Seasonal development of phytoplankton at a high latitude oceanic site

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SARSIA

A three-year time series of hydrography, nutrients, chlorophyll *a*, Secchi depth and phytoplankton composition taken at the Ocean Weather Station Mike (OWSM)(66°N, 2°E) was investigated. The pattern in the seasonal development of phytoplankton biomass was very similar in all three years, despite some differences in the magnitude of the spring bloom. From January to March typical winter conditions prevailed with low water mass stability, high and homogeneously depth distributed nutrient concentrations, and phytoplankton biomass below 0.05 mg m^{-3} chlorophyll *a*. During April a pre-bloom situation still prevailed, characterised by still low, but now steadily increasing biomass. The spring bloom started in May concurrent with incipient thermal stratification. Maximum phytoplankton biomass was observed between mid May and mid June, but the Chl *a* concentrations never exceeded 2.8 mg m^{-3}. By July the biomass had decreased to pre-bloom levels. Generally nutrients were not depleted at this time. The decrease in phytoplankton biomass was followed by a smaller second bloom of short duration in early autumn, with Chl *a* concentrations around 1 mg m^{-3}. After the autumn bloom the biomass decreased to winter levels. The winter and pre-bloom period were dominated by small nanoplankton (< 5 µm), and coccolithophorids, where *Emiliania huxleyi* accounted for a considerable proportion. The spring bloom was dominated by small diatoms, either *Fragilariopsis pseudonana* (1990, 1992) or *Thalassiosira bioculata* var. *raripora* (1991). The absence of large diatoms seemed to be a common feature of the winter and spring all three years. After the bloom, small nanoplankton (<5 µm) again became increasingly important. Dinoflagellates were also occasionally an abundant component of the phytoplankton community but the succession did not seem to reach a "dinoflagellate phase" at Stn M during summer. The autumn samples did not reveal any major changes in the composition of the phytoplankton community compared to summer.

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INTRODUCTION

Since the end of the last century the Norwegian Sea has periodically been subject of great interest for physical as well as biological studies. Around the turn of the century several qualitative investigations on the phytoplankton were undertaken (Cleve 1897, 1900a, 1900b; Jørgensen 1900; Gran 1901, 1902; Paulsen 1904, 1909, 1918; Ostenfeld 1903, 1913). Already in these early investigations the close connection between plankton and the physical environment was acknowledged. Cleve (1897), for instance, tried to use phytoplankton species as a characteristic of different water masses in order to elucidate the circulation pattern of the area. Gran (1902), on the other hand, divided the Norwegian Sea into biogeographical regions characterised by different phytoplankton communities.

These early investigations were limited by the fact that the smaller size fractions of the phytoplankton escaped most of the common sampling gears used at that time. The development of the centrifuge method (Lohmann 1908) and later the sedimentation method (Utermöhl 1931) made it possible to extend the study to the whole phytoplankton community. After the introduction of these quantitative methods several investigations (Gran 1915; Braarud 1935; Steemann Nielsen 1935) revealed the importance of the nanoplankton (2-20 µm), and particularly the coccolithophorids in this area.

In 1948 the Ocean Weather Ship Station Mike (Stn M) came into service in the southeastern part of the Norwegian Sea (66°N, 2°E). The weather ship offered a unique opportunity for continuous studies of both the hydrographical and biological conditions. The plankton investigations of Halldal (1953) and Østvedt (1955) provided important information on the seasonal devel-

opment of phyto- and zooplankton. These investigations were partly the basis for Sverdrup's theory considering the role of physical conditions in the onset of the spring phytoplankton bloom (Sverdrup 1953). Later studies showed considerable yearly variations and regional differences in both the qualitative and quantitative aspects of the spring phytoplankton development in the Norwegian Sea (Paasche 1960a, 1961; Ramsfjell 1960).

Although general knowledge about the major factors regulating ocean primary production is reasonably good, there is still need to get more specific information about issues like timing of blooms, factors controlling the primary production, and dominant algal types in this particular area. The present investigation treats the results from a three-year sampling programme that included hydrography, nutrients, Chl *a*, Secchi depth and phytoplankton samples. The aim of this investigation was primarily to describe the seasonal development of the phytoplankton, both quantitatively and qualitatively and to address the factors that might control the development of both the phytoplankton abundance and species composition. Further our aim was to try to identify common patterns in the seasonal development in the three years. The material was investigated as a master's thesis in marine biology at the Department of Fisheries and Marine Biology, University of Bergen by the first author (Dale 1995) under supervision of the third and second authors.

MATERIAL AND METHODS

STUDY AREA

The Norwegian Sea, Greenland Sea and Iceland Sea form what is known as the Nordic Seas (Fig. 1). The area is separated from the North Atlantic by the submarine ridge between Greenland and Scotland, whose deepest connections are the Faroe-Shetland channel (850 m) and the Greenland Strait (620 m). Stn M is located at 66°N, 2°E in the Norwegian Basin, the southernmost of two deep basins in the Norwegian Sea. Maximum depth in the basin is almost 4000 m while the depth at Stn M is 2150 m.

The principal water masses in the Norwegian Sea are partly of Atlantic and partly of Arctic origin. The Norwegian Atlantic Current (NAC) brings warm saline Atlantic Water (AW) from the south and this water mass makes up the surface layer at Stn M. AW is generally defined as having salinity above 35.00 and temperature above 0 °C. When entering through the Faroe-Shetland Channel the salinity is between 35.27 and 35.45 (Dooley & al. 1984) and the temperature above 8 °C. NAC flows northwards along the Norwegian continental shelf. Due to the bottom topography, the current forms several branches on its way northwards. At around 64°N one

branch turns northwest then westwards and forms together with the East Icelandic Current the large cyclonic eddy of the Norwegian Sea at which eastern edge Stn M is located. Heavier Arctic Surface Water (ASW) makes up the surface layer of the Iceland Sea (Stefánsson 1962), but sinks below the AW on its way to the east and makes up the intermediate layer at Stn M. ASW has a salinity between 34.7 and 34.9 and temperature below 3 °C although with some year to year variation (Malmberg 1969). Occasionally, Norwegian Coastal Water (NCW) reaches as far west as Stn M (Halldal 1953; Helland 1963; Brettum 1969). NCW is carried northwards along the Norwegian coast with the Norwegian Coastal Current (NCC). There are considerable variations both in salinity and temperature due to seasonal variations in its fresh water component, but salinity is always less than 35.00

SAMPLING AND ANALYSIS

The material was collected at the Ocean Weather Station Mike (OWSM)(Stn M), covered by M/S *Polarfront* during the period 1 April 1990 to 22 December 1992. Surface samples were collected with a bucket while the rest of the samples were collected by means of Nansen water bottles equipped with reversing thermometers. The temperature was read immediately after retrieving the bottles and corrected onboard. Water samples for salinity were collected at standard ICES depths at least three times a week down to 2000 m and analysed ashore at the Department of Geophysics at the University of Bergen. Calculation of sea water density, sigma-t, was done according to Millero & Poisson (1981). Here only data from the upper 200 m are presented.

Water samples for nutrient analyses (nitrite, nitrate, phosphate, and silicate) were collected about once a week in 20 ml polyethylene vials with screw stoppers and added 0.2 ml chloroform for preservation (Hagebø & Rey 1984). The samples were analysed ashore according to standard methods (Strickland & Parsons 1972) adopted to an autoanalyser developed at the Institute of Marine Research in Bergen (IMR) (Føyn & al. 1981). Water samples for phytoplankton pigment analyses were collected on 263 ml plastic bottles, filtered through GF/C filters and kept frozen until analysis ashore. The pigments were extracted in 90 % acetone in darkness at 4 °C for 24 hours. They were further centrifuged and analysed fluorometrically using a Turner Design fluorometer calibrated against commercial chlorophyll *a* (Sigma Inc.). The extracts were measured both before and after the addition of 0.2 ml of a 5 % v/v solution of HCl and, Chl *a* concentrations were calculated according to Strickland & Parsons (1972). The chlorophyll data from 1990 did not pass the quality control at IMR and were therefore not available.
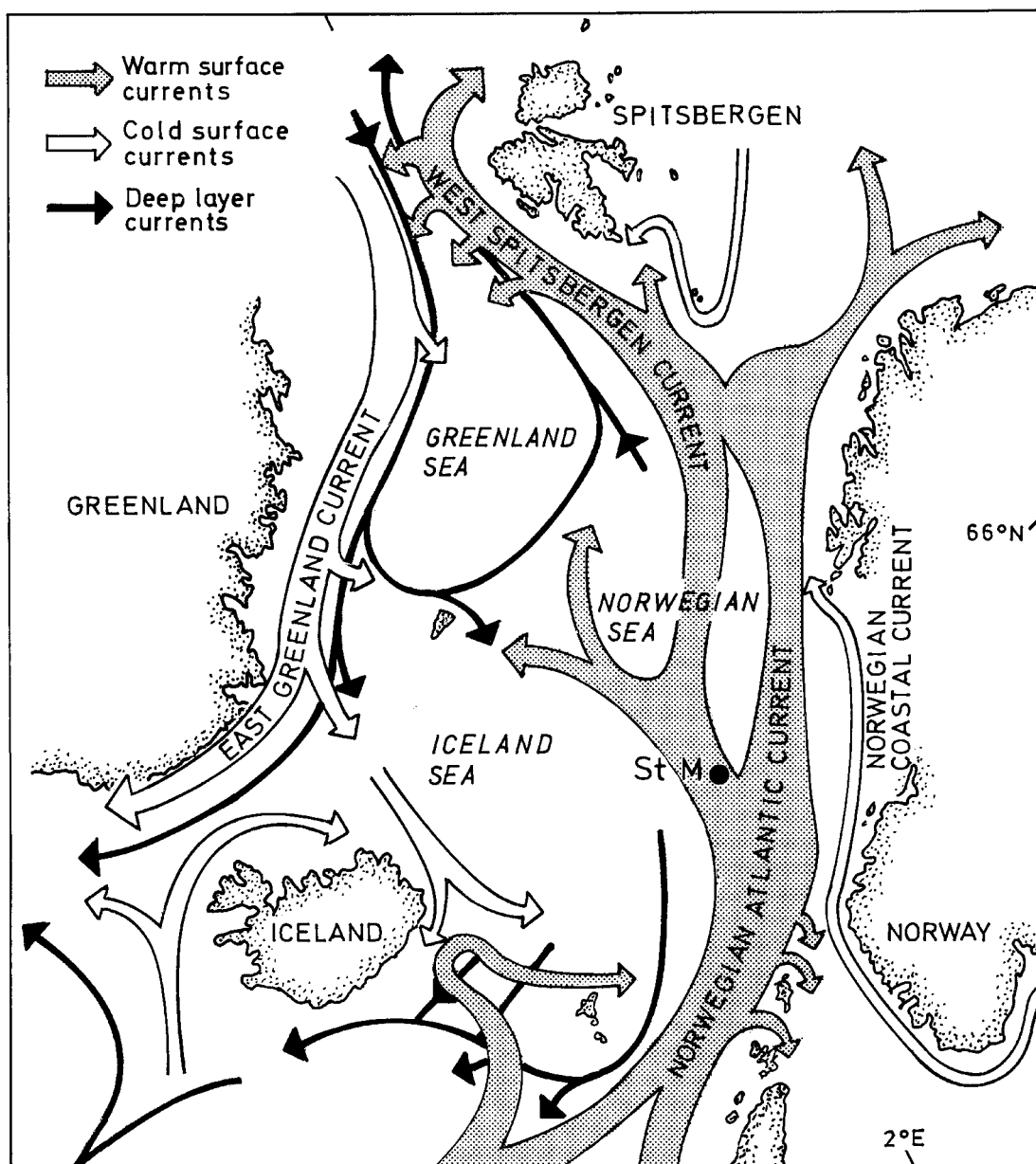
Fig. 1. The main current systems (schematic) in the Nordic Seas. Warm surface currents are shaded and cold surface currents are white. Subsurface circulation is marked black. Østerhus and Myking (pers. commn).

Secchi disc readings were carried out daily at 1200 UTC using a 30 cm disc.

Water samples for phytoplankton enumeration and identification were collected with the same frequency as nutrient and pigment samples, but only at surface, 10, and 30 m (25 m in 1990). The samples were col-lected in amber glass bottles and preserved with 20 % hexamine neutralised formaldehyde. In order to reduce the amount to be analysed, a selection was first made on the basis of the Chl *a* distribution in the water col-umn throughout the different phases of the seasonal development. Further, the samples were selected at cor-
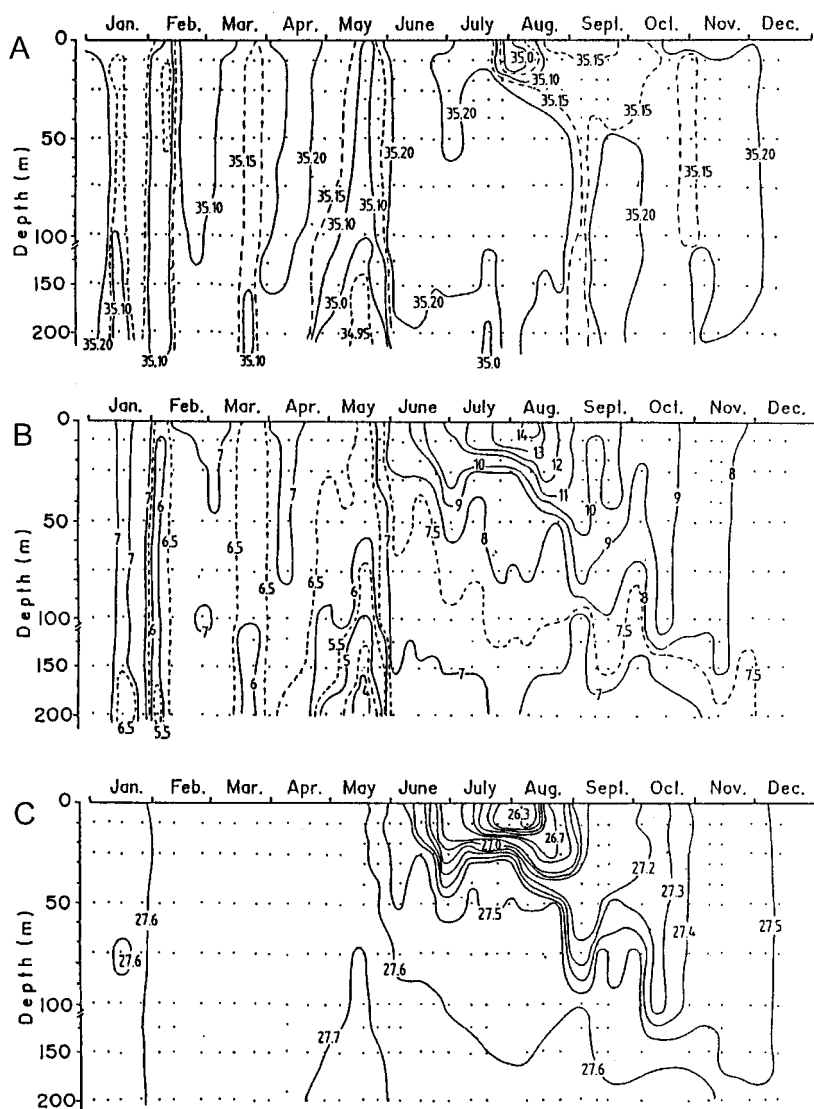
Fig. 2 A-C. Isopleth diagrams for A: salinity, B: temperature (°C), C: sigma-t (σ_t) observed in the upper 200 m at Stn M in 1991. Sampling depths are denoted by dots.

responding dates each year to facilitate a year to year comparison. Some additional samples were also analysed for time periods where environmental data indicated possible changes in the phytoplankton composition. During periods when nutrients and Chl *a* were homogeneously distributed in the upper 200 m, only surface samples were examined; when stratification and Chl *a* gradients was more pronounced samples from all three depths were examined.

Standing stock of phytoplankton was determined from 50 ml subsamples sedimented according to the Utermöhl

(1931) method. Enumeration was carried out at 600 times magnification using a Wild 40 inverted microscope, where 6 diagonals equivalent to 2 ml sample were counted. The phytoplankton was as far as possible identified to species level. When this was impossible, the identification was made to family or genus level, and in some cases collective terms were used. *Flagellate* is used for flagellated cells where it was uncertain how many flagella that were originally present. The term *monad* is used for any, more or less spherical cell, with no flagellum and no particular discernible shell.
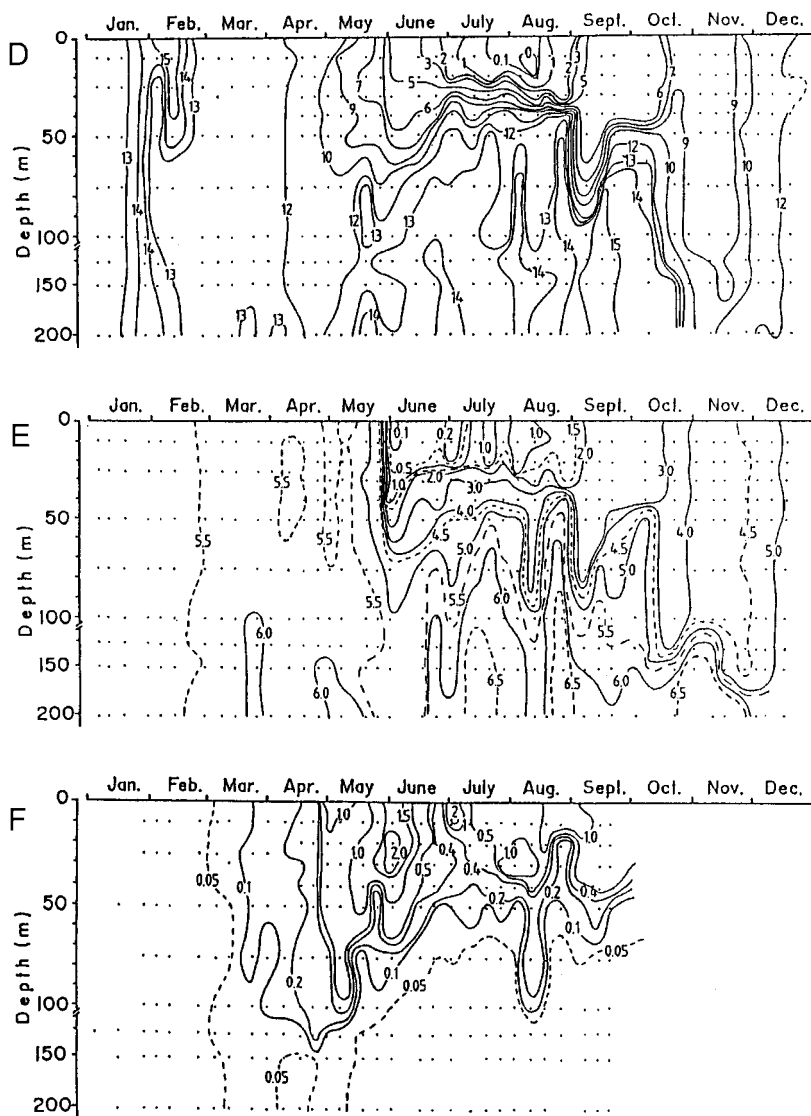
Fig. 2 D-F. Isopleth diagrams for D: nitrate (μmol l^{-1}), E: silicate (μmol l^{-1}), F: chlorophyll *a* (mg m^{-3}) observed in the upper 200 m at Stn M in 1991. Sampling depths are denoted by dots.

RESULTS AND DISCUSSION

SEASONAL DEVELOPMENT IN PHYTOPLANKTON BIOMASS

Winter (January-March)

The seasonal development of phytoplankton at Stn M could roughly be divided into five phases. First the winter season from January to March. During winter Atlantic Water (AW) with temperatures between 6-7 °C (Fig. 2) prevailed in the upper 200 m (only shown for 1991), and vertical stability was low (Figs 2 & 3). Nitrate concentrations were generally above 12 μmol l^{-1}, phosphate above 0.9 μmol l^{-1} and silicate above 5.5 μmol l^{-1} and homogeneously distributed with depth (Figs 2 & 3). The biomass was low, with Chl *a* concentrations below 0.05 mg m^{-3} throughout the homogenous upper 200 m (Figs 2 & 3). During winter light becomes a limiting factor for phytoplankton growth (Ryther 1956). By March however there should be sufficient
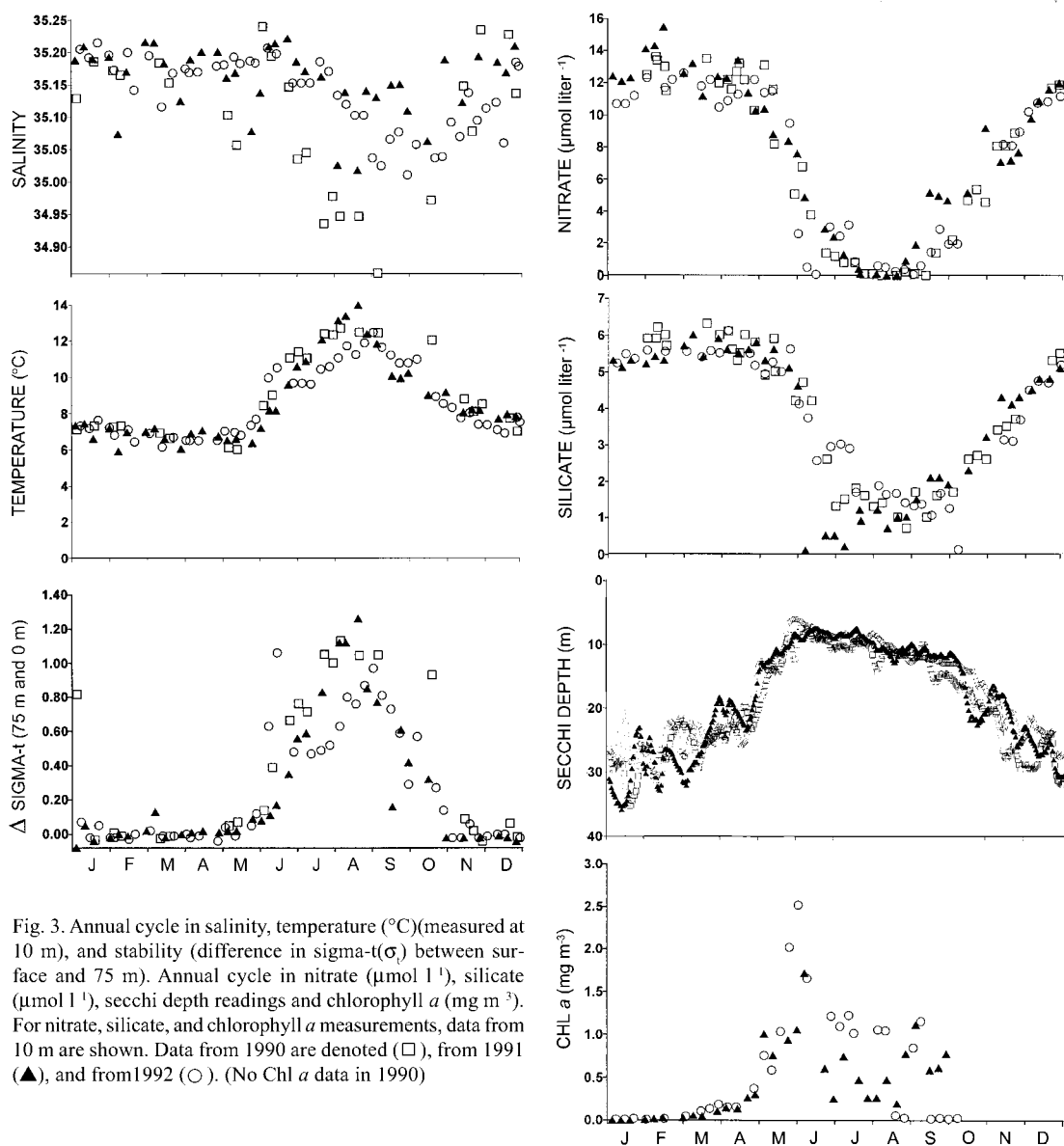
Fig. 3. Annual cycle in salinity, temperature (°C)(measured at 10 m), and stability (difference in sigma-t(σ_t) between surface and 75 m). Annual cycle in nitrate (µmol l⁻¹), silicate (µmol l⁻¹), secchi depth readings and chlorophyll *a* (mg m⁻³). For nitrate, silicate, and chlorophyll *a* measurements, data from 10 m are shown. Data from 1990 are denoted (□), from 1991 (▲), and from1992 (○). (No Chl *a* data in 1990)

light to initiate the spring bloom at Stn M. Minimum average incoming light intensities between 120 and 145 Ly d⁻¹, suggested as a requirement for the initiation of the spring bloom at Norwegian coastal localities between 60 and 69°30'N, occurs already between mid February and mid March (Sakshaug & Myklestad 1973; Eilertsen & Taasen 1984; Erga & Heimdal 1984; Erga 1989).

Phytoplankton biomass above winter levels was indeed present in March (Figs 2 & 3), and the subsequent weak increase indicates that the phytoplankton popula-

tion was no longer light limited although no bloom occurred at this time. Our results are in accordance with Halldal (1953) and Brettum (1969) who observed an increase in phytoplankton population from February to March. There were no indications of increased stability in the upper 200 m at this time (Figs 2 & 3). Since the depth of the mixed layer generally is at its maximum in February, and being deeper than 100 m until the end of April (Johannessen & Gade 1984), it is assumed that the phytoplankton population growth was kept low due to deep vertical mixing.

The pre-bloom period (April)

The second phase can be characterised as a pre-bloom period. It started in April, with a marked and faster increase in the phytoplankton biomass, and a concurrent weak reduction in both dissolved nutrient concentrations (Figs 2 & 3) and Secchi depth (Fig. 3). In April there was still no sign of thermal stratification. However, reduced thickness of the AW layer (Fig. 2, only shown for 1991) probably due to entrainment of a colder, less saline water mass, was observed. This lead to a weak increase in stability in the upper 100 m, probably sufficient to start a small bloom. Traditionally, the formation of a pycnocline together with increased solar radiation have been regarded as a prerequisite for the initiation of the spring bloom in offshore waters (Gran & Braarud 1935; Sverdrup 1953; Riley 1957). Several authors have indicated that small blooms can start in short-lived periods of increased stability prior to the vernal development of stratification (Colebrook 1979; Townsend & al. 1992; Garside & Garside 1993; Townsend & al. 1994). With wind speed below a certain threshold, the critical depth is deeper than the mixing depth and thus favours small spring bloom pulses (Townsend & al. 1994). The Norwegian Sea is in the path of the northern atmospheric low-pressure belt where rough weather and strong wind alternates with calmer periods. The wind-driven vertical mixing will have a rhythm with a period of 8-10 days (Skjoldal & al. 1993). While phytoplankton sampling probably have been too separated in time to reveal any pulses, the more frequent observations of dissolved nutrients and Chl *a* data indicate a gradual increase in biomass (Figs 2 & 3). This is in agreement with the observations of Halldal (1953) and Brettum (1969).

Despite the increase in biomass, the Chl *a* concentrations in April and May were still relatively low and homogeneously distributed down to 75-135 m (Fig. 2, only 1991 shown). However, integrated over the entire water column the biomass was considerable. This agrees with model runs of the primary production at Stn M, indicating that phytoplankton growth prior to stratification is an important part of the production available for transfer to higher trophic levels (Broström 1997). Correspondingly, Garside & Garside (1993) argue that as much as half of the total spring production in the Atlantic occurs prior to stratification.

"Top down" control of phytoplankton by grazers during the pre-bloom period is possible, depending on zooplankton population size and the timing of life history events in spring relative to phytoplankton development (cf. Frost & al. 1983; Miller & al. 1984; Vidal & Smith 1986; Fasham 1995*)*. At Stn M *Calanus finmarchicus* and *Pseudocalanus minutus* is the domi-

nating herbivorous copepods during spring (Wiborg 1955; Østvedt 1955; Beyer 1962). They ascend from overwintering in deep waters for spawning in surface sometime between February/March and mid June. Bathmann & al. (1990) observed two populations of *C. finmarchicus* in February at the Vøring plateau, one in strata from 500-1000 m and another apparently actively feeding in the surface layer (see also Hirche 1983; Head & Harris 1985).

The spring bloom (May-June)

A third phase, the spring bloom, started in early May in all three years (Fig. 3). From mid May there was an increase in stability due to warming of the upper layers (Figs 2 & 3). The mixed layer depth normally decrease considerably during May (Johannessen & Gade 1984). Although there appears to be a close connection between increased stability and increase in biomass, a strong vertical density gradient in the upper part of the water column, did not seem to be a prerequisite even for the vernal bloom at Stn M.

The Chl *a* and nutrient concentrations, and the far more frequent Secchi depth readings, indicate small annual variations in the timing of the bloom the three years (Figs 2 & 3). The timing of the bloom agrees with the observations of Brettum (1969), while the bloom according to Halldal (1953) did not occur until June. In an area reaching from 63-66°N and from 1-5°E, means from time series between 1948-1965 (Continuos Plankton Recorder) showed a peak abundance already in April (Robinson 1970). Also closer to the Norwegian coast, variations in the timing of the vernal bloom are observed (Braarud & al. 1958; Sakshaug 1972; Rey 1981).

Grazing may have a significant impact on the vernal bloom in areas with a slow build-up of thermal stratification such as at Stn M. The prolonged bloom period in such regions may give zooplankton the necessary time to mature and feeding stages to develop in phase with the progression of the spring bloom. This has been shown for Atlantic water masses in the Barents Sea (Rey & al. 1987). The zooplankton investigations of Østvedt (1955) parallel to the phytoplankton investigations of Halldal (1953) showed that the zooplankton maximum closely matched that of phytoplankton.

Phytoplankton maximum seems to occur in early June all three years (Figs 2 & 3). The Chl *a* concentrations never exceeded 2.8 mg m^{-3}, observed in 1992. In 1991 the maximum concentrations were 2.1 mg m^{-3}. Based upon the pattern of decrease in nutrient concentrations and Secchi depth, the order of magnitude of the spring bloom probably were the same in 1990 as in the proceeding years. There was a subsequent decrease in biomass after the maximum was achieved; though less pronounced in 1992 where Chl *a* concentrations re-

mained above 1 mg m^{-3} until mid August.

Nutrient depletion is often the cause of bloom culmination, but it did not seem to cause the decline in the present investigation since considerable amounts of nutrients were available in the mixed layer when the bloom culminated. With exception of silicate, which reached a minimum in early June 1991, the lowest mixed layer nutrient concentrations were observed in July-August (Figs 2 & 3). A possible explanation for the decline is that grazing again control the phytoplankton biomass. The decline in nutrient concentrations should, in absence of grazers, yield a larger increase in Chl *a* than measured during this investigation. Colebrook (1982) also have suggested that the phytoplankton in the North Atlantic and the North Sea north of 60°N was not nutrient limited but controlled by grazing.

Post bloom period (July-August)

By the end of June the water column was well stratified in the upper 50 m (Figs 2 & 3). This marks the introduction to the fourth phase, the post bloom period. The most pronounced change in hydrographical conditions that occurred during summer was the period of reduced salinity seen in 1990 and partly in 1991, which further enhanced the stratification in the upper 50 m (Figs 2 & 3). The reduced salinity was probably due to an advection of water masses from the Norwegian Coastal Current (NCC). This seems to be a common feature during summer (Halldal 1953; Helland 1963; Brettum 1969), while the NCC runs close to the coast during winter. Whether NCC water reaches as far as Stn M depends on the wind conditions, where wind from north or northeast drives the surface water away from the coast. Periods of salinity lower than 35.00 coincided with wind from northeast (Helland 1963; Brettum 1969). According to Brettum (1969) the 35.00 isohaline is driven back and forth around Stn M at this time of the year depending on wind strength and direction.

The admixture of coastal water did not seem to extensively alter the development in the phytoplankton compared to what one would expect during one month at this time of the year. The same pattern of reduction in phytoplankton abundance was seen each year, although the June sample in 1990 was taken in AW while the July sample was taken in the less saline water mass (Fig. 3). The total abundance in July was in the same order of magnitude all three years despite hydrographical differences.

During summer the bulk of the biomass was concentrated within the upper mixed layer (Fig. 2, shown only for 1991), which generally is between 20-40 m during this period (Johannessen & Gade 1984). Subsurface Chl *a* maxima were measured at a few occasions in 1991, possibly connected to the periodically low nutrient concentrations measured this year (c.f. Pingree & al. 1977; Harrison & al. 1983). At Stn M relatively strong vertical convection probably made the periods of low nutrient concentrations quite short, and thus no lasting deep Chl *a* maximum. In the northern North Atlantic surface Chl *a* maximum was observed when stratification was weak, while maximum was constantly observed deeper when mowing southwards (Veldhuis & al. 1993; Weeks & al. 1993a, 1993b).

Autumn (September-October)

The fifth and last phase is autumn. There appeared to be a small autumn bloom of short duration in August/September 1991 and 1992, with Chl *a* concentrations around 1 mg m^{-3} (Figs 2 & 3). Halldal (1953) also described an autumn maximum but this seemed to occur later than during the present investigation. The autumn bloom did not seem to be caused by increased nutrient concentrations alone since only small changes in nutrient concentrations were observed prior to the bloom (Figs 2 & 3). According to Østvedt (1955) the abundance of *Calanus finmarchicus* in the upper 100 m decreased quickly during the last half of August so reduced grazing pressure might have been a contributing factor. By mid September 1992 Chl *a* concentrations were reduced to ~0.1 mg m^{-3}, levels typical for the period prior to the spring bloom. At the same time in 1991 Chl *a* concentrations were still between 0.5 and 0.7 mg m^{-3} (Fig. 3). Concurrent with the decrease, the upper mixed layer depth increased from 40-50 m to 80-100 m both in 1991 and 1992 (Fig. 2, only shown for 1991). The somewhat higher phytoplankton abundance in September 1990 (Fig. 4) might have been due to the fact that no similar reduction in the mixed layer depth occurred and therefore gave a less pronounced dilution effect (Fig. 3). In 1990 mixed layer depth stayed around 50 m until late October.

SEASONAL DEVELOPMENT IN THE COMPOSITION OF THE PHYTOPLANKTON COMMUNITY

The seasonal development in the composition of the phytoplankton community was quite similar the three years. Early season (Jan-April) was dominated by monads/flagellates (1990) and coccolithophorids (1991, 1992) followed by dominance by small diatoms during the bloom. After the decline of diatoms flagellated cells were again dominating (Fig. 4). This pattern very much resembles the succession previously described for the North Atlantic (Sieracki & al. 1993; Taylor & al. 1993).

The few vertically resolved sampling series did not reveal any consistent seasonal changes in the vertical distribution of the different groups. Diatoms and dinoflagellates generally had their maximum abundance in the upper 10 m (Fig. 5), which is in agreement with

Halldal (1953). Also monads/flagellates appear to have maximum in the upper 10 m (Fig. 5). Brettum (1969) showed that the abundance of this group was highest in surface and quickly decreasing with depth, while monads/flagellates according to Halldal (1953) had somewhat deeper maxima, most often between 10 and 50 m. Coccolithophorids had a more ambiguous pattern with unsystematic variations between surface and deeper maxima (Fig. 5).

Winter and pre-bloom

The low diatom abundance observed during this period (Fig. 4) seems to be a general feature of the phytoplankton community prior to the vernal bloom (Halldal 1953; Brettum 1969) even though low stability, high nutrient concentrations and partly low irradiance characterising the spring situation at Stn M expectedly would favour diatoms (Margalef 1978; Egge & Aksnes 1992; Sieracki & al. 1993; Langdon 1988). Selective grazing may offer an explanation for this apparent contradiction. Bathmann & al. (1990) suggested that copepods overwintering in the surface was a possible explanation for the low diatom abundance during their investigation, and argued that in years with high copepod abundance in the surface together with a favourable timing of the upward migration might result in low diatom abundance.

Copepods may feed on a range of prey sizes, defined by the morphology and movement of the feeding appendages (Landry & Fagerness 1988; Hansen & Tiselius 1992). These optima are generally from about 15 μm to 80 μm (Hansen & al. 1994). In the North Sea *Calanus finmarchicus* basically grazed on particles in the range of 20-30 μm (Gamble 1978). The few diatoms present during early spring were generally small species, < 15 μm. The most abundant species of coccolithophorids were *Emiliania huxleyi* (Lohmann) Hay & Mohler and *Algirosphaera* sp. (Tables 1-3). *E. huxleyi* and *Algirosphaera sp.*, both < 10 μm were important components of the algal community at the time, but they were probably not heavily grazed upon. Using the feeding rates of *Pseudocalanus elongatus* and *C. helgolandicus* provided by Harris (1994) on data from an *E. huxleyi* bloom in the North Atlantic (i.e. Holligan & al. 1993a), less than 1 % of a *E. huxleyi* population will be grazed daily. Furthermore, when offered to *C. finmarchicus* at concentrations observed during the present investigation *E. huxleyi* was, according to Nejstgaard & al. (1997) barely ingested at all.

Spring bloom

The vernal bloom was dominated by small diatoms, either *Fragilariopsis pseudonana* (Hasle) Hasle or a form of *Thalassiosira bioculata* var. *raripora* Gaarder. Dur-
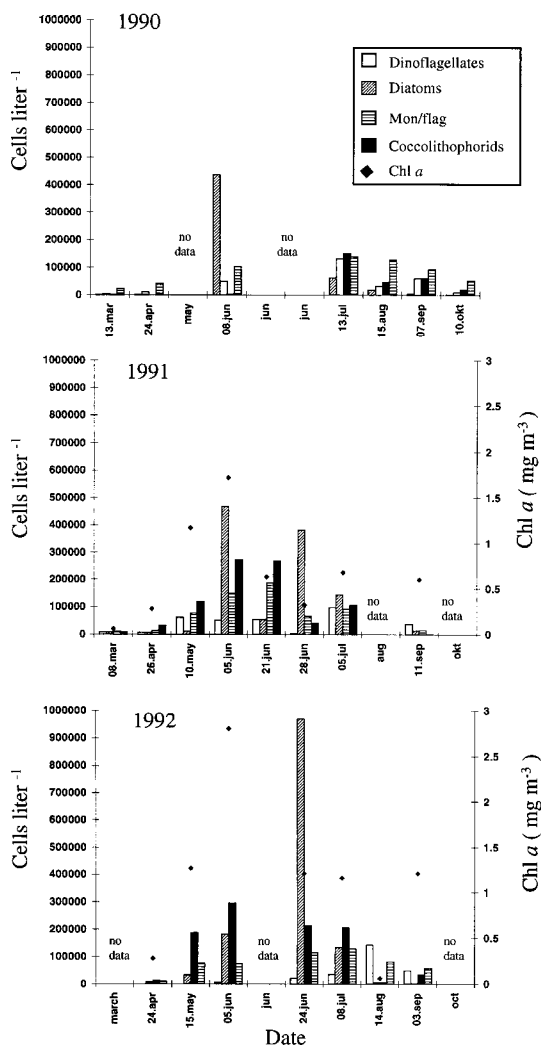

Fig. 4. The changes in the major phytoplankton groups (cells l⁻¹), identified by light microscopy, and the chlorophyll *a* standing stock (mg m⁻³) in the surface during the period from March to October in 1990, 1991 and 1992.

ing the bloom in 1990 and 1992 *F. pseudonana* represented 98 and 95 % of the diatoms respectively, while *T. bioculata* var. *raripora* constituted 97 % of the diatoms in 1991 (Tables 1-3). This species composition deviated somewhat from earlier investigations. *T. bioculata* var. *raripora* is common in large areas in the Norwegian Sea (Ramsfjell 1960; Paasche & Rom 1962), but has only occasionally (Paasche 1961) been recorded in concentrations corresponding to the present investigation (Halldal 1953; Ramsfjell 1960; Brettum 1969). The pennate diatom *F. pseudonana* is described as common in the area by some authors (Halldal 1953; Paasche
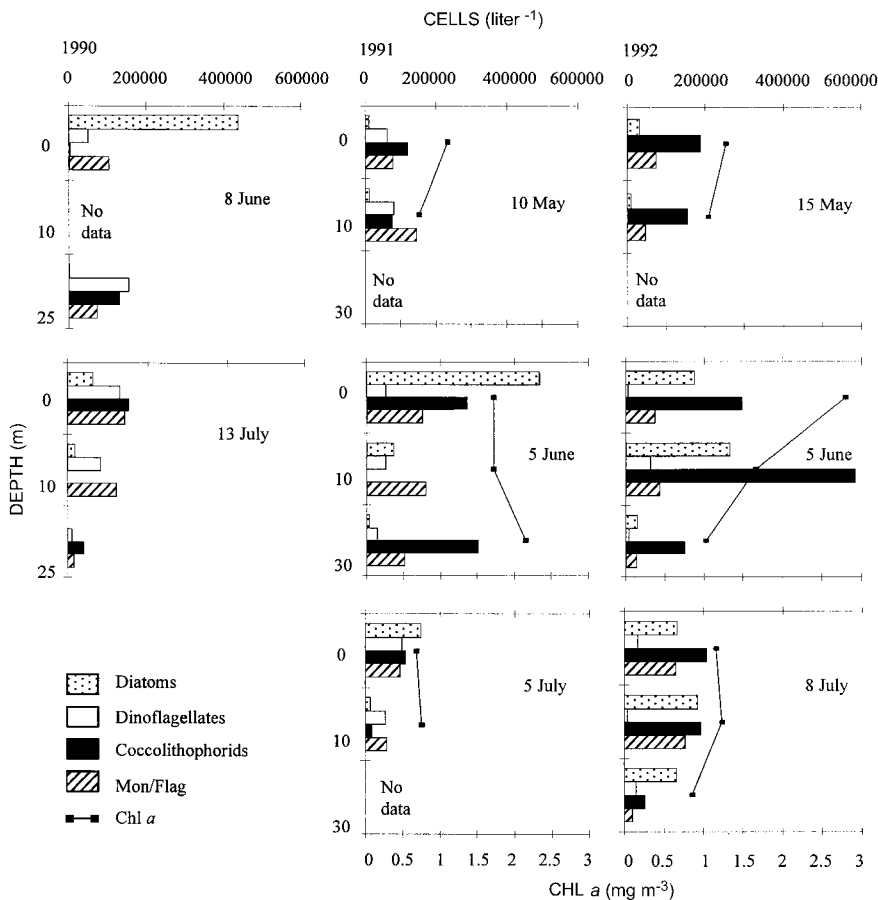
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CELLS (liter $^{-1}$)

Fig. 5.Vertical profile of the major phytoplankton groups (cells l ^{1}), identified by light microscopy, and the chlorophyll *a* standing stock (mg m ^{3})(1991 and 1992) in1990 (left), 1991 (middle) and 1992 (right).

1960b; Ramsfjell 1960) while not mentioned by others (Gran 1929; Braarud & al. 1953). *Chaetoceros* spp. were only recorded in insignificant numbers during the present investigation while i.e. *Chaetoceros convolutus* (Halldal 1953; Nygaard 1963; Brettum 1969) and *C. debilis* prevailed in other investigations from the Norwegian Sea (e.g. Paasche 1960b; Ramsfjell 1960; Nygaard 1963).

The differences in the dominating species described in literature indicate that the species present in the water masses when the hydrographical conditions become favourable for their production, is vital for the subsequent taxonomic composition of the bloom. This is exemplified by the *T. bioculata* var. *raripora* bloom in 1991. This year *T. bioculata* var. *raripora* was already present in April (Table 2), and when water masses reached sufficient stability this species bloomed to considerably high concentrations. There appeared to be a

continuous supply of *T. bioculata* var. *raripora* with the NAC this year. The two other years *T. bioculata* var. *raripora* did not appear until June and never reached the numbers seen in 1991. Since AW normally is the dominant water mass at Stn M during this period, the actual species seeded into the AW will be important for the composition of the phytoplankton community at Stn M. The vegetation of the Norwegian Sea is a mixture of neritic species from bordering coastal areas, and oceanic species entering with the Atlantic water inflow (Braarud & al. 1953). For instance, *E. huxleyi* and *Algirosphaera sp.*, two important species in the Norwegian Sea, are both described as abundant in the inflowing AW and in the mixed water masses in the Faroe-Shetland Channel (Braarud & al. 1953). Other species observed in high numbers in the Norwegian Sea, as e.g. *Chaetoceros debilis* (Paasche 1960b; Brettum 1969) and *Phaeocystis pouchetii* (Paasche 1960b; own unpub-

lished results), do as well appear to be important components of the phytoplankton along the coasts of the Faroe Island (Gran 1915; Steemann Nielsen 1935; Braarud & al. 1953). Thus physical and biological conditions early during the season in the southern Norwegian Sea and the North Atlantic are probably of considerable importance for the species composition at Stn M. Occasionally water masses of origin other than Atlantic prevail in the surface at Stn M also during spring. Brettum (1969) observed a large bloom of *Rhizosolenia fragilissima*, a species previously only recorded in low numbers (Halldal 1953; Paasche 1960b; Ramsfjell 1960). This bloom was apparently caused by the introduction of coastal water containing *R. fragilissima* at the time when conditions were favourable for a bloom (Brettum 1969).

Since *F. pseudonana* and *T. bioculata* var. *raripora* were the only diatoms that occurred quite regularly in high numbers (Tables 1-3), a species succession pattern was difficult to identify. Halldal (1953) shows that *Chaetoceros* sp. reached maximum first, then *F. pseudonana* followed by *Rhizosolenia* sp., but also in his work only *F. pseudonana* reached high numbers.

Both the present investigation and that of Halldal (1953) indicate that the succession of diatoms at Stn M show little resemblance to the general pattern described by Margalef (1978); a diatom bloom consisting of several species with a succession proceeding from large fast growing species to smaller, and where each species dominate for a short period. However the pattern described by Brettum (1969) resembles more the general pattern of Margalef (1978).

The relatively numerous coccolithophorids and monads/flagellates seemed to have a more continuous presence throughout the season without blooming in the common sense of the word. This is in accordance with both Halldal (1953) and Brettum (1969). Also during spring bloom the most abundant coccolithophorids were *E. huxleyi* and *Algirosphaera* sp. (Tables 1-3).

Post-bloom and autumn

A considerable amount of diatoms was present at the end of June both in 1991 and 1992 (Fig. 4), where *F. pseudonana* was the most abundant species (Tables 2 & 3). No late June sample was taken in 1990, but the continued decline in silicate concentrations during June

Table 1. The species composition in surface, 10 m and 25 m in 1990 expressed as cells l⁻¹. For a complete species list see Dale (1995).

Depth (m)				0				10	25	
Date	13.03	24.04	08.06	13.07	15.08	07.09	10.10	13.07	08.06	13.07
Class Bacillariophyceae										
Corethron hystrix	-	-	-	-	18216	-	-	-	-	-
Fragilariopsis pseudonana	-	506	431112	12650	-	-	-	-	-	-
Cylindrotheca closterium	506	-	-	11638	-	-	-	506	-	-
Thalassiosira bioculata										
var *raripora*	-	-	1012	9180	-	-	-	-	-	-
Bacillariophyceae (others)	506	506	5060	28842	1012	3542	506	15180	2530	506
Class Dinophyceae										
Gymnodinium sp.	-	-	1012	7590	2530	-	-	6578	7590	1012
Heterocapsa sp.	-	-	-	-	-	11638	506	-	3542	-
Prorocentrum balticum	1012	2024	23276	5060	1012	3036	506	6578	11132	506
Protoperidinium sp.	506	-	-	1518	-	-	-	4048	1518	506
O. Gymnodiniales (unident.)	-	1012	5060	7084	-	12144	-	-	1518	3036
Dinophyceae(athecat others)	2024	6578	15686	109296	28336	32384	4048	58190	122958	5566
Dinophyceae(thecat others)	-	-	4554	506	-	-	3542	7084	7590	506
Class Prymnesiophyceae										
Algirosphaera sp.	-	-	2530	6578	-	-	1518	-	10626	11638
Calyptrolithophora papillifera	-	-	-	4048	7590	7084	4048	-	-	-
Coccolithus pelagicus	-	-	-	7590	-	-	506	-	1518	3542
Emiliania huxleyi	-	-	-	76406	8602	12144	5566	-	117392	21758
Helladosphaera cornifera	-	-	-	29348	5566	1012	-	-	-	-
Syracosphaera cf. *nodosa*	-	-	-	-	-	22264	3036	-	-	-
Coccolithophorids (others)	506	-	506	27324	24794	17710	5060	-	-	1518
Class Cryptophyceae										
Leucocryptos marina	-	-	-	7590	-	-	-	10626	4048	-
Class Chlorophyceae										
Trochiscia sp.	-	-	-	-	-	10120	12650	-	-	-
Monads / flagellates	22264	41492	103730	139150	127442	69322	28842	118910	72358	10120

indicated that diatoms were present also in late June 1990 (Fig. 3). By July the proportion of diatoms was less than 30 % all years with coccolithophorids, dinoflagellates and flagellates dominating (Fig. 4). The bulk of dinoflagellates comprised at this time unidentified athecate species, while *E. huxleyi* and *Helladosphaera cornifera* (Schiller) Kamptner were the most important coccolithophorids (Tables 1-3). Within all groups the highest species diversity was observed during the post-bloom period. Both in 1991 and 1992 the heterotrophic crytophyte *Leucocryptos marina* (Braarud) Butcher was a quite abundant a species during summer (Tables 2 & 3). Silicate deficiency often causes a shift from diatoms to flagellates (Officer & Ryther 1980; Smayda 1980; Sieracki & al. 1993), and dominance of smaller cells apparently occur because of their more efficient nutrient uptake (Sakshaug & Holm-Hansen 1977; Smith & Kalff 1982). In mesocosm experiments diatoms seems to dominate whenever silicate concentrations are above 2 µmol l^{-1}, while diatoms were replaced by flagellates at lower concentrations (Egge & Aksnes 1992; Jacobsen & al. 1995). However, the large number of *F. pseudonana* in late June 1991 occurred at silicate concentrations far less than 2 µmol l^{-1} (Table 2, Fig. 3), which shows that diatom blooms may occur at low silicate concentrations given a species as small as *F. pseudonana*.

Dinoflagellates had a scattered seasonal distribution with varying species diversity. Only *Prorocentrum balticum* (Lohmann) Loeblich III and some small unidentified species of order Gymnodiniales occurred relatively regularly throughout the season (Tables 1-3). This agrees with Halldal (1953) who reported only isolated observations of dinoflagellates except from *P balticum* which was present throughout his entire investigation. The scattered observations indicate that a dinoflagellate phase in the succession was never reached any of the years. This is furthermore reflected by the dominance of small species such as *P. balticum*, a species that, together with *E. huxleyi* is described as part of the early summer community in the Atlantic (Braarud & al. 1953; Holligan & Harbour 1977; Ayres & al. 1982). A community like this is according to Holligan (1987) associated with medium turbulent water masses. Wind probably causes considerable turbulence in the upper layer in summer at Stn M. High turbulence does not create optimal conditions for large dinoflagellates, these slow growing species are reported to occur in high numbers when there is a steep nutrient gradient and a shallow pycnocline (Holligan 1987). In the North Atlantic the dinoflagellate phase of succession was only reached south of 60°N where nutrient concentrations were lower

Table 2. The species composition in surface, 10 m and 30 m in 1991 expressed as cells l^{-1}. For a complete species list see Dale (1995).

Depth (m)		0							10			30	
Date	08.03	26.04	10.05	05.06	21.06	28.06	05.07	11.09	10.05	05.06	05.07	05.06	16.08
Class Bacillariophyceae													
Fragilariopsis pseudonana	-	-	5566	1012	31372	375958	123970	7590	2024	-	7590	-	-
Cylindrotheca closterium	506	-	506	1012	8602	1012	3542	-	-	-	1012	-	506
Thalassiosira bioculata													
var *raripora*	-	1012	2024	453376	7590	-	15180	3542	5566	65780	-		
Bacillariophyceae (others)	8096	6072	3036	12144	6578	4554	6578	1518	3036	5566	6072	5566	6072
Class Dinophyceae													
Gymnodinium sp.	-	-	2024	-	-	-	10626	-	-	-	506	506	-
Gyrodinium sp.	-	-	-	4048	-	-	1518	1012	-	3542	-	506	-
Prorocentrum balticum	-	-	27324	20746	3868	-	10120	4554	45034	15686	5060	-	506
O. Gymnodiniales (unident.)	4048	1518	4554	5060	-	-	8602	11132	7084	8602	-	5566	-
Dinophyceae (athecat others)	4554	5566	27324	21252	49588	4048	66792	20746	27324	22770	45044	19228	8602
Dinophyceae (thecat others)	-	-	-	-	-	-	-	-	-	-	2024	4554	-
Class Prymnesiophyceae													
Algirosphaera sp.	2024	7084	25300	7590	-	-	-	-	2024	-	-	13156	4554
Emiliania huxleyi	1012	23782	82478	233260	264132	36938	99176	506	66792	506	113850	261096	-
Coccolithophorids (others)	5566	1012	11638	31878	4048	2530	6578	-	7084	506	4048	29348	30866
Class Cryptophyceae													
Leucocryptos marina	-	1012	3036	5060	26312	18216	68816	3036	4554	4048	17710	3036	-
Class Craspedophyceae													
Monosiga marina	-	-	506	-	1518	-	1518	-	2530	-	-	-	-
Unident heterotophic	-	-	-	22264	-	-	-	1012	-	-	506	-	-
Monads/flagellates	11132	14674	78936	148764	187726	66286	92092	15180	144716	159390	57684	100188	92092

and vertical stratification stronger (Taylor & al. 1993; Weeks & al. 1993b).

The autumn bloom in 1992 was probably caused by dinoflagellates and coccolithophorids, both due to introduction of new species and by a general increase in abundance in species already present. In 1991 no samples were taken between early June and mid September, these two samples were however quite similar considering species composition so it is likely that the autumn bloom this year was caused by an increase in some of the species already present in July (Tables 1-3).

GENERAL PATTERNS IN THE SEASONAL DEVELOPMENT

The seasonal development in the phytoplankton community followed a mixed pattern of a "successions" and "sequences". "Succession" refers to the seasonal change in species composition in a well defined water mass, while "sequence" means changes in species composition resulting from changes in water masses (Braarud 1935).

Admixture of water masses other than AW, and thus "sequence", most likely occurs during summer (Halldal 1953; Helland 1963). The slight changes in water masses during summer did, however, hardly change the development of the phytoplankton community compared to what one would expect in one well-defined water mass.

This may indicate that biomass and partly species composition are the same in large areas in the southeastern part of the Norwegian Sea in summer, which is in agreement with Paasche (1960b) and Halldal (1953).

"Sequence" might be more easily detected in situations when e.g. the admixture of coastal water occur earlier in the season due to larger differences in stability between different areas. This is exemplified by the admixture of coastal water in May described by Brettum (1969). Local differences in hydrographic conditions in spring may cause differences in the developmental stage of the phytoplankton community between areas. These differences are far less pronounced in summer and the phytoplankton community is probably more stable.

A striking difference between the present and several earlier investigations (Halldal 1953; Paasche 1960b; Ramsfjell 1960; Brettum 1969) was the low abundance and species diversity of large diatoms i.e. in the genus *Chaetoceros* and *Rhizosolenia*. According to Reid (1977) considerable changes in the phytoplankton occurred between 1958-1974 in the south east Norwegian sea with a trend towards lower diatom abundance, a trend that later reversed (Colebrook & al. 1984). Dickson & al. (1988) suggested that a long term increase in northerly wind component over the North At-

Table 3. The species composition in surface, 10 m and 30 m in 1992 expressed as cells l^{-1}. For a complete species list see Dale (1995).

Depth (m)	0							10			30	
Date	24.04	15.05	05.06	24.06.	08.07	14.08	03.09	15.05	05.06	08.07	05.06	08.07
Class Bacillariophyceae												
Fragilariopsis pseudonana	-	-	-	917884	32890	506	506	-	38456	117392	-	78430
Cylindrotheca closterium	-	-	20240	506	2530	-	-	-	33396	2024	506	1012
Pseudo-nitzschia sp.	-	-	7590	7084	9614	-	-	-	5566	9108	-	3036
Thalassiosira bioculata var *raripora*	-	-	83996	20746	70840	506	506	-	178112	50600	23276	47564
Bacillariophyceae (others)	6384	32384	70334	22770	16192	4048	-	9120	8096	6072	4048	10120
Class Dinophyceae												
Gymnodinium sp.	-	-	-	1012	-	62744	-	-	3036	2024	6072	1518
O. Gymnodiniales (unident)	-	-	6578	-	18216	78936	9614	-	44528	4048	2530	3036
Dinophyceae (athecat others)	-	-	-	19228	15686	-	37444	-	16192	-	18722	26312
Dinophyceae (thecat others)	-	-	-	1012	-	-	-	-	-	2024	506	506
Class Prymnesiophyceae												
Algirosphaera sp.	608	25300	1518	3036	506	-	2024	26752	2024	2024	48070	5060
Coccolithus pelagicus	-	2024	-	-	-	-	13156	3648	-	-	3036	506
Emiliania huxleyi	608	41998	179630	201388	132066	4554	15180	39520	447810	171534	76912	44022
Syracosphaera sp.	-	-	-	3036	6578	-	-	-	-	13662	-	-
cf Corymbellus	-	-	-	49082	-	-	-	-	-	-	-	-
Coccolithophorids (others)	11248	118404	113850	5566	67804	-	2024	83904	132572	5566	21758	2024
Class Cryptophyceae												
Leucocryptos marina	-	-	90574	3036	39468	-	8602	-	111320	16698	3542	1012
Class Craspedophyceae												
Monosiga marina	-	-	24288	-	6578	-	-	-	26312	30866	-	506
Unident. heterotrophic	-	-	-	-	-	1518	5566	-	-	2024	-	-
Monads/other flagellates	8816	75364	72358	64262	127512	79442	57684	47424	82984	150788	26312	16698

lantic from 1950 to 1980 induced a decline both in phyto- and zooplankton. It is difficult to decide whether the present investigation represent a period with successful overwintering and favourable timing of migration to the surface for grazers relative to the increase in phytoplankton biomass, or indicate a trend towards a smaller phytoplankton biomass and less dominance by large diatoms. To achieve this a much longer observation period is needed.

REFERENCES

Ayres PA, Seaton DD, Tett PB. 1982. Plankton blooms of economic importance to fisheries in UK waters 1968-1982. *ICES Council Meeting* 1982/L:38. 12 p.

Bathmann UV, Noji TT, Bodungen B von. 1990. Copepod grazing potential in late winter in the Norwegian Sea - a factor in the control of spring phytoplankton growth. *Marine Ecology Progress Series* 60:225-233.

Beyer F. 1962. Absorption of water in crustaceans and the standing stock of zooplankton. *Rapports et Procès-Verbaux des Réunions Conseil permanent International pour l'Exploration de la Mer* 153:79-85.

Braarud T. 1935. The "Øst" Expedition to the Denmark Strait 1929. II. The phytoplankton and its conditions of growth. *Det Norske Videnskaps Akademi. Hvalrådets skrifter* 10:1-173.

Braarud T, Ringdal, Gaarder K, Grøntvedt J. 1953. The phytoplankton of the North Sea and adjacent waters in May 1948. *Rapportes et Procès-Verbaux des Réunions Conseil permanent International pour l'Exploration de la Mer* 133:1-89.

Braarud T, Ringdal, Gaarder K, Nordli O. 1958. Seasonal changes in the phytoplankton at various points off the Norwegian West coast. *Report on Norwegian Fishery and Marine Investigations* 12(3):1-77.

Brettum P. 1969. *En undersøkelse over fytoplanktonet på værskiposisjonene "A" og "M" i Nord-Atlanteren, 0-1000m* [Cand.scient. thesis]. University of Oslo. 150 p.

Broström G. 1997. *Interaction between mixed layer dynamics, gas exchange and biological production in the oceanic surface layer with application to the northern North Atlantic* [Doctoral thesis]. Göteborg University.

Cleve PT. 1897. *A Treatise on the Phytoplankton of the Atlantic and its Tributaries, and on the Seasonal Changes of the Plankton of the Skagerak.* 27 p.

Cleve PT. 1900a. The seasonal Distribution of Atlantic Plankton Organisms. *Kungliga Vetenskaps och Vitterhets Samhälles Handlingar.* Göteborg. 368 p.

Cleve PT. 1900b. Report on the Plankton Collected by the Swedish Expedition to Greenland in 1899. *Kungliga Svenska Vetenskapsakademis Handlingar* 34(3):1-21.

Colebrook JM. 1979. Continuous plankton records: Seasonal variations in the distribution and abundance of plankton in the North Atlantic and the North Sea. *Marine Biology* 51:23-32.

Colebrook JM. 1982. Continuous plankton records: Seasonal variations in the distribution and abundance of plankton in North Atlantic and the North Sea. *Journal of Plankton Research* 4:435-462.

Colebrook JM, Robinson GA, Hunt HG, Roskell J, John AWG, Botrell HH, Lindley JA, Collins NR, Halliday NC. 1984. Continuous plankton records: A possible reversal in the downward trend in the abundance of the plankton of the North Sea and the Northeast Atlantic. *Journal du Conseil permanent International pour l'Exploration de la Mer* 41:304-306.

Dale T. 1995. *Planteplanktonets sesongutvikling på Stasjon M i årene 1990-1992* [Cand.scient. thesis]. University of Bergen. 103 p.

Dickson RR, Kelly PM, Colebrook JM, Wooster WS, Cushing DH. 1988. North winds and production in the eastern North Atlantic. *Journal of Plankton Research* 10(1):151-169.

Dooley HD, Martin JHA, Ellett DJ. 1984. Abnormal hydrographic conditions in the north east Atlantic during the 1970s. *Rapportes et Procès-Verbaux des Réunions Conseil permanent International pour l'Exploration de la Mer* 185:179-187.

Egge JK, Aksnes D. 1992. Silicate as regulating nutrient in phytoplankton competition. *Marine Ecology Progress Series* 83:281-289.

Eilertsen HC, Taasen JP. 1984. Investigations on the plankton community of Balsfjorden. Northern Norway. The phytoplankton 1976-1978. Environmental factors. Dynamics of growth and primary production. *Sarsia* 69:1-15.

Erga SR. 1989. Ecological studies of the phytoplankton in Boknafjorden, western Norway. II. Environmental control of photosynthesis. *Journal of Plankton Research* 11:785-812.

Erga SR, Heimdal BR. 1984. Ecological studies of the phytoplankton of Korsfjorden, western Norway. The dynamics of a spring bloom seen in relation to hydrographical conditions and light regime. *Journal of Plankton Research* 6:67-90.

Fasham MJR. 1995. Variations in the seasonal cycle of biological production in subarctic oceans: A model sensitivity analysis. *Deep-Sea Research* 42:1111-1149.

Føyn L, Magnussen M, Seglem K. 1981. Automatisk analyse av næringsalter med "on-line" databehandling. En presentasjon av oppbygging og virkemåte av systemet i bruk på Havforskningsinstituttets båter og i laboratoriet. *Fisken og Havet* Serie B 4:1-40.

Frost BW, Landry MR, Hassett RR. 1983. Feeding behaviour of large calanoid copepods *Neocalanus cristatus* and *N. plumchrus* from the subarctic Pacific ocean. *Deep-Sea Research* 32:899-915.

Gamble JC. 1978. Copepod grazing during a declining spring phytoplankton bloom in the North Sea. *Marine Biology* 49:303-315.

Garside C, Garside JC. 1993. The f-ratio on 20°W during the North Atlantic Bloom Experiment. *Deep- Sea Research* II 40:75-90.

Gran HH. 1901. Über die Verbreitung einiger wichtiger Planktonformen im Nordmeere. In: Hjort J, editor. *Die erste Nordmeerfahrt des Norwegishen Fischereidampfers "Michael Sars" im Jahre 1900 unter Leitung von Johan Hjort.* Dr. A. Petermanns Geographische Mitteilungen Hefte IV. p 73-83.

Gran HH. 1902. Das Plankton des Norwegischen Nordmeeres von biologischen und hydrografischen Gesichtpunkten behandelt. *Report on Norwegian Fishery and marine Investigations* 2(5):1-223.

Gran HH. 1915. The plankton production of the North European Waters in the spring of 1912. *Bulletin planktonique pour l'année 1912. Conseil permanent International pour l'Exploration de la Mer.* 142 p.

Gran HH. 1929. Quantitative plankton investigations carried out during the expedition with the "Michael Sars", July-Sept 1924. *Rapports et Procès-Verbaux des Réunions Conseil permanent International pour l'Exploration de la Mer* 56(5):1-50.

Gran HH, Braarud T. 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine (including observations on hydrography, density and turbidity). *Journal of the Biological Board of Canada* 1(5):279-467.

Hagebø M, Rey F. 1984. Lagring av sjøvann til analyser av næringsalter. *Fisken og Havet* 4:1-12.

Halldal P. 1953. Phytoplankton investigations from Weather ship M in the Norwegian Sea, 1948-1949. *Det Norske Videnskaps Akademi. Hvalrådets Skrifter* 38:1-91.

Hansen B, Bjørnsen PK, Hansen PJ. 1994. The size ratio between planktonic predators and their prey. *Limnology and Oceanography* 39:395-403.

Hansen B, Tiselius P. 1992. Flow through the feeding structures of suspension feeding zooplankton: a physical model approach. *Journal of Plankton Research* 14:821-834.

Harris RP. 1994. Zooplankton grazing on the coccolithophore *Emiliania huxleyi* and its role in inorganic carbon flux. *Marine Biology* 119:431-439.

Harrison WG, Douglas D, Falkowski P, Rowe G, Vidal J. 1983. Summer nutrient dynamics of the Middle Atlantic Bight: nitrogen uptake and regeneration. *Journal of Plankton Research* 5:539-556.

Head EJH, Harris LR. 1985. Physiological and biochemical changes in *Calanus hyperboreus* from Jones Sound NWT during the transition from summer feeding to overwintering condition. *Polar Biology* 4:99-106.

Helland P. 1963. Temperature and salinity variation in the upper layers at Ocean Weather Ship M (66°N, 2°E). *Årbok for Universitetet i Bergen 1963. Matematisk-Naturvitenskaplig Serie* 16:1-26.

Hirche HJ. 1983. Overwintering of *Calanus finmarchicus* and *Calanus helgolandicus. Marine Ecology Progress Series* 11:281-290.

Holligan PM. 1987. The physical environment of exceptional phytoplankton blooms in the Northeast Atlantic. *Rapportes et Procès-Verbaux des Réunions Conseil permanent International pour l'Exploration de la Mer* 149:148-157.

Holligan PM, Fernandez E, Aiken J, Balch WM, Boyd P, Burkhill PH, Finch M, Groom SB, Malin G, Muller K, Purdie DA, Robinson C, Trees CS, Turner SM, Wal P van der. 1993a. A biogeochemical study of the coccolithophore, *Emiliania huxleyi,* in the North Atlantic. *Global Biogeochemical Cycles* 7:879-900.

Holligan PM, Harbour DS. 1977. The vertical distribution and succession of phytoplankton in the Western English Channel in 1975 and 1977. *Journal of the Marine Biological Association of the United Kingdom* 57:1065-1073.

Jacobsen A, Egge JK, Heimdal BR. 1995. Effects of increased concentration of nitrate and phosphate during a springbloom experiment in mesocosm. *Journal of Experimental Marine Biology and Ecology* 187:239-251.

Jørgensen E. 1900. Protistenplankton aus dem Nordmeere in den Jahren 1897-1900. *Bergen Museums Aarbok* 1900(4). 37 p.

Johannessen JA, Gade HG. 1984. A case study of the variations in the upper ocean at Ocean Weather Ship Mike (66°N, 2°E) in the Norwegian Sea. *Geophysica Norvegica* 32(5):165-175.

Landry MR, Fagerness VL. 1988. Behavioural and morphological influences on predatory interactions among marine copepods. *Bulletin of Marine Science* 43:509-529.

Langdon C. 1988. On the causes of interspecific differences in the growth-irradiance relationship of phytoplankton. II. A general review. *Journal of Plankton Research* 10:1291-1312.

Lohmann H. 1908. Untersuchungen zur Feststellung des vollständigen Gehaltes des Meeres an Plankton. *Wissenschaftliche Meeresuntersuchungen der Kommission zur wissenschaftlichen Untersuchung der deutschen Meere.* Abt Kiel, N.F.10.

Malmberg SA. 1969. Hydrographical changes in the waters between Iceland and Jan Mayen in the last decade. *Jøkul* 19:30-43.

Margalef R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta* 1:493-509.

Miller CB, Frost BW, Batchelder HP, Clemons MJ, Conway RE. 1984. Life histories of large, grazing copepods in a subarctic ocean gyre: *Neocalanus plumchruns, Neocalanus cristatus* and *Eucalanus bungii* in the Northeast Pacific. *Progress in Oceanography* 13:201-243.

Millero FJ, Poisson A. 1981. International one-atmosphere equation of state of seawater. *Deep-Sea Research* 28(6A):625-629.

Nejstgaard JC, Gismervik I, Solberg PT. 1997. Feeding and reproduction by *Calanus finmarchicus*, and microzooplankton grazing during mesocosm blooms of diatoms and the coccolithophore *Emiliania huxleyi. Marine Ecology Progress Series* 47:197-217.

Nygaard I. 1963. *Fytoplanktonet i den sydlige delen av Norskehavet i juni 1959* [Cand.scient. thesis]. University of Oslo, Norway. 124 p.

Østvedt OJ. 1955. Zooplankton investigations from Weather Ship M in the Norwegian Sea, 1948-1949. *Det Norske Videnskaps Akademi. Hvalrådets skrifter* 40. 99 p.

Officer CB, Ryther JH. 1980. The possible importance of silicon in marine eutrophication. *Marine Ecology Progress Series* 3:83-91.

Ostenfeld CH. 1903. Phytoplankton from the Sea around the Farøes. *Botany of the Faroes*. II. 558-612.

Ostenfeld CH. 1913. On the distribution of Bacillariales (Diatoms) in the plankton of the North European waters according to international sea investigations with special relation to the hydrographical conditions. *Conseil International pour l'Exploration de la Mer. Bulletin trimestriel des resultats acquis pendant les Croisieres periodiques et dans les periodes intermediares. Resume des observations sur le Plankton* 3:403-508.

Paasche E. 1960a. On the relationship between primary production and standing stock of phytoplankton. *Journal du Conseil permanent International pour l'Exploration de la Mer* 26(1):33-48.

Paasche E. 1960b. Phytoplankton investigations in the Norwegian Sea in June, 1954, related to hydrography and compared with primary production data. *Fiskeridirektoratets Skrifter Serie Havsundersøkelser* 2. 77 p.

Paasche E. 1961. Notes on phytoplankton from the Norwegian Sea. *Botanica Marina* 2(3/4):197-214.

Paasche E, Rom A-M. 1962. On phytoplankton vegetation of the Norwegian Sea in May 1958. *Nytt Magasin for Botanikk* 9:33-60.

Paulsen O. 1904. Plankton Investigations in the Waters round Iceland in 1903. *Meddelelser fra Kommissionen for Havsundersøkelser Serie Plankton* 1(1):1-41.

Paulsen O. 1909. Plankton Investigations in the Waters round Iceland and in the North Atlantic in 1904 *Meddelelser fra Kommissionen for Havsundersøkelser Serie Plankton* 1(8):1-57.

Paulsen O. 1918. Plankton and other Biological Investigations in the Sea around the Færoes in 1913 *Meddelelser fra Kommissionen for Havsundersøkelser Serie Plankton* 1(13):1-27.

Pingree RD, Maddock L, Butler EI. 1977. The influence of biological and physical stability in determining the chemical distributions of inorganic phosphate, silicate and nitrate. *Journal of the Marine Biological Association of the United Kingdom* 57:1065-1073.

Ramsfjell E. 1960. Phytoplankton distribution in the Norwegian Sea in June, 1952 and 1953. *Report on Norwegian Fisheries and Marine Investigations* 12(10):1-113.

Reid PC. 1977. Continuous Plankton Records: Changes in the Composition and Abundance of the Phytoplankton of the North-Eastern Atlantic Ocean and North Sea, 1958-1974. *Marine Biology* 40:337-339.

Rey F. 1981. The development of the spring phytoplankton outburst at selected sites off the Norwegian coast. In: Sætre R, Mork M, editors. *The Norwegian Coastal Current*. Proceedings from the Norwegian coastal current symposium; 1980 Sep 9-12; Geilo, Norway. p 649-680.

Rey F, Skjoldal HR, Slagstad D. 1987. Primary production in relation to climatic changes in the Barents Sea. In: Loeng H, editor. *The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea*. Proceedings of the 3rd Soviet-Norwegian symposium; 1986 May 26-28; Murmansk. p 29-46.

Riley GA. 1957. Phytoplankton of the North Sargasso Sea, 1950. *Limnology and Oceanography* 2:252-270.

Robinson GA. 1970. Continuous plankton records: Variation in the seasonal cycle of phytoplankton in the North Atlantic. *Bulletin of Marine Ecology* 6:333-345.

Ryther JH. 1956. Photosynthesis in the ocean as a function of light intensity. *Limnology and Oceanography* 1:61-70.

Sakshaug E. 1972. Phytoplankton investigations in Trondheimsfjord, 1963-1966. *Det Kongelige norske videnskaps selskaps Skrifter* 1:1-56.

Sakshaug E, Holm-Hansen O. 1977. Chemical composition of *Skeletonema costatum* and *Pavlova (Monochrysis) lutheri* as function of nitrate-, phosphate-, and iron-limited growth. *Journal of Experimental Marine Biology and Ecology* 29:1-34.

Sakshaug E, Myklestad S. 1973. Studies on the phytoplankton ecology of the Trondheimsfjord. III. Dynamics of phytoplankton bloom in relation to environmental factors, bioassay experiments and parameters for the physiological state of the populations. *Journal of Experimental Marine Biology and Ecology* 11:157-187.

Sieracki ME, Verity PG, Stroecker DK. 1993. Plankton community response to sequential silicate and nitrate depletion during the 1989 North Atlantic spring bloom. *Deep-Sea Research* II 40:213-225.

Skjoldal HR, Noji TT, Giske J, Fosså JH, Blindheim J, Sundby S. 1993. *"Mare cognitum" Science Plan for Research on the Marine Ecology in the Norwegian Sea*. Bergen: Institute of Marine Research. 162 p.

Smayda TJ. 1980. Phytoplankton species succession. In: Morris I, editor. *The physiological ecology of phytoplankton*. Los Angeles: University of California Press. p 493-570.

Smith REH, Kalff J. 1982. Size-dependent phosphorus uptake kinetics and cell quota in phytoplankton. *Journal of Phycology* 18:275-284.

Steemann Nielsen E. 1935. The production of the Faroe Isles, Iceland, East Greenland and the waters around. *Meddelelser fra Kommissionen for Danmarks Fiskeri og Havsundersøkelser Ser Plankton* 3(1):1-93.

Stefánsson U. 1962. North Icelandic Waters. *Rit Fiskideildar* 3:1-269.

Strickland JDH, Parsons TR. 1972. A practical Handbook of seawater Analysis (2nd ed). *Bulletin of the Fisheries and Research Board of Canada* 167:1-310.

Sverdrup HU. 1953. On conditions of vernal blooming of phytoplankton. *Journal du Conseil permanent International pour l'Exploration de la Mer* 18:287-295.

Taylor AH, Harbour DS, Harris RP, Burkhill PH, Edwards ES. 1993. Seasonal succession in the pelagic ecosystem of the North Atlantic and the utilization of nitrogen. *Journal of Plankton Research* 15:875-891.

Townsend DW, Cammen LM, Holligan PM, Campell DE, Pettigrew NR. 1994. Causes and consequences of the timing of spring phytoplankton blooms. *Deep-Sea Research* 41:747-765.

Townsend DW, Keller MD, Sieracki ME, Ackleson SG. 1992. Spring phytoplankton blooms in the absence of vertical water column stratification. *Nature* 360:59-62.

Utermöhl H. 1931. Neue Wege in der quantitativen Erfassung des Planktons (Mit besoderer Berücksichtigung des Ultraplanktons). *Verhandlungen der Internationalen Vereiningung für theoretische und angewandte Limnologie* 5:567-596.

Veldhuis MJW, Kraay GW, Gieskes WWC. 1993. Growth and fluorescence characteristics of ultraplankton on a north-south transect in the eastern North Atlantic. *Deep-Sea Research* II 40:609-626.

Vidal J, Smith SL. 1986. Biomass, growth, and development of herbivorous zooplankton in the Eastern Bering Sea during spring. *Deep-Sea Research* 33:523-556.

Weeks A, Conte MH, Harris RP, Bedo A, Bellan I, Burkhill PH, Edwards ES, Harbour DS, Kennedy H, Llewellyn C, Mantoura RFC, Morales CE, Pomroy AJ, Turley CM. 1993a. The physical and chemical environment and changes in community structure associated with bloom evolution: the Joint Global Flux Study North Atlantic Bloom Experiment. *Deep-Sea Research* II 40:347-368.

Weeks A, Fasham MJR, Aiken J, Harbour DS, Read JF, Bellan I. 1993b. The spatial and Temporal development of the spring bloom during the JGOFS North Atlantic Bloom Experiment,1989. *Journal of the Marine Biological Association of the United Kingdom* 73:253-282.

Wiborg KF. 1955. Zooplankton in relation to hydrography in the Norwegian Sea. *Fiskeridirektoratets Skrifter Serie Havundersøkelser* 11. 66 p.