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Microzooplankton in the pelagic food web of the East Greenland Sea and its role in sedimentation processes

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1. INTRODUCTION

Studies of the vertical flux of organic matter from the upper layers of the ocean have, in the past decades, been numerous (Knauer et al. 1979, Smetacek 1980, Honjo 1982). It is now recognised that the spatial and temporal variations in observed patterns of sedimentation are closely related to biological processes operating within the euphotic zone (Bathmann et al. 1988, v.Bodungen 1989). An understanding of the structure of the pelagic system, and trophic interactions within its various compartments, therefore, is essential in the study of export processes to deeper water layers. Primary among these are heterotrophic processes which control herbivory and facilitate the packaging of small particles into larger aggregates, thus determining their potential for export. Metazooplankton are known to enhance the sedimentation of autotrophic biomass from the euphotic zone by the formation of large, rapidly sinking faecal pellets, thus leading to the loss of minerals essential for autotrophic growth.

The classical paradigm of marine food chains has been drastically altered in the past two decades, leading to the proposal of the "microbial loop" by Azam et al. in 1983. This has been brought about by the realization that autotrophs < 5 μm in size can account for a large proportion of primary production (Joint and Pomroy 1983, Li et al. 1983, Weber and El-Sayed 1987). These organisms are largely unavailable to larger metazoan grazers due to morphological contraints in the filtration of small particles (Nival and Nival 1976). Further, it has been demonstrated in a number of studies that autotrophic production of larger phytoplankton groups is often insufficient to support observed metazoan biomass (Joint and Williams 1985). It has now been established that microzooplankton, defined as that part of the zooplankton assemblage between 20 and 200 μm in size, are dominant herbivores on nano- and picoautotrophs.

The role of the microzooplankton in vertical flux studies, however, has largely been neglected. Due to their small size and negligible role in aggregate formation, as well as their known capacity as primary remineralizers in the pelagial, they have long been thought to hinder transport of organic matter to deeper water layers. This, however, is an incomplete evaluation of their trophic role. Elucidation of the fate of the organic matter in the microzooplankton compartment of the food chain is crucial in an understanding of the balance between processes that either enhance or hinder its export from the euphotic zone. Recent research indicates that a significant proportion of microzooplankton biomass serves as a food source to higher trophic levels in a number of marine environments (Sherr et al. 1986, Stoecker and Egloff 1987, Gifford and Dagg 1991), thus facilating the transfer of smaller particles which are otherwise unavailable to metazooplankton. In this capacity, microzooplankton could serve as enhancers, rather than hinderers, of sedimentation.

The purpose of the present study has been to identify and quantify processes between the microzooplankton, their prey and predators, that determine the fate of particulate matter in relation to its sedimentation out of or retention within the euphotic zone, with the help of field and laboratory studies. Field investigations were conducted in the East Greenland Sea, where an a long-term sediment trap mooring is deployed. Investigations were conducted along the path of drifting sediment trap arrays in June/July 1989 and August/September 1990, where rate measurements in the pelagial were coupled to an analysis of particulate material sedimenting at the base of the euphotic zone. These were complemented by laboratory studies to investigate the degradation of algal pigments by protozoan grazers, and determine the formation of faecal material by microprotozoans.

This study was carried out within the Sonderforschungsbereich 313 of the University of Kiel, in the subproject A1 (Flux of particles from the pelagial).

2. MATERIALS AND METHODS

Field data presented in this thesis were collected during two expeditions; the METEOR cruise 10 leg 3, between 15.06.1989 and 12.07.1989 and POSEIDON cruise 173 leg 2, from 14.08.1990 to 10.09.1990. On both cruises investigations were concentrated in the East Greenland Sea, in open water between 72°N and 72°30'N and 7°W and 8°W. Drift experiments of 11 (1989) and 9 (1990) days were conducted by the deployment of a drifting trap array with sediment traps at 60 µm (1989) or 100 and 300m (1990), and daily water column sampling at the position of the drifter. Maps of the investigation area, with the path of the drifters are illustrated in Fig. 1.

2.1 Physical parameters

Temperature and salinity were measured at all stations using a CTD (Mark III-sensors in 1989 and ME-CTD in 1990) mounted on a rosette water sampler, as part of the subproject A1 of the SFB 313.

2.2 Bulk parameters

Water samples were taken from the water column in the upper 100 m during both cruises M10/3 and POS173/2, as shown in Appendix 1. Depths for sampling were determined after taking a Secchi depth reading at the beginning of the stations, and samples corresponded to the 50, 30, 20, 10, 5, 1 and 0.1 % light levels. Additional samples provided a finer vertical resolution within the euphotic zone. 10 l Niskin bottles mounted on a multiple rosette were used for sampling.

Samples of 1 l each for the measurement of particulate organic carbon (POC) were filtered onto GF/F filters (25mm diameter) and stored frozen until analysis on the laboratory. Samples of 0.5 l for the measurement of chlorophyll (chl) *a* were filtered onto GF/F filters (25mm diameter), and stored frozen until analysis within 48 hours. Filters were extracted in 90% acetone, homogenized using glass beads, centrifuged in a temperature-controlled centrifuge at 3,000 r.p.m. for 10 min, and measured fluorometrically using the acidification technique of Holm-Hansen et al. (1965).

POC was measured as part of the subproject A1 of the SFB 313. Analysis was conducted on a high-combustion Hereus Rapid CHN analyser.

Primary production was measured using the ^{14}C uptake technique of Steeman and Nielsen (1958). Incubations were conducted *in situ* using a rig which was attached to the drifting trap array.

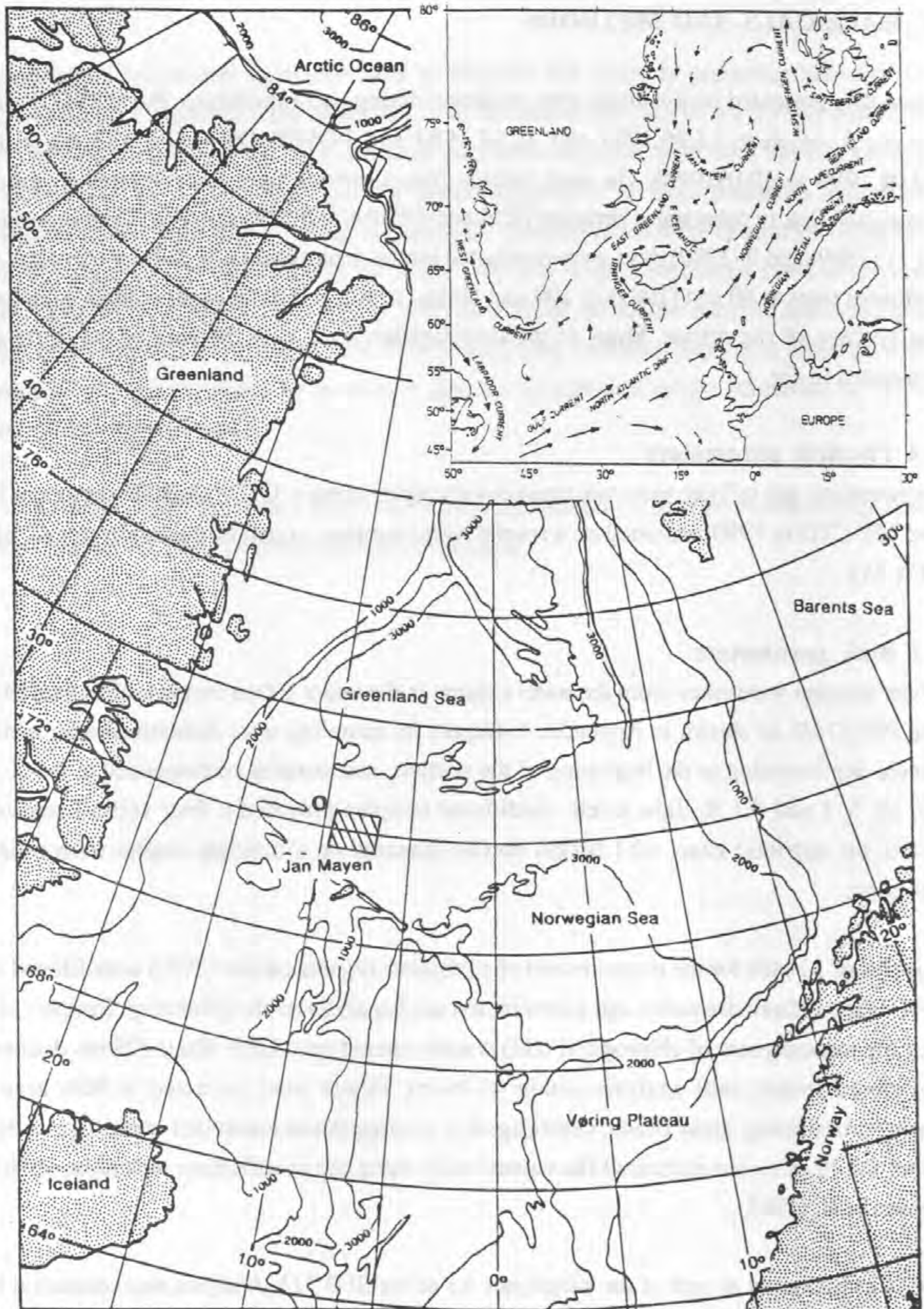


Fig. 1: Map showing the investigation area with surface currents illustrated in the insert. The shaded box indicates the position at which drift experiments were carried out in June/July 1989 and August/September 1990. The position of the annual mooring is marked by a circle.

Chl *a* was measured fluorometrically both in water column samples and experiments using a Turner Designs fluorometer. The fluorometer was calibrated on board using pure chl *a* extract from SERVA Chemicals. Calibrations were conducted according to Edler (1979), and linear regressions yielded correlation coefficients >0.95, with an X-axis intercept <0.005. The fluorometer was calibrated against a LKB Photometer and chl *a* concentrations calculated using the molar extinction coefficient for chl of 87.67.

Fractionated chl *a* was measured in water column samples from the layer of chl maximum. Nylon gauzes 50 mm in diameter and with pore sizes of 20 µm, 10 µm, 5 µm and Nucleopore filters of 2 µm pore size were used to fractionate particulate matter. 0.5 l of water was passed through these gauzes, filtered onto GF/F filters and chl *a* measured as described above.

Primary production measurements were conducted using the ^{14}C- incorporation technique of Steemann Nielsen (1952). Incubations were conducted in situ for 24 hours.

Measurements of nutrient (nitrate, silicate, and phosphate) concentrations were conducted using the techniques described in Grasshoff (1983), adapted for use with an autoanalyser. Ammonium concentrations were measured by the hand-method similarly described by Grasshoff (1983).

2.3 Microzooplankton distribution

Water samples of 200 - 250 ml were gently filled into brown sampling bottles, taking care to avoid bubbling as this is known to rupture delicate cells. Lugols iodine solution (2g KI + 1g I in 200 ml distilled water, + 20 ml glacial acetic acid) was added to each bottle as a fixative to a final concentration of 4 %. Bottles were stoppered tightly and stored in the dark until later analysis in the laboratory.

An inverted light microscope was used to enumerate microprotozoans larger than 10 µm. Samples were mixed gently, and 50 ml allowed to settle according to the technique of Utermöhl (1958). Individual species were enumerated under a magnification of 160 X or 250 X. Identification was based on the following literature: Leegard 1915, Lee et al. 1985, Kahl 1930-1935, Corliss 1979, Montagnes et al. 1988; Maeda and Carey 1985, Maeda 1986. Linear measurements of individual species were noted, together with their shapes, and these were converted on the basis of conventional geometric forms to volume. A factor of 0.14 pgC μm^{-3} (Putt and Stoecker 1989) was used to convert volume to carbon biomass. In some cases where identification was not possible to the species level, orders have been listed with the suffix "unidentified". Where tintinnids were present, body volume of the protozoan cell has been used to calculate biomass, as lorical volume can lead to gross inaccuracies (Gilron and Lynn 1989).

Samples for biomass measurements from incubation experiments were treated in the manner described above.

2.4 Dilution experiments

The seawater dilution method to estimate microzooplankton grazing involves the serial dilution of natural seawater with filtered water from the same source. I describe here the experimental protocol, followed by an explanation of the theory of this technique.

2.4.1 Experimental protocol

The experimental setup involves the addition of prefiltered seawater to natural water samples in a serial dilution and subsequent incubation on board ship. Water was obtained using 10-l Niskin bottles from a rosette water sampler. Up to 40 l of water was collected a day prior to each experiment, filtered through a 0.2 µm polycarbonate membrane with a GF/F prefilter, and stored at *in situ* temperature on board. Water for the experiments was sampled from the chl *a* maximum, as this was seen to have coincided with the depth of maximal microzooplankton abundance. The Niskin bottles were gently emptied into clean containers using a broad-diameter (2.5 cm) silicon tubing. This water was prescreened through a 200 µm mesh to eliminate macrozooplankton grazers, and added to the prefiltered water in 10 l carboys, in dilutions of 1:0, 3:1, 1:1 and 1:3, corresponding to 1.0, 0.75, 0.5, and 0.25 fractions of undiluted water. Samples were taken from each canister at the start of the experiments for microscopy and the determination of chl *a* and nitrate concentrations. Actual dilutions of chl *a* were often different from those made up by volume, and measured dilution factors were used in subsequent calculations. Water from each of the four carboys was transfered to 1.8 l glass (in 1989) or 2.2 l polycarbonate (in 1990) flasks (3 replicates for each dilution) and incubated on deck at *in situ* temperature and light for 24 hours. On cruise M10/3 this was done in slowly rotating zooplankton incubators in a temperature-controlled laboratory on board; during the cruise POS 173/2 incubation flasks were placed in deck incubators shaded with neutral-density foil to 13 % incident light, which corresponded to that at the collection depth. Periodic exchange of water in the deck incubators with *in situ* water ensured a constant temperature, whereas the gentle rolling of the flasks with the ships' movement ensured that particles were held in suspension. At the end of 24 hours 0.5 l water from each flask was filtered onto GF/F Filters for the fluorometric determination of chl *a*. Nitrate concentrations were measured in the three flasks with undiluted seawater to confirm that nutrient depletion did not hamper phytoplankton growth. A schematic presentation of the experimental design is shown in Fig. 2.

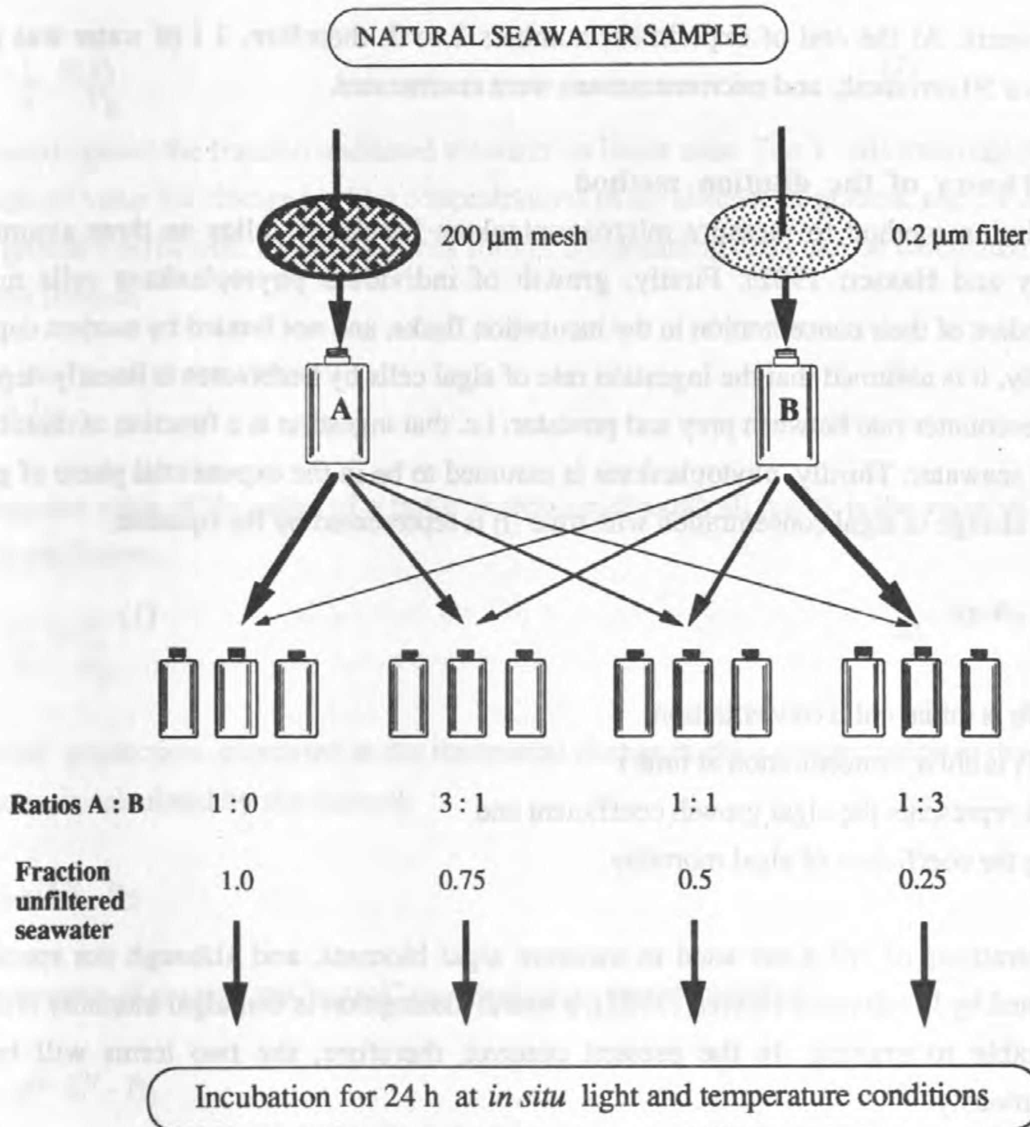


Fig. 2: Schematic presentation of the experimental protocol for the seawater dilution technique to measure microzooplankton herbivory. Samples for chl *a* were taken at the beginning and the end of incubations from all flasks. Nutrients (NO_3, PO_4) concentrations were measured at the beginning and the end of the experiment from flasks with undiluted seawater (A : B = 1 : 0).

This basic dilution approach was modified at Sta 885 on 26.8.1990 in the following manner:

a) HPLC determination of algal pigments:

Samples for the HPLC determination of algal pigments were taken parallel to those for fluorometric chl *a* measurements in order to determine grazing rates on specific algal taxa as characterized by their carotenoids and accessory pigments.

b) Enumeration of microprotozoan grazers. During POS173/2 microscopy of Apstein net samples on board revealed the presence of numerous metazoans between 80 and 200 µm in length, which were able to pass through a 200 µm mesh, and were thus included in the grazing

experiments. At the end of experiment numbers 2 to 7, therefore, 1 l of water was passed through a 50 µm mesh, and micrometazoans were enumerated.

2.4.2 Theory of the dilution method

The dilution method to measure microzooplankton herbivory relies on three assumptions (Landry and Hassett 1982). Firstly, growth of individual phytoplankton cells must be independant of their concentration in the incubation flasks, and not limited by nutrient depletion. Secondly, it is assumed that the ingestion rate of algal cells by herbivores is linearly dependant on the encounter rate between prey and predator, i.e. that ingestion is a function of dilution with filtered seawater. Thirdly, phytoplankton is assumed to be in the exponential phase of growth, and the change in algal concentration with time (t) is represented by the equation

$$P_t = P_0\, e^{(k-g)t} \qquad (1)$$

where P_0 is initial chl *a* concentration
P_t is chl *a* concentration at time t
k represents the algal growth coefficient and
g the coefficient of algal mortality

Concentrations of chl *a* are used to measure algal biomass, and although not specifically mentioned by Landry and Hassett (1982), a fourth assumption is that algal mortality is directly attributable to grazing. In the present context, therefore, the two terms will be used synonymously.

It follows, then, that in incubations of 1.0, 0.75, 0.5, and 0.25 fractions undiluted seawater, changes in algal concentrations with time can be represented by the equations

$$P_t = P_0\, e^{(k-1*g)t} \qquad (1a)$$
$$P_t = P_0\, e^{(k-0.75*g)t} \qquad (1b)$$
$$P_t = P_0\, e^{(k-0.5*g)t} \text{ and} \qquad (1c)$$
$$P_t = P_0\, e^{(k-0.25*g)t} \qquad (1d)$$

respectively.

Any two of these equations can be solved as simultaneous equations to give values of k and g; however a larger number of dilutions and replicates provides an estimate of linearity and correlation.

Chl *a* is used as an indicator of phytoplankton stocks, and chl *a* concentrations are measured at the start and end of the experiment in all bottles. Apparent growth rate, or the net rate of change in chl *a* concentration (k-g), is calculated as

$$(k-g) = \frac{1}{t} \ln \frac{P_t}{P_0} \quad (2)$$

and plotted against the fraction undiluted seawater on linear axes. The Y-axis intercept yields an extrapolated value for change in chl *a* concentrations in the absence of grazers, and its value "k" is the growth coefficient. Doubling times for chl *a* containing cells can be calculated in days using the formula

$$\mu = \frac{k}{\ln 2} \quad (3)$$

The negative value of the slope of a linear regression through all points is the value of "g", the grazing coefficient.

$$g = -k - \frac{1}{t} \ln \frac{P_t}{P_0} \quad (4)$$

"Potential" production, expressed as the theoretical change in chl *a* concentration in the absence of grazers, is calculated by the formula

$$P_t = P_0\, e^{(k)t} - P_0 \quad (5)$$

In the presence of grazers, the "actual" production can be calculated as

$$P_t = P_0\, e^{(k-g)t} - P_0 \quad (6)$$

Since production by autotrophs and grazing by herbivores are simultaneous processes, a cumulative grazing rate must take into account that part of standing stock, that has been consumed as well as the increase in algal cells during the time frame of the experiment. Potential production, as described above, represents the increase in chl *a* concentrations due to algal production. Actual production, similarly, quantifies the change in chl *a* concentrations in the presence of herbivores. The absolute difference in the two values provides an estimate of the impact of herbivory on algal stocks.

Mathematically, the cumulative grazing rate can be calculated by a subtraction of equation 6 from equation 5. Thus, change in chl *a* concentration with time is represented by

$$P_t = [P_0\, e^{kt} - P_0] - [P_0\, e^{(k-g)t} - P_0], \text{ or}$$

$$P_t = P_0(1 - e^{gt}) \quad (7)$$

2.5 Copepod grazing upon microzooplankton

During cruise M10/3, incubations of natural seawater were conducted in the presence and absence of copepods. Water was taken from the chl *a* maximum, screened gently through a 200 µm mesh, filled in 1.8 l glass flasks and stoppered without air bubbles. Adults of the dominant copepod species, *Calanus hyperboreus*, were collected using a multiple opening-closing net in the upper 100 m of the water column. Individual copepods were added to three flasks, whereas the other three were incubated without copepods. All flasks were slowly rotated in a zooplankton incubator for 24 hours. 200 ml from each flask was fixed for microscopy at the beginning and end of each experiment. A schematic representation of the experimental protocol is shown in Fig. 3.

In 1990, on cruise POS 173/2, copepods were likewise collected from the water column using a multinet. Water from the chl *a* maximum was prescreened through a 200 µm mesh, and added to twelve 2.25 l polycarbonate flasks. Three bottles contained no copepods; three each contained one, two and three copepods respectively. All flasks were incubated in deck incubators as described above for 24 hours, and samples for microscopy taken at the beginning and end of the experiment.

For these experiments a different approach was used to measure copepod grazing from that mentioned above. I made the same three assumption as those for the seawater dilution method used to measure microzooplankton grazing: a) that copepod grazing is linearly proportional to food (in this case microzooplankton prey) abundance; b) that growth of microzooplankton is constant in all incubation flasks, and c) that microzooplankton growth can be represented by the equation for exponential growth used in the Section above. Laboratory experiments serve as a basis for the first assumption. By exposing microzooplankton in the incubation containers to the same phytoplankton concentrations, their growth remains constant regardless of grazing pressure from copepods. Instead of diluting prey organisms, I concentrated predator organisms. This was necessary in order to ensure that microzooplankton growth was not limited by dilution of their algal prey.
Apparent change in microzooplankton abundance with time can therefore be represented by the equation:

$$Z_t = Z_0 \, e^{(\mu - c)t}$$

where Z_0 is initial microzooplankton concentration,
Z_t is microzooplankton concentration at time t,
μ represents the microzooplankton growth coefficient and
c the coefficient of microzooplankton mortality.

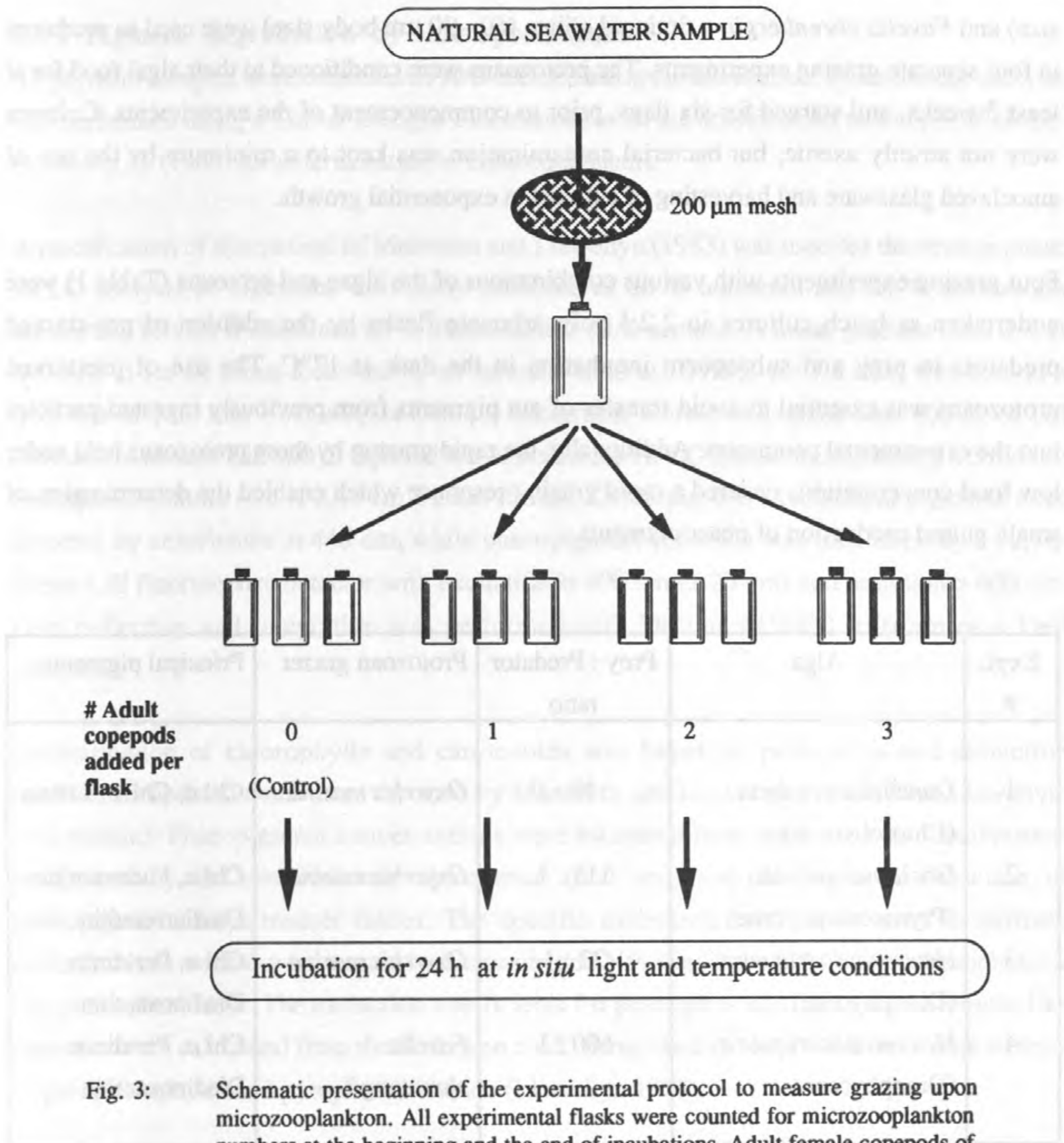


Fig. 3: Schematic presentation of the experimental protocol to measure grazing upon microzooplankton. All experimental flasks were counted for microzooplankton numbers at the beginning and the end of incubations. Adult female copepods of the species *Calanus hyperboreus* were used in all experiments.

Calculations of net grazing and growth rates folllow from this equation as those mentioned in Section 2.4.2 above.

2.6 Laboratory culture experiments

Three strains of algae, *Dunaliella tertiolecta* (Chlorophyceae), *Isochrysis galbana* (Prymnesiophyceae) and *Heterocapsa triquetra* (Dinophyceae) were grown in F/2 medium using filtered (0.2 µm) seawater. Seawater of reduced salinity ($26 * 10^{-3}$) was used in all experiments with *H. triquetra*. *Oxyrrhis marina*, a heterotrophic dinoflagellate (15 - 30 µm in

size) and *Favella ehrenbergii*, a tintinnid ciliate (60 - 90 µm body size) were used as predators in four separate grazing experiments. The protozoans were conditioned to their algal food for at least 3 weeks, and starved for six days, prior to commencement of the experiments. Cultures were not strictly axenic, but bacterial contamination was kept to a minimum by the use of autoclaved glassware and harvesting of cultures in exponential growth.

Four grazing experiments with various combinations of the algae and protozoa (Table 1) were undertaken as batch cultures in 2.2 l polycarbonate flasks by the addition of pre-starved predators to prey and subsequent incubation in the dark at 17°C. The use of prestarved protozoans was essential to avoid transfer of gut pigments from previously ingested particles into the experimental containers. Additionally, the rapid grazing by these protozoans held under low food concentrations ensured a rapid grazing response which enabled the determination of small, pulsed production of phaeopigments.

Expt. #	Alga	Prey : Predator ratio	Protozoan grazer	Principal pigments
1	*Dunaliella teriolecta* (Chlorohyceae)	149 : 1	*Oxyrrhis marina*	Chl *a*, Chl *b*, Lutein
2	*Isochrysis galbana* (Prymnesiophyceae)	111 : 1	*Oxyrrhis marina*	Chl *a*, Fucoxanthin, Diadinoxanthin
3	*Heterocapsa triquetra* (Dinophyceae)	22 : 1	*Oxyrrhis marina*	Chl *a*, Peridinin, Diadinoxanthin
4	*Heterocapsa triquetra* (Dinophyceae)	600 : 1	*Favella ehrenbergii*	Chl *a*, Peridinin, Diadinoxanthin

Table 1: Combinations of prey and predator, prey : predator ratios and principal algal pigments for experiments 1 to 4.

Control flasks contained algae diluted to the same concentrations as the experimental containers using filtered seawater. All flasks were gently inverted several times a day and sampled at intervals of 6 to 24 hours for up to 140 hours. Aliquots of between 10 and 200 ml were removed for pigment analysis and filtered onto GF/F filters for HPLC and fluorometry. Parallel samples were taken for numerical and volume analysis by a Coulter Multisizer (expt. 1 & 2) or fixed with acid Lugol solution for enumeration by light microscopy (expt. 3 & 4).

2.6.1 Pigment degradation by microprotozoans

All pigment samples were extracted in 90% acetone using ultrasonication. Fluorometric analysis was performed using a Turner Designs Fluorometer with the acidification technique of Holm-Hansen et al. (1965) for determination of chl *a* equivalents.

A modification of the method of Mantoura and Llewellyn (1983) was used for the reverse phase HPLC analysis of pigments. Solvent A consisted of 80 % methanol and 20 % ammonium acetate and solvent B contained 60 % methanol and 40 % acetone. A linear gradient from 0 % B to 100% B for 10 mins, followed by an isocratic hold at 100% B for 7.5 min, was used at a flow rate of 1 ml min^{-1}. An aliquot (300 µl) of clarified extract was mixed with 300 µl of 1M ammonium acetate and 100 µl injected into a Shimadzu HPLC system incorporating a 3 micron Pecosphere column (3.5 X 0.45 cm, Perkin Elmer). Chlorophyll and carotenoid pigments were detected by absorbance at 440 nm, while phaeopigment detection was monitored by a Perkin Elmer LSI fluorescence detector with excitation at 400 nm (± 20 nm) and emission > 600 nm. Data collection and integration was performed with Phillips PU6000 software on a Dell computer.

Quantification of chlorophylls and carotenoids was based on peak areas and extinction coefficients updated from those reported by Mantoura and Llewellyn (1983) (C.A.Llewellyn, pers.comm.). Phaeopigment concentrations were estimated from peak areas and calibrations performed by the simultaneous absorbance (667 nm) and fluorescence detection of phaeopigments from mussel faeces. The specific extinction coefficients used to estimate concentrations were those reported by Lorenzen and Newton Downs (1986) for phaeophytin *a* and phaeophorbide *a*. The extinction coefficients for phaeophorbide-like and phaophytin-like pigments were calculated from the extinction coefficients used above and the molecular weights of pyrophaeophytin and pyrophaeophorbide (Llewellyn 1989).

2.6.2 Particle formation by microprotozoans

In the experiments described above particle formation by the two protozoan species used was investigated. At the time intervals at which sampling was conducted, additional samples of 10 - 20 ml were taken, fixed with formaldehyde to a final concentration of 4%, and examined by epifluorescence and light microscopy.

2.7 Particle formation in a natural microzooplankton assemblage

The use of fluorescently labelled inert particles as tracers to measure phagotrophic processes is widespread (McManus and Fuhrman 1986, Pace and Bailiff 1987, Sherr et al. 1987). Many studies have used such particles to quantify uptake of natural particles of similar size by

protozoan grazers. In the experiments conducted in this study, however, I have used fluorescence latex beads to qualitatively follow the processes of uptake and packaging of small particles by a mixed microzooplankton assemblage.

Fluorescent latex beads from POLYSCIENCE (fluoresebrite tm carboxylate) in two size classes (0.51 µm ± 0.008 µm and 2.0 µm ± 0.005 µm; excitation maximum 458 nm, emmision maximum 540 nm) were used in feeding experiments with field-collected microzooplankton. Beads were presuspended in bovine serum albumin to ensure even dispersion in seawater (Pace and Bailiff 1987). Hauls in the upper 50 µm of the water column using a 20 µm mesh size Apstein net gave concentrated samples of microzooplankton. This was observed live in sterile culture flasks of 50 ml under a dissecting microscope, and where necessary, filtered seawater was added to samples that appeared too concentrated. Beads of both sizes were added to a final concentration of approximately 10^6-10^7 cc^{-1} (2.0 µm diameter) and 10^7-10^8 cc^{-1} (0.5 µm diameter). Up to seven parallel bottles, with addition of beads, were incubated in a deck incubator as described above. At intervals of 15 min, 30 min, 60 min, 2, 8, 24, 48 and 97 hours the experiment was stopped in one of the bottles by the addition of glutaraldehyde (final concentration 2.5%).

To observe bead uptake by individual zooplankton, samples were placed in a settling chamber and viewed with an inverted epifluorescence microscope (Zeiss Axiovert 35) under blue light excitation. Individual fluorescent beads could be counted within the guts of the herbivores; where a precise counting was not possible bead numbers have been grouped in the following manner: 1-5 , 6-10, 11-15, 16-20, 21-50, >50, >100 beads per individual.

2.8 Microzooplankton sedimentation

Sediment traps modified from the original design of Zeitzschel et al. (1978) were deployed in the Greenland Sea both as annual and short term moorings and drifting traps below the euphotic zone. The sampling jars of traps from the mooring OG2 (1988-1989) in 500 and 2000 m, as well as samples from the traps during drift experiments in 1989 and 1990 were enumerated for microzooplankton remains. Entire samples were split to fractions of 1/16 to 1/125; the splits were filled to a discrete volume, diluted further, and 50 ml was allowed to settle in a chamber for 24 hours and counted using an inverted light microscope under 160X or 250X according to the method of Utermöhl (1958). Hard parts of microzooplankton were comprised almost exclusively of tintinnid loricae, and in the case of the 1990 drift experiment, some thecae of heterotrophic dinoflagellates.

Material from sediment traps was analysed using Scanning Electron Microscopy. 10 to 30 ml sample was gently injected onto a nucleopore filter (2 µm pore diameter), dehydrated with

successive washings in 10, 30, 50, 75, 90, and 100 % Alcohol, and then air-dried, according to the method of Bathmann and Liebezeit (1986). Filters were mounted on aluminum plates, coated with a thin layer of gold-palladium, and scanned using a Zeiss electron microscope.

3. RESULTS

Data in this thesis were collected on two cruises in the East Greenland Sea. In Section 3.1 I present data from METEOR Cruise 10/3, between 15.6.1989 and 12.7.1989; in Section 3.2 data from POSEIDON Cruise 173/2 from 19.8.1990 to 10.9.1990. Firstly, I describe the pelagic system in terms of its hydrography and biological activity using bulk parameter measurements in the water column. Against this background microzooplankton abundance, biomass and species composition is presented, and the results of experiments to determine herbivory by the microzooplankton, followed by estimates of their mortality by grazing pressure of copepods. The following Section (3.3) presents the results of laboratory experiments with two protozoan species to investigate patterns of pigment degradation due to protozoan grazing (Section 3.3.1) and their formation of faecal material (Section 3.3.3). Section 3.4 is concerned with the qualitative estimates of the uptake and packaging of nano-sized particles by metazoan and protozoan members of a natural microzooplankton community using a fluorescent microsphere technique. Section 3.5 decribes observations of the microscopy of sediment trap material. Sedimentation patterns of microprotozoans in the study area are then presented in Section 3.6.

3.1 The drift experiment during June/July 1989

3.1.1 Physical parameters

Isolines of salinity and temperature along the path of the drifter (x-axis in days) are shown in Figure 4. At the start of the drift period there was a sharp stratification of the water column at 22 m depth. Warmer, less saline water overlay a colder, denser water mass. This underlying water mass appeared uniform between 40 and 100m. A break in this density gradient was seen on 4.7.1989, with isolines of salinity ($34.4 * 10^{-3}$) and temperature (0.9 °C) dipping from 22 m to ca. 30 m. During the second half of the drift experiment stratification was restored at ca 25 m, with a stronger gradient in salinity and temperature around this depth.

The path of the drifting sediment traps (Fig. 5) appeared to follow two different eddy-like structures. During the first half of the drift experiment the drifter trajectory described a cyclonal track, between Stations 649 and 661. Its direction changed in the two days thereafter, turning to drift onwards in a clockwise manner, apparently influenced by currents in an anticyclonal eddy-like structure. The discontinuities in isolines of temperature and salinity between Stations 661 and 665 indicate that a disturbance in stratification in the upper 50 m of the water column took place, a typical feature for such a proposed frontal system.

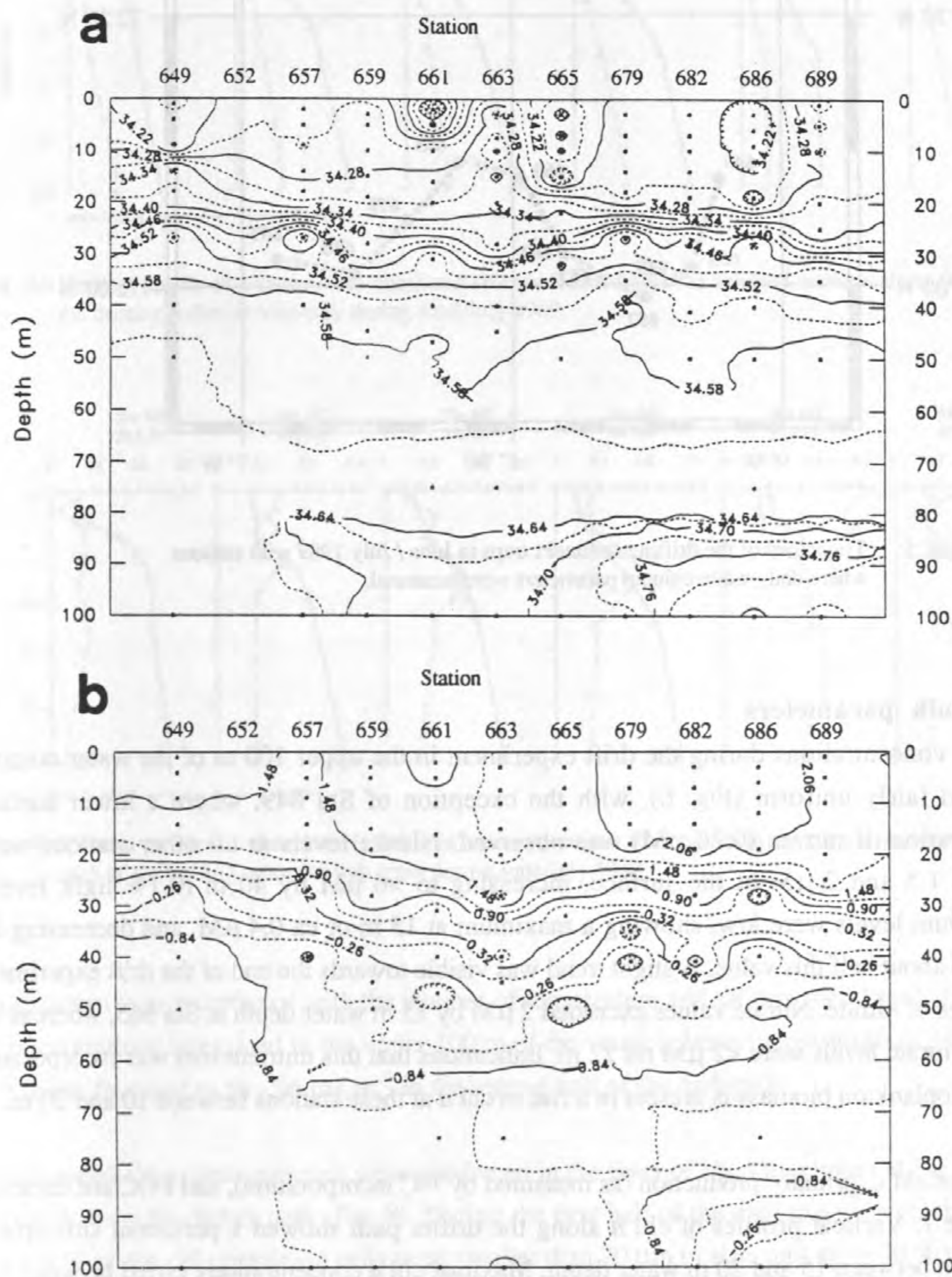


Fig 4: Isolines of salinity (∗ 10^{-3}) and temperature (°C) along the path of the drifting sediment trap array during June/July 1989, shown in Fig 4 a) and b) respectively.

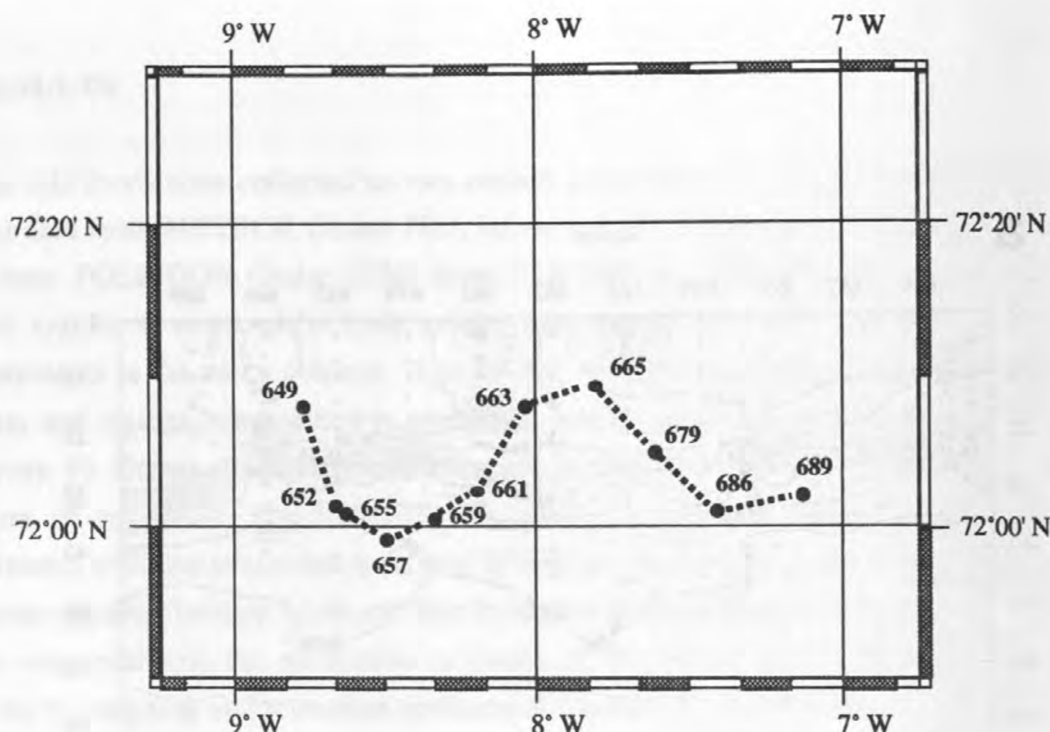


Fig. 5: Trajectory of the drifting sediment traps in June / July 1989 with stations where daily water column parameters were measured.

3.1.2 Bulk parameters

Nutrient concentrations during the drift experiment in the upper 100 m of the water column remained fairly uniform (Fig. 6), with the exception of Sta 649, where a lower surface concentration of nitrate (0.26 µM) was observed. Nitrate levels at all other stations were between 1.5 and 2 µM at the surface, increasing to >6 µM by 40 m (0.1% light level). Ammonium levels were low, showing a maximum at 15 m of ca 0.4 µM, and decreasing by 100 m to about half this value. A slight trend was visible towards the end of the drift experiment in profiles of nitrate. Nitrate values exceeded 2 µM by 15 m water depth at Sta 665, whereas by Sta 689 nitrate levels were <2 µM till 22 m. Indications that this nutrient loss was incorporated into phytoplankton biomass is present in a rise in chl *a* at these stations between 10 and 20 m.

Profiles of chl *a*, primary production (as measured by ^{14}C incorporation), and POC are depicted in Figure 7. Vertical profiles of chl *a* along the drifter path showed a persistent subsurface maximum between 15 and 20 m water depth. Maximal chl *a* concentrations varied between 1.5 and 2.5 µg dm^{-3}, increasing during the second half of the drift experiment. This depth of maximum chl *a* concentration changed during Sta 661 to 665, with a penetration of higher chl *a* levels (0.5 - 1.0 µg dm^{-3}) to 40 - 50 m. By Sta 689 a pronounced gradient was once again seen between 20 and 30 m, with lower concentrations (ca. 2.0 µg dm^{-3}) below 30 m.

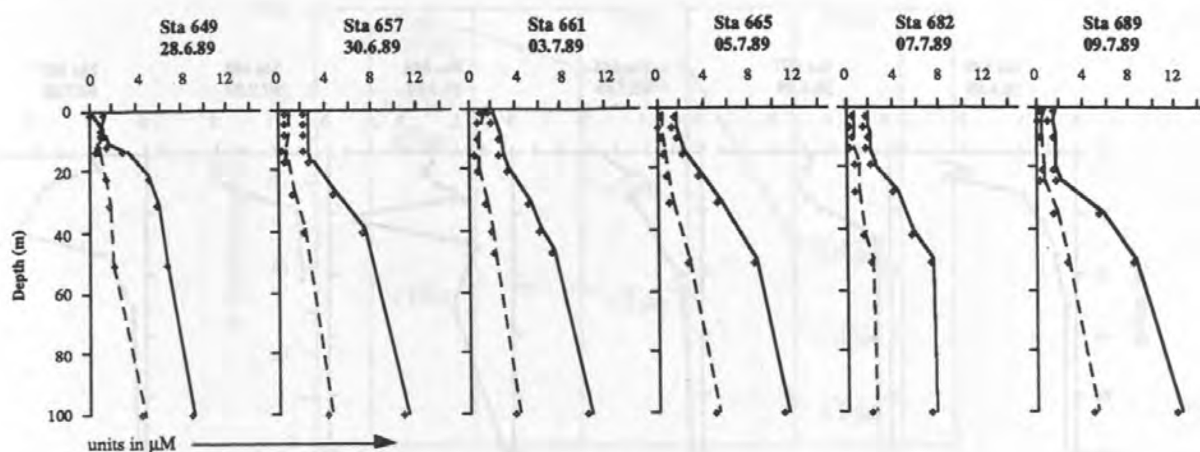


Fig. 6a: Vertical profile of nitrate (solid lines) and silicate (dashed lines) at selected stations along the path of the drifting sediment trap aray during June/July 1989.

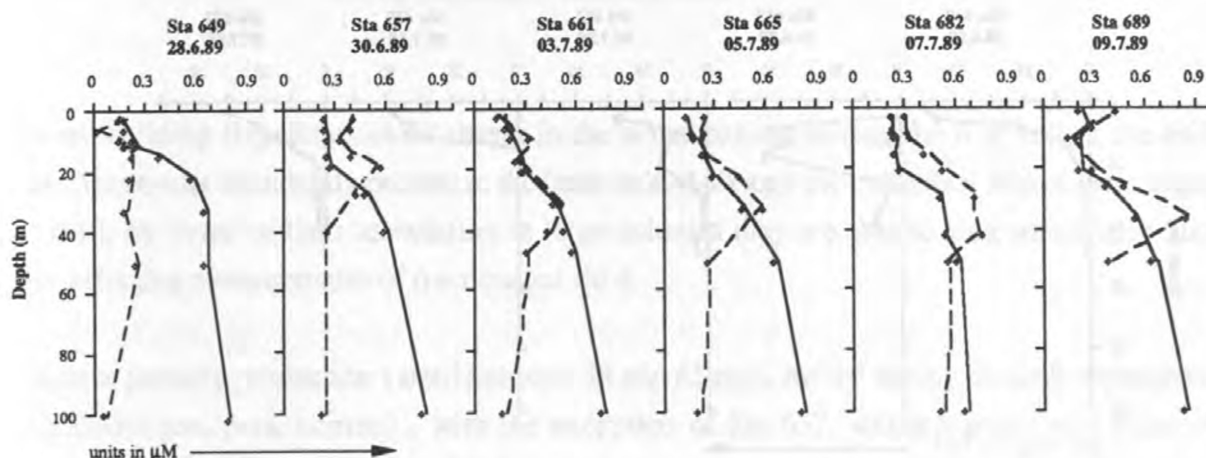


Fig. 6b: Vertical profiles of phosphate (solid lines) and ammonium (dashed lines) at selected stations along the path of the drifting sediment trap array during June/July 1989.

This pattern is in accordance with the isolines of temperature and salinity mentioned above. Chl *a* concentrations integrated in the upper 100 m of the water column increased from 34 - 49 mg m^{-2} in the first half to 56 - 96 mg m^{-2} in the second half of the drift path.

Fractionated chl *a* measurements were conducted in the layer of chl *a* maximum at Sta 651, 661 and 679 along the drifter path (Fig. 8). During the first half of the drift experiment, at Sta 651, 80 - 90 % of the chl-containing cells were smaller than 20 µm in size, and up to 30 % were able to pass through a 2 µm filter. This pattern changed during the latter part of the drift experiment, with over 50 % of chl *a* being contained in cells larger than 20 µm. At Sta 679 about 10 % of the chl-containing algae were in the size class <2 µm. This feature could be accounted for in the observed species composition of the phytoplankton (Arndt 1990). *Phaeocystis pouchetii*, a

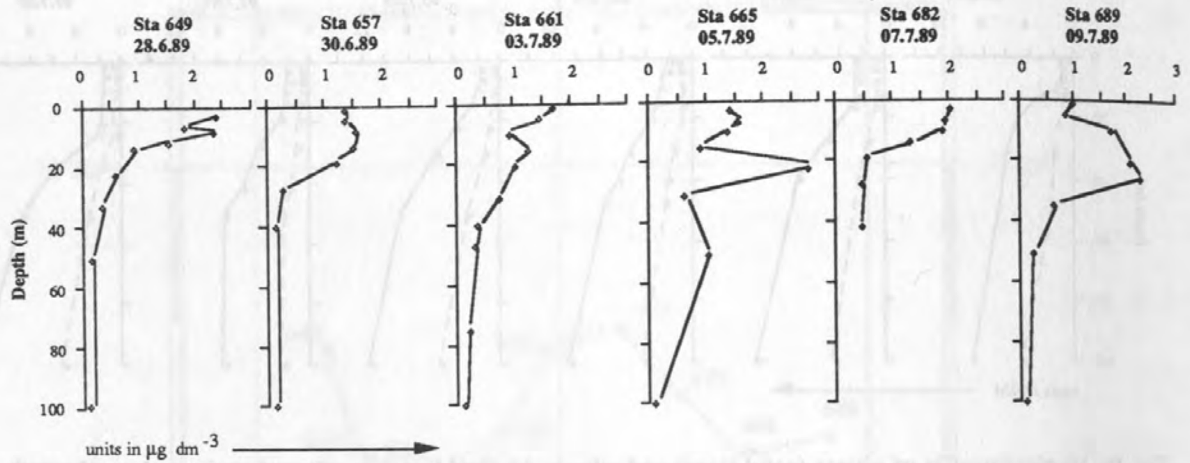


Fig. 7a: Vertical profiles of chlorophyll *a* at selected stations along the path of the drifting sediment trap array during June/July 1989.

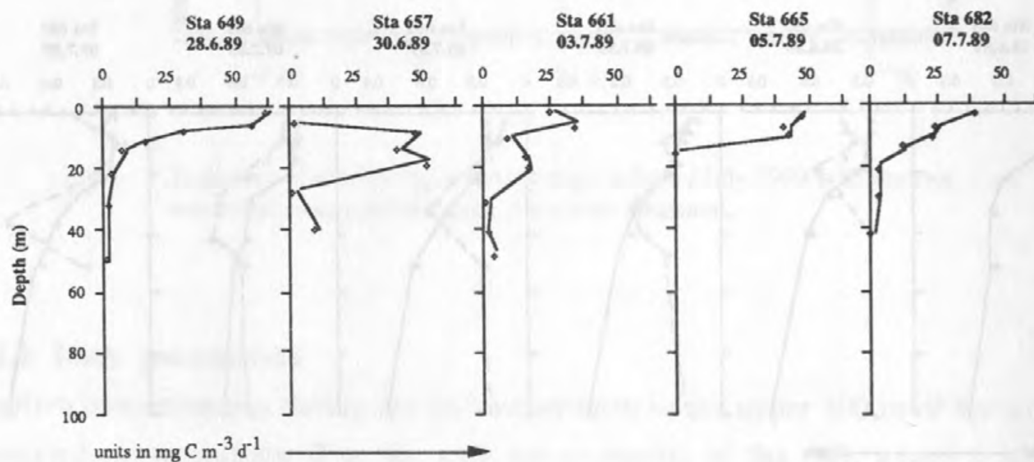


Fig. 7b: Vertical profiles of primary production at selected stations along the path of the drifting sediment trap array during June/July 1989.

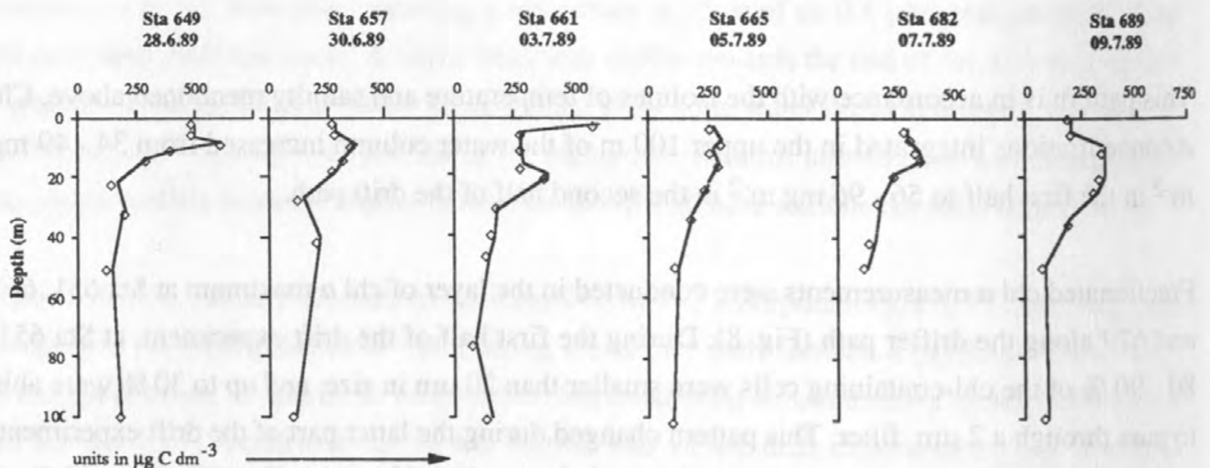


Fig. 7c: Vertical profiles of particulate organic matter at selected stations along the path of the drifting sediment trap array during June/July 1989.

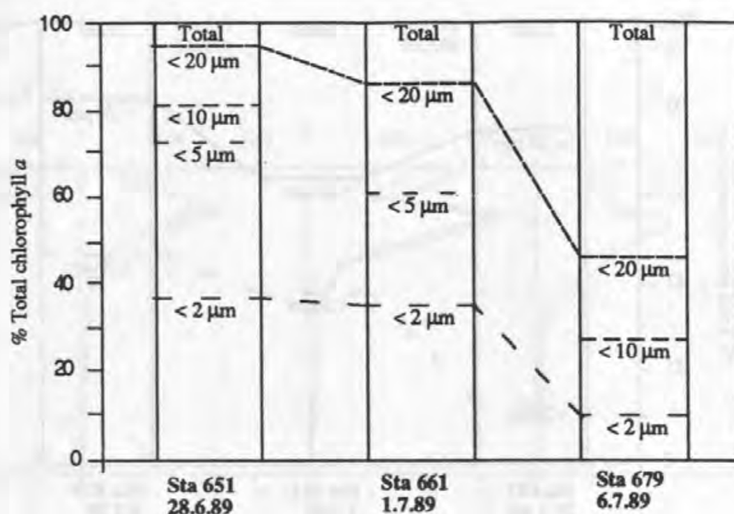


Fig. 8: Stacked graphs of the percentual contribution of size fractions to total chl a at three stations along the path of the drifting trap array in June/July 1989

colony-building flagellate, while absent in the water column during the first half of the drift experiment, was abundantly present in the latter half. Although the individual size of these algae is small, by virtue of their association in large colonies they are able to clog small mesh-size nets, affecting measurements of fractionated chl *a*.

Maximal primary production varied between 35 and 65 mgC $m^{-3}d^{-1}$ during the drift experiment (B.v.Bodungen, pers. comm.) , with the exception of Sta 657, where a maximum value of 10.5 mgC $m^{-3}d^{-1}$ was observed. Production maxima were consistently in surface (0 - 3 m) waters, again with the exception of Sta 657 at which a subsurface maximum at 10 m was seen. The occurance of maximal production above the maximum of biomass accumulation (chl *a* max) is indicative of a faster growing algal population at higher light levels. The relative contribution of phytoplankton size classes to total primary production is shown in Figure 9 at Sta 652, 661 and 682, at the depths of chl *a* maximum. Whereas at the start of the drift experiment the smaller size classes of phytoplankton (< 5 µm) contained up to 75 % of total chl *a* , they contributed to only 25 % of primary productivity. This pattern was inversed during the latter part of the experiment, where almost half of the productivity was in the size class < 2 µm, although this fraction contained less than 10 % of total chl *a*.

Particulate organic carbon (POC) showed a similar distribution pattern as chl *a* in the upper 30 m, but declined less rapidly at the base of the euphotic zone. A deeper maximum of POC was seen at Sta 663, similar to the profile for chl *a*. There was no significant change in POC in the upper 60 m (integrated values), and these fluctuated between 16 and 20 mg m^{-2} during the entire drift experiment. POC : chl ratios in the upper 30 m of the water column ranged between

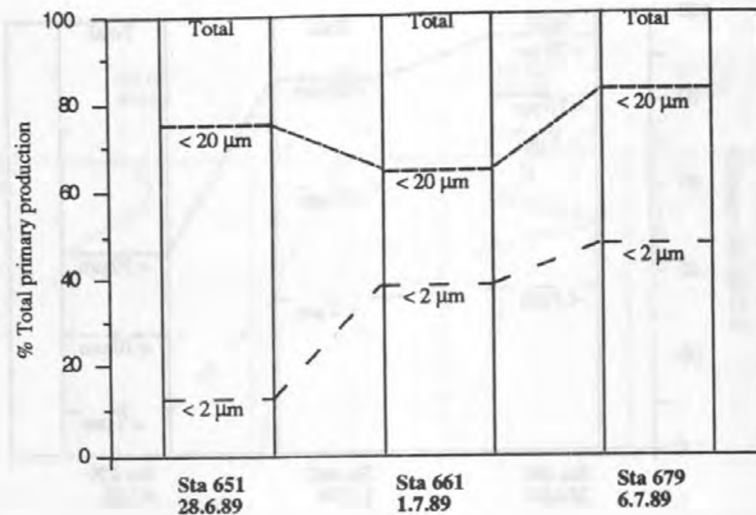


Fig. 9: Stacked graphs of the percentual contribution of size fractions to total primary production at three stations along the path of the drifting trap array in June/July 1989

200:1 and 350:1. Below this depth they increased gradually, reaching ratios of 600:1 to 800:1 at 100 m. This may be explained by a higher proportion of heterotrophic material and detritus in the lower layers of the euphotic zone.

The differences in the above mentioned parameters between both halves of the drift experiment indicate that the drifter passed through zones of water differing in their pelagic biological components. Measurements of new production indicated that the first situation was fuelled by processes of regenerated nutrients (f-ratio 0.1 - 0.2; W.Koeve, pers. comm.), whereas "new" (nitrate-based) production characterized the second situation (f-ratios >0.5).

3.1.3 Microzooplankton distribution

Distribution of microzooplankton was measured at five stations along the path of the drifting sediment trap array (Fig. 10). At all stations maximum abundances of microzooplankton and their biomass was found between 9 and 18 m, which corresponded to the depth of maximal chl *a*. A secondary maximum was found at the surface (0 - 3 m), and was often accompanied by a sub-surface minimum at 4 to 8 m. Microzooplankton concentrations decreased sharply with depth below the maximum number, and were negligible by 100 m. Profiles of abundance and biomass closely parallelled one another, indicating a uniform size distribution with depth. During the second half of the drift experiment, however, there was a divergence in this pattern in surface samples, with the number of microzooplankton relatively greater than biomass in surface samples. This is indicative of the predominance of smaller forms in surface samples.

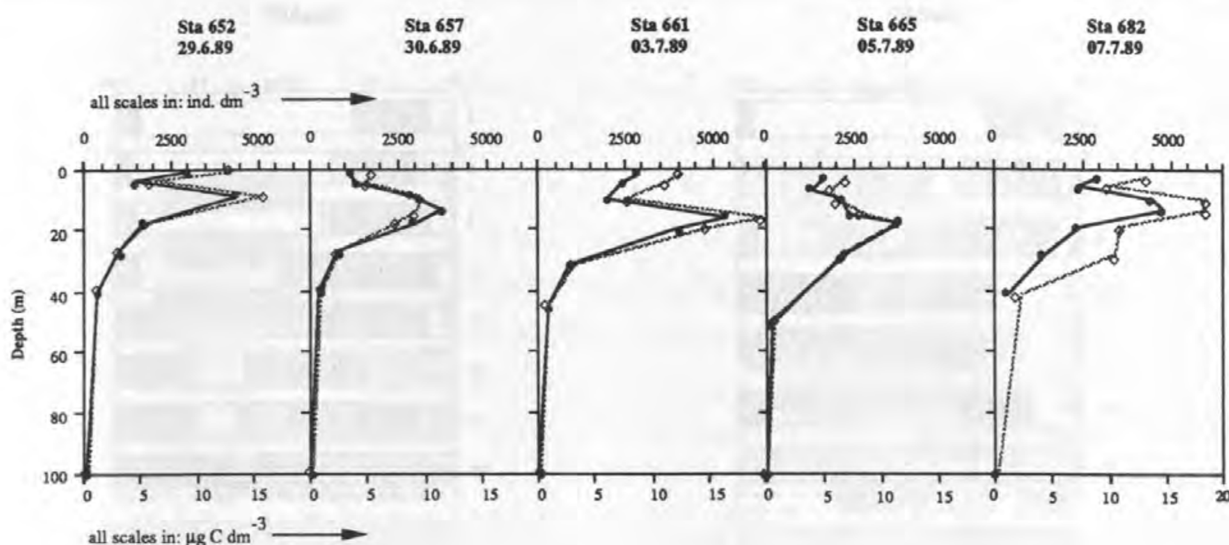


Fig. 10: Vertical profile of microzooplankton numbers (dashed lines) and microzooplankton biomass (solid lines) at selected stations along the path of the drifting sediment trap aray during June/July 1989.

Figure 11 shows the relative contribution of individual groups to total microzooplankton numbers. During the drift experiment heterotrophic dinoflagellates, primarily *Gyrodinium* spp., were dominant in the upper 15 - 20 m of the euphotic zone, comprising over 50 % of total microzooplankton numbers. This decreased by 30 m to about 10 % of total microzooplankton, and *Gyrodinium* was rarely present below 50 m water depth. Tintinnids were the dominant microprotozoans at lower depths, forming the major part of the microzooplankton assemblage between 40 and 100 m. The relative contribution of naked oligotrichs of the genus *Strombidium* was constant in the upper layers at between 5 and 20 %. *Laboea* species showed a subsurface dominance in abundance, comprising up to 40 % of microzooplankton numbers at 20 m. Less abundant species have been grouped in the category "others", and consisted of individuals of *Lohmaniella oviformis*, *Didinium* spp., and unidentified hypotrich ciliates. Their combined contribution to microzooplankton biomass was negligible, at below 5 % of the total.

When the relative contribution of different groups of protozoans to microzooplankton biomass is seen (Fig. 12), it is apparent that *Laboea* spp. comprised a dominant part of the protozoan carbon in the upper euphotic zone. *Strombidium* species, too, were more dominant in terms of carbon biomass than in numbers, whereas the relative contribution of the smaller heterotrophic dinoflagellates to total microzooplankton carbon was smaller. Below the subsurface maximum at 20 m, tintinnids were the prominent protozoans both in terms of number and carbon content. Integrated abundances of microzooplankton in the upper 100 m increased slightly during the second half of the drift experiment, from an initial 0.78 - 1.15 $*10^5$ m^{-2} to 1.6 $*10^5$ m^{-2} by Sta 682. Integrated biomass also increased from ca. 250 mgC m^{-2} at the beginning to ca. 300 mgC m^{-2} at the end of the experiment.

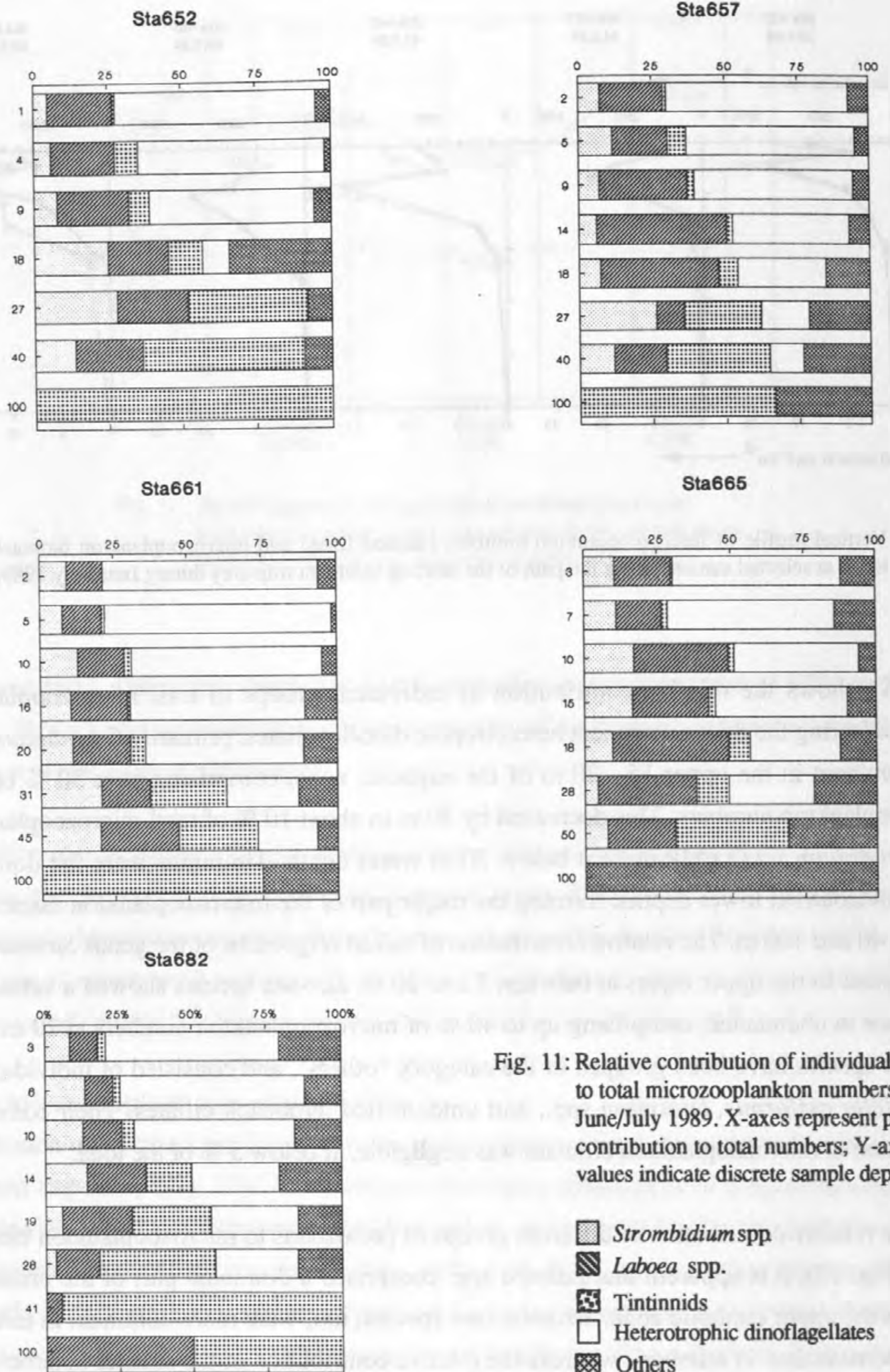


Fig. 11: Relative contribution of individual groups to total microzooplankton numbers during June/July 1989. X-axes represent percentual contribution to total numbers; Y-axes values indicate discrete sample depths.

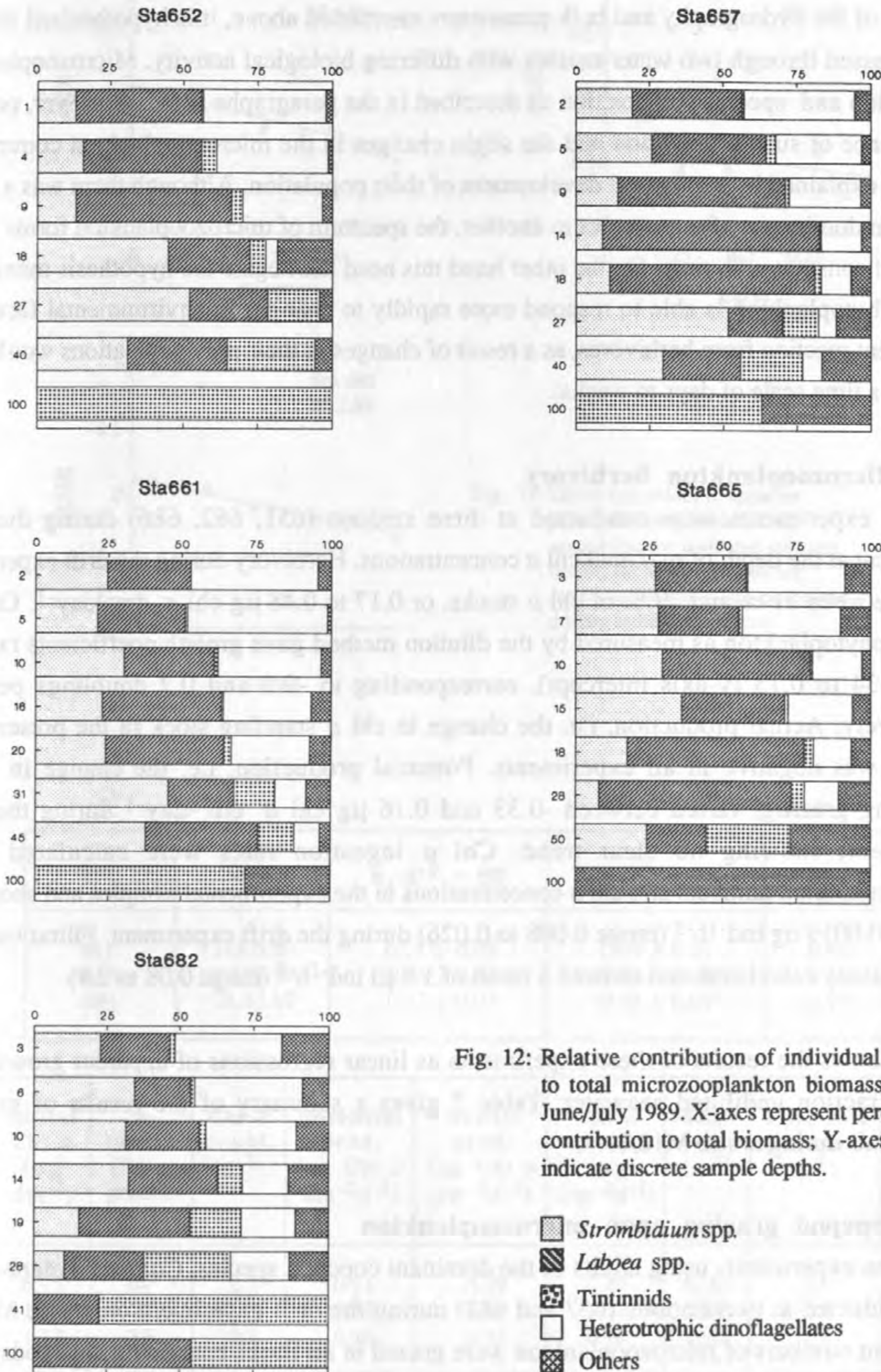


Fig. 12: Relative contribution of individual groups to total microzooplankton biomass during June/July 1989. X-axes represent percentual contribution to total biomass; Y-axes values indicate discrete sample depths.

In terms of the hydrography and bulk parameters mentioned above, it is hypothesized that the drifter passed through two water masses with differing biological activity. Microzooplankton distribution and species composition as described in the paragraphs above, however, provide no evidence of such a transition and the slight changes in the microzooplankton community could be explained by a temporal development of their population. Although there was a slight shift from dominance of one species to another, the spectrum of microzooplankton forms found remained constant with time. On the other hand this need not negate the hypothesis mentioned above. Phytoplankton is able to respond more rapidly to changes in environmental factors; a subsequent reaction from herbivores, as a result of changes in their prey populations would take place on a time scale of days to weeks.

3.1.4 Microzooplankton herbivory

Dilution experiments were conducted at three stations (651, 662, 686) during the drift experiment at the depth of maximal chl *a* concentrations. Herbivory during the drift experiment varied between 21 % and 39 % of chl *a* stocks, or 0.17 to 0.48 µg chl *a* $dm^{-3}day^{-1}$. Growth rates of phytoplankton as measured by the dilution method gave growth coefficients ranging from -0.34 to 0.13 (y-axis intercept), corresponding to -0.5 and 0.2 doublings per day respectively. Actual production, i.e. the change in chl *a* standing stock in the presence of grazers, was negative in all experiments. Potential production, i.e. the change in chl *a* discluding grazing, varied between -0.33 and 0.16 µg chl *a* $dm^{-3}day^{-1}$ during the drift experiment, showing no clear trend. Chl *a* ingestion rates were calculated from microzooplankton numbers and chl *a* concentrations in the experimental samples and showed a mean of 0.0019 ng $ind^{-1}h^{-1}$ (range 0.008 to 0.026) during the drift experiment. Filtration rates were similarly calculated, and showed a mean of 1.8 µl $ind^{-1}h^{-1}$ (range 0.08 to 2.9).

Fig. 13 shows the results of these experiments as linear regressions of apparent growth rate against fraction undiluted seawater. Table 2 gives a summary of the results of grazing experiments during cruise M10/3.

3.1.5 Copepod grazing upon microzooplankton

Incubation experiments using adults of the dominant copepod species, *Calanus hyperboreus*, were conducted at two stations (657 and 682) during the drift experiment on cruise M10/3. Significant numbers of microzooplankton were grazed in all flasks containing copepods, with 35 % of microzooplankton standing stocks being grazed at Sta 657, and 27 % grazed at Sta 682. In incubation flasks containing no copepods, no increase in microzooplankton numbers were seen. Expressed in terms of microzooplankton biomass, 39 % was grazed in incubation flasks with copepods at Sta 657, and 27 % at Sta 682.

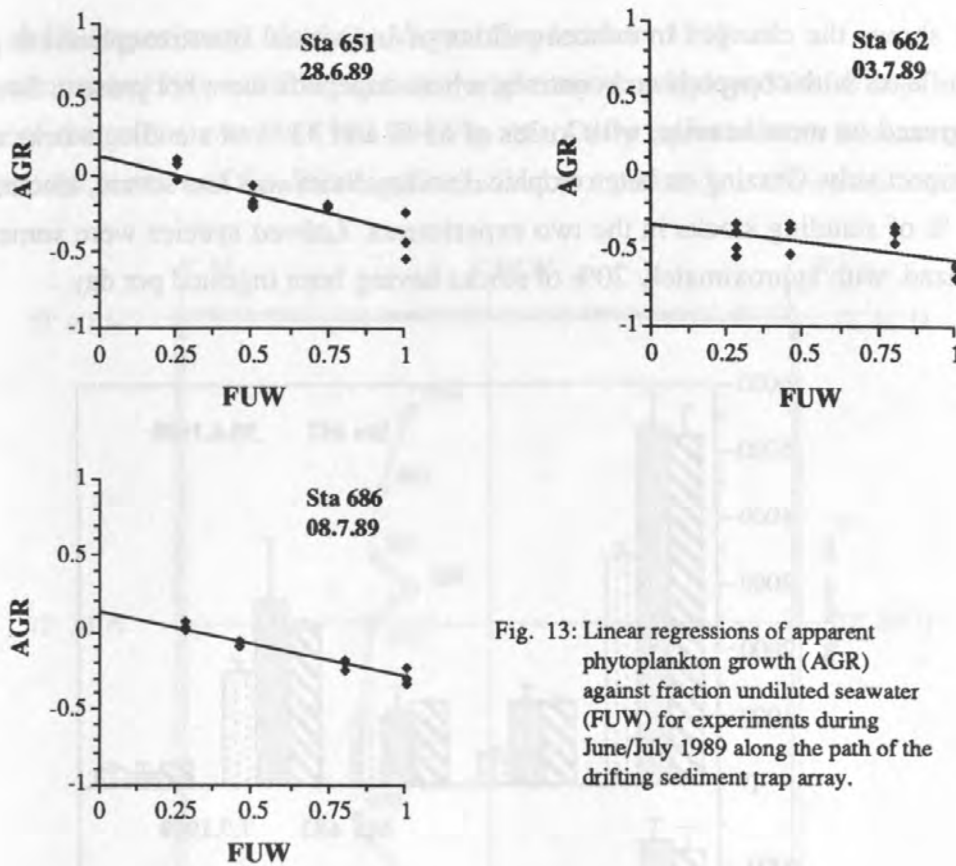


Fig. 13: Linear regressions of apparent phytoplankton growth (AGR) against fraction undiluted seawater (FUW) for experiments during June/July 1989 along the path of the drifting sediment trap array.

Sta	Date	k d^{-1} ± SD	g d^{-1} ± SD	| r |
651	28.06.89	0.11 ± 0.05	0.49 ± 0.08	0.86
662	03.07.89	-0.34 ± 0.06	0.23 ± 0.09	0.56
686	08.07.89	0.13 ± 0.03	0.43 ± 0.04	0.97

Sta	Initial Chl *a* (µg dm^{-3})	% Initial Chl *a* grazed d^{-1}	Chl *a* doubl. d^{-1}	Potential prod. (µg Chl *a* $dm^{-3}d^{-1}$)	Actual prod. (µg Chl *a* $dm^{-3}d^{-1}$)	Chl *a* grazed (µg $dm^{-3}d^{-1}$)	MZP* (# dm^{-3})	Filt. rate (µl ind^{-1} h^{-1})	Ingest. rate (µl ind^{-1} h^{-1})
651	0.93	39	0.2	0.11	-0.29	0.40	6240	2.9	0.0026
662	1.15	21	-0.5	-0.33	-0.50	0.17	8000	0.8	0.0008
686	1.19	35	0.2	0.16	-0.31	0.48	9360	1.8	0.0021

Table 2: Tabulated results of dilution experiments to determine microzooplankton herbivory, conducted during June/July 1989. "k" is the coefficient of algal growth, "g" the coefficient of algal mortality and "r" the value of the correlation coefficient. * Microzooplankton

Figure 14 shows the changes in concentrations of individual microzooplankton groups in incubation flasks with copepods and controls, where copepods were not present. ***Strombidium*** spp. was grazed on most heavily, with losses of 65 % and 33 % of standing stocks at Sta 657 and 682 respectively. Grazing on heterotrophic dinoflagellates was less severe, amounting to 29 % and 27 % of standing stocks in the two experiments. ***Laboea*** species were somewhat less rapidly grazed, with approximately 20% of stocks having been ingested per day.

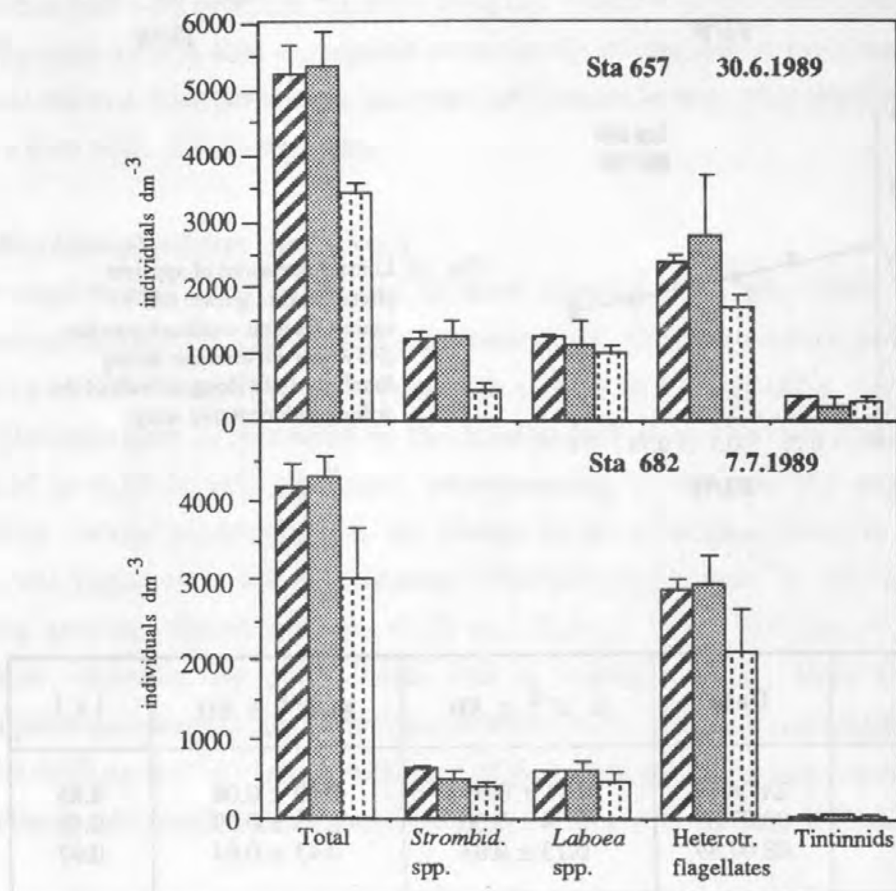


Fig. 14: Results of incubation experiments to determine grazing of copepods (adult female *Calanus hyperboreus*) on microzooplankton.
Microzooplankton number at 0 hours
Microzooplankton number in controls at 24 hours
Microzooplankton number in flasks containing copepods at 24 hours

In flasks containing no copepods, heterotrophic dinoflagellates were seen to increase by 16 % and 11 % respectively during the 24-hour incubation. *Strombidium* species did not increase in number, showing rather a loss of 2 % and 14 % at Sta 657 and 682 respectively. Small losses of *Laboea* spp. were also seen (9 % and 7 % respectively), but were not significantly different from zero.

3.2 The drift experiment during August/September 1990

During the cruise in 1990, a drifting sediment trap array was deployed for 10 days at a position very close to that of the array in 1989 (see Fig. 15). Daily water column measurements were conducted at the position of the drifter, which moved in a primarily southwards direction.

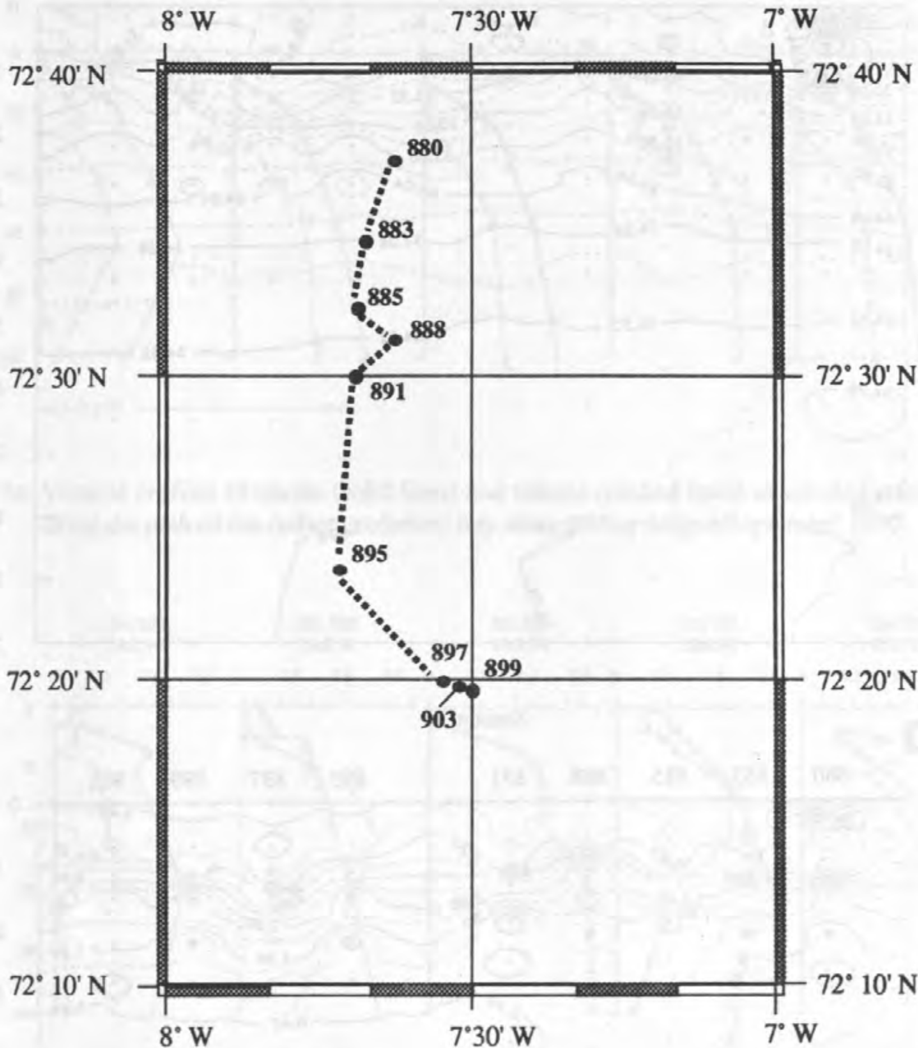


Fig. 15: Trajectory of the drifting sediment traps in August/ September 1990 with stations where daily water column parameters were measured.

3.2.1 Physical parameters

Figure 16 shows isolines of temperature and salinity along the path of the drifting sediment traps during cruise POS 173/2. Conspicuous was the surface layer of low salinity ($32.8 * 10^{-3}$) and high temperature (5.8 - 6.0 °C) which is attributable to a lens of fresh water from melted ice from the ice edge off the coast of Greenland. A gradual gradient in both parameters was seen between 10 and 30 m, covering a uniform water mass with a salinity of $>34.5 * 10^{-3}$ and

temperature of 0.4 °C. A uniformity in hydrographical conditions and bulk parameters were seen in the euphotic zone during the time of this drift experiment .

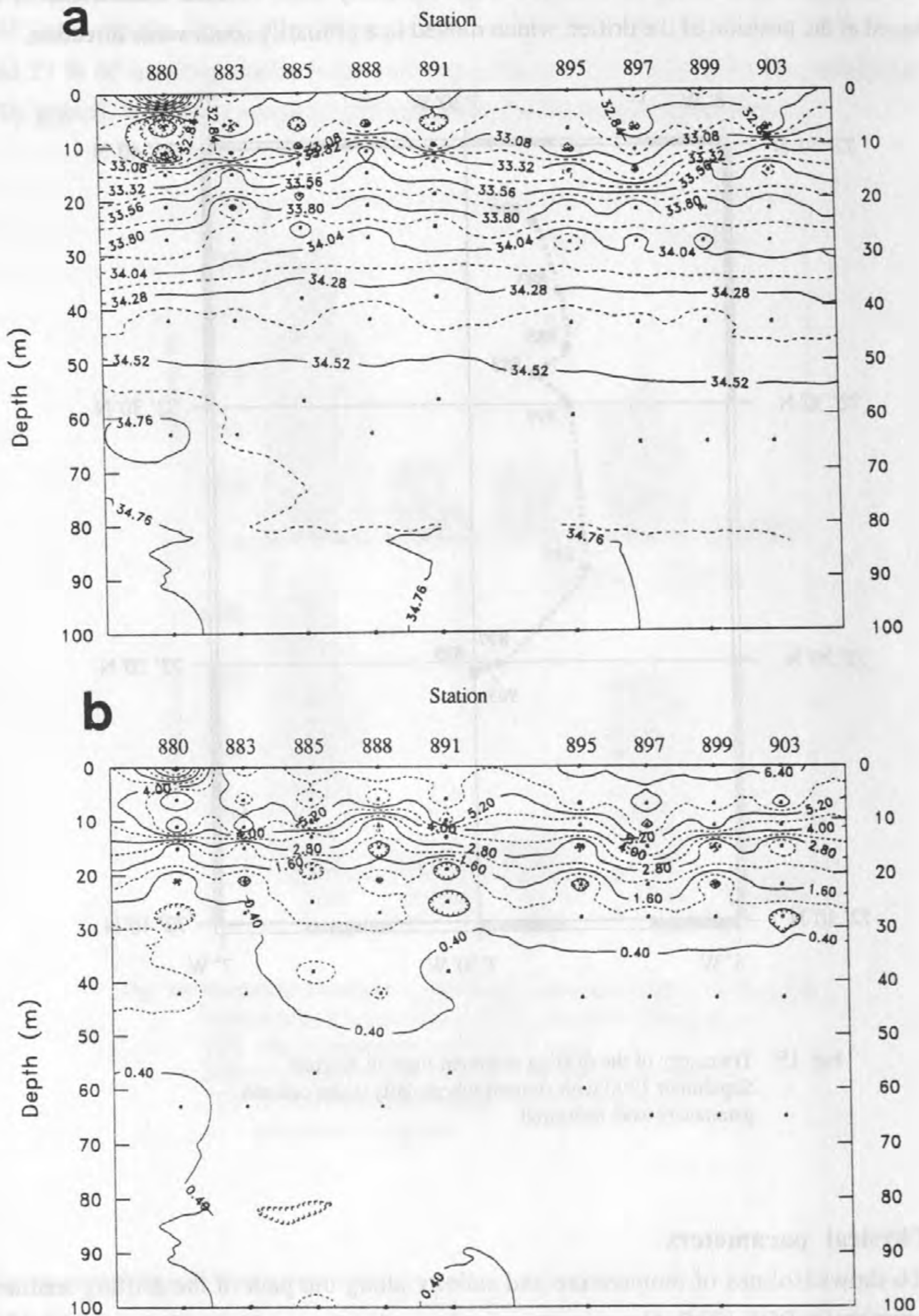


Fig. 16: Isolines of salinity (* 10^{-3}) and temperature (°C) along the path of the drifting sediment trap array during August/September 1990, shown in Fig. 16 a) and b) respectively.

3.2.2 Bulk Parameters

Nutrient levels were low in the upper 20 m, where production was highest, with NO_3 concentrations < 1 µM. Below 10 m, nutrient concentrations increased rapidly (Fig. 17).

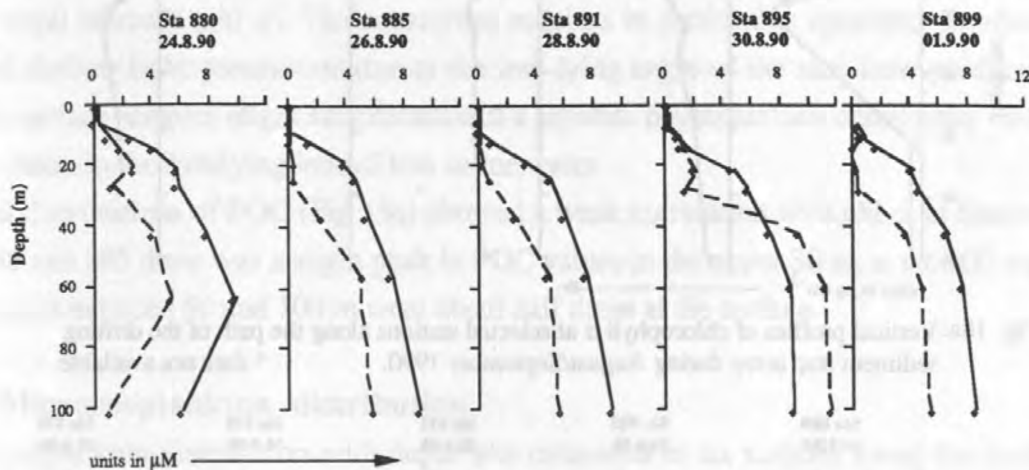


Fig. 17a: Vertical profiles of nitrate (solid lines) and silicate (dashed lines) at selected stations along the path of the drifting sediment trap array during August/September 1990.

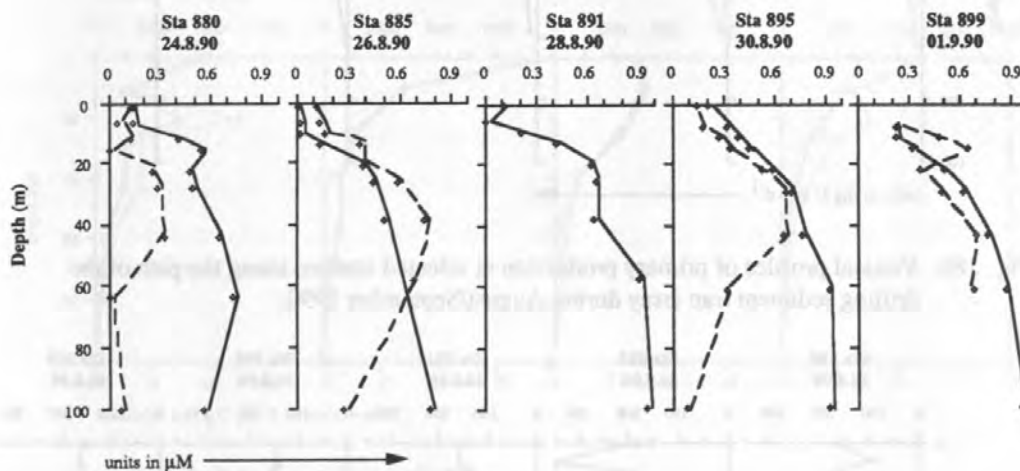


Fig. 17b: Vertical profiles of phosphate (solid lines) and ammonium (dashed lines) at selected stations along the path of the drifting sediment trap array during August/September 1990.

Chl *a* levels during the drift experiment were lower than those seen in 1989 (Fig. 18a). With the exception of Sta 880 and Sta 883 chl *a* concentrations remained below 1 µg dm^{-3}. At the first station (Sta 880) a pronounced subsurface maximum was seen at 22 m water depth; subsequently, chl *a* was distributed more evenly down to 50 - 60 m, with occasional slight peaks around 40 m. Chl *a* concentrations at 100 m varied between 0.1 and 0.67 µg dm^{-3} and corresponded to about half those at the surface.

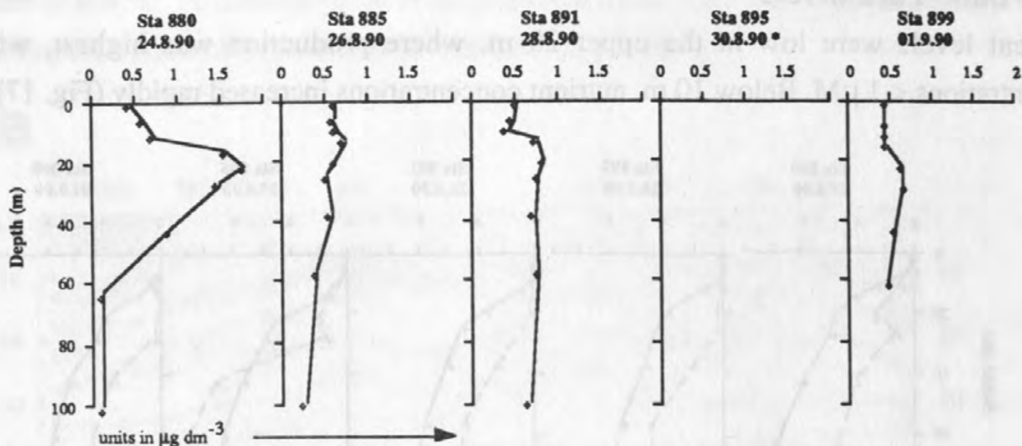


Fig. 18a: Vertical profiles of chlorophyll *a* at selected stations along the path of the drifting sediment trap array during August/September 1990. * data not available

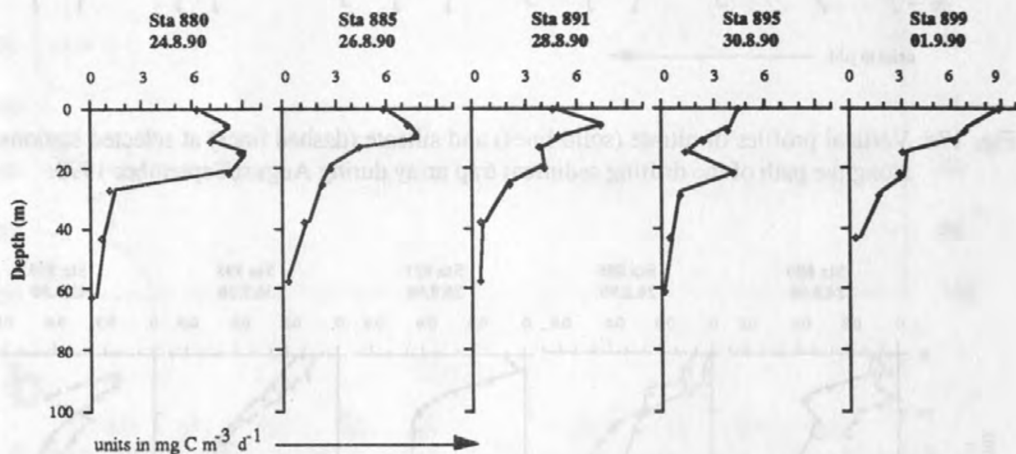


Fig. 18b: Vertical profiles of primary production at selected stations along the path of the drifting sediment trap array during August/September 1990.

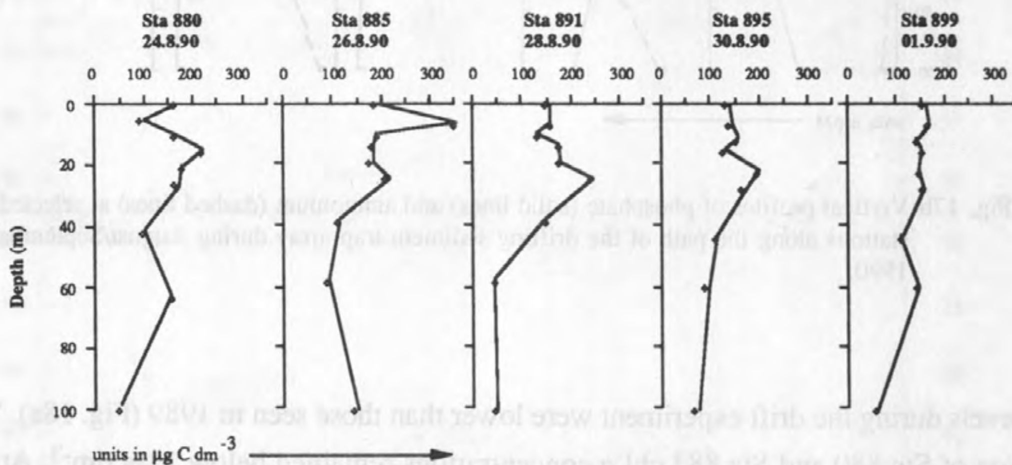


Fig. 18c: Vertical profiles of particulate organic matter at selected stations along the path of the drifting sediment trap array during August/September 1990.

Fractionated chlorophyll measurements showed that 65 % of total chl was able to pass through a 20 µm mesh; 10 % of the total was smaller than 2 µm.
Primary production values (Fig 18b) were below 10 mgC $m^{-3}d^{-1}$, a factor of five lower than in June/July 1989. As in the previous year, the depth of maximal primary production lay above that of algal biomass (chl *a*). The subsurface maxima in production appeared paradoxical in view of shallow light penetration due to the low-lying angle of the sun. Low productivity of algae in surface samples might be indicative of a separate phytoplankton community with lower growth rates, in the overlying lens of less saline water.
Vertical distributions of POC (Fig 18c) showed a weak correlation with chl *a*; at Stations 880, 883, 888 and 895 there was a slight peak in POC values in the upper 30 m, at ca. 200 mg dm^{-3}. POC values between 50 and 100 m were about half those at the surface.

3.2.3 Microzooplankton distribution

Microzooplankton distribution with depth was measured at six stations along the path of the drifting sediment traps (Fig. 19).

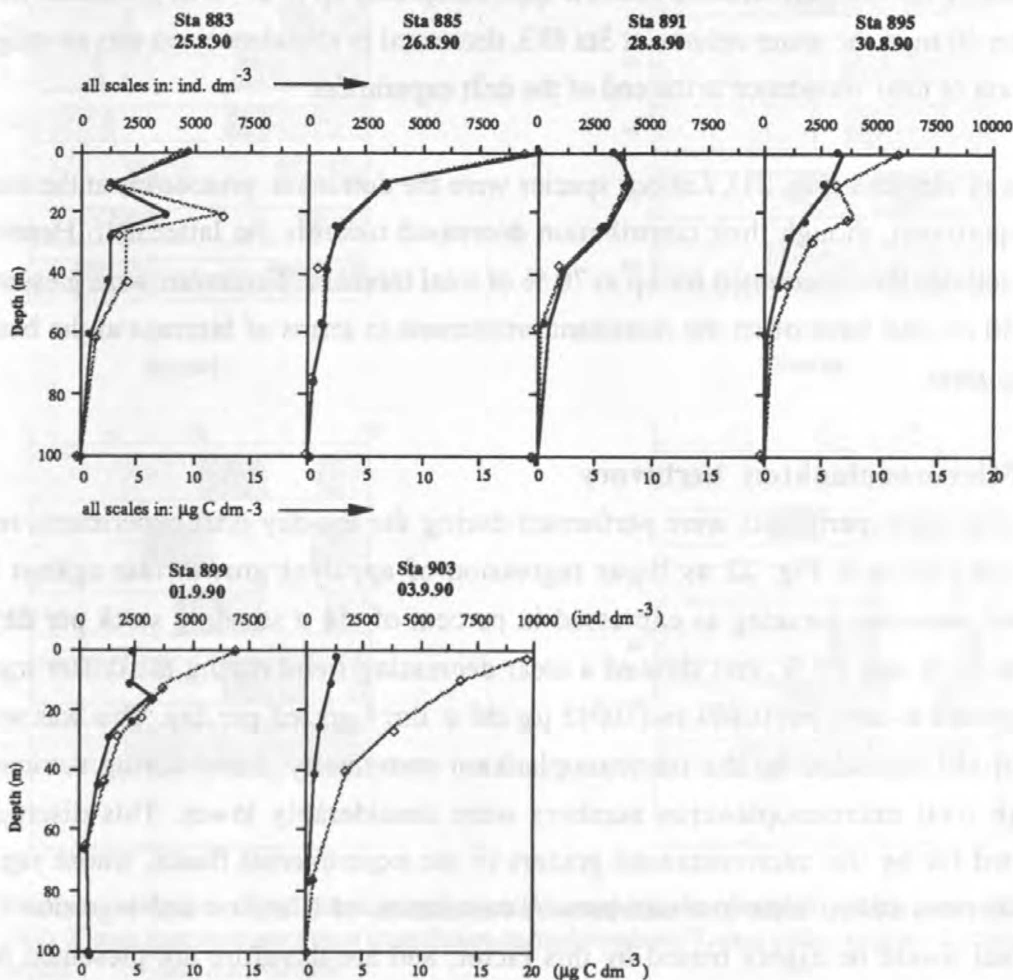


Fig. 19: Vertical profile of microzooplankton numbers (dashed lines) and microzooplankton biomass (solid lines) at selected stations along the path of the drifting sediment trap array during August/September 1990.

Maximum numbers of protozoans were found in surface waters (0 - 3 m) with the exception of Sta 883, where a subsurface maximum at 20 m was seen. The curves of abundance and biomass closely followed each other, diverging at the surface with biomass relatively lower than number of individuals. This trend increased during the drift path, and at Sta 899 the relative biomass was significantly less than abundance, showing an increased dominance of smaller forms at the end of the drift experiment. The depth distributions of individual groups accounted in large part for this trend. *Lohmaniella oviformis* (17 µm in size) and *Laboea* spp. (60 - 110 µm in size), showed pronounced surface maxima whereas *Strombidium* spp. were most abundant at 15 - 20 m. As seen during the drift experiment of 1989, tintinnids were most abundant at deeper layers (40 - 60 m).

The relative contribution of different groups to total protozoan numbers and biomass is shown in Figs. 20 and 21 respectively. *Strombidium* spp. accounted for up to 50 % of microprotozoan numbers at the start of the experiment; this decreased to between 20 and 30 % by Sta 899. The relative contribution of heterotrophic dinoflagellates, ca. 20 % at Sta 883, increased to 30-40 % at the end of the drift experiment. *Laboea* spp., comprised up to 27 % of protozoan number in the upper 10 m of the water column at Sta 883, decreased in abundance and was an insignificant proportion of total abundance at the end of the drift experiment.

In terms of biomass (Fig. 21), *Laboea* species were the dominant protozoans at the start of the drift experiment, though their contribution decreased towards the latter half. Heterotrophic dinoflagellates then accounted for up to 70 % of total biomass. Tintinnids were present mainly below 30 m, and were often the dominant protozoans in terms of biomass at the base of the euphotic zone.

3.2.4 Microzooplankton herbivory

Seven dilution experiments were performed during the ten-day drift experiment, results of which are shown in Fig. 22 as linear regression of apparent growth rate against fraction undiluted seawater. Grazing as expressed in percent of chl *a* standing stock per day varied between 10 % and 40 %, and showed a clear decreasing trend during the drifter track. This corresponded to between 0.369 and 0.043 µg chl *a* dm^{-3} grazed per day. This was within the range of chl ingestion by the microzooplankton community found during summer 1989, although total microzooplankton numbers were considerably lower. This discrepancy is accounted for by the micrometazoan grazers in the experimental flasks, whose rapid chl *a* ingestion rates belied their low numbers. A calculation of filtration and ingestion rates per individual would be highly biased by this factor, and are therefore not presented for these experiments. Chl *a* standing stocks, in the incubation bottles showed a steady reduction with time, decreasing from an initial 1.29 µg dm^{-3} at Sta 880 to 0.46 µg dm^{-3} at Sta 903.

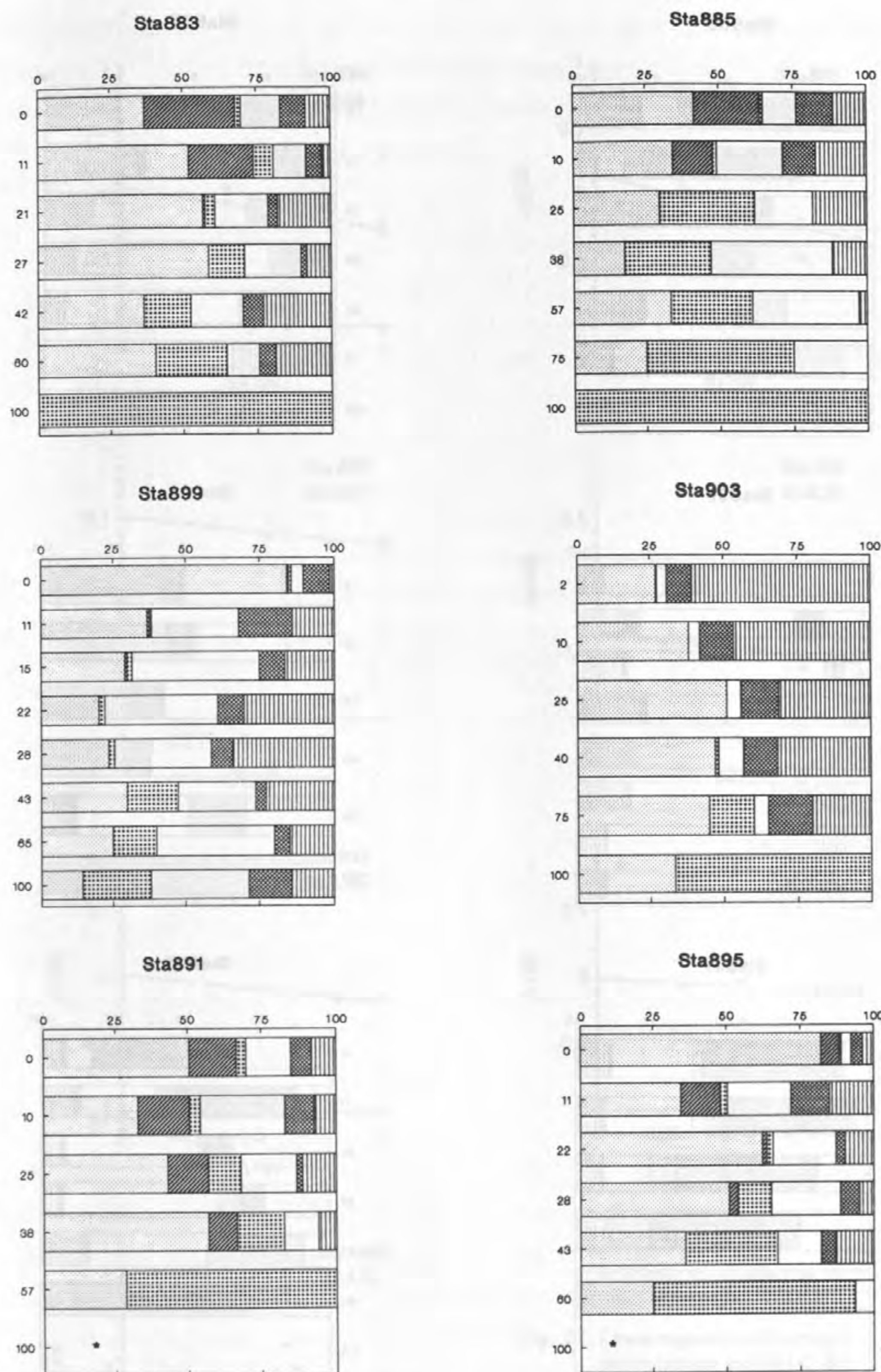


Fig. 20: Relative contribution of individual groups to total microzooplankton numbers during August/September 1990. X-axes represent percentual contribution to total numbers; Y-axes values indicate discrete sample depths. * data not available

Strombidium spp. *Laboea* spp. Tintinnids Heterotrophic dinoflagellates Others

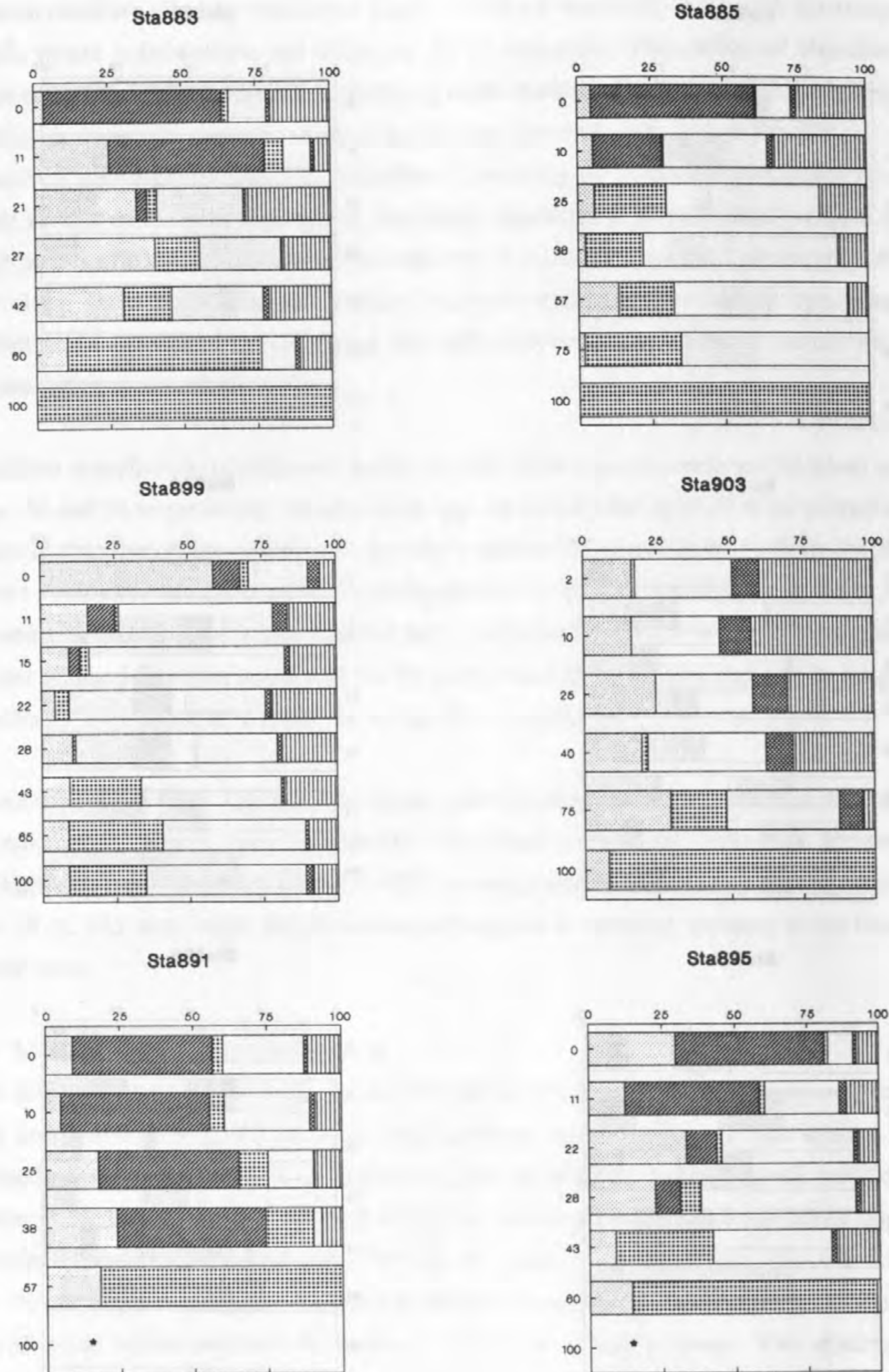


Fig. 21: Relative contribution of individual groups to total microzooplankton biomass during August/September 1990. X-axes represent percentual contribution to total biomass; Y-axes values indicate discrete sample depths. * data not available

Strombidium spp. *Laboea* spp. Tintinnids Heterotrophic dinoflagellates Others

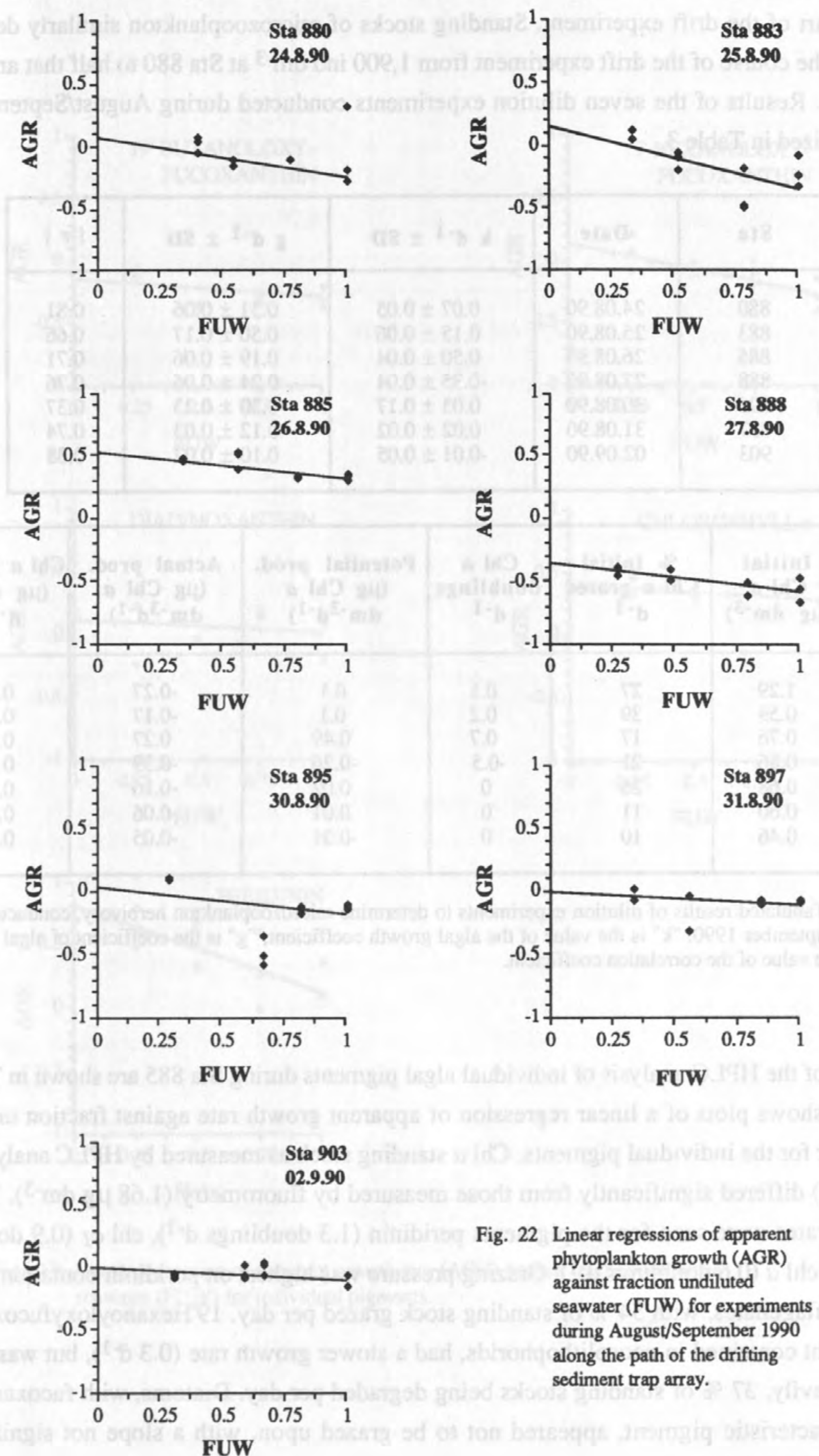


Fig. 22 Linear regressions of apparent phytoplankton growth (AGR) against fraction undiluted seawater (FUW) for experiments during August/September 1990 along the path of the drifting sediment trap array.

Phytoplankton growth varied between 0 and 0.7 doublings per day, and decreased during the latter part of the drift experiment. Standing stocks of microzooplankton similarly decreased during the course of the drift experiment from 1,900 ind dm^{-3} at Sta 880 to half that amount at Sta 903. Results of the seven dilution experiments conducted during August/September are summarized in Table 3.

Sta	Date	k d^{-1} ± SD	g d^{-1} ± SD	|r|
880	24.08.90	0.07 ± 0.05	0.31 ± 0.06	0.81
883	25.08.90	0.15 ± 0.06	0.50 ± 0.17	0.66
885	26.08.90	0.50 ± 0.04	0.19 ± 0.06	0.71
888	27.08.90	-0.35 ± 0.04	0.24 ± 0.06	0.76
895	30.08.90	0.03 ± 0.17	0.30 ± 0.23	0.37
897	31.08.90	0.02 ± 0.02	0.12 ± 0.03	0.74
903	02.09.90	-0.01 ± 0.05	0.10 ± 0.07	0.38

Sta	Initial Chl *a* (µg dm^{-3})	% Initial Chl *a* grazed d^{-1}	Chl *a* doublings d^{-1}	Potential prod. (µg Chl *a* $dm^{-3}d^{-1}$)	Actual prod. (µg Chl *a* $dm^{-3}d^{-1}$)	Chl *a* grazed (µg dm^{-3} d^{-1})
880	1.29	27	0.1	0.1	-0.27	0.37
883	0.59	39	0.2	0.1	-0.17	0.27
885	0.76	17	0.7	0.49	0.27	0.22
888	0.86	21	-0.5	-0.26	-0.39	0.13
895	0.68	26	0	0.02	-0.16	0.18
897	0.60	11	0	0.01	-0.06	0.07
903	0.46	10	0	-0.01	-0.05	0.04

Table 3: Tabulated results of dilution experiments to determine microzooplankton herbivory, conducted during August/September 1990. "k" is the value of the algal growth coefficient; "g" is the coefficient of algal mortality and "r" the value of the correlation coefficient.

Results of the HPLC analysis of individual algal pigments during Sta 885 are shown in Table 4. Fig. 23 shows plots of a linear regression of apparent growth rate against fraction undiluted seawater for the individual pigments. Chl *a* standing stock as measured by HPLC analysis (0.5 µg dm^{-3}) differed significantly from those measured by fluorometry (1.68 µg dm^{-3}). Highest growth rates were seen for the pigments peridinin (1.3 doublings d^{-1}), chl c_1 (0.9 doublings d^{-1}) and chl *a* (0.6 doublings d^{-1}). Grazing pressure was highest on peridinin-containing algae, i.e. dinoflagellates, with 54 % of standing stock grazed per day. 19'Hexanoyloxyfucoxanthin, a pigment contained in coccolithophorids, had a slower growth rate (0.3 d^{-1}), but was grazed upon heavily, 37 % of standing stocks being degraded per day. Diatoms, with fucoxanthin as the characteristic pigment, appeared not to be grazed upon, with a slope not significantly different from zero.

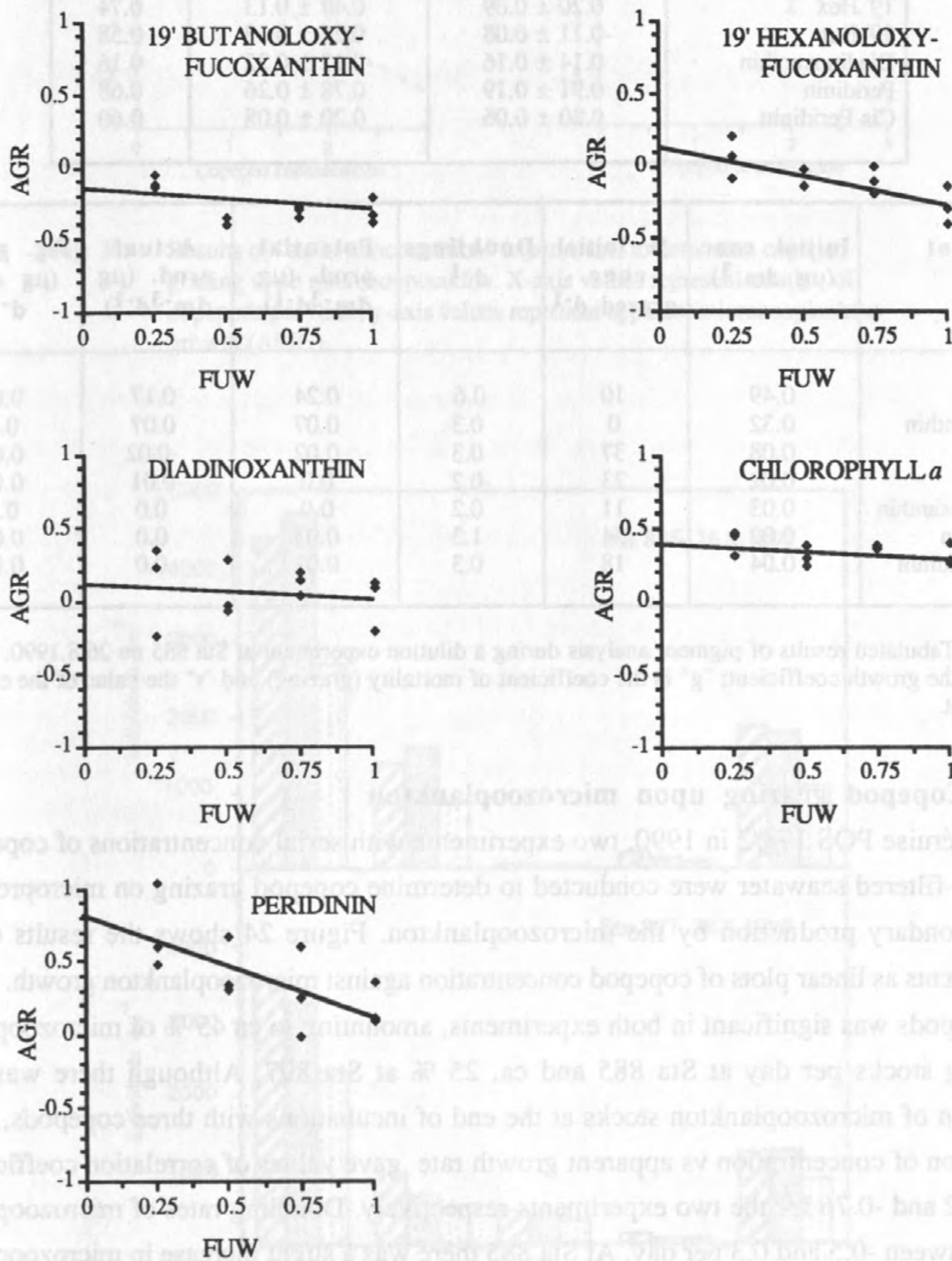


Fig. 23: Linear regression of apparent growth rate (AGR) against fraction undiluted seawater (FUW) for individual pigments.

Pigment	k d^{-1} ± SD	g d^{-1} ± SD	| r |
Chl *a*	0.41 ± 0.06	0.11 ± 0.08	0.37
Fucoxanthin	0.20 ± 0.08	0.00 ± 0.12	0.01
19' Hex	0.20 ± 0.09	0.47 ± 0.13	0.74
19' But	-0.11 ± 0.08	0.26 ± 0.12	0.58
Diadinoxanthin	0.14 ± 0.16	-0.12 ± 0.22	0.16
Peridinin	0.91 ± 0.19	0.78 ± 0.26	0.68
Cis-Peridinin	0.20 ± 0.06	0.20 ± 0.08	0.60

Pigment	Initial conc. (µg dm^{-3})	% Initial conc. grazed d^{-1}	Doublings d^{-1}	Potential prod. (µg $dm^{-3}d^{-1}$)	Actual prod. (µg $dm^{-3}d^{-1}$)	Pig. grazed (µg dm^{-3} d^{-1})
Chl *a*	0.49	10	0.6	0.24	0.17	0.07
Fucoxanthin	0.32	0	0.3	0.07	0.07	0.0
19' Hex	0.08	37	0.3	0.02	-0.02	0.04
19' But	0.02	23	-0.2	0.0	-0.01	0.01
Diadinoxanthin	0.03	11	0.2	0.0	0.0	0.0
Peridinin	0.02	54	1.3	0.03	0.0	0.03
Cis-Peridinin	0.04	18	0.3	0.01	0.0	0.01

Table 4: Tabulated results of pigment analysis during a dilution experiment at Sta 885 on 26.8.1990. "k" is the value of the growth coefficient; "g" is the coefficient of mortality (grazing) and "r" the value of the correlation coefficient.

3.2.5 Copepod grazing upon microzooplankton

During cruise POS 173/2 in 1990, two experiments with serial concentrations of copepods in 200 µm-filtered seawater were conducted to determine copepod grazing on microprotozoans and secondary production by the microzooplankton. Figure 24 shows the results of these experiments as linear plots of copepod concentration against microzooplankton growth. Grazing by copepods was significant in both experiments, amounting to ca 45 % of microzooplankton standing stocks per day at Sta 885 and ca. 25 % at Sta 897. Although there was severe depletion of microzooplankton stocks at the end of incubations with three copepods, a linear regression of concentration vs apparent growth rate gave values of correlation coefficients of r = -0.92 and -0.76 for the two experiments respectively. Doubling rates of microzooplankton were between -0.5 and 0.3 per day. At Sta 885 there was a slight increase in microzooplankton numbers in the absence of copepods, giving a doubling of 0.1 per day. However, at Sta 897 microzooplankton stocks decreased even in the absence of copepods. Grazing of copepods on specific groups of protozoans was also quantified, and the results are illustrated in Figure 25. Tintinnids appeared not to be grazed as heavily as naked ciliates, with 30 % and 8 % ingested per day at Sta 885 and 897 respectively. Heterotrophic flagellates were somewhat more heavily grazed upon (40 % and 31 % respectively); there appeared to be no significant trend in food selectivity among the other protozoan groups.

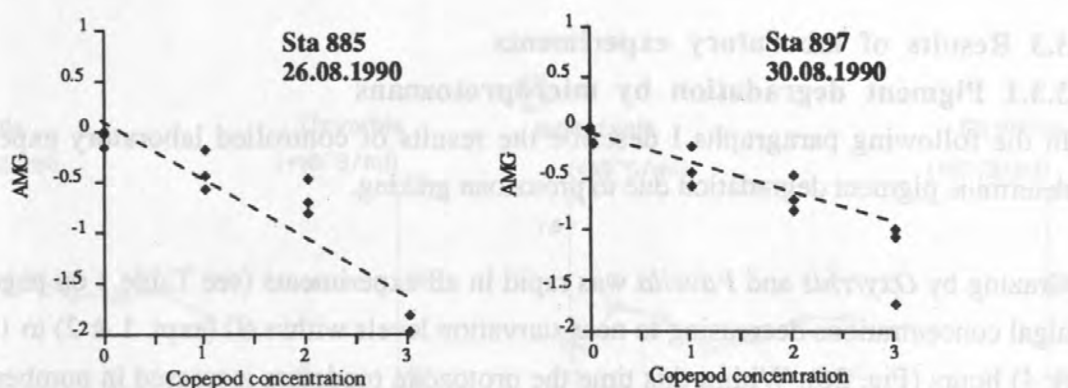


Fig. 24: Results of "serial concentration" experiments to determine copepod grazing upon microzooplankton. X-axis values represent number of copepods per flask; y-axis values represent apparent microzooplankton growth (AMG).

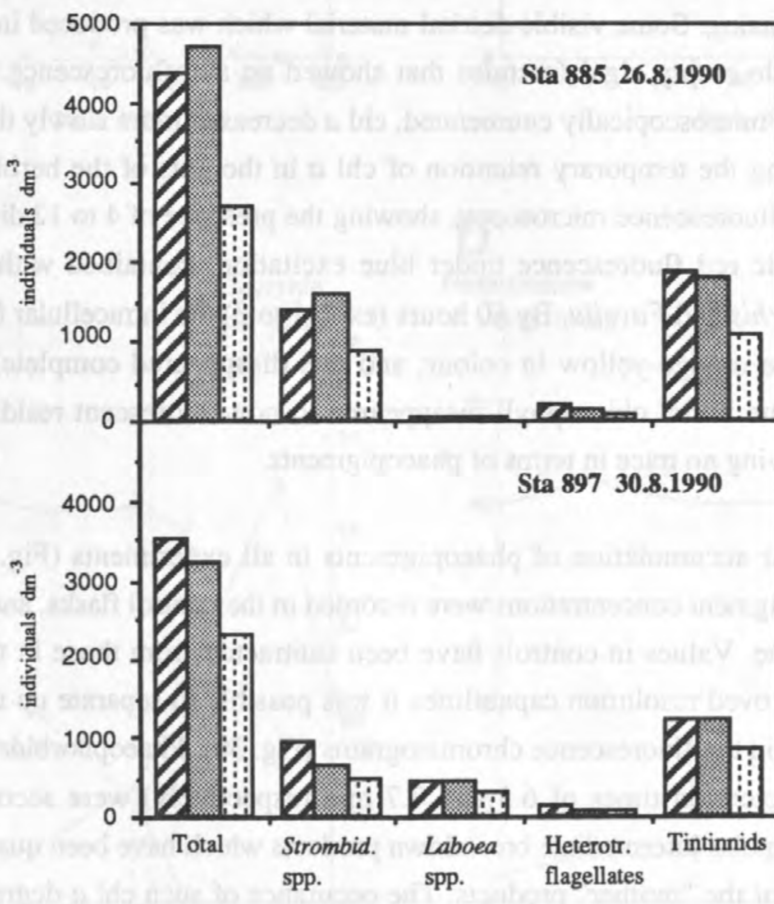


Fig. 25: Bar diagrams showing the grazing pressure of copepods (adult female *Calanus hyperboreus*) on different groups of microzooplankton.
- Microzooplankton number at 0 hours
- Microzooplankton number in controls at 24 hours
- Microzooplankton number in flasks containing copepods at 24 hours

3.3 Results of laboratory experiments

3.3.1 Pigment degradation by microprotozoans

In the following paragraphs I describe the results of controlled laboratory experiments to determine pigment degradation due to protozoan grazing.

Grazing by *Oxyrrhis* and *Favella* was rapid in all experiments (see Table 1 on page 12), with algal concentrations decreasing to near starvation levels within 60 (expt. 1 & 2) to 100 (expt. 3 & 4) hours (Fig. 26). Within this time the protozoan predators increased in numbers although there was a noticeable lag phase. During this lag phase the volume per predator (*Oxyrrhis*) cell showed a steady rise followed by a decrease following division (Fig. 27).

Chl *a* degradation followed a similar pattern compared to cell numbers, albeit at a faster rate in expt 1 & 2 (Fig. 28). The lower rate for cell numbers can be attributed to an overestimate in prey concentration using the Multisizer, due to interference by detrital particles of similar size formed during grazing. Some visible detrital material which was produced in all experiments consisted of single empty algal frustules that showed no autofluorescence. In expt. 3 & 4, where algae were microscopically enumerated, chl *a* decreased more slowly than did algal cell number, indicating the temporary retention of chl *a* in the guts of the herbivores. This was confirmed by epifluorescence microscopy, showing the presence of 4 to 12 discrete algal cells with characteristic red fluorescence under blue excitation, contained within the digestive vacuoles of *Oxyrrhis* and *Favella*. By 60 hours (expt. 1 to 3) the intracellular fluorescence was dimmer and more orange-yellow in colour, and this disappeared completely by 100 hours About 50 % of the initial chlorophyll disappeared to non-fluorescent residues by 15 hours (expt. 1 & 2), leaving no trace in terms of phaeopigments.

There was a clear accumulation of phaeopigments in all experiments (Fig. 29). Negligible (<0.01%) phaeopigment concentrations were recorded in the control flasks, and these remained constant with time. Values in controls have been subtracted from those in the experimental flasks. With improved resolution capabilities it was possible to separate up to 10 breakdown products of chl *a* in the fluorescence chromatograms (Fig. 30). Phaeophorbide and pyrophaeophorbide (with retention times of 6.5 and 7.7 min respectively) were accompanied by the formation of less polar intermediate breakdown products which have been quantified using the response factors of the "mother" products. The occurance of such chl *a* degradation products intermediate in polarity between chlorophyllide *a* and chl *a* have been reported using both thin layer chromatography (Hallegraf and Jeffrey 1985, Gieskes et al. 1978) and HPLC (Gieskes and Kraay 1983). Phaeophytin *a* and phaeophytin were produced in all experiments and a single peak eluting at 17.4 min was formed in expt 4, which was characterized as phaeophytin like. These intermediate products constituted between 13 and 59 % of the total breakdown products.

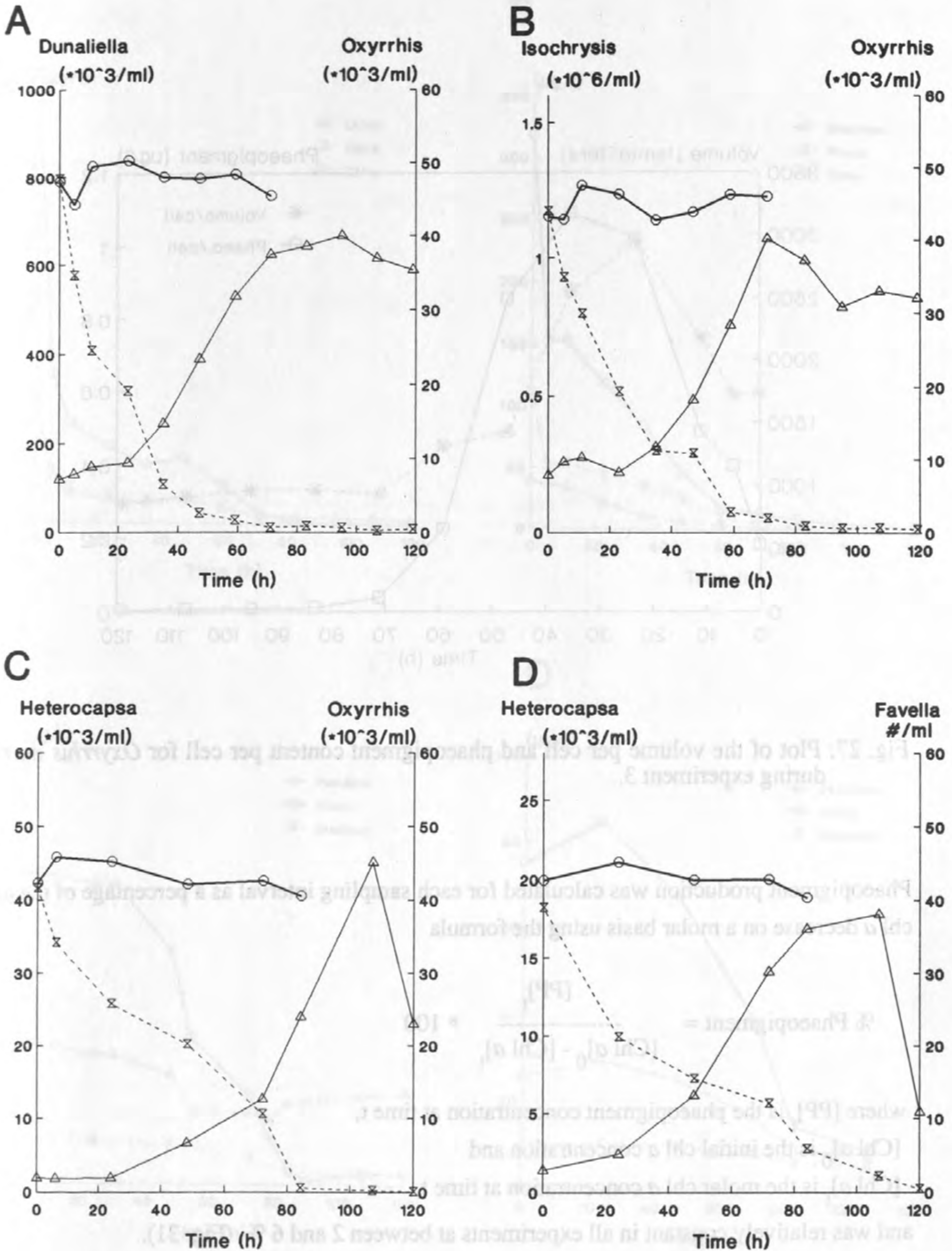


Fig. 26: Changes in algal and protozoan concentrations with time for experiments 1 to 4, (A) to (D) respectively. Dashed line: algal number, solid line: protozoan number, bold line algal number in control flasks.

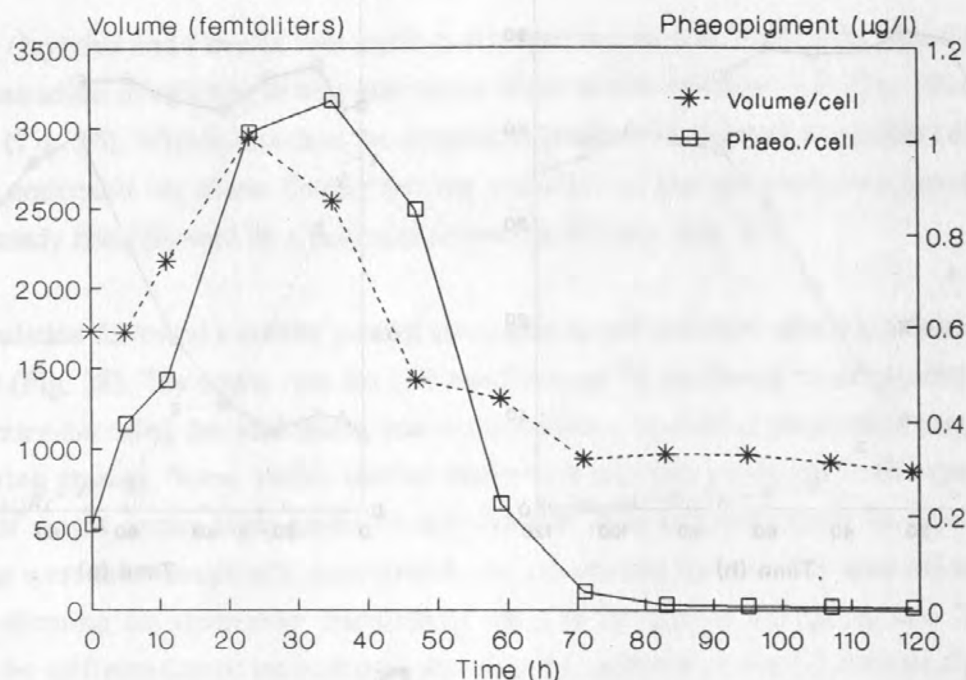


Fig. 27: Plot of the volume per cell and phaeopigment content per cell for *Oxyrrhis marina* during experiment 3.

Phaeopigment production was calculated for each sampling interval as a percentage of the total chl *a* decrease on a molar basis using the formula

$$\% \text{ Phaeopigment} = \frac{[PP]_t}{[\text{Chl } a]_0 - [\text{Chl } a]_t} * 100$$

where $[PP]_t$ is the phaeopigment concentration at time t,
$[\text{Chl } a]_0$ is the initial chl *a* concentration and
$[\text{Chl } a]_t$ is the molar chl *a* concentration at time t,
and was relatively constant in all experiments at between 2 and 6 % (Fig. 31).
In expt. 1, 2 & 3 phaeopigments were further degraded to colourless residues not detectable by HPLC, and by 100 hours phaeopigments had almost completely disappeared. A similar pattern of phaeopigment buildup was seen in expt. 4, but the experiment was terminated before a decrease in phaeopigment concentrations could be observed.

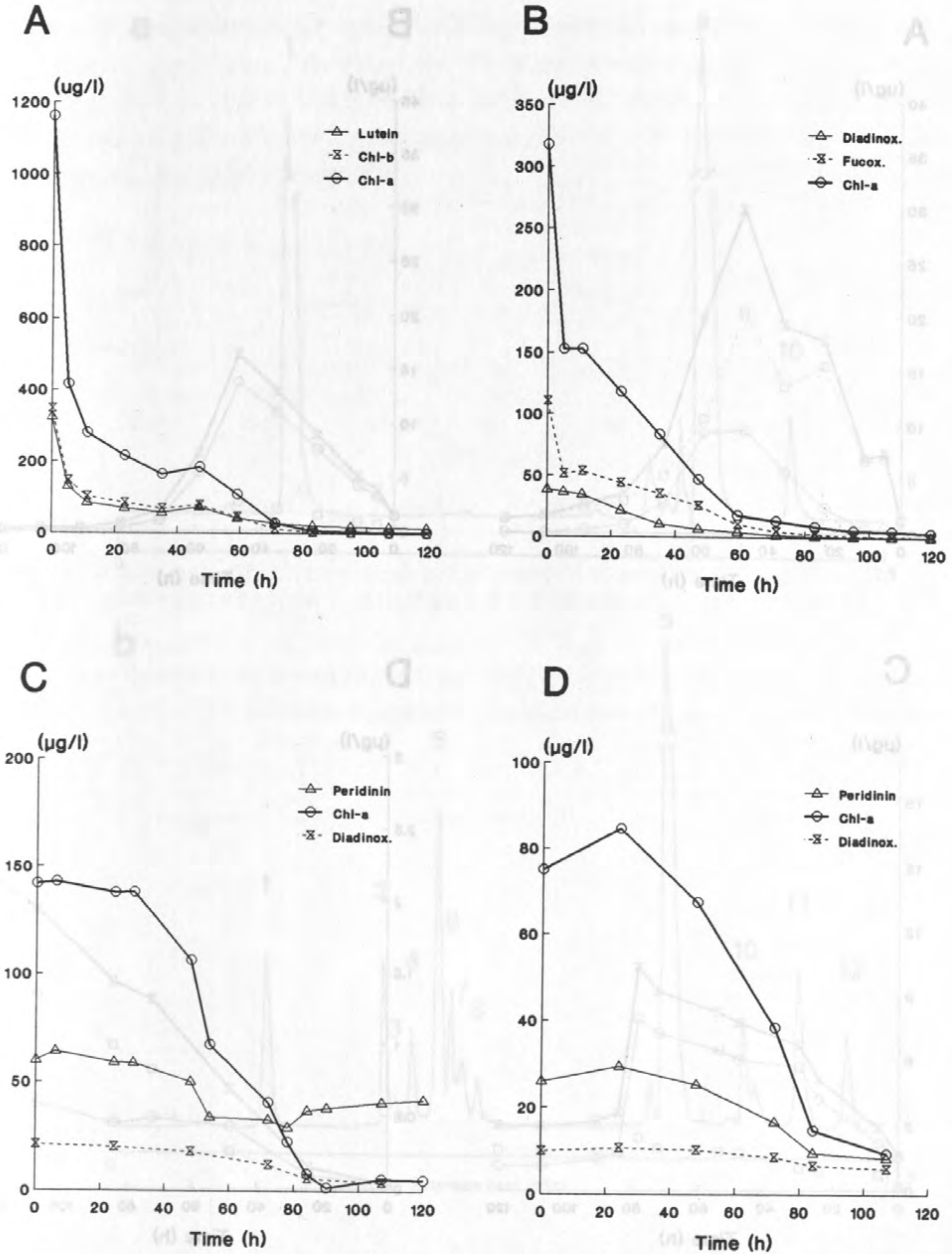


Fig. 28: Attrition of chlorophyll *a* and major accessory pigments in experiments 1 to 4, (A) to (D) respectively.

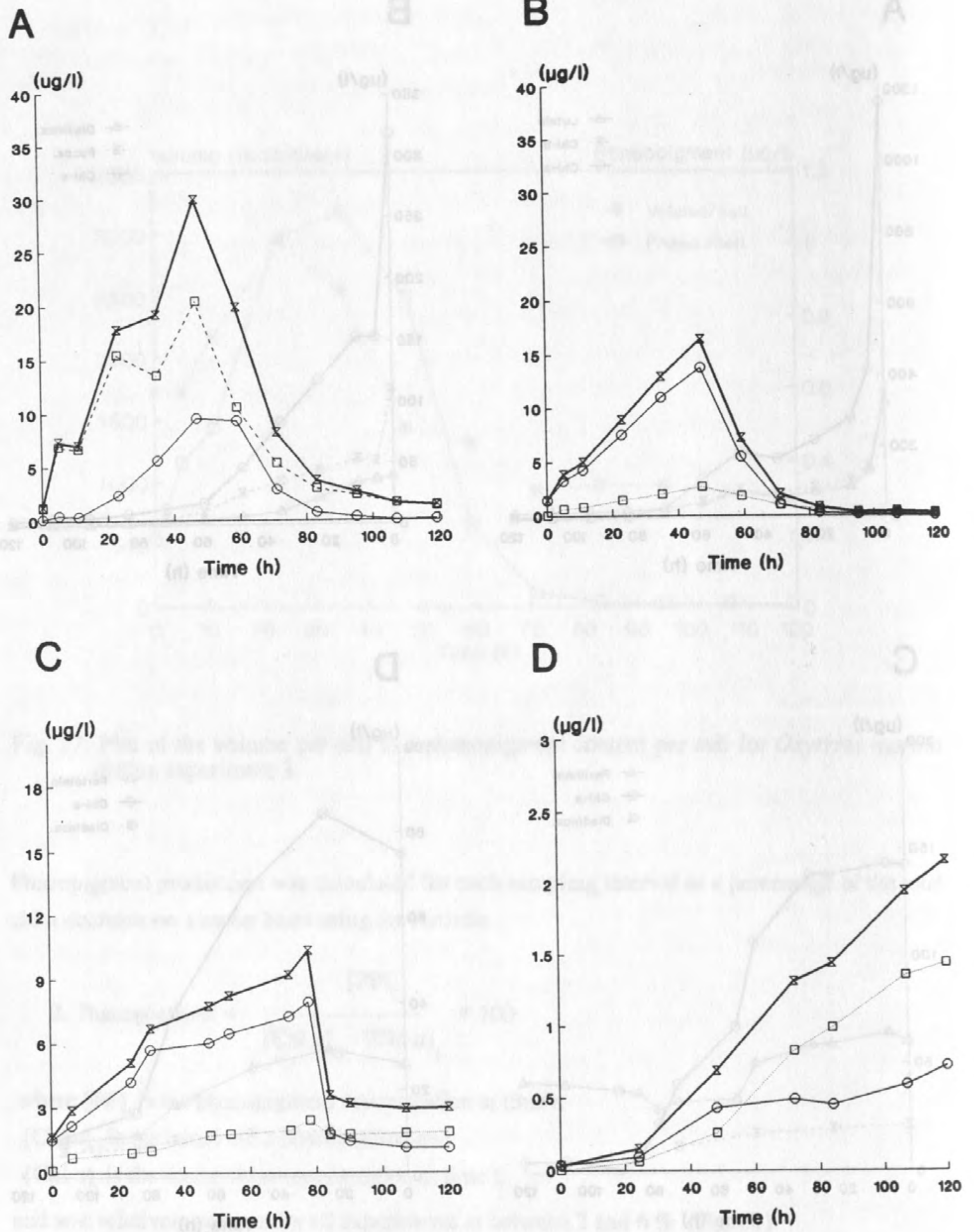


Fig. 29: Phaeopigment production during experiments 1 to 4, (A) to (D) respectively. Dashed line: phaeophorbide *a* and phaeophorbide *a* - like pigments, solid line: phaeophytin *a* and phaeophytin *a* - like pigments, bold line: total pigments.

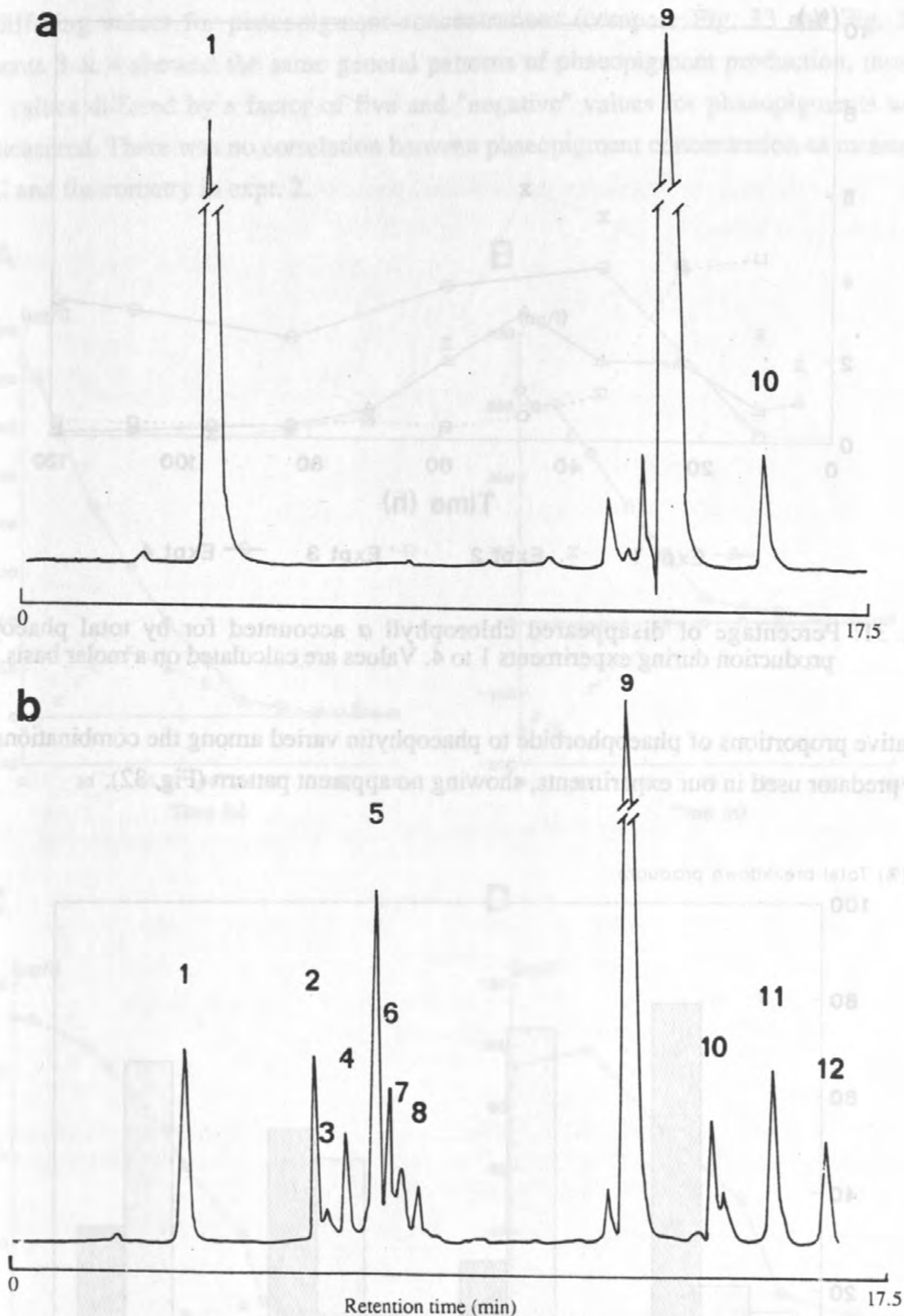


Fig. 30: Fluorescence chromatograms at 0 hours (A) and 120 hours (B) of experiment 4. Peaks are identified as follows: **1**, Chlorophyll c_1c_2 ; **2**, Phaeophorbide *a*; **3**, Phaeophorbide *a*-like 1; **4**, Phaeophorbide *a*-like 2; **5**, Phaeophorbide *a*-like 3; **6**, Phaeophorbide *a*-like 4; **7**, Phaeophorbide *a*-like 5; **8**, Phaeophorbide *a*-like 6; **9**, Chlorophyll *a*; **10**, Phaeophytin *a*; **11**, Phaeophytin *a*-like 1; **12**, Phaeophytin *a*-like 2.

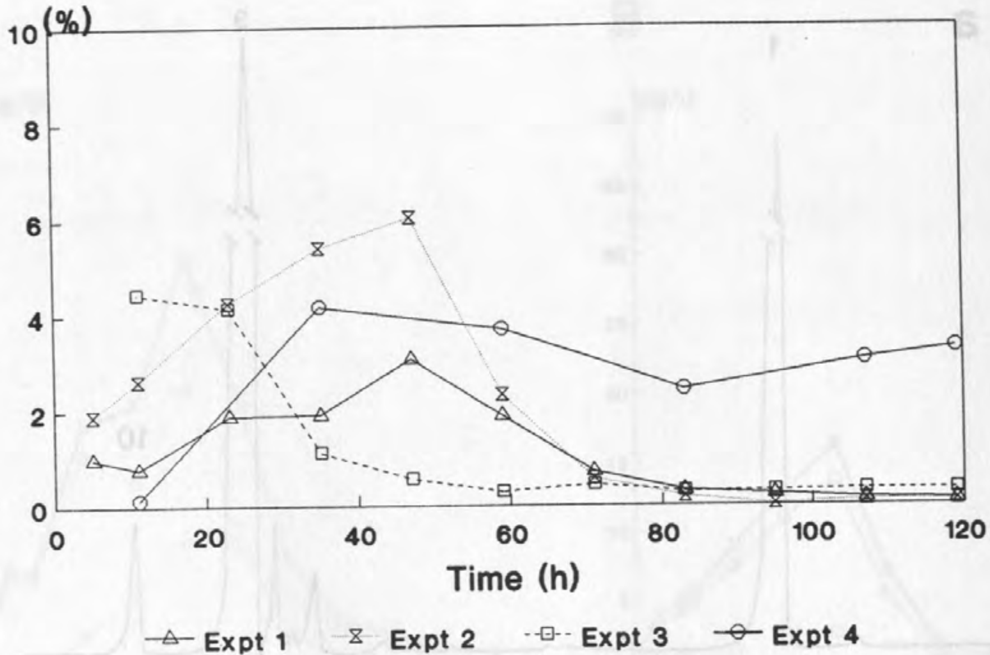


Fig. 31: Percentage of disappeared chlorophyll *a* accounted for by total phaeopigment production during experiments 1 to 4. Values are calculated on a molar basis.

Relative proportions of phaeophorbide to phaeophytin varied among the combinations of prey and predator used in our experiments, showing no apparent pattern (Fig. 32).

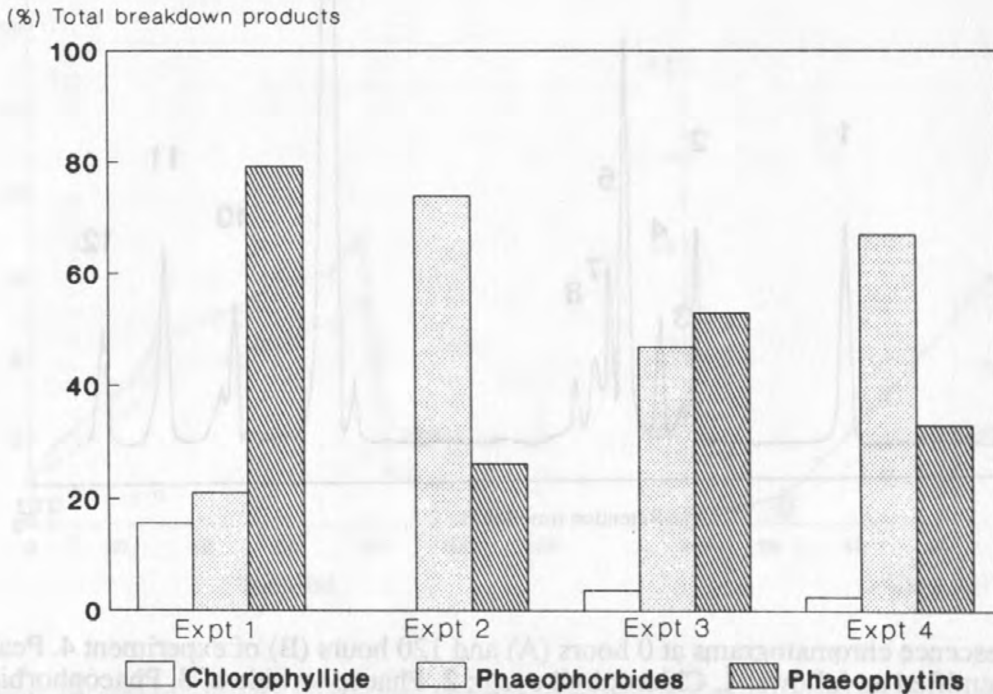


Fig. 32: Relative proportions of individual degradation products expressed as a percentage of total breakdown products.

Fluorometric measurements agreed with HPLC analysis of chl *a*, but the two techniques gave widely differing values for phaeopigment concentrations (compare Fig. 33 and Fig. 28). Experiments 3 & 4 showed the same general patterns of phaeopigment production, though absolute values differed by a factor of five and "negative" values for phaeopigments were always measured. There was no correlation between phaeopigment concentration as measured by HPLC and fluorometry in expt. 2.

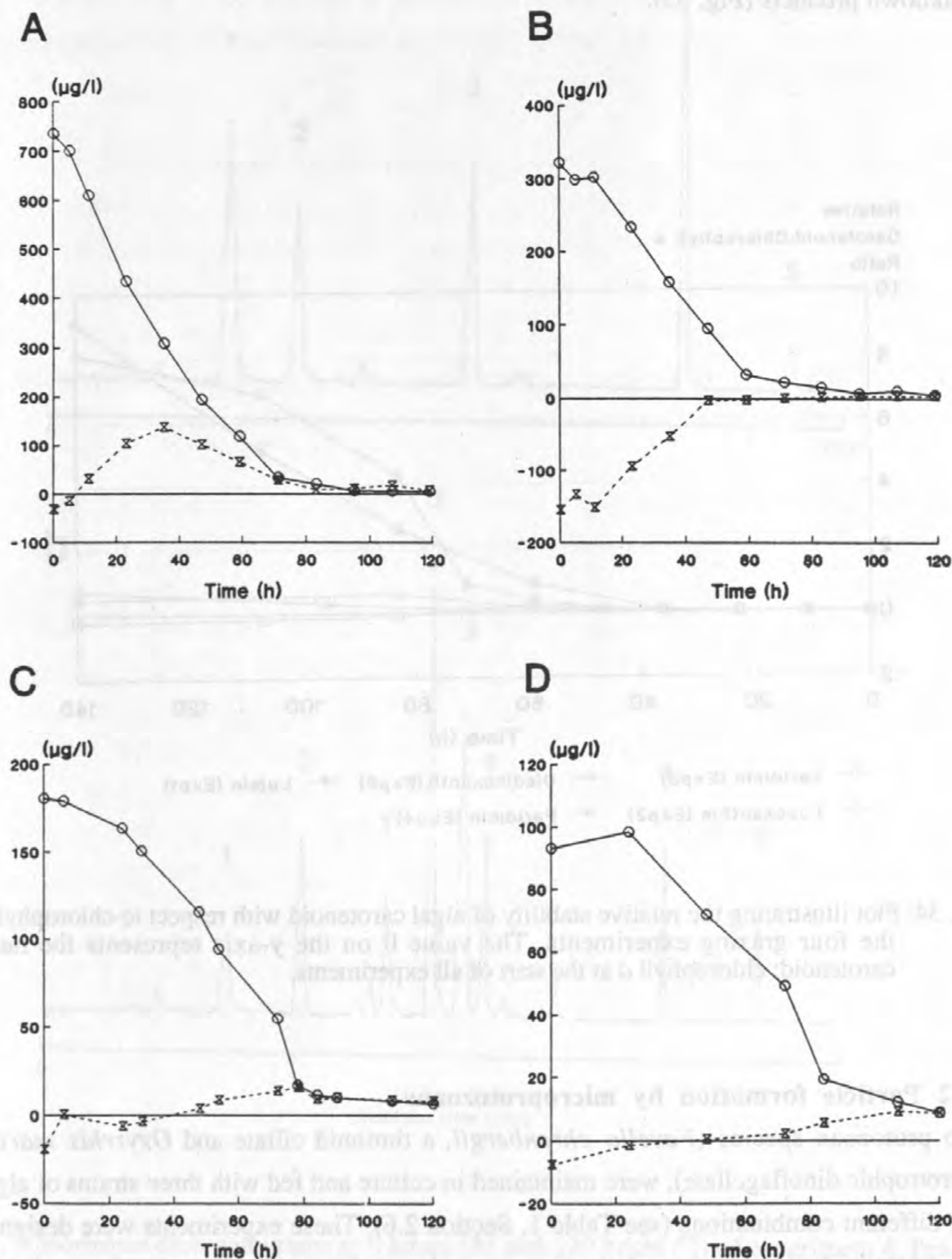


Fig. 33: Fluorometric determinations of chlorophyll *a* (solid line) and chlorophyll *a* - equivalents (dashed line) in experiments 1 to 4, (A) to (D) respectively.

The disappearance of accessory pigments deviated from rates of degradation of chl *a* in experiments 1 and 3 (Fig. 34). Initial rates of disappearance (0 - 6 h) were parallel for all pigments. Relative proportions of diadinoxanthin and lutein subsequently increased, indicating that these were broken down more slowly than chl *a*. These pigments accumulated in the guts of herbivores till termination of the experiments. Absorbance chromatograms during these experiments showed the production of additional peaks which may be attributable to carotenoid breakdown products (Fig. 35).

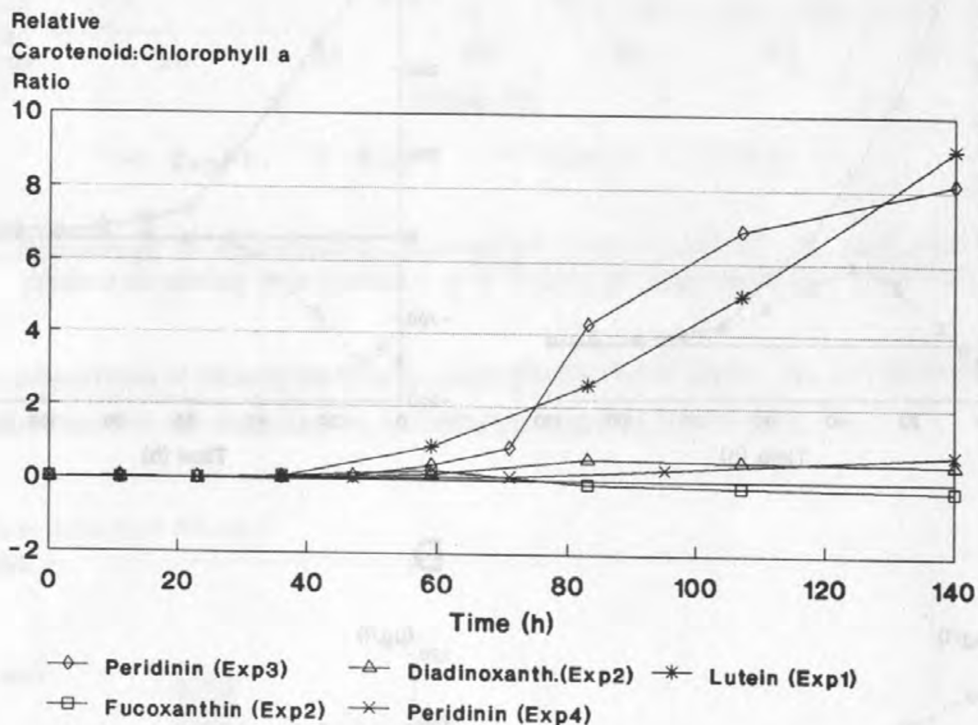


Fig. 34: Plot illustrating the relative stability of algal carotenoid with respect to chlorophyll *a* in the four grazing experiments. The value 0 on the y-axis represents the ratio of carotenoid: chlorophyll *a* at the start of all experiments.

3.3.2 Particle formation by microprotozoans

Two protozoan species (*Favella ehrenbergii*, a tintinnid ciliate and *Oxyrrhis marina*, a heterotrophic dinoflagellate), were maintained in culture and fed with three strains of algae in four different combinations (see Table 1, Section 2.6). These experiments were designed to investigate both pigment degradation (reported above) due to protozoan grazing and particle formation by the grazers in the form of faecal pellets or aggregates.

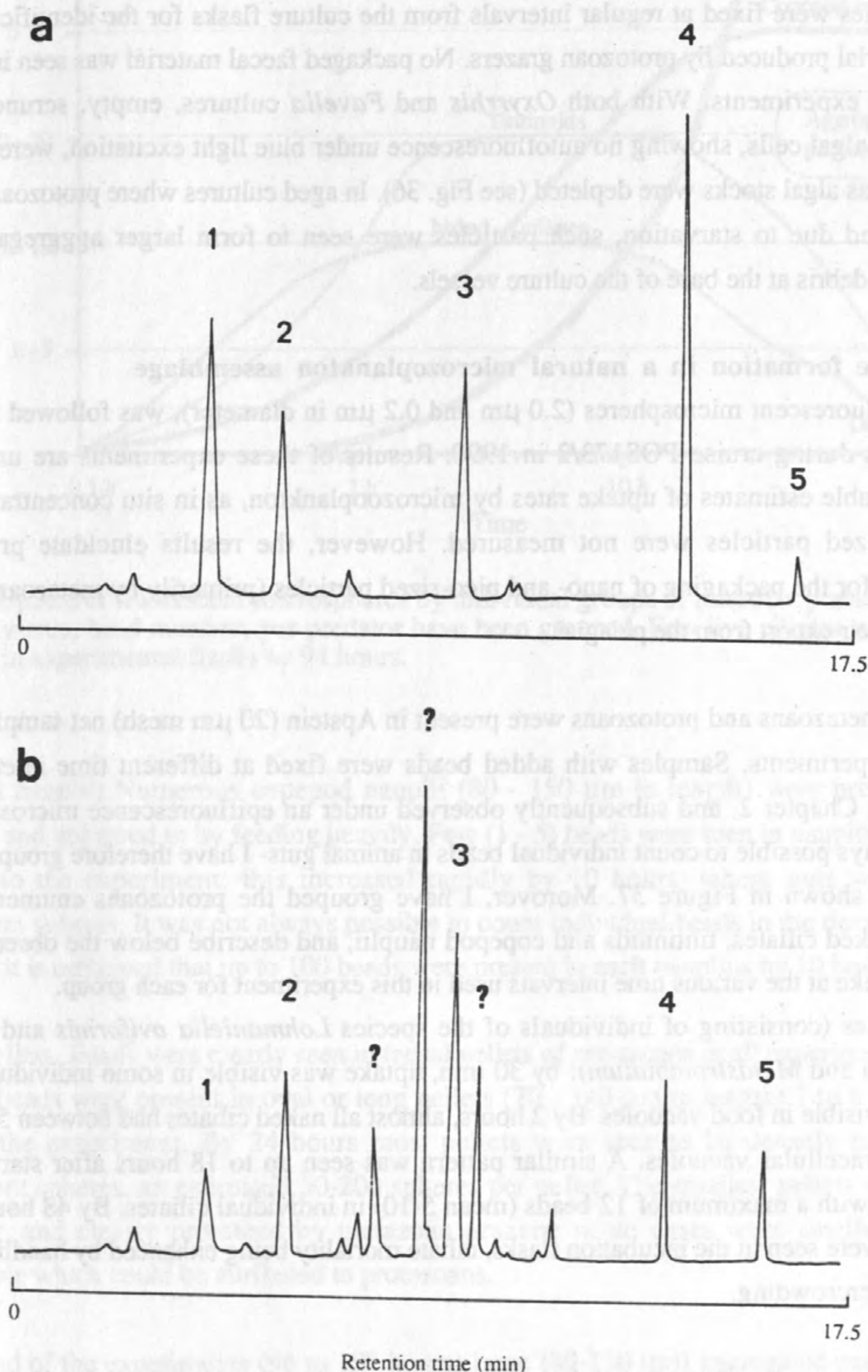


Fig. 35: Absorbance chromatograms at 0 hours (A) and 120 hours (B) of experiment 4. Peaks are identified as follows: **1**, Chlorophyll *c1c2*; **2**, Peridinin; **3**, Diadinoxanthin; **4**, Chlorophyll *a*; **5**, ß-carotene. ? denote unidentified pigments thought to be carotenoid breakdown products.

Ingestion rates were rapid in all cases, with algal stocks being depleted within 48 hours (expt. 1 & 2) to 120 hours (expt. 4). There was little visible accumulation of faecal material during this time. Samples were fixed at regular intervals from the culture flasks for the identification of faecal material produced by protozoan grazers. No packaged faecal material was seen in any of the grazing experiments. With both *Oxyrrhis* and *Favella* cultures, empty, scrunched-up frustules of algal cells, showing no autofluorescence under blue light excitation, were seen to accumulate as algal stocks were depleted (see Fig. 36). In aged cultures where protozoan stocks were reduced due to starvation, such particles were seen to form larger agggregates and appeared as debris at the base of the culture vessels.

3.4 Particle formation in a natural microzoplankton assemblage

Uptake of fluorescent microspheres (2.0 µm and 0.2 µm in diameter), was followed in three experiments during cruise POS173/2 in 1990. Results of these experiments are unable to provide reliable estimates of uptake rates by microzooplankton, as in situ concentrations of similarly sized particles were not measured. However, the results elucidate processes responsible for the packaging of nano- and pico-sized particles (primarily by metazoans), thus leading to their export from the pelagial.

Numerous metazoans and protozoans were present in Apstein (20 µm mesh) net samples used for these experiments. Samples with added beads were fixed at different time intervals as described in Chapter 2, and subsequently observed under an epifluorescence microscope. It was not always possible to count individual beads in animal guts- I have therefore grouped bead numbers as shown in Figure 37. Morover, I have grouped the protozoans enumerated as followes: naked ciliates, tintinnids and copepod nauplii, and describe below the observations for bead uptake at the various time intervals used in this experiment for each group.

Naked ciliates (consisting of individuals of the species *Lohmaniella oviformis* and genera *Strombidium* and *Metastrombidium*): by 30 min, uptake was visible in some individuals, 1-5 beads were visible in food vacuoles. By 2 hours, almost all naked ciliates had between 5 and 10 beads in intracellular vacuoles. A similar pattern was seen up to 18 hours after start of the experiment, with a maximum of 12 beads (mean 5-10) in individual ciliates. By 48 hours, few living cells were seen in the incubation flasks, ciliate mortality being enhanced by handling and, possibly, overcrowding.

Tintinnids (primarily represented by *Acanthostomella norvegica, Parafavella* sp. and *Ptychocylis obtusa*): tintinnids showed a similar pattern of bead uptake as naked ciliates, although the number of ingested beads was larger (15 - 20) 3 hours after start of the experiment. Tintinnid mortality was high 2 to 3 days after start of the experiment, and numbers approached zero by 4 days.

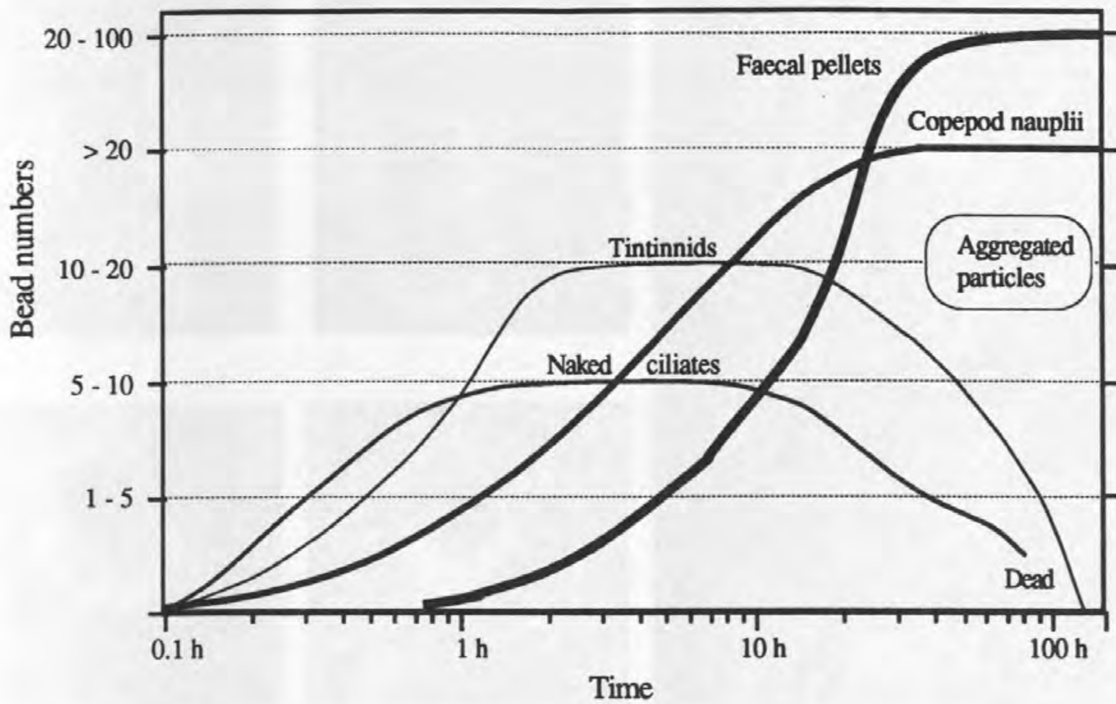


Fig. 37: Uptake of fluorescent microspheres by individual groups of microzooplankton. On the y-axis, bead numbers per predator have been grouped. Few live ciliates were present in experimental flasks by 94 hours.

Copepod nauplii: Numerous copepod nauplii (80 - 150 µm in length) were present in the samples, and appeared to by feeding heavily. Few (1 - 5) beads were seen in nauplii guts 3 to 4 hours into the experiment: this increased rapidly by 10 hours, where guts were full of fluorescent spheres. It was not always possible to count individual beads in the densely packed guts, but it is estimated that up to 100 beads were present in each nauplius by 10 hours.

Faecal pellets: Beads were clearly seen in faecal pellets of metazoans in all experiments. A few (5 - 15) beads were present in oval or long pellets (70 - 140 µm in length) 7 to 8 hours after start of the experiment. By 24 hours most pellets were seen to be densely packed with fluorescent spheres, an estimated 50-200 spheres per pellet. The smallest pellets were ca. 40 µm long, and clearly produced by metazoan grazers; in no cases were smaller particles identifiable which could be attributed to protozoans.

At the end of the experiments (96 to 107 hours) large (80-150 µm) aggregated particles were seen in the experimental flasks, containing phytoplankton and debris. Attached to these particles were numerous beads of both diameters (2 and 0.2 µm). It is presumed that these particles were formed by the clumping of senescent and damaged algal cells, and that the beads observed on their surface were attached by adhesion.

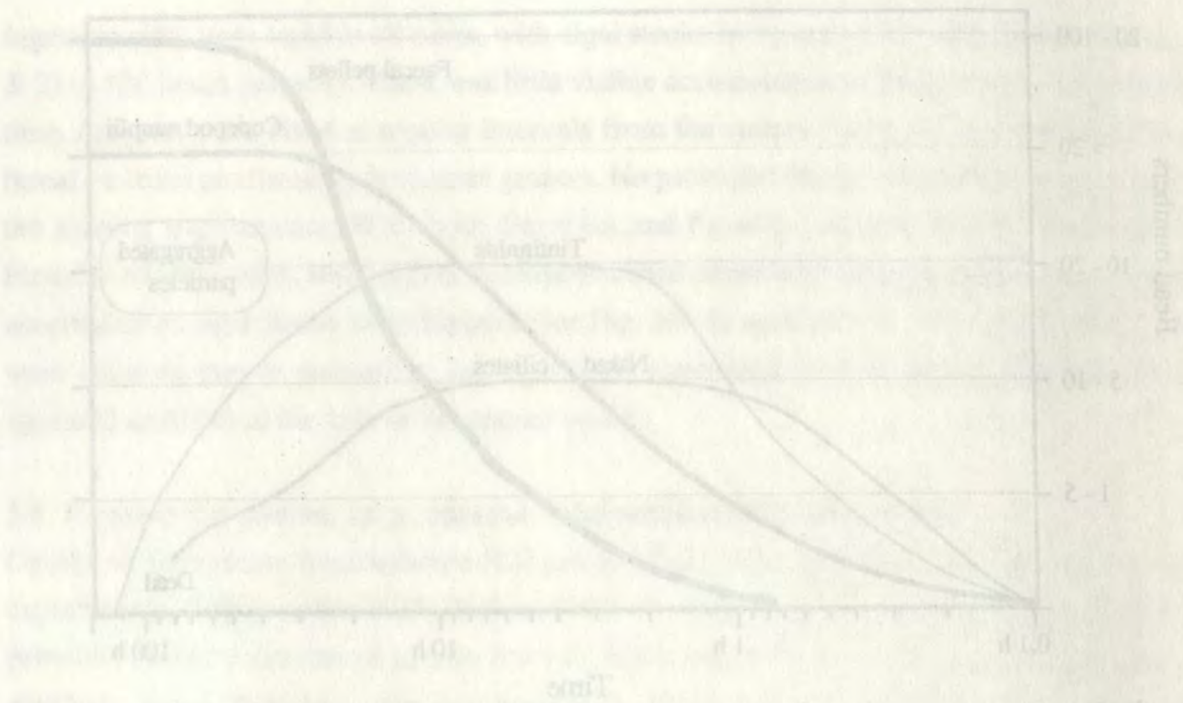


Fig. 36: **Light micrographs of laboratory cultures (a to e) and natural samples (f to j).**
Scale bars 20 µm. All samples were fixed with formaldehyde to a final concentration of 4%.

a) to d) Loricae of differing forms built by individuals of the same strain of tintinnid, *Favella ehrenbergii*.

c) the cell body of the tintinnid is present inside the lorica.

e) Detrital material formed by feeding of *Favella ehrenbergii* on the thecate dinoflagellate *Heterocapsa triquetra*. Coloured cells are healthy algae; empty frustules, such as those indicated by arrows, were the only visible faecal material produced by grazing of *Favella ehrenbergii*.

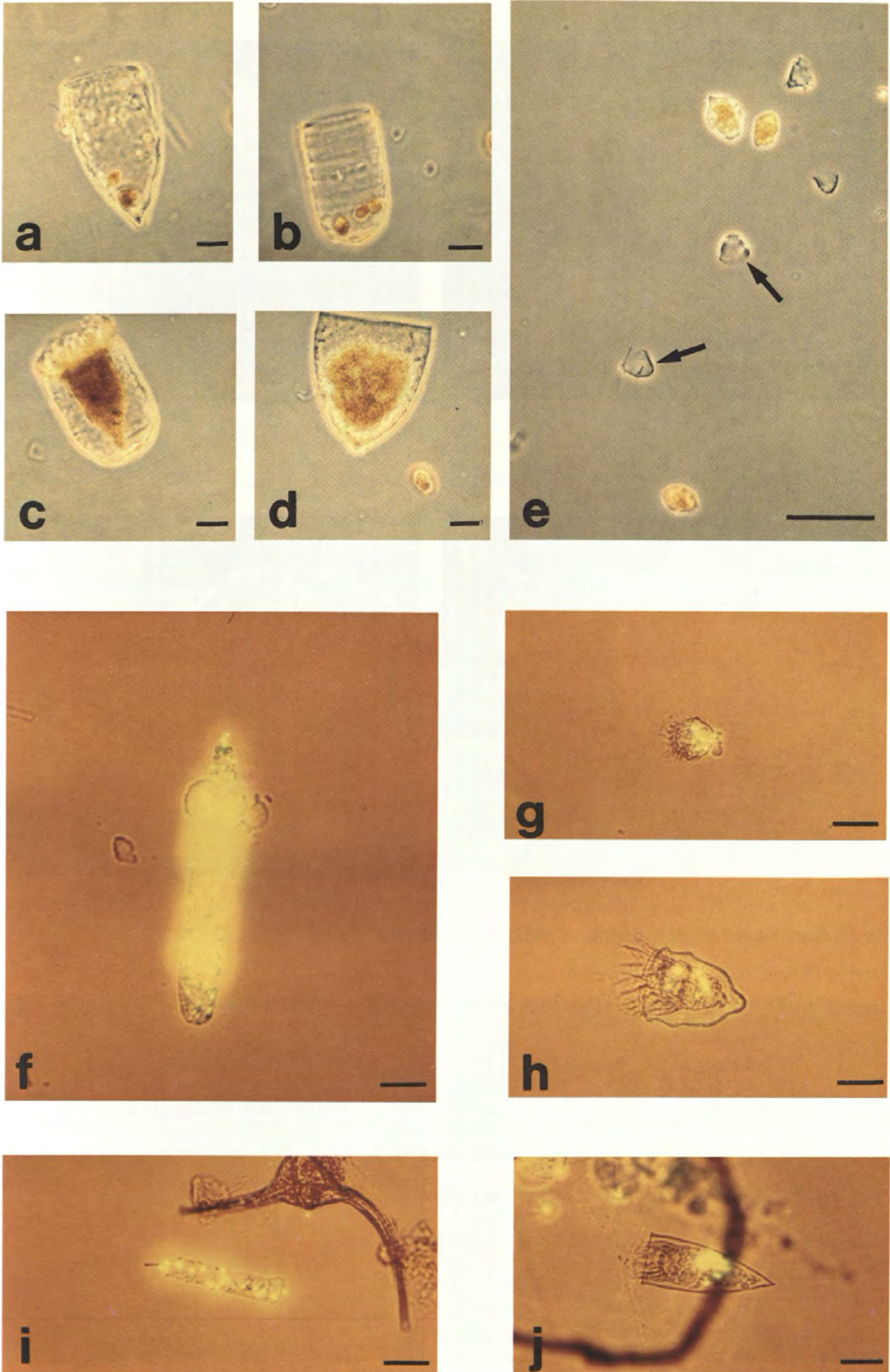
Fluorescent beads seen under UV-excitation in faecal pellets and protozoan food vacuoles are seen in f) to j).

g) Naked ciliate of the genus Strombidium with ca. 10 beads in food vacuoles (48 hours after addition of beads).

h) Tintinnid ciliate of the species *Ptychocylis obtusa* (48 hours after addition of beads).

j) Tintinnid ciliate of the genus Parafavella (48 hours after addition of beads).

f) and i) Faecal pellets of metazoan microzooplankton (small copepods and copepod nauplii), 107 hours after addition of beads (f) and 72 hours after addition of beads (i).


a
b
c
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j

3.5 Microscopy of sediment trap material

Light and scanning electron microscopy were used to enumerate protozoans in the water column and their remains in sediment trap samples. The appendix lists the common forms of naked ciliates and tintinnids in the water column. In some cases a precise identification to the species level was not possible in iodine-stained samples, and tintinnids present a special problem. In laboratory experiments with the tintinnid *Favella ehrenbergii*, various forms of loricae were seen in individual cells of the same species (Fig. 36 a to d). Morover, cells that had lost their lorica were no longer identifiable on the basis of iodine stains. In natural samples, many empty loricae of various forms were found, and often the cell body left its shell due to the shock inherrant in fixation. Caution is therefore advised in the identification of protozoans in natural samples.

Although light microscopy gives a quantitative view of sedimentation patterns, electron microscopy is indispensible in the detail of information it provides about the qualitative forms that this sedimenting material takes. The primary transport mechanism of tintinnids to deeper waters appears to be as individually sinking loricae, which are visible using light microscopy in trap samples. A second transport mechanism of these hard parts, in the faecal pellets of metazoan grazers, was evident in scanning electron microscopic pictures (Fig. 38 b). Many faecal pellets between 100 and 300 μm in length were seen to have tintinnid loricae visible through their membranous covering.

The production of faecal pellets by protozoan grazers has been the subject of some controversy in recent years, and will be dealt with in Section 4.6 below. In general, the size of faecal material has been taken to be indicative of its origin, leading to the proposal that pellets smaller than ca. 80 μm are produced by protozoans. Such small pellets, 10 to 80 μm in size, were often seen to be numerous in sediment trap material. Some of these pellets are shown in Figure 38 (c to f), and are seen to be densely packed with diatom and coccolithophorid remains.

3.6 Microzooplankton sedimentation

Both annual moorings, short term moorings and multiple drifting sediment trap arrays were deployed during the time of this study in both years. For the purposes of this work, however, the annual mooring in the East Greenland Sea, and drifting trap arrays below the euphotic zone, where water column parameters were measured daily, will be considered.

3.6.1 Annual sedimentation patterns

The position of the annual mooring deployed from 5.9.1988 to 27.6.1989 is shown in Figure 1 on page 4. Due to malfunction of various moored traps, data are only available from 500 m water depth. Seasonal patterns of sedimentation were apparent in terms of dry weight and POC content of collected material, with maximum sedimentation rates during May 1989. The

composition of this sedimentation pulse was reflected partly in the particulate silica (PSi) values of collected material (Puch 1990), as being largely composed of diatomaceous material. It is possible, from a view of the yearly sedimentation profile, that, on our arrival at the site in June 1989, a sedimentation event dominated by a pulse of diatoms, had recently taken place.
Annual patterns of tintinnid sedimentation were similar to those for dry weight, except for the absence of a large peak in May 1989 (Fig. 39). Highest values of tintinnid sedimentation were reached during September. Due to low light levels at 72°N at this time of the year, autotrophic growth in the pelagial would be low, and herbivorous activity may be a dominating trophic activity.

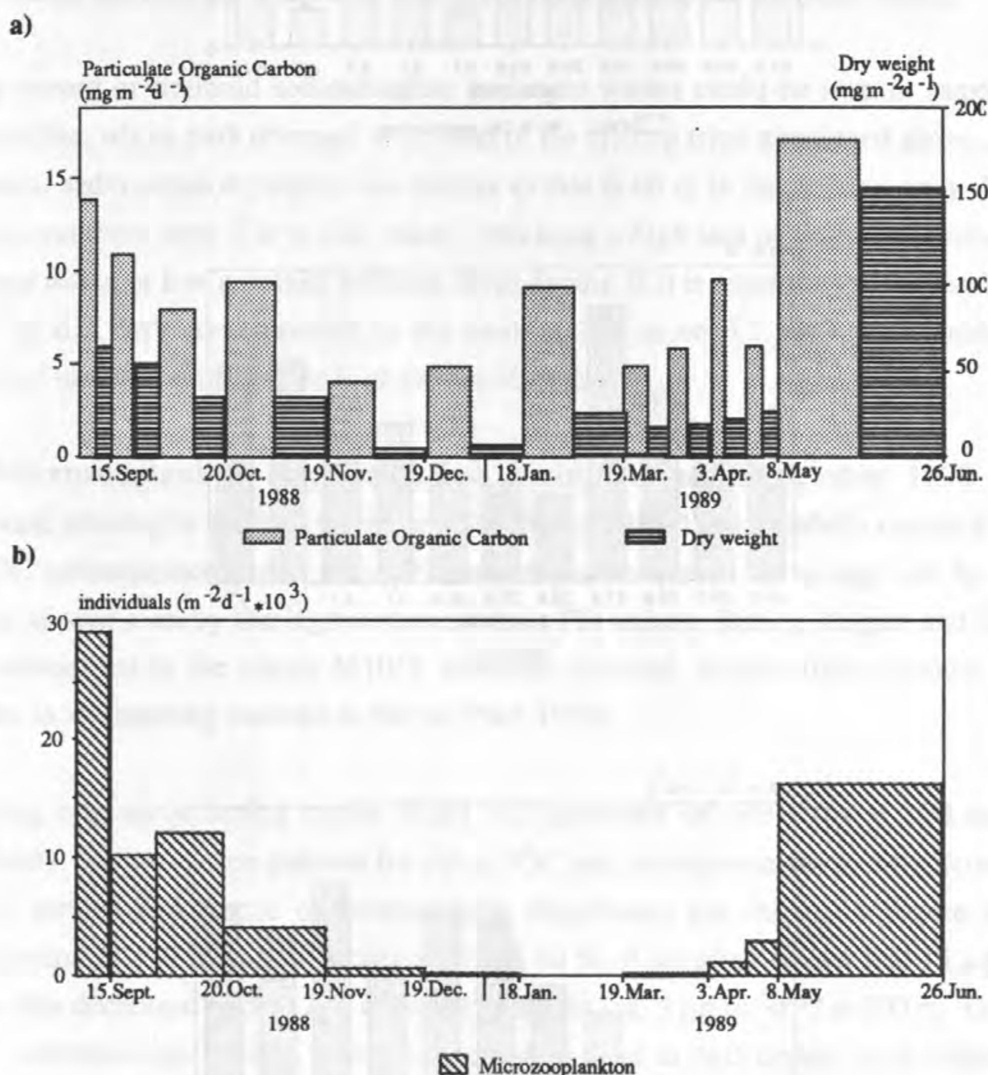

Fig. 39: Annual sedimentation patterns of particulate organic carbon and dry weight (a), and microzooplankton number (b) at 500 m in the annual mooring in the East Greenland Sea between 5.8.1988 and 26.6.1989. Bar width corresponds to the duration of sampling intervals.

3.6.2 Microzooplankton sedimentation during June/July 1989

Drifting sediment traps at 60 m, above which daily water column measurements were conducted, gave a fine temporal resolution of tintinnid sedimentation rates. These results, together with those for daily sedimentation of chl *a* and POC, are shown in Fig. 40.

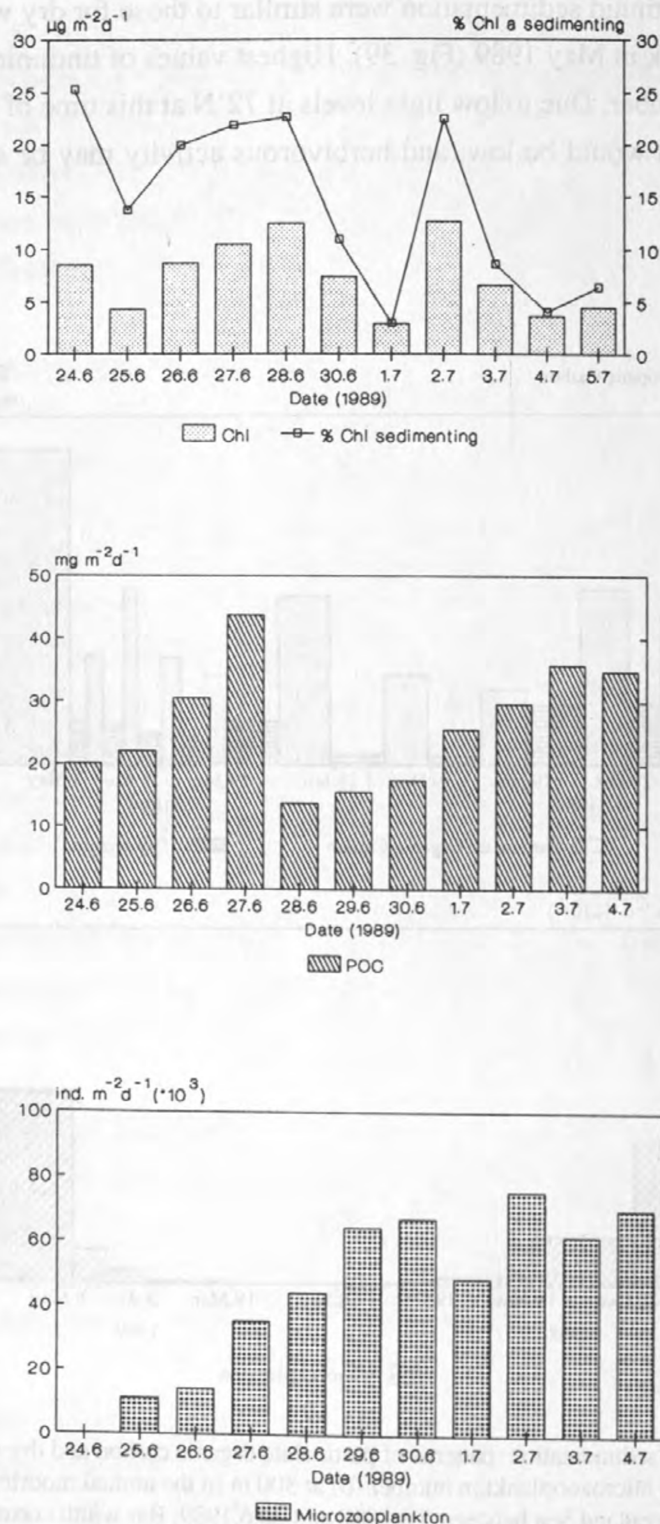

Fig. 40: Daily sedimentation patterns of Chlorophyll *a* (a), Particulate Organic Carbon (b), and Microzooplankton (c), in the drifting sediment trap at 60 m during June/July 1989.

Chl *a* sedimentation appeared to differ between the first and second half of the drift experiment. During the first half, between 15 and 25 % of chl *a* standing stocks (0 - 60 m) reached the trap at 60 m. This fell to 3 % on 3.7.1989 and, with the exception of high percentual sedimentation on 6.7.1989, remained between 5 and 10 % of overlying standing stocks. Particulate silica values in these traps, as indicative of diatomaceous material, showed no particular trend during this time (Puch 1990), with the exception of a peak in values on 1.7.1989, and a decrease during the end of the drift period. POC sedimentation was higher during the first half of the experiment (average $30*10^3$ µg m^{-2}), fell on 3.7.1989 to $13*10^3$ µg m^{-2}, and then rose again to initial values. The sedimentation of tintinnids in this drifter showed a clear trend, increasing from an initial 12,000 ind. m^{-2} to 70,000 ind. m^{-2} towards the end of the experiment. Distinct phases within this time, as seen in the profiles of other parameters were not visible.

A daily record of tintinnid sedimentation to deeper waters could be seen in samples of the second drifter, whose path diverged somewhat of the drifting traps mentioned above. At 100 m, the general sedimentation pattern was similar to that at 60 m in the drifting array. By 300 m, however, numbers were 5 to 6-fold lower, indicating a high loss of tintinnid numbers (either the empty lorica or live animals) between these depths. If it is assumed that the peak reaching 300 m on 6.7.1989 corresponded to the peak at 100 m on 3.7.1989, this yields a rough estimate of tintinnid sinking speeds of around 70 m day^{-1}.

3.6.3 Microzooplankton sedimentation during August/September 1990

The annual mooring in the East Greenland Sea during 1989-1990 showed a repeated pattern of high POC sedimentation during May 1990, which was accounted for in large part by a pulse of diatoms, as was seen by the high concommittant PSi values. During August and September 1989, subsequent to the cruise M10/3, siliceous material, largely from diatoms, was also dominant in sedimenting material at 500 m (Puch 1990).

A drifting trap array during cruise POS173/2 consisted of two traps at 100 and 300 m respectively. Sedimentation patterns for chl *a*, POC and microprotozoan remains (consisting of tintinnid loricae and thecae of heterotrophic flagellates) are shown in Figure 41. Chl *a* sedimentation at 100 m varied between 10 and 40 % of standing stocks (ca. 15 µg $m^{-2}d^{-1}$), whereas this decreased to 3 - 12 % of standing stocks (ca. 5 µg $m^{-2}d^{-1}$) at 300 m. The profiles of POC sedimentation showed a relatively constant trend in both depths, with slightly higher average values in 300 (30,685 µg $m^{-2}d^{-1}$) than in 100 m (29,714 µg $m^{-2}d^{-1}$). This anomaly was repeated in the pattern of tintinnid sedimentation, where numbers in 300m were an astonishing factor of three higher (average 312,687 ind. $m^{-2}d^{-1}$) than at 100m (average 95,940 ind. $m^{-2}d^{-1}$). This feature may be explained in terms of a patchy distribution of tintinnids in the pelagial, where sub-populations were intercepted by the traps in the two depths.

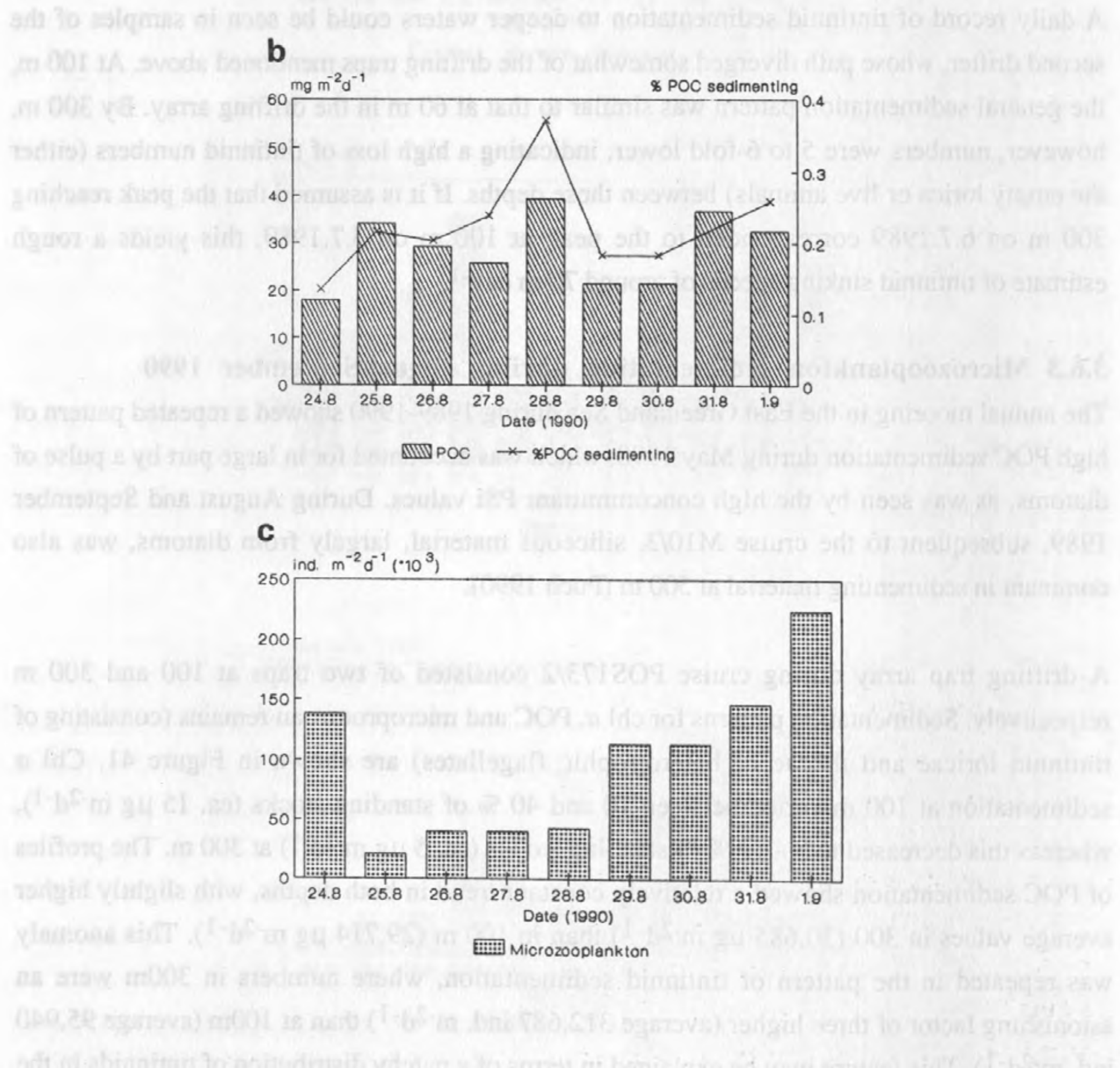

Fig. 41: Daily sedimentation patterns of Chlorophyll *a* (a), Particulate Organic Carbon (b) and Microzooplankton (c) in the drifting sediment trap at 100 m during August/September 1990.

4. DISCUSSION

4.1 Microzooplankton distribution and species composition

The term microzooplankton is operationally defined as that part of the total zooplankton between 20 µm and 200 µm in size (Sieburth et al. 1986), and has been used in this context in the present study. Zooplankters within this size fraction constitute a diverse assemblage, including metazoans (such as larval, naupliar and other developmental stages of crustaceans) and protozoans (primarily ciliates and heterotrophic dinoflagellates). The relative contribution of these members to total microzooplankton numbers and biomass can differ widely both spatially and temporally. Basic differences in morphology, life cycles and pelagic activity among the individual groups must be taken into account in consideration of the trophic role of the entire microzooplankton community.

In the present study protozoans were seen to be the most dominant members of the microzooplankton assemblage, although copepod nauplii were present in August/September 1990. In the following discussion the term microprotozoans shall be used to denote protozoans (ciliates and heterotrophic flagellates) between 20 and 200 µm in size (with the exception of some small ciliates ca. 15 µm in diameter.) Although larger protozoans, such as foraminifera, acantharia and radiolaria, have been included by some authors among the microzooplankton (Beers and Stewart 1971), I have excluded them on the basis of their size and inability to pass through a 200 µm mesh. These forms can be amply present in the East Greenland Sea, and have been dealt with in other studies (Bock 1990, Antia et al. manuscript). At the lower end of the scale, nano- and pico-heterotrophs are also known to contribute to herbivory in the pelagial; they have, however, not been enumerated in this study (again with the exception of some small ciliate species ca 15 µm in diameter).

With improved techniques for sampling, preservation and enumeration of microprotozoans, their abundance and distribution has been shown to be ubiquitous in the worlds´ oceans, establishing them as dominant members of pelagic food webs. In general, the abundance of microzooplankton in the euphotic zone shows a decreasing trend with higher latitudes, whereas coastal and nearshore waters have higher abundances than those encountered in the open ocean.

Few data exist, however, on microzooplankton numbers in Arctic waters and the Greenland Sea, and an intercomparison of available data is complicated by the differences in sampling methods used and species spectrum enumerated. Paranjape (1988) summarizes some of the literature on microzooplankton biomass in polar regions, with values of between 1 to 10 µg C dm^{-3}, which show good agreement with this study.

Two recent studies dealing with ciliated protozoa, with an emphasis on mixotrophic forms, in the East Greenland Sea (Auf dem Venne 1990, Putt 1990) provide data on species spectra that are comparable to those found in this study. Among the naked oligotrichs in the above mentioned studies, many species were also found in the course of this investigation, notably *Strombidium dalum, S.compressum, S.delicatissium, S. capiitatum, Laboea strobila, and Laboea* spp., suggesting that these may be indigenous to this region. Auf dem Venne (1990), in a study of auto-, mixo- and heterotrophic ciliates in open water and at the ice edge off the coast of Greenland, found maximum ciliate numbers of 3,000 individuals dm^{-3} during late spring in surface waters, dominated by heterotrophic oligotrich ciliates. Putt (1990), concentrating on chlorophyll-containing ciliates in the Iceland/Greenland Sea during July/August 1988, found ciliate numbers of around 820 ind. dm^{-3} in surface waters, of which ca. 50 % were plastidic (or mixotrophic) forms.

Mixotrophy in ciliated protozoa has been suspected since the early works of Lohmann (1908) and Faure-Fremiet (1969), but has only recently received renewed attention as an alternative mode of nutrition in heterotrophic protozoa. The ability of phagotrophic protozoans to sequester chloroplasts from their algal prey has been demonstrated in an ever increasing number of species both in laboratory (Laval-Peuto et al. 1986, Stoecker et al. 1987, Jonsson 1987, Laval-Peuto and Rassoulzadegan 1988, Stoecker and Silver 1990, Stoecker and Michaels 1991) and field (Putt 1990) populations. Table 5 lists these species, from which it is evident that many of the forms found in the course of this study are potentially mixotrophic in nature. Photosynthesis by the sequestered chloroplasts, however, cannot provide phagotrophic protozoans with sufficient nutrition to support their growth (with assimilation rates of 0.8 - 2.8% body C h^{-1}; Stoecker 1989, Putt 1990), but provides such forms with a means to enhance their chances of survival under suboptimal conditions. These findings open up exciting new possibilities of links within the microbial loop which suggest that pelagic dynamics in this small size fraction could be more complex than previously supposed. Mixotrophy is not considered as a nutritional form in the present study, and is assumed not to have affected estimates of the rates of herbivory and biomass transfer between microzooplankton, their prey and predators, which forms the basis for the present work. With more data on phototrophic phagotrophs, however, it may be necessary to reevaluate their role in oceanic food webs.

During this study naked ciliates dominated over tintinnids in the upper euphotic zone both in summer and autumn in the East Greenland Sea, which is in accordance with reports in the literature for the Arctic regions (Taniguchi 1984, Tibbs 1967, Auf dem Venne 1990). The species composition of tintinnids found in this study, consisting primarily of *Acanthostomella norvegica*, *Ptychocylis* sp. and *Parafavella* sp., and their predominance at the base of the euphotic zone, has similarly been reported in the literature and appears to be a recurrent feature.

MIXOTROPHIC SPECIES	HETEROTROPHIC SPECIES	REFERNCES
Laboea strobila		Blackbourn 1973, McManus & Fuhrman 1986, Jonsson 1987, Stoecker et al. 1987, Dale 1988, Gifford 1988, Putt 1990(b), Stoecker & Michaels 1991,
Str. oculatum		Faure-Fremiet 1969,
Str. reticulum		Jonsson 1987,
	Str. vestitum	Jonsson 1987, Blackbourn et al. 1973,
Str. sp.		Jonsson 1987,
Str. conicum		Jonsson 1987, Stoecker and Michaels 1991,
Str. capitatum		Stoecker and Silver 1990, Stoecker and Michaels 1991,
Str. (Lohmaniella) spiralis		Blackbourn et al. 1973,
	Helicostomella sp.	Jonsson 1987,
Tontonia appendiculariformis		Laval-Peuto et al. 1986,
	Tintinnopsis tubulosa	Blackbourn et al. 1973,
	Tintinnidium mucicola	Blackbourn et al. 1973

Table 5: Tabellation of ciliate species seen to be mixotrophic or strictly heterotrophic, compiled from a review of the literature. Excluded from this list is the autotrophic ciliate *Mesodinium rubrum* which, it has recently be suggested, be included among the phytoplankton (Crawford 1989). *Str.* = *Strombidium*

Tintinnid numbers at high latitudes have been consistantly shown to be lower (20-200 ind. dm^{-3}; Tibbs 1967, Auf dem Venne 1990, Leakey et al. 1988, Stoecker et al. 1989) than in temperate and coastal waters, where they can reach abundances of up to 700 - 2000 $ind.ml^{-3}$ (Dale and Dahl 1987; see also Burkill 1982, Verity 1986). Growth and doubling rates of tintinnid populations are suppressed at low temperatures, and their small reported abundance in Arctic areas has led to the speculation that these species are not indigenous to high latitudes, relying rather on seeding populations from the warmer waters of the Gulf Stream and North Atlantic Current (Taniguchi 1984). Due to their low numbers, and thus negligible grazing impact, tintinnids appeared not to play a major role in the euphotic zone during the investigations presented here. Their significance, however, may lie in their hard shells, or loricae, which are the only remains of the microprotozoan community that are found in sediment trap samples and preserved in the geologic record at the sea bottom (Reid 1981).

Conspicious by their presence in large numbers in this study were heterotrophic dinoflagellates of the genera *Gyrodinium*, *Protoperidinium* and *Dinophysis*, accounting for up to 70% and 40% of the total microzooplankton community in terms of numerical abundance and biomass respectively. These were identified in unfixed natural water samples by their characteristic

brilliant green fluorescence (Lessard and Swift 1986, Carpenter et al. 1991). Although heterotrophic dinoflagellates are known to dominate the protozooplankton biomass in certain coastal and oceanic areas, scant data are available on their role in polar waters. A possible explanation for the abundances reported here may lie with the food preference of heterotrophic dinoflagellates, which are known to be capable of preying upon large diatoms (Jacobson and Anderson 1986), and have been found to be associated with diatom blooms (Taylor 1987, Lessard 1991). During the drift experiment in summer 1989 reported here, diatoms were found to be abundant in the phytoplankton (Arndt 1990), and increased during the latter half of the drift experiment to account for 45 % of phytoplankton biomass. These were dominated by individuals of the genera *Chaetoceros* and *Rhizosolenia*. During this time heterotrophic dinoflagellates were abundantly present among the microzooplankton. A predominance of heterotrophic dinoflagellates following spring blooms has been reported in the Canadian Arctic (Bursa 1961) and Antarctic waters (Lessard and Rivkin 1986, Nöthig and v.Bodungen 1989).

Significantly, diatoms are unsuitable prey items for aloricate ciliates, probably due to the morphological constraints in ingestion of their spines (Verity and Villareal 1986, Stoecker et al. 1986). Heterotrophic dinoflagellates, using pseudopodal extentions or extracellular digestion to overcome this obstacle are thus able to take advantage of an abundant food source unavailable to the ciliates. Morever, by feeding on bacteria, nanoflagellates and even ciliates themselves, heterotrophic dinoflagellates can serve both as competitors and predators within the microzooplankton community. A recent publication (Hansen 1991), documents the ability of dinoflagellates of the genus *Dinophysis*, that can act both as prey and predator of a ciliate. Once again, indications point to the need to investigate loops within the microbial food chain which may modify established concepts of compartmentalised prey-predator dynamics.

The close coupling, both regionally and vertically in the water column between prey organisms and their predators, is a well known feature in the ocean (Napp et al. 1988 a). The maximum in chl *a* concentrations, often corresponding to a maximum in phytoplankton biomass (Cullen 1982) is thought to attract herbivorous zooplankton by its high nutritional content (Napp et al. 1988b). Unlike their crustacean counterparts, which are able to migrate large distances vertically in the water column, microzooplankton are confined to the upper, chl-rich layers of the water, and their abundance at discrete depths within this layer is often seen to be significantly correlated with chl *a* concentrations (Beers and Stewart 1971, Sorokin 1981, Burkill 1982, Taniguchi 1984, Paranjape 1988). During summer 1989 in the East Greenland Sea, where a pronounced maximum in chl *a* concentrations at around 20m was found, correlations of microzooplankton abundance and biomass with chl *a* gave r-values of 0.73 and 0.72 respectively (at 95% confidence limits; see Fig. 42). This, however, is not always the case. During autumn in the following year, when chl *a* concentrations were more evenly distributed

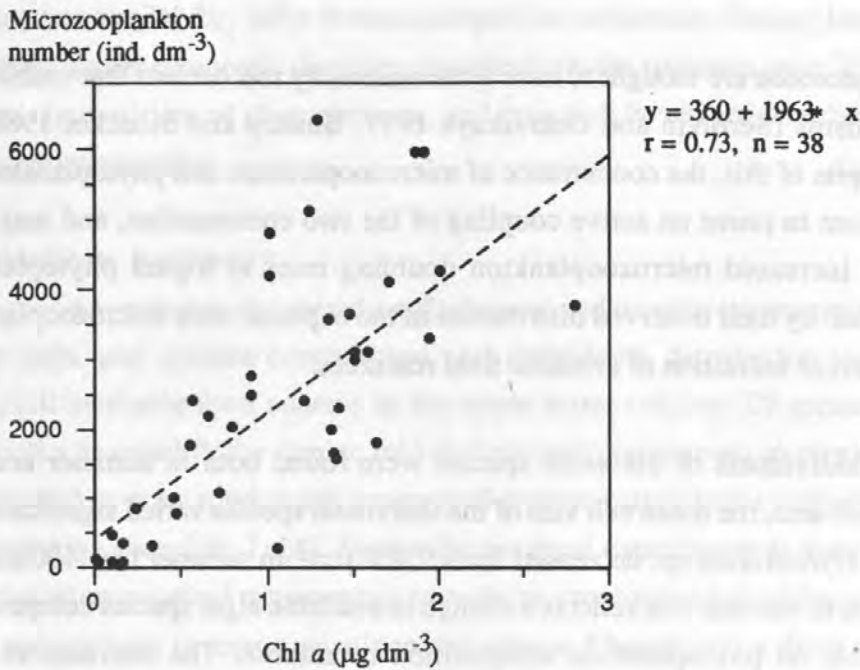

Fig. 42: Linear regression of chl *a* concentrations with microzooplankton numbers. Values were taken from samples at discrete water depths. Included are all samples from the path of the drifting sediment trap array during June/July 1989.

in the upper 100 m, the distribution of microzooplankton was only loosely correlated with chl *a* ($r = 0.29$). In July/August 1988 in the same region, Putt (1990) similarly found no correlation of ciliate occurance with chl *a* concentrations. The concentration of phytoplankton biomass by hydrographic conditions, nutrient and light availability, to the upper layers, and the formation of a distint layer of maximum algal biomass and production (such as seen in 1989), may lead to a better entrainment of their predator populations (the microzooplankton). A less rigid distribution in the water column (such as seen in 1990), would thus be less likely to show good correlation of prey and predator.

The entire spectrum of chlorophyll-containing autotrophs is, however, not available to the microzooplankton community due to the physical constraints mentioned above and may not reliably reflect prey-predator correlations. Naked ciliated protozoa are known to feed selectively on small (2-20 µm) phytoplankton with a preference for dinoflagellates over other taxa (Jonsson et al. 1986, Burkill et al. 1987, see also Section 4.2.3 this study). This has been demonstrated in laboratory studies for many of the species present in this study (e.g. *Strombidium* sp., *Laboea* sp., Jonsson 1986), and indicates that fractionated chl *a* measurements (< 20 µm) may more closely represent available ciliate food sources. During both drift experiments in this study, algae passing through a 10 µm mesh accounted for a large part (60-90%) of total chl *a* values, indicating that a substantial proportion of algal biomass was available as prey for the protozoans.

Predatory protozoa are thought to have a chemosensory mechanism that enables them to detect prey organisms (Serravin and Orlovskaya 1977, Buskey and Stoecker 1988, Sibbald et al. 1988). In spite of this, the concurrance of microzooplankton and phytoplankton biomass alone is insufficient to prove an active coupling of the two communities, and may conceivably be caused by increased microzooplankton doubling rates at higher phytoplankton densities. Nevertheless, by their observed distribution in the euphotic zone microzooplankton are clearly able to optimize utilization of available food resources.

Although individuals of the same species were found both in summer and autumn in the investigation area, the mean cell size of the individual species varied significantly. The average volume of *Gyrodinium* sp. decreased from 9,400 μm^3 in summer to 1,400 μm^3 in autumn. It is unclear as to whether this reflects a change in available algal species composition, as data are not available on phytoplankton composition in autumn. The decrease in cell volume of *Gyrodinium* individuals mentioned above was countered by an increase in mean cell volume of *Laboea* sp. in autumn. *Laboea strobila* had a mean cell volume of 50,000 μm^3 in summer, which increased by 60 % to 82,000 μm^3 in autumn; *Laboea conica* similarly increased in volume from 11,363 μm^3 per cell in summer to 25,338 μm^3 per cell in autumn. The change in body volume of populations of protozoans under conditions of differing food availability has been documented in tintinnid and oligotrich ciliate populations and is clearly seen in the laboratory cultures used in this study (see Section 3.3.1), and it is speculated that a shift in prey spectrum may have lead to this occurence in the field populations encountered here. However, since species and size distribution of algal taxa and food preference of microzooplankton groups was not determined, this remains as yet inconclusive.

A comparison of the entire species spectrum of microprotozoans encountered during summer and autumn reveals an interesting feature; although the same taxa of ciliates and dinoflagellates were encountered in both seasons, the diversity of genera is noticeably greater in autumn. Heterotrophic dinoflagellates, represented almost solely by large individuals of *Gyrodinium* sp. in summer, was more diverse in autumn, with larger numbers of ***Protoperidinium*** and *Dinophysis* sp. present. The number of naked oligotrich ciliate species (primarily *Strombidium* spp.) was also considerably larger in autumn (see Appendix). Whereas 10 species contributed to the microzooplankton community in summer, a total of 21 species were represented in autumn.

A shift towards greater species diversity in more developed ecosystems is widely known to occur in both terrestrial and marine habitats (Raymond 1976, Parsons and Takahashi 1979). The development of a pelagic system is often dominated by large, competitive forms in spring

when light and nutrient availability offer them a competitive advantage. During late summer, smaller forms with of higher taxonomic diversity may dominate the spectrum seen. This is often seen in the species composition of phytoplankton, and may well be reflected in their predator community, the microzooplankton.

4.2 Microzooplankton herbivory

In the Section above I have shown that microzooplankton abundances in the investigation area considered were high, and species composition and their depth distribution indicates an adaptation to exploit available food sources in the upper water column. Of greater interest, however, is the ability to quantify the trophic role of these microprotozoans in relation to food web dynamics that lead to consumption and turnover of organic matter in the euphotic zone. In the following paragraphs, therefore, I shall discuss the results of experiments to determine rates of herbivory of the microzooplankton community with an emphasis on the biomass of prey (phytoplankton) and predator (microzooplankton) organisms. I begin with a short assessment of the seawater dilution method, and attempt to point out its weaknesses and limitations.

4.2.1 Critique of the dilution method

Since its conception a decade ago (Landry and Hassett 1982), the seawater dilution method to estimate microzooplankton herbivory has been widely applied and its assumptions repeatedly reviewed. Mathematical modelling to test the assumption of linearity in grazing response of microzooplankton at different dilutions, and its effect on estimations of algal growth have been dealt with elsewhere (Gallegos 1989, Evans and Paranjape manuscript), and tests of linearity will not be considered here.

Critical in the assumptions of the seawater dilution method is that algal growth not be limited during the experimental time frame. Limitation of algal gowth in undiluted water would result in lower apparent growth rates, an exaggeration of the slope of regression, and thus overestimation of grazing pressure. To ensure that algal growth is not limited in incubation flasks, many authors (Landry and Hassett 1982, Burkill et al. 1987, Gallegos 1989) have added nutrients at the start of the experiments. This, however, may result in artificially high rates of algal growth in undiluted seawater, where nutrient limitation would be greatest, thus deceasing the slope of the regression, and leading to an underestimate in grazing. Morever, mortality of some species of oligotrich ciliates is known to occur due to the addition of excess nutrients or due to trace contaminants in nutrient stocks (Landry and Hassett 1982, Gifford 1988). Additionally, the applicability of algal growth estimates in the presence of added minerals to *in situ* growth rates is open to question. A correct estimate of algal growth is crucial in considering the balance between growth and grazing *in situ,* and the potential disadvantages in the addition of nutrients overweigh arguments in its favour. In the experiments in this study,

therefore, I chose not to add nutrients and present here indications that this did not affect the results obtained.

With ambient NO_3 concentrations of > 2 µM at the sampling depths used, it was clear that this factor was not limiting to phytoplankton growth in the water column or experimental flasks. This is in accordance with the findings of Paranjape (1990), who found that algal growth was not lower in 48 hour as compared to 24 hour incubations in water samples where nitrate concentrations (1.0 µM) were lower than those encounterd in this study. Measurements of NO_3 at the end of 24 hours in undiluted seawater showed that concentrations exceeding 1.9 µM were still present. An indirect estimate of algal growth using chl *a* standing stocks and ^{14}C-mediated primary production measurements was able to provide parallel estimates of phytoplankton growth as a comparison to those obtained from the dilution experiments. Although primary production measurements were conducted from separate sampling bottles to those used in the dilution experiments, and were often taken at adjacent stations, ^{14}C uptake was relatively constant at the depths considered for these experiments, allowing for a rough comparison of the two methods. Table 6 shows the results of these calculations and, with the exception of individual stations (Sta 662 in 1989, Sta 885 and 888 in 1990), there is reasonable agreement of the figures.

Sta	Date	Depth (m)	Doublings d^{-1} (SWDil*)	Doublings d^{-1} (^{14}C**)
651	28.06.89	15	0.2	0.17
662	03.07.89	10	-0.5	0.23
686	08.07.89	15	0.2	0.10
880	24.08.90	20	0.1	0.10
883	25.08.90	20	0.2	0.15
885	26.08.90	20	0.7	0.08
895	30.08.90	20	-0.5	0.05
897	31.08.90	20	0.02	0.06
903	02.09.90	20	0.01	0.06

* Doublings per day as measured by the seawater dilution technique.
** Doublings per day as calculated from primary production.

Table 6: A comparison of estimates of algal doublings per day using the seawater dilution technique and values of chlorophyll *a* and primary production. A conversion factor of 50 was used to convert Chl *a* to phytoplankton carbon with the following formula:

$$\text{doublings day}^{-1} = \frac{\text{Primary Prod. (mg m}^{-2}\text{d}^{-1})}{50 * \text{Chl } a \text{ (mg m}^{-2})}$$

Phytoplankton growth is assumed to be exponential with time, an assumption that is generally fulfilled in coastal areas, but nevertheless not easy to verify. During at least one drift experiment of this study (cruise POS 173/2 in Aug/Sept 1990), phytoplankton stocks were seen to decline with time, light levels were low in subsurface water layers and the pelagic situation resembled one of decline at the end of the growth season. Algal growth in such a situation may not be adequately described by the conventional equation for exponential growth that forms the basis of the dilution method. Morever, this is complicated by the processes of differing growth rates among the algal taxa, and selective grazing by microzooplankton (as demonstrated in this study, see Section 4.2.3). By averaging the growth of all algal taxa, the growth-grazing dynamics between microzooplankton and their prey are incompletely quantified.

Perhaps a more significant criterion in this technique is that a decrease in chl *a* stocks is directly linked to algal mortality by grazing. Recent research (Barlow et al 1988, see also Section 4.4, this study) into pigment degradation patterns indicates that this may not be the case. Microzooplankton consists of a diverse assemblage of proto- and metazooplankters, whose basic digestion patterns and thus ability to degrade ingested pigments, varies. The temporal scale of pigment retention and degradation within herbivore guts and the persistance of chl *a* within fecal pellets of metazoan grazers has an impact on the use of chl *a* as a parameter to estimate algal growth and mortality. This consideration is discussed further in Section 4.4.

Gallegos (1989), in his evaluation of the dilution method, mentions the implications of changes in predator concentration during the incubation period. An increase in microzooplankton stocks due to growth is thought to have been negligible in the present study, where doubling times far exceeded 1 day (10 - 14 days). More likely, the *in situ* microzooplankton population suffers losses due to predation pressure from metazoans. Elimination of the latter by prescreening of incubation samples, may overestimate grazing pressure, and it may be necessary to view these rates as "potential" values compared to the *in situ* situation.

Lastly, non-algal sources of nutrition to the microzooplankton community (detritus, bacteria, nano-heterotrophs and ciliates themselves are some of the recognized possibilites), are not considered in the diluton technique. Although this consideration does not affect results calculated by this method, it may restrict the use of herbivory to evaluate trophic food dynamics. The seasonal importance of bactivory, detritivory and carnivory and its effect on selection of algal prey has not been studied, but may play an important role in pelagic food webs.

4.2.2 Impact of microzooplankton herbivory in the pelagial

Microzooplankton grazing rates reported in the literature encompass the entire spectrum from 0 - 100% primary production per day (Gifford 1988) and are seen to account for between 10 and 60% of the annual phytoplankton productivity (summary in Gifford 1988). Although an increasing body of data is collecting on microzooplankton abundances in polar waters and in particular the Greenland Sea (Tibbs 1967, Tanuguchi 1984, Putt 1990, Auf dem Venne 1990), the trophodynamic role of these communities has not been investigated in any detail. Paranjape (1988), working in the Canadian Arctic, found that between 8 and 15 % of phytoplankton standing stocks were ingested by microzooplankton per day. Results from grazing experiments reported in this study show that arctic open-ocean microzooplankton communities are comparable in their grazing impact on phytoplankton stocks with those reported from coastal and temperate areas.

Grazing by microzooplankton on algal biomass was high both in summer and autumn in the East Greenland Sea as measured at the depth of maximal chl *a* concentration. I attempt here to quantify grazing by the microzooplankton in terms the ingestion of phytoplankton carbon and relate this to the biomass of the microzooplankton itself.

In June/July 1989, between 20 and 40% of chl *a* standing stocks were ingested per day by the microzooplankton, and showed no trend during the 10-day drift experiment (see Section 3.1.4). Using a C:Chl conversion factor of 50:1 (Arndt 1990) this corresponds to 10-20 $\mu gC\ dm^{-3}\ d^{-1}$. Microzooplankton standing stocks at this time were relatively high, at 11 $\mu gC\ dm^{-3}$, and ingestion corresponded to ca. 180% of body carbon per day on a community basis. During the middle of August microzooplankton stocks were considerably lower (3 $\mu gC\ dm^{-3}$), and their feeding pressure amounted to 27 - 39% of chl *a* standing stocks per day. In terms of carbon ingested, this corresponded to 14 - 18.5 $\mu gC\ dm^{-3} d^{-1}$, or 500 - 700% of microzooplankton biomass (including metazoans) at the community level. During the end of August, during the latter part of the drift experiment, both chl *a* and microzooplankton standing stocks steadily decreased, and grazing of microzooplankton amounted to 10% of chl standing stocks d^{-1} by September 2., corresponding to ca. 140% of microzooplankton biomass d^{-1}.

This apparent discrepancy, where a low numerical abundance of microzooplankton in autumn shows a higher ingestion in relation to their own biomass than a 5-fold larger community in summer, is explained in terms of the species composition of the microzooplankton. Copepod nauplii, absent in summer in experimental containers, were present at concentrations of 4-12 ind. dm^{-3} during autumn. This reflected their abundance in the water column, as enumerated in net hauls in the upper 100 m (Fürderer 1991). Bead uptake experiments during the autumn experiment (see Section 3.4) showed that these nauplii were ingesting large numbers of

particles as small as 2 µm in size, thus contributing to microzooplankton herbivory to an extent comparable to the entire protozoan commmunity. Their contribution to ingestion rates could, therefore, far exceed that of protozoans in biomass per individual. A comparison of ingestion by protozoans alone may, therefore, show more constant rates between the two investigations, with about twice their own biomass being ingested per day. This is in accordance with values from laboratory and field investigations (Heinbokel 1978), suggesting that theoretical turnover rates in protozoan populations may well approximate those *in situ*. Fig. 43 shows the relationship between algal growth and grazing for the experiments in 1989 and 1990, from which it is evident that the latter dominated in almost all experiments. The consequences of this deviation from steady state condition and its possible causes will be discussed later.

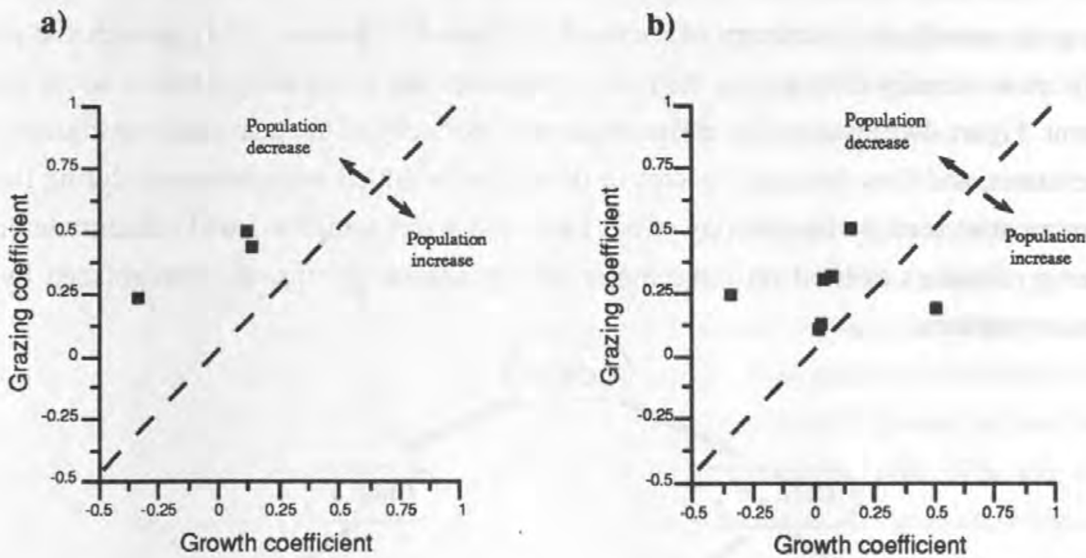

Fig. 43: Linear plots of algal growth coefficients vs coefficients of algal mortality (grazing) for individual experiments during 1989 (a) and 1990 (b). The dashed line indicates steady state conditions, where growth = grazing.

Using values for chl *a* concentration, microzooplankton number and grazing rates it was possible to calculate mean ingestion and filtration rates of 0.0019 ng chl *a* ind^{-1}h^{-1} and 1.8 µl ind^{-1}h^{-1} respectively during June/July 1989. These ingestion rates show agreement with those in the literature (0.001 to 0.017 ng ind^{-1}h^{-1}; Capriulo and Carpenter 1980). Filtration rates of microzooplankton in this study lie at the lower end of those found in the literature (0.5 - 8.5 µl ind^{-1}h^{-1}; Spittler 1973: 1 - 85 µl ind^{-1}h^{-1}; Capriulo and Carpenter 1980: 1 - 11 µl ind^{-1}h^{-1}; Burkill et al. 1987). The higher values cited in the literature, morover, are based on populations dominated by tintinnids which, due to their larger oral aperture may be capable of higher filtration rates than smaller ciliates. Measured rates for oligotrich ciliates lie in the range of 2 to 9 µl ind^{-1}h^{-1} (Rassoulzadegan 1982, Jonsson 1987), which are in better agreement with this study.

4.2.3 Selective grazing processes

In terms of production, turnover and export of organic carbon, measurements of microzooplankton herbivory quantify an important process in the consumption of autotrophic biomass. Bulk chl *a* measurements in incubations with natural water samples, however, ignore the processes of selective grazing mentioned above and differing growth rates of individual phytoplankton taxa, which in turn may have a decisive impact on retention or loss rates from the pelagial. Accessory algal pigments and carotenoids provide a useful biochemotaxonomic marker which can be exploited, using HPLC analysis, to follow production and loss rates of discrete groups of algae. This approach was used at Sta 885 during the experiment in autumn 1990 to investigate grazing activity of microzooplankton in more detail.

As can be seen from a summary of the results, (Table 4 in Section 3.2.4), growth and grazing coefficients varied widely among the various pigments, and thus the algal taxa in which they are present. Figure 44 illustrates the chemotaxonomic hierarchy of the pigments investigated in this experiment, and lists the algal species in these groups which were dominant during the drift experiment as seen by microscopy of net hauls and water samples. I will concentrate here on grazing pressures exerted on three major phytoplankton groups, as distinguished by their pigment markers.

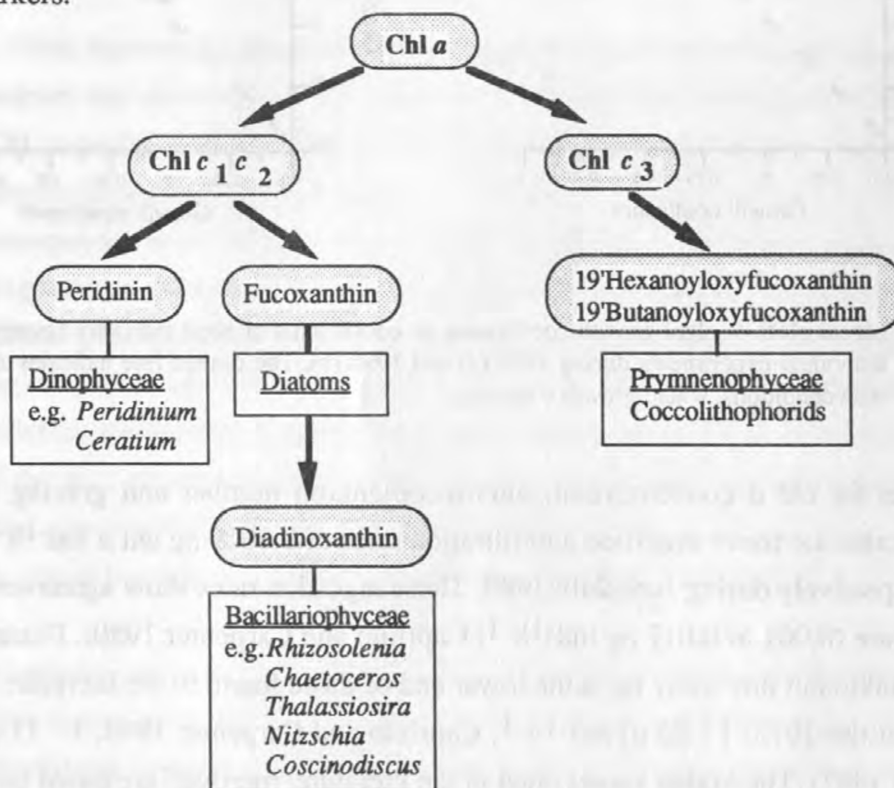

Fig. 44: Schematic illustration of the chemotaxonomic heirachy of algal pigments. Algal groups and species found in the water column are listed along with their characteristic pigments.

Diatoms, prymnesiophytes, and chrysophytes share the common pigment fucoxanthin, with additional pigments specific to particular groups dividing this spectrum furthar. The diatoms (bacillariophytes) are characterized by the possession of diadinoxanthin, and were represented in the water column by large forms (see Fig. 44). The fucoxanthin derivative 19'Hexanoyloxyfucoxanthin is the major carotenoid of the prymnesiophyte *Emiliania* (*Coccolithus*) *huxleyi* (Arpin et al. 1976, Gieskes and Kraay 1984, Haxo 1985). Although 19'Hexanoyloxyfucoxanthin is also present in the dinoflagellate *Gymnodinium aureolum* (Tangen and Björnland 1981) and the colonial prymnesiophyte *Corymbellus aureus* (Gieskes and Kraay 1986), the abundance of coccolithophorids of the species *Coccolithus pelagicus* and *E.huxleyi* in water samples during the drift study (Antia et al. 1990) is taken to indicate that these were the primary organisms containing 19'Hexanoyloxyfucoxanthin in the water column. Dinoflagellates, the third group considered here, are recognizable in their pigment composition by their characteristic carotenoid peridinin. In the following paragraphs, therefore, these pigments will be used to discuss grazing on the above mentioned algal groups.

Significant differences in growth and grazing were seen among the fucoxanthin derivatives; although fucoxanthin was present at high ambient concentrations (0.32 μg dm^{-3}) grazing on this pigment was not significantly different from zero. Loss rates for diadinoxanthin amounted to 11% of standing stocks per day, indicating that there was some grazing of the larger diatom species. 19'Hexanoyloxyfucoxanthin and 19'Butanoyloxyfucoxanthin, present at low ambient concentrations (0.08 and 0.02 μg dm^{-3}) were grazed upon heavily, with 37% and 23% of standing stocks depleted per day, and loss rates exceeded those of growth, indicating a population decrease among this group. Peridinin was present at low ambient concentrations (0.2μg dm^{-3}), yet showed the highest turnover rates in the grazing experiment (1.3 doublings per day, 54% of standing stocks grazed per day).

This preference of microzooplankton for dinoflagellates over diatoms in a heterogenous algal population is in accordance with reports of selective feeding in laboratory cultures and has been demonstrated by Burkill et al. (1987) in a field population. Stoecker et al. 1984, found indirect support for this relationship in the fine-scale spatial correlations between planktonic ciliates and dinoflagellates in a natural population. The ability of microzooplankton to graze heavily on fast-growing algal taxa, thus controlling their stocks, has been suggested as indicative of a feedback-coupling effect among the microzooplankton predators and their prey (Burkill et al. 1987). By the process of selective grazing among the algal taxa, microzooplankton may be instrumental in determining seasonal species succession among the phytoplankton.

In Fig. 45 the specific rates of growth and grazing on different pigments has been plotted. As can be seen a decrease in stocks of 19'Hexanoyloxyfucoxanthin and 19'Butanoyloxy-

fucoxanthin indicates a higher grazing pressure than can be compensated for by their growth. Peridinin, cis-Peridinin and Diadinoxanthin, although showing variable growth and grazing coefficients, approach steady state conditions.

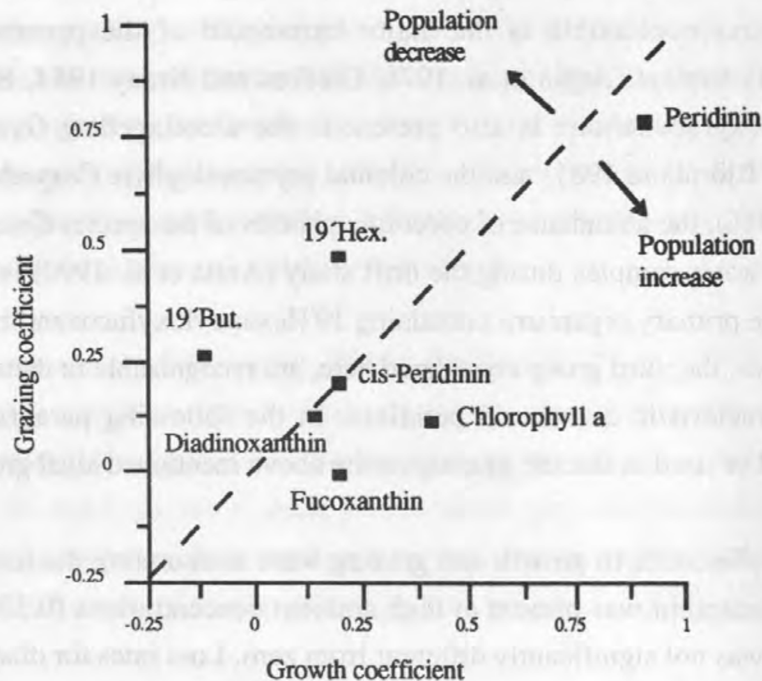

Fig. 45: Plot of the coefficients of algal growth vs grazing for individual pigments as measured using HPLC analysis. The dashed line indicates steady state conditions, where growth = grazing.

4.3 Microzooplankton growth and doubling

Microzooplankton growth during the two studies presented here was determined in incubation experiments in the absence of copepods (see Materials and Methods, Section 2.5) and was low during both the time series considered, with doubling times on the order of 10 days. It must be considered here that the handling of these delicate organisms can lead to an underestimate of growth. Although large metazoan grazers were excluded in experimental flasks used to measure growth rates, it cannot be discounted that some losses in ciliate populations by predation of heterotrophic dinoflagellates occurred (eg. loss of oligotrichs, Gifford 1985, dinoflagellate predation, Hansen 1991).

Growth and doubling rates of microzooplankton species have been shown to be potentially high under optimal conditions in the laboratory (Verity 1986, Gilron and Lynn 1989, see also Section 3.3 this study). Doubling times of tintinnid ciliates in field populations of between 12 hours and 3 days have been reported (Heinbokel 1987 & 1988, Stoecker et al. 1983). Growth of natural populations, however, is limited by a number of environmental conditions; low

temperatures, as those seen in arctic waters, are known to slow doubling times (Hamilton and Preslan 1969, Laybourn and Stewart 1974, Wickham 1985). Recently, however, a number of authors have suggested that food quality and quantity may be more important in controlling the reproduction of natural populations (Banse 1982, Fenchel 1987), and may be the major limiting factor in oligotrophic parts of the ocean. Verity (1986) suggests that chl *a* concentrations below 2 - 4 $\mu g\ dm^{-3}$ (such as those found in this study) may curb protozoan growth. It is tenuous at best to characterize food concentrations as limiting to growth in a system where prey-predator populations are closely coupled. The balance between available food and predator biomass in such a system approaches stady state conditions, and the total quantity of available algal prey will at best determine the absolute level at which the biomass of the two communities stabilises. The label "prey-limited" can at most be a comparison with theoretically or experimentallly determined ingestion rates and should be used with caution to describe natural populations.

4.4 Pigment degradation by microprotozoans

In the Section above I have emphasized the study of selective herbivory in the water column using pigments as chemotaxonomic biomarkers. Of these chl *a*, which is present in all algae and can be easily measured by routine methods, is widely used to quantify ingestion rates of both microzooplankton (by the dilution method used in this study) and macrozooplankton (by the gut fluorescence method of Mackas and Bohras 1976). Both these methods have found wide acceptance and have been applied in numerous field studies; they are based on the critical assumption that the attrition of chl *a* is linearly related to its rate of ingestion. Similarly, in the HPLC experiments described in the previous Section, it is assumed that attrition of accessory pigments proceeds parallel to that of chl *a*, i.e. that the ratios of individual pigments remain constant during digestion by microzooplankton. This assumption has, however, seldom been tested, and will be further dealt with below.

Another important application of pigments as biomarkers involves the use of phaeopigments (the degradation products of chl *a*) to trace the fate of algal biomass in the water column. Phaeopigments are produced primarily by herbivorous activity and are routinely found in the guts and faecal pellets of copepods and other metazoans. Recent models by Welschmeyer and Lorenzen (1985) and SooHoo and Kiefer (1982) have proposed pathways for the flux of phaeopigments to deeper waters, implicating metazoans in the production of large, rapidly sinking faecal pellets and microzooplankton as the source of phaeopigments in small faecal pellets that remain in suspension. Additionally, the ratios of Chlorophyll:Phaeopigment and Carbon:Phaeopigment (Downs and Lorenzen 1985) have been proposed as indicators of herbivorous assimilation efficiency and activity in the water column. Central to these models is the assumption that chl *a* is a conservative tracer, with a 100% molar conversion to its breakdown products. Although Schuman and Lorenzen (1975) found a 100% molar

conservation between total chlorophyll and phaeopigments during copepod grazing, loss rates of chl *a* to colourless residues of between 8% and 30% have also been reported (Helling and Baars 1985, Kiörboe and Tiselius 1987, Lopez et al. 1988). Most recently, the degradation by copepods of ingested chl *a* has been shown to be dependent on their history of food acclimation and ingestion rate (Penry and Frost 1991). These authors demonstrate a 2-3 fold higher chl *a* degradation in animals adapted to high food concentrations than those adapted to low food concentrations.

The production of phaeopigments by microzooplankton, morover, is unclear, with conflicting reports in the literature. Working with the heterotrophic dinoflagellate *Oxyrrhis marina*, Klein et al. (1986) found that a small amount of phaeophytin was produced in the dark and this was further degraded to colourless residues. On the other hand, Barlow et al. (1988), working with the same protozoan, found no phaeopigment production. In contrast, Goldman and Caron (1985), using the microflagellate *Paraphysomonas imperforata* and fluorometric analysis, measured significant phaeopigment production. I discuss here the results of experiments with two protozoan predators and three algal prey, to determine degradation of chl *a* and accessory pigments in laboratory grazing experiments using HPLC and fluorometric analysis (see Section 3.3.1 for results).

Using improved capabilities in resolution of the HPLC chromatograms it was possible to verify phaeopigment production in all experiments, although they accounted for a minor fraction (2 to 6 %) of chl *a* losses. Their transient accumulation and then disappearance to non-fluorescent residues was correlated to the increase in volume of predator (*Oxyrrhis*) cells (expt. 1-3), and their subsequent phased division. The initial (0 to 6 hours) disappearance of up to 90% of chl *a* standing stocks to colourless residues without accumulation of pigmented intermediates can thus be related to the rapid and efficient digestion by starved *Oxyrrhis* cells, while in contrast, the subsequent accumulation of small amounts of phaeopigments occurred in large, "satiated" protozoa. Further breakdown of the phaeopigments to colourless residues was seen to have occurred when algal stocks were depleted, and the predator population approached starvation.

Since faecal pellet formation during these experiments was not observed (see also Section 3.3.2 this study), we were able to rule out the possibility that this formed a pool of phaeopigments in the cultures. Phaeopigments in these experiments were contained within the digestive vacuoles of the protozoans. Epifluorescence microscopy confirmed the presence of red fluorescent (chl *a*) food vacuoles, changing in colour to yellow-orange in older vacuoles. The abrupt decrease in phaeopigment concentrations (expt. 1-3) also supports this fact; if phaeopigments were contained in extracellular pellets, their concentration would be expected to decrease more slowly. These results contradict the assumptions of Welschmeyer and Lorenzen (1985) and

SooHoo and Kiefer (1982), that implicate the microzooplankton in the production of small, suspended particles which form a reservoir of phaeopigments in natural waters. A second assumption of these models, namely that photooxidation is responsible for loss of phaeopigments in these small pellets, is not borne out by these experiments. Clearly light degradation of phaeopigments does not need to be invoked, and complete degradation of the chlorophyll *a* molecule can occur in the dark due to protozoan digestion.

Relative proportions of phaeophorbide to phaeophytin varied among the combinations of prey and predator used in these experiments, showing no apparent pattern (see Fig 32 on page 48). Phaeophorbide has been found to be the primary phaeopigment in the guts and faecal pellets of herbivorous copepods, and its distribution in natural waters is often positively correlated to metazooplankton abundance (Bigidare et al. 1986). In natural waters phaeophorbide has been found to occur at concentrations four to ten times higher than phaeophytin (Vernet & Lorenzen 1987a, Bigidare et al. 1986).

In an attempt to consolidate results of these experiments with literature values for phaeopigment production by both protozoan and metazoan grazers, the following scheme is proposed: the known degradation pathways of the chl *a* molecule are shown in Fig. 46.

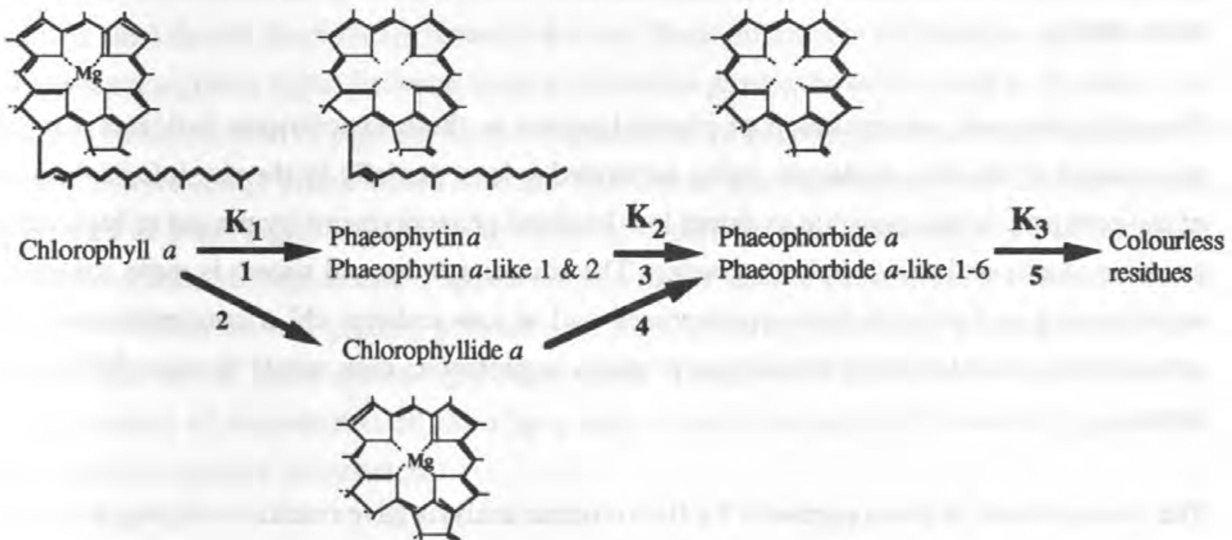

Fig. 46: Degradation pathways of Chlorophyll *a*, and intermediate products formed during protozoan grazing. Reactions 1 and 4 are mediated by the presence of $[H^+]$; reactions 2 and 3 are mediated by the activity of hydrolases and chlorophyllase.

Assuming that the ultimate fate of chl *a* in the marine environment is its disappearance as colourless residues, it may be argued that the accumulation of intermediate degradation products depends on the rate constants K1, K2 and K3, and the relative stability of the phaeopigments in

the prevailing chemical environment (i.e. either herbivore guts or faecal pellets). Since chl *a*, constituting only a fraction of total cellular carbon, is broken down incidentally during the digestive process, it may be expected that the degree of its degradation is coupled to efficiency of total food digestion. Basic differences in the digestive processes between protozoans and metazoans may thus result in different rate constants for these reactions.

Loss of the central Mg^{++} atom from the tetrapyrrhole molecule, giving rise to phaeophytin, is mediated by acidic conditions such as those commonly seen in digestive tracts, where the presence of a Mg -removing enzyme has been suggested. Buildup of phaeophytin in the marine environment, however, is seldom seen, although it may be the primary degradation product of grazing by salps and some larger zooplankton (Jeffrey 1980). It appears, therefore, that furthar loss of the phytol chain from phaeophytin, gives rise to phaeophorbide, occurs in most metazoan digestive tracts. Phaeophorbide then accumulates in their guts and faecal pellets, and the reaction K3 (Fig. 7) proceeds more slowly, perhaps due to a high energetic requirement in cleaving the tetrapyrrhole ring. Differences in the digestive chemistry of gut enzymes due to preconditioning history (Penry and Frost 1991) could thus account for the different patterns in chl *a* degradation seen in copepod guts. The accumulation of phaeopigments in metazoan faecal material can thus at least partly be attributed to the incomplete digestion in metazoan guts and egestion of whole or partially intact algal cells, in which pigment degradation then proceeds more slowly.

The only transient accumulation of phaeopigments in these experiments indicates a rapid degradation of the chl *a* molecule, being controlled at least partially by the physiological status of the protozoa. It was possible to detect low levels of phaeopigments by the use of high chl *a* standing stocks and rapid, pulsed, grazing. The situation in natural waters is more complex, with grazing and division less synchronized and at low ambient chl *a* concentrations, the accumulation of chlorophyll breakdown products in protozoan cells would be more difficult to detect.

The measurement of phaeopigments by fluorometric analysis gave results of varying accuracy as compared to those measured by HPLC. The overestimation of phaeopigments using the fluorometer was most pronounced in the presence of chl b (expt.1), a feature that has previously been reported by Vernet & Lorenzen (1987b). The widespread use of flourometry as a quick and easy method to measure phaeopigments in natural water samples should thus be tempered with caution.

In summary, phaeopigments are highly transient tracer intermediates in the degradation of algal chlorophyll by microprotozoan grazing. Pigment diagenesis is rapid and occurs almost

completely within the food vacuoles of the protozoan, without the production of pigmented faecal aggregates. This is in direct contrast to metazoan zooplankton, whose large, membrane-bound faecal pellets contain intact and partially broken algal remains which form a pool of phaeopigments in the water column and a rapid transport mechanism to deeper waters. The fate of the chl *a* molecule during digestion needs to be more thoroughly investigated to ascertain if there is a systematic production of chemical precursors which can be related to specific herbivorous taxa. If, as reported in the case of photodegradation, the tetrapyrrhole structure is fragmented to low molecular weight organic acids which may be incorporated into grazer cells (Llewellyn et al. 1990), loss of this pigment tracer may be absolute.

The degradation of accessory pigments due to protozoan grazing accentuates the problems in using pigments as conservative markers in rate measurements. The change in ratios of chl *a* to carotenoids due to grazing has implications on the method used above (Section 4.2.3) to measure selective herbivory among algal taxa. Additionally, the presence of carotenoids and accessory pigments in the water column and sediment trap material may not accurately reflect algal taxa in the water column.

As a note of caution it should be remembered that microzooplankton form a diverse assemblage in natural waters, consisting of both protozoans and metazoans, and current methods to estimate grazing rates do not discriminate between the two. Basic differences in digestion and alteration of the algal pigment signal between these herbivorous groups, however, need to be taken into account in the creation of pigment budgets, and the use of phaeopigment ratios as indicators of biological processes in the water column. The use of the fluorometer can yield erroneous estimates of phaeopigment standing stocks, and should be supplemented by HPLC analysis where possible. Microprotozoans appear to be a major sink of chl *a* in natural waters where their concentrations and grazing pressures are high, possibly exceeding photooxidation and senescence as loss pathways of algal chlorophyll. Clearly we need to know more about the stoichiometry of degradation of chl *a* by grazers in order to exploit the use of pigments as biomarkers in aquatic ecosystems.

4.5 Copepod grazing upon microzooplankton

In the Section above I have discussed the grazing impact of microzooplankton on algal standing stocks in the East Greenland Sea. Additional pressures of herbivory from metazooplankton would be expected to further deplete algal biomass. Copepod herbivory during the 1989 drift experiment was measured using the gut fluorescence technique of Mackas and Bohrer (1976) in the dominant copepod species *Calanus hyperboreus* (Zeller 1990), and was seen to account for 0.02 % to 4.6 % (mean 1.32 %) of chl *a* standing stock per day in the upper 25 m of the water column. Even if this figure is increased to account for other copepod species present, it still lies

an order of magnitude lower than measured rates of microzooplankton herbivory. Macrozooplankton biomass, on the other hand, accounted for 19 % of total POC in the upper 25 m of the water column, far exceeding that of the microzooplankton (2.5 - 4 % total POC). Two questions arise: firstly, how does the macrozooplankton maintain its higher biomass in the water column, and secondly, what is the fate of the large amount of autotrophic biomass that is seen to pass through the microzooplankton loop of the food chain, especially since no accumulation of microzooplankton biomass is observed? In the following paragraphs I invoke a mechanism leading to loss rates of microzooplankton as prey to larger crustaceans, which supplies a partial explanation for the situation described above.

High standing stocks of copepods are seen in many pelagic environments; Burkill et al. (1982) found that they accounted for over 90% of total biomass in the Celtic Sea in summer. These stocks have often been shown to be in excess of the autotrophic biomass available to support their growth. Macrozooplankton are inefficient feeders on particles < 10 µm in size (Nival and Nival 1976), and primary production in the algal fraction > 5 µm is often inadequate to support macrozooplankton nutritional demands. There is a growing awareness that crustaceans, and copepods in particular, are omnivorous and not strictly herbivorous in nature, as previously thought. This has led to the proposal that microprotozoans, which are able to avail of nano- and picoplankton material, form a vital link of photosynthetic biomass to higher trophic levels (Sherr et al. 1986, Stoecker and McDowell 1990). Indirect evidence of this in natural populations was seen by Smetacek (1981) in the negative correlation between copepod and protozooplankton biomass, indicating that larger metazoans were capable of controlling microzooplankton standing stocks. Although nauplii and small metazoans are known to contribute to the diet of copepods (Landry 1981, Daan et al. 1988), their predation on protozoa has only recently received attention. Tintinnid loricae have been seen in copepod faecal pellets (Turner and Anderson 1983, see also Section 3.5 this study) and guts (Mullin 1966, Zeitzschel 1967, Harding 1974), but these make up only a small part of the protozoan community in arctic areas.

Grazing experiments of the dominant copepod species, *Calanus hyperboreus*, on microzooplankton, were thus conducted during this study to test the hypothesis that protozoans form an important part of the copepod diet and that copepod grazing is capable of regulating protozoan stocks in the upper euphotic zone. The feeding pressure of adult female *C.hyperboreus* amounted to 5-6 % of protozoan standing stocks per day; this is, however, a minimum value for the entire metazoan community. Taking into account the abundance of all copepod species, (which includes copepods of *Calanus* sp., *Metridia* sp. and *Pseudocalanus*; data from Zeller 1990), and assuming similar ingestion rates, about 18 % of the microzooplankton community was being ingested per day in the upper 25 m of the water

column. Using the values for chl *a* ingestion in Zeller (1990) and a Carbon:Chlorophyll conversion factor of 50 (Arndt 1990), I calculated an ingestion rate of ca. 0.6 to 1.4 µgC individual copepod^{-1}day^{-1}.As opposed to this, protozooplankton ingestion supplied the copepods between 2.5 and 6.5 µgC ind.$^{-1}$d^{-1}. Based on these conservative estimates, protozoans are seen to form a vital component in the diet of copepods in the East Greenland Sea, supplying the metazoans with up to 3-fold organic carbon more than from phytoplankton. In addition to providing an additional food source to enhance growth, protozoans may be crucial in enabling copepods to overwinter in polar areas, where a short autotrophic growth season is followed by a longer period of low pelagic activity, during which heterotrophic organisms may form a large proportion of existing biomass. By their grazing activity, in turn, metazoans can be instrumental in regulating protozoan standing stocks.

Gifford and Dagg (1991) working with the dominant copepod species in natural samples from the Gulf of Maine, similarly found that they were capable of clearing between 11 and 16 % of protozoan stocks on a daily basis, and that the copepods obtained 28 to 59 % of their daily metabolic requirements from this protozoan food source. In incubation experiments, a selection in favour of ciliated protozoa as compared to algal food has been shown for *Acartia tonsa*, a coastal copepod species (Stoecker and Sanders 1985, Wiadnyana and Rassoulzadegan 1989). Due to their high content of storage products and nitrogen-rich nutritional value (Gifford and Dagg 1991), ciliates could be a preferred food source for many copepod species. A number of studies have similarly shown high consumption rates of heterotrophic protozoans by various metazooplankton such as jellyfish, ctenophores and amphipods (Stoecker et al. 1987a, 1987b, Stoecker and Egloff 1987). High predatory pressure on microzooplankton could control their standing stocks, which in turn can regulate pressures of herbivory on the algae. Low microzooplankton standing stocks are compensated for by rapid turnover rates, and their high assimilation efficiencies ensures efficient transfer of nanoplankton biomass to higher trophic levels.

The estimation of herbivory by microzooplankton using methods which exclude larger organisms that graze upon the microzooplankton, and the application of these results to *in situ* situations, may also be influenced by the high rates of consumption of protozoans in the water column. If a close coupling between these grazer populations exists, such incubations would result in a decoupling of the phytoplankton-microzooplankton -metazoan chain, overestimating herbivory in relation to the field situation. The dominance of grazing over phytoplankton growth (seen in Fig. 43 on page 73) may thus be partially explained, and further efforts in modelling such interactions will enhance our understanding of trophic coupling between autotrophs, herbivores and carnivores. It may be useful to view the rates of microzooplankton

herbivory by the methods described above as "potential" rates, which should be extrapolated to the field situation in view of concomitant loss rates of microzooplankton.

The pelagic situation in the upper 100 m of the water column has been described in terms of the major compartments in Table 7, for the summer and autumn situations investigated in this study.

	JUNE / JULY 1989	AUG / SEPT 1990	NOV. 1989	FEB. 1991
PRIMARY PRODUCTION (euphotic zone) (mg C m^{-2})	500	150	-	-
POC * (0 - 100 m) (mg C m^{-2})	15.87	12.78	8.8	7.41
PHYTOPLANKTON-CARBON ** as % POC	23	17	-	-
MICROZOOPLANKTON-CARBON as % POC	2.4	3.8	-	-
MACROZOOPLANKTON-CARBON as % POC	19 (0 - 25 m)	19 (0 - 50 m)	-	-
% POC SEDIMENTING	0.05 (at 60 m)	0.23 (at 100 m) 0.14 (at 300 m)	-	-
MICROZOOPLANKTON-CARBON as % Phytoplankton-carbon (0 - 30 m)	10.5	22	-	-
MICROZOOPLANKTON-CARBON as % Macrozooplankton-carbon (0 - 30 m)	10	16	-	-

* POC measurements were conducted with the exclusion of large metazooplankton.
** Calculated as Chl *a* conc (µg l^{-1}) * 50.

Table 7: Values of primary production, POC, and relative contribution of phytoplankton-, microzooplankton-, and metazooplankton carbon to total POC in different seasons in the East Greenland Sea.

Relative contributions of phytoplankton carbon to total POC were slightly higher in summer than in autumn, which reflects the lower primary productivity in the latter season. The relative contribution of microzooplankton to total POC was small in both situations, not exceeding 4 % of total POC. Macrozooplankton biomass, however, was a dominant part of particulate carbon in the euphotic zone, constituting 19 % of the total. This may appear at first contradictory to the

high rates of herbivory exerted by microzooplankton, and the contrast with low rates of herbivory by the metazoans. This can, however, be explained in terms of the close coupling between the two grazer communities, where the microzooplankton serve as an efficient trophic link between phytoplankton and macrozooplankton. Fast turnover rates within the microzooplankton compartment belies their small biomass, and can ensure optimal utilization of algal biomass within the entire heterotrophic community. A four-fold decrease in productivity between the two situations discussed in this study did not lead to a substantial decrease in pelagic biomass. Heterotrophic processes in the pelagial that accentuate retention of particulate matter may thus buffer changes in autotrophic production, and maintain pelagic activity when low light levels do not allow for photosynthesis. Total POC values during November and February amount to half of the maximum seen during summer, which cannot be accounted for by algal production alone during winter. It is speculated that a heterotrophic system, which can retain nutrients and particulate matter in the upper water layer, may fuel such a winter situation. The empirical relationship between productivity and sedimentation is thus compromised by high levels of heterotrophic activity, leading to decreased sedimentation rates at the end of the autotrophic growth period.

4.6 Particle formation by microprotozoans

In the Sections above I have shown that high grazing rates of microzooplankton and their role in the close coupling of autotrophic biomass to higher trophic levels characterized the pelagic systems studied in the East Greenland Sea. A more recent area of research is concerned with the production of faecal aggregates by microzooplankton, and their contribution to particulate fluxes in the water column; it is this question that I shall address in more detail in the following paragraphs.

The formation of faecal pellets by marine protozoa has only in the past five years received attention, with the identification of large numbers of "minipellets" (defined as between 3 and 50 µm in size) in water samples and sediment traps (Gowing and Silver 1985). Some of these pellets were seen to originate from protozoan (spumellarian and phaeodarian radiolaria) and metazoan (juvenile hydromedusae) grazers. Due to their small size they did not account for significant proportions of the total organic flux; however, their content of intact algal cells and bacteria is thought to provide a source of high quality organic matter to midwater feeders.
In addition to radiolaria (mentioned above), pelagic foraminifera are also known to produce membrane-bound fecal pellets (Lee et al. 1988). Pellets from juvenile metazoans (eg. copepod nauplii) as produced in laboratory experiments (Marshall and Orr 1956, Paffenhöfer and Knowles 1979) overlap in size with the "minipellets", and a characterization of such particles in natural samples is tenuous.

Gowing and Silver (1985), however, were able to find numerous "minipellets" in the bodies of sarcodine protozoa in the water above their sediment traps, establishing beyond doubt their biological origin. Nöthig and v.Bodungen (1989), in water and sediment trap samples in the Weddell Sea found numerous small faecal pellets between 30 and 300 µm in size, which they ascribe to protozoan grazers (ciliates, dinoflagellates, radiolaria and foraminifera). In their picture in Fig 1(a) (Nöthig and v.Bodungen 1989), they show the ingestion of large numbers of pennate diatoms by a heterotrophic dinoflagellate of the *Gyrodinium* species, and a membrane-coated pellet that is thought to be egested by this form (Fig 1(c)). Similarly, Buck et al. (1990) found abundant sheath-covered pellets from a phagotrophic dinoflagellate in sea ice and the water column in the Weddell Sea, and were able to observe ingestion of diatoms by this species. In scanning electron micrographs of sediment trap material in the East Greenland Sea (this study), numerous minipellets with diatom, dinoflagellate, coccolithophorid and bacterial content (see Fig. 38 c to f) were similarly seen. In particular, sheathed aggregates very similar in form to those observed by Nöthig and v.Bodungen (1989, their Fig 1(c)) are thought to have originated from heterotrophic dinoflagellates, which were abundant in the pelagial during the time of the investigations. The content of these pellets, at times consisting of single algal groups, is also indicative of selective feeding processes among the phytoplankton.

Aggregate formation by heterotrophic dinoflagellates and ciliates is likely to assume different forms due to the differing capabilities of prey engulfment and digestion in these two groups. Dinoflagellates are able to form large food vacoules by virtue of an extrathecal feeding mechanism (Dodge and Priddle 1987), and use pseudopodal extentions for capture and digestion of prey; some forms are known to secrete a "feeding veil" or pallium to enclose food particles (Gaines and Taylor 1984, Jacobson and Anderson 1986). Feeding in ciliated protozoa, on the other hand, is restricted to phagotrophy and food particles are enclosed in individual vacuoles where digestion takes place. In older food vacuoles, where digestion is complete, membrane building blocks and enzymes are "recycled" to the peristomal region, where invaginations of fresh vacuoles takes place. Remains of the food vacuoles are egested through the cytopharynx. It is morphologically unlikely, therefore, that compact, ensheathed faecal aggregates are excreted by the ciliates. Particle production by phagotrophic ciliates has been recognized (Hamilton and Preslan 1969, Soldo et al. 1978, Stoecker 1984) in the form of amorphous aggregates, similar in size to their algal food (Stoecker 1984). These pellets differ from those of heterotrophic flagellates and larger protozoan groups in the absence of a discrete membrane and thus lack of structural integrity.

The production of fecal matter by the tintinnid ciliate *Favella ehrenbergii*, investigated in this study (see Results Section 3.3.2), corroborates the pattern of protozoan aggregate formation mentioned above. End-products of grazing by *Favella* were in the form of empty, non-

fluorescent thecae of their prey, the autotrophic dinoflagellate *Heterocapsa triquetra* (Fig. 36 e). In grazing experiments with *Oxyrrhis*, similarly, no packaged faecal pellets were seen, and scrunched-up remains of the algal prey were the only visible faecal material. These particles can degrade rapidly due to microbial activity (Stoecker 1984), and are thus unlikely to contribute to the particulate pool in the water column.

From the above discussion it is evident, therefore, that different protozoan groups exhibit conflicting roles in the packaging of ingested particles. Although the pellets formed, with their low sinking speeds (0.07 - 20 $m^{-1}d^{-1}$ calculated according to Stokes' Law; Gowing and Silver 1985) are not expected to contribute significantly to total vertical particulate flux, their abundance in sediment traps indicates that they reach mid-water layers where they may provide a food source to other organisms. Micrometazoans, due to their small size, have also been implicated in the formation of minipellets (see above), which was studied in a qualitative manner in this study, using fluorescent latex spheres in particle uptake experiments with a natural microzooplankton assemblage. Concentration of particles in the incubation flasks used in these experiments was seen to occur almost exclusively by copepod nauplii. By 109 hours numerous faecal pellets 60 - 160 µm in length were densely packed with fluorescent beads (Fig. 36 f and i), whereas faecal material that could be ascribed to the smaller protozoans was absent. Among the microzooplankton assemblage, therefore, basic differences among protozoan groups and between proto- and metazoans must be considered, both in terms of their modification of particulate matter in physical form as well as their alteration of pigment signals discussed in Section 4.4.

Microprotozoans, thus, by their activity in the pelagial play a dual role in the processing of particulate matter as concerns its transport to deeper water layers. On the one hand, by their high known rates of recycling and absence of faecal pellet formation, they lead to retention of biomass and nutrients in the euphotic zone. On the other hand, by forming a link between nanoplankton and larger metazoans, they facilitate transfer of autotrophic biomass to higher trophic levels, from where it can be partly recycled or exported in the form of rapidly-sinking faecal pellets.

4.7 Microzooplankton sedimentation

Remains of microprotozoans themselves are rarely seen in sediment trap samples, with the exception of the hard parts of tintinnids (and, more seldomly, thecate heterotrophic flagellates). These, however, formed a negligible part of the entire microzooplankton community. The presence of these organisms in trap samples have been repeatedly reported and, aside from shells of larger protozoans such as radiolaria and foraminifera, are the only traces of protozoans in the water column.

I have on no occasion found naked or "sheathed" ciliates (eg. *Laboea* spp.) in trap material. These organisms must either be consumed by metazoan grazers as shown above (Section 4.5), or be degraded by microbial activity upon their death. The only report in the literature that notes such species in sediment traps was in shallow water layers (20 -30 m; Taylor 1988), following a storm event in the North Pacific. The bulk of microprotozoan species in the euphotic zone were absent in sediment trap material in the present study, making it impossible to ascertain their activity in the pelagial over annual cycles from the composition of sedimenting material. The patterns of tintinnid sedimentation as recorded in daily intervals during the drift experiments showed no correlation with other parameters (chl *a*, POC, SiO_2). In the short term, therefore, the presence of their loricae in sedimenting material may not be a sensitive indicator of the state of their population in the pelagial. On an annual basis, however, a distinct pattern in sedimenting numbers is clearly visible, and has been reported for other areas, for example the Norwegian Sea (Bathmann et al. 1990). The coincidence of maximal tintinnid sedimentation with the end of the annual light period in September, as seen in this study, is explainable in terms of the general collapse of the heterotrophic population, of which the tintinnids are a part. This has similarly been hypothesized in the Norwegian Sea (Bathmann et al. 1990), where a pulse in tintinnid sedimentation occurred in July. This is not inherrantly contradictory to the hypothesis presented here, which postulates a heterotrophic community carrying on into the winter months, and leading to a retention of biomass in the pelagial. The transition from a pelagic scenario fuelled by autotrophic production to one in which heterotrophic organisms, and possibly phytodetritus, dominate, can well be accompanied by a pulse of sedimentation, reducing the absolute leves of suspended POC in the upper water layers.

Annual sedimentation patterns, therefore, may qualitatively reflect heterotrophic dynamics in the euphotic zone. The use of tintinnids as "indicators" of microzooplankton activity is compromised by their accumulation lower than the depth of maximal microzooplankton biomass, and their small contribution to total microzooplankton numbers. The quantitative contribution of tintinnids and heterotrophic dinoflagellates to total particulate flux, however, is thought to be negligible due to their small size and the absence of cell bodies within the shells.

The study of organic matter sedimentation from the pelagial has been rigorously pursued in the past decades (Smetacek 1980, Honjo 1982, Peinert et al. 1987, Bathmann et al. 1990, v.Bodungen et al. 1986) and has recently received renewed attention, albeit disputably, as an agent in global climate change. Variability within annual cycles of sedimentation has been explained in a number of models (Dugale and Goering 1967, Eppley and Peterson 1979) as being linked to biological and physical dynamics in the upper ocean. It has been recognized,

however, that observed patterns in the qualitative and quantitative nature of vertical flux is much more complex than can be explained by simple parameters (v. Bodungen 1989).

The role of herbivory in regulating both algal stocks and CO_2 fixation is crucial in a consideration of pelagic biology, which in turn determines flux rates out of the upper waters. Among the herbivorous organisms, differences in packaging of particulate matter determines its export potential. Copepods, by the formation of large faecal pellets, have long been thought to accelerate the sinking of organic matter. Whether these particles do in fact reach deeper layers is dependant on the degree of their integrity in the water column and is beyond the scope of this study. This has recently been brought into debate with the recognition of processes leading to fragmentation of these pellets by coprophagy, coprorhexy and coprochaly (Lampitt et al. 1990, Noji et al. 1991a). A review of the role of macrozooplankton in sedimentation is given in Noji (1991b).

4.8 The role of microzooplankton in particle flux

The role of the microzooplankton in vertical flux studies, however, has received scant attention. This may be due to their absence in sediment trap material, and the acknowledgement of their role as primary remineralizers in the euphotic zone. This is, however, an incomplete evaluation of their trophic activity.

Although the microzooplankton are thought to primarily play a role in hindering export of particles, this may not always be the case. I suggest that the degree of coupling between the microzooplankton and larger grazers may regulate this process. If microzooplankton serve largely as a food source to higher trophic levels, they may play an indirect role in the formation of larger particles, with higher potential for export. The concept of the microbial loop, as the prime mediator of processes of remineralization and particle retention in the upper ocean layers may thus need to be expanded to include non-microbial members. The substitution of the **web** concept for the traditional **chain** to describe pelagic trophodynamics is evidence of the recognition that marine systems are characterized by a myriad of interacting communities. The realization that larger metazoans interact closely with "microbial loop" members should thus be no surprize, and furthar research into such dynamics will enhance our understanding of the pelagic system as a whole.

In terms of turnover within the pelagic carbon cycles, the importance of the microzooplankton in the East Greenland Sea during summer and autumn is indisputable. The processes of recycling of nutrients, although hindering sedimentation of the particles that have been directly ingested, increases the retention of essential elements vital to phytoplankton growth. Thus, as long as incident irradiation supports photosynthesis, heterotrophic processes can enhance

autotrophic biomass production. Large pulses of sedimentation, on the other hand, counteract this process and by leading to the export of essential elements can limit further growth even when light conditions are optimal. It is possibly these periodic events, generally following spring blooms and also caused by heavy grazing by swarmer populations (eg. krill, pteropods see Bodungen et al. 1987, Bathmann et al. 1988) that account for much of the annual sedimentation, and decisively alter pelagic food dynamics. The heterotrophic system described in this study, of which the microzooplankton form an important part, could thus provide a "background" with near steady-state conditions.

Sedimentation at the base of the euphotic zone during the drift experiments reported in this study was negligible (<1 % POC standing stocks), and did not decrease drastically during winter. POC standing stocks in the upper 100 m during the winter months were also relatively high (8.8 mg m^{-2} in November 1989, 7.41 mg m^{-2} in February 1991), and, with the low light levels at the high latitude, cannot be accounted for in terms of autotrophic biomass. It may be plausible to suggest that these high POC values were in part accounted for by detrital matter and small, suspended particles, and that a heterotrophic system dominated these communities. Data do not exist to support this hypothesis, and it would require heterotrophic production in excess of known capacities to support a pelagic community. Slow turnover rates, controlled by low temperatures and limited food availability could maintain some biomass, providing a seeding population for the following spring. In the absence of winter investigations, this remains but a speculation.

Given our present knowledge of protozoan behaviour and modification of particulate matter, and in view of the uncertainties in isolating processes in natural water samples, laboratory studies are indispensible to complement field investigations. How, then, can one determine the role of the microzooplankton in vertical flux studies, if their most abundant species are not seen in sedimenting material? The use of pigments as biomarkers to trace their activity is severely compromised by their pigment degradation ability demonstrated in this study. It may be necessary to investigate the use of more stable biomarkers characteristic to protozoan communities if one is to elucidate their contribution in sediment trap material.

During a short-term drift experiment in 1989, differences in autotrophic dynamics as seen in the f-ratio, and phytoplankton composition did not lead to changes in the pelagic system as a whole. Seasonal pelagic investigations showed large differences in incident irradiation, primary production and phytoplankton standing stocks, but pelagic biomass remained relatively constant. It is suggested that heterotrophy, dominated by the microzooplankton community, can act as a "buffer" in such systems, compromising the empirical relationship between production and export.

5. Summary

Microzooplankton form an integral component of pelagic food chains in the East Greenland Sea. Using experimental techniques to determine rate processes between microzooplankton, their predators and prey, it was possible to demonstrate a close coupling of the three communities, which characterized pelagic food web dynamics during summer and autumn in the investigation area. High rates of microzooplankton herbivory did not lead to increases in their standing stocks, but served rather as a link of phytoplankton carbon to higher trophic levels. Although they constituted less than 4 % of total biomass in the euphotic zone, their high turnover rates established them as dominant members of the pelagic food web in the investigation area.

The species composition of microzooplankton in the East Greenland Sea was dominated by naked ciliates and heterotrophic dinoflagellates, with tintinnids comprising less than 10 % of total number. Although the same genera were represented in both June/July 1989 and August/September 1990, species diversity was significantly higher during the latter investigation. Copepod nauplii, present among the microzooplanton in August/September 1990, were absent in June/July 1989.

Rates of herbivory of microzooplankton were measured by the seawater dilution technique of Landry and Hassett (1982), and amounted to between 21 - 39 % and 10 -39 % of chl *a* standing stocks on a daily basis. A modification of this technique using HPLC analysis of algal pigments in August 1990 showed processes of selective grazing among the algae. High rates of consumption of dinoflagellates and prymnesiophytes were seen.

Additionally, the rate of consumption of microprotozoans by copepods of the dominant species, *Calanus hyperboreus*, was investigated, and amounted to ca. 18 % of microprotozoan standing stocks per day in the upper 25 m of the water column.

In controlled laboratory experiments the degradation of algal pigments by microprotozoan grazers was investigated using HPLC analysis. A rapid and complete degradation of chl *a* was seen in all experiments, accompanied by the transitional accumulation of intermediate breakdown products. Degradation of algal carotenoids occurred at rates different from those for chl *a*, altering the Chl:Carotenoid ratio during the experiments. It is postulated that microprotozoans could be a major pathway for the loss of chl *a* in marine environments.

The production of faecal particles by microzooplankton was investigated in a field population using fluorescent microspheres as tracer, as well as in culture experiments in the laboratory. Among the microzooplankton assemblage metazoans such as copepod nauplii were the only producers of aggregated particles; no pellet formation was seen by protozoan grazers in either of the experiments.

An analysis of sediment trap material does not accurately reflect heterotrophic processes within the euphotic zone, as seen by the absence of dominant members of the microzooplankton community. Shipboard and laboratory experimentation are thus essential in understanding the processes which lead to retention of organic carbon or its loss to deeper water layers.

Finally, it was seen that microzooplankton play a dual role in the export of organic matter from the productive layer of the ocean. Due to their small size and negligible aggregation of ingested particles, they hinder export processes, leading rather to the retention of particles and essential nutrients in the euphotic zone. This is countered by their trophic role as a significant link in the transfer of small particles to larger metazoans, which are capable of enhancing sedimentation by the formation of large faecal aggregates. The degree of coupling between the microzooplankton, their predators and prey, is thus seen to play an important role in the relationship between productivity and export.

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Appendix. Table 1: Microzooplankton abundance (ind. dm^{-3}) during the drift experiment in June/July 1989

Depth [m]	[--------- *Strombidium* sp. --------- *S.dalum*	*S.constric-tum*	---------] *S.emergens*	*Lohm. oviformis* [1]	[----- *Laboea* sp. *L.strobilia*	----] *L.conica*	*Mesod.* sp. [2]	*Ac. norvegica.* [3]	[-- Het. flagellates *Protoperidinium* sp.	--] *Gyrodinium* sp.	Total number
Sta 640 23.06.1989											
2	200	0	480	720	0	0	40	0	100	60	1600
7	240	0	620	840	20	40	100	0	260	360	2480
14	120	0	1000	1420	0	40	240	160	300	440	3720
28	160	0	380	580	40	20	300	440	180	80	2180
40	0	0	120	140	0	0	180	200	0	0	640
100	0	0	0	20	0	0	60	20	0	0	100
Sta 652 29.06.1989											
1	0	0	200	120	440	480	80	40	0	2840	4200
4	0	0	120	0	200	240	40	160	0	1280	2040
9	80	80	240	0	960	280	280	360	80	2760	5120
18	80	0	360	0	160	200	600	200	0	160	1760
27	0	0	280	0	80	160	80	400	0	0	1000
40	0	0	60	0	40	60	40	240	0	0	440
100	0	0	0	0	0	0	0	120	0	0	120
Sta 657 01.07.1989											
2	0	0	120	0	140	220	120	20	0	1040	1660
5	0	0	180	0	200	100	80	100	40	880	1580
9	0	0	220	0	660	280	180	80	80	1640	3140
14	0	0	180	0	1180	160	220	60	0	1220	3020
18	0	0	180	0	880	100	380	160	80	660	2440
27	0	0	220	0	60	20	180	220	60	80	840
40	0	0	40	0	20	40	80	120	0	40	340
100	0	0	0	0	0	0	20	40	0	0	60
Sta 661 03.07.1989											
2	0	0	380	0	320	180	240	0	120	2860	4100
5	0	0	280	0	280	200	60	40	60	2720	3640
10	0	0	320	0	220	180	120	60	20	1600	2520
16	0	0	660	0	880	360	680	60	100	3700	6440
20	0	0	520	0	640	300	540	240	120	2440	4800
31	0	0	220	0	60	120	140	280	80	180	1080
45	0	0	60	0	40	40	20	80	0	60	300
100	0	0	0	0	0	0	20	60	0	0	80
Sta 665 05.07.1989											
3	0	0	240	0	160	280	280	20	40	1280	2300
7	0	0	200	0	120	160	260	40	0	1040	1820
10	0	0	340	0	420	220	120	40	0	860	2000
15	0	0	460	0	260	460	280	60	40	1220	2780
18	0	0	360	0	860	620	480	280	0	1160	3760
28	0	0	100	0	640	100	480	240	0	640	2200
50	0	0	20	0	0	60	80	100	0	0	260
100	0	0	0	0	0	0	20	0	0	0	20
Sta 682 07.07.1989											
3	0	0	360	0	280	120	880	120	0	2520	4280
6	0	0	440	0	160	160	400	80	0	2040	3280
10	0	0	760	0	400	400	920	240	0	3240	5960
14	0	0	840	0	480	720	1240	920	0	1760	5960
19	0	0	200	0	280	560	520	960	0	1040	3560
28	0	0	80	0	120	240	360	960	0	680	2440
41	0	0	0	0	40	0	0	720	0	0	760
100	0	0	0	0	0	40	0	40	0	0	80

[1] *Lohmaniella oviformis*

[2] *Mesodinium* sp.

[3] *Acanthestomella norvegica*

Appendix. Table 2: Microzooplankton biomass (µg C dm^{-3}) during the drift experiment in June/July 1989

Depth	[--------- *Strombidium* sp. ---------]			*Lohm.*	[----- *Laboea* sp. ----]		*Mesod.*	*Ac. nor-*	[-- Het. flagellates --]		Total
[m]	*S.dalum*	*S.constrictum*	*S.emergens*	*oviformis* [1]	*L.strobilia*	*L.conica*	sp. [2]	*vegica.* [3]	*Protoperidinium* sp.	*Gyrodinium* sp.	biomass
Sta 640 28.06.89											
2	0.699	0.000	2.755	0.415	0.000	0.000	0.064	0.000	0.069	0.078	4.080
7	0.839	0.000	3.558	0.485	0.140	0.064	0.161	0.000	0.179	0.467	5.893
14	0.419	0.000	5.739	0.819	0.000	0.064	0.386	0.218	0.207	0.571	8.423
28	0.559	0.000	2.181	0.335	0.280	0.032	0.483	0.598	0.124	0.104	4.696
40	0.000	0.000	0.689	0.081	0.000	0.000	0.290	0.272	0.000	0.000	1.331
100	0.000	0.000	0.000	0.012	0.000	0.000	0.097	0.027	0.000	0.000	0.135
Sta 652 29.06.1989											
1	0.000	0.000	1.148	0.069	3.082	0.764	0.129	0.054	0.000	3.683	8.929
4	0.000	0.000	0.689	0.000	1.401	0.382	0.064	0.218	0.000	1.660	4.414
9	0.280	0.119	1.377	0.000	6.725	0.445	0.451	0.489	0.055	3.580	13.521
18	0.280	0.000	2.066	0.000	1.121	0.318	0.965	0.272	0.000	0.208	5.230
27	0.000	0.000	1.607	0.000	0.560	0.255	0.129	0.544	0.000	0.000	3.094
40	0.000	0.000	0.344	0.000	0.280	0.095	0.064	0.326	0.000	0.000	1.111
100	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.163	0.000	0.000	0.163
Sta 675 01.07.1989											
2	0.000	0.000	0.689	0.000	0.981	0.350	0.193	0.027	0.000	1.349	3.588
5	0.000	0.000	1.033	0.000	1.401	0.159	0.129	0.136	0.028	1.141	4.027
9	0.000	0.000	1.263	0.000	4.623	0.445	0.290	0.109	0.055	2.127	8.912
14	0.000	0.000	1.033	0.000	8.266	0.255	0.354	0.082	0.000	1.582	11.571
18	0.000	0.000	1.033	0.000	6.164	0.159	0.611	0.218	0.055	0.856	9.097
27	0.000	0.000	1.263	0.000	0.420	0.032	0.290	0.299	0.041	0.104	2.449
40	0.000	0.000	0.230	0.000	0.140	0.064	0.129	0.163	0.000	0.052	0.777
100	0.000	0.000	0.000	0.000	0.000	0.000	0.032	0.054	0.000	0.000	0.087
Sta 661 03.07.1989											
2	0.000	0.000	2.181	0.000	2.242	0.286	0.386	0.000	0.083	3.709	8.887
5	0.000	0.000	1.607	0.000	1.961	0.318	0.097	0.054	0.041	3.528	7.607
10	0.000	0.000	1.836	0.000	1.541	0.286	0.193	0.082	0.014	2.075	6.028
16	0.000	0.000	3.788	0.000	6.164	0.573	1.094	0.082	0.069	4.799	16.568
20	0.000	0.000	2.984	0.000	4.483	0.477	0.869	0.326	0.083	3.165	12.387
31	0.000	0.000	1.263	0.000	0.420	0.191	0.225	0.381	0.055	0.233	2.768
45	0.000	0.000	0.344	0.000	0.280	0.064	0.032	0.109	0.000	0.078	0.907
100	0.000	0.000	0.000	0.000	0.000	0.000	0.032	0.082	0.000	0.000	0.114
Sta 665 05.07.1989											
3	0.000	0.000	1.377	0.000	1.121	0.445	0.451	0.027	0.028	1.660	5.109
7	0.000	0.000	1.148	0.000	0.841	0.255	0.418	0.054	0.000	1.349	4.065
10	0.000	0.000	1.951	0.000	2.942	0.350	0.193	0.054	0.000	1.115	6.606
15	0.000	0.000	2.640	0.000	1.821	0.732	0.451	0.082	0.028	1.582	7.335
18	0.000	0.000	2.066	0.000	6.024	0.986	0.772	0.381	0.000	1.504	11.734
28	0.000	0.000	0.574	0.000	4.483	0.159	0.772	0.326	0.000	0.830	7.145
50	0.000	0.000	0.115	0.000	0.000	0.095	0.129	0.136	0.000	0.000	0.475
100	0.000	0.000	0.000	0.000	0.000	0.000	0.032	0.000	0.000	0.000	0.032
Sta 682 07.07.1989											
3	0.000	0.000	2.066	0.000	1.961	0.191	1.416	0.163	0.000	3.268	9.066
6	0.000	0.000	2.525	0.000	1.121	0.255	0.644	0.109	0.000	2.646	7.299
10	0.000	0.000	4.362	0.000	2.802	0.636	1.480	0.326	0.000	4.202	13.809
14	0.000	0.000	4.821	0.000	3.362	1.145	1.995	1.251	0.000	2.283	14.858
19	0.000	0.000	1.148	0.000	1.961	0.891	0.837	1.305	0.000	1.349	7.491
28	0.000	0.000	0.459	0.000	0.841	0.382	0.579	1.305	0.000	0.882	4.448
41	0.000	0.000	0.000	0.000	0.280	0.000	0.000	0.979	0.000	0.000	1.259
100	0.000	0.000	0.000	0.000	0.000	0.064	0.000	0.054	0.000	0.000	0.118

[1] *Lohmaniella oviformis*

[2] *Mesodinium* sp.

[3] *Acanthestomella norvegica*

Appendix. Table 3: Linear dimensions (µm) and volume calculations (µm³) for individual protozoan species in June/July 1989

	Length	SD±	Diameter	SD±	Shape	Volume
Strombidium S.emergens	39.95	3.20	34.86	7.74	cylinder	38.130
	9.00		34.86		cone	2.863
					Total	40.993
Strombidium S.constrictum	43.38	3.97	30.55	2.93	cone	10.599
Strombidium S.dalum	48.66	4.42	44.27	3.04	cone	24.967
Mesodinium sp.			28.00	4.48	sphere	11.494
Lohmaniella oviformis			19.89	1.57	sphere	4.120
Laboea L.strobila	52.55	7.86	44.40	2.54	cone	27.121
			44.40		1/2 sphere	22.915
					Total	50.036
Laboea L.conica	36.45	2.70	26.30	2.40	cone	6.601
			26.30		1/2 sphere	4.763
					Total	11.363
Unidentified *Strombidium* sp.	37.90	7.50	24.13	4.40	ellipsoid	11.555
Acanthestomella norwegica	30.00	2.39	18.60	0.84	cylinder	8.152
	6.20		18.60		cone	0.562
					Total	8.713
Ptychocyclis obtusa	31.05	4.88	39.21	8.54	cylinder	37.493
	30.00		39.21		cone	12.075
					Total	49.568
Gyrodinium sp.	50.16	8.10	26.56	3.90	2 cones	9.264
Protoperidinium sp.	32.00	4.42	20.50	3.76	ellipsoid	7.041
					-30 %	4.929

Appendix. Table 4: Microzooplankton abundance (ind. dm^{-3}) during the drift experiment in August/September 1990

Depth	[------ *Strombidium* sp.				------]	*Metast.*	*Lohm.*	[-- *Laboea* sp.	--]	*Didinium*	[-- Heterotrichs	--]	[---- Tintinnids		----]	[--- Het. flagellates		---]	[--- Unidentified		---]	Total
[m]	*S.emergens*	*S.conicum*	*S.delicatissimus*	*S.acuminatum*	*S.cornicopiae*	*sp.* [1]	*oviformis* [2]	*L.strobila*	*L.conica*	sp.	> 40 µm	< 30 µm	*Ac. norvegica* [3]	*Parafavella* sp.	*Ptycho. obtusa* [4]	*Gyrodinium* sp.	*Protop.* sp. [5]	*Dinophysis* sp.	*flagellate*	*Strombidium* sp.	*Didinium* sp.	number
Sta 883 25.08.1990																						
0	60	40	1460	20	40	100	380	140	1220	60	20	0	20	60	0	260	200	120	0	180	0	4380
11	420	260	40	0	40	40	80	40	280	0	0	0	60	40	0	100	40	20	0	0	0	1460
21	1620	1100	600	20	200	520	200	20	20	260	140	100	200	0	20	600	500	20	0	100	0	6240
27	560	440	120	0	40	80	40	0	0	40	20	0	180	40	20	220	140	20	0	20	0	1980
42	320	320	80	20	0	140	140	0	0	100	100	60	280	20	20	200	160	0	0	0	60	2020
60	140	0	100	20	40	20	40	0	0	60	20	40	80	40	60	60	20	0	0	0	0	740
100	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	20
Sta 885 26.08.1990																						
0	200	180	3380	40	140	440	1160	520	1580	100	80	0	80	20	0	500	420	160	0	440	20	9460
10	0	100	960	20	80	240	380	0	460	120	40	0	40	0	0	200	480	80	0	180	0	3380
25	0	40	340	20	20	120	0	0	0	80	60	0	360	100	0	0	280	0	0	0	0	1420
38	80	0	40	0	0	40	0	0	0	0	40	0	140	60	0	60	220	0	0	0	0	680
57	40	80	120	0	0	20	0	0	0	0	0	0	160	40	0	80	160	20	0	0	0	720
75	0	0	60	0	0	0	0	0	0	0	0	0	100	20	0	0	60	0	0	0	0	240
100	0	0	0	0	0	0	0	0	0	0	0	0	40	0	0	0	0	0	0	0	0	40
Sta 891 28.08.1990																						
0	100	200	1560	0	20	160	260	160	440	0	60	60	60	60	0	120	380	60	0	20	0	3720
10	260	80	840	20	60	140	380	220	460	0	80	40	80	20	40	600	460	40	0	20	0	3840
25	500	420	280	40	0	180	60	180	220	40	40	60	240	40	40	360	180	0	0	0	0	2880
38	140	240	200	0	0	20	0	100	0	0	40	0	120	0	40	100	0	20	0	0	0	1020
57	40	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	140
100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

[1] *Metastrombidium* sp.
[2] *Lohmaniella oviformis*
[3] *Acanthestomella nervegica*
[4] *Ptychocylis obtusa*
[5] *Protoperidinium* sp.

Appendix. Table 4: continued

Depth [m]	Strombidium sp. S.emergens	S.conicum	S.delicatissimus	S.acuminatum	S.cornicopiae	Metast. sp.[1]	Lohm. oviformis[2]	Laboea sp. L.strobila	L.conica	Didinium sp.	Heterotrichs > 40 µm	< 30 µm	Tintinnids Ac. norvegica[3]	Parafavella sp.	Ptycho. obtusa[4]	Het. flagellates Gyrodinium sp.	Protop. sp.[5]	Dinophysis sp.	flagellate	Unidentified Strombidium sp.	Didinium sp.	Total number
Sta 895 30.08.1990																						
0	320	720	3680	60	0	100	220	280	80	40	80	0	20	20	0	40	100	60	0	0	0	5820
11	280	260	480	60	20	100	420	140	280	280	100	0	60	20	0	340	260	80	0	0	0	3180
22	880	320	1040	60	100	40	120	20	40	300	40	0	80	0	0	480	320	20	0	0	0	3860
28	240	200	620	0	20	20	140	0	60	80	0	0	240	0	0	200	260	40	0	0	0	2120
43	40	20	380	0	0	40	60	0	0	80	40	0	340	40	0	80	100	0	0	0	0	1220
60	0	20	60	0	0	0	0	0	0	0	0	0	180	40	0	20	0	0	0	0	0	320
100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sta 899 01.09.1990																						
0	480	1120	4300	60	0	40	620	40	0	60	0	0	20	40	0	60	180	60	0	0	0	7080
11	260	280	800	80	0	100	700	40	0	280	120	40	0	20	0	540	460	140	0	0	0	3860
15	340	200	340	100	0	200	280	20	0	100	160	100	0	60	0	520	840	100	0	0	0	3360
22	100	40	300	20	80	120	240	0	0	280	420	0	20	20	20	400	620	20	0	0	0	2700
28	140	100	140	0	60	20	140	0	0	120	180	320	40	0	0	180	380	60	0	0	0	1880
43	100	40	180	20	0	100	40	0	0	160	0	0	160	0	40	140	160	0	0	0	0	1140
65	0	20	60	0	20	20	20	0	0	40	0	0	0	60	0	100	60	0	0	0	0	400
100	20	40	0	0	0	0	60	0	0	20	20	20	60	20	20	20	100	20	0	0	0	420
Sta 907 03.09.1990																						
2	440	20	2160	0	0	60	840	0	0	0	0	0	40	0	0	20	140	160	3820	0	0	7700
10	160	0	2480	0	0	60	780	0	0	20	40	0	0	0	0	0	60	200	1100	0	0	4900
25	160	20	1800	0	0	40	500	0	0	0	0	0	0	0	0	40	60	80	180	0	0	2880
40	120	0	680	0	0	20	200	0	0	0	0	0	20	0	0	60	40	40	120	0	0	1300
75	40	20	120	0	0	0	60	0	0	0	0	0	60	0	0	0	20	0	80	0	0	400
100	0	0	20	0	0	0	0	0	0	0	0	0	40	0	0	0	0	0	0	0	0	60

1 *Metastrombidium* sp.
2 *Lohmaniella oviformis*
3 *Acanthestomella nervegica*
4 *Ptychocylis obtusa*
5 *Protoperidinium* sp.

Appendix. Table 5: Microzooplankton biomass ($\mu g\ C\ dm^{-3}$) during the drift experiment in August/September 1990

Depth [m]	[----- *Strombidium* sp. *S.emergens*	*S.conicum*	*S.delicatissimus*	*S.acuminatum*	*S.corniocopiae* -----]	*Metast. sp.* [1]	*Lohm. oviformis* [2]	[-- *Laboea* sp. *L.strobila*	*L.conica* --]	*Didinium* sp.	[-- Heterotrichs > 40 µm	< 30 µm --]	[---- Tintinnids *Ac. norvegica* [3]	*Parafavella* sp.	*Ptycho. obtusa* [4] ----]	[---- Het. flagellates *Gyrodinium* sp.	*Protop.* sp. [5]	*Dinophysis* sp. ----]	[---- Unidentified *flagellate*	*Str.* sp.	*Didinium* sp. ----]	Total biomass
Sta 883 25.08.1990																						
0	0.025	0.076	0.197	0.008	0.018	0.263	0.131	1.617	4.328	0.012	0.029	0.000	0.015	0.201	0.000	0.047	0.950	0.276	0.000	1.383	0.000	9.576
11	0.176	0.496	0.005	0.000	0.018	0.105	0.028	0.462	0.993	0.000	0.000	0.000	0.046	0.134	0.000	0.018	0.190	0.046	0.000	0.000	0.000	2.671
21	0.681	2.097	0.081	0.008	0.089	1.369	0.069	0.231	0.071	0.052	0.203	0.019	0.152	0.000	0.139	0.109	2.375	0.046	0.000	0.768	0.000	7.743
27	0.235	0.839	0.016	0.000	0.018	0.211	0.014	0.000	0.000	0.008	0.029	0.000	0.137	0.134	0.139	0.040	0.665	0.046	0.000	0.154	0.000	2.484
42	0.134	0.610	0.011	0.008	0.000	0.368	0.048	0.000	0.000	0.020	0.145	0.011	0.213	0.067	0.139	0.036	0.760	0.000	0.000	0.000	0.000	2.571
60	0.059	0.000	0.013	0.008	0.018	0.053	0.014	0.000	0.000	0.012	0.029	0.008	0.061	0.134	0.416	0.011	0.095	0.000	0.000	0.000	0.000	0.930
100	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015
Sta 885 26.08.1990																						
0	0.084	0.343	0.456	0.016	0.062	1.158	0.399	6.008	5.605	0.020	0.116	0.000	0.061	0.067	0.000	0.091	1.995	0.368	0.000	3.381	0.000	20.229
10	0.000	0.191	0.129	0.008	0.036	0.632	0.131	0.000	1.632	0.024	0.058	0.000	0.030	0.000	0.000	0.036	2.280	0.184	0.000	1.383	0.000	6.753
25	0.000	0.076	0.046	0.008	0.009	0.316	0.000	0.000	0.000	0.016	0.087	0.000	0.274	0.334	0.000	0.000	1.330	0.000	0.000	0.000	0.000	2.496
38	0.034	0.000	0.005	0.000	0.000	0.105	0.000	0.000	0.000	0.000	0.058	0.000	0.107	0.201	0.000	0.011	1.045	0.000	0.000	0.000	0.000	1.565
57	0.017	0.153	0.016	0.000	0.000	0.053	0.000	0.000	0.000	0.000	0.000	0.000	0.122	0.134	0.000	0.014	0.760	0.046	0.000	0.000	0.000	1.314
75	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.076	0.067	0.000	0.000	0.285	0.000	0.000	0.000	0.000	0.436
100	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030
Sta 891 28.08.1990																						
0	0.042	0.381	0.210	0.000	0.009	0.421	0.089	1.848	1.561	0.000	0.087	0.011	0.046	0.201	0.000	0.022	1.805	0.138	0.000	0.154	0.000	7.025
10	0.109	0.153	0.113	0.008	0.027	0.368	0.131	2.542	1.632	0.000	0.116	0.008	0.061	0.067	0.278	0.109	2.185	0.092	0.000	0.154	0.000	8.150
25	0.210	0.801	0.038	0.016	0.000	0.474	0.021	2.080	0.780	0.008	0.058	0.011	0.183	0.134	0.278	0.065	0.855	0.000	0.000	0.000	0.000	6.010
68	0.059	0.458	0.027	0.000	0.000	0.053	0.000	1.155	0.000	0.000	0.058	0.000	0.091	0.000	0.278	0.018	0.000	0.046	0.000	0.000	0.000	2.242
57	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.076	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.093
100	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

1 *Metastrombidium* sp.
2 *Lohmaniella oviformis*
3 *Acanthestomella nervegica*
4 *Ptychocylis obtusa*
5 *Protoperidinium* sp.

Appendix. Table 5: continued

Depth [m]	[--- *Strombidium* sp. --- *S.emergens*	*S.conicum*	*S.delicatissimus*	*S.acuminatum*	*S.cornicopiae* ---]	*Metast. sp.* [1]	*Lohm. oviformis* [2]	[-- *Laboea* sp. -- *L.strobila*	*L.conica* --]	*Didinium* sp.	[-- Heterotrichs -- > 40 µm	< 30 µm --]	[--- Tintinnids --- *Ac. norvegica* [3]	*Parafavella* sp.	*Ptycho. obtusa* [4] ---]	[--- Het. flagellates --- *Gyrodinium* sp.	*Protop.* sp. [5]	*Dinophysis* sp. ---]	[--- Unidentified --- *flagellate*	*Str.* sp.	*Didinium* sp. ---]	Total biomass
Sta 895	**30.08.1990**																					
0	0.134	1.373	0.496	0.024	0.000	0.263	0.076	3.235	0.284	0.008	0.116	0.000	0.015	0.067	0.000	0.007	0.475	0.138	0.000	0.000	0.000	6.711
11	0.118	0.496	0.065	0.024	0.009	0.263	0.144	1.617	0.993	0.056	0.145	0.000	0.046	0.067	0.000	0.062	1.235	0.184	0.000	0.000	0.000	5.523
22	0.370	0.610	0.140	0.024	0.044	0.105	0.041	0.231	0.142	0.060	0.058	0.000	0.061	0.000	0.000	0.087	1.520	0.046	0.000	0.000	0.000	3.540
28	0.101	0.381	0.084	0.000	0.009	0.053	0.048	0.000	0.213	0.016	0.000	0.000	0.183	0.000	0.000	0.036	1.235	0.092	0.000	0.000	0.000	2.450
43	0.017	0.038	0.051	0.000	0.000	0.105	0.021	0.000	0.000	0.016	0.058	0.000	0.259	0.134	0.000	0.014	0.475	0.000	0.000	0.000	0.000	1.188
60	0.000	0.038	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.137	0.134	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.321
100	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sta 899	**01.09.1990**																					
0	0.202	2.135	0.580	0.024	0.000	0.105	0.213	0.462	0.000	0.012	0.000	0.000	0.015	0.134	0.000	0.011	0.855	0.138	0.000	0.000	0.000	4.886
11	0.109	0.534	0.108	0.032	0.000	0.263	0.241	0.462	0.000	0.056	0.174	0.008	0.000	0.067	0.000	0.098	2.185	0.322	0.000	0.000	0.000	4.658
15	0.143	0.381	0.046	0.040	0.000	0.526	0.096	0.231	0.000	0.020	0.232	0.019	0.000	0.201	0.000	0.094	3.989	0.230	0.000	0.000	0.000	6.249
22	0.042	0.076	0.040	0.008	0.036	0.316	0.083	0.000	0.000	0.056	0.609	0.000	0.015	0.067	0.139	0.072	2.945	0.046	0.000	0.000	0.000	4.550
28	0.059	0.191	0.019	0.000	0.027	0.053	0.048	0.000	0.000	0.024	0.261	0.061	0.030	0.000	0.000	0.033	1.805	0.138	0.000	0.000	0.000	2.748
43	0.042	0.076	0.024	0.008	0.000	0.263	0.014	0.000	0.000	0.032	0.000	0.000	0.122	0.000	0.278	0.025	0.760	0.000	0.000	0.000	0.000	1.644
65	0.000	0.038	0.008	0.000	0.009	0.053	0.007	0.000	0.000	0.008	0.000	0.000	0.000	0.201	0.000	0.018	0.285	0.000	0.000	0.000	0.000	0.626
100	0.008	0.076	0.000	0.000	0.000	0.000	0.021	0.000	0.000	0.004	0.029	0.004	0.046	0.067	0.139	0.004	0.475	0.046	0.000	0.000	0.000	0.918
Sta 907	**03.09.1990**																					
2	0.185	0.038	0.291	0.000	0.000	0.158	0.289	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	0.004	0.665	0.368	0.465	0.000	0.000	2.493
10	0.067	0.000	0.334	0.000	0.000	0.158	0.268	0.000	0.000	0.004	0.058	0.000	0.000	0.000	0.000	0.000	0.285	0.460	0.134	0.000	0.000	1.769
25	0.067	0.038	0.243	0.000	0.000	0.105	0.172	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.285	0.184	0.022	0.000	0.000	1.124
40	0.050	0.000	0.092	0.000	0.000	0.053	0.069	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.011	0.190	0.092	0.015	0.000	0.000	0.586
75	0.017	0.038	0.016	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.046	0.000	0.000	0.000	0.095	0.000	0.010	0.000	0.000	0.242
100	0.000	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.033

1 ***Metastrombidium* sp.**
2 ***Lohmaniella oviformis***
3 ***Acanthestomella nervegica***
4 ***Ptychocylis obtusa***
5 ***Protoperidinium* sp.**

Appendix. Table 6: Linear dimensions (µm) and volume calculations (µm³) for individual protozoan species in August/September 1990

	Length	SD±	Diameter	SD±	Shape	Volume
Strombidium S.emergens	12.82	3.20	15.38	7.74	cylinder	2.381
	10.00		15.38		cone	0.619
					Total	3.001
Strombidium S.conicum	46.21	5.52	33.55	8.06	cone	13.617
Strombidium S.delicatissimus	16.62	4.02	14.88	3.62	cone	0.963
Strombidium S.acuminatum	24.24	3.10	21.15	4.08	cone	2.838
Strombidium S.cornicopiae	73.32	6.61	12.86	4.21	cone	3.174
Metastrombidium sp.			32.99	5.42	sphere	18.799
Lohmaniella oviformis			16.74	3.28	sphere	2.456
Laboea L.strobila	110.54	2.06	53.40	6.47	cone	82.522
Laboea L.conica	62.00	5.84	39.51	3.87	cone	25.338
Didinium sp.	21.05	3.68	12.74	1.53	ellipsoid	1.788
					-20 %	1.431
Heterotrichs (> 40µm)	40.68	3.31	24.66	5.64	ellipsoid	12.952
					-20 %	10.362
Heterotrichs (< 30µm)	25.13	3.31	11.34	1.68	ellipsoid	1.692
					-20 %	1.353
Acanthestomella norwegica	18.42	5.78	17.85		cylinder	4.609
	10.00		17.85		cone	0.834
					Total	5.443
Parafavella sp.	65.21	6.08	37.40	8.26	cone	23.879
Ptychocyclis obtusa	31.05	4.88	39.21	8.54	cylinder	37.492
	30.00		39.21		cone	12.074
					Total	49.567
Gyrodinium sp.	27.93	8.51	13.31	6.85	2 cones	1.295
Protoperidinium sp.	46.28	7.30	44.72	6.81	ellipsoid	48.461
					-30 %	33.923
Dinophysis sp.	40.78	3.15	33.17	1.08	ellipsoid	23.492
					-30 %	16.445
Unidentified *flagellate*	6.22	1.00	13.34	1.02	cylinder	0.869
Unidentified *strombidium*	35.71	8.83	40.61	4.90	cylinder	46.253
	20.00		40.61		cone	8.635
					Total	54.888

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