic Marine Biologists (1979) with a difference in that the homogenisation was carried out with a Soniprep 140 ultrasound homogeniser. When computing the results, the equation of Jeffrey and Humphrey (1975) was applied.

The algae were preserved in 0.4% neutralised formaldehyde and were counted in 2, 5 or 10 ml of seawater after overnight settlement using an inverted microscope.

Results

The primary production in the Faroe Shelf water started earlier in spring and also declined earlier in autumn than outside the front (Fig. 2). The phytoplankton biomass during spring and summer was significantly higher in the Faroe Shelf water and in the frontal region than outside the front and at the same time the nutrient concentrations decreased much in this water and were much lower in the shelf water than in the open area outside the front.

The highest phytoplankton biomass in spring was found in the northern region of the shelf water (Fig. 3a) and the spring bloom, apparently, has started in this region. The primary production clearly affected the nutrient concentrations and they decreased very much in this area (Fig. 3.b). The results indicate that the water masses in the northern region were more isolated than in the southern region. This is also supported by the nutrient distribution in mid summer (Fig. 3c). The nitrate concentrations in the shallowest part in the northern region of the Faroe Shelf were between 2 and 3 μmol l^{-1}. The concentrations in the southern region were more than twice as high.

Both the nutrient gradients and the distribution pattern of the phytoplankton biomass were related to the hydrographic features (Fig. 4). The north-western transect showed strong horizontal density gradients in the frontal area and very high phytoplankton biomass above the pycnocline. However, in the eastern region, there was weaker thermal stratification, stronger vertical gradients, and low phytoplankton biomass outside the front.

The concentrations of nutrients in the central region of the shelf water (station S) decreased dramatically during spring and early summer 1995 (Fig. 5). The primary production in particular affected the nitrate concentrations, which decreased rapidly during early May and reached zero around mid July in the shallow areas. Only at the very beginning of the sampling period (ear-

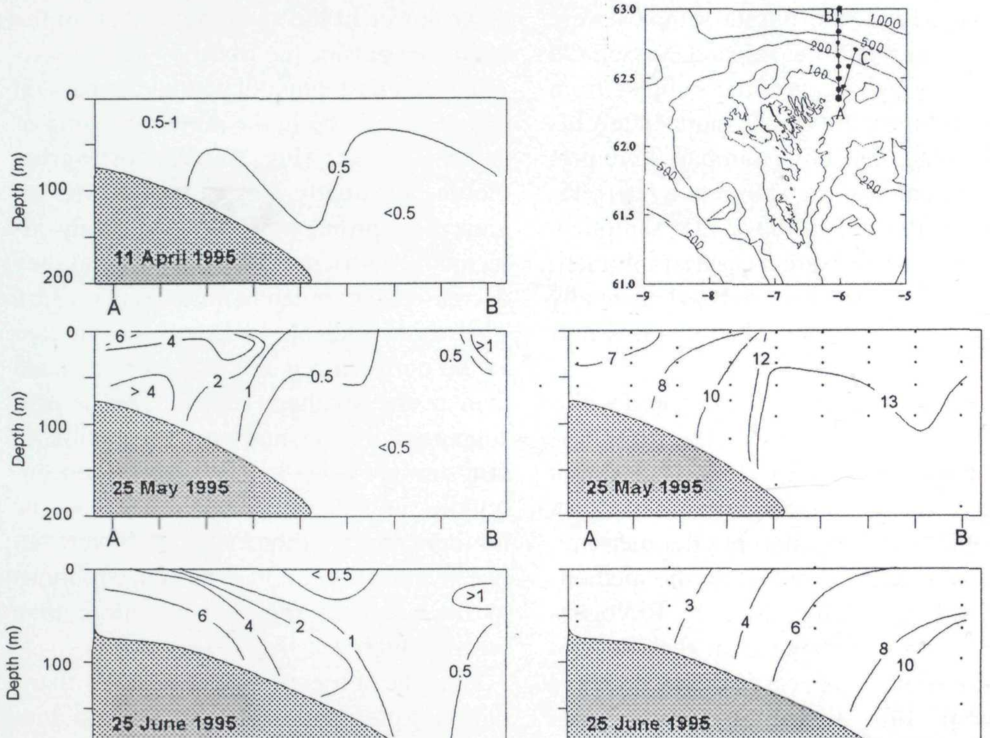


Fig. 2. *Vertical distributions of fluorescence (µg chl.* a *l*$^{-1}$*) and nitrate (µM) on transects A-B and A-C from April to November 1995.*

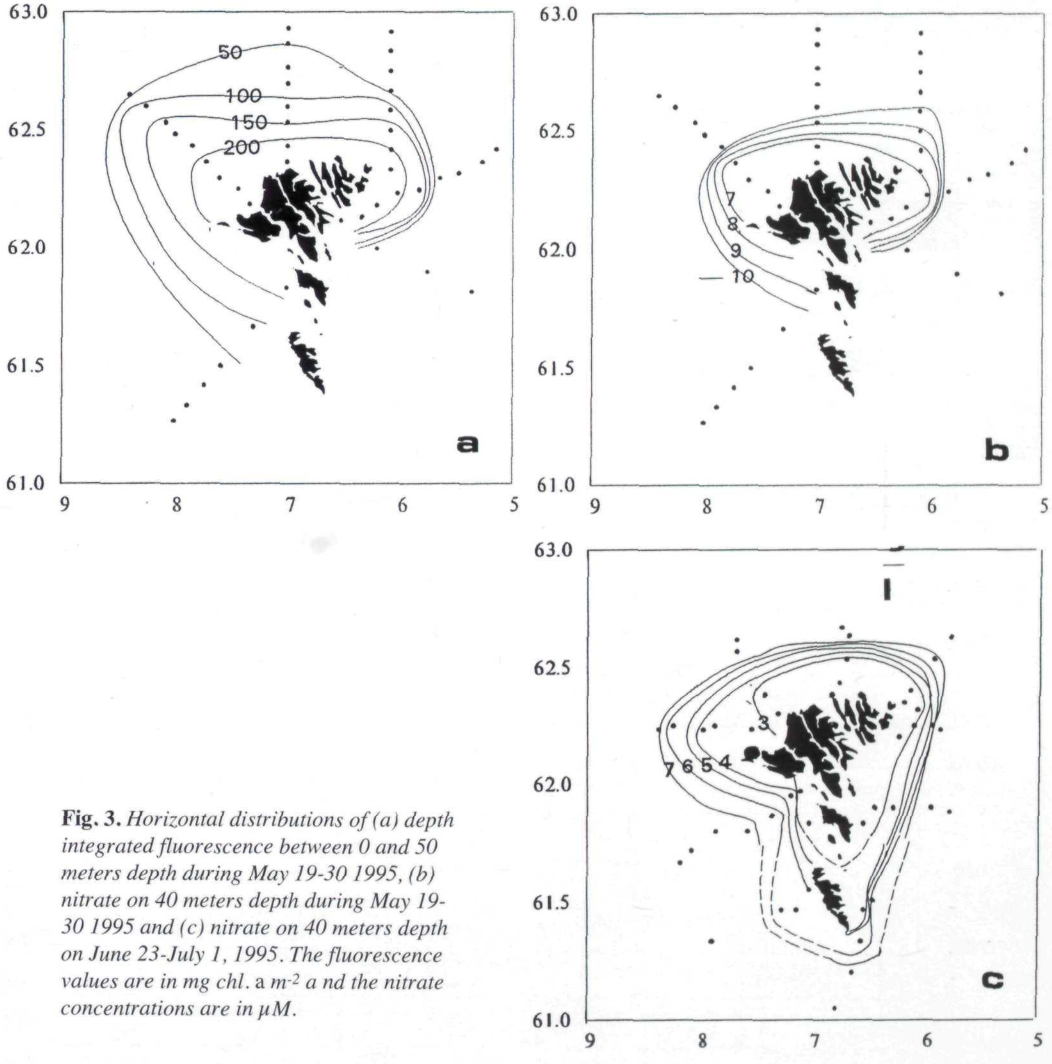


Fig. 3. *Horizontal distributions of (a) depth integrated fluorescence between 0 and 50 meters depth during May 19-30 1995, (b) nitrate on 40 meters depth during May 19-30 1995 and (c) nitrate on 40 meters depth on June 23-July 1, 1995. The fluorescence values are in mg chl.* a *m*$^{-2}$ *a nd the nitrate concentrations are in μM.*

ly May) did the silicate concentration decrease more rapidly than the nitrate concentration and it never reached zero. During autumn and early winter, the nitrate concentration gradually increased again to about 12 μmol l^{-1} and the silicate concentration to about 5 μmol l^{-1}.

On May 3rd, when the sampling series on station S started, the phytoplankton community was dominated by the diatom *Thalassiosira nordenskioeldii* and contained lower concentrations of diatoms of

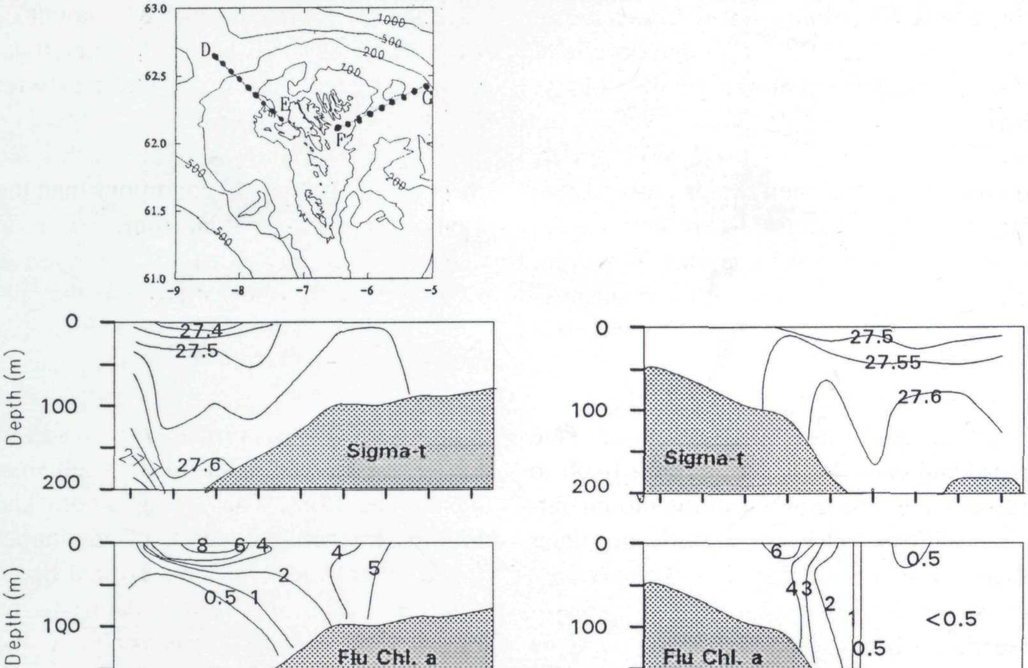


Fig. 4. *Vertical distributions of density, fluorescence, nitrate and silicate along transect D-E on May 29 and transect F-G on May 30, 1995.*

the genus *Rhizosolenia* and *Chaetoceros*. 1-2 weeks later, the diatoms decreased rapidly and were replaced by the colony-forming prymnesiophyte *Phaeocystis pouchetii* (Fig. 5). This species then totally dominated in the shelf water until around late July-early August, when they too decreased much in concentrations. This coincided with the very low nitrate concentrations what were found in the water at that time.

The diatom spring bloom on the Faroe Shelf in 1995 thus peaked between late April and early May. It is more difficult to identify the timing of the spring bloom outside the front but it was significantly later than in the shelf region. Fig. 4 shows that the thermal stratification outside the front (section F-G) was weak in late May and the phytoplankton biomass was low. On May 29-30 (well after the collapse of the diatom bloom in the shelf water) measurements along a section going towards north-west off the shelf edge showed that the concentrations of diatoms were still high in this frontal area (Fig. 6). Outside this frontal region, only very low concentrations of phytoplankton were found at this time.

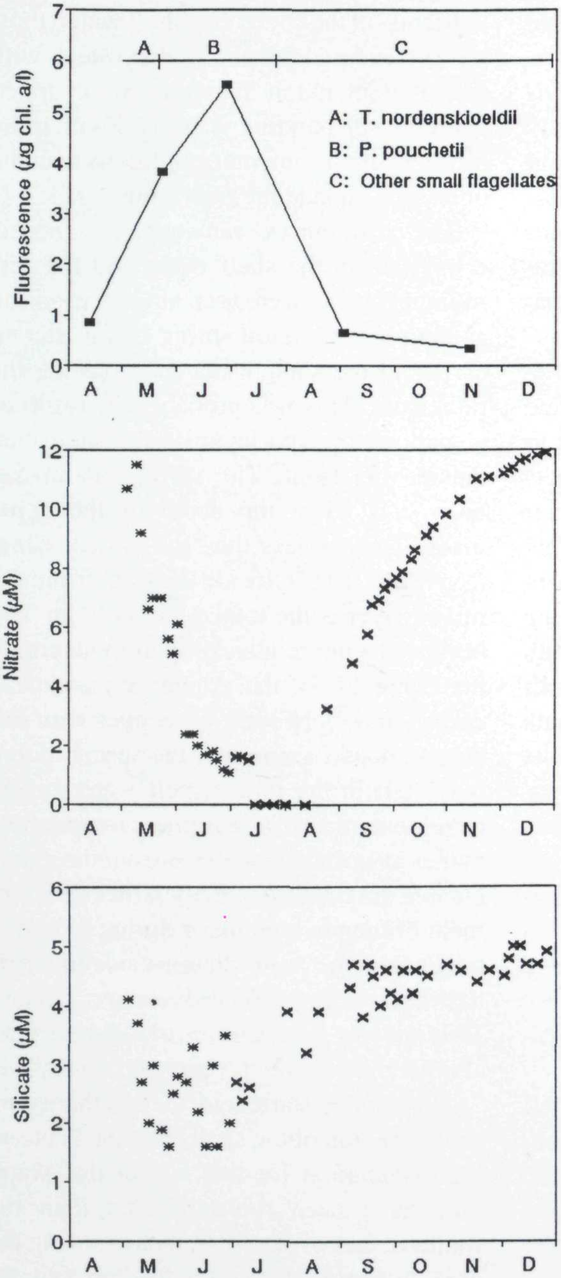
Discussion

Environmental influences on the phytoplankton

The well-mixed water column on the shelf provides quite different hydrographic conditions for the phytoplankton than in the area outside the tidal front. Furthermore, the isolation of the water mass inside the front may cause limitation of the potential new primary production (Dugdale and Goering, 1967) due to the limited amount of nutrients on the shelf. The shelf water, thus, has an isolated plankton ecosystem with the phytoplankton community separated from the surrounding water and with quite different environmental conditions than the open area outside the tidal front.

The differences between the neritic ecosystem in the shelf water and the surrounding ocean were seen already in spring as the phytoplankton spring bloom started earlier in the shelf water than outside the tidal front. This was probably the result of a shallower mixed layer on the shelf than outside the front. The spring bloom can only start when the depth of the upper mixed layer is less than the critical depth (Sverdrup, 1953). Inside the tidal front, the mixed layer is the total water column, and because of the relatively shallow depth on the Faroe Shelf, the critical depth during spring may very well be deeper than the bottom depth. Therefore, the spring bloom may start in the Faroe Shelf water before development of a summer thermocline makes it possible in the surrounding area outside the tidal front. This earlier development of the phytoplankton spring bloom in the Faroe Shelf water than outside the front has also been observed earlier (Gaard, 1994) but the timing of the bloom may vary significantly between years.

The bloom started in the northern and central region of the shelf (Fig. 3). A possible explanation for this is that this water may have been more isolated than the southern part of the shelf, thus allowing the phytoplankton stocks to develop and increase in concentration during spring.



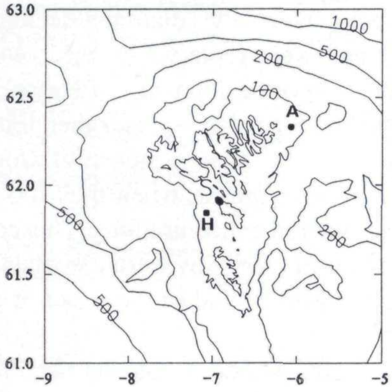


Fig. 5. *Mean fluorescence on 0-50 meters depth on station A and H and dominant phytoplankton, nitrate and silicate on monitoring station S during 1995.*

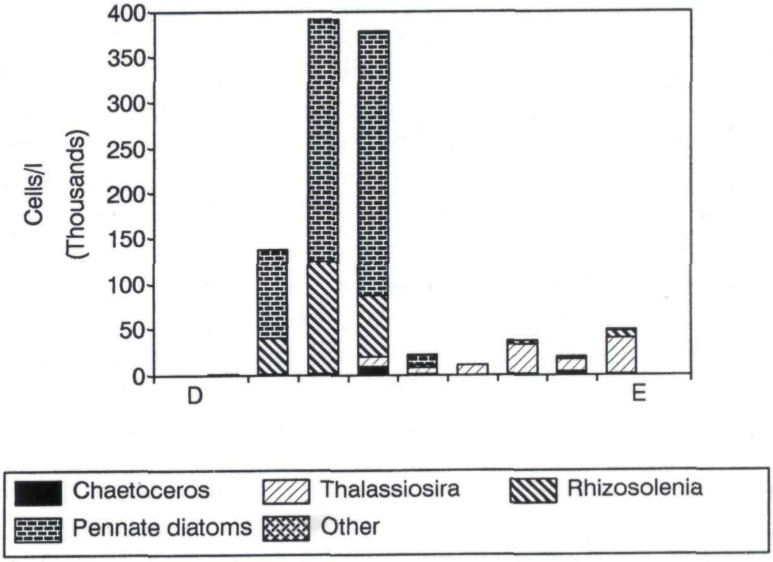


Fig. 6. *Algal concentrations on 20 meters depth on transect D-E on May 29, 1995. (See fig. 4).*

The concentration gradients shown in Figs. 3. and 4 indicate that advection into the shelf water was most pronounced in the eastern part of the shelf. This fits well with current measurements which have shown import to the eastern part of the shelf (Hansen, 1992).

Both in May and late June-early July 1995, the nitrate concentrations were significantly higher in the southern region of the Faroe Shelf than in the central and northern region. Part of the explanation for this may be the narrow shelf in the southern region, facilitating transport of nutrient-rich water to the shelf. This is also supported by measurements of zooplankton which have shown high advection of copepods to the southern region of the shelf (Gaard and Reinert, 1996).

Succession of the algae

It is well known that hydrographic conditions highly influence the phytoplankon composition. Normally, large chain-forming diatoms are more abundant in turbulent water, while dinoflagellates and smaller flagellates are more common in stratified water. Most diatoms are large and unable to swim. They tend to sink and turbulence or upwelling may therefore be a necessary requirement for large diatoms to remain in the euphotic zone. Furthermore, turbulence may increase the advective transport of nutrients to the cell surface and hence, increase the nutrient availability to the phytoplankton. This may be important for large non-swimming diatoms (Kiørboe, 1993). However, in stratified water turbulence is reduced and diatoms not favoured. Dinoflagellates and smaller flagellates, on the other hand, normally are able to swim and therefore these algae are favoured in stratified waters (Margalef, 1978; Holligan, 1987; Fogg, 1991). Such favorisation of the diatoms in turbulent environment is also seen on the Faroe Bank, which is a similar ecosystem to the Faroe Shelf (Gaard and Mortensen, 1993).

The strong turbulence on the Faroe Shelf should therefore favour diatoms. Nevertheless, diatoms were only abundant on the shelf during the spring bloom period. Already in mid-late May they declined in concentrations and instead *Phaeocystis* dominated the phytoplankton flora on the shelf during most of the summer.

Egge and Aksnes (1992) have shown that silicate concentrations may be a regulating nutrient in the phytoplankton competition. They found that diatoms, as a group, were outcompeted by flagellates at silicate concentrations below a threshold of about 2 μM. Our measurements showed that the diatoms in the shallow part of the shelf (station S) collapsed around mid May at the same time as the silicate concentrations reached this value. However, even if the summer concentrations, which were around 2-3 μM, may have slowed down the production rate of the diatoms, this factor alone is not a sufficient explanation for the diatom collapse and the almost total dominance of *Phaeocystis*.

The nutrient uptake by the algae is much affected by the cell size and is most efficient in small cells due to their higher specific surface area (Kiørboe, 1993). Thus, large celled phytoplankters such as most diatoms that are common in spring blooms may be outcompeted by smaller algal species when the nutrient concentrations are low.

Other possible advantages which may be important for the colony-forming *Phaeocystis* compared to diatoms may be lower predation pressure by mesozooplankton (Estep *et al*., 1990; Lancelot, 1995).

Potential new primary productivity

The primary production occurrs almost entirely in the summer period. Measurements of the primary production during 1985 (Vandkvalitetsinstituttet, 1987) showed that about 80% of the total primary production was within the four months period from May to August. Outside this period the primary production was light limited.

Some fraction of the primary production is derived from new nitrogen (primarily nitrate) and another fraction is derived from recycled nitrogen (primarily ammonia and urea) (Dugdale and Goering, 1967). The harvestability is related to the size of the new primary production, i.e. the fraction of the primary production that is based on new nutrients.

Figure 5 shows that the nitrate concentrations the shallow area of the Faroe Shelf reached approximately zero in mid and late summer, 1995. The potential new primary production is, therefore, limited to the nutrient pool in this water in spring plus advection of nutrients into the shelf water during the summer.

The winter concentration of nitrate in the Faroe Shelf water is about 12-12.5 μmol l^{-1}. Using the Refield ratio of C:N = 106:16 and assuming a mean bottom depth on the shelf to about 80m, this corresponds to a potential new production of about 1gC m^{-3} or about 80 gC m^{-2}. In addition to this, there is a contribution of nutrients to the area through advection from outside the shelf water. The magnitude of this advection is not well known and may vary between years. However, it is assumed to be in the same order of magnitude during the summer period as the nutrient pool in the shelf water prior to the onset of the primary production in spring. The potential new primary production can therefore be roughly estimated to be about 150 gC m^{-2}, from April to September this year. By far the most of the new production was in spring and early summer, and measurements of nitrate during 1995 showed that the nitrate pool in the shelf water was emptied after about 70-80 days. This gives a mean potential new primary production of about 1.5 gC m^{-2} d^{-1} during the spring and early summer period.

Based on Fig. 5, about half of the new production was based on the diatom spring bloom (mainly *Thalassiosira nordenskioeldii* and *Chaetoceros sp.*) during the first 3-4 weeks of the spring bloom period. The daily new production of diatoms in this period therefore has been as high as 2-3 gC m^{-2} d^{-1}. The rest of the new production was mainly by the colony-forming Prymnesiophycea *Phaeocystis pouchetii*.

Large phytoplankton, such as diatoms, are more effectively grazed by the mesozooplankton than small. Thus, there is a greater potential for the classical food chain to develop when the large species are present (Fenchel, 1988). Smaller species, such as *Phaeocystis* are thought to primarily be indicative of a microbial loop food chain structure, with much waste of energy (e.g. Azam *et al.*, 1983; Kiørboe *et al.*; 1990, Kiørboe and Nielsen, 1994). Therefore, even if the production time of diatoms was short and apparently was limited to only 3-4 weeks in spring, it may have been of major importance as food supply to the higher trophic level on the Faroe Shelf.

The primary production and nutrient concentrations in the Shelf water may vary significantly between years. Some years may be highly productive, causing distinct nutrient depletion, but other years may show lower productivity, resulting in higher nutrient concentrations and a more diatom based flora (Gaard and Hansen, unpubl.). The year discussed in this work has to be considered as one of the most productive for the shelf, since the nitrate concentrations in the shallow parts of the shelf reached approximately zero.

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