

Phytoplankton variability on the Faroe Shelf

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Mixing by the strong tidal currents on the Faroe Shelf causes the shallower part of the shelf water to be vertically and horizontally almost homogeneous. This water mass is separated from the surrounding, seasonally stratified, waters by a tidal front. The system is maintained by a persistent anticyclonic circulation system of currents driven by tidal rectification. Since 1990, nutrient concentrations and phytoplankton biomass and species composition in the shelf water have been studied in a systematic monitoring programme. The observations demonstrate large variations. In some years, nitrate becomes almost totally depleted in summer and the diatoms that dominate during the spring bloom are replaced by flagellates (e.g. *Phaeocystis pouchetii*). In other years, nitrate concentrations remain fairly high and diatoms continue to dominate the phytoplankton through summer. The inter-annual differences are more likely caused by variations in primary production rather than by variations in nutrient inflow. Furthermore, variations in primary production are more likely caused by grazing, due to the large differences in zooplankton abundance, rather than by variations in light conditions or stratification as affected by winds and tidal currents.

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Key words: Faroe Shelf, grazing, nutrients, phytoplankton variability, solar radiation, wind.

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Introduction

The Faroe Plateau is usually surrounded by waters of Atlantic origin down to depths of 400–500 m. On the shallow parts of the shelf, strong tidal currents lead to intense mixing and create a water mass that is vertically and horizontally fairly homogeneous. This water mass, which we term “shelf water”, is separated from offshore waters by a tidal front (Fig. 1), evident on infrared satellite images and usually situated between the 100 and 150 m isobath.

The well-mixed shelf water is maintained as a separate water mass by a persistent anticyclonic circulation (Hansen, 1992). Thus, the shelf water has a phytoplankton community which is separated from the surrounding area: primary production, the initiation of the spring bloom, and species composition exhibit characteristic differences (Gaard, 1994, 1996a). The zooplankton communities are also quite different. The species composition in the shelf water is usually dominated by neritic copepods (by number) and production, abundance, and seasonal development of the species exhibit characteristic patterns. Outside the front, the

zooplankton is always dominated by the copepod *Calanus finmarchicus*, whereas the abundance of this species in the shelf water is more variable (Gaard, 1994, 1996b; Gaard and Reinert, 1996). The late copepodite stages are advected in variable numbers during spring and early summer into the shelf water, where they reproduce (Gaard, 1994). In some years, the copepod is relatively sparse in this ecosystem, while in others it is more abundant. Because of its much larger size than the other species, zooplankton biomass in the shelf water is much affected by its numerical abundance.

Because of the limited amounts of nutrients in the shelf water, the primary production strongly affects the nutrient concentrations during spring and summer. Since the new primary production is primarily based on nitrate as nitrogen source (Dugdale and Goering, 1967), variability in the decrease of nitrate concentrations during spring and summer may be used as a proxy for the new primary production but other effects also need to be taken into account.

The different timing of the phytoplankton spring bloom in the shelf water and in the surrounding area

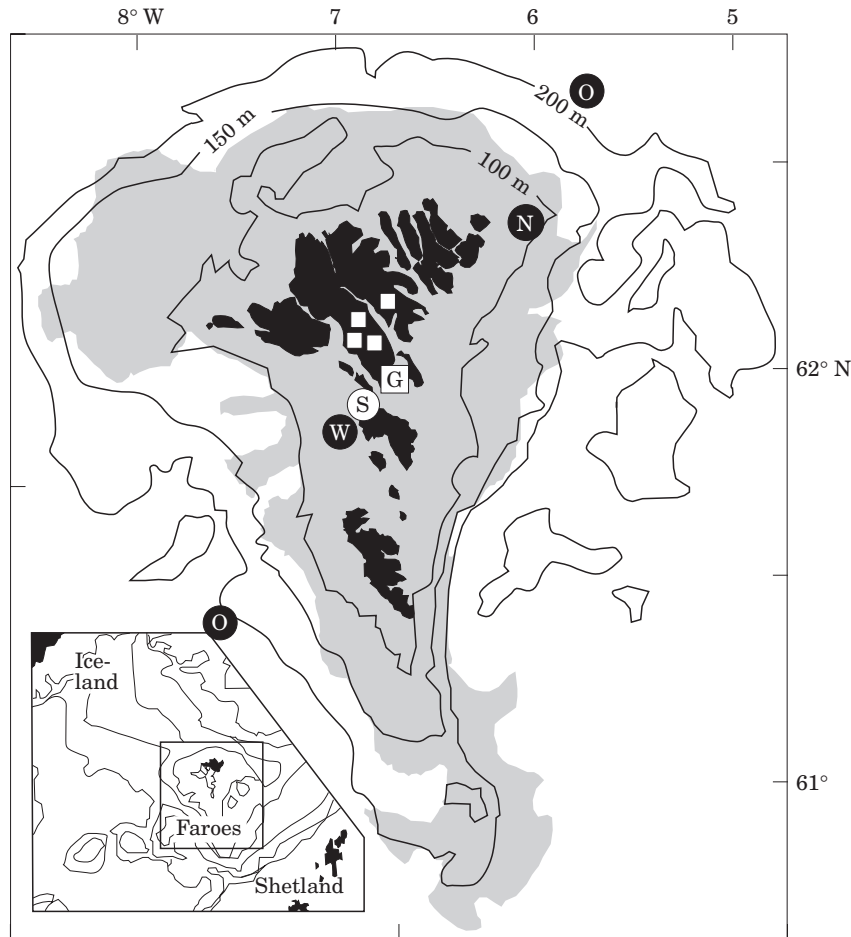


Figure 1. Topography of the Faroe Shelf. Shaded area indicates the extent of the well-mixed shelf water on 17 May 1980, 0849 GMT according to infrared satellite image. Stations W and N lie inside the shelf water while the two stations marked O are oceanic. Coastal station S at Skopun and measuring station G at Glyvursnes for wind and solar radiation are also indicated. Small white squares represent measuring stations for solar radiation.

(Gaard, 1994, 1996a, b) is apparently due to the differences in bottom depth and hydrographic conditions in these two environments. According to the Sverdrup (1953) model, the spring bloom can only start when the critical depth is greater than the depth of the upper mixed layer. In the open area outside the tidal front, this may happen after the summer thermocline has developed. However, the mixed layer in the shelf water is equal to the total water column and light is therefore sufficient for the spring bloom to develop on the shelf when the critical depth exceeds bottom depth.

If light conditions were the same every spring, a similar development of the spring bloom might be expected in the shelf water each year. However, this is not the case. Observations on nutrient concentrations and phytoplankton for the period 1990–1996 are used to illustrate the inter-annual variability during spring and early summer. In an attempt to identify the

main causal factors, observations on solar radiation, stratification, wind, tidal currents, and zooplankton biomass are used.

Material and methods

The data used fall into three groups: (1) oceanic observations on nutrients, phytoplankton, zooplankton, and stratification; (2) observations at a coastal station on nutrients and phytoplankton; (3) land-based observations of solar radiation and wind.

The oceanic observations were collected on board RV “Magnus Heinason” during a number of cruises in 1990–1996. A large number of stations were sampled, but two in particular (W, N) within the shelf water (Fig. 1). The map also shows the location of two offshore stations (O), the coastal station (S), where observations

have been collected twice week⁻¹ since May 1995, and the land-based meteorological stations (G).

Water samples for nutrient measurements were collected with Niskin bottles on a CTD rosette. The samples taken in 1990 were stored in a refrigerator and analysed 7–11 days after sampling. In 1991–1994 they were frozen immediately after sampling and analysed ashore. In 1995 and 1996, nitrate samples were analysed onboard, while silicate samples were preserved with 12 drops of chloroform 100 ml⁻¹ and analysed ashore. Samples taken at the coastal station for nitrate analysis were also preserved in 12 drops chloroform 100 ml⁻¹, stored in a refrigerator and analysed within 5–30 days. Nitrate+nitrite was measured automatically and silicate was measured manually using methods described by Grasshoff *et al.* (1983).

In situ fluorescence was measured with a Sea Tech fluorimeter interfaced to the CTD. Fluorescence was calibrated against Chl *a* by means of selected samples. Chl *a* measurements followed the methods described by Baltic Marine Biologists (1979) but with the modification that a Soniprep 140 ultrasound homogenizer was used. The Jeffrey and Humphrey (1975) equation was applied in the computations.

Phytoplankton samples were collected from 20-m depth, preserved in 0.4% neutralized formaldehyde and counted in 2, 5 or 10 ml of sea water after overnight settlement using an inverted microscope. Mesozooplankton was sampled in vertical hauls from 50 m depth to the surface. A Hensen net was used in 1990–1991 and a WP2 net in 1992–1996. Both nets had a mesh size of 200 µm and the hauling speed was 0.3–0.5 m sec⁻¹.

The temperature difference between 5 and 50 m depth at station W (Fig. 1) according to CTD observations was used as a measure of stratification of the shelf water. The Office of Public Works in the Faroes has operated eight automatic measuring stations (Aanderaa) since 1987, which include measurements of solar radiation in the 300–2500 nm spectral range. Results, including most of 1996, have been published by Heinesen (1997). Data for four of these stations, which have close to 100% data coverage during spring throughout the 1990–1996 period, will be used here.

Wind observations are available from the automatic (Aanderaa) station at Glyvursnes (Fig. 1), where average wind is recorded for every 10 min. This station is considered to be the least directionally sensitive site of those for which data are available. The data set is complete except for a period in mid-April 1996.

Results

The nutrient concentrations in the shelf water during winter are fairly constant between years (nitrate: 12 µM; silicate: 5–6 µM). However, during spring and summer the concentrations may vary considerably. The seasonal

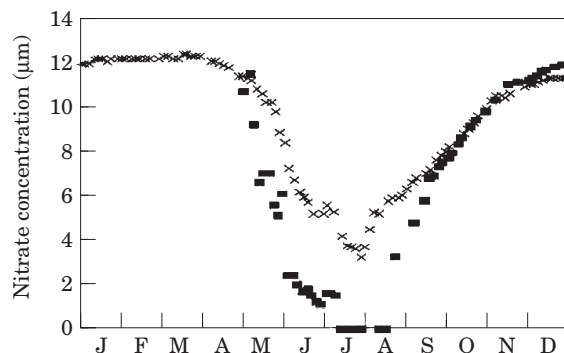


Figure 2. Nitrate concentrations at station S during 1995 (■) and 1996 (×).

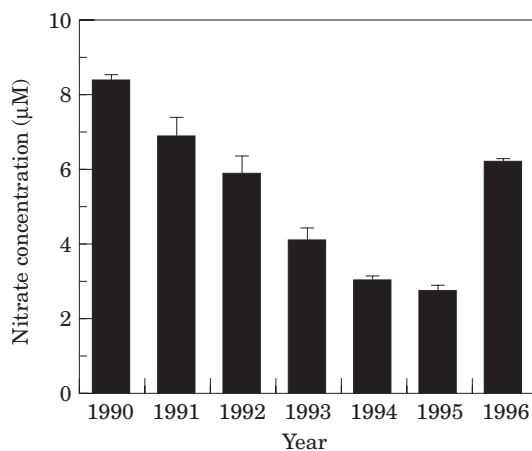


Figure 3. Mean nitrate concentrations in the shelf water (stations W and N) in late June, 1990–1996, based on samples collected between 21 June and 2 July. Bars indicate standard error.

development of nitrate concentrations at the coastal station S in 1995 and 1996 (Fig. 2) show marked differences, both in respect of the time when nitrate concentrations decrease in spring and of the minimum values during summer. The variations have been even greater in previous years (Fig. 3). With the exception of 1990, nitrate concentrations in the upper layers were higher outside the tidal front than in the shelf water (Fig. 4).

Based on a combination of a comparison between the nutrient concentrations in spring and winter, the phytoplankton biomass (fluorescence converted to Chl *a*), and a comparison between the years (Table 1, Fig. 2), estimates of the onset of the phytoplankton spring bloom varied by about one month over the 1990–1996 period (Table 2). During spring, diatoms dominate the phytoplankton. In years when nutrients remained fairly high (1990, 1991, and 1996), diatoms remained dominant in June–July, but in years with relatively low

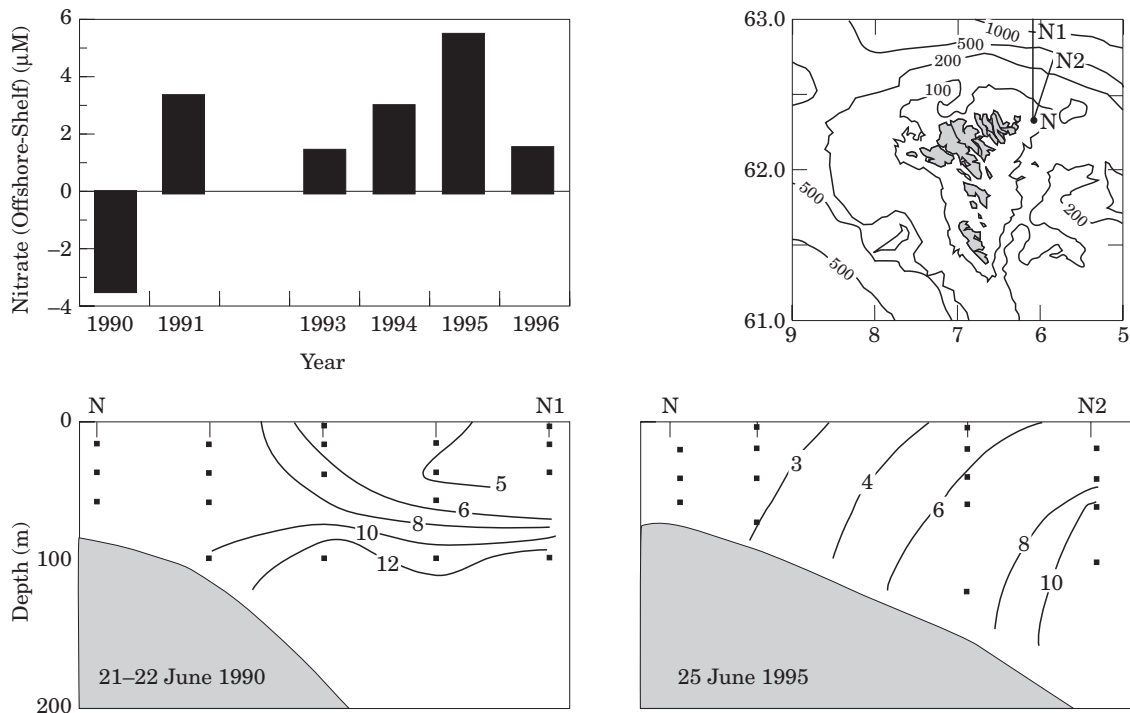


Figure 4. Difference in nitrate concentrations in the upper 60 m of the water column between the oceanic water outside the tidal front (>200 m bottom depth) and the shelf water (stations W and N) in late June, 1990–1996 (upper left), and nitrate concentrations on transects from the northern part of the Faroe Shelf and out through the tidal front in late June 1990 and 1995 (lower figures).

Table 1. Mean concentrations of nitrate and silicate (stations W and N) and average Chl *a* concentrations in the upper 50 m of shelf stations of less than 100 m bottom depth during spring and early summer 1990–1996.

Date	Nitrate (μM)	Silicate (μM)	Chl <i>a</i> ($\mu\text{g l}^{-1}$)
4–11 May 1990	11.0	4.8	0.3
21 Jun. 1990	8.7	2.0	0.6
18 May 1991			1.1
28 May 1991	8.9		2.2
30 Jun.–2 Jul. 1991	6.4		4.2
22 May–2 Jun. 1992	6.8	2.2	4.5
19–24 Jun. 1992			2.9
17–26 May 1993	6.6	2.9	3.3
4–10 Jun. 1993			3.6
9 Apr. 1994			0.8
23–29 Apr. 1994	8.1		2.0
14–18 May 1994	4.4	0.7	0.9
11–14 Apr. 1995		3.6	0.8
19–25 May 1995	7.9	2.2	3.8
28–30 Apr. 1996	11.3	4.0	0.5
5 May 1996			0.9

nutrient concentrations (1993–1995), the species composition shifted to smaller flagellates, mainly *Phaeocystis* (Table 3).

Table 2. Estimated timing of the phytoplankton spring bloom in the shelf water.

Year	Timing of the spring bloom
1990	Late May
1991	Late May
1992	Mid–Late May
1993	Early May
1994	Late April
1995	Beginning of May
1996	Mid May

Zooplankton biomass also varied considerably between years (Fig. 5). These data refer to late June/early July, for which the most complete data set was available, but the May data showed the same tendencies. The inter-annual differences were almost entirely accounted for by the copepod *Calanus finmarchicus*.

Solar radiation averaged over the April–May period each year showed consistent inter-annual variations at the four measuring sites (Fig. 6a) indicating that these observations are representative of a wider area. Although data on stratification are sparse, the index did not exceed 0.3°C in the series (Fig. 6b), which is

Table 3. The dominant phytoplankton species in May and late June to early July in shelf water, 1990–1996. The most abundant species is listed first (D: diatoms; F: flagellates).

Year	May	June–July
1990	D: <i>Rhizosolenia</i> , <i>Nitzschia</i>	D: <i>Rhizosolenia</i> , <i>Nitzschia</i> F: Coccoliths
1991	D: Small pennate; F: Coccoliths and small naked spp.	D: <i>Triceratium</i> , <i>Nitzschia</i> (no data)
1992	D: <i>Thalassiosira</i> , <i>Chaetoceros</i>	F: <i>Phaeocystis</i>
1993	D: <i>Thalassiosira</i> , <i>Chaetoceros</i>	F: <i>Phaeocystis</i>
1994	D: <i>Thalassiosira</i>	F: <i>Phaeocystis</i>
1995	D: <i>Thalassiosira</i> , <i>Chaetoceros</i>	F: <i>Phaeocystis</i>
1996	D: <i>Chaetoceros</i>	D: <i>Chaetoceros</i>

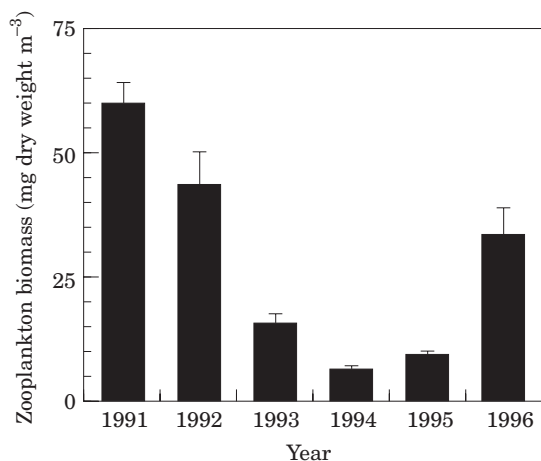


Figure 5. Zooplankton biomass in the upper 50 m of the shelf water (stations <100 m bottom depth) in late June–early July, 1991–1996. Bars indicate standard error.

consistent with the view that shelf water is a generally well-mixed water mass. Energy transfer from tides to mixing supposedly varies with current speed to the third power. Current speeds were simulated every half hour based on current meter measurements on the shelf corrected for nodal modulation (Hansen, 1992). Average values of this parameter cubed for the period 15 April to 25 June suggest only very small inter-annual variation (Fig. 6c). The energy transfer from winds is similarly supposed to depend upon the windspeed cubed. This parameter showed a considerably larger inter-annual signal (Fig. 6c).

Discussion

Algal succession

Hydrographic conditions are known to influence phytoplankton composition. Because of poor swimming abilities, diatoms are usually favoured by turbulent conditions, while dinoflagellates and smaller flagellates are more common in stratified waters (Margalef, 1978;

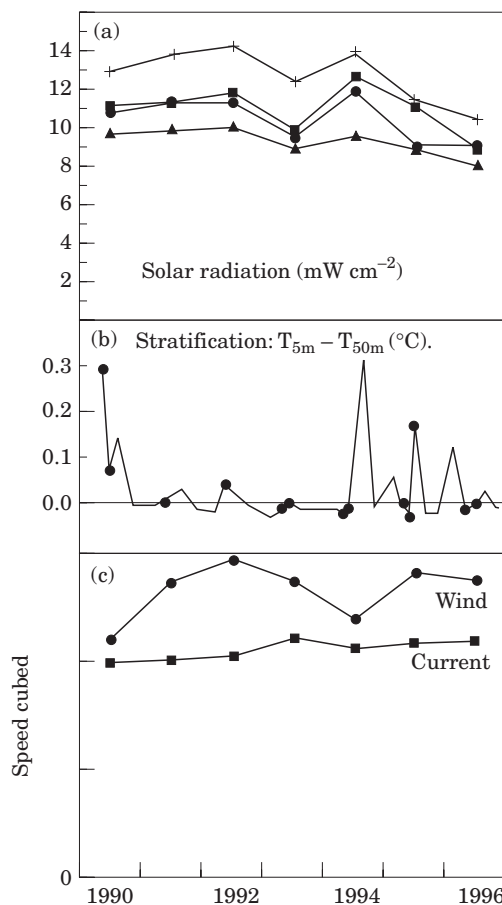


Figure 6. Variation in environmental parameters in spring, 1990–1996. (a) Solar radiation averaged over April and May at four selected sites. (b) Temperature difference between 5 and 50 m depth at station W based on CTD observations. Filled circles indicate observations between 1 April and 2 July. (c) Indices of energy input due to winds (filled circles) and tidal currents (filled squares) during the period 15 April to 25 June. Vertical scales are in relative units (see also text).

Fogg, 1991; Kiørboe, 1993). Given the strong turbulence on the Faroe Shelf, it is not surprising that the spring blooms are always dominated by diatoms. However,

nutrient concentrations also affect the algal succession. Nutrient uptake is more effective in small cells than in large cells because of the higher specific surface area in the former (Kiørboe, 1993). Thus, large-celled phytoplankters common in spring may be outcompeted by smaller species when nutrient concentrations become low. Furthermore, diatoms need silicate and growth rates of diatoms as a group are reduced significantly when concentrations fall below about $2 \mu\text{M}$ (Egge and Aksnes, 1992).

In the years 1993–1995, the diatoms that were common in spring were apparently outcompeted by smaller algal species (mainly *P. pouchetii*) during summer. The data suggest that the low summer nutrient concentrations in the shelf water during these years are responsible for this effect (Fig. 3). The available nutrient data have shown stable winter concentrations of about 12 and $5\text{--}6 \mu\text{M}$ of nitrate and silicate, respectively, and do not indicate significant inter-annual variations in either of the two nutrients during this time of year.

The predation pressure by mesozooplankton has been shown to be lower on colony-forming *Phaeocystis* than on diatoms (Estep *et al.*, 1990; Weisse *et al.*, 1994; Lancelot, 1995). Although the potentially low palatability may have been a possible advantage for *P. pouchetii* compared to diatoms, this factor does not by itself explain the change in dominance, since the diatoms were only outcompeted by flagellates in years when the zooplankton biomass was low.

Variability in primary production

The nutrient measurements indicate large variations in the summer concentrations in different years (Fig. 3). If these values are subtracted from the typical winter concentration of nitrate ($12 \mu\text{M}$), we obtain a time series of the “nitrate loss” in the shelf water during the spring bloom (Fig. 7). This nitrate loss is largely the result of two processes, phytoplankton uptake and the net nitrate transport (“nitrate inflow”) from the offshore water into the shelf water either by mixing or advection. Whatever the process, a qualitative expectation would be that the nitrate inflow equals the “exchange rate” of water times the offshore concentration minus the concentration in the shelf water. Assuming that the exchange rate does not vary too much, the nitrate inflow may be expected to depend on the concentration difference between offshore and shelf water. This difference is plotted versus nitrate loss in Figure 8. If inter-annual variations in the nitrate inflow were the main cause of the variations in nitrate loss, then an inverse relationship would be expected between nitrate loss and the concentration difference. However, Figure 8 indicates the opposite, implying that variations in nitrate loss are mainly caused by variations in phytoplankton uptake, whereas variation in nitrate

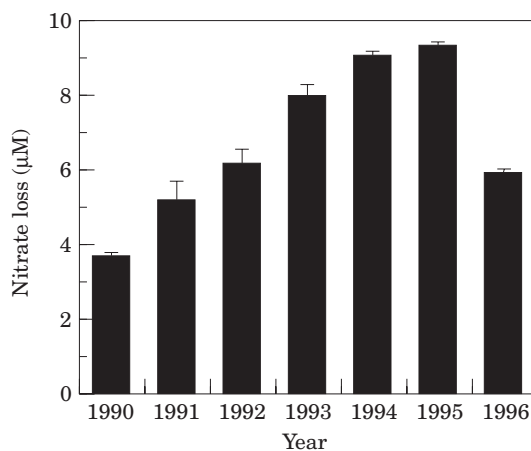


Figure 7. Nitrate loss in the shelf water (stations N and W) from the winter value ($12 \mu\text{M}$) until 26 June, 1990–1996. Bars indicate standard error.

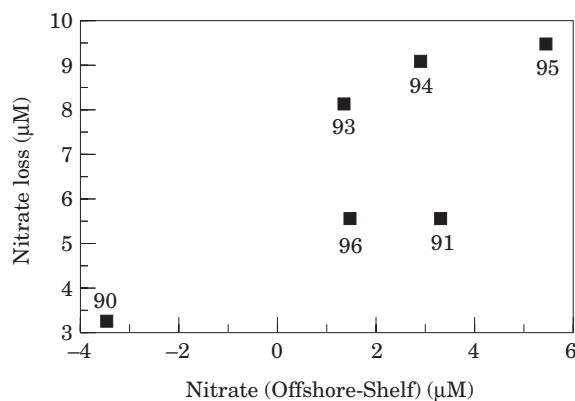


Figure 8. Nitrate loss in the shelf water plotted against the difference in nitrate concentrations in the upper 60 m of the water column between the oceanic water and the shelf water (1990–1996).

inflow would rather tend to smooth out variation in nitrate loss.

The above argument presupposes a more or less horizontal exchange of water with fairly constant exchange rate. Although this assumption is at present not supported by direct evidence, variations in the exchange process would have to be fairly dramatic to invalidate the conclusion. Therefore, the large inter-annual variations in nitrate loss (Fig. 7) are probably caused by variations in phytoplankton uptake. Because of the smoothing effect of nitrate inflow, the variability in phytoplankton uptake may even be underestimated by the nitrate loss.

Thus, the uptake of nitrate by phytoplankton in spring and early summer may vary by at least a factor of 2 between years. With nutrients abundant, phytoplankton uptake of nitrate depends upon the physical conditions

Table 4. Average values of environmental parameters for "low-productive" (1990–1991) and "high-productive" (1993–1995) years (nitrate loss until 26 June; average solar radiation given for three periods; windspeed cubed and tidal current speed cubed averaged over the period 15 April to 25 June; zooplankton biomass for June – no data for 1990).

Period	1990–1991	1993–1995
Nitrate loss (μM)	4.4	8.8
Solar radiation (mW cm^{-2})		
May	13.9	13.3
Apr/May	11.4	10.8
Apr/Jun	12.8	11.8
Wind energy ($\text{m}^3 \text{s}^{-3}$)	336	365
Tidal energy ($\text{dm}^3 \text{s}^{-3}$)	100	106
Zooplankton biomass (mg dW m^{-3})	60	10

for growth (light and stratification) and upon the number of algae affected by grazing. In the following we therefore discuss the possible effects of inter-annual variations in abiotic factors and grazing by zooplankton.

Abiotic factors

The seven years may be split into three groups characterized by small, intermediate, and large nitrate losses. Table 4 compares average values for the different parameters in "low-productive" (1990–1991) and "high-productive" (1993–1995) years according to the estimated nitrate loss as an index of phytoplankton uptake.

Solar radiation was averaged over three different periods (May; April–May; April–June). The large differences in nitrate loss are clearly not associated with variations in solar radiation for any period considered, confirming the lack of resemblance between the temporal variation in solar radiation (Fig. 6a) and in nitrate loss (Fig. 7). Thus, insofar as land-based measurements represent conditions over the shelf, solar radiation cannot be held responsible for variations in nitrate loss.

The limited number of hydrographic observations (Fig. 6b) prohibits the establishment of a good time series for the stratification index. Therefore, a causal relationship between nitrate loss and stratification may not be completely excluded on this basis. However, the available data do not support such a relationship, because stratification during the critical April–June period appears to have been most marked in 1990, when nitrate loss reached its smallest value.

Stratification is enhanced by solar radiation, while wind and tidal energy represent forces that breakdown stratification. A comparison of nitrate loss (Fig. 7) and winds or tidal currents (Fig. 6c) does not indicate a correlation with either of the two factors. Also, when average values are computed for the low- and high-

productive periods (Table 4), there is no evidence of a causal link.

The observations at the coastal station for 1995 and 1996 provide a more detailed picture of the development in the nitrate concentration, which may be compared to solar radiation and energy input from winds, averaged over the periods between nitrate measurements (Fig. 9). The emerging picture is not easy to interpret. For some periods, changes in nitrate concentration appear to be linked to wind and/or solar radiation, but such links are not consistent. Neither wind nor light explain the large difference between 1995 and 1996 in the course of the nitrate concentration during early May.

Grazing

The large inter-annual variation in zooplankton biomass in June (Fig. 5) suggests large differences in grazing pressure on phytoplankton. Indeed, the clear negative relationship between nitrate loss and zooplankton biomass (Fig. 10) indicates a causal effect of grazing on nutrient uptake by phytoplankton.

The years with the lowest zooplankton biomass (Fig. 5) were also observed to have the earliest timing of the spring bloom (Table 2). It might be argued that zooplankton abundance in these years had already peaked before late June. This hypothesis requires high zooplankton abundance in May in years with an early spring bloom. However, although the data for May were less complete, this possibility is not supported by the available data, since the May and June zooplankton biomass values showed essentially the same tendencies. No zooplankton estimates are available for June 1990, which was the year with the lowest nitrate loss in the series. However, in May 1990 the zooplankton biomass value was the highest ever observed (40 mg dW m^{-3}). This indicates that 1990 would probably fit nicely into the estimated relationship (Fig. 10).

A key question is whether the grazing pressure can be expected to be sufficiently high to affect the growth of the phytoplankton stock to the extent observed. Measurements of the grazing rate on the Faroe Shelf during pre-spring bloom periods are not available, but measurements of the zooplankton community respiration (mean biomass $30 \text{ mg dry weight m}^{-3}$) during late May 1992 have given values of $15 \text{ mg O}_2 \text{ m}^{-3} \text{ d}^{-1}$, which is equivalent to a calculated carbon demand of about $5 \text{ mg C m}^{-3} \text{ d}^{-1}$ or $2 \mu\text{M NO}_3^- \text{ month}^{-1}$. This amount is comparable to 30–50% of the nitrate loss, which strongly supports the view that inter-annual variability in the spring bloom development is most likely due to differences in grazing pressure. In the summers of 1993–1995, the grazing rates may have been decreased further due to a relatively lower predation pressure on colony-forming *Phaeocystis* than on diatoms (Estep *et al.*, 1990; Weisse *et al.* 1994; Lancelot, 1995).

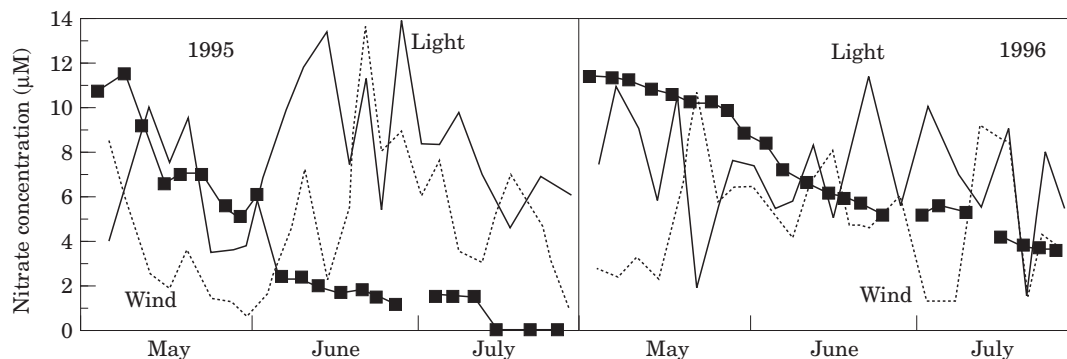


Figure 9. Trends in nitrate concentration (coastal station S; filled rectangles), solar radiation (station G; thick line), and windspeed cubed (station G; dotted line) in May–July, 1995 and 1996. Solar radiation and windspeed were both averaged over the period between consecutive nitrate measurements and are shown on the same relative scales for both years.

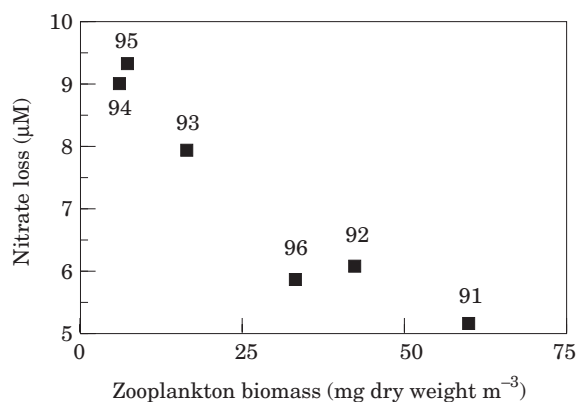


Figure 10. Nitrate loss in the shelf water plotted against zooplankton biomass in late June, 1991–1996.

Conclusions

When attempting to link inter-annual variations of nitrate loss to inter-annual variations of physical parameters and grazing, it is important to note that the processes linking primary production to the abiotic and biotic environment are of a multivariate and non-linear nature. Therefore, there is no guarantee that the approach followed here will identify the underlying relationships even when they exist. Nevertheless, two conclusions may be drawn:

- The large inter-annual variations of nitrate loss in the shelf water are most likely due to large (more than a factor of 2) variations in the (new) productivity of phytoplankton.
- The variations in productivity are most likely due to grazing by the highly variable zooplankton stocks. However, the processes responsible for the variations in the latter have not yet been identified.

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