SEASONAL DEVELOPMENT OF PLANKTON IN THE BARENTS SEA:
A CONCEPTUAL MODEL

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ABSTRACT

Capelin (Mallotus villosus) is a small salmonid fish that forms the basis of one of the most important fisheries in the Barents Sea. Relatively large variations in growth of capelin prompted ecological investigations on the feeding conditions of capelin and these were initiated by the Institute of Marine Research in 1979. The studies were expanded in 1984 with the start of the Norwegian Research Program for Marine Arctic Ecology (PRO MARE). A conceptual model for the seasonal development of plankton has provided a framework for our studies in the Barents Sea. The model emphasizes the importance of the ice edge spring phytoplankton bloom for the spawning and development of zooplankton and for the northwards seasonal feeding migration of capelin. The model is reviewed in light of field observations and some remaining key questions for our further studies are pointed out. While the main elements of the model have in broad terms been verified, it will in the future be necessary to put more emphasis on large scale processes such as transport of plankton by dominant currents and the ecological feedback interactions such as predation by capelin and grazing by zooplankton.

INTRODUCTION

The Barents Sea is a high latitude ecosystem located approximately

between 70° and 80°N on the North European shelf. It has an area of about 1.4 10^6 km^2 and an average depth of 230 m (Loeng,1987). The physical oceanographic conditions in the Barents Sea are characterized by meeting and mixing of relatively warm Atlantic water flowing in from south-west and cold Arctic water in north (Midttun and Loeng, 1987).

The Barents Sea is an important feeding and nursery area for large commercial fish stocks, e.g. of cod, haddock, redfish and capelin (Loeng, 1987; Dragesund and Gjøsæter, 1987). Capelin (<u>Mallotus villosus</u>), which is a small and short-lived salmonid fish (Forberg and Tjelmeland, 1984; Gjøsæter and Loeng, 1987), is the dominant pelagic planktivorous species with a stock size of 3 to 7 million tonnes in the period 1973-1983 (Hamre, 1984). The growth of capelin has shown marked interannual variability (Gjøsæter, 1984; Gjøsæter and Loeng, 1987), and this has great consequences for maturation and thereby the management of the capelin fishery (Hamre, 1984; Tjelmeland, 1984). With the aim to predict capelin growth conditions, biological oceanographic investigations were initiated by the Institute of Marine Research in 1979 and expanded as part of the Norwegian Research Program on Marine Arctic Ecology (PRO MARE) in 1984.

These investigations have been based on a conceptual model of ice edge spring phytoplankton bloom, zooplankton reproduction and development, and capelin feeding migration. Here we present a detailed description of this model, review some of its basic concepts and assumptions in light of field observations, and point to some remaining key questions that will direct our future research in the Barents Sea.

THE CONCEPTUAL MODEL

A large but variable part of the Barents Sea is influenced by seasonal ice (Loeng, 1987; Midttun and Loeng, 1987). Freezing and thawing of ice are therefore prominent processes of great consequences for the biological development in this area. Our conceptual model for the seasonal development of the plankton,

which starts with a phytoplankton bloom associated with the retreating ice edge, is shown schematically in Fig. 1. The successional time axis coincides ideally with the N-S gradient. Thus different stages in the plankton development can be found at a transect perpendicular to the ice edge. This is a valuable asset from a scientific point of view and makes the ice edge region a suitable place for detailed studies of plankton development.
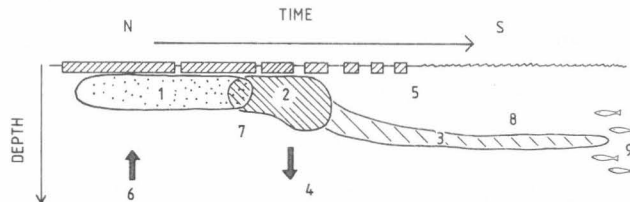

Fig. 1. A conceptual model for the seasonal plankton development in the Barents Sea. The receding ice edge acts as a biological time setter, and various stages of the seasonal plankton development can be found along a N-S gradient.

    1 - prebloom phytoplankton growth predominantly by flagellates,

    2 - ice edge phytoplankton bloom typically dominated by diatoms,

    3 - postbloom deep chlorophyll maximum,

    4 - sedimentation of part of the spring bloom,

    5 - oligotrophic surface layer with production based mainly on regenerated nutrients,

    6 - upwards migration of overwintering zooplankton,

    7 - spawning of zooplankton,

    8 - development and growth of the new generation of zooplankton,

    9 - capelin feeding migration.

Melting of ice usually starts fairly late in the spring when light conditions are already good. The earliest stage of the phytoplankton development is found in the northern areas with dense ice cover prior to any substantial melting. Some growth of phytoplankton will occur in this prebloom situation which is assumed to be dominated by small flagellates. With the thawing of ice in the ice edge region the abrupt increases in light and water column stability results in the eruption of the spring phytoplankton bloom. This ice edge bloom is typically dominated by diatoms.

Depletion of nutrients from the upper layer causes the ice edge bloom to culminate. Massive sedimentation of ungrazed algal material occurs at this stage. Towards the end of the bloom the phytoplankton biomass is concentrated in the lower part of the euphotic zone where it forms a pronounced subsurface maximum. This maximum continues as a subsurface chlorophyll maximum in the stratified summer situation, although both physiological adaptation and species selection are probably involved in the transition between the late bloom and summer situations. The pronounced pyknocline caused by the light meltwater layer effectively restricts upwards transport of nutrients from the deeper layer in summer. After the spring bloom, therefore, oligotrophic conditions prevail in the upper layer with low rates of production based on regenerated nutrients and with flagellates as the dominant phytoplankters.

Calanoid copepods are the dominant component of the zooplankton, with Calanus finmarchicus and C. glacialis as the most important species south and north of the polar front, respectively. The overwintering of zooplankton takes place in deeper water followed by a seasonal upwards migration in early spring. Grazing on phytoplankton in the prebloom and early bloom phases benefits maturation and egg laying, and spawning is assumed to occur early in the bloom. The developing young stages utilize the later stage of the spring bloom as well as production during the following summer situation.

The immature capelin overwinters mainly in and south of the polar front region. The northwards feeding migration starts in early summer, but the most extensive migration takes place in late summer and early autumn (July - September). This migration of capelin is delayed relative to the receding ice edge and ice edge bloom, which allows capelin to exploit the zooplankton in its later developmental stages.

PRO MARE

The Norwegian Research Program for Marine Arctic Ecology - PRO

MARE - was initiated in 1984 and will be a six years ecological study program ending in 1989. PRO MARE is composed of approximately 20 separate research projects covering physical oceanography, plankton, ice biota, fish, sea birds and mammals. It consists of long-range basic research which aims at improving the basis for management and protection of economic or otherwise valued resources. The program is funded by the Norwegian Research Council for Science and the Humanities, the Norwegian Fisheries Research Council and the Norwegian Ministry of Environment, and has an annual budget of 7 million Nkr. In addition comes an equally large indirect funding from participating institutions in the form of ship-time, etc.

The plankton studies in PRO MARE has had the conceptual model described above as a central element in order to achieve integration of the separate projects in a larger system ecological perspective. PRO MARE has sponsored detailed studies including microbiology, phytoplankton growth dynamics, nutrients cycling, zooplankton grazing, and sedimentation. A comprehensive review of all these aspects must await further integrative data analysis.

PHYTOPLANKTON SPRING BLOOM

Phytoplankton blooms in the ice edge zone appears to be a general phenomenon associated with melting and retreating ice distribution. Such blooms have been described for both arctic and antarctic environments (Alexander, 1981; Niebauer et al., 1981; Schandelmeier and Alexander, 1981; Horner and Schrader, 1982; Sakshaug and Holm-Hansen, 1984; Smith and Nelson, 1985, 1986). Because a large, although variable, part of the Barents Sea is influenced by freezing and thawing of seasonal ice (Vinje, 1983; Midttun and Loeng, 1987), one would expect an ice edge phytoplankton bloom to be a pronounced feature in the seasonal production cycle of this sea area. Marshall (1958) presented a short analysis of the ice edge bloom development using the model of Sverdrup (1953). Rey and Loeng (1985) presented further documentation of the Barents Sea ice edge bloom, which has also been the subject of simulations with a mathematical model (Slagstad 1985).

The investigations both prior to and in PRO MARE have clearly demonstrated the ice edge bloom as a prominent and consistent feature in the seasonal plankton development of the Barents Sea. This is examplified by results from cruises with R/V "G.O. Sars" and M/S "Lance" in May-June 1983 (Fig. 2). The hydrographical sections show the sharp polar front which separates the cold arctic water in north from the warmer and more saline Atlantic water in south (Fig. 2 A,B) and the surface layer of light meltwater south of and in the ice edge zone (Fig. 2 B). The phytoplankton growth is reflected by the nutrient depletion in the meltwater region (Fig. 2 C, D). The actual ice edge bloom is seen as a fairly narrow zone of high chlorophyll concentration in the upper layer some 15-20 km into the ice covered waters (Fig. 2 E). This corresponds to an area with sharp horizontal gradients in nutrient concentrations (Fig. 2 C, D), reflecting their consumption by the developing bloom.

In the Atlantic water south of the polar front the stability of the water column was low and due to a weak temperature gradient reflecting the seasonal warming (Fig. 2 A). This resulted in a delayed bloom development and culmination here (Fig. 2 C-E). Analysis of data from late spring and early summer in the years 1979 to 1984 has revealed the great importance of stability formation in determining spring bloom development in the Barents Sea (Rey et al., 1987; Skjoldal et al., 1987). There is considerable variability among areas and years depending upon differences in physical conditions. Stability formation occurs by three major mechanisms: (1) warming of the surface layer; (2) melting of ice in "warm" Atlantic water; (3) melting of ice in Arctic water due to insolation and atmospheric heating. In cold years with much ice formation, ice will drift south of the polar front and melt in the Atlantic water. This is more or less independent of the atmospheric conditions and melting can take place in winter time. The resulting stabilization of the water column allows the spring bloom to take place as early as April (Skjoldal, 1986; Skjoldal et al., 1987). In contrast, in Atlantic water of homogeneous salinity, the peak of the bloom usually occurs in June (Marshall, 1958; Rey and Loeng, 1985; Rey et al., 1987; Skjoldal et al., 1987). Somewhat paradoxically, therefore, the
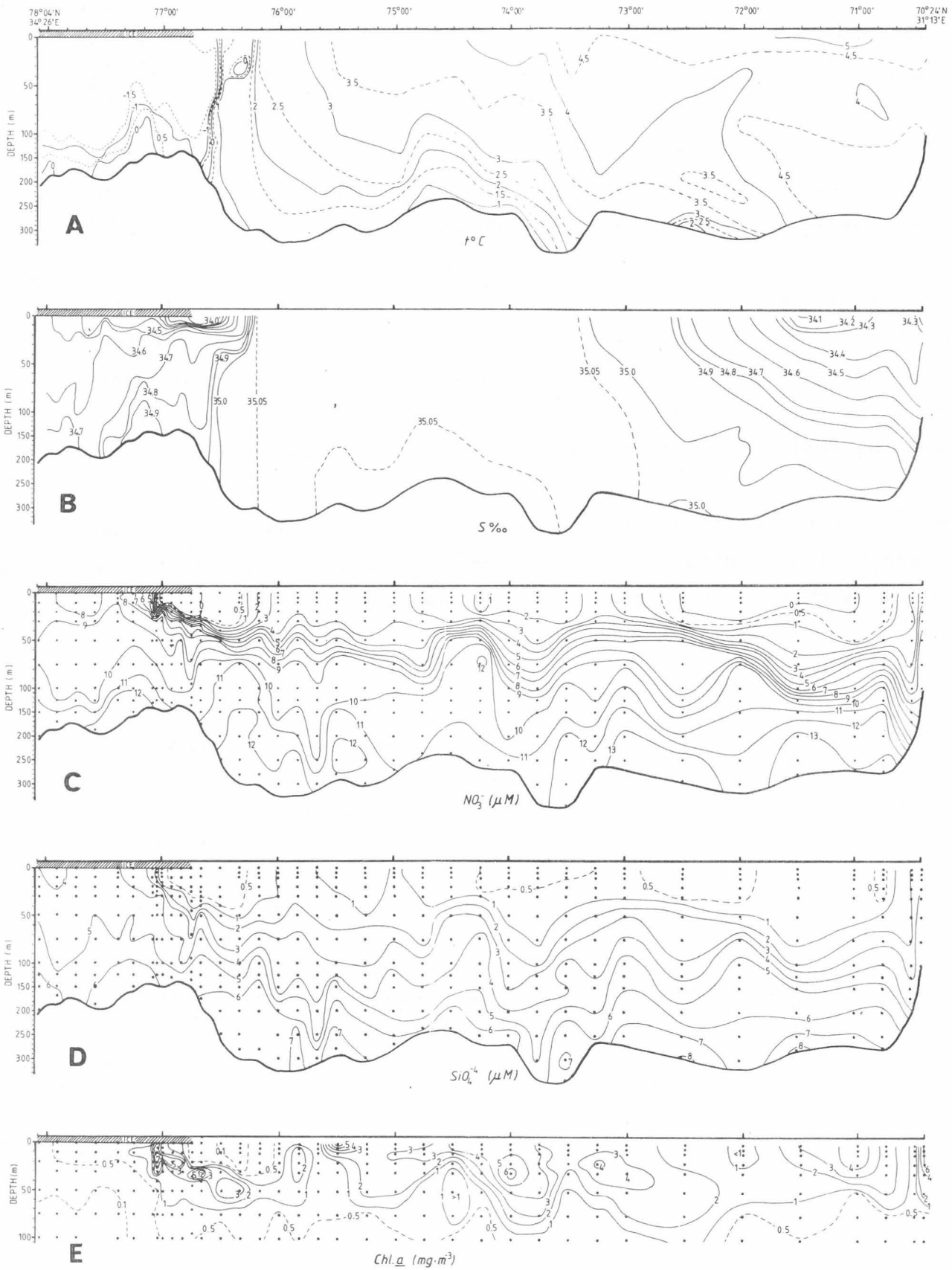
Fig. 2. Distributions of temperature (A), salinity (B), nitrate (C), silicic acid
(D), and chlorophyll a (E) along a N-S section from the coast of Finmark to
78°04'N in early June 1983. Results from cruises with R/V "G.O. Sars" and M/S
"Lance" (Gjøsæter et al., 1983).

spring bloom starts earliest in the southern areas of water influenced by ice in cold years whereas the bloom can be at least six weeks delayed in the Atlantic water further south (Skjoldal et al., 1985).

The effect of vertical mixing due to cooling and freezing in winter is to homogenize the water column. To what degree the mixing extends to the bottom is probably variable depending on bottom topography as well as hydrographic and atmospheric conditions. Mixing reaches the bottom over the shallow bank areas. Vertical profiles obtained in January 1985 revealed a pronounced two-layering of the Arctic water (Fig. 3 A). Breakdown of this layering would depend on the extent of ice formation during rest of the winter. Ice formation over shallow bank areas results in heavy water that floats down the bank slopes to form bottom water in the deeper basins (Midttun, 1985; Midttun and Loeng, 1987). This is a mechanism that tends to stabilize the deeper part of the water
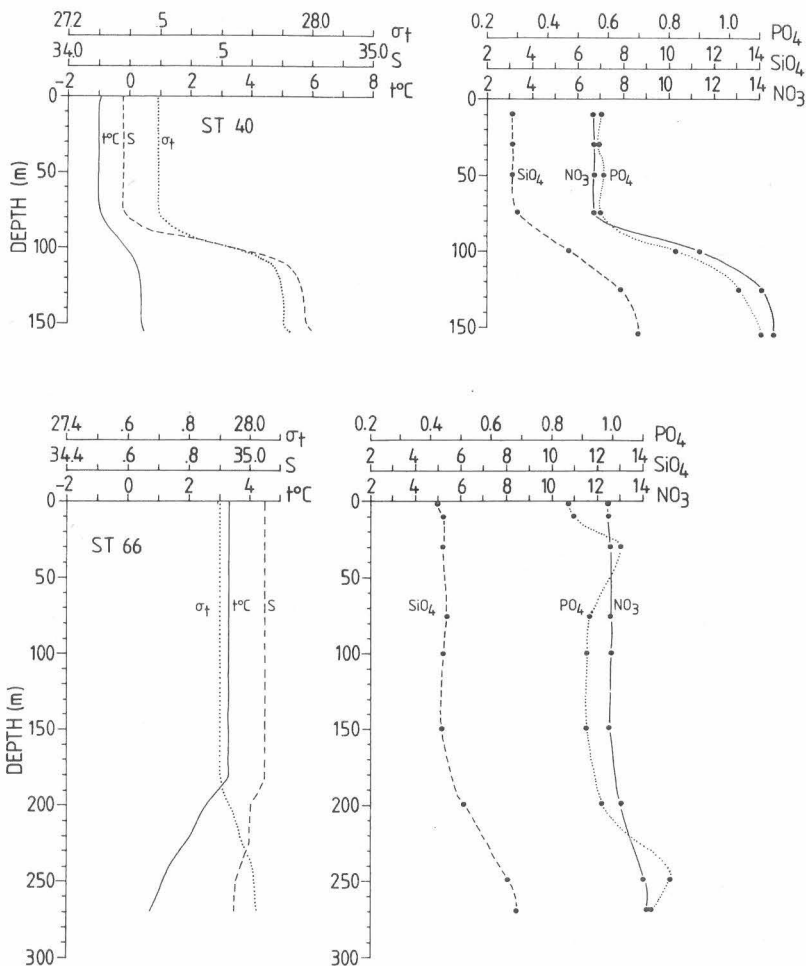
Fig. 3. Vertical profiles of hydrographical features (left) and nutrients (right) at station 40 in Arctic water (A) and station 66 in Atlantic water (B) in January 1985. From Hassel et al. (1986).

column, isolating the bottom from the homogenous upper layer (Fig. 3 B). In terms of reintroducing sedimented resting spores into the upper water column, this could be of great ecological significance. The shallow bank areas might serve as nucleus areas for growth of bloom diatoms with resting spores in their life cycle, such as the dominant species Chaetoceros socialis.

Typical concentrations of nutrients in the Atlantic water in winter are 12-14 uM nitrate, 6-7 uM silicate and 0.8-1.0 uM phosphate (Fig. 3 B). The concentrations are somewhat lower in the Arctic water where nitrate is typically about 10 uM. The phytoplankton biomass in mid winter is very low with chlorophyll concentration of 0.01 ug L^{-1} or less (Hassel et al., 1986). Flagellates and monads < 5 um occurred in fairly high numbers, 0.5-1.5 10^6 cells L^{-1} (Table 1), and a large part of these was probably living heterotrophically. Heterotrophic forms dominated the microplankton counts, and fairly large dinoflagellates occurred in numbers of 10-20 10^3 cells L^{-1}. Diatoms were rarely seen except at stations on the Central Bank with homogenous water column from surface to bottom (Table 1).

Table 1. Taxonomic composition of phytoplankton (numbers of cells 1^{-1}) at a station in Atlantic water in the western Barents Sea (Stn 31) and at a station in mixed Atlantic-Arctic water on the Central Bank (Stn 78) in January 1985 (Hassel et al., 1986).

Taxon	Stn 31			Stn 78	
	10 m	100 m	300 m	10 m	125 m
Cryptophyceae	591	1730	148	2307	3223
Gyrodinium grenlandicum	-	1154	2307	4614	1154
Athecate dinoflagel. 10-30 um	4614	5768	6922	12690	21918
Other dinoflagellates	160	160	160	200	320
Prymnesiophyceae	3904	7498	1154	-	-
Diatoms	-	-	-	2508	4645
Prasinophyceae	-	-	-	1626	443
Flagellates & monads <5 um	736000	637000	1592000	547000	1024000
Flagellates & monads >5 um	71500	72000	100000	60000	227000
Zoomastigophorea	1154	1154	-	9230	2307

The model postulates predominance of small flagellates in the

early pre-bloom phase of phytoplankton development (Fig. 1). Evidence in support of this has been obtained from field observations. During a cruise in April 1986 in ice-covered melt water and open Atlantic water , a progressive decrease in the relative contribution of flagellates, and an increase in the proportion of autotrophic biomass, occurred with increasing development in the early stages of the spring bloom (C.D. Hewes, unpubl. results; Fig. 4). Small flagellates of about 2 um size were also found to be dominant in the pre-bloom situation in ice-covered Arctic water during the cruise with M/S "Lance" in 1983 (Fig. 2). This was reflected in relatively larger consumption of nitrate than of silicate (Fig. 5 B). Predominance of flagellates in pre-bloom situations has also been found in other studies in arctic and boreal waters (Braarud, 1935; Throndsen and Heimdal, 1976; Schandelmeier and Alexander, 1981; Horner and Schrader 1982).
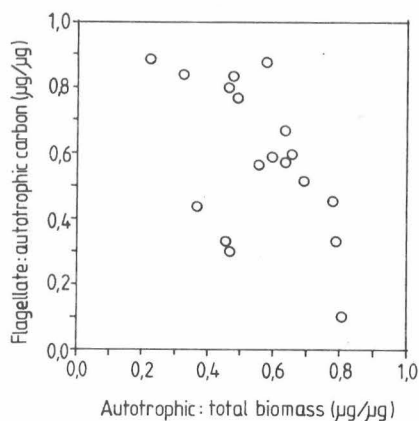

Fig. 4. Relationship between the proportion of phytoflagellate to total autotrophic biomass and the proportion of autotrophic to total nanoplankton (<10 um) biomass during the early phase of the spring bloom in April 1986. From Christopher D. Hewes (unpubl. results).

The role of ice algae in the initiation of ice edge phytoplankton blooms in the Barents Sea is not clear. It has been suggested for the Bering Sea that algae originating from the ice may act as an inoculum early in the spring bloom (Alexander and Chapman, 1981; Schandelmeier and Alexander, 1981). However, the ice community is generally dominated by pennate diatoms, while the spring phytoplankton bloom consists primarily of centric diatoms (Horner and Schrader, 1982). Much of the ice in the Barents Sea is seasonal ice that forms in late autumn and winter, and is apparently poor in ice algae. Syvertsen (1985) observed a thin layer of planktonic diatoms at the underside of the ice in early spring and suggested

that this represented a growing layer that could be of great
importance for the ensuing spring bloom in the water column.
Positive buoyancy could be a possible mechanism for such a
concentration of diatoms (Lännergren, 1979; Smetacek 1985). Our
data for the pre-bloom stations in 1983 revealed a positive
relationship between integrated chlorophyll a in the water column
and nitrate consumed, with an intercept close to the origo (Fig. 5
A). This is not indicative of any marked consumption of nutrients
by algae associated with the ice. Suspension of algae due to the
disturbance of the ship prior to sampling is, however, a possible
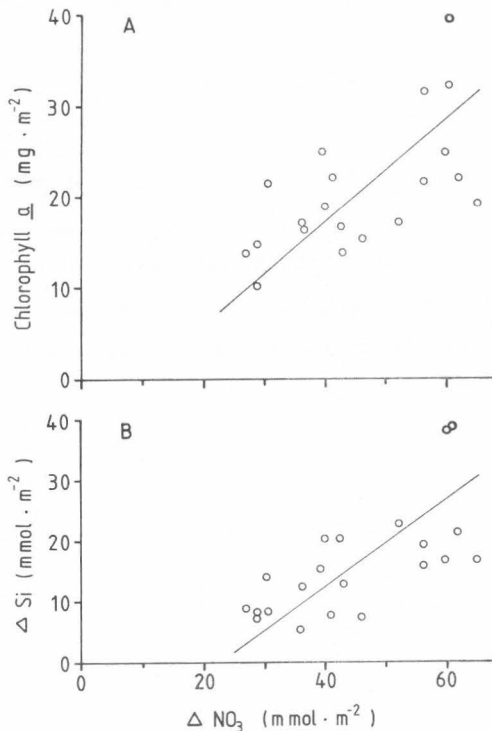complicating factor for this interpretation.

Fig. 5. Relationships between depth-
integrated (0-50 m) content of
chlorophyll a and consumed nitrate
(A) and between consumed silicic
acid and consumed nitrate (B) at
stations in ice-covered water with
prebloom conditions in late May and
early June 1983. Data from cruise
with M/S "Lance" (Gjøsæter et al.,
1983).

The spring phytoplankton bloom is typically dominated by diatoms
of the genera Chaetoceros, Nitzschia and Thalassiosira along with
the colony-forming phytoflagellate Phaeocystis pouchetii. This is
similar to the spring bloom composition in the Bering Sea (Goering
and Iverson, 1981). The detailed patterns of occurrence of
Phaeocystis and diatoms in the Barents Sea have not been
systematically analysed as yet. Due to their different ecological
properties in terms of sinking, sedimentation and trophic fate, the
relative occurrence and competition between diatoms and Phaeocystis
is an important aspect that needs clarification in future studies.

Some indications of the relative importance of diatoms on one hand and Phaeocystis (and other flagellates) on the other can be gained from nutrients consumption patterns. Data from the spring and early summer period in 1980-1984 (Fig. 6) indicate a marked interannual variability that ranges from apparent nitrate limitation of the system in some years (1980, 1981) to silicate limitation in others (1983, 1984). We assume that diatoms are more important in years with indicated silicate limitation. There is possibly a succession in such years with Phaeocystis taking over after the diatoms, continuing to grow until the nitrate has been used up. Such a pattern of Phaeocystis bloom following the spring diatom peak has also been reported from the North Sea (Cadée and Hegeman, 1986; Veldhuis et al., 1986).
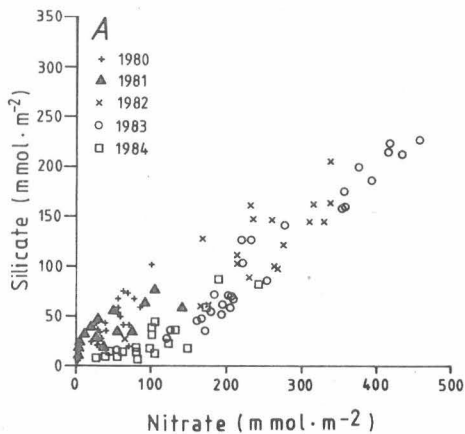

Fig. 6. Relationship between contents of silicic acid and nitrate in the upper 50 m at stations along a N-S section during or just after the spring bloom in the years 1980-1984 (Skjoldal et al., 1987).

GRAZING AND SEDIMENTATION

Grazing and sedimentation are the main fates of the spring phytoplankton blooms. Our data for the years 1979-1984 indicate a large variation in the relative importance of these two opposing processes. The time course of the spring phytoplankton bloom development and the stock size of overwintering zooplankton which participate in spawning are the two major factors determining the proportion of the spring bloom that is being grazed. The spring phytoplankton development ranges from rapid and short-lived blooms under conditions of high water column stability such as in the ice

edge meltwater region, to slowly developing and prolonged blooms under conditions of low stability such as in Atlantic water south of the meltwater area (Skjoldal et al., 1987; Rey et al., 1987). The potential impact of grazing is evidently greatest in the latter case with a low phytoplankton population growth rate.

The zooplankton biomass in late spring or early summer has shown a 10-fold range of variation among years in the period 1979-1984 in waters in and south of the polar front region (Rey et al., 1987). This was mainly due to variations in the stock size of the new generation of developing young copepodites of Calanus finmarchicus (Skjoldal et al., 1987; Fig. 13). The zooplankton biomass was about 20 g dry weight m^{-2} in the years 1979-1981. This represents a minimum estimate of the accumulated secondary production during spring, and, when compared to a primary production of 30-50 g C m^{-2}, suggests an efficient transfer from primary to secondary production (Rey et al., 1987). This further suggests a heavy grazing pressure on the phytoplankton that could markedly prolong the spring bloom. Thus both physical and biological factors influence the time course of the spring bloom development.

To generalize, one would expect the closest coupling of energy transfer in the pelagic zone in warm years with large inflow of Atlantic water or in years when the overwintering zooplankton biomass is high. Little would be left ungrazed to sediment to the bottom under such circumstances. In contrast, in cold years with extensive ice melting in the spring or when zooplankton biomass is low, grazing will have a relatively small impact and much of the bloom will sediment out from the euphotic zone, representing input of energy and matter to the benthic and demersal food chain. The situation in the Barents Sea is therefore somewhat similar to that in the Bering Sea where different regions with pelagic and benthic dominated secondary production have been reported (Iverson et al., 1979; Goering and Iverson, 1981; Cooney, 1981; Cooney and Coyle, 1982; Sambrotto and Goering,1983).

Massive sedimentation of the ice edge spring bloom was observed in 1983 and particularly 1984 , which were years with low biomass of zooplankton in the investigated area. The sequence of vertical

profiles in Fig. 7 shows the introduction of a considerable amount of chlorophyll below the nitracline following culmination of the bloom in the surface layer. Another feature of this sequence is the separation of the nitrate and silicic acid gradients. Apparent utilization of silicic acid below the nitracline is a common phenomenon in the Barents Sea and has been suggested as due to silicic acid consumption associated with resting spore formation of the bloom forming diatom Chaetoceros socialis (Rey and Skjoldal, 1987).

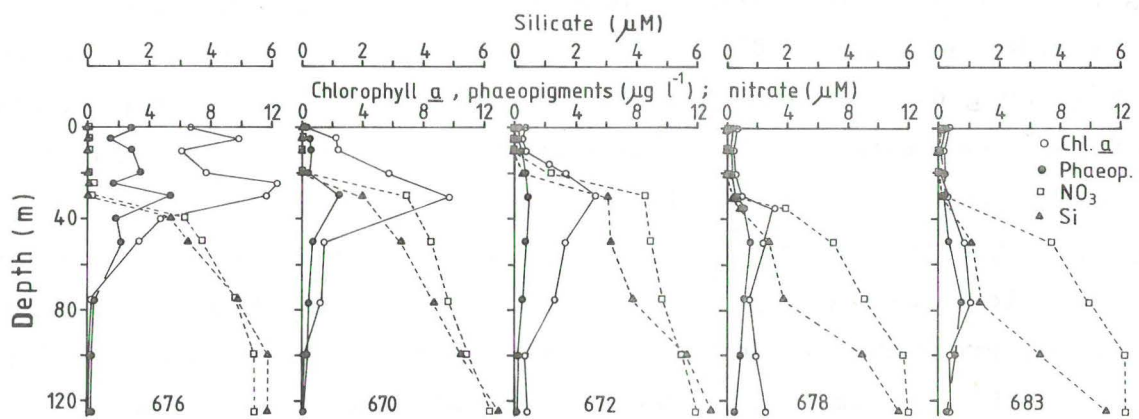Fig. 7. Vertical profiles of chlorophyll a, phaeopigment, nitrate and silicic acid at selected stations from a gradient from bloom to postbloom situations along a N-S section in early June 1984. Data from cruise with R/V "G.O. Sars" (Hassel et al., 1984).

Besides its quantitative effects on bloom production, grazing can also have more qualitative effects, e.g. on the species composition of the phytoplankton. Selective grazing of diatoms by larger zooplankton was considered the reason for dominance of Phaeocystis poucheti in the Bering Sea (Goering and Iverson, 1981). It has been a common contention that Phaeocystis is discriminated against by pelagic grazers. Such a discrimination has not been obvious, however, in recent experiments with Calanus hyperboreus and Calanus finmarchicus as grazers (Huntley et al., 1987; Tande and Båmstedt, 1987).

Our data from the Barents Sea show a relationship between the Si/NO_3 ratio of the nutrients remaining in the water column during or after the spring bloom and the zooplankton biomass (Fig. 8).

Selective grazing on diatoms is one possible explanation for this relationship. A large biomass of zooplankton that has been produced during spring assumedly represents a heavy grazing pressure on the spring bloom. Selective grazing on diatoms could have resulted in low silicic acid consumption and a high Si/NO_3 ratio, reflecting that the system was on the side of nitrate limitation such as in 1980 and 1981 (Fig. 6). In contrast, the relative consumption of silicic acid was much larger in 1983 and 1984 when the zooplankton biomass was low. Low grazing pressure could have favoured the growth of diatoms, leading to silicate depletion (Fig. 6) and massive sedimentation of the diatom bloom.
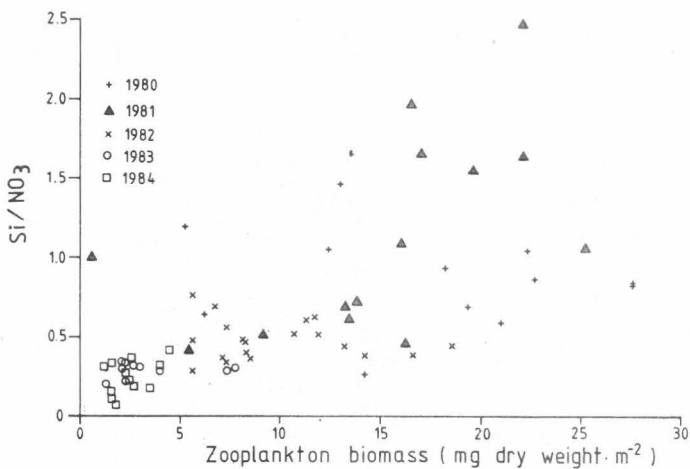

Fig. 8. Relationship between the molar ratio of silicic acid to nitrate content in the upper 50 m and zooplankton biomass (0-200 m) at stations along a N-S section during or just after the spring bloom in the years 1980-1984. Data from Rey et al. (1987) and Skjoldal et al. (1987).

The interrelated aspects of grazing impact on spring bloom development, composition, culmination and fate, and alternate pathways for transfer of primary production into the pelagic food web through grazing or into the benthic/demersal food web through sedimentation form a prominent area for future ecosystem research in the Barents Sea. Better knowledge of these relationships will be an important contribution to the multi-species fisheries research and management problems.

OLIGOTROPHIC SUMMER SITUATION

Following the spring bloom the upper layer is depleted of
nutrients. The melt water layer formed in waters that have been
covered by ice results in a very pronounced pyknocline typically at
a depth of 10-30 m. The melt water layer is only slowly eroded in
its southern extension and covers therefore an extensive area of
the Barents Sea in late summer (Rey et al., 1987). Due to the
shallow depth of the strong pyknocline, light conditions allow
growth of phytoplankton which depresses the nutriclines deeper than
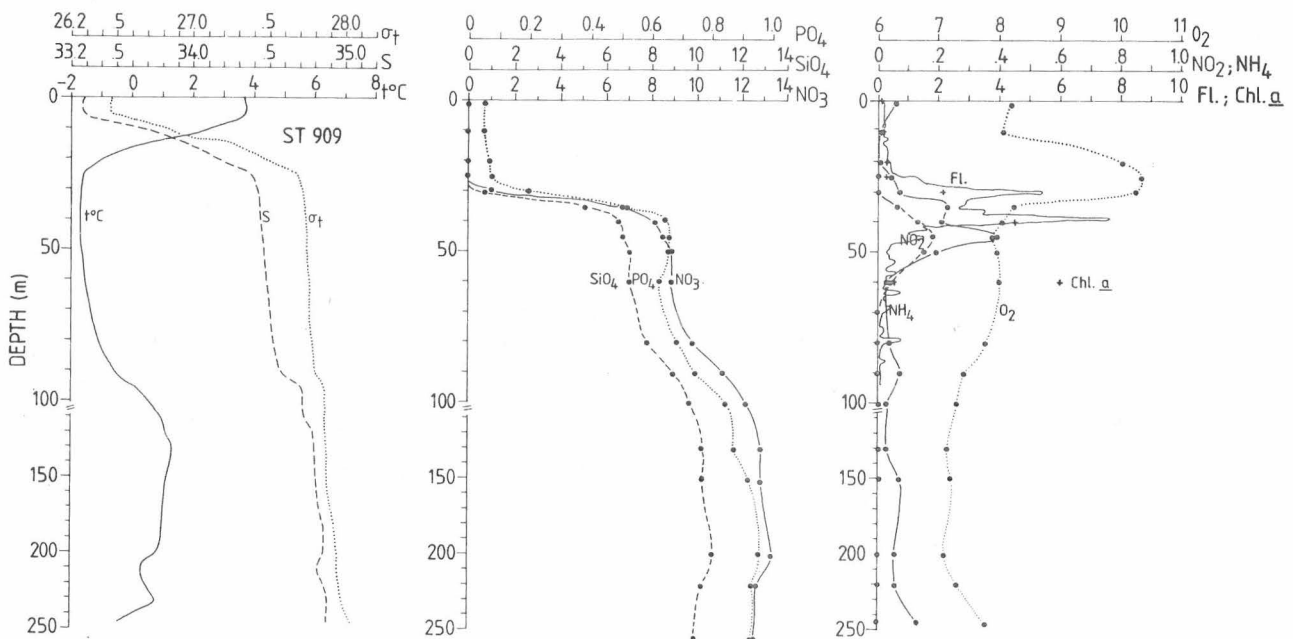the pyknocline (Fig.   9; Rey and Loeng, 1985).

Fig. 9. Vertical distribution of physical structure (left), nutrients (uM)
(middle), and in situ chlorophyll fluorescence (Fl.), chlorophyll a (ug l^{-1}),
oxygen (ml l^{-1}), ammonium and nitrite (uM) (right) at a station in Arctic water
in August 1985. From Loeng et al. (1986).

A deep chlorophyll maximum is usually associated with the
nitracline (Fig. 9). This maximum is typically more sharp and
pronounced in early summer just following the bloom than it is in
late summer (Gjøsæter et al., 1983; Loeng et al., 1986). In our
model we conceive the deep chlorophyll maximum as a continuous
structure from the culmination of the spring bloom when the main
phytoplankton biomass is concentrated towards the bottom of the
euphotic zone (Fig. 1). The growth of phytoplankton is then to a

great extent light limited, and this could be a stage when the
system is very sensitive to the meteorological conditions with
regard to the fate of the accumulated phytoplankton biomass. Good
weather with high light intensities may allow the phytoplankton to
sustain their biomass and to adapt to the dim light conditions at
the bottom of the euphotic zone. In contrast, overcast weather and
fog with light intensities an order of magnitude lower than on
clear days, may cause the accumulated biomass to wither and sink
out from the euphotic zone. Selection plays probably an important
role in the establishment and maintenance of the deep chlorophyll
maximum. Such a selection could occur according to physiological
conditions and ecological properties both within and among species.

The nutrient depleted surface layer typically has a low
chlorophyll content following the spring bloom (Rey and Loeng,
1985; Skjoldal et al., 1987). The sharp pyknocline effectively
reduces the upwards transport of nutrients through the nutricline,
and production in the oligotrophic upper layer is mainly based on
regenerated nutrients. Most of the chlorophyll is contained in
nanoplankton organisms less than 10 um in size, and the proportion
of heterotrophs in the nanoplankton is high (Loeng et al., 1986;
Hewes, 1986).

The deep chlorophyll maximum at or just above the nutricline acts
assumedly as a trap for the upwards transport of "new" nutrients
such as nitrate from the deeper layer. This results in a more or
less clear vertical separation of "new" production in the bottom
layer of the euphotic zone and "regenerated" production in the
upper layer. The nutrients and plankton dynamics in this
oligotrophic summer situation have been important areas of research
within PRO MARE, and the vertical aspects have been particularly
emphasized on cruises in August 1984 and 1985 (Hassel et al.,
1984; Loeng, 1986). The results from these cruises have not been
finally synthesized and it is therefore premature to draw any firm
conclusions. Fig. 9 shows some features which are often observed.
These include a structured chlorophyll maximum layer with two or
occasionally more peaks, a pronounced oxygen maximum above the
chlorophyll maximum, and maxima in ammonium and nitrite in and
below the chlorophyll maximum region. Similar patterns have been

observed also in temperate and tropical environments (Herbland and Voituriez, 1979; Schulenberger and Reid, 1981; Holligan et al., 1984), suggesting that this could be quite general patterns for stratified water columns.

Because of the high stability of the meltwater layer, ice edge blooms are typically hectic and of short duration. As a consequence, much of the copepodite development of the dominant copepods takes place during the oligotrophic situation following the spring bloom. Important questions here are how much of this secondary production is based on respectively new and regenerated production, and how the grazing and production interacts both vertically and temporally.

ZOOPLANKTON REPRODUCTION AND DEVELOPMENT

As is typical for high latitude ecosystems (Longhurst, 1985), copepods constitute the most important group in terms of zooplankton biomass. Calanus finmarchicus is the dominant species in the Atlantic water of the southern Barents Sea, while the closely related C. glacialis is a true arctic species which dominates north of the polar front (Jaschnov, 1972; Tande et al., 1985; Hassel, 1986). Other common copepods are Pseudocalanus sp., C. hyperboreus, Metridia longa, Euchaeta glacialis and Oithona similis.

Euphausids are another important component of the zooplankton, with Thysanoessa inermis and T. raschi as the predominant species occurring mainly in the Atlantic water of the southern Barents Sea and in the polar front and mixed water regions (Hassel, 1986; Loeng et al., 1986). Amphipods are another important group dominated by Parathemisto spp. which occur also in Arctic water north of the polar front.

Among invertebrate predators, chaetognaths occur in fairly high abundance both in the Atlantic and Arctic water masses. Gelatinous forms such as hydromedusae (Sarsia princeps, Euphysa flammea) and ctenophores (Mertensia ovum, Bolinopsis sp., Beroe sp.) can occur

in high abundance in late summer (Loeng et al. 1986).

It has been generally accepted that zooplankton overwinter in deep water, migrating upwards in late winter or spring to spawn in the upper layer (Fomin, 1985; Tande et al., 1985). Such a pattern has been clearly demonstrated for Calanus finmarchicus in Norwegian coastal waters (Sømme, 1934; Skreslet and Rød, 1986) and the Norwegian Sea (Østvedt, 1955). From this one could expect that the dominant Calanus species occurred in the deep water and possibly close to the bottom in winter. However, results from January 1985 revealed fairly even distributions in the water column of both total zooplankton biomass and abundance of Calanus spp. in the central and northern Barents Sea (Fig. 10; Hassel et al., 1986).

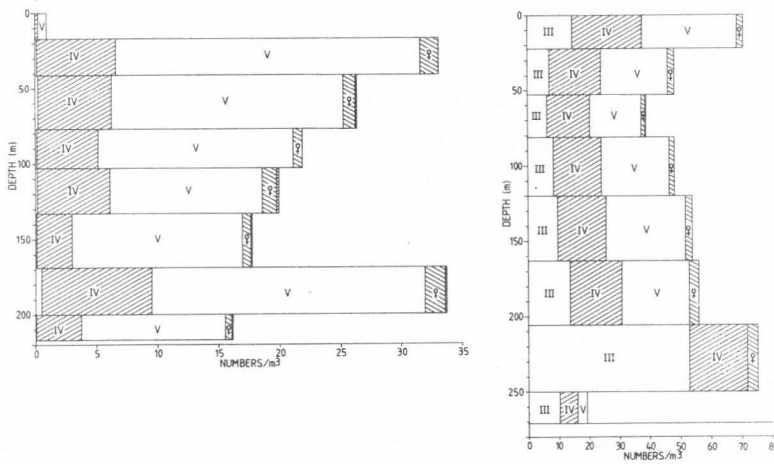Fig. 10. Vertical distribution of copepodite stages of Calanus finmarchicus at stations in the western (A) and eastern (B) Barents Sea in January 1985. From Hassel et al. (1986).

An upwards migration evidently takes place as most of the zooplankton is found concentrated in the upper layer in late winter or spring (Gjøsæter et al., 1983; Melle et al., 1987). According to our model, spawning and development of the early juvenile stages occur in association with the spring phytoplankton bloom. As the ice recedes northwards in summer, one would therefore expect to find the early developmental stages of zooplankton near the ice edge, with a succession of gradually older stages away from the edge. Such a pattern has been observed on several occasions, most clearly for Calanus spp. and euphausids (Ellertsen et al., 1981, 1982; Hassel, 1986).

Calanus finmarchicus overwinters mainly as copepodite stages III-V
(Fomin, 1985). In January 1985, stage V was dominant in the western
Barents Sea (Fig. 10 A). In mixed Atlantic-Arctic water in the
eastern Barents Sea, there was a greater proportion of stages III
and IV (Fig. 10 B).

Calanus glacialis seems to have a two-years life cycle in the
Barents Sea (Tande et al., 1985), as it also has in the Canadian
Arctic (Longhurst et al., 1984). In a prebloom situation in ice
covered waters, the population of C. glacialis was comprised mainly
of copepodite stage IV and adult females, representing presumably
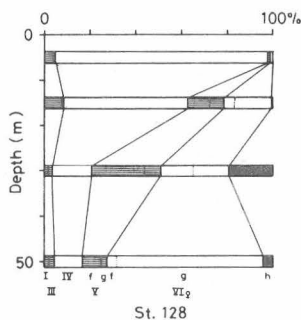one and two years old individuals, respectively (Fig. 11).

Fig. 11. Relative copepodite stage
composition of Calanus glacialis (g),
C. finmarchicus (f) and C. hyperboreus
(h) in the upper 50 m of ice-covered
Arctic water with prebloom condition
in early June 1983 (Gjøsæter et al.,
1983).

Reproduction of zooplankton in relation to spring phytoplankton
development was studied during a cruise in Atlantic and ice covered
waters in April 1986 (Skjoldal, 1986; Melle et al., 1987).
Integrated nitrate consumption was taken as a measure of the
phytoplankton development and the number of eggs per adult female
in the water column was used as an index of spawning activity of
the copepods. The results suggested that the maximum spawning
activity occurred in the early phase of bloom development for both
Calanus finmarchicus and C. glacialis (Fig. 12 A, B). In accordance
with this there was a general increase in the number of nauplii as
the bloom progressed (Fig. 12 C).

Observations on zooplankton development along a N-S transect in
late spring or early summer in the years 1979-1984 have been
analysed in relation to hydrographical conditions and phytoplankton
development (Skjoldal et al., 1987). These results also suggested
early spawning of the Calanus species and, except for 1982,
copepodite stages III-IV were dominant in June or early July (Fig.
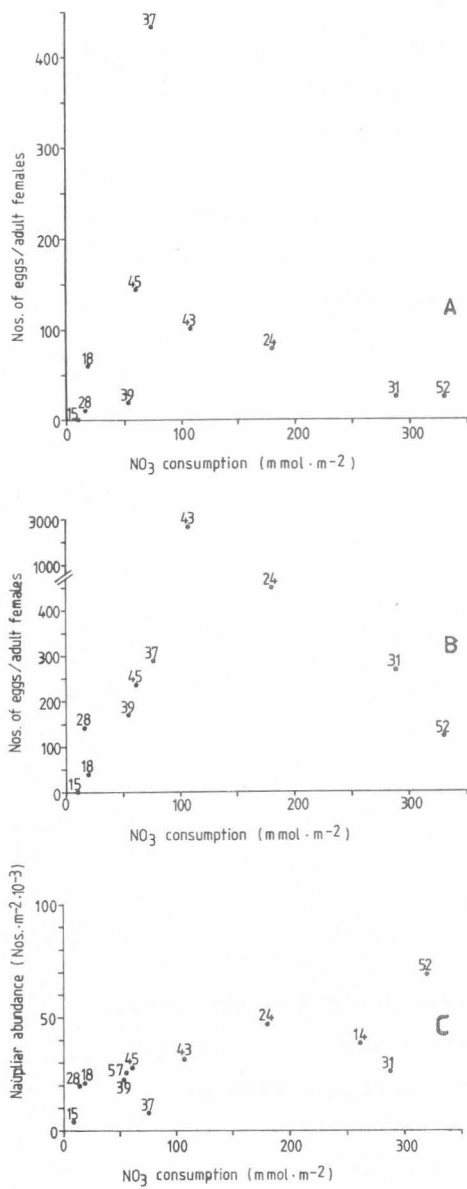
Fig. 12. Reproduction of Calanus finmarchicus and C. glacialis in relation to early spring phytoplankton bloom development. Numbers of eggs in the water column (0-100 m) per adult female of C. finmarchicus (A) and C. glacialis (B) and number of nauplii (0-100 m) for the two Calanus species combined (C) versus estimated nitrate consumption by the developing bloom. From Melle et al. (1987).

13). The copepodite stage development showed a weak relationship with the integrated nitrate utilization and also a relationship with the water temperature at the time of sampling (Fig. 14).

From the above data it seems clear that there exists a dependency of the reproduction of Calanus spp. on the spring phytoplankton development. Intrinsic physiological factors plays probably also a role. Due to the great contribution of Calanus spp. to the total secondary production, further clarification of these functional relationships is important for realistic modelling of the zooplankton production (Slagstad, 1981). The spring bloom development and the climatic conditions as reflected in water temperature is interrelated (Rey et al., 1987; Skjoldal et al.,
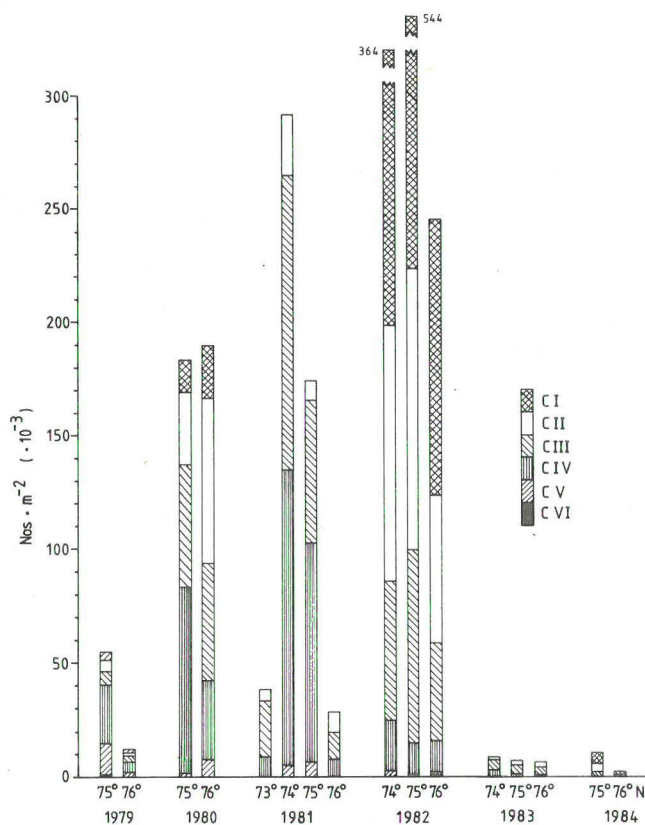
Fig. 13. Abundance of copepodites of <u>Calanus finmarchicus</u> plus <u>C. glacialis</u> at selected stations along a N-S section in the years 1979-1984. From Skjoldal <u>et</u> <u>al</u>. (1987).

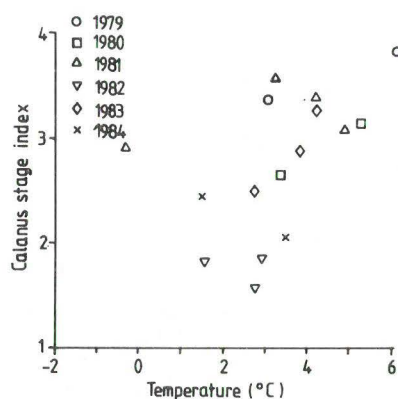Fig. 14. Relationship between average copepodite stage number (stage index) of <u>Calanus finmarchicus</u> plus <u>C. glacialis</u> and temperature of the upper mixed layer at the time of coverage of a N-S section in June or early July in 1979-1984. From Skjoldal <u>et</u> <u>al</u>. (1987).

1987), and their effects on the zooplankton reproduction are therefore difficult to separate. It is likely, however, that the relationship in Fig. 14 at least partly reflects a direct effect of temperature on zooplankton metabolism and rate of development. Such a temperature effect has also been reported for the development of zooplankton in the Bering Sea (Smith and Vidal, 1984, 1986; Vidal and Smith, 1986; Walsh and McRoy, 1986).

The ocean climate of the Barents Sea shows great interannual variability, with large variation in ice cover and area influenced by melting of ice in spring (Midttun and Loeng, 1987). In general terms, the spring bloom in the central Barents Sea tends to occur earlier and be of shorter duration in cold than in warm years. At the same time the rate of early development of zooplankton is retarded by the low temperature. As a consequence, one would expect the optimal match between phytoplankton development and production of Calanus finmarchicus to occur in warm years (Rey et al., 1987; Skjoldal et al., 1987). However, the data on stock size of C. finmarchicus in the years 1979-1984 does not lend support to this generalization. Thus the stock was lower in the warm years 1983 and 1984 than in the cold years 1979 and 1981 (Fig. 13; Skjoldal et al., 1987). One reason for this could be the influence of other factors strongly influencing the stock size, such as predation by capelin and variable transport of zooplankton by the inflowing Atlantic water (Skjoldal et al., 1987).

Towards the end of the active growth period, the seasonal downwards migration out of the surface layer takes place. A vertical profile of Calanus finmarchicus distribution in early June 1984 suggests that this migration can take place shortly after the spring bloom with participation also by the younger copepodite stages (Fig. 15). The relative distribution of zooplankton biomass
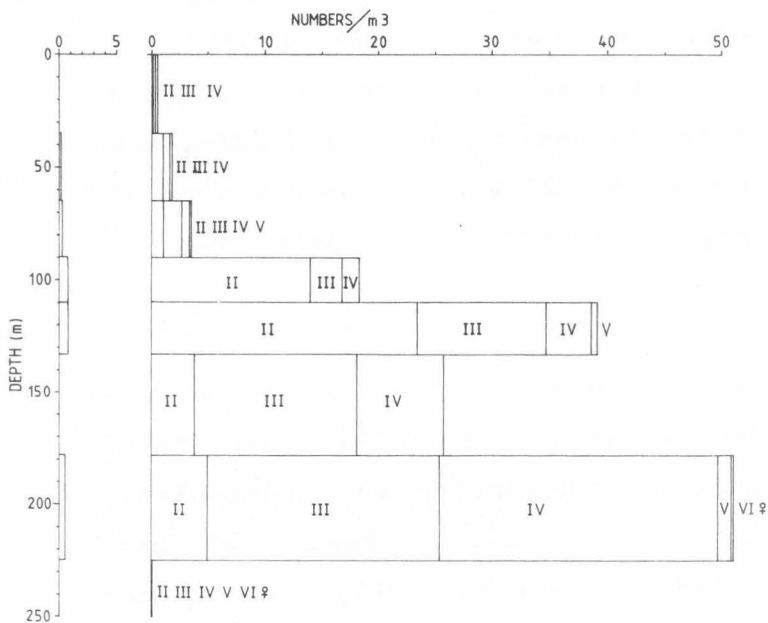

Fig. 15. Vertical distributions of copepodite stage I of Calanus spp. (left) and stages II-VI of C. finmarchicus (right) in Atlantic water at 74°30'N, 30°15'E in early June 1984. Data from cruise with R/V "G.O. Sars" (Hassel et al., 1984).

between the upper 50 m and the layer below showed marked variation among years in the period 1979-1984 (Rey et al., 1987). It is possible that the downwards migration is influenced by the culmination and sedimentation of the spring phytoplankton bloom. We have observed a clear downwards shift in the vertical distribution of zooplankton on the transition from surface bloom to subsurface chlorophyll maximum conditions (Gjøsæter et al., 1983; Skjoldal et al., 1987b). Whether massive sedimentation of a spring bloom could trigger C. finmarchicus to leave the euphotic zone and migrate to deeper water remains to be seen.

CAPELIN FEEDING MIGRATION

Capelin (Mallotus villosus) is an important predator on zooplankton in the Barents Sea. It spawns at the coast of Murman and northern Norway in late winter whereas the immature stock overwinters in the central Barents Sea. In summer and autumn the capelin performs an extensive feeding migration that can extend north to 78-80°N (Ozhigin and Luka, 1984; Ozhigin and Ushakov, 1984; Dommasnes and Røttingen, 1984). The necessity of this feeding migration can be illustrated by a rough calculation. Assuming an annual P/B ratio of 1 (Banse and Mosher, 1980) and a growth efficiency of 1/3, a stock of 4 million tonnes wet weight (Hamre, 1984) would require about 1.2 million tonnes of food in units of carbon. Assuming further an annual secondary production of 20 g C m^{-2} and that 1/4 of this would be suitable and available as food for capelin, this food requirement is equivalent to a feeding area of 2.4 10^5 km^2. This represents almost 20 % of the total area of the Barents Sea and an even larger fraction of that part inhabited by capelin.

Calanoid copepods, euphausids and amphipods are the major food items of capelin (Fig. 16). Most planktonic forms have been found in the stomach contents of capelin, suggesting an opportunistic feeding behavior although there is a clear element of size selection in its diet (Hassel, 1984; Panasenko, 1984). Capelin does not seem to feed during the dark winter months. Low stomach content was observed in May and June 1981 (less than 1 % of body weight),
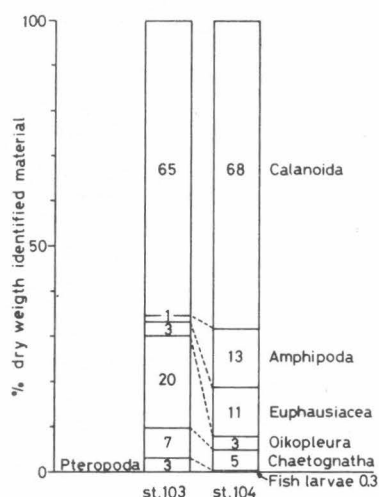
Fig. 16. Per cent dry weight of different prey categories in capelin stomachs from two stations in the northern Barents Sea in August 1981. From Hassel (1984).

whereas contents up to 9 % was found in August in northern areas where large individuals of Calanus were abundant (Hassel, 1984).

The distribution of capelin has often been found to end abruptly in north as a narrow band with high abundance of capelin (Fig. 17). This "capelin front" moves northwards with speeds up to 6 nautical miles per day (Ellertsen et al. 1981, 1982; Loeng et al., 1986). A strong increase in zooplankton biomass in and north of the capelin front has been seen on several occasions (Hassel, 1986; Loeng et al., 1986). A difficulty in interpreting such an inverse relationship between zooplankton and capelin biomass is the fact that the capelin front has been in the vicinity of the polar front at the time of the investigation (Loeng et al., 1986). There is little doubt, however, that capelin has the potential to severely graze the zooplankton, causing the inverse relationship. The average biomass of capelin over 30 or more nautical miles in the capelin front region generally exceed the zooplankton biomass. Considering this in relation to the residence time of the capelin front in a given area, and stomach contents of almost 10 % of the capelin body weight, it is to be expected that the stock of larger zooplankton is markedly reduced by the grazing of the migrating capelin front.

The condition factor (wet weight $* 10^3/length^3$) of capelin in June 1981 was uniformly low (3.3-3.5) in the area between 72 and 75°N. The condition factor was higher in August that year and
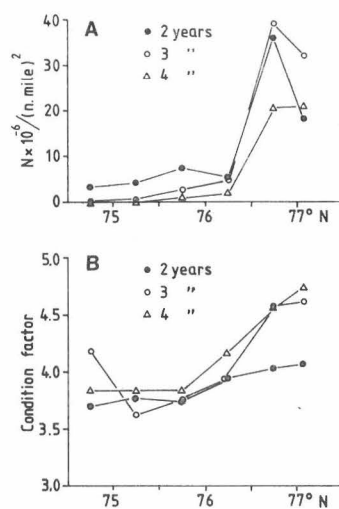
Fig. 17. Abundance (A) and condition factor (B) of capelin along a N-S section in August 1981.

showed a marked increase in the capelin front region (Fig. 17 B). We interpret this as reflecting the superior feeding conditions in north. The capelin up front encounter the rich zooplankton stocks and feed vigorously on these. As a result of this grazing the zooplankton biomass is much reduced and the feeding conditions for the capelin trailing the capelin front is therefore inferior. Capelin has therefore, in our view, a strong negative feedback on its own feeding conditions. In addition to the short-term effect, this could also affect the stock of overwintering zooplankton that takes part in reproduction the following spring. This can possibly limit the production of the larger zooplankton forms such as Calanus spp. the following season (Slagstad, 1981; Rey et al., 1987).

Capelin feeds in the three major water masses in the Barents Sea: Atlantic water, Arctic water, and mixed Atlantic-Arctic water. In order to fully understand the feeding conditions of capelin, it will be necessary to emphasize the large-scale geographical and temporal ecological aspects to a greater extent than done up to now in our studies. Transport of plankton with the Atlantic water flowing from southwest and the Arctic water flowing from north is one important issue. The migrating fronts of feeding capelin as well as other planktivorous fishes such as herring, is another important issue. These processes and their interaction with biological production processes require mathematical simulation modelling as an integrated part of the research activity. Such work

is now being initiated and our hope is that this will contribute to the multispecies modelling and management of the fisheries resources of the Barents Sea.

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