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Diel variations in some important phytoplankton parameters during a 24 hours sampling period in Balsfjorden, Tromsø and Skjomenfjorden, Nordland, North Norway

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Abstract

Every fourth hour in 24 h periods measurements were made of temperature, salinity, plant nutrients, incident radiation at three m depth, sub-surface light extinction, chlorophyll a, phaeophytin, particulate carbon and nitrogen, cell counts, zooplankton dry weight biomass, *in situ* primary production (^{14}C), incubator carbon assimilation (^{14}C), heterotrophic activity (^{14}C glucose assimilation), and horizontal variation in chlorophyll a over one nautical mile. The marked variations in all parameters were probably generated by the combined effects of wind-driven circulation of water masses in the fjord and phytoplankton patches. This study stresses the presence of spatial and temporal changes in fjords, and that data conducted from one or few stations should be interpreted with care.

Introduction

The presence of spatial structure and short-term variations in the phytoplankton populations and biological and physical environment is a well-known phenomenon (RICHERSON et al. 1970, PLATT 1975, MEYER-REIL et al. 1979). Most phytoplankton investigations are based on samples taken at weekly or monthly intervals, and phytoplankton workers often tend to neglect the occurence of spatial and temporal variations.

This pilot study, aimed at the presence and the magnitude of spatial and temporal changes in several measured phytoplankton parameters, summarizes the results from 24 h sampling periods in Balsfjorden (69°29'N – 19°06'E) and Skjomen (68°22'N – 17°14'E) (Fig. 1). Maximum depth in Balsfjorden (B5) is approx. 190 m, and in Skjomen (O5) 120 m. The investigations were carried out at the time of the spring phytoplankton bloom, at a time when fjord hydrography was about to change from a winter situation with homogeneous water masses to a summer situation with estuarine circulation.

Material and methods

Sampling

Samples were collected at 4 h intervals during 24 h periods in Balsfjorden (April 8–9, 1980) and Skjomen (April 22–23, 1980). Water samples were taken with a 5 l plastic Niskin sampler. Sampling depths were determined from data on hydrography and continuous fluorescence (chlorophyll a) profiles (50–0 m). In Balsfjorden samples were taken from 0, 3, 10 and 25 m and in Skjomen from 4 m instead of 3 m.
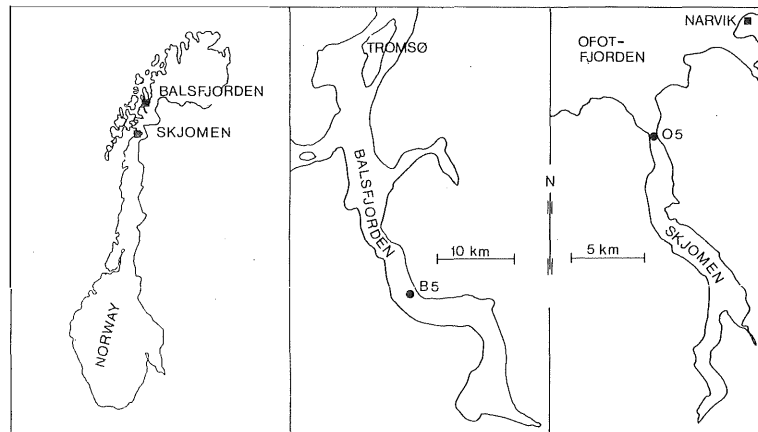
Figure 1

Map of Balsfjorden and Skjomen showing the sampling stations.

Hydrography

Data on temperature, salinity and density for each metre were obtained using a Neil Brown Instruments Mark III CTD Sonde coupled to a Nord-10 computer.

Water chemistry

Nitrate (No_3 + NO_2 − N), orthophosphate and silicate were analysed immediately on board the vessel according to the methods described by STRICKLAND and PARSONS (1972).

Light

Sub-surface light extinction was measured in micro-Einsteins $(\mu E)^+$ $m^{-2} \cdot sec^{-1}$ in the 400–700 nm waveband with a Lambda LI-185 quantum meter and underwater quantum sensor LI-1925. Light in μE at 3 m (4 m in Skjomen) during the *in situ* carbon assimilation and incubator experiments was measured with a Lambda LI-500 integrator coupled to Lambda LI-1925 underwater quantum sensor.

Chlorophyll a, phaeophytin, and continuous *in vivo* fluorescence profile

Water samples of 250 ml were filtered on Whatman GF/C filters. Chlorophyll a and phaeophytin were extracted in 90 % acetone and determined on board the vessel by fluorescence technique (EDLER 1979) using a Turner 111 fluorometer. *In vivo* fluorescence profiles (50–0 m) were taken with the same fluorometer, with a recorder coupled to pump and hose.

Particulate carbon and nitrogen

Carbon and nitrogen content of 500 ml water samples filtered on precombusted GF/C filters were determined in a Carlo Erba Elemental Analyser Mod 1104.

Cell density and species composition

Water samples of 100 ml were preserved with 2 ml of neutralized formalin. Subsamples of 2 ml and 50 ml were examined within 3 weeks of sampling by the inverted microscope technique (UTERMÖHL 1931).

$^+$ 1 microeinstein ($1\mu E$) = 6.02 x 10^{17} quanta (photons).

Carbon assimilation *in situ* and incubation experiments

The method for ^{14}C uptake followed procedures outlined by STRICKLAND and PARSONS (1972). Carbonate content of seawater was determined by measuring pH immediately after sampling. In *in situ* and incubator experiments 100 ml light and dark bottles were inoculated with 0.5 ml of 5 μCi (1 μCi = 2.22 x 10^6 dpm) $NaH^{14}CO_3$, and kept in light for 4 hours. Water for measurement of maximum photosynthetic rates (incubator, kept in daylight at surface temperature) was collected at 3 m depth. Light in the incubator bottles corresponded by means of different nets to 75, 30, 15 and 2 % of surface irradiance. After incubation the phytoplankton was filtered on to Millipore HA type 47 mm filters which were desiccated and stored frozen for up to 1 month before further analysis. Filters were treated with fuming hydrochloric acid and the activity was measured by liquid scintillation (Packard Tri-Carb) using Schint Hei-3 as a scintillator.

Glucose assimilation

Heterotrophic glucose assimilation (uptake rate) was measured by adding 0.5 ml of uniformly labelled d-glucose ^{14}C solution (0.0125 μCi) and incubating for 4 h in darkness at the surface water temperature. The filters were treated in the same manner as described for carbon assimilation measurements. Concentration of glucose in the seawater was not measured, and hence turnover rate could not be calculated. The concentration of added glucose probably does not correspond to *in situ* values, and the measured uptake rates must be considered as relative values.

Zooplankton biomass

Zooplankton was collected with a WP-2 net (0.25 m²) with 200 μm mesh. Vertical hauls were taken from 70 m to surface every 4 hours, and samples were kept frozen at –20 °C. Dry weight was determined after desiccation with silica gel for 2 weeks.

Random errors

The coefficients of variation of the various analyses were estimated after the analysis of 20 replicates (Table 1).

Table 1

Parameter	C.V. (%)
Nitrate (No_3 + NO_2 − N)	1.2
Orthophosphate	1.1
Silicate	3.7
Chlorophyll a, phaeophytin	5.1
Particulate carbon and nitrogen	2.0
Carbon assimilation	7.2
Cell counts, *Phaeocystis* colonies, 10·2ml samples	40
1 % of surface light, calm cloudless weather, 10 measurements	3.7

Results and discussion

Hydrography

Hydrographical data from both stations showed marked changes during the 24 h sampling period (Fig. 2). No marked pycnocline was observed in Balsfjorden at the beginning of the sampling period, indicating thorough mixing with the underlying
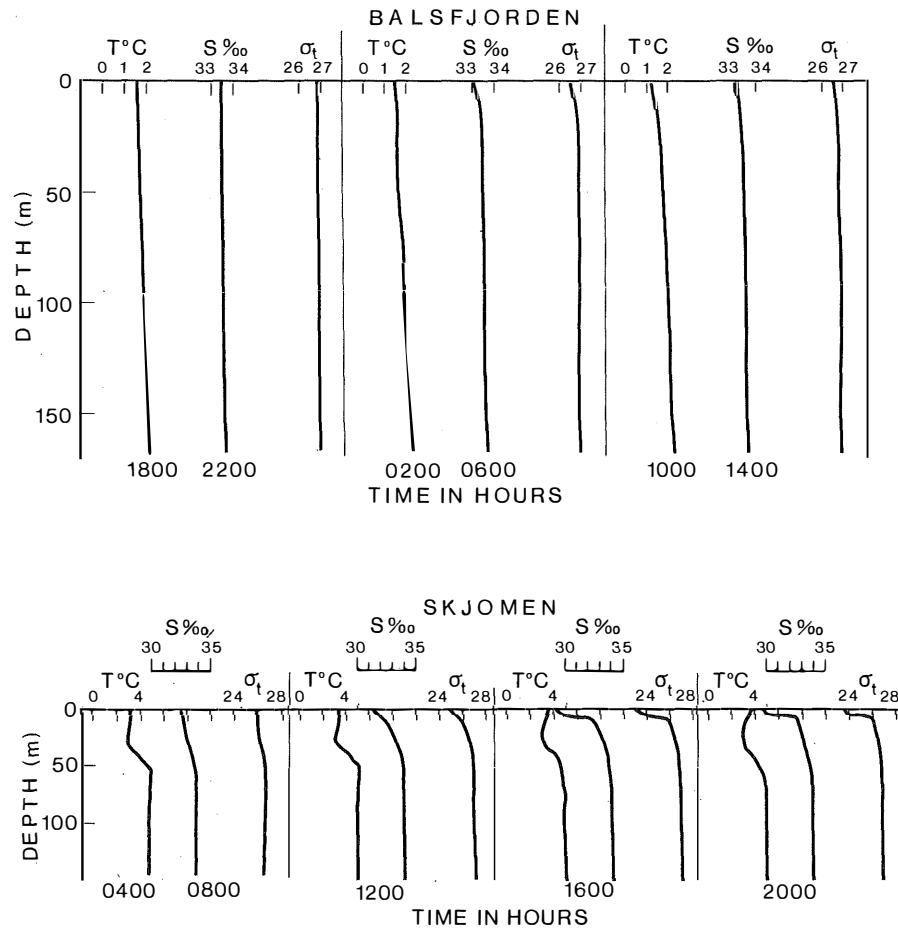
Figure 2

Hydrography during the 24 h sampling periods

water masses. The greatest variations in salinity were at 0 m (33.400 $^0/_{00}$ 1800 hr and 33.047 $^0/_{00}$ 0200 hr) in Balsfjorden. In Skjomen surface salinity varied from 32.500 $^0/_{00}$ 0400 hr to 29.300 $^0/_{00}$ 1600 hr and there was a marked pycnocline present (c. 5–10 m). During the sampling periods less saline water could be measured at both stations in the surface layers, occurring in Balsfjorden from c. 0100 hr and in Skjomen from 1200 hr, leading to increased surface stability (Fig. 3). The salinity in the surface increased again towards the end of the sampling periods. Extended sampling on hydrography before and after the 24 h period in Balsfjorden suggested that variations in surface salinity had a diel character. Current measurements from Skjomen (Fig. 3) indicate that surface layer currents are correlated to winds of diel periodicity.

During winter high barometric pressure centres over northern Scandinavia cause strong, cold winds ("boras") to blow out of the fjords in North Norway. In summer these "boras" are absent, and winds of diel periodicity caused by heating of the land may blow into the fjords (SVENDSEN 1977, EILERTSEN et al. 1981). In Ryfylkefjordene
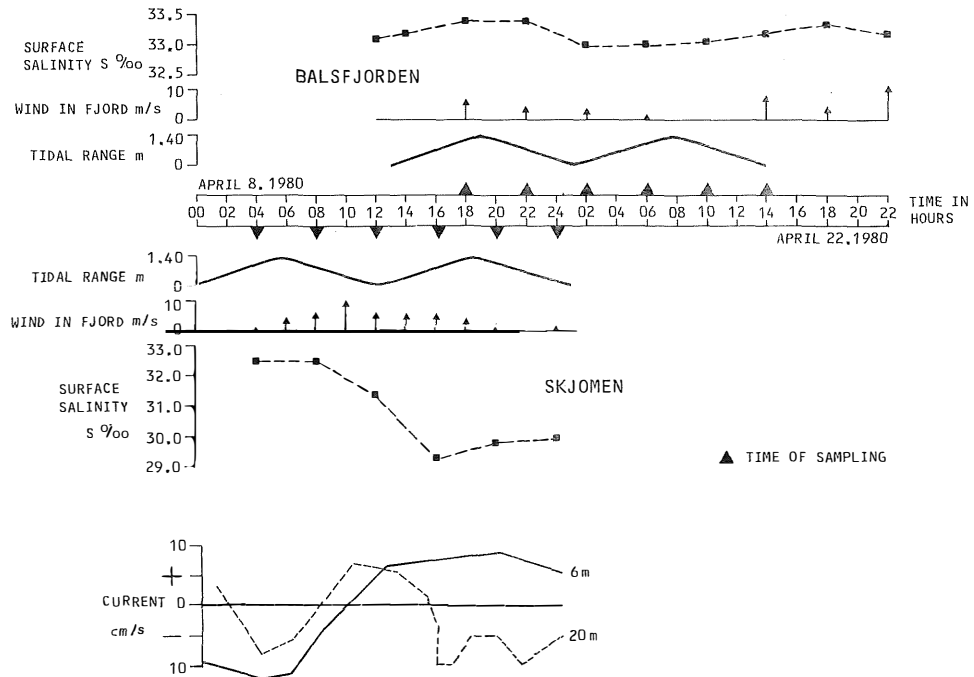
Figure 3

Variation in surface salinity with wind and tide, '+' denotes current into the fjord and '–' out of the fjord

surface drifts caused by winds of diel periodicity were observed, and it was concluded that wind was by far the most important factor in setting up the current system of the upper layers of the fjord (SVENDSEN 1977, SVENDSEN and UTNE 1979). In Skjomen, yearly inflow of coastal water has been positively correlated with wind blowing out of the fjord (SKRESLET and SCHEI 1976).

Diel winds blowing from the mouth to the head of Balsfjorden and Skjomen causes accumulation of brackish surface water inside the fjord, leading to decreased surface salinity and increased stability. This may be enhanced by more freshwater run-off due to increased temperatures during the day. The wind-generated surface drifts may be counteracted or strengthened by the tidal waves. According to SKRESLET and SCHEI (1976) water coming in at high tide may restrict outflow of brackish water at the surface in both Skjomen and Balsfjorden. The great decrease in surface salinity in Skjomen during the day must be the result of a wind-generated surface current in the fjord combined with the incoming tidal movement.

Plant nutrients

In both fjords great variations were recorded in all the measured plant nutrients. Measurements showed increasing values of all parameters towards the end of the sampling period at both stations, except for high phosphate values in Balsfjorden at 2200 hr (Fig. 4). In Skjomen there were very high nitrate values at 2000 hr and 2400 hr.
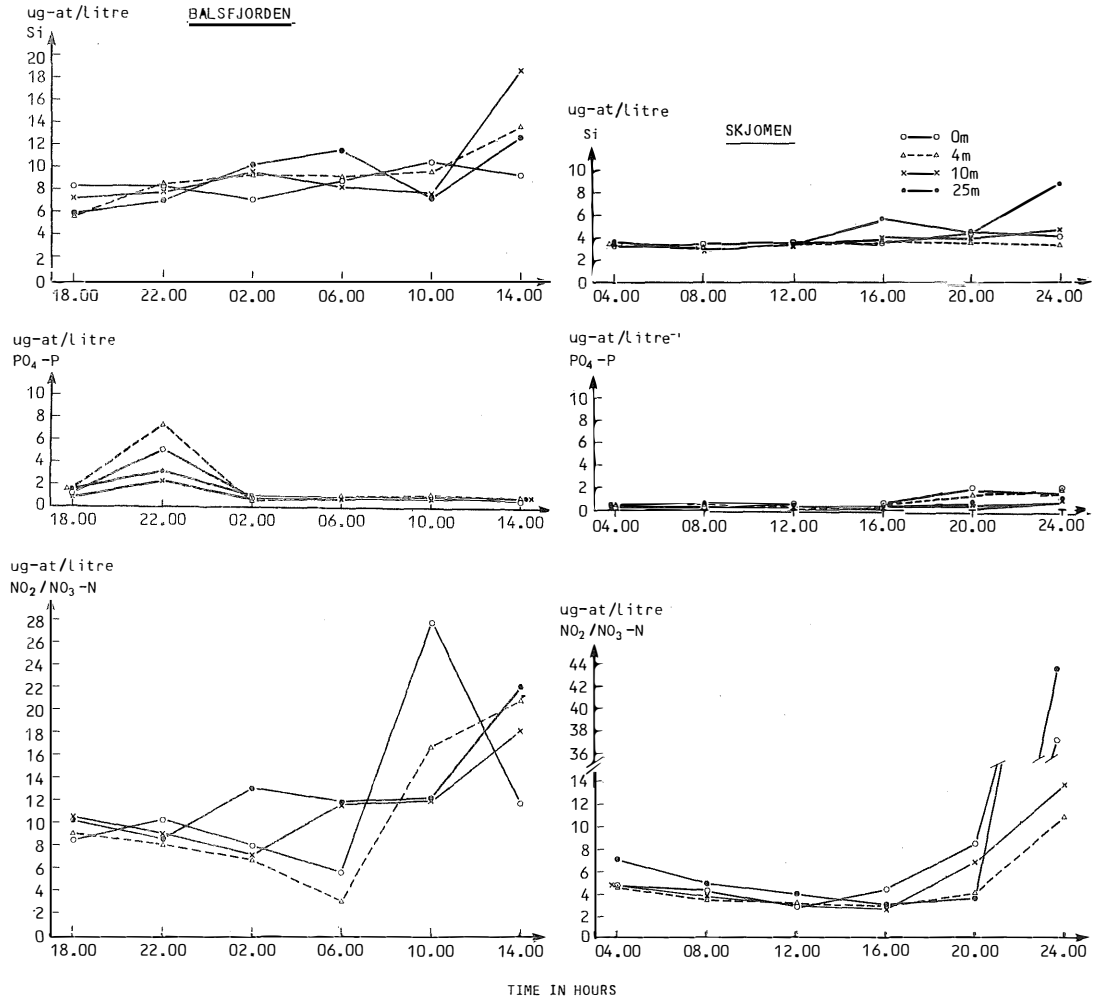
Figure 4

Plant nutrients in Balsfjorden and Skjomen

The increased nutrient values at all depths towards the end of the sampling period in both fjords were probably due to admixture of nutrient-richer deep water to the surface layers resulting from increased turbulent diffusion between water bodies moving in opposite directions (Fig. 3).

The water in Balsfjorden generally showed greater content of nutrients than the water in Skjomen. Skjomen is situated further south than Balsfjorden, and has reached a later stage in the phytoplankton spring bloom development and consequently there were lower concentrations of nutrients in the upper water layers.

Sub-surface light extinction

In Balsfjorden the depth at which 1 % surface irradiance occurred decreased from c. 38 m to c. 30 m at the end of the sampling period (Fig. 5). This coincided with an increase in phytoplankton biomass (see chl. a measurements). Underwater light measurements at varying and low solar elevations are uncertain and may lead to differences in the determination of 1 % depth of surface irradiance (JERLOV and NYGÅRD 1969). In Balsfjorden solar elevation at midday 8 April was only 27°, and in Skjomen 22 April 35°. In Skjomen significant changes in 1 % depth of surface irradiance could not be recorded.
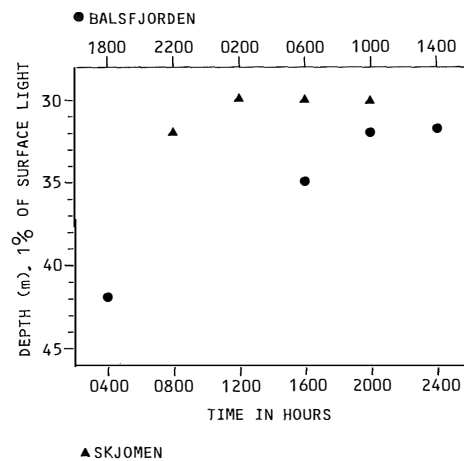

Figure 5

Sub-surface light extinction in Balsfjorden and Skjomen

Cell density and species composition

The standing crop at both stations was dominated by the colony-forming haptophycean *Phaeocystis pouchetii*. Small numbers of diatoms and flagellates were also present. Cell counts from Skjomen, as expected, were higher than in Balsfjorden (Fig. 6). No significant correlation could be observed between cell counts and chlorophyll a values, probably due to counting errors and uneven distribution of *Phaeocystis* colonies.

Towards the end of the sampling period Chl a values decreased down to 25 m in Skjomen (Fig. 7). At the same time salinity decreased. If an accumulation of freshwater occurred (Fig. 3), biomass in the upper layers was 'diluted', and lower Chl a values were measured. In Balsfjorden Chl a was quite evenly distributed down to 25 m, and the decrease in biomass did not show the same trend as in Skjomen. Freshwater run-off into Balsfjorden was neglible at this time of year (Fig. 2), and no marked pycnocline was observed. In Skjomen phytoplankton growth above the pycnocline (c. 10 m) was favoured, as shown by lower Chl a values at 25 m.

Particulate carbon and nitrogen varied to a high degree in both fjords (Table 2). It can be noted that C/N-ratios at 0 m were similar to ratios at 3 m, and ratios at 15 m similar to 25 m. This may again be explained by the presence of two different water bodies, with different pre-histories, moving in opposite directions.
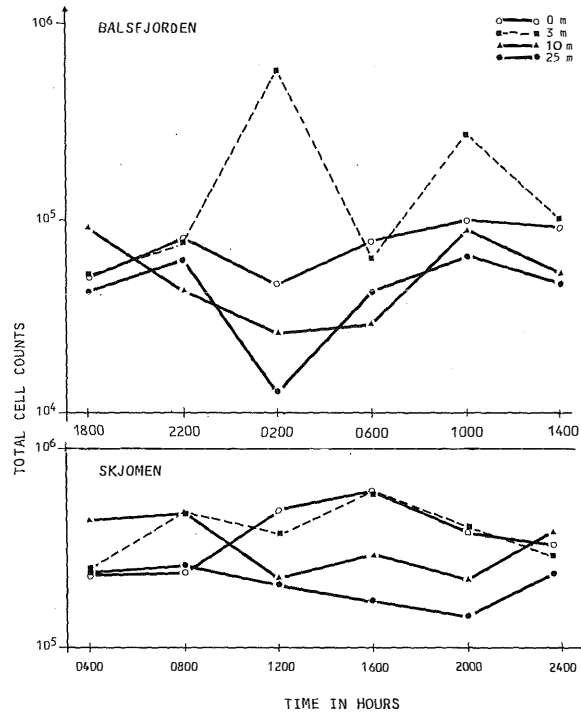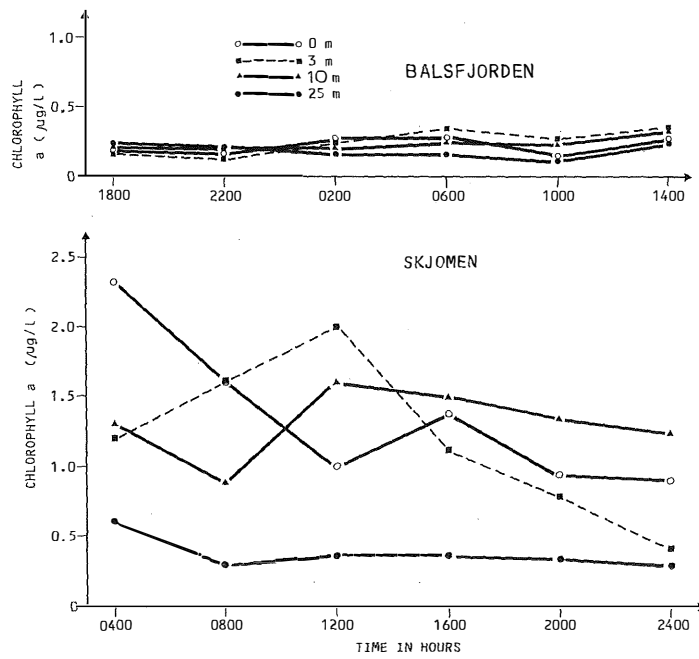
Figure 6

Total cell counts

Figure 7

Chlorophyll a measurements

Table 2

Particulate C and N, C/N-ratio (atomic). Triplicate measurements from each depth

Balsfjorden

Depth m	1800 h μg C/l	μg N/l	C/N	2200 h μg C/l	μg N/l	C/N	0200 h μg C/l	μg N/l	C/N	0600 h μg C/l	μg N/l	C/N	1000 h μg C/l	μg N/l	C/N	1400 h μg C/l	μg N/l	C/N
0	245.2	23.6	12.2	322.6	58.8	6.3	355.3	20.5	20.2	210.9	25.4	9.7	215.13	19.5	12.8	296.1	12.1	28.5
3	428.3	44.2	11.3	304.3	42.7	8.3	496.2	39.0	14.8	389.3	51.0	8.9	367.9	41.3	10.4	262.5	12.7	24.1
15	299.9	62.2	5.6	363.5	29.3	14.5	502.6	34.9	16.8	375.2	36.9	11.9	431.8	32.2	15.6	601.3	22.4	31.3
25	326.4	57.9	6.6	255.9	11.8	25.3	268.6	3.6	86.9	303.6	28.2	12.6	224.7	11.0	23.8	323.0	16.9	22.3

Skjomen

Depth m	0400 h μg C/l	μg N/l	C/N	0800 h μg C/l	μg N/l	C/N	1200 h μg C/l	μg N/l	C/N	1600 h μg C/l	μg N/l	C/N	2000 h μg C/l	μg N/l	C/N	2400 h μg C/l	μg N/l	C/N
0	223.8	38.3	6.8	1124.5	195.5	6.7	794.1	117.0	7.9	335.3	26.1	15.9	473.5	53.8	8.9	449.5	47.5	11.0
4	259.7	45.2	6.7	935.1	238.8	4.6	899.9	117.1	9.0	496.2	39.02	14.8	456.5	61.8	10.3	564.2	48.5	11.3
10	361.5	56.6	7.4	774.0	156.8	5.8	493.2	44.5	12.9	564.2	71.3	9.2	521.6	43.3	14.0	414.1	62.0	7.8
25	485.7	58.8	9.6	788.7	144.3	6.4	452.0	41.3	12.8	514.4	73.3	8.2	424.8	20.6	24.1	234.2	43.2	6.3

Chlorophyll a, particulate carbon and nitrogen have all been frequently used as estimates of phytoplankton biomass and their ratios as indices of phytoplankton growth status (nutrient deficiency etc.) (SAKSHAUG 1978).

Variations in the ratios C/Chl. a were; Balsfjorden: 2500–750, Skjomen: 700–100 and N/Chl a; Balsfjorden 300–37, Skjomen 100–17. There was no correlation between the changes in the ratios C/Chl a, N/Chl a and C/N with either time of sampling or depth, and no conclusions regarding phytoplankton growth status and physiology will be drawn from these ratios. The great variations in the absolute values of C, N and Chl.a and their ratios must result from inhomogenities in the water masses, i.e. varying amounts of detritus from different water bodies, freshwater run-off, and from patchy distribution of phytoplankton. All the ratios are lower in Skjomen than in Balsfjorden. This must be a result of phytoplankton being a greater part of total particulate organic material. The rapid and unpredictable changes in the ratios C/Chl a, N/Chl a and C/N observed in this investigation show that it is very difficult to estimate ratios between these chemical constituents characterizing the growth status of natural phytoplankton. BANSE (1974) has stressed the importance of interpreting results on ratios involving carbon and nitrogen from natural phytoplankton with care, partly because of the presence of microzooplankton and aggregates of organic matter produced as byproducts of photosynthesis. *Phaeocystis pouchetii*, being the dominant algae in both fjords, is known to excrete up to 64 % of its photo-assimilated carbon (GUILLARD and HELLEBUST 1971).

The presence of phytoplankton patches was confirmed by the results obtained both from Balsfjorden and Skjomen, and shows up to 100 % variation over 1/3 nautical mile (Table 3).

Table 3

Balsfjorden	1/3	2/3	3/3	n.m. (1852 m)
Chl a µg/l[+]	0.21	0.17	0.32	
Skjomen				
Chl a µg/l	0.52	0.56	0.95	

[+] Each measurement mean of four replicate samples.

Zooplankton grazing is often believed to be one factor producing uneven distribution of phytoplankton. The main species of the standing stock of zooplankton were *Pseudocalanus elongatus*, *Microsetella norwegica*, *Microcalanus* sp. and *Calanus finmarchicus*. In Balsfjorden there was a peak in zooplankton abundance at 0200 hr and in Skjomen at 1600 hr (Fig. 8). Several species of zooplankton are known to undergo diurnal migration in Balsfjorden (HOPKINS et al. 1978). The increased biomass at 0200 hr was mainly composed of *Calanus finmarchicus*. This species is known to increase in number at this time of the year, and probably represents an increased grazing pressure on the phytoplankton standing crop, especially during the night.

In situ ^{14}C assimilation, incubation experiments and heterotrophic glucose assimilation

The highest primary production values were measured around midday (Fig. 9) with 10.4 mg C/m²/h in Balsfjorden 1000 – 1400, and 68.3 mg C/m²/h 1200 – 1600 in Skjomen. In Balsfjorden, production around midnight (2200 – 0200 hr) amounted to 1.7 % of the production mg C/m²) at midday. Some of the values are underestimated due to lack of
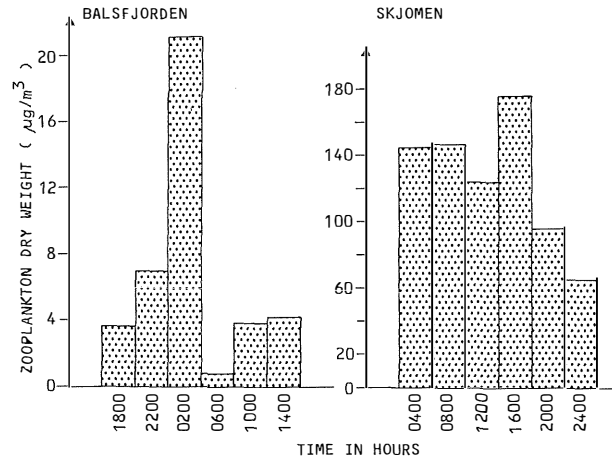
Figure 8
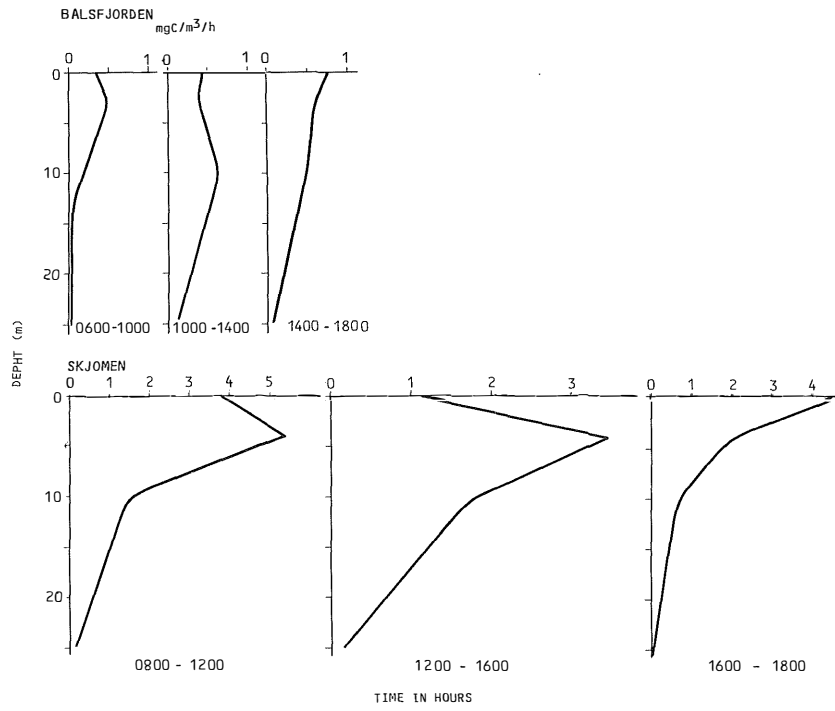Variations in zooplankton dry weight

Figure 9
Variations in *in situ* primary production

sampling depths under 25 m, but this error does not affect any of the preceding conclusions. The results also show that at high solar elevations (midday), maximum production rate is found at greater depths, indicating surface light inhibition. This was also confirmed by the incubator experiments.

The ratio between light-saturated photosynthesis and weight of chlorophyll a has frequently been used as a measurement of photosynthetic capacity. Incubation experiments at the stations showed higher photosynthetic rates after noon than before (Fig. 10). The light at the period of lowest light irradiance during the day (Balsfjorden 0600 – 1000 hr) corresponded to c. 4.0 x 10^{15} quanta $cm^{-2}sec^{-1}$. It is expected that at least algae near the surface underwent light-saturated photosynthesis. In the incubator the greatest photosynthetic rates were found in bottles corresponding to 75 % of surface irradiance, and after noon in bottles corresponding to 100 %. The *in situ* experiments showed the same tendency of light adaption: before noon maximum photosynthesis was found at 3 (4 m) depth, and after noon at 0 m.

Phytoplankton populations have long been known to undergo daily rhythms in photosynthetic rates (see SOURNIA 1974). Some workers report this phenomenon as the "afternoon depression", and it is often assumed that this periodicity decreases with higher latitudes (SOURNIA 1974). The mechanisms govering diurnal variations in photosynthesis are not yet fully understood. STROSS (1975) states that the diurnal variations are results of intrinsic rhythms (chl. a reorganization, enzyme activity) and oscillations in external nutrient concentrations. The results of this study suggest that there is an afternoon maximum in photosynthetic efficiency in the investigated fjords. STROSS (1975) found that arctic phytoplankton from tundra ponds had a photosynthetic maximum during the afternoon, and NEWHOUSE et al. (1967) reported that phytoplankton from inshore environments near Hawaii had a maximum around 1600 hr.

Heterotrophic glucose assimilation values varied to a great extent at both stations (Table 4). The highest values encountered were at noon or afternoon, coinciding with the greatest phytoplankton production. Dissolved organic matter may immediately be incorporated in microheterotrophs resulting in instant increased bacterial growth (WIEBE and SMITH 1977). This may lead to short term variations in bacterial growth which again result in quick changes in the material cycle in the sea (MEYER-REIL et al. 1979).
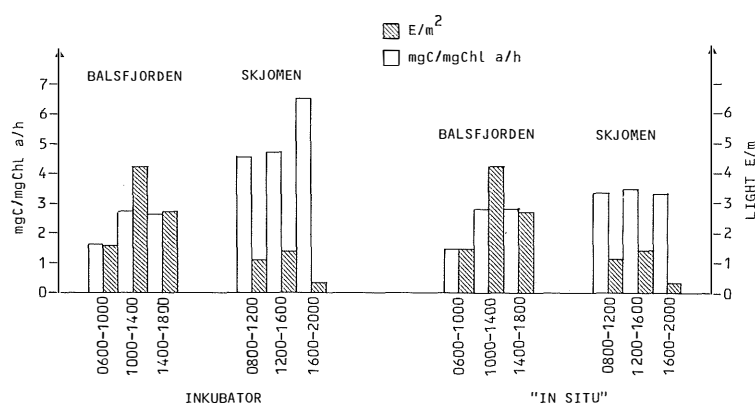

Figure 10
Photosynthetic rates and light

Table 4

Heterotrophic glucose assimilation (μg $\cdot$ l^{-1} h^{-1}, integrated values)

Balsfjorden

	1800–2200	2200–0200	0200–0600	0600–1000	1000–1400	1400–1800
0–25 m	0.05	0.11	0.11	0.08	0.14	0.12

TIME

Skjomen

	0400–0800	0800–1200	1200–1600	1600–2000	2000–2400	2400–0400
0–25 m	0.24	0.23	0.39	0.37	0.17	0.16

Concluding remarks

It is a well-known phenomenon that phytoplankton populations are distributed in nonrandom or patchy fashion on moderate scales, though the mechanisms involved are not yet fully understood. RICHERSON et al. (1970) explains this by the "contemporaneous disequilibrium".

The aquatic environment consists of contiguous microhabitats (with different growth characteristics) which tend towards diversity, whilst physical processes tend towards uniformity.

The variations in the parameters measured in this investigation must result from water replacements and phytoplankton patches. Wind-generated diel currents in the surface layers are found up the fjord. Freshwater accumulated in the surface layer (S^0/$_{oo}$ decreased) biomass decreased due to 'dilution' and nutrients were transported upwards from the deeper layers. The understanding of patches and temporal variations in fjords is complicated by the fact that the physical factor in the "contemporaneous disequilibrium" concept is constantly changing during spring and summer. Marine biologists often tend to neglect short-term variations, and that investigations are often not carried out in the same water (same microhabitat). This study stresses the importance of understanding the physical environment of phytoplankton, the nature of temporal biological changes in the sea, and shows that data collected from a limited number of stations should be interpreted with care. Sampling programmes, expecially in investigations involving studies of phytoplankton growth dynamics, should be designed to sample many stations or to sample within short intervals so than conclusions based on the results have reasonable validity.

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