Seasonal patterns in composition and biomass of autotrophic and heterotrophic nano- and microplankton communities on the north Norwegian shelf

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From monthly transects on the shelf off northern Norway, data describe the size, abundance, and biomass of photosynthetic nano- and picoplankton, heterotrophic (aplastidic) nanoplankton, and ciliates. Samples were analyzed using a state-of-the-art color imaging system. The numerically dominant phytoplankton were pico- and nanoplankton. Highest biomasses occurred in summer, and increased earlier in the year and attained higher values in inshore stations compared to offshore stations. Mean cell sizes were small, 2-5 µm diameter nanoplankton and 1 µm eucaryotic picoplankton; cyanobacteria were comparatively unimportant contributors to biomass. The dominant herbivores appeared to be heterotrophic flagellates, which were generally similar in size, concentration, and biomass to the phototrophic forms. Their temporal and spatial distribution mimicked their putative prey, except that they often occurred in abundance deeper than the photosynthetic nanoplankton. Oligotrich ciliates were also abundant. The ratio of photosynthetic: heterotrophic plankton (P:H) biomass exhibited spatial and temporal trends. P:H in surface waters was low in March (< 0.5), increased to maxima (2-3) in June-July, and decreased again during late summer and into October (0.4-0.6). Contrary to expectations, small-celled auto- and heterotrophs apparently dominated nutrient uptake, remineralization, and likely reduced vertical fluxes of microplankton-derived organic matter from the euphotic zone of the north Norwegian shelf. It is suggested that the significance of small cells was exacerbated by significant grazing of large phytoplankton and protozoans by meso- and macrozooplankton.

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INTRODUCTION

Studies of plankton dynamics in Norwegian fjords have been undertaken for much of the 20th century (reviewed in Tande 1991 and Wassmann & al. 1996a, 1996b). The majority of these efforts focused on larger phytoplankton and zooplankton, primarily due to philosophical and methodological biases. The resulting conceptual model of pelagic processes in fjords incorporates a spring bloom of large-celled diatoms and colonial *Phaeocystis*, dinoflagellates and ciliates in summer, and often a second diatom bloom in autumn, all grazed by mesozooplankton. Studies beyond the coastal fjords on the continental shelf are fewer (see Wassmann & al. 1999), and it has generally been assumed that plankton dynamics in fjord and shelf waters are similar. Moreover, such interpretations are often extended according to water temperature: cold waters are generically identified with large organisms and short food chains (Lenz 1992). There are indications, however, that such broad generalizations can be misleading (Verity & Vernet 1992; Verity & al. 1993; Stoecker & al. 1995).

As part of the European OMEX (Ocean Marginal EXchange) program, a study of processes and fluxes was conducted on Nordvestbanken, a portion of the north Norwegian shelf, from March to October of 1994. The Norwegian Coastal Current (NCC) flows northward on the shelf, while more saline Norwegian Atlantic Water (NAW) occasionally intrudes at depth from offshore onto the shelf. Topography and hydrography of the region are described in Nordby & al. (1999). Here we provide the composition, abundance, and biomass of autotrophic and heterotrophic cells from monthly transects across the shelf. From these and related data on plankton structure, we infer an unexpected conceptual model of plankton dynamics in these cold subarctic shelf waters.

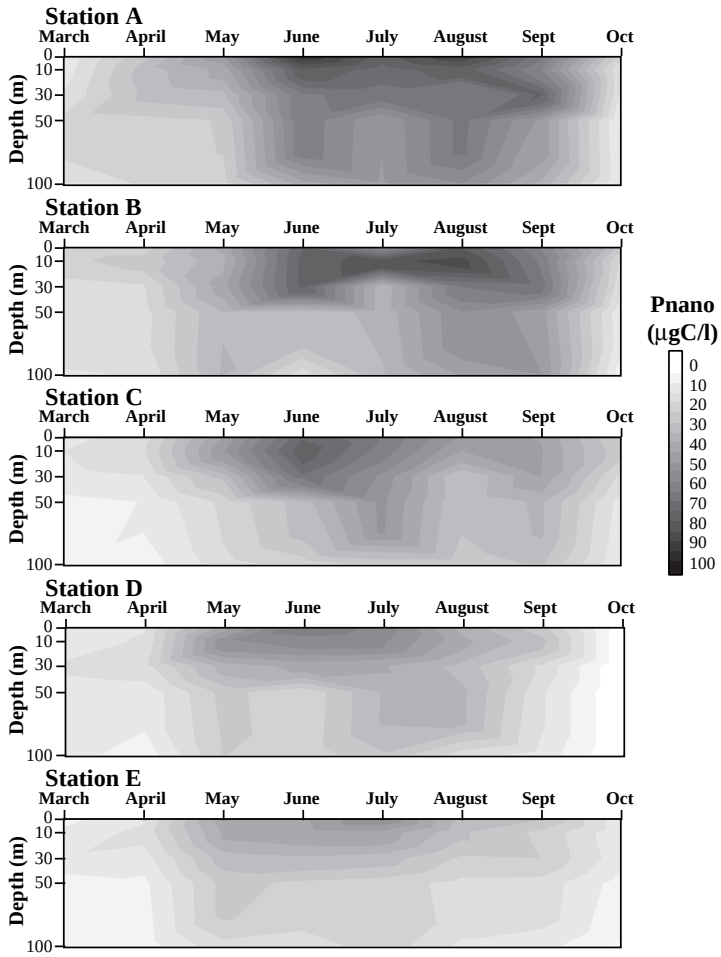

Fig. 1. The temporal and vertical distribution of carbon biomass of photosynthetic nanoplankton (Pnano) across the north Norwegian shelf in 1994. Contours generated by DeltaGraph v4.0 (DeltaPoint, Inc.).

METHODS

Water samples were collected at monthly intervals in 1994 across a five station transect on Nordvestbanken. The transect line was ca. perpendicular to the shelf break, and stations included the inner shelf (Stn A), mid shelf (Stn B), and three stations at the shelf edge: 200 m (Stn C), 300 m (Stn D), and 500 m (Stn E) isobaths. Distances between stations were ca. 30 km, 20 km, 5 km, and 5 km, respectively (see Wassmann & al. 1999). Samples from near-surface, 10 m, 30 m, 50 m, and 100 m were treated using two methods. One set was preserved in 0.2 % final concentration glutaraldehyde, stained with DAPI and proflavin according to Verity & Sieracki (1993), and gently collected on 0.4 μm black Nuclepore filters. Each was mounted onto a glass microscope slide under a drop of low fluorescence immersion oil and a #1 cover slip, and frozen at –20 °C for subsequent analysis of small auto- and heterotrophic plankton (see below). The other sample from each depth was fixed in glutaraldehyde-Lugol's solution (Rousseau & al. 1990) and used to enumerate and measure larger cells (diatoms, dinoflagellates, and protozoans) and *Phaeocystis* colonies.

Using the fluorescently stained samples on filters, the abundances and dimensions of the following plankton trophic groups were measured: photosynthetic nano- and picoplankton; cyanobacteria; heterotrophic nanoplankton; and hetero- and mixotrophic ciliates. Samples were analysed using a quasi-automated colour image analysis system similar to that described by Verity & Sieracki (1993), with contemporary upgrades. Basically, a powerful desktop computer housed several integrated software packages which operated microscope-mounted

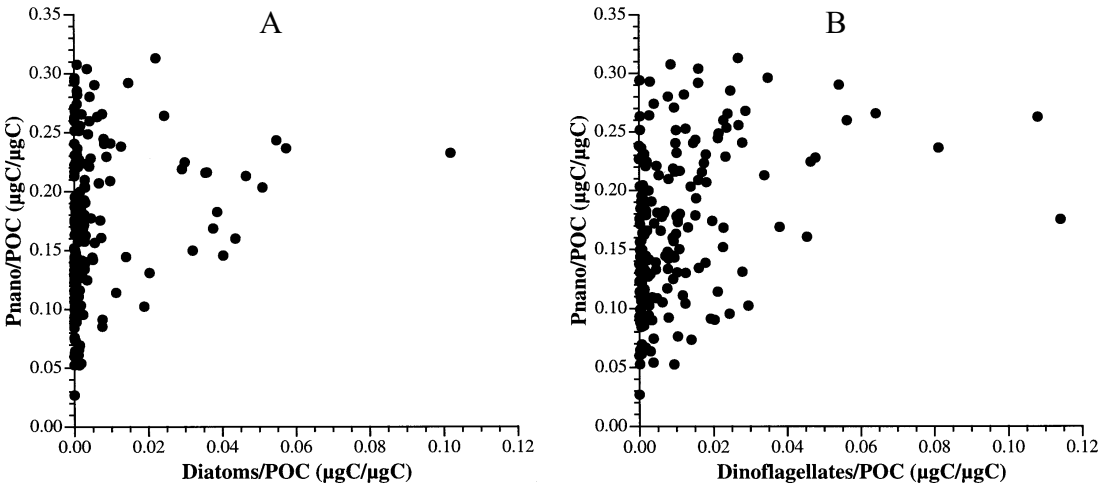

Fig. 2. A. The fractions of total particulate organic carbon (POC) composed of photosynthetic nanoplankton (Pnano) and diatoms. Individual data points represent mean values for each depth and station (N = 194). B. Same as A but for photosynthetic dinoflagellates.

hardware and additionally performed image processing functions. An Optronics DEI-470 integrating 2/3" CCD captured analogue RGB colour images from an Olympus BX-60 epifluorescence microscope. A Windows-based imaging software package, Image Pro Plus (IPP) for Windows v2.0 (Media Cybernetics, Inc.) controlled image capture, enhancement, measurement, analysis, and output.

For analysis, a new field was located, either randomly or on a transect (see below), and focused on the video monitor visually. It was then rapidly digitized into the computer, avoiding significant fluorescence fading, and then edited if necessary to remove detrital particles or to separate adjoining cells. Two types of analyses were used depending upon the density on the slide of the particular cell population being analysed. For cells which were numerous per field and relatively uniform in brightness in a given sample (e.g. cyanobacteria), randomly chosen whole fields were measured automatically. This approach required that a single threshold be used for all cells in the image, but was faster than automatically finding individual cell thresholds.

For more rare cells, transects of the slide were scanned and individual cells were isolated and identified by the operator interactively. The computer automatically selected single or multiple random locations on the slide (and could return to each location +/–1 µm), and also kept record of the exact fraction of sample analysed. The entire process (moving to a given location, focusing, opening an electronic shutter, grabbing an image, closing the shutter, and moving to a new location) was automated and computer-controlled. Sub-images containing the individual cells were temporarily stored and analysed automatically overnight. Typically, 200 cells of each type were measured in each sample. The analysis procedure for these sub-images used automatic threshold determination via the second derivative method (Sieracki & al. 1989a), segmentation and cell measurement. Individual cell biovolume measurements (Sieracki & al. 1989b) were converted to carbon biomass using conversion factors based on literature values of carbon density (Bratbak & Dundas 1984; Børsheim & Bratbak 1987; Putt & Stoecker 1989; Lessard 1991; Verity & al. 1992).

Larger phytoplankton and protozoans were counted in the glutaraldehyde-Lugol's samples using bright field microscopy (Semina 1978). Samples were allowed to settle for a week and then were slowly decanted. Cells were enumerated and measured at 10-20 × magnification. The biovolumes of algal cells and protozoa were calculated from the volumes of appropriate stereometrical bodies (Smayda 1978). All the taxonomic identifications were carried out in fluid samples according to morphology of cells and colonies. Biomass was estimated assuming 0.2 pg C μm^{-3} (Putt & Stoecker 1989; Verity & al. 1992).

Chlorophyll *a* was measured by methanol extraction in the dark of samples collected on Whatman GF/F filters. Particulate organic carbon (combustible POC) and nitrogen were analyzed using a Leeman Lab 440 CHN elemental analyzer, after fuming with HCl to remove carbonate (Wassmann & al. 1999).

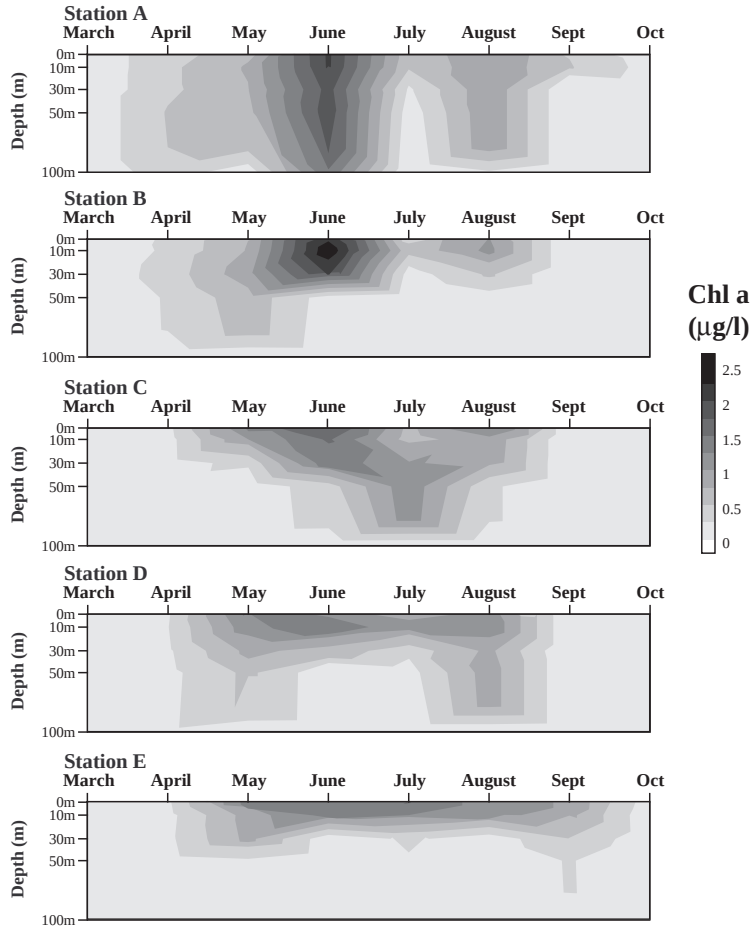

Fig. 3. The temporal and vertical distribution of chlorophyll *a* (Chl *a*) across the north Norwegian shelf in 1994. Contours as in Fig. 1.

RESULTS

The numerically dominant phytoplankton during most of the study period were pico- and nanoplankton. Abundances were typically 10^4-10^5 and 10^3-10^4 cells ml^{-1} in the upper euphotic zone, respectively, and decreased with depth (data not shown). Lowest abundances occurred in March and October, and highest concentrations in June-August. The same trends occurred in biomass (Fig. 1), with nanoplankton contributing most to biomass because of their larger cell size (typically 2-5 µm in diameter). The biomass of photosynthetic nanoplankton increased gradually during March-June and maintained high concentrations (100 µg C l^{-1}) during the summer. Highest biomass occurred on the inner shelf at shallow depths (0-10 m), and decreased offshore and with depth. Biomass decreased into the autumn to low levels by the last sample date in October. Cyanobacteria occurred at 10^2 cells ml^{-1} with negligible biomass due to their small size (1 µm). They were most abundant in late spring and summer in near surface waters (data not shown).

Diatoms and photosynthetic dinoflagellates were less important numerically and in terms of biomass. Both groups exhibited annual peaks in June-July, and occurred at similar biomass levels contributing a maximum of 10-20 % of photosynthetic nanoplankton biomass (Fig. 2). Whereas photosynthetic nanoplankton contributed 1-60 % of POC, diatoms comprised 0-10 %, and only occasionally in excess of 2 %; dinoflagellates were equally unimportant. *Phaeocystis* colonies were also not significant components of the plankton communities, although *Phaeocystis* solitary cells were important in the nanoplankton.

Accordingly, patterns in chlorophyll *a* concentrations (Fig. 3) were similar to those of phototrophic nanoplank-

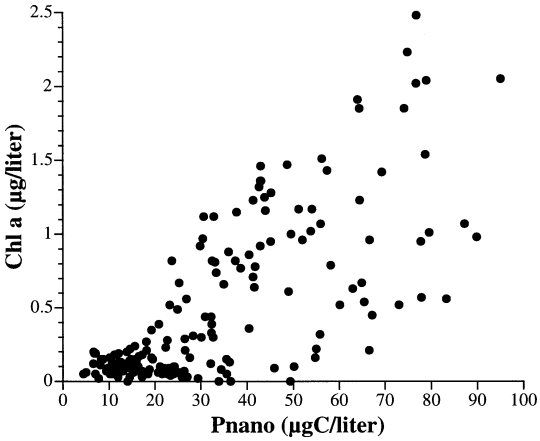

Fig. 4. Relationship between chlorophyll *a* (Chl *a*) and carbon biomass of photosynthetic nanoplankton (Pnano). Individual data points represent mean values for each depth and station ($r^2 = 0.54$, $P < 0.01$, $n = 194$).

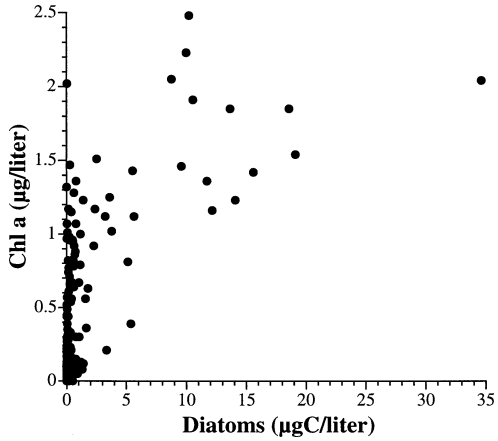

Fig. 5. Relationship between chlorophyll *a* (Chl *a*) and carbon biomass of diatoms. Individual data points represent mean values for each depth and station ($r^2 = 0.21$, $P < 0.1$, $n = 194$).

ton. Chl *a* was highest on the inner shelf at 0-10 m, decreasing with depth and distance offshore. Peaks occurred in June in the inner and mid shelf, with secondary peaks in August. At the shelf break, these temporal peaks merged into a broad summer maximum, and were typically confined to shallower depths than on the inner shelf (Fig. 3). A significant positive linear correlation was observed between photosynthetic nanoplankton and Chl *a* (Fig. 4). In contrast, correlations between Chl *a* and biomass of diatoms (Fig. 5) and dinoflagellates (Fig. 6) were less significant, although the highest biomasses of diatoms generally coincided with higher Chl *a* concentrations.

The dominant herbivores appeared to be heterotrophic flagellates (Fig. 7). These aplastidic cells were typically similar in size and concentration to the phototrophic forms, i.e. 3-6 µm cells occurring at 10^3-10^4 cells ml^{-1}. Their temporal and spatial biomass distribution (Fig. 7) mimicked those of their putative prey (Fig. 1), except that they often occurred deeper. A highly significant ($P < 0.01$) positive correlation between photosynthetic and heterotrophic nanoplankton implies strong trophic coupling between these groups (Fig. 8). Heterotrophic nanoplankton were frequently found with clearly recognizable phototrophic pico- and nanoplankton in their digestive vacuoles.

Oligotrich ciliates and heterotrophic dinoflagellates were commonly present, but were much less abundant than nanoflagellates. Ciliate concentrations were 0.5-10 cells ml^{-1} (data not shown). Mixotrophic specimens were typically 30-40 % of total ciliate numbers. Highest ciliate biomass occurred in summer months in surface waters, and lowest biomass was found in spring and fall, and in deeper waters. Small ciliates (8-15 µm diameter) were the most abundant, generally 3-5 times more than larger ciliates, but larger ones were often the most salient contributors to total ciliate biomass. Heterotrophic (aplastidic) dinoflagellates accounted for 5-50 cells ml^{-1} (data not shown) with distributions similar to ciliates. The biomasses of ciliates and dinoflagellates were each ca. 5 % of the biomass of heterotrophic nanoplankton, but occasionally their combined biomass was 20-25 %.

The biomass of heterotrophic nanoplankton, ciliates, and dinoflagellates was significantly correlated ($P < 0.01$) with the total biomass of phototrophs (Fig. 9). Microheterotrophs biomass was also positively corre-

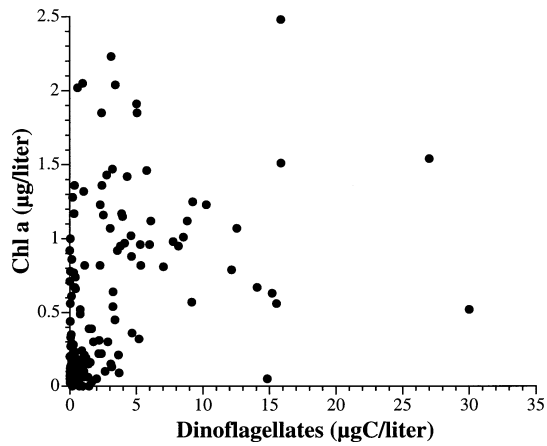

Fig. 6. Relationship between chlorophyll *a* (Chl *a*) and carbon biomass of photosynthetic dinoflagellates. Individual data points represent mean values for each depth and station ($r^2 = 0.17$, $P < 0.1$, $n = 194$).

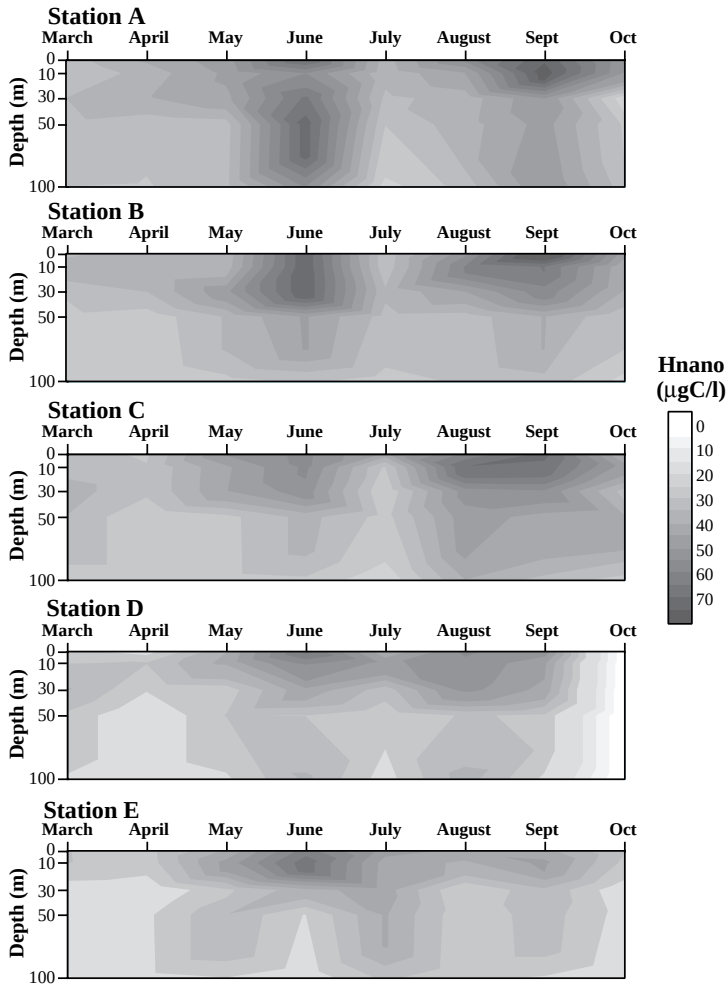

Fig. 7. The temporal and vertical distribution of carbon biomass of heterotrophic (aplastidic) nanoplankton (Hnano) across the north Norwegian shelf in 1994. Contours as in Fig. 1.

lated ($P < 0.01$) with Chl *a* concentration (Fig. 10). Both relationships imply close coupling between these producers and consumers. The positive y-axis intercepts in both cases suggests that, beneath a certain minimum threshold, the small heterotrophs feed on non-algal food, i.e. detritivory or carnivory.

The biomass ratio of photosynthetic:heterotrophic plankton (P:H) exhibited definitive spatial and temporal trends (Fig. 11). The carbon content of the photosynthetic plankton community was estimated by summing the biomasses of phototrophic nanoplankton, picoplankton, diatoms, dinoflagellates, and cyanobacteria. The carbon content of the phagotrophic plankton community was estimated as the sum of aplastidic flagellates and dinoflagellates, and all ciliates. Thus calculated, the P:H ratios in surface waters were low in March (< 0.5), gradually increased through the spring to maxima (2-3) in July, and decreased again during late summer and into October (0.4-0.6). The P:H ratio was greatest at 0-10 m and decreased with depth, i.e. the plankton community structure was generally more autotrophic in the upper water column and more heterotrophic at depth.

The P:H ratio was positively correlated with total POC (Fig. 12). The significant linear relationship ($P < 0.05$) indicated that POC accumulated as the plankton community became increasingly autotrophic. The estimated carbon biomass of the total autotrophic (Fig. 13) and heterotrophic (Fig. 14) communities was significantly correlated ($P < 0.01$) with POC. The positive y-axis intercept in the phototroph carbon vs. POC relationship (Fig. 13) implies that other forms of POC

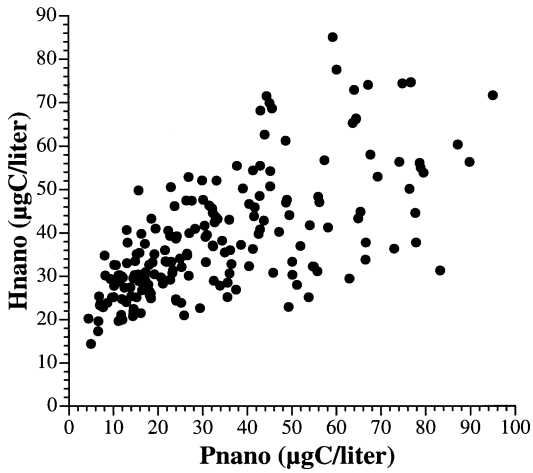

Fig. 8. Relationship between carbon biomasses of photosynthetic (Pnano) and heterotrophic (Hnano) nanoplankton. Individual data points represent mean values for each depth and station ($r^2 = 0.44$, $P < 0.01$, $n = 194$).

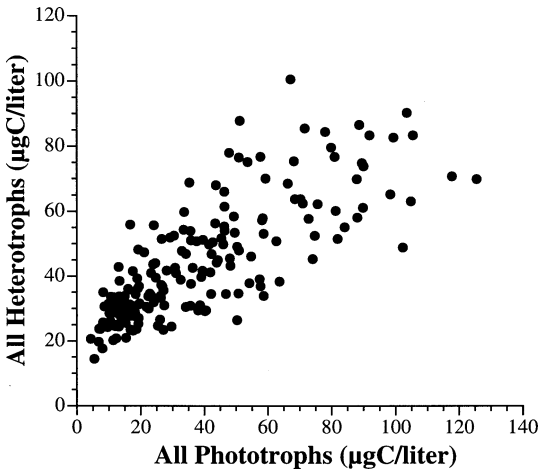

Fig. 9. Relationship between carbon biomasses of all photosynthetic cells (nanoplankton, diatoms, dinoflagellates, cyanobacteria) and all heterotrophic cells (nanoplankton, dinoflagellates, ciliates). Individual data points represent mean values for each depth and station ($r^2 = 0.62$, $P < 0.01$, $n = 194$).

(heterotrophs, detritus) were present when phototrophs were rare. The near-zero intercept in the microheterotroph carbon vs. POC relationship (Fig. 14) suggests a particle-depauperate environment when heterotrophs were absent. POC was strongly correlated with total plankton biomass auto- and heterotrophic communities (Fig. 15), the regression slope indicated that these cells contributed an average of 60 % of total POC.

DISCUSSION

Early plankton studies in productive high latitude waters provided the quantitative basis for the traditional conceptual model of cold water food webs consisting primarily of large phytoplankton (diatoms, *Phaeocystis*) and zooplankton (*Calanus*, euphausiids) (Gran 1902). Such short food chains were hypothesised to account for the extensive sustained fisheries (Legendre 1990). Despite early admonitions that such scenarios were simplistic (Lohmann 1908), this high latitude-large organism model became entrenched. Moreover, in the absence of supportive data, this conceptual model was even exported to temperate and tropical waters (e.g. Steele 1974; Raymont 1980). It was not until the last quarter of the 20th century that technological improvements, primarily epifluorescence microscopy, permitted re-evaluation of the large organism-short food chain model (Pomeroy 1974; Azam & al. 1983).

Perhaps the final bastion for such conceptual revision is where it all began: the subarctic. The data presented here and by Ratkova & al. (1999) and Wassmann & al. (1999) clearly indicate that north Norwegian shelf waters in 1994 were dominated by small-celled phytoplankton and nano/microzooplankton: the microbial food web was responsible for much of the production and consumption of particulate organic matter in the euphotic zone. In this respect, shelf waters were similar to subarctic fjord waters in late spring (Verity & Vernet 1992, and citations therein). But more importantly, the high productivity but low chlorophyll biomass

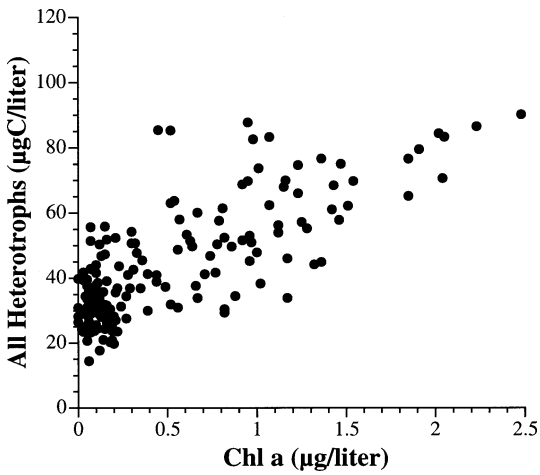

Fig. 10. Relationship between carbon biomasses of all heterotrophic cells (nanoplankton, dinoflagellates, ciliates) and chlorophyll *a* (Chl *a*). Individual data points represent mean values for each depth and station ($r^2 = 0.60$, $P < 0.01$, $n = 194$).

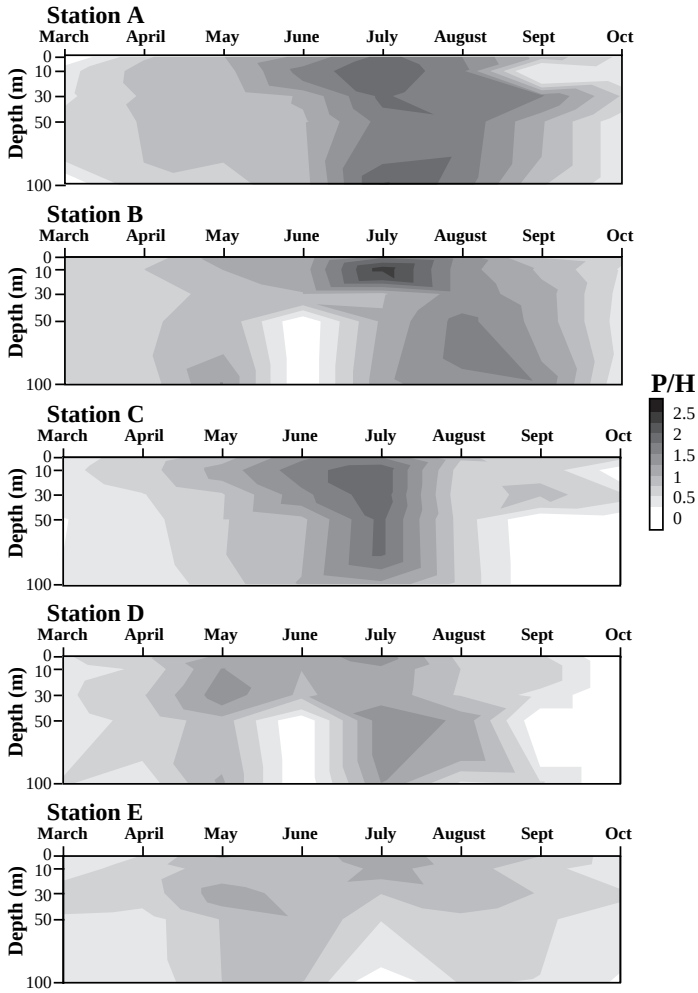

Fig. 11. The temporal and vertical distribution of the ratio of carbon biomass of photosynthetic nanoplankton to heterotrophic (aplastidic) nanoplankton (P/H) across the north Norwegian shelf in 1994. Contours as in Fig. 1.

(Fig. 3 and Wassmann & al. 1999), coupled with small cell size, is similar to observations in several large regions of the global ocean, e.g. the high nutrient/low chlorophyll (HNLC) Antarctic, subarctic Pacific, and equatorial Pacific waters (Miller & al. 1991; De Baar & al. 1995; Landry & al. 1997). Thus the importance of the microbial food web in assimilating and regenerating nutrients, and therefore in enhancing retention of these essential elements in the euphotic zone, can no longer be ascribed only to oligotrophic gyres.

The present data includes an extensive spatial and temporal description of ratios of phototrophic:heterotrophic (P:H) biomass in an aquatic ecosystem. As calculated here, the P:H ratio is certainly a simplification of *in situ* relationships, due to the unknown magnitude of contributions by mixotrophs. To the extent that such cells were important in these boreal waters (see Havskum & Riemann 1996), then the P:H ratios provided here are underestimates. Nevertheless, the general temporal and spatial patterns are instructive. The mean P:H ratio in the upper 100 m increased through the spring, peaked in July, and decreased into autumn; P:H was typically largest at shallow depths. While perhaps intuitively predictable, these data quantitatively imply that the north Norwegian shelf is net autotrophic for a brief period of ca. three months (assuming similar production/biomass by autotrophs and heterotrophs). The food web is apparently net heterotrophic for the remainder of the year, operating increasingly on stored detrital material, heterotrophic recycling, allochthonous

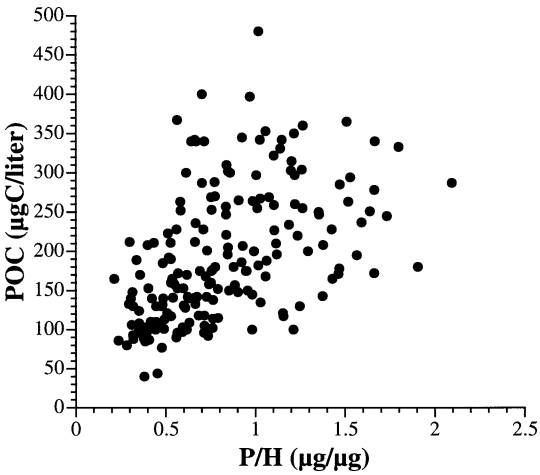

Fig. 12. Relationship between combustible POC and the ratio of carbon biomass of photosynthetic nanoplankton to heterotrophic (aplastidic) nanoplankton (P/H). Individual data points represent mean values for each depth and station ($r^2 = 0.25$, $P < 0.05$, $n = 194$).

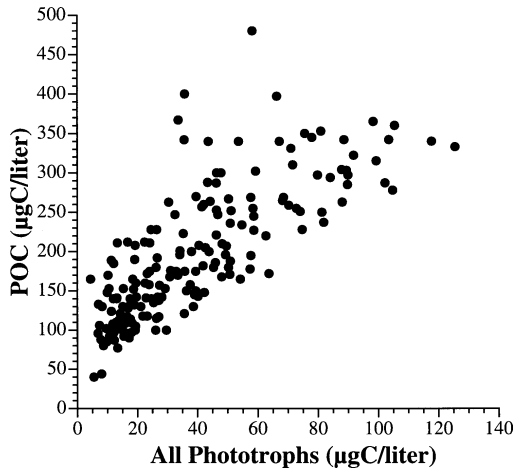

Fig. 13. Relationship between combustible POC and the carbon biomass of all photosynthetic cells (nanoplankton, diatoms, dinoflagellates, cyanobacteria). Individual data points represent mean values for each depth and station ($r^2 = 0.61$, $P < 0.01$, $n = 194$).

inputs, and benthic-water column exchanges. The observation that significant amounts of suspended POC remained when phototrophic biomass was extrapolated to zero (Fig. 12) supports this notion.

Another salient conclusion from the OMEX program concerns the apparent regulation of pelagic trophic structure. A major corollary of the traditional large organism food chain model is that each trophic level is primarily resource-limited, thus providing more nutrients will yield higher biomasses of phytoplankton, zooplankton, and fish (e.g. Legendre & Le Fèvre 1989). This perspective has been challenged for its universal applicability in both fresh (Carpenter & al. 1987) and marine waters (Verity & Smetacek 1996). On the north Norwegian shelf in 1994, the structure of the food web suggests that top-down control was as important as resource limitation:

1. a dearth of large phytoplankton such as diatoms and colonial *Phaeocystis*, despite significant NO_3 and $Si(OH)_4$ consumption (Wassmann & al. 1999)
2. similar low abundances of large protozoans (Ratkova & al. 1999), despite tremendous abundances of their prey (Figs 1 & 7)
3. high concentrations of mesozooplankton (Halvorsen 1997) which cannot feed efficiently on small flagellates (Hansen & al. 1994).

Thus understanding the structure of the autotrophic and heterotrophic nano- and microplankton communities is partially dependent on dynamics of the mesozooplankton.

Currently there is vigorous debate about the relative roles of meso- and microzooplankton in grazing of phytoplankton (e.g. Banse 1994), and it would appear that in many situations that microzooplankton exert the dominant grazing pressure (e.g. Burkill & al. 1993; Verity & al. 1996). These uncertainties indicate that we do not fully understand the consequences of phytoplankton size structure, protozoan and metazoan grazing and ultimately their relationship to vertical flux out of the surface layer (Wassmann 1998). In order to comprehend the dynamics of biogenic matter in the upper water column, it is therefore essential to improve our understanding of the distribution of various classes of zooplankton, their feeding pressure and their productivity.

Assuming that the daily ration of larger protozooplankton grazed by mesozooplankton is equivalent to protozooplankton standing stock times its specific growth rate, a grazing seasonal rate of about 19 g C m^{-2} of protozooplankton by mesozooplankton was calculated. Diatom abundance was kept low and only a small maximum in June was recorded; Si budget calculations argue strongly that a major diatom bloom was not missed in between sampling dates (Wassmann & al. 1999). The estimate of the carbon equivalent based on $Si(OH)_4$ consumption may be used to approximate the grazing rate of mesozooplankton on diatoms, i.e. > 25 g C m^{-2} (Wassmann & al. 1999). The combined grazing estimates indicate that mesozooplankton graze seasonally ca. 44 g C m^{-2} of a mixed diatom and protozoa diet. Other forms such as dinoflagellates, *Phaeocystis pouchetii* and coccolithophorids as well as detritus, fae-

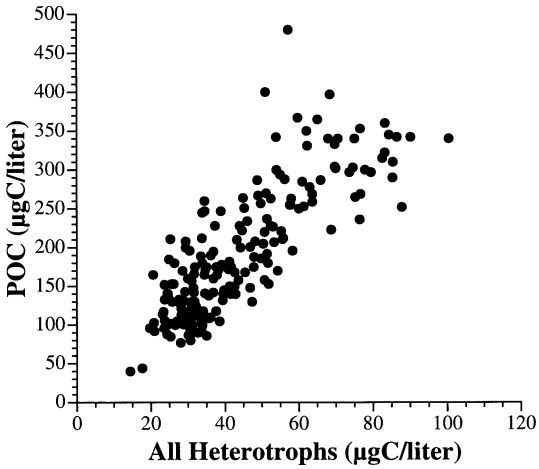

Fig. 14. Relationship between combustible POC and the combined carbon biomass of all heterotrophic cells (nanoplankton, dinoflagellates, ciliates). Individual data points represent mean values for each depth and station ($r^2 = 0.67$, $P < 0.01$, $n = 194$).

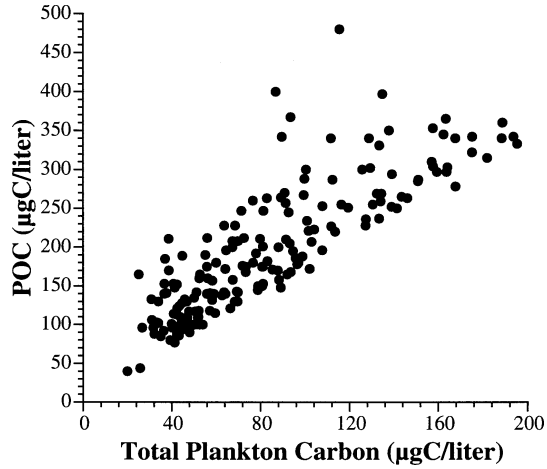

Fig. 15. Relationship between combustible POC and the combined biomasses of all photosynthetic cells (nanoplankton, diatoms, dinoflagellates, cyanobacteria) and all heterotrophic cells (nanoplankton, dinoflagellates, ciliates). Individual data points represent mean values for each depth and station (POC = 1.67 (Biomass) + 54.9, $r^2 = 0.71$, $P < 0.005$, $n = 194$).

cal pellets and aggregates further contribute to the diet of mesozooplankton.

To approximate the grazing impact of larger protozooplankton on Nordvestbanken, a specific growth rate of 0.4 d^{-1} was assumed, similar to those determined experimentally by Hansen & al. (1995) in the Barents Sea. Based on their biomass and assuming a gross growth efficiency of 0.3-0.5 (Verity 1985 1991), the grazing rate of larger protozooplankton from March to October 1994 was calculated to be ca. 37-61 g C m^{-2}. For comparison, assuming a daily ration of 5-15 % of mesozooplankton body carbon (Huntley & al. 1987) and the standing stock along the transect (seasonal average: 2.5 g C m^{-2}; E. Nordby & K.S. Tande, unpubl. data), the average seasonal grazing rate of mesozooplankton may be 31-94 g C m^{-2}. From faecal pellet production estimates, Urban-Rich & al. (1999) calculated an even higher seasonal grazing rate of 250 g C m^{-2} for zooplankton > 500 µm on Nordvestbanken. These approximations suggest that the grazing impact of larger protozooplankton was less than that of mesozooplankton on Nordvestbanken in 1994. Thus it would appear that larger microzooplankton did not exert the dominant grazing pressure on phytoplankton, but that mesozooplankton, grazing on both phyto- and protozooplankton, executed a pivotal role in carbon flux.

However, it must be remembered that the grazing rates estimated here for protozooplankton reflect the contribution only of the larger cells, e.g. ciliates and dinoflagellates. Smaller heterotrophic nanoplankton, which do not compete for prey with mesozooplankton, were much larger contributors to protozooplankton biomass. Assuming a growth rate of 0.4 d^{-1} (Verity & Vernet 1992) and a gross growth efficiency of 0.3-0.5 (Parslow & al., 1986; Goldman & Dennett, 1990), nanoflagellates (mean biomass = 38.6 µg C l^{-1}) were estimated to have ingested 704-1170 g C m^{-2} during the March-October period. Since their diet includes bacteria and other nanoflagellates as well as phytoplankton, in unknown quantities, strict comparisons with mesozooplankton cannot be made. Furthermore, these calculations include only truly heterotrophic flagellates, because mixotrophs were not distinguished from obligatory autotrophic flagellates, i.e. incubation experiments with fluorescently-labelled prey would have been required for such discrimination. Hence the total biomass of phagotrophic nanozooplankton is underestimated by an unknown amount corresponding to mixotrophic cells. However, it seems reasonable to hypothesize that their grazing was responsible for the low biomass of photosynthetic nanoplankton, which dominated the microplankton community. The inferred dominance of the phagotrophic protozoan community by small flagellates is similar to observations in other diverse environments (Andersen & Sørensen 1986; Verity & al. 1993, 1996; Sherr & Sherr 1994).

Thus, multiple independent measurements and calculations indicate that north Norwegian shelf waters in 1994 did not represent the traditional concept of a large organism pelagic food web. Rather, the abundance and

biomass of phytoplankton and herbivores were dominated by small cells, and the dynamics of microautotrophs and heterotrophs were apparently closely linked. Net primary production by small phototrophs led to accumulations of small autotrophs, heterotrophs, and total suspended POC, evidenced as P:H ratios exceeding 1.0, which subsequently declined as the major driving force (irradiance) waned in autumn. Substantial nitrate and silicate uptake (Wassmann & al. 1999) and high abundances of nanoplankton (Figs 1 & 7) suggests that the production of large phytoplankton and phagotrophic protozoans, respectively, was also substantial, but their biomass did not accumulate due to grazer control by meso/macrozooplankton. It is likely that mesozooplankton on the north Norwegian shelf pursue an omnivorous feeding strategy in order to survive. They graze extensively on large phytoplankton cells, but supplement their food demand by grazing on detritus and protozoa. The situation on Nordvestbanken represents a scenario by which energy is channelled back into the grazing food web by the microbial loop (Azam & al. 1983). If this hypothesis is correct, mesozooplankton on the north Norwegian shelf controlled the fraction of primary production channelled into large cells such as diatoms (new production) and protozooplankton, leaving copious amounts of ammonia for incorporation into the microbial food web (regenerated production). The food web was both unexpected but understandable: joint regulation by resource availability and predation (Verity & Smetacek 1996). This dual dependency, coupled with changing P:H ratios, indicates that the structure of the food can indeed complicate relationships between primary production, grazing, and sedimentation (Silver & Gowing 1991; Wassmann 1993; Andreassen & al. 1996; Andreassen & al. 1999).

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