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Plankton variability on the Faroe Shelf during the 1990s

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A mixture of neritic copepod species, meroplanktonic larvae, and ichthyoplankton usually dominates the zooplankton on the Faroe Shelf during spring and summer. The ecosystem, however, is very much affected by the interannually variable influx of *Calanus finmarchicus*. During the 1990s, the plankton production, abundance, and species composition fluctuated greatly, the zooplankton biomass on the Shelf (which is mainly *C. finmarchicus* biomass) by a factor of 10. When the abundance of *C. finmarchicus* was high, the abundance of neritic zooplankton was generally low and *vice versa*. Interannually, there is a strong inverse relationship between zooplankton biomass on the Shelf and new primary production. During the 1990s, new primary production from spring to mid-summer fluctuated by a factor of about 5, inversely related to the zooplankton biomass. The good relationship between primary production and fish reproduction and growth and is most likely the result of variable production of zooplankton of a suitable size for fish larvae during spring.

Keywords: ecosystem, Faroe Shelf, ichthyoplankton, phytoplankton, solar radiation, zooplankton.

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Introduction

The tides on the Faroe Shelf are primarily semidiurnal with peak currents of about 1 m sec^{-1} inside the 100 m bottom contour (Figure 1). The currents are even stronger in the shallow areas and, locally, can exceed 4–10 knots (Hansen, 1992; Simonsen, 1999). This leads to intense mixing, resulting in homogeneous water masses. The well-mixed shelf water is separated from the offshore stratified waters by a persistent tidal front located at about the 100–130 m contour (Gaard *et al.*, 1998). In addition, residual currents have a persistent anticyclonic circulation around the islands, with typical speeds of about 0.1–0.15 m s^{-1} (Hansen, 1992; Hansen and Larsen, 1999; Simonsen, 1999; Gaard and Hansen, 2000).

The extreme turbulence of the Faroe Shelf Water, and the separation of the Shelf Water from the offshore led to maintenance of a shelf planktonic community that is quite different from that offshore. Both the phytoplankton production and species composition in these two regions are quite different. Most years the phytoplankton spring bloom starts earlier on the Shelf than offshore (Gaard, 1996, 2000). Since the nutrient pool is limited, the primary production decreases nutrient concentrations during spring and summer (Gaard, 1996; Gaard *et al.*, 1998). In high nutrient concentrations, diatoms dominate in the Shelf Water; however, when the nutrient concentrations decrease much smaller flagellates tend to take over (Gaard *et al.*, 1998).

The zooplankton species composition, production, and abundance on the Shelf are also usually quite different from the offshore environment. The Shelf community is essentially a mixture of neritic copepod (mainly *Acartia* spp. and *Temora longicornis*) and meroplanktonic larvae (Gaard, 1999; Debes, 2000), and ichthyoplankton (Gaard and Steingrund, 2000; Gaard and Reinert, 2002) during spring and summer. The ecosystem is also affected by advection of zooplankton from the surrounding offshore environment, e.g. the copepod *Calanus finmarchicus* may be advected onto the Shelf in highly variable abundance (Gaard and Hansen, 2000). The abundance of *C. finmarchicus* is usually much lower on the Shelf than offshore.

The Faroe Shelf Water can be characterized as a relatively isolated, well-defined, small (approximately 8,000–10,000 km^2) and uniform ecosystem which is suitable for ecological studies.

The aim of this article is to demonstrate the interannual variability of phytoplankton, zooplankton, and ichthyoplankton during the period 1990–2000. Possible environmental causes and their effects on higher trophic levels in the Faroe Shelf ecosystem are discussed.

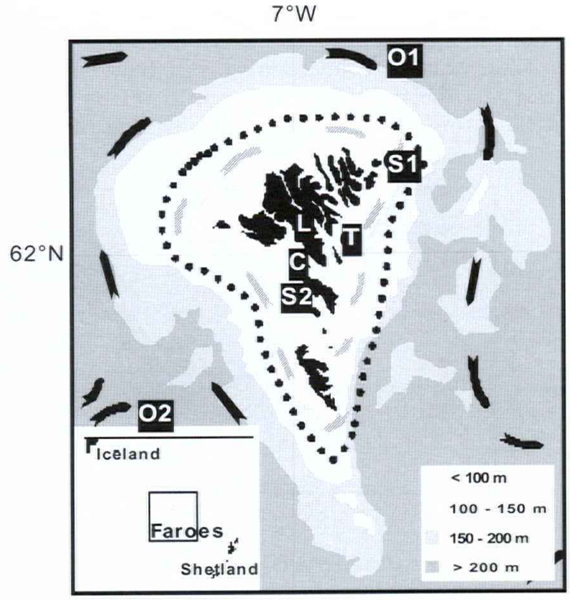

Figure 1. Bottom topography and main features of the flow field. The dotted line indicates a typical position of the tidal front that separates the Shelf Water from the open ocean. The black squares with letters refer to observational sites visited for monitoring of time-series investigations.

Materials and methods

Oceanic observations and measurements of hydrography, nutrients, and plankton were carried out in late June 1990–2000 at about 50 stations distributed around the Faroe Shelf and slope. In addition, time-series of salinity were collected at two shelf stations (S1 and S2) and at two offshore stations (O1 and O2) in May 1990–2000 (Figure 1).

At a coastal station (Station C in Figure 1), nutrients and chlorophyll *a* were collected twice a week at 18-m depth. Nutrient samples were collected from May 1995 and chlorophyll *a* samples during spring and summer from 1999. In addition, chlorophyll *a* was frequently collected at station T during 1997. Solar radiation in the 300–2500 nm spectral range was measured from 1990 to 1999 at station L with an automatic measuring weather station (Anderaa). Salinity was obtained by CTDs. An EG&G CTD was used until May 1995 and a Seabird Electronics SBE 911 plus CTD afterwards.

The nutrient samples from 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. Since 1995 the samples that were collected onboard the research vessel were analysed onboard, and the samples that were taken at the coastal station (C) were preserved with 12 drops of chloroform per 100 ml of sample. Nitrate + nitrite were measured with an autoanalyzer in accordance with the method of Grasshoff *et al.* (1983).

Chlorophyll *a* was measured following the method of the Baltic Marine Biologists (1979) and the Jeffrey and Humprey equation (1975).

Zooplankton was sampled by vertical hauls from 50-m depth to the surface. A Hensen net was used in 1989–1991 and a WP2 net in 1992–2000. Both nets had a mesh size of 200 μm and operated at a towing speed of 0.3–0.5 m sec^{-1}. The samples were preserved in 4% formaldehyde. Subsamples were identified and counted, and biomass obtained after drying at 60–65°C until they reached constant weight.

Results

The average solar radiation for March, April, May, and June 1990–1999 showed increasing values during the seasons (Figure 2). During spring, the interannual variability was generally smaller than differences between the months.

The salinity is always lower in the Faroe Shelf Water than in the surrounding ocean (Figure 3A). This salinity gradient is maintained by precipitation and run-off from the islands, retention of the water masses on the shelf and shallower bottom depths on the Shelf. The front between the oceanic and the Shelf Water can be identified based on the isohalines. The average salinity difference in the upper 50 m of the water column between the shelf stations (S1 and S2) and offshore stations (O1 and O2) in May 1990–2000 was 0.10. However, there was interannual variability in salinity with a difference of between 0.05 and 0.13. This variability is due to variable retention of the Shelf Water or variable precipitation.

The amounts of nutrients on the Shelf are limited to those available to the spring bloom plus the net

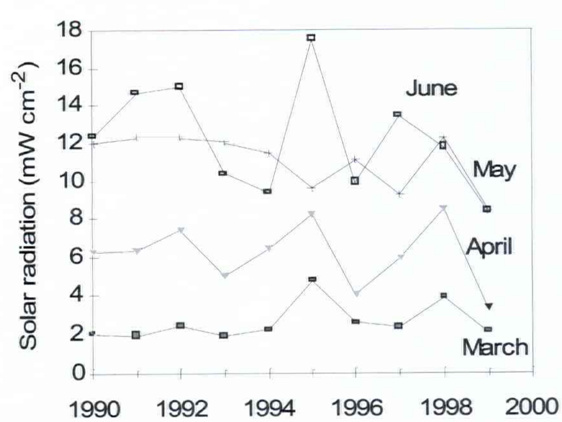

Figure 2. Mean solar radiation (300–2500 nm spectral range) at station L in March, April, May, and June 1990–1999.

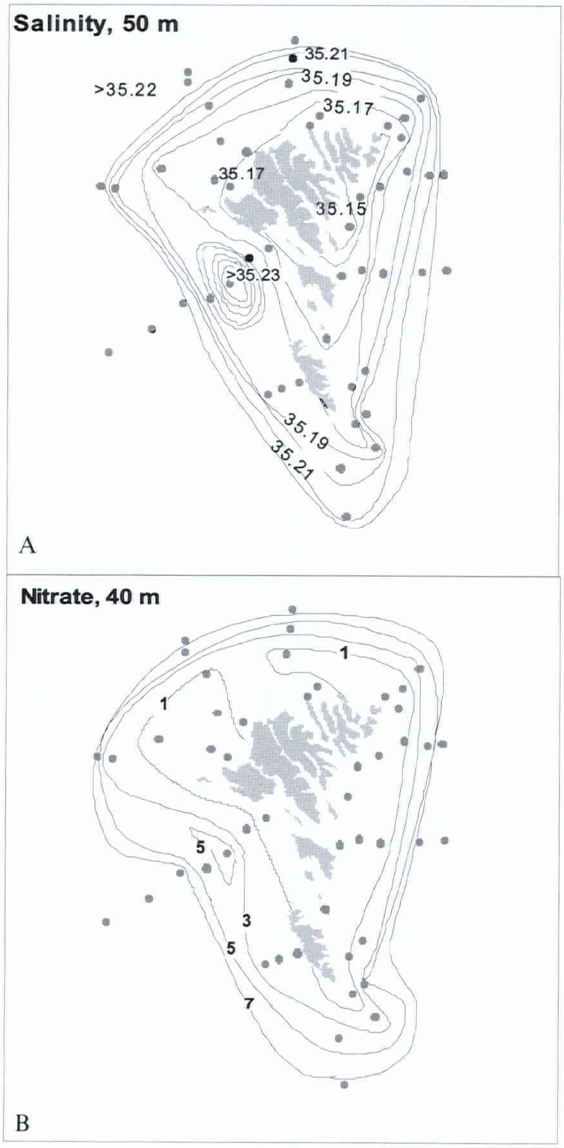

Figure 3. Salinity at 50 m depth (A) and nitrate (μM) at 40 m depth (B) around the Faroe Shelf, 23 June to 1 July 2000.

influx of nutrients from offshore during the productive season. During summer, the nutrient concentrations may decrease to very low levels in the Shelf Water (Figure 3B).

In most years, shelf nitrate concentrations begin to decrease in May – rapidly during the spring bloom and generally more than offshore. Nitrate concentrations reach a minimum in July and then slowly increase again. By November they again reach winter levels of around 12.0–12.5 μM (Figure 4). The timing of the spring bloom and decrease of the nitrate concentrations as well as the phytoplankton biomass can vary significantly between years. Generally the years with the earliest spring bloom had the lowest nitrate concentrations during summer, and *vice versa* (Figures 4 and 5).

There was high interannual variability in (decrease of) the nitrate concentrations on the Faroe Shelf during the 1990s (Figure 6). During the early

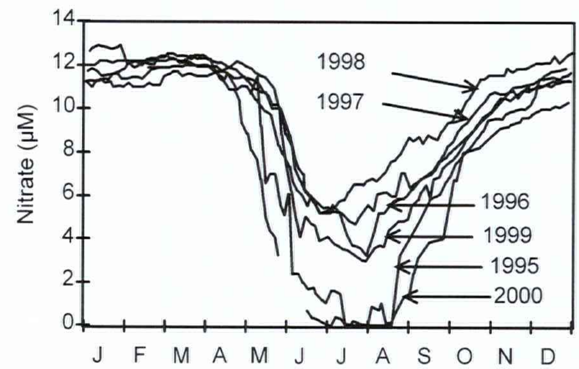

Figure 4. Nitrate concentrations at station C from May 1995 to December 2000.

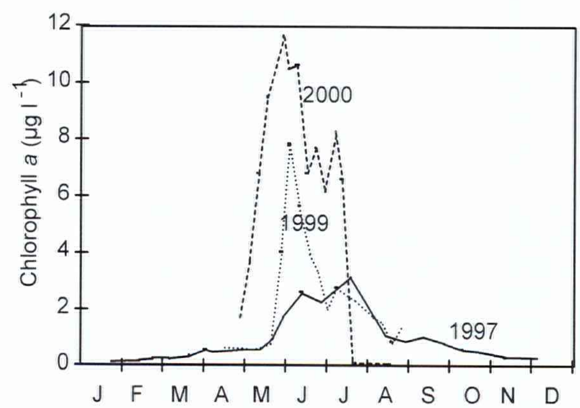

Figure 5. Chlorophyll *a* concentrations at station T during 1997 and station C from April to August 1999 and 2000.

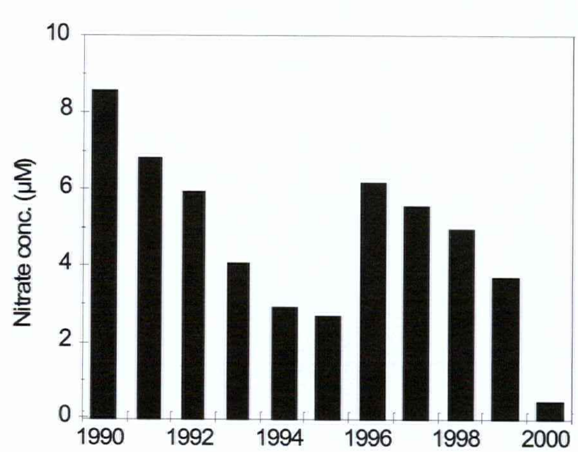

Figure 6. Mean nitrate concentrations on stations S1 and S2 in late June 1990–2000.

1990s, the nitrate concentrations remained high throughout the year. However, during the early-mid-1990s and again in 2000 the nitrate concentrations decreased greatly in the Shelf Water during summer.

Between 1989 and 2000, the interannual abundance of oceanic species (mainly *C. finmarchicus*) and neritic species (mainly the copepods *Acartia* spp. and *Temora longicornis* and barnacle larvae) on the Faroe Shelf fluctuated greatly (Figure 7). During the first few years of the period, the ecosystem was dominated by *C. finmarchicus*. The mid-summer abundance of *C. finmarchicus* fluctuated from about 400 copepods m^{-3} in 1989 to about 25 in 1994 and up again to about 150 copepods m^{-3} in the late 1990s. At the same time the neritic zooplankton fluctuated inversely, from about 120 in late June 1989 to 960 in 2000. Relatively, the system fluctuated from 80% of *C. finmarchicus* + *Oithona* and 20% neritic species in 1989 to 10% of *C. finmarchicus* + *Oithona* and 90% neritic species in 2000.

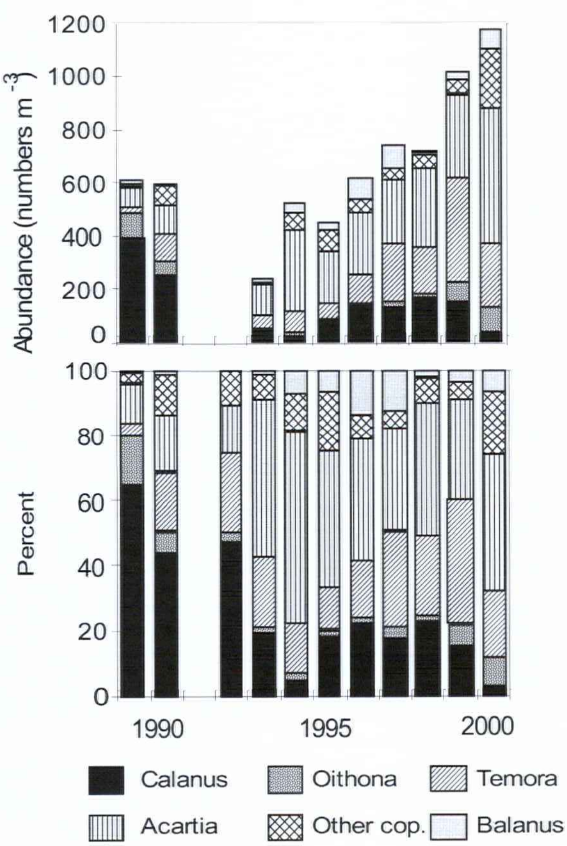

Figure 7. Mean absolute (upper) and relative (lower) abundance of the dominant copepod species and barnacle larvae in the upper 50 m of the water column at stations S1 and S2 in June 1989–2000.

Since *C. finmarchicus* is a much bigger copepod than the neritic species, it dominates the zooplankton biomass. Therefore the changes in abundance of *C. finmarchicus* on the Shelf during the 1990s dominated the zooplankton biomass, which, during this period, fluctuated by a factor of 10 on the Shelf while remaining relatively constant in the oceanic environment outside the tidal front (Figure 8).

Discussion

Phytoplankton variability

In most years, the primary production increases in May and decreases again in August or September. Phytoplankton production usually increases earlier in spring on the Shelf than offshore, and is believed to be the result of a shallower mixed layer on the Shelf compared to outside the tidal front during early spring (prior to establishment of a summer thermocline offshore). According to Sverdrup's (1953) theory, the spring bloom can only start when the depth of the upper mixed layer is less than the critical depth. Inside the tidal front on the Faroe Shelf, the mixed layer is the total water column (mean depth 70–80 m) and in spring the critical depth may exceed the bottom depth. The spring bloom may therefore start on the Shelf before the development of a summer thermocline makes this possible in the surrounding offshore area. The spring bloom usually starts in the central and northern shelf regions (Gaard, 1996, 2000) and then spreads over the entire Shelf.

Nitrate concentrations during spring and summer on the Faroe Shelf varied dramatically during the 1990s, because of variable new primary production (Dugdale and Goering, 1967), variable net influx

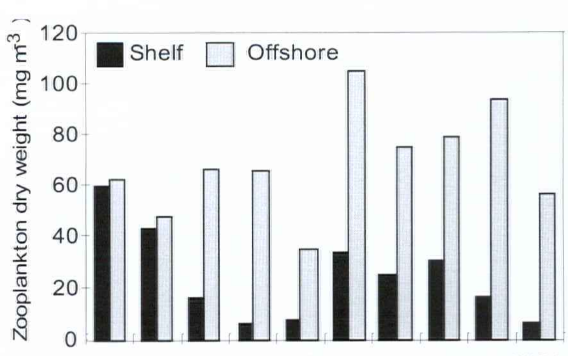

Figure 8. Mean zooplankton dry weight in the upper 50 m of the water column on the Faroe Shelf (inside the 100 m bottom contour) and offshore (outside the 150 m bottom contour) in June 1990–2000. The data derive from stations similar to those in Figure 3.

of nitrate from offshore or a combination of both. An approximation of relative nitrate assimilation (potential new primary production) during the high-productive period can be calculated as the sum of the nitrate decrease in the Shelf Water and net nitrate inflow. The latter can be expressed as the renewal rate of the Self Water multiplied by $[NO_3^-]_{offshore}$ minus $[NO_3^-]_{shelf}$ during the investigated period.

The amount of nitrate in shallow regions on the Faroe Shelf is limited and interannual variability in its decrease during spring and summer is fairly easily monitored. The flushing rate of the Shelf Water can be approximated from salinity on the Shelf and offshore water, precipitation, and depth of the Shelf Water column (Gaard and Hansen, 2000). Assuming a mean precipitation of 1000 mm $year^{-1}$, the average flushing time in spring during the 1990s is estimated to be about 2.5 months, but is variable. The flushing time is only an approximation, due to the averaging period used and the difficulty in obtaining representative precipitation measurements.

The above calculations can be used as a proxy for a relative potential new primary production (Figure 9). The index is based on calculation from spring to a fixed date (26 June) each year. Variable nitrate influx (owing to variable renewal rates of the Shelf Water) is markedly lower than the nitrate loss. This therefore suggests that the nutrient changes are due mainly to variable assimilation. Potential new primary production thus appears to have varied by a factor of about 5 during the 1990–2000 decade.

The primary production index only provides relative values, from spring to midsummer. Using a Redfield ratio of C:N = 106:16, and assuming that the mean bottom depth is 75 m, the index corresponds to a mean potential new primary production ranging from about 17 gC m^{-2} in 1990 to 95 gC m^{-2} in 2000. During the period from about 10 May to 26 June, the mean daily potential new production on

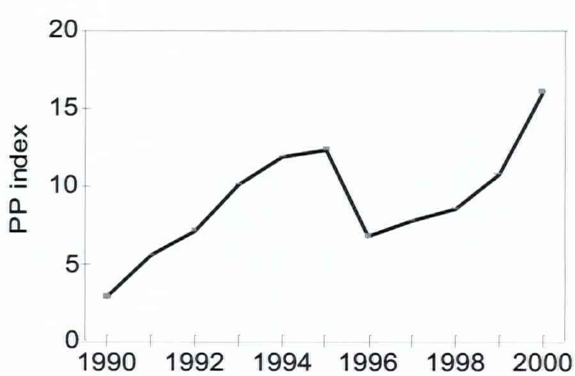

Figure 9. Calculated index of the potential new primary production on the Faroe Shelf.

the central Faroe Shelf varied between about 0.4 mgC m^{-2} day^{-1} (1990) and 2 gC m^{-2} day^{-1} (2000).

The onset of primary production on the Shelf varied by more that a month during the years 1990–2000 (Gaard *et al.*, 1998; Figures 4 and 5). The timing of the spring bloom is thought to have important ecological consequences for copepod reproduction (e.g. Diel and Tande, 1992; Kiørboe *et al.*, 1990; Kiørboe and Nielsen, 1994; Hirche, 1996; Niehoff *et al.*, 1999; Niehoff and Hirche, 2000), and therefore also for feeding and survival of fish larvae (e.g Ellertsen *et al.*, 1980; Cushing, 1990; Leggett and DeBlois, 1994; Gaard and Steingrund, 2000).

The initiation and evolution of the spring bloom are determined by a combination of events that reflect a balance between the amount of solar radiation received by the phytoplankton population, the variability in concentrations of dissolved inorganic nutrients, and phytoplankton losses associated with respiration, grazing, and sedimentation (Smetacek and Passow, 1990; Platt *et al.*, 1991) and, in this case, possible flushing out of the area.

Unfortunately, no data-series are available for light penetration on the Faroe Shelf during spring. However, data-series from meteorological stations ashore (Figure 2) indicate that the variability in timing of the spring bloom onset and the calculated new primary production are not related to variability in intensity in solar radiation.

The depth (or stratification) of the upper, mixed layer is often an important factor in determining the photosynthetic rate, and hence the development of the spring bloom (e.g. Sakshaug and Slagstad 1991). However, on the Faroe Shelf, variability in physical forces (e.g. wind, tidal currents, and stratification) does not correlate with the variability of timing of the spring bloom development or the primary production (Gaard *et al.*, 1998). This is not surprising, since the strong tidal currents do not permit any marked stratification on the Shelf. Consequently the depth of the (productive) water column on the Faroe Shelf is fairly constant, and not influenced by forcing. Therefore effects from variable phytoplankton loss seem to be a more likely reason for the observed variability in phytoplankton growth. Losses may be due to flushing out of the ecosystem and grazing.

Although the flushing rates of seawater on the Faroe Shelf may vary, they seem to be too low to be the main factor affecting the observed variability in spring bloom development and primary production.

Sakshaug *et al.* (1991) showed in a mathematical model that variable loss rates of phytoplankton may affect the timing of spring bloom development, and Yin *et al.* (1997) reported an impact by the large oceanic copepod, *Neocalanus plumchrus*, during early spring from the Strait of Georgia, British Columbia. The presence of a high biomass of this copepod prior to the spring bloom may be able to repress, and thus delay, spring bloom development in that area. Bathmann *et al.* (1990) also suggested that copepod grazing may influence spring bloom development in the Norwegian Sea. On the other hand, other researchers have stated the opposite and concluded that the grazer community cannot control or postpone a spring bloom (e.g. Smith *et al.*, 1985; Hirche *et al.*, 1991; Nielsen and Hansen, 1995).

There is a strong inverse relationship between the zooplankton biomass and the nitrate loss, i.e. new primary production (Figure 10). In years with low zooplankton biomass, the primary production developed early and levels were high, while in years with high zooplankton biomass, the spring bloom occurred later and the production was reduced. The variability in zooplankton biomass is dominated by *C. finmarchicus*. During early spring, substantial (but interannually highly variable) amounts of overwintered *C. finmarchicus* are advected onto the Shelf (Gaard and Hansen, 2000). A key question is whether grazing by *C. finmarchicus* could have delayed the spring bloom and decreased the total new primary production during spring and early summer. Unfortunately, simultaneous measurements of copepod ingestion rates and primary production *in situ* during pre-bloom and bloom periods are not available, and without such data a final conclusion is not possible. However, the inverse relationship between zooplankton biomass (largely *C. finmarchicus* biomass) and primary production supports this.

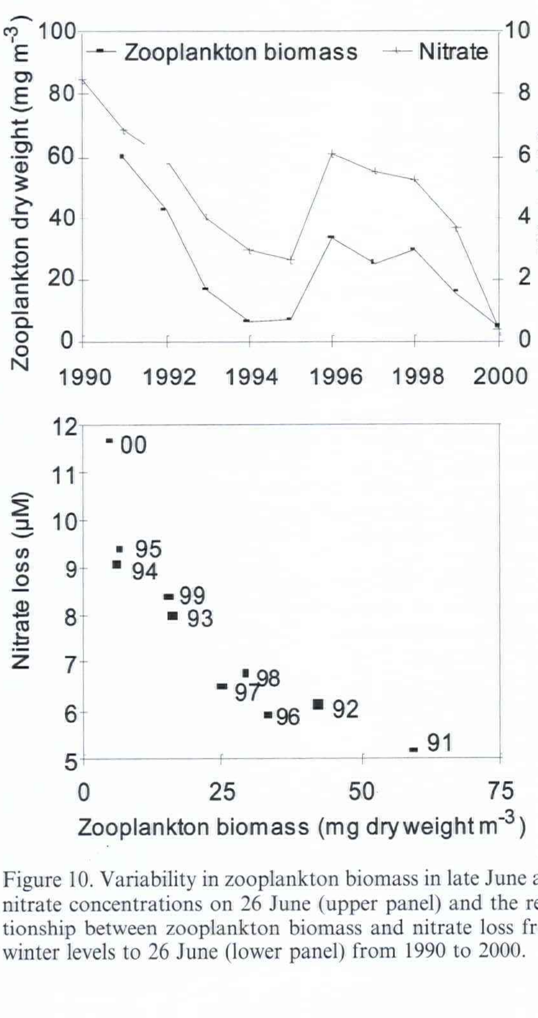

Figure 10. Variability in zooplankton biomass in late June and nitrate concentrations on 26 June (upper panel) and the relationship between zooplankton biomass and nitrate loss from winter levels to 26 June (lower panel) from 1990 to 2000.

Zooplankton variability

During the period 1989–2000, considerable variability was observed in zooplankton abundance and species composition. The ecosystem fluctuated interannually between high influence of the oceanic environment and neritic dominance with lower oceanic influence.

During 1989–1990, the ecosystem was dominated by *C. finmarchicus*, while neritic zooplankton species were of minor importance. Differences between the Shelf area and the surrounding offshore area were generally small. However, during the early 1990s the species composition on the Faroe Shelf changed and the area gradually became more and more neritic (Figure 7). *C. finmarchicus*, which was still the dominant copepod outside the tidal front (Gaard, 1999), gradually became less abundant inside the tidal front, while other copepod species, mainly *Acartia longiremis* and *Temora longicornis*, increased in numbers. *C. finmarchicus* was scarce on the shelf, especially during the period 1993–1995 and in 2000. Although predation on *C. finmarchicus* obviously must have affected its abundance in the ecosystem, variable advection of individuals from offshore is presumed to be a main reason for the changes in abundance. The main inflow area seems to be on the western shelf slope (Gaard and Hansen, 2000).

Egg production of copepods is highly affected by food availability (e.g. Kiørboe *et al.*, 1990; Kiørboe and Nielsen, 1994; Hirche 1996 and references therein; Niehoff *et al.*, 1999). This effect is also seen on the Faroe Shelf, where development of the copepods reflects the seasonal production of phytoplankton (Gaard, 1999, 2000). However, there is a considerable pre-bloom reproduction of overwintered *C. finmarchicus*, mainly on the western and northwestern shelf slope region that is advected from the offshore (Gaard, 2000; Gaard and Steingrund, 2000). Thus copepod reproduction and development seems to start with *C. finmarchicus* in early spring and then, as the phytoplankton biomass increases during spring, the neritic species increase their reproduction.

Effect on higher trophic levels

During the 1990s, fish reproduction, growth, and catches on the Faroe Shelf have undergone quite extensive and dramatic changes. The annual landings of cod and haddock, which in the long term fluctuate between 20 000 and 40 000 and between 15 000 and 25 000 tonnes, respectively, decreased in the early 1990s to historically low levels of only ~6000 and ~4000 tonnes, respectively, in 1993. Landings of both species increased rapidly to maximum levels in 1996 and 1998, respectively, and then fell to average levels by the end of the 1990s (ICES, 2000). Although high fishing mortality undoubtedly influenced these trends, their main cause seems to have been variable recruitment and growth rates induced by environmental changes (Gaard *et al.*, 2002; Steingrund *et al.*, 2003). During the late 1980s and the beginning of the 1990s there was a general recruitment collapse of many fish species and their food in the ecosystem. At the same time as the recruitment was low, fish growth was low, and seabirds also declined (Gaard *et al.*, 2002). The production of their main food sources also seems to have been low. By the mid-1990s the recruitment and growth rates had increased again. Variability coincided well with variability in the calculated new primary production (Gaard *et al.*, 2002; Steingrund *et al.*, 2003), which, during the 1990s. was reflected in trophic levels throughout the ecosystem, including fish and seabirds. The entire ecosystem changed between low-production and high-production periods in all trophic levels.

The negative relationship between zooplankton biomass (largely *C. finmarchicus* variability) and fish recruitment and growth may seem contradictory. However, first-feeding fish larvae depend on high concentrations of small-sized zooplankton. Spawning of the main fish species on the Shelf (cod, haddock, sandeel, and Norway pout) takes place in early spring and the successful survival and feeding conditions of the larvae depend largely on high copepod reproduction in spring. During the first years of the period for which plankton data are available (mainly 1989–1991), production was at a very low level and zooplankton on the Shelf was mainly composed of oceanic plankton. The zooplankton was dominated by *C. finmarchicus* and its reproduction during early spring seems to have been low. Thus, although the zooplankton biomass on the shelf was quite high during that period, to a large extent it consisted of large-sized *C. finmarchicus* during spring. Such a food environment does not favour feeding conditions for small fish larvae. Gradually, however, during the early 1990s, primary production markedly improved at the same time as the ecosystem gradually became more and more dominated by small-sized neritic zooplankton. It is hypothesized that an increased production of small-sized zooplankton organisms (both *C. finmarchicus* and neritic species), mainly during spring, has caused a corresponding increase in food availability for fish larvae in general on the Faroe Shelf during the early 1990s and that this has been a major reason for the fish recruitment and growth recovery. Environmental conditions may not only affect survival of cod and haddock larvae, but also of their prey species (e.g. sandeel). A negative relationship between zooplankton abundance and cod and haddock recruitment has also been observed on the Scotian Shelf (Drinkwater *et al.*, 2000).

In summary, primary production has fluctuated very much during the 1990s, and the fluctuations are reflected through all trophic levels, including fish and seabird growth and reproduction. The production was negatively correlated with abundance of *C. finmarchicus* and it is hypothesized that a potential grazing effect may delay and reduce the phytoplankton production. During years with high advection of overwintered *C. finmarchicus* onto the Shelf the abundance of small-sized zooplankton was low. The general decrease in fish production during the period from the 1980s to the beginning of the 1990s may have been due to low abundance on the Shelf of suitable sized prey for fish larvae during spring.

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