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Climatic effects on plankton and productivity on the Faroe Shelf

Bogi Hansen, Sólvá K. Eliasen, Eilif Gaard, and Karin M. H. Larsen

Previous investigations have shown that new primary production on the Faroe Shelf during the spring bloom varies considerably from one year to another, both with regard to timing and intensity. It has also been found that variations in new primary production are transmitted up the food chain to top predators such as cod and haddock. An observed inverse relationship between new primary production and zooplankton biomass, especially *Calanus finmarchicus*, might be due to grazing, but could also reflect a dependence of both new primary production and *C. finmarchicus* import on the horizontal exchange between waters on the shelf and off it. Here, we investigate this question, using observations and an idealized numerical model. We find that the large variability in new primary production is most likely due to the direct effect of variable horizontal exchange rates on phytoplankton reproduction (horizontal Sverdrup mechanism), rather than grazing. Enhanced horizontal exchange flushes phytoplankton from the shallow areas and limits primary production. Horizontal exchange rate seems most sensitive to horizontal density differences between on-shelf and off-shelf waters, which is governed by atmosphere−ocean heat exchange and precipitation. For the primary observational period from 1990 to 2003, a close relationship was found between air temperature in January−April and new primary production. Cold winters produced large density differences, small horizontal exchange rates, and intensive new primary production. Other, less direct, evidence indicates, however, that this relationship may not have been valid in a period before 1990.

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Introduction

Located between Iceland and Scotland (Figure 1), the Faroe Islands are an archipelago of only small areal extent above sea level, but with a large oceanic region within its economic zone. Fish catches from this region remain the main economic basis for Faroese society, and understanding their variations is a research imperative. Only a small percentage of the total economical zone is shallower than 200 m, but these areas have a disproportionate importance for exploited fish stocks as well as other components of the Faroese marine ecosystem (Gaard *et al.*, in press).

The most important of these shallow areas is the Faroe Shelf, which surrounds the islands and covers 5300 km^2 out to the 100 m, and 20 000 km^2 out to the 200-m depth contours. Tidal rectification and other effects drive a current system, which circles the islands in a clockwise direction (Hansen, 1992). During most of the year, the surface water is considerably colder over the shallow parts of the shelf than farther offshore (Larsen *et al.*, 2002), and a front—the Shelf-front—separates the two regimes, which here will be termed on-shelf and off-shelf, respectively.

The Shelf-front provides a fair, although variable, degree of isolation between the on-shelf and the off-shelf areas (Larsen, 2003). This allows the on-shelf areas to support an ecosystem, which in many ways is distinct from off-shelf waters (Gaard *et al.*, 2002). One distinguishing feature is the earlier establishment of the spring bloom, but observations (Gaard *et al.*, 1998; Gaard, 2003) have shown that the timing and intensity of this bloom can vary a great deal from one year to another.
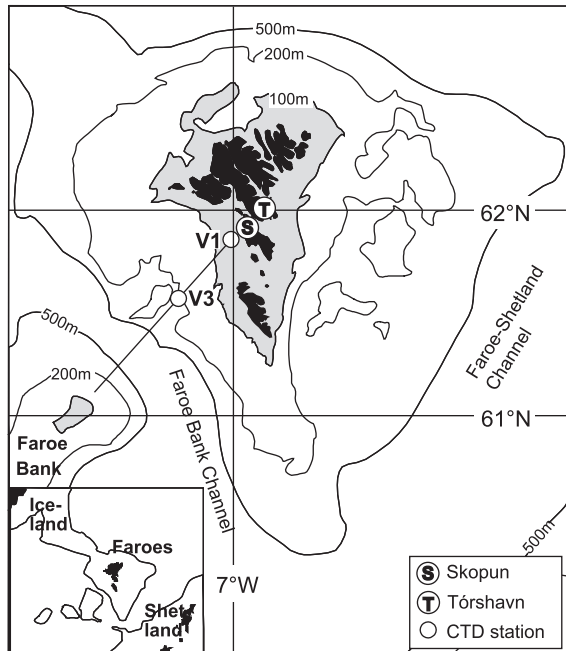
Figure 1. The Faroe Shelf (grey areas are shallower than 100 m) with indications of the coastal monitoring station in Skopun, the meteorological station in Tórshavn, and two CTD Stations V1 and V3 on a standard section. The map in the lower left-hand corner shows the location of the Faroe Shelf between Iceland and Shetland.

A characteristic feature of this variability is a high correlation between the onset and intensity of new primary production. In years with an early spring bloom, the total new primary production from April to late June may be several times greater than in years with a late spring bloom development (Gaard, 2003). It has, furthermore, been observed that this high variability is transmitted upwards through the food chain. The production of both cod and haddock correlates fairly well with new primary production. Other components of the ecosystem, such as seabirds, are also affected by the variation in new primary production (Gaard *et al.*, 2002; Steingrund and Gaard, 2005).

Explanations for interannual variability in the spring bloom have been eagerly sought. At the time of the spring bloom, Faroese waters are generally well-mixed and unstratified, both on-shelf as well as off-shelf down to a depth of several hundred metres, and observations also indicate that stratification is not the controlling parameter for the primary production on-shelf (Gaard *et al.*, 1998). The most obvious candidate for causing the variations might be solar radiation, but available observational data do not support this (Gaard *et al.*, 1998). On the other hand, an inverse relationship between new primary production and zooplankton biomass was reported (Gaard *et al.*, 1998). In terms of biomass, the most important zooplankton species

in spring is the copepod *Calanus finmarchicus*, which over-winters in deep waters and is imported to the shelf in spring. Observed interannual variability in zooplankton biomass on the shelf is generated by *C. finmarchicus*, and the relationship implies a link between new primary production and *C. finmarchicus* abundance.

An obvious explanation for this relationship would be grazing. In years with high *C. finmarchicus* abundance, they could be imagined to exert such a heavy grazing pressure that the spring bloom would be delayed and reduced in magnitude (Gaard *et al.*, 1998). Alternatively, new primary production and *C. finmarchicus* abundance could both be controlled by horizontal exchange mechanisms. In years with large horizontal exchange rates, there would be a large import of *C. finmarchicus* to the shelf, and also export of phytoplankton, which could retard and limit the spring bloom. Even if grazing were to be the most important controlling mechanism for new primary production, a vari-able horizontal exchange rate might be the mechanism responsible for the highly variable *C. finmarchicus* abundance observed (Gaard and Hansen, 2000).

In this paper, we seek the answer to these questions. Is the new primary production on the Faroe Shelf in spring controlled by grazing, by the direct effects of horizontal exchange, or by something else? Is there any observational evidence of variable horizontal exchange rates? What climatic factors, if any, affect the horizontal exchange rate? To answer these questions, we present results from biological, hydrographic, and meteorological observations, and compare these with an idealized numerical primary production model, which includes both grazing and horizontal exchange.

Observational material

The oceanic observations presented here were obtained at a coastal station (Skopun) (Figure 1) by the research vessel RV "Magnus Heinason". At the coastal station, samples were obtained twice a week since May 1995, and analysed for salinity and nitrate content. Since 1997, chlorophyll *a* has also been determined at weekly intervals (Gaard, 2003). The water intake for these samples was taken at a depth of 18 m in an area with strong tidal currents. The samples should therefore represent the inner parts of the Faroe Shelf fairly well.

Research vessel cruises included CTD profiles along a standard section extending westwards from the Faroe Islands. CTD stations have been occupied approximately four times a year since 1988. In all years since 1990, there has also been a cruise in late June occupying about 50 stations on- and off-shelf with CTD profiles, water samples that were analysed for nitrate content, and plankton hauls (50-m depth to surface) with a WP2 net (Tranter and Smith, 1968) to determine zooplankton abundance. In addition to the oceanic observations, we use wind observations from

the NCAR/NCEP reanalysis and monthly mean air temperature observations in Tórshavn, obtained from the Danish Meteorological Institute.

Observational results

Based on chlorophyll *a* measurements at Skopun, seasonal variation of the phytoplankton biomass on-shelf can be obtained for all the years in the period 1997−2003 (Figure 2a). Large interannual variation in phytoplankton biomass and the onset of the spring bloom is evident, supporting the earlier conclusion that the timing of the spring bloom and its peak intensity are linked. In years with a high spring bloom (large peak chlorophyll *a* concentration), the bloom starts early. A similar conclusion may be drawn from the nitrate measurements at Skopun (Figure 2b), since the nitrate loss on-shelf during spring is a measure of the accumulated new primary production, to the extent that exchanges of nitrate with off-shelf waters can be ignored. Comparing Figure 2a and b, it can be verified that the years with an early and large loss of nitrate are those that exhibit an early and large increase of phytoplankton biomass.

Using nitrate observations from the late June cruises, an index of new primary production (PP-index) can be determined for each year (Figure 3). The index is mainly based on the nitrate reduction on-shelf, but is corrected for horizontal nitrate import to the shelf, as described by Gaard *et al.* (2002) and Gaard (2003). This correction assumes constant horizontal exchange rates, which is not very realistic, but the correction is relatively small. Varying the horizontal exchange rate within realistic bounds (Gaard and Hansen, 2000) gives only small changes to the index, as indicated by the error bars in Figure 3. Since this index is derived from the total uptake of nitrate, it represents the accumulated new production from the beginning of the production period until late June.
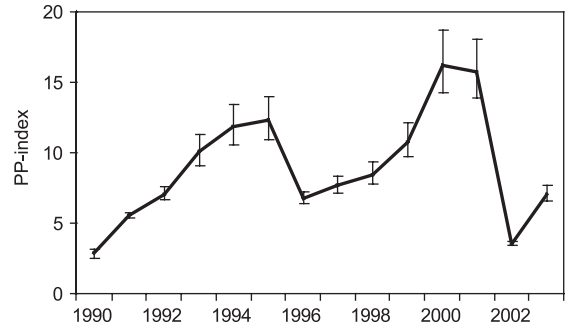

Figure 3. An index for new primary production (the PP-index) on the Faroe Shelf 1990−2003. Error bars indicate the uncertainty attributable to variable horizontal exchange rates.

Consistent with previous results (Gaard, 2003), zoo-plankton biomass on-shelf in late June varied interannually by about an order of magnitude and more (coefficient of variation = 0.77) than the off-shelf zooplankton biomass (coefficient of variation = 0.40) (Figure 4). Since *C. finmarchicus* is a much bigger copepod than the neritic species, it dominates zooplankton biomass, and the on-shelf biomass values in Figure 4 may be seen as indicators of *C. finmarchicus* abundance.

Salinity observations at Skopun should represent the well-mixed inner parts of the on-shelf water. For off-shelf salinity, we used CTD observations from a standard Station V3 (Figure 1). At this station, the waters may become temperature-stratified in summer, but usually without any significant salinity stratification. In order to compare them with on-shelf conditions, we used the average salinity between 10- and 100-m depth from the CTD profiles.

Both on-shelf and off-shelf salinity observations (Figure 5) show increasing trends, which may have significant climatic impacts (Hansen *et al.*, 2004). In the context of this work, the parallel trend of both curves on Figure 5 indicates
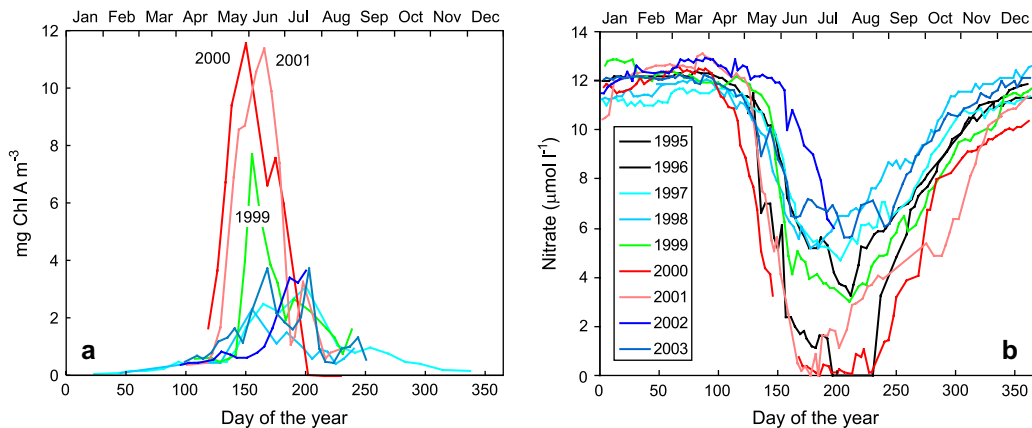

Figure 2. Seasonal variation at Skopun of the chlorophyll *a* concentration (a) 1997−2003 and the nitrate concentration (b) 1995−2003. The colours represent the same years on both panels, as indicated by the legend in panel b. The "good" years, 2000 and 2001 in reddish colours, and the intermediate year, 1999 in green, are emphasized in panel a.
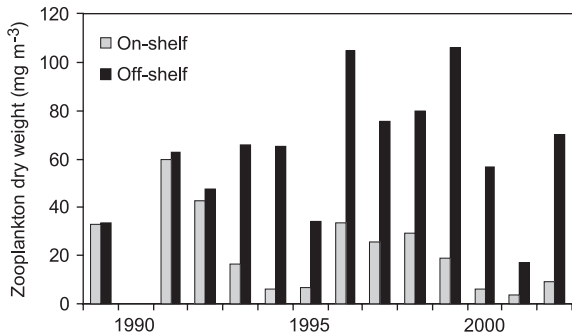
Figure 4. Mean zooplankton dry weight in the uppermost 50 m of the water column on-shelf (inside the 100-m isobath) and off-shelf (outside the 150-m isobath) in late June, 1989−2002.

Figure 6. Seasonal variation of the density difference across the Shelf-front. Each rectangle indicates the density difference between 10- and 100-m depth layer (or bottom, if shallower) at standard Stations V3 and V1 (Figure 1), observed on one cruise.

that off-shelf salinity determines on-shelf salinity on time scales of years or more. On shorter time scales, both curves indicate seasonal variation, which is especially pronounced for on-shelf salinity. This is not surprising, since precipitation varies seasonally. From orographic effects, one would expect higher precipitation over and close to land, and therefore lower salinities on-shelf than off-shelf. This is verified when comparing the salinity at Skopun with that at V3, farther offshore. Salinity differences between these two sites increase with increased precipitation and decrease with increased horizontal exchange. Therefore, some of the salinity difference variations derive from variable precipitation, but the very rapid salinity increases on-shelf, which are sometimes observed, e.g. in 1998 (Figure 5), indicate that horizontal exchange rates occasionally may become much higher than usual.

Lower on-shelf salinity would seem to imply less dense water on-shelf than off-shelf. This is usually the case during autumn, but not in the early months of the year (Figure 6). The reason for this is that cooling by the atmosphere during winter makes on-shelf water colder and therefore denser

than off-shelf, since atmospheric cooling is more efficient in shallow than deep water. In February−March, on-shelf waters are typically about 2 °C colder than off-shelf, and the temperature has more of an effect on density than salinity. This seasonal variation implies a reversal of the cross-shelf density difference around the time of the spring bloom, which may explain the large variation of the density difference in May (Figure 6).

Primary production model

The numerical model presented here (Eliasen, 2004; Eliasen *et al.*, in press) is a highly idealized model of the Faroe Shelf. In it, waters on the shelf are represented by a series of concentric annular domains (Figure 7) within which water is assumed to be vertically and horizontally homogeneous in all physical and biological parameters. Through each interface between two domains, there is an exchange of water, dissolved properties, such as nutrients, and plankton. It is assumed that the exchanges are proportional to the area of the interface and the difference in concentration across the interface. As an example, the loss of phytoplankton from domain number i to domain number i + 1, during a time interval Δt is given by:

$$L_i \times \Delta t = -k \times A_{i+1,i} \times (P_{i+1} - P_i) \times \Delta t \quad (1)$$

where P is the phytoplankton biomass and A is the interface area between the two domains. The parameter k represents the rate of horizontal exchange of water through each square metre of interface. Its magnitude is on the order of the eddy diffusivity divided by a length scale, which is the typical width of the annular domains. Since it represents advective and turbulent (but not molecular) exchange of water, the same value of k should be used for all parameters. It could be taken to vary between domains and with time, but in our implementations of the model, a unique value for k has been used in every run, although it varied from one run to another.
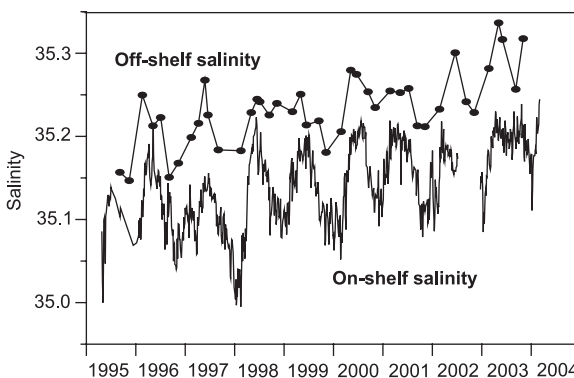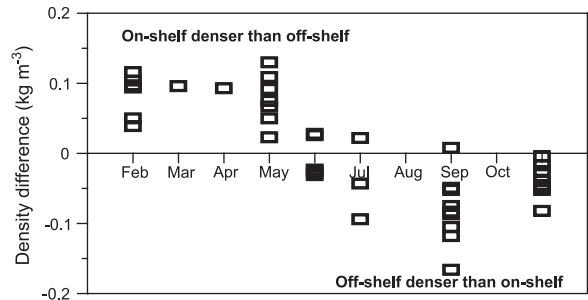

Figure 5. Salinity difference across the Shelf-front. The lower continuous curve shows salinity in Skopun (with a gap in 2002), whereas the upper filled ellipses connected by straight lines show average salinity between 10- and 100-m depth at standard Station V3 (Figure 1).
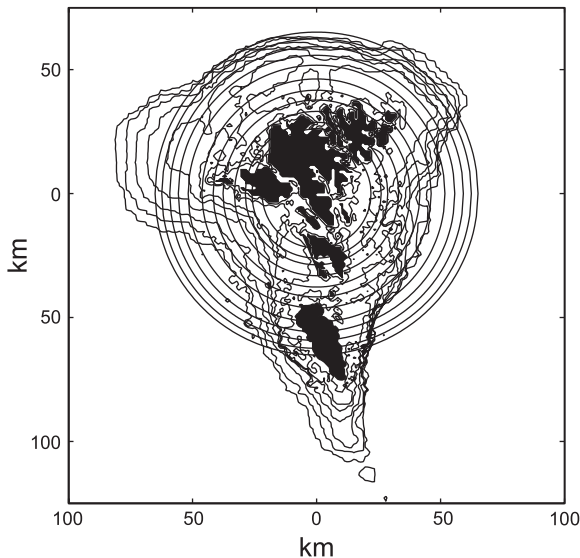
Figure 7. The geometry of the numerical model consists of a circular area of zero depth, surrounded by 11 concentric annular domains. The innermost of these represents depths between 0 and 50 m, whereas each of the outer domains represents a 10-m depth interval. The area and depth of each domain are adjusted to the real topography. Outside the outermost annular domain, the offshore waters are modelled as one homogeneous domain.

Larsen (2003) showed that a typical value for the horizontal exchange rate can be estimated by simulating the seasonal temperature variation on-shelf and off-shelf and using tabulated ocean−atmosphere heat fluxes. This typical value ($k_{typ} = 1450 \, m \, day^{-1}$), which may be considered a long-term average, implies a flushing time[1] of 77 days. This is consistent with the results of Gaard and Hansen (2000), but on time scales of a few months, they found fluctuations which indicate that the horizontal exchange rate varies considerably.

In addition to gains or losses from neighbouring domains, the model includes a biological component where the time evolution of nutrients, phytoplankton, phytoplankton grazers, and detritus is modelled. Phytoplankton is divided into two major groups: flagellates and diatoms. The grazers are also divided into two major groups: benthic fauna in one group, and *C. finmarchicus*, which is advected from offshore, in the other group.

To reflect the off-shelf origin of *C. finmarchicus*, the model is initiated on 1 April with no *C. finmarchicus* in any of the annular domains. Outside the off-shelf, *C. finmarchicus* abundance is assumed to follow temporal variations consistent with the maximal abundances observed off-shelf in different months of the year (Eliasen, 2004). In other

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[1] Defined as the time from a sudden addition of some property applied uniformly to the off-shelf waters, until the innermost domain reaches half the concentration of the off-shelf area.

model runs, *C. finmarchicus* was set to zero everywhere. The model was also run with different horizontal exchange rates.

The effect of *C. finmarchicus* grazing on the modelled spring bloom is illustrated in Figure 8a. A high horizontal exchange rate is needed to import sufficient *C. finmarchicus* to shallow water. Even in that case, grazing does not seem capable of delaying the spring bloom or reducing its peak by the amounts observed. To check the robustness of this result, the model was run with prescribed high *C. finmarchicus* abundances also in the innermost domains. Still, the spring bloom was only minimally delayed or reduced in peak intensity.

In this model, grazing on phytoplankton by *C. finmarchicus* does not seem capable of explaining the observed variations in the spring bloom. Varying the horizontal exchange rate by a factor of 5.4, from ½ to 2.7 times the typical value, did give changes in the modelled spring bloom, which approach the changes observed (Figure 8b). Thus, the model indicates that flushing of phytoplankton in years with a high horizontal exchange rate is sufficiently intense to delay the spring bloom and reduce its peak sufficiently to explain the observations. This mechanism can be compared to the Sverdrup (1953) mechanism, only operating horizontally instead of vertically, and Eliasen et al. (in press) used the term "horizontal Sverdrup mechanism" to describe it.

Discussion

An inverse relationship between new primary production in spring and zooplankton biomass has been indicated from field observations on the Faroe Shelf. Originally (Gaard et al., 1998), this was based on observations from only a few years, but succeeding observations continued to show the same relationship until the very last year (2002) for which we have zooplankton biomass values (Figure 9). This last year clearly does not fit the pattern and will be discussed in more detail below. Except for 2002 high-production years have been associated with large zooplankton biomasses and *vice versa*.

Zooplankton biomass is dominated by *C. finmarchicus*, which derives from off-shelf waters and, *a priori*, its variability might arise from processes far away from the Faroe Shelf. No correlation, however, is found between zooplankton biomass (or *C. finmarchicus* abundance) on the shelf and in the Norwegian Sea (Ellertsen et al., 2004), and Figure 4 does not indicate that zooplankton biomass variation on-shelf is controlled by the variation off-shelf.

This indicates that the *C. finmarchicus* abundance on-shelf is determined either by top-down control through predation or by the horizontal exchange rate between on-shelf and off-shelf waters. In the first case, the link to primary production would have to be through zooplankton grazing on phytoplankton. In the second case, grazing might also provide the link between zooplankton and
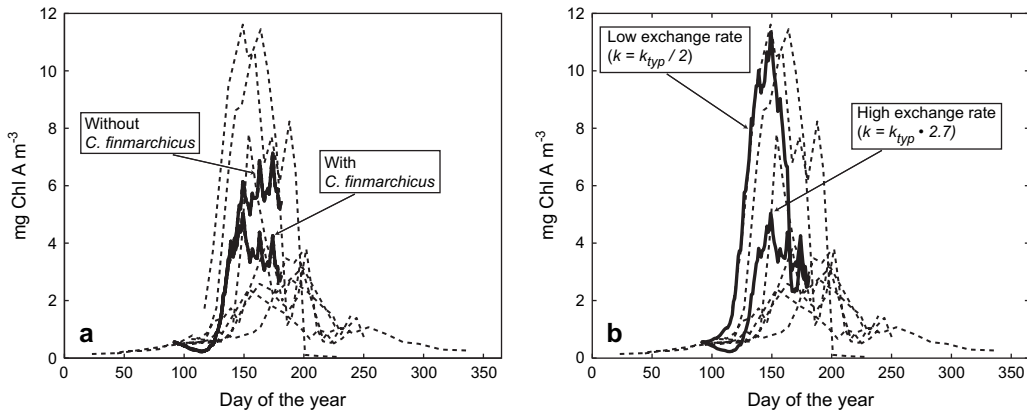
Figure 8. Modelled chlorophyll *a* concentrations (thick lines) in the innermost annular domain compared with the observations from Skopun (thin dashed lines copied from Figure 2a). In panel a, the horizontal exchange rate is 2.7 times the typical value and the two thick curves represent runs with no *Calanus finmarchicus* and with maximal observed *C. finmarchicus* abundance offshore, respectively. In panel b, the two thick curves represent two extreme horizontal exchange rates with maximal observed *C. finmarchicus* abundance offshore.

phytoplankton, but alternatively a variable horizontal exchange rate might control primary production as well as zooplankton biomass. Thus, there seem to be different mechanisms, which all could explain the relationship (excluding 2002) in Figure 9:

(i) *Hypothesis I*: Zooplankton grazing controls the spring bloom. Interannual variation in zooplankton biomass (*Calanus finmarchicus* abundance) is controlled by predation from, e.g., sandeel during spring, which itself may be controlled by predation by demersal fish, e.g. cod.

(ii) *Hypothesis II*: Zooplankton grazing controls the spring bloom. Interannual variations in abundance of *C. finmarchicus* are controlled by physical variations in the horizontal exchange rate between on-shelf and off-shelf waters.

(iii) *Hypothesis III*: The spring bloom and zooplankton biomass (*C. finmarchicus* abundance) are not causally related, but both depend on the horizontal exchange rate. Thus, when exchanges are large, there is a large import of *C. finmarchicus* to the shelf, but also a large export of phytoplankton and large exchanges between shallow and deep parts of the shelf (the horizontal Sverdrup effect).

Results of the primary production model (Figure 8a) indicate that grazing by zooplankton cannot explain the observed interannual variations in phytoplankton biomass (Figure 2a). In late spring and summer, a large zooplankton biomass can apparently depress the phytoplankton peak somewhat, but it does not appear capable of delaying the spring bloom appreciably or reducing the peak sufficiently. Variations in the horizontal exchange rate of the model do induce variations in the phytoplankton biomass that seem to reflect observed variations fairly well (Figure 8b).

The first two hypotheses above are therefore in conflict with the model results, whereas hypothesis III is supported. Since the model is highly idealized compared with nature, this result must be treated with caution, but it does indicate that variable horizontal exchange rates, common to hypotheses II and III, may well be the most important cause of the variability in the spring bloom on the Faroe Shelf.

In years with large horizontal exchange rates, this mechanism keeps the PP-index low, whereas large numbers of *C. finmarchicus* are imported on-shelf. This can explain the typical relationship in Figure 9. It should be noted, however, that the zooplankton biomass values in Figure 9 are from late June. This is because this zooplankton biomass time-series is the highest quality available, but this also means that the values may be affected by their feeding conditions and predation, as well as the import rate. Previous investigations indicated that zooplankton biomass in late June is positively correlated to zooplankton biomass earlier
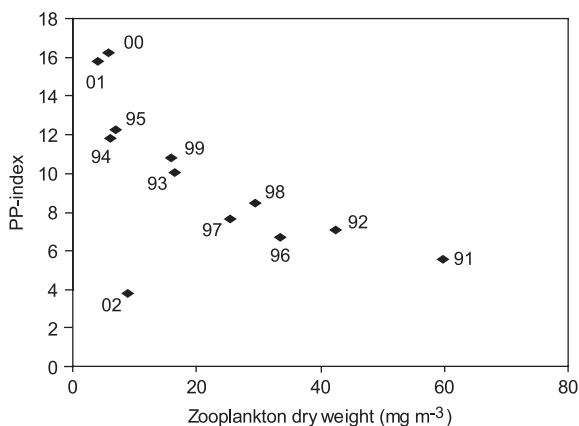

Figure 9. The association between PP-index and on-shelf zooplankton biomass in late June, 1991–2002. Numbers indicate the years.

in spring (Gaard *et al.*, 1998), and zooplankton import rate seems to be the dominant factor determining the biomass, also in late June. In years with an exceptionally low spring bloom, such as 2002 (Figures 2, 3), there might not be sufficient food to maintain a large imported zooplankton biomass until late June. This could, conceivably, explain the outlier in Figure 9, but enhanced predation on zooplankton although unobserved, is another possible, cause and more observations are needed to clarify this. Whatever the explanation for the anomaly in 2002, it does weaken the earlier assumption of grazing as the main controlling factor for the spring bloom, as do the modelling results.

In Figure 8b, the high-production year was achieved by reducing the horizontal exchange rate in the model to one half of its typical value, whereas the low-production year had a horizontal exchange rate 2.7 times the typical value. The ratio between these two (5.4) is of the same order of magnitude, although slightly larger than the variation in flushing time of the inner shelf water found by Gaard and Hansen (2000). They based their estimates on measurements of the salinity difference between on-shelf and off-shelf waters (Figure 5), combined with observed precipitation over land. This method cannot yield very precise estimates of the horizontal exchange rate, but according to the model, it indicates that variations in horizontal exchange rate are of the order of magnitude needed to yield the variations observed for the spring bloom.

The PP-index is calculated from the nitrate reduction on-shelf plus the net import of nitrate from off-shelf, assuming a constant horizontal exchange rate (Gaard *et al.*, 2002). If the new primary production and the horizontal exchange rate are inversely related, then this assumption will tend to exaggerate the difference between good and bad years. The real variation between years of new primary production until late June is therefore probably less than what Figure 3 indicates. From the error bars in Figure 3, it can be seen that the import correction to the PP-index is relatively small. Thus, the large interannual variation in new primary production remains valid and consistent with the variation in Figure 2a.

Thus, it appears that horizontal exchange, through the horizontal Sverdrup mechanism, can explain the spring bloom variations if the horizontal exchange rate varies sufficiently. Observations indicate that it does vary on the required order of magnitude. This raises the question, what causes the variations in horizontal exchange rate? This question was addressed by Gaard and Hansen (2000), who found a significant correlation to windstress. This relationship was established for the whole year but, for an effect on the spring bloom, we would look for a relationship between windstress and production in the critical months: April, May, and June. We have therefore compared the PP-index with the NCAR/NCEP wind data from a point on the Faroe Shelf. In line with Gaard and Hansen (2000), we computed six-hourly values for a windstress index by squaring windspeed and assuming that stress was in the wind

direction. These values were vectorially averaged to produce monthly averaged windstress estimates, which were compared with the PP-index. By this procedure, we were not able to identify any link between windstress and new primary production. On annual time scales, winds may well influence the exchanges between on-shelf and off-shelf waters (Gaard and Hansen, 2000), but they do not seem to explain the large interannual variations in the spring bloom.

Dynamically, the primary isolating factor between the on-shelf and the off-shelf waters is the density difference $\Delta\rho$ between the two water masses (Figure 10). The typical seasonal variation of this parameter (Figure 6) implies a sign reversal close to the time of the spring bloom. Without going into detailed discussion of the processes involved, this reversal is likely to imply a relatively large cross-shelf exchange (Figure 10). Early reversal would therefore seem to imply large exchanges during spring, prior to and during the spring bloom development.

It seems likely that large values for $\Delta\rho$ in early spring would tend to reduce the horizontal exchange and thus increase the primary production. The number of years with data available for testing this idea is limited, but the data that do exist support the hypothesis (Figure 11). In early spring, $\Delta\rho$ is mainly generated by winter cooling. Therefore, it makes sense to compare the PP-index with the air temperature over the shelf in late winter–early spring. This is done in Figure 12, and again the correspondence is reasonably good, with a correlation coefficient of -0.66 (statistically significant at $p < 0.01$).

This result might appear somewhat counter-intuitive when taking into account the positive effect of temperature on phytoplankton turn-over rates, and it should be noted that the temperature shown in Figure 12 is the air temperature before the spring bloom and not the water temperature during the spring bloom. These two temperatures are, no doubt, related, but apparently the effect of air temperature on horizontal exchange rates dominates over the temperature effect on turn-over rates.

A tentative conclusion from this data set would be that the main factor controlling the spring bloom on the Faroe Shelf is the air temperature during the first months of the year. In cold years, large horizontal density differences would isolate the on-shelf waters from those off-shelf and allow an early and intensive spring bloom. Warm years would have the opposite effect with a delayed spring bloom and low production.
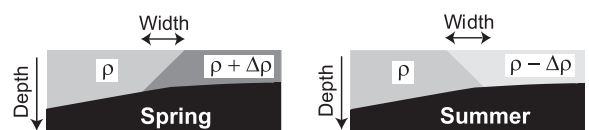

Figure 10. A schematic vertical section crossing the Shelf-front. The density difference across the front changes sign from spring to summer. This also implies that the tilt of the front and its width change, if geostrophic balance applies.
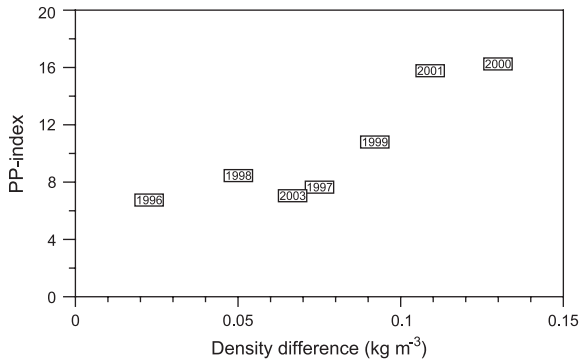
Figure 11. The association between PP-index and the density difference between standard Stations V3 and V1 in May.

From the data presented here, this fairly simple mechanism would seem to explain a large part of the variability in the spring bloom on the Faroe Shelf. Unfortunately, other evidence indicates that this conclusion may be somewhat premature. Observations needed to compute the PP-index do not extend to the period before 1990, but data on recruitment and weight-at-age for cod extend back to 1960. From this, one can generate a time-series of cod production back to 1960 (Steingrund, pers. comm.). If the relationship between new primary production and cod production holds, as it has done since 1990 (Steingrund and Gaard, 2005), and if the proposed mechanism is valid, then we would expect a negative correlation between cod production and winter air temperature. When this was checked, however, no correlation was found.

Conclusions and future perspectives

Although not conclusive, the model discussed in this paper indicates that the main factor controlling new primary
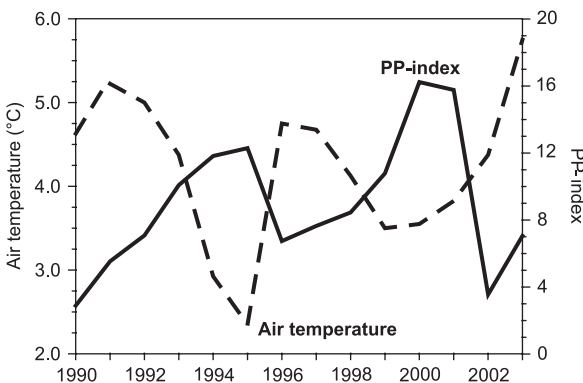

Figure 12. The association between PP-index (continuous line) and average air temperature January−April (dashed line) for the years 1990−2003.

production on the Faroe Shelf in spring is the horizontal exchange rate between on-shelf and off-shelf waters. From the observations, horizontal exchange rate appears to be controlled by the density difference between on-shelf and off-shelf waters, which seems to be controlled by the air temperature in the first months of the year. In cold years, on-shelf waters become well isolated from off-shelf waters, and horizontal exchange is reduced, allowing an early and intensive spring bloom. This mechanism, which opens the possibility for prediction, is well supported by the main data set treated in this paper, covering the period 1990−2003. Fisheries data covering an earlier period do not support it, however. It is not known whether this is because the tight coupling between new primary production and fish production was not valid in this earlier period, whether factors other than air temperature dominated the horizontal exchange rate, or whether the proposed basic mechanism is not appropriate. These questions will be the main focus of future research.

Acknowledgements

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