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Contribution of algal sinking and zooplankton grazing to downward flux in the Lazarev Sea (Southern Ocean) during the onset of phytoplankton bloom: a lagrangian study

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ABSTRACT: Hydrography, chlorophyll *a*, phytoplankton and zooplankton dynamics and the vertical flux of particulate organic carbon (POC) and pigments in the upper 200 m were investigated for 12 consecutive days during a drogue study conducted in the open waters of the ice-edge zone of the Lazarev Sea during the austral summer (December/January) 1994/95. Results of the study indicate that during the experiment, primary production, although variable, increased from ~300 to ~800 mg C $m^{-2} d^{-1}$. This increase could likely be related to development of a shallow pycnocline. Analysis of sediment trap data showed that the vertical carbon flux resulting from sedimentation and grazing activity was greatest in the upper water column (<80 m). The importance of grazers to total POC flux was highest at the beginning and the end of the investigation and accounted for up to 15% of total carbon flux. The contribution of grazers to vertical flux was negligible (<2%) during the intermediate part of the Southern Ocean Drogue study. Lower contribution of grazers to sedimentation of POC at depth can likely be related to community composition of zooplankton. Sedimentation of phytoplankton cells from the upper water column increased during the study. Here, downward POC flux resulting from sedimentation of microphytoplankton was equivalent to 15–75% of the total. Increase in sedimentation of phytoplankton during the study can be related to an increase in the average size of phytoplankton cells. Transport of POC from surface waters to deeper depths resulting from sedimentation or grazing activity was equivalent to <48% of total daily primary production, measured at 50 m, while the same value for phytoplankton flux did not exceed 27% of the total. Zooplankton density was insufficient to exert either a positive (via faecal pellets) or negative (via reducing suspended phytoplankton concentration) effect on particulate carbon sedimentation. This resulted in algal sink being the most important mechanism in downward POC flux during the onset of the phytoplankton bloom period in the Marginal Ice Zone, even in the presence of pelagic tunicates.

KEY WORDS: Seasonal ice zone · Antarctica · Lazarev Sea · Vertical flux · POC · Phytoplankton · Zooplankton · Grazing

INTRODUCTION

Each year about $^1/_3$ of the Southern Ocean (the region south of the Subantarctic Front) experiences an advance and retreat of the sea-ice (Comiso & Zwally 1984). Dense phytoplankton blooms often accompany the receding ice and may persist in the Marginal Ice Zone (MIZ) for several weeks, extending for up to 200 n miles in width (Smith & Nelson 1985). It has been suggested that production associated with the MIZ may contribute between 40 and 60% to the annual primary production of the Southern Ocean (Smith & Nelson 1986, Savidge et al. 1996). The fate of the photo-

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synthetically fixed carbon in this region is therefore of particular importance for the total carbon budget of the Southern Ocean (Smetacek et al. 1990). It was recently shown that in the continental seas the majority of primary production is partitioned through particulate rather than dissolved organic carbon, postulating the importance of zooplankton grazing in carbon transfer (Carlson et al. 1998).

Boyd & Harrison (1999) suggested that the fate of phytoplankton in inshore regions of the ocean during the post-bloom periods is sedimentation and that pelagic recycling predominates outside bloom periods, while in offshore regions pelagic recycling predominates year-round. In the Southern Ocean, Smetacek et al. (1990) identified 2 basic loss type systems, e.g. 'loss' and 'retention' sensu Peinert et al. (1989), which eventually determined the magnitude and composition of vertical flux. The loss type system is characterized by the high downward carbon flux through either sedimentation of phytoplankton cells and phyto-detritus or feces of large metazoans, such as krill and salps. In the retention type system, high grazing pressure by copepods appears to induce high retention of carbon in the top layers of water and consequently low downward carbon flux (Smetacek et al. 1990).

Preliminary calculations conducted in the Lazarev Sea using the gut fluorescence technique suggested that prior and immediately after the 1994/95 drogue study, the sinking of phytoplankton cells may have represented the most important mechanism for the downward carbon transfer to depth (Froneman et al. 1997). However, results of other sediment trap studies indicate that within the MIZ, krill and copepods may contribute substantially to total downward particle flux (Schnack 1985, von Bodungen et al. 1986, Wefer 1989, Bathmann et al. 1991, Cadée et al. 1992).

From late December 1994 to early January 1995, a drogue with sediment traps was deployed for 12 d within the MIZ of the Lazarev Sea to investigate, in a 'lagrangian mode', the fate of biogenic material in the top 200 m layer of water during the onset of the phytoplankton bloom. This region is generally characterized by high krill biomass, and consequently the downward carbon flux was expected to be mainly grazer-mediated (Makarov & Sysoeva 1983, Bathmann et al. 1991, Knox 1994). However, during the 1994/95 summer season, krill densities in the area of investigation were extremely low, never exceeding 0.7 ind. m^{-3} (Froneman et al. 1997). In contrast, concentrations of the salp *Salpa thompsoni* reached levels of ca. 4 ind. m^{-3}, suggesting that regional carbon flux may have been altered as salps are considered to be more efficient repackagers of pelagic particles than krill (Perissinotto & Pakhomov 1998a,b). The time series measurements in a lagrangian mode, e.g. following a drifting sediment trap to minimize the effects of horizontal advection, are scarce in the Southern Ocean (Karl et al. 1991) and elsewhere (Bender et al. 1992, Fasham et al. 1999). The main aims of this investigation are: (1) to study composition of sedimented material, and (2) to quantify the role played by biotic components of the ecosystem (algal sinking and grazing) in downward carbon flux during the onset of phytoplankton bloom in the ice-edge zone of the Lazarev Sea.

MATERIALS AND METHODS

Phytoplankton, chlorophyll *a* (chl *a*), phaeopigments and particulate organic carbon (POC) dynamics and fluxes were investigated during the Southern Ocean Drogue and Ocean Flux Study (SODOFS) aboard the MV 'SA Agulhas' (Voyage 57), conducted between 28 December 1994 and 8 January 1995, in the seasonal ice zone of the Lazarev Sea (see Fig. 1). In order to track the same water body, a drogue (parachute type) was deployed at 300 m depth on 28 December 1997 and was followed for 12 d. While tracking the drogue, continuous temperature and salinity measurements as well as phytoplankton, chl *a* and POC samples were collected at fixed depths twice daily (around midday and midnight) using a Neil Brown MK III CTD-profiler with 8 l Niskin bottles mounted on a 12 bottle rosette system (General Oceanics, Miami Florida). In order to avoid diel variability, results of the day and night sampling were averaged (except for POC) to represent daily observations. At each station, water samples were collected at 6 standard depths: 0, 10, 20, 50, 100, 125 and 200 m.

Water column phytoplankton, pigments, primary production and POC. Fifty millilitre aliquots of seawater from each standard depth were fixed with a glutaraldehyde-Lugol solution for taxonomic analysis of phytoplankton (Rousseau et al. 1990). In the laboratory, phytoplankton cells were counted with a non-inverted light microscope furnished with a counting grid (Semina 1978). The whole sample was gently mixed and pico- (<2 µm) and the most abundant nanoplankton (2 to 20 µm) algae were counted in a Fuchs-Rosental counting chamber at 400× magnification. The samples were then left to settle for a week and slowly decanted through a glass tube covered with 2 layers of fine mesh nylon gauze. After gentle mixing, part of the remaining sample was removed with a glass tube and placed into a 0.05 ml chamber. Microplankton cells (>20 µm) were counted at 200× magnification. In order to count rare phytoplankton forms, a special 1.0 ml chamber was used. Many algae could, however, only be identified to genus level. Flagellates and coccolithiphorides were encountered in the size groups

2–4, 4–6, 6–10, 10–15 and 15–30 µm only. The biovolume of algae cells was calculated from the volumes of appropriate stereometrical bodies (Smayda 1978). The average cell volume of each group was used to calculate the carbon content of the cells according to Strathmann (1967). No attempt was made to distinguish between heterotrophic and autotrophic cells. Thus, estimates of dinoflagellate and flagellate abundance and carbon content, and thereby the total phytoplankton carbon (PPC), may include mixotrophic and heterotrophic cells.

Water column (0 to 200 m) chl *a* and phaeopigments were extracted from 250 ml aliquots in 90% acetone for 12 h in the dark at –18°C. Concentrations were calculated from fluorescence readings on a Turner Designs 111 fluorometer before and after acidification with HCl (Parsons et al. 1984). Pigment fractionation into pico- (<2 µm), nano- (2 to 20 µm) and micro- (>20 µm) size classes was carried out by serial filtration (vacuum <5 cm Hg) at all stations. For this purpose, Whatman GF/C, 2.0 µm Nucleopore and 20 µm Nitex filters were used in a multiple serial filtration manifold.

Estimates of primary production rates were carried out daily following the Joint Global Ocean Flux Study protocol (JGOFS 1990). A detailed description of the procedure can be found in Froneman et al. (1997).

For analysis of total POC, 200 ml aliquots from each standard depth were filtered on pre-combusted Whatman GF/F filters, stored in a freezer (–20°C) and later analysed on a Leeman Laboratory CEC 440 CHN analyser after removal of carbonate with fumes of concentrated HCl.

Sediment trap phytoplankton, pigments and POC. Nine sets of sediment traps were deployed during the drogue study (see Fig. 1). Vertical flux of particulate organic material and pigments were collected at 6 depths between 20 and 80 m (at 10 m intervals) and at 3 depths between 80 and 200 m (at 40 m intervals) using sediment traps. The sediment traps (KC maskiner og laboratorieudstyr, Copenhagen, Denmark) comprised of parallel cylinders mounted in a gimballed frame, equipped with a vane to ensure that the cylinders were always positioned vertically and never shaded each other. The traps measured 0.072 m in diameter and 0.45 m in height (H/D ratio = 6.25). The traps were deployed for 47 to 48 h. Poison was not applied and therefore grazing and bacterial decomposition may have occurred in the sediment traps during the deployment.

After recovery, contents of the sediment traps were transferred to bottles and kept cold and dark. Samples were never kept more than 4 h before subsampling. Each sample was thoroughly mixed and a bird pipette was used for subsampling. Fifty ml aliquots of the sample from each depth were fixed with a glutaraldehyde-Lugol solution for taxonomic analysis of phytoplankton as described above. Total PPC was calculated using the average cell volume:carbon content ratio of each group according to Strathmann (1967). Quadruplicate samples (~200 ml) from each cylinder were taken and filtered for analysis of POC, chl *a* and phaeopigments on pre-combusted Whatman GF/F filters followed by manual removal of all visible metazoans. Samples for chl *a* and phaeopigments were analysed immediately after subsampling using a Turner Designs AU-10 fluorometer as described above. POC samples were stored in a freezer (–20°C) and were later analysed on a Leenam Laboratory CEC 440 CHN analyser after removal of carbonate with fumes of concentrated HCl.

Fifty ml aliquots of the trap sample from 50, 70, 120, 160 and 200 m depths (e.g. below the euphotic zone) were used to enumerate faecal pellets, metazoan (mainly Copepoda) eggs and foraminiferans. These were counted and measured using a dissecting microscope. The length and width of pellets were measured to calculate faecal pellet volume (FPV) according to Edler (1979). To calculate faecal pellet carbon (FPC), the total FPV and an average POC:FPV ratio of 0.069 mg C mm^{-3} was applied (E. Arashkevich unpubl. results). An average value of 0.32 µg C egg^{-1} and 0.08 µg C $foraminifera^{-1}$ were applied to calculate metazoan egg and foraminiferan carbon (EFC) (E. Arashkevich unpubl. results).

Daily loss rates (%) were calculated using integrated concentrations of chl *a* from the depth above the sediment trap or using depth integrated primary production. Potential faecal pellet production was estimated from herbivorous zooplankton grazing rates assuming an average assimilation efficiency of 70% (Downs & Lorenzen 1985).

Zooplankton grazing. Meso- (0.5 to 20 mm) and macrozooplankton (>20 mm) were collected and grazing rates of the most abundant herbivorous species were measured at the three 24 h stations. Samples were collected every 4 h with oblique Bongo net (300 and 500 µm mesh) tows between 300 and 0 m. The 24 h stations coincided with Drogues 2, 4 and 6. The 300 µm mesh sample was immediately fixed in 4% hexamine buffered formalin for taxonomic identification and enumeration of zooplankton in the laboratory. The 500 µm mesh sample was used to estimate zooplankton grazing impact on phytoplankton using the *in situ* gut fluorescence technique (Perissinotto 1992, Perissinotto & Pakhomov 1996).

At each 24 h station, 3 to 10 specimens of each species were processed within 5 min of collection to monitor initial gut pigment concentrations. The gut evacuation rate experiments consisted of *in vitro* incubations of freshly caught specimens of the 10 most abundant herbivorous species in 20 l polyethylene containers,

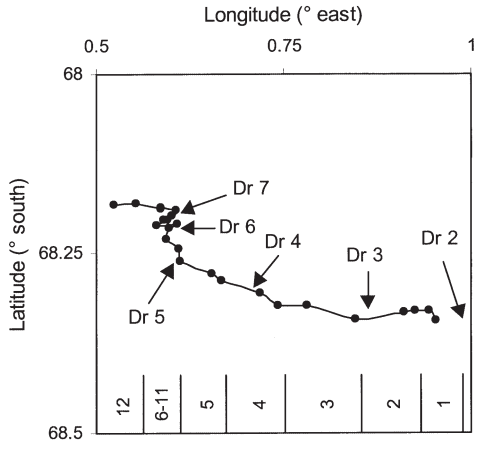

Fig. 1. Drogue track in the Lazarev Sea between 28 December 1994 and 12 January 1995. Points and arrows show the CTD stations and drogue deployment locations respectively

filled with surface water and filtered through a 0.2 µm Milli-Q filtration system to which charcoal particles (<100 µm) were added to keep zooplankton under continuous feeding conditions (Perissinotto & Pakhomov 1996). The incubations ranged from 1 to 5 h, with gut fluorescence measured at 5 to 20 min intervals for the first 1 to 2 h and at 0.5 to 1 h intervals thereafter until the end of the experiment. Three to 5 specimens were collected at each time interval. Gut evacuation rate constants (k, h^{-1}) were then derived from the slope of the regression versus time (Perissinotto & Pakhomov 1996).

To estimate gut pigment destruction efficiency (b'), freshly caught animals were incubated in particle-free seawater for 4 to 24 h to allow the animals to empty their guts. Specimens (5 to 10 copepods and 1 to 2 euphausiids or salps per jar) were then incubated for 1 to 2 h in 1 l polyethylene containers containing natural seawater. The gut pigment destruction efficiency was estimated using the 2 compartment (phytoplankton and grazer) pigment budget approach. A comparison of the pigment budgets in the control (without grazers) and experimental treatment was then carried out. Any significant loss in the pigment budget from the experimental treatment (with grazers) was then attributed to gut destruction of phytoplankton pigments (Perissinotto & Pakhomov 1996). Previous studies conducted in the Antarctic have demonstrated that the gut passage time of copepods may be <1 h, suggesting that the gut destruction efficiency of the copepods may have been overestimated during this study. However, since no faecal pellets were observed at the end of the incubations, the overestimation appears to have been negligible.

In all the experiments, gut pigments were extracted in 10 ml polyethylene tubes (1 ind. $tube^{-1}$ for macroplankton; 3 to 10 ind. $tube^{-1}$ for mesozooplankton) with 8 to 10 ml of 100% methanol and stored at –20°C for 12 h. After centrifugation at 5000 rpm (1745 × g), the pigment content of the methanol was measured before and after acidification using a Turner Designs 111 fluorometer (Mackas & Bohrer 1976). Pigment contents were then expressed in terms of total pigments per individual and calculated according to Strickland & Parsons (1968) as modified by Conover et al. (1986). Where the chlorophyll:phaeopigment ratio in the gut content was higher than 0.25, total pigment levels were corrected according to Baars & Helling (1985).

Daily ingestion rates (I, ng pig. $ind.^{-1}$ d^{-1}) were estimated from the relation of Perissinotto (1992): $I = kG/(1-b')$, where G is an integrated value (over 24 h period assuming a linear decay in gut pigment) of gut pigments (ng pig $ind.^{-1}$ d^{-1}), k is the gut evacuation rate

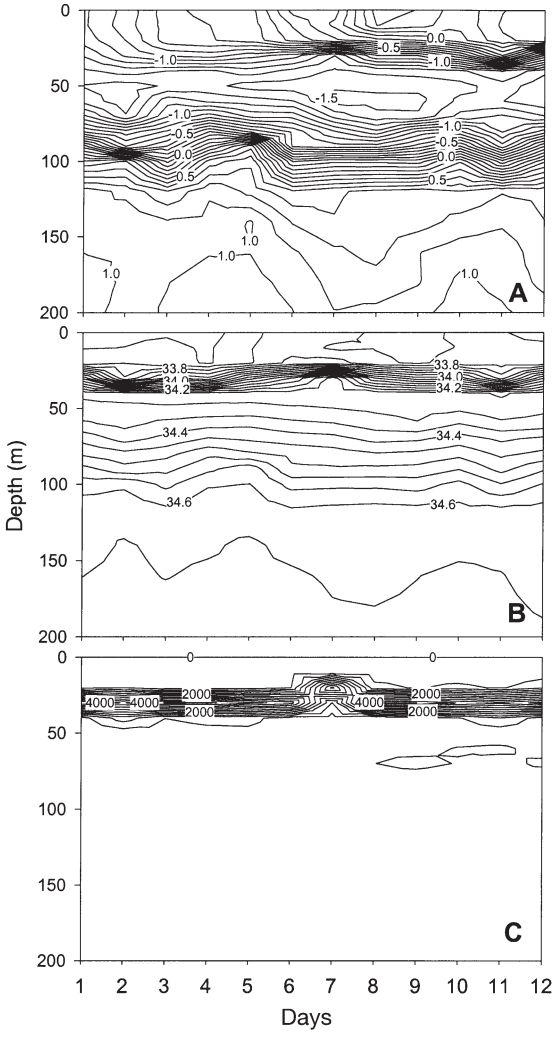

Fig. 2. Vertical distribution (m) of (A) temperature (°C), (B) salinity (psu) and (C) stability (×10^{-8} m^{-1}) during the 1994/95 drogue study in the Lazarev Sea

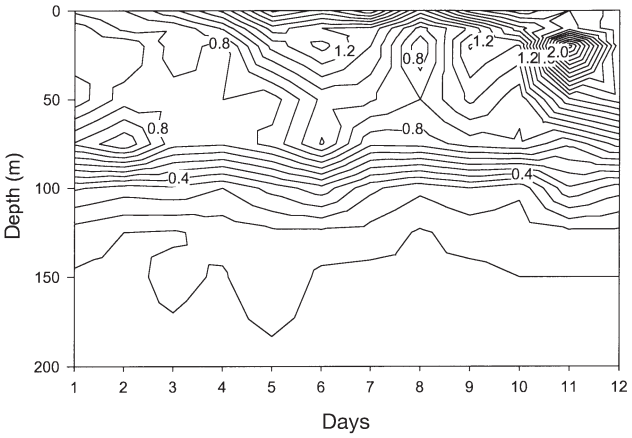

Fig. 3. Vertical distribution (m) of total chl *a* during the 1994/95 drogue study in the Lazarev Sea

constant (h^{-1}), and b' is efficiency of gut pigment destruction. In order to estimate the community grazing impact, species abundance data were combined with the individual ingestion rates. To convert pigment concentrations into autotrophic carbon (C), the POC:pigment (chl *a* + phaeopigments) ratio, obtained during Drogues 2, 4 and 6 in the top 200 m water column (137, 118 and 112 respectively), was employed. The grazing impact was then expressed as % integrated chl *a* stock and % daily primary production consumed per day.

RESULTS

Physical environment

During the course of the study, the drogue drifted ~25 n miles in a westerly direction for 12 d (Fig. 1). Conditions during the entire experiment were characterised by low wind speeds, ranging from 1.4 to 19.8 knots, and high surface light intensities, varying between 564 and 2797 µE m^{-2} d^{-1} (Froneman et al. 1996). At the time of the drogue deployment, the sea surface was free of pack ice. The pack ice edge was found approximately 20 n miles to the south from the point of the drogue deployment (G. Rigg pers. comm.).

At the beginning of the drogue study, seawater temperatures ranged from below zero down to 100 m and were only half a degree colder between 40 and 70 m depths than in the upper layer (Fig. 2A). No strong thermocline was evident at the beginning of the study, while a well-developed halocline was already established (Fig. 2B). The distinct trend was an increase in the surface seawater temperature, clearly indicating that the summer capping of colder winter waters had occurred during the study (Fig. 2A,B). From Day 5 onwards, the upper water column appeared to be strongly stratified with a sharp pycnocline evident in the upper 20 to 30 m layer (Fig. 2). A subsurface (40 to 60 m) colder and more saline water intrusion occurred between Days 5 and 10, being most extensive during Days 7 to 9 (Fig. 2A). This intrusion did not dramatically affect the physico-chemical structure of the upper water column. However, coupled with the summer capping the intrusion resulted in the shallowing of pycnocline after Day 7 (Fig. 2C).

Chl *a* and primary production dynamics

With the exception of the first 3 d of the experiment, >50% of total chl *a* biomass was concentrated within the top 50 m (Fig. 3). A subsurface (at ~75 m) enhancement of chl *a* was also observed at the beginning of the drogue study. However, after the development of a strong pycnocline on Day 5, chl *a* concentrations exceeding 1 mg m^{-3} were found almost exclusively in the upper mixed layer (Fig. 3). After Day 10, however, maximum chl *a* biomass was recorded at depths corresponding to approximately 50 m (Fig. 3). Surface total chl *a* biomass doubled between Day 1 and 5 (from 0.8 to 1.6 mg m^{-3}) and then showed a tendency to stabilise (Fig. 4A). However, the depth-integrated chl *a* biomass displayed an increasing trend throughout the experiment (Fig. 4B). Size-fractionated surface chl *a* data indicate that all the changes in biomass were

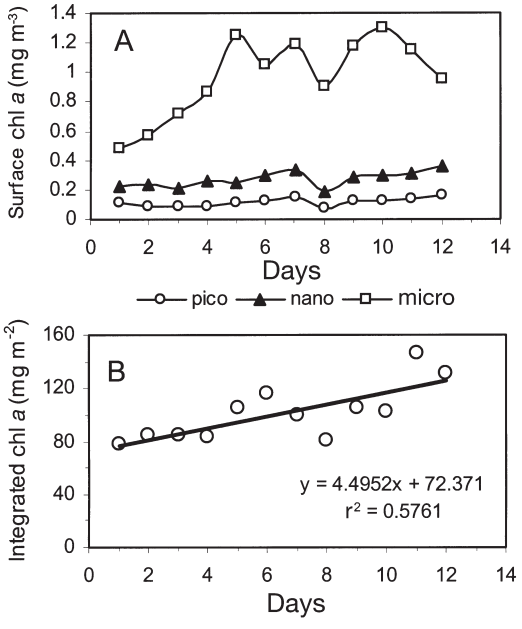

Fig. 4. (A) Surface size-fractionated and (B) total depth-integrated chl *a* temporal distribution during the 1994/95 drogue study in the Lazarev Sea

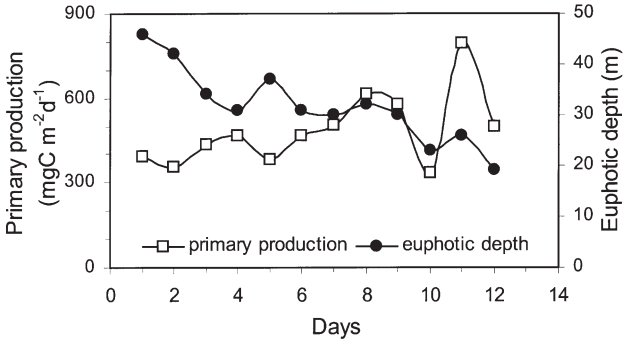

Fig. 5. Daily primary production and euphotic depth temporal variability during the 1994/95 drogue study in the Lazarev Sea

associated with the microphytoplankton size fraction (Fig. 4A). Surface- and depth-integrated chl *a* densities showed significant positive correlation ($p < 0.05$) with temperature (surface and depth averaged) and surface salinity, which accounted for ≥58% of chl *a* variability. During the course of the drogue study the euphotic depth decreased from 46 to 20 m (Fig. 5). Total primary production raged from 355 to 796 mg C m^{-2} d^{-1} with the highest values recorded towards the completion of the study (Fig. 5).

Suspended and sedimented phytoplankton

Flagellates of nano- and pico-size classes dominated the phytoplankton community, accounting for >90% of total cells counted during the drogue study. Their abundance decreased by ~3.5-fold throughout the experiment. This explained 97% of total phytoplankton abundance variability ($r^2 = 0.97$, $p < 0.005$) during the drogue study.

Total PPC flux at 200 m depth ranged from 24 to 48 mg C m^{-2} d^{-1} and was the lowest during Drogue 5. Phytoplankton composition recovered in the sediment trap at 200 m was similar to that found in the top 200 m layer of water with flagellates and diatoms accounting for 49 to 85 and 8 to 48% of total PPC, respectively (Fig. 6).

Vertical flux of particulate biogenic matter

During the entire drogue study, the vertical flux of POC and chl *a* was the highest in the upper water column (<80 m) and decreased with depth (Figs. 7 & 8). The vertical flux of phaeopigments was generally highest between 50 and 80 m depths and only on 2 occasions (Drogues 3 and 7) at 20 m (Fig. 8). The chlorophyll:phaeopigment ratio was highest (>1.5) in the 20 and 30 m depth strata. The ratio decreased with increasing depth, with values <1 below 80 m depth with only 2 exceptions observed during Drogues 2 and 7 (Fig. 9). POC flux ranged from 155 to 295 mg C m^{-2} d^{-1} and from 60 to 110 mg C m^{-2} d^{-1} at 20 and 200 m depths, respectively (Fig. 7). During the course of the drogue study POC flux almost doubled, while chl *a* and phaeopigment fluxes nearly tripled. Chl *a* and phaeopigment fluxes ranged from 0.55 to 1.59 mg m^{-2} d^{-1} and from 0.26 to 0.76 mg m^{-2} d^{-1} at 20 m depth respectively (Fig. 8).

Contribution of PPC flux to the total POC flux was generally highest either in the upper 70 m of the water column (range 11 to 70% of the total) or between 160 and 200 m (15 to 86%) (Fig. 10, Table 1). With the exception of Drogue 7, contribution of FPC flux to total POC flux was always <1% within the top 160 m. The highest contribution of faecal pellets (up to 9%, Drogue 2) was generally observed at 200 m depth (Fig. 10, Table 1). During Drogue 7, FPC contribution was consistently higher throughout the water column, accounting for 6 to 16% of the total POC flux (Fig. 10, Table 1). Throughout the drogue study, oval faecal pellets (mainly copepod pellets, 100 × 50 µm in size) accounted for >70% of all pellets found in the sediment traps at all depths. Metazoan EFC generally contributed ≤7% to the total POC flux, with the highest contribution (<13%) recorded during Drogues 5 and 7 (Fig. 10, Table 1).

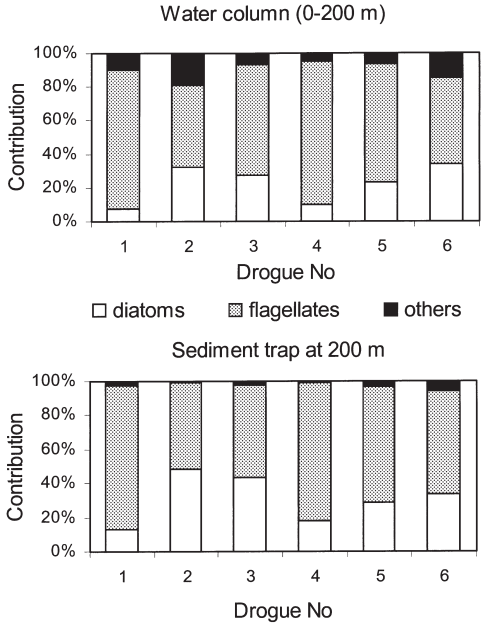

Fig. 6. Phytoplankton group composition (by phytoplankton carbon [PPC]) in the 0 to 200 m water column and in the 200 m sediment trap during the 1994/95 drogue study in the Lazarev Sea

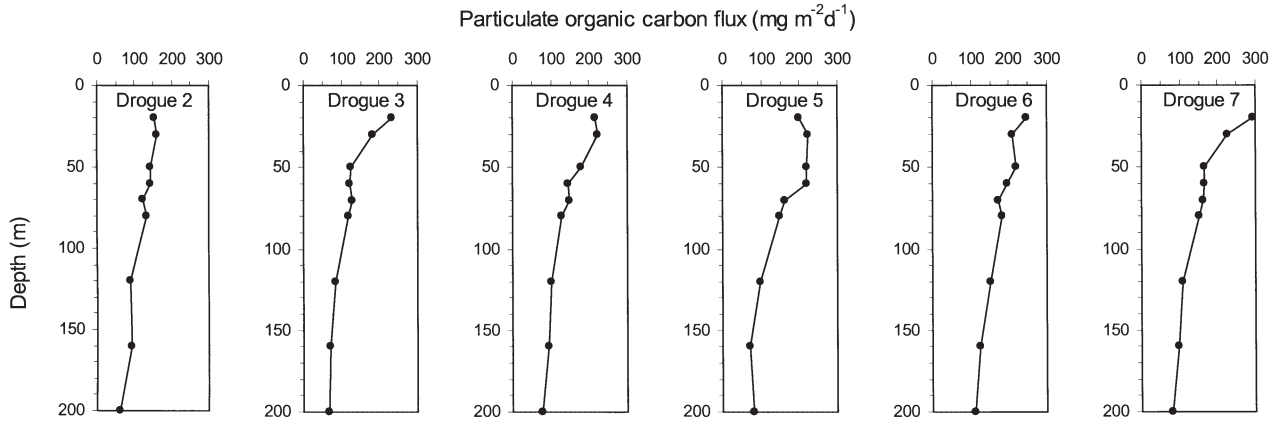

Fig. 7. Downward flux of particulate organic carbon measured in sediment traps in Drogues 2 to 7 during the 1994/95 drogue study in the Lazarev Sea

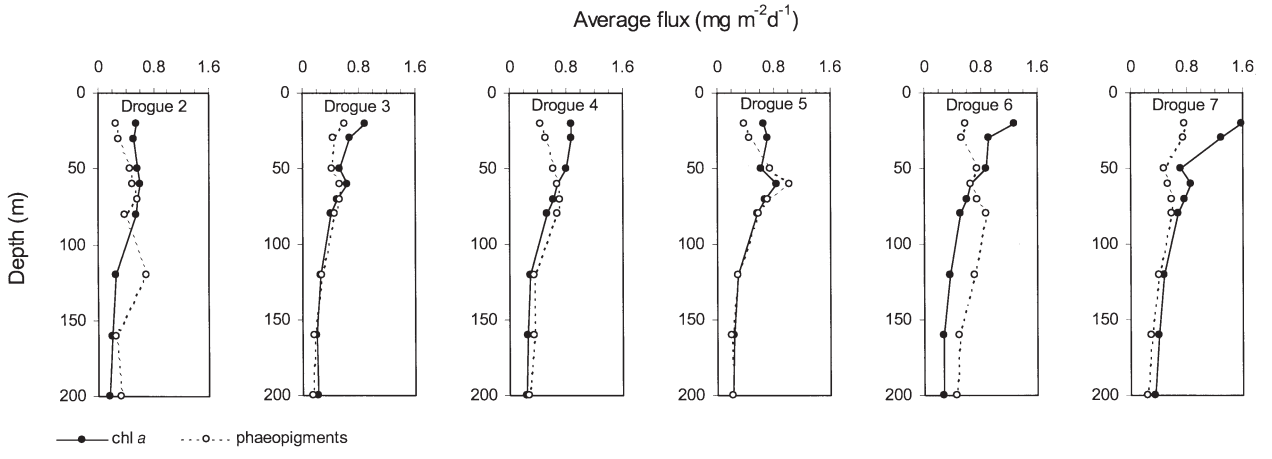

Fig. 8. Downward flux of chl *a* and phaeopigments measured in sediment traps in Drogues 2 to 7 during the 1994/95 drogue study in the Lazarev Sea

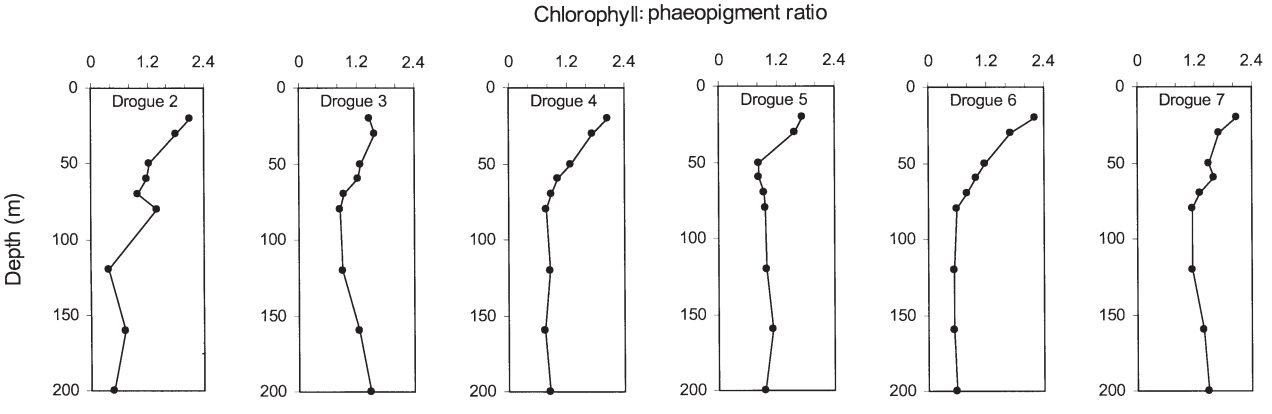

Fig. 9. Chlorophyll:phaeopigment ratio measured in sediment traps in Drogues 2 to 7 during the 1994/95 drogue study in the Lazarev Sea

Table 1. Summary of the impact of algal sinking (phytoplankton carbon, PPC), faecal pellet flux (FPC) and metazoan egg/foraminiferan flux (EFC) on algal production and biomass and their impact on total particulate organic carbon (POC) stock and flux during the1994/95 drogue study in the Lazarev Sea. pFPP: potential faecal pellet production estimated from zooplankton ingestion rates assuming 70% assimilation efficiency

Drogue	Year 1994/95	Trap depth (m)	Euphotic depth (m)	Chl *a* stock (mg m^{-2})	Chl *a* flux from traps (mg m^{-2} d^{-1})	Phaeo flux from traps (mg m^{-2} d^{-1})	Loss due to chl *a* flux (% d^{-1})	Loss due to phaeo flux (% d^{-1})	POC stock (mgC m^{-2})	POC flux (mgC m^{-2} d^{-1})	Loss due to POC flux (% d^{-1})	Contribution of PPC to POC flux (%)	Contribution of FPC to POC flux (%)	Contribution of EFC to POC flux (%)	Zooplankton pFPP (mgC m^{-2} d^{-1})	Contribution of pFPP to POC flux (%)
2	28–29.12	50	44	35.2	0.58	0.47	1.64	1.34	8 570	144.1	1.68	70.1	1.0	3.0		
		120		76.5	0.26	0.70	0.33	0.92	14 256	90.3	0.63	15.3	0.3	3.2		
		200		81.5	0.16	0.33	0.20	0.40	16 416	60.9	0.37	52.2	9.1	0	43.3	71.1
3	30–31.12	50	33	42.4	0.53	0.42	1.25	0.99	10 037	126.1	1.26	27.8	0.1	0		
		120		78.6	0.26	0.28	0.33	0.36	14 947	83.6	0.56	59.2	0.2	1.7		
		200		83.9	0.22	0.15	0.27	0.32	17 087	68.6	0.40	57.0	0.2	4.3		
4	1–2.01	50	34	58.0	0.79	0.62	1.37	1.07	10 814	177.6	1.64	40.9	0.2	5.1		
		120		104.1	0.29	0.34	0.28	0.33	15 992	99.8	0.62	35.5	0.8	0		
		200		110.9	0.23	0.26	0.21	0.23	18 327	77.3	0.42	32.2	0.1	1.9	23.65	30.6
5	3–4.01	50	31	49.6	0.62	0.75	1.25	1.51	11 892	219.6	1.85	29.2	0.3	4.6		
		120		85.1	0.29	0.29	0.34	0.34	18 067	96.6	0.53	17.8	0.6	3.4		
		200		90.8	0.21	0.22	0.23	0.24	20 521	79.8	0.39	29.8	2.0	10.8		
6	5–6.01	50	27	58.5	0.87	0.74	1.48	1.27	11 430	218.6	1.91	50.9	0.2	0.3		
		120		98.7	0.37	0.71	0.38	0.72	16 646	151.8	0.91	14.2	0.3	2.8		
		200		103.6	0.27	0.46	0.26	0.44	19 040	111.8	0.59	43.2	1.5	0	20.5	18.3
7	7–8.01	50	23	82.6	0.72	0.48	0.87	0.58	12 590	166.4	1.32	19.3	7.4	6.5		
		120		133.2	0.46	0.41	0.35	0.31	18 234	107.9	0.59	39.9	15.0	7.3		
		200		138.8	0.35	0.24	0.25	0.17	20 590	79.5	0.37	46.8	15.4	5.4		

Daily loss rates of biogenic material and microplankton

Daily loss of POC expressed as % of total POC standing stock was highest at 50 m depth and relatively constant (1.3 to 1.9%) throughout the entire drogue study. It decreased with increasing depth and was lowest, range 0.4 to 0.6%, at 200 m depth (Table 1). Similarly to POC, daily loss of chl *a* expressed as % of total chl *a* stock was the highest immediately below the euphotic zone (at 50 m) ranging from 0.9 to 1.6% of total. The lowest values at 50 m were observed during Drogue 7 (Table 1). POC decreased with the increasing depth, accounting for only 0.2 to 0.3% of total chl *a* stock at 200 m depth (Table 1). Daily loss of phaeopigments expressed as % of total chl *a* stock was almost identical to chl *a* loss, ranging from 0.6 to 1.3 and 0.2 to 0.4% at 50 and 200 m depths respectively (Table 1).

During the drogue study, daily loss of CPP estimated via chl *a* flux ranged from 5.5 to 9.5 and 1.9 to 3% at 50 and 200 m depths respectively (Table 2). Daily loss of CPP via POC flux was substantially higher, ranging from 26 and 48 and 12 to 25% at 50 and 200 m depths, respectively (Table 2). Daily loss of CPP via PPC flux generally decreased during the drogue study and was equivalent to 5–27 and 4–11% at 50 and 200 m depths respectively (Table 2). In contrast, daily loss of CPP via FPC flux increased towards the end of the study, ranging from <0.1 to ~2% of the total (Table 2).

During the experiment, daily loss rates of microplankton at 200 m depth ranged from 0.1 to 2.3%, showing a clear increasing trend towards the end of the investigation (Table 3). Group-specific daily loss rates were the highest (range 0.1 to 2.5%) for diatoms, which displayed an identical trend with loss rates of total microplankton. *Phaeocystis* sp. cells showed the highest loss rates (0.7 to 1.2%) during Drogues 2 and 7 (Table 3). Daily loss rates for the remaining microplankton groups ranged from <0.1 to 0.2% (Table 3).

Zooplankton composition and grazing

Total abundance of zooplankton in the top 200 or 300 m water layer varied between

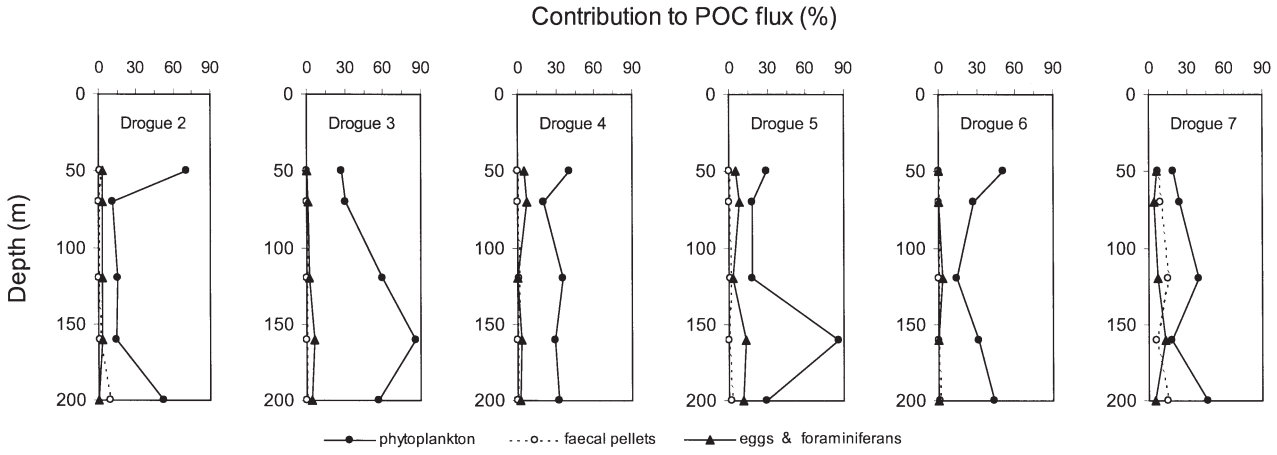

Fig. 10. Phytoplankton (PPC), faecal pellet (FPC) and metazoan eggs/foraminiferans (EFC) contribution to total downward particulate organic carbon (POC) flux measured in sediment traps in Drogues 2 to 7 during the 1994/95 drogue study in the Lazarev Sea

Table 2. Loss rates of chl *a*, POC, phytoplankton (PPC), FPC and zooplankton grazing expressed as % of primary production during the 1994/95 drogue study in the Lazarev Sea

Drogue	Depth (m)	Primary production (mg C m^{-2} d^{-1})	Loss due to chl *a* flux (% d^{-1})	Loss due to POC flux (% d^{-1})	Loss due to PPC flux (% d^{-1})	Loss due to FPC flux (% d^{-1})	Loss due to zooplankton grazing (% d^{-1})
2	50	375	7.7	38.4	26.9	0.4	
	120		3.4	24.1	3.7	0.1	
	200		2.1	16.3	8.5	1.5	36.6
3	50	451	5.9	27.9	7.8	0.03	
	120		2.9	18.5	11.0	0.03	
	200		2.5	15.2	8.7	0.03	
4	50	422	8.7	42.1	17.2	0.1	
	120		3.4	23.6	8.4	0.2	
	200		2.7	18.3	5.9	0.02	17.0
5	50	559	5.5	39.3	11.5	0.1	
	120		2.6	17.3	3.1	0.1	
	200		1.9	14.3	4.3	0.3	
6	50	455	9.5	48.1	24.5	0.1	
	120		4.1	33.4	4.8	0.1	
	200		3.0	24.6	10.6	0.4	15.0
7	50	647	5.5	25.7	5.0	1.9	
	120		3.6	16.7	6.7	2.5	
	200		2.7	12.3	5.8	1.9	

Table 3. Loss rates of different groups of phytoplankton at 200 m depth expressed as % of total phytoplankton stock in the 0 to 200 m water layer during 1994/95 drogue study in the Lazarev Sea

Drogue	Diatoms	Flagellates	Dinoflagellates	*Phaeocystis* sp.	Silicoflagellates	Total
2	0.1	0.1	<0.1	1.2	<0.1	0.1
3	0.2	<0.1	<0.1	<0.1	0.1	0.2
4	0.1	0.1	0.1	0.1	<0.1	0.1
5	0.7	0.1	<0.1	<0.1	<0.1	0.6
6	2.5	0.2	0.2	<0.1	0.1	2.3
7	2.2	0.1	0.2	0.6	<0.1	2.0

Table 4. Mean abundance (ind. m^{-3} ± SD) of the 11 most important zooplankton species during the 1994/95 drogue study in the Lazarev Sea. –: not recorded

Taxon	Drogue 2	Drogue 4	Drogue 6
Rhincalanus gigas	0.711 ± 0.294	2.167 ± 0.080	0.676 ± 0.278
Calanus propinquus	0.681 ± 0.553	1.252 ± 0.210	0.601 ± 0.913
Calanoides acutus	4.266 ± 2.121	3.169 ± 0.255	1.706 ± 0.727
Metridia gerlachei	3.370 ± 1.228	4.835 ± 0.091	3.833 ± 2.477
Clausocalanus and *Ctenocalanus*	0.927 ± 0.625	0.500 ± 0.084	0.923 ± 0.529
Oithona spp.	1.556 ± 1.295	6.589 ± 0.719	3.594 ± 3.793
Euphausia superba, juveniles	0.002 ± 0.004	–	0.001 ± 0.001
E. superba, subadults/adults	0.002 ± 0.004	–	–
Thysanoessa macrura, juveniles	0.100 ± 0.065	0.467 ± 0.101	0.624 ± 0.434
T. macrura, subadults	0.024 ± 0.025	0.008 ± 0.004	0.060 ± 0.124
T. macrura, adults	0.003 ± 0.009	–	0.001 ± 0.005
Limacina spp.	0.006 ± 0.010	0.008 ± 0.004	0.009 ± 0.014
Salpa thompsoni	0.618 ± 0.274	0.836 ± 0.086	0.049 ± 0.023
Total herbivores	12.265 ± 4.381	19.831 ± 1.435	12.077 ± 5.763
Total zooplankton	15.646 ± 5.495	26.478 ± 1.802	16.833 ± 7.055
Depth sampled (m)	0–300	0–200	0–300

15.6 and 26.5 ind. m^{-3}. The lowest and highest zooplankton abundances were recorded during Drogues 2 and 4 respectively (Table 4). Copepods, represented mainly by *Rhincalanus gigas* (copepodites IV–VI), *Calanus propinquus* (mainly adults), *Calanoides acutus* (mostly copepodites III–IV), *Metridia gerlachei* (copepodites IV–V), *Oithona* spp., *Clausocalanus* spp. and *Ctenocalanus* spp. were the most numerous, contributing between 67 and 73% to the total abundance (Table 4). Contribution of other groups, particularly euphausiids, pteropods and salps, never exceeded 5% of the total. During the drogue study, the 11 most abundant taxa which were used in grazing studies comprised 72 to 78% of total zooplankton abundance (Table 4).

Individual ingestion rates of herbivorous zooplankters are presented in Table 5. In general, ingestion rates of *Rhincalanus gigas*, *Calanus propinquus* and *Metridia gerlachei* decreased, while ingestion rates of *Calanoides acutus* and *Limacina* spp. increased during the course of the drogue study (Table 5).

The potential community grazing impact of the 4 most abundant zooplankton groups during the drogue study are presented in Table 6. Total ingestion rate ranged from 0.6 to 1.1 mg pig. m^{-2} d^{-1} and 68.4 to 144.2 mg C m^{-2} d^{-1} (Table 6). These ingestion rates cor-

Table 5. Ingestion rates of 11 most abundant herbivorous zooplankton species during the 1994/95 drogue study in the Lazarev Sea. Roman numerals show different zooplankton stages

Taxon	Ingestion rates (ng pig. ind.$^{-1}$ d^{-1})			
	Drogue 2	Drogue 4	Drogue 6	Drogues 2 to 6
Rhincalanus gigas (IV–VI)	184.8	95.6	109.5	–
Calanus propinquus (V–VI)	945.7	401.6	395.9	–
Calanoides acutus (III–IV)	125.9	240.4	490.7	–
Metridia gerlachei (IV–VI)	193.0	66.1	93.2	–
Clausocalanus spp.	–	–	–	265.2
Ctenocalanus spp.	–	–	–	152.0
Oithona spp.	–	–	–	31.9
Euphausia superba, juveniles	–	–	–	507.8
E. superba, subadults/adults	–	–	–	1889
Thysanoessa macrura, juveniles	–	–	–	131.5
T. macrura, subadults	–	–	–	216.1
T. macrura, adults	–	–	–	665.9
Limacina spp.	2204	2429	5980	–
Salpa thompsoni, 1–2.5 cm long	–	–	–	1700
S. thompsoni, 2.5–5 cm long	–	–	–	3300
S. thompsoni, >5 cm long	–	–	–	65 000

Table 6. Summary of metazoan grazing impact (mg pig. m^{-2} d^{-1}) during the 1994/95 drogue study in the Lazarev Sea

Groups	Drogue 2	Drogue 4	Drogue 6
Copepoda	0.674	0.416	0.544
Euphausiidae	0.008	0.012	0.029
Pteropoda	0.004	0.004	0.016
Tunicata	0.362	0.238	0.024
Total grazing (mg pig. m^{-2} d^{-1})	1.048	0.670	0.613
Chl *a* stock (mg m^{-2})	76.75	116.35	103.03
Grazing impact (%)	1.4	0.6	0.6
Total grazing (mg C m^{-2} d^{-1})	144.2	78.86	68.41
Primary production (mg C m^{-2} d^{-1})	394.2	464.2	454.9
Grazing impact (%)	36.6	17.0	15.0

respond to a loss between 0.6 and 1.4% of the total integrated chl *a* standing stock or between 15 and 37% of the daily primary production (Table 6). Among the grazers, copepods were the most important, utilising between 62.1 and 88.7% d^{-1} of total pigment ingested. Salp grazing was substantial (~35%) during Drogues 2 and 4 and significantly decreased (3.9%) during Drogue 6. The contribution of euphausiids and pteropods varied between 0.7–4.8 and 0.4–2.6% respectively (Table 6).

Impact of algal sinking and zooplankton herbivory on algal biomass and total POC flux

To investigate the relationships among sedimenting pigment fluxes, water column algal biomass and total downward POC fluxes, the inputs of PPC and FPC in the traps were compared with the chl *a* biomass in the top 50 m layer and with the total downward POC flux found in the traps (Table 1). The potential FPC contribution from the most abundant taxa of zooplankton (Table 4) was also compared to the total downward POC flux.

Overall, the fraction of the chl *a* from the top 50 m layer that sedimented daily below the top 200 m was consistent throughout the drogue study and never exceeded 0.6% of total POC flux (Table 1). The proportion of chl *a* that reached the traps in the form of phaeopigments ranged between 0.3 and 0.9%, with highest values recorded during Drogues 2 and 6 (Table 1). At 50 m depth, the PPC contribution to the total downward POC flux ranged from 19 to 70% during the experiment, with lowest and highest contribution observed during Drogues 7 and 2 respectively (Table 1). At 200 m, the PPC contribution to total POC flux varied between 30 and 57%, with the highest level observed during Drogue 3. The contribution of FPC to the total downward POC flux was generally low (≤2%), with the highest contribution (<15%) observed during Drogue 2 at depth 200 m and Drogue 7 at all depths (Table 1). During Drogue 2, ca. 71% of total downward POC flux at 200 m depth could be explained by the potential flux of zooplankton FPC. The potential contribution of FPC flux to total POC flux at 200 m decreased to 31 and 18% during Drogues 4 and 6 respectively (Table 1).

DISCUSSION

Although the drogue was deployed with the aim of studying biochemical processes within a specific, gradually modifying water mass, it is evident that on Days 5 (Drogue 4) to 9 (Drogue 6), a subsurface intrusion of colder, more saline water may have occurred (Fig. 2). The intrusion coincided with a change in the direction and speed of the drogue drift, but did not dramatically affect the physico-chemical structure of the upper 300 m water column. There are, however, indications that this intrusion resulted in a change in the phytoplankton structure as the region of investigation was exposed to a similar but successionally more advanced algal assemblage (Pakhomov et al. 2001). Coupled with this was a change in the zooplankton density (Table 4). Therefore, precautions should be taken comparing the results from the water column and sediment traps because traps may have encountered areas with patchy distribution of both phytoplankton and zooplankton.

Overall POC and chl *a* vertical fluxes observed during the drogue study were in the range previously recorded in the spring/summer sediment trap studies from a variety of Antarctic ecosystems (e.g. Schnack 1985, von Bodungen et al. 1988, Bathmann et al. 1991, Karl et al. 1991). A notable exception was the study conducted in the Bransfield Strait, where the flux of up to 1400 mg C m^{-2} d^{-1} was documented (von Bodungen et al. 1986). Considerable short-term variability in the downward biogenic flux was evident during the period of investigation (Table 1), which is consistent with studies conducted in other oceanic regions, reflecting complexity of processes in the upper water column (e.g. Welschmeyer et al. 1984, Corn et al. 1994, Sasaki et al. 1997, Nodder & Alexander 1998, Pusceddu et al. 1999).

The vertical flux of both chl *a* and POC decreased with depth with only a small fraction of intact phytoplankton reaching deeper waters. The proportion of phytoplankton sedimented out daily from the upper

20 m water column (data not shown) was equivalent to between 2 and 4% of the phytoplankton stock above the trap. The flux may have been overestimated, as growth of phytoplankton in the 20 m trap might have occurred. Indeed, little material (<2%) escaped from the top 50 m water column and only <0.5% of both chl *a* and POC sedimented beyond the 200 m depth layer. The loss rates were therefore similar to those identified in other oceanic regions (e.g. Nöting & von Bodungen 1989, Bathmann et al. 1991, Karl et al. 1991, Andreassen & Wassmann 1998, Smith & Dunbar 1998). Higher loss rates of chl *a* could be found in regions where the bulk of plant pigments was either found in FPC of large metazoans (Schnack 1985, Thibault et al. 1999) or represented by sinking of phytoplankton in the ice zone (Sasaki & Hoshiai 1986, Smith & Nelson 1986, Tremblay et al. 1989, Handa et al. 1992).

Coupled with low chl *a* losses, no extensive phytoplankton recycling occurred within the euphotic zone during the drogue study. This was supported by the similar loss rates of phytoplankton (as chl *a*) and total POC at 50 m depth (Table 1). In contrast with the upper 50 m water column, at 200 m depth the loss rates of POC were 1.5- to 2-fold higher than phytoplankton loss rates (Table 1), pointing to the substantial recycling of phytoplankton within the 50 to 200 m layer. Furthermore, the chl *a*:phaeopigment ratio in the top 60 to 70 m was generally >1, indicating that sinking consisted mainly of phytoplankton rather than more decomposed material. This pattern changed below the 70 m depth, providing evidence for zooplankton grazing within the 70 to 200 m layer. The amount of POC, which disappeared between 50 and 200 m, ranged from 13 to 25% of the total primary production (average 20.1 ± 5.5%, Table 1) and may crudely represent the grazing impact of metazoan zooplankton. These values are very similar to our herbivorous zooplankton grazing estimates obtained using the gut fluorescence method (range 15 to 37%, average 22.9 ± 11.9%, Table 6).

PPC comprised 15 to 70% of the vertical POC flux throughout the entire 0 to 200 m water column, confirming that identifiable phytoplankton cells represented on average $^1/_3$ of the total biogenic flux. Contribution of FPC was generally <3% of total POC and never exceeded 16% of the total downward POC flux. The C:chl *a* ratios generally exceeded 180 in the entire water column, suggesting the presence of a substantial pool of detritus in the euphotic zone. Our calculations indicate that the unaccounted POC fraction (POC–PPC–FPC) in the upper 50 m (Table 1), tentatively representing the detritus pool, varied between 26 and 72% (mean 55 ± 17%). This is in the same range (16 to 64%) observed in Norwegian fjords (Reigstad et al. 2000). There are, however, possible sources of overestimation of the detritus contribution, as a major part of detritus pool could include broken faecal pellets and/or bacterial aggregates and protozoans.

The potential contribution of faecal pellets at 200 m depth, calculated from zooplankton ingestion rates assuming 70% assimilation efficiency, should be substantially higher, ranging from 18 to 71% of total POC flux (Table 1). Simple calculations demonstrate that between 87 and 99% of faecal pellets were remineralized in the upper 200 m layer. These rates are similar to values reported in the literature (e.g. Viitasalo et al. 1999), implying that faecal pellets are either extensively broken down and/or efficiently recycled, probably through coprophagy, coprorhexy and coprochaly (Fortier et al. 1994, Bathmann 1998). The latter situation normally occurs under conditions of low food concentration and high zooplankton densities, particularly cyclopoids (Fortier et al. 1994, Bathmann 1998). Unfortunately, densities of small calanoids and cyclopoids during this study were likely substantially underestimated due to the sampling gear employed. More important for the downward flux could be faecal pellets of large metazoans, such as the tunicate *Salpa thompsoni* (Perissinotto & Pakhomov 1998a,b). However, salp faecal pellets were never encountered in sediment traps during the drogue study. This points to the inefficiency of small sediment traps in collecting rare faecal pellets of large metazoans. Nevertheless, natural breakage of pellets and/or extensive coprophagy on them in the water column cannot be discounted.

Interestingly, according to sediment trap data, the grazer-mediated flux increased by at least one order of magnitude between Drogues 3 and 7, probably demonstrating an increasing role of zooplankton grazing in the carbon sink. This, however, was in contradiction to actual measurements using the gut fluorescence method, which showed a decrease in grazing impact during the course of the drogue study (Table 6). The decrease in zooplankton grazing coincided with a significant drop in tunicate abundance and grazing impact, while copepod grazing remained stable. An increase in faecal pellet contribution to total POC flux may therefore reflect better feeding conditions for copepods, which probably allowed them to switch from coprophagy to a mainly herbivorous feeding mode.

The physico-chemical environment during the period of the drogue study was characterized by the presence of a well-developed pycnocline at ~30 m depth, high nutrient concentrations (M. Lucas unpubl.) and favorable light conditions. The area recently became ice free and therefore the development of a phytoplankton bloom was anticipated (Smith & Sakshaug 1990, Sakshaug et al. 1991, Goosse & Hecq 1994). Sediment trap data show that between 5 and 27% of pri-

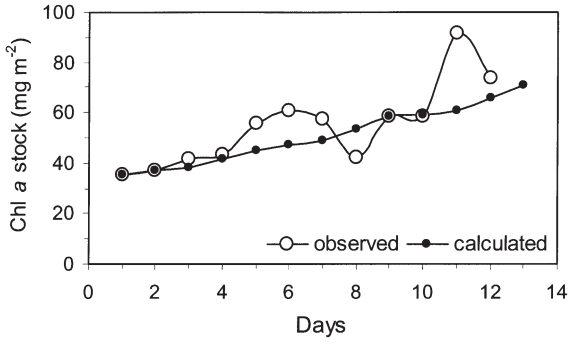

Fig. 11. Measured and predicted chl *a* standing stock in the top 0 to 50 m water layer. Predicted chl *a* stock for Day 2 was calculated using daily budget approach as follows: chl *a* stock for Day 1 + daily primary production – phytoplankton cell lysis (assumed as 8% d^{-1} after Murphy et al. 1998) – pigment flux at 50 m sediment trap (Table 1)– microzooplankton grazing (ca. 0.8 mg pig. m^{-2} d^{-1}, after Froneman et al. 1996) – metazoan grazing (Table 5)

mary production left the euphotic zone in the form of PPC and ≤42% of primary production escaped this layer in the form of POC (Table 1). This allowed an accumulation of phytoplankton (see Fig. 4B) in the upper surface layers during the drogue study. Predictions (for the following day, see legend of Fig. 11) for the chl *a* stock build-up in the top 50 m layer described the measured chl *a* stock dynamics well, suggesting that our measurements are accurate and assumptions valid (Fig. 11). The duration of the drogue study appeared to be insufficient for the proper development of a phytoplankton bloom (Moline et al. 1997). This is supported by chl *a* concentrations of >2.5 mg m^{-3} reported during the post-drogue grid survey (Perissinotto & Pakhomov 1998a) and during previous surveys in the same area (Laubscher et al. 1993, Perissinotto et al. 1997).

Grid surveys conducted in the region of drogue deployment prior and immediately after the drogue experiment described a clear shift in the size composition of phytoplankton assemblage from a community dominated by nano- and picophytoplankton to one dominated by microphytoplankton (Froneman et al. 1997). Our findings show that this shift occurred largely during the drogue study (Fig. 4A). Zooplankton abundance and community grazing impact increased during the same period (Table 7). Although no sediment traps were deployed, it has been postulated that grazer-mediated downward carbon flux was twice as efficient during the pre-drogue survey (Froneman et al. 1997). The results of the drogue study clearly demonstrated that despite increase in zooplankton grazing (Table 7) and FPC flux (Table 1), phytoplankton sinking dominated overall flux during the onset of the MIZ bloom (Table 1). The findings of the drogue study thus point out that estimates of vertical carbon flux obtained from the gut fluorescence technique alone might be misleading.

CONCLUSION

Major export events in the seasonally ice-covered waters include the release and sedimentation of ice algae during the time of ice melt (e.g. Sasaki & Hoshiai 1986, Matsuda et al. 1987, Tremblay et al. 1989), massive sinking of ice-edge blooms (e.g. Smith & Nelson 1986, Wilson et al. 1986, Bathmann et al. 1991), and sedimentation of algae from the spring-summer phytoplankton bloom (e.g. Schnack et al. 1985, Sasaki & Hoshiai 1986, von Bodungen et al. 1986, Handa et al. 1992). It is generally accepted that outside these periods, the sinking of faecal material largely dominates the downward vertical flux of POC (Schnack 1985, von Bodungen et al. 1988, Bathmann et al. 1991, Karl et al. 1991, Cadée 1992). The results of the drogue study show that the contribution of grazing-mediated POC flux was insignificant during the onset of the MIZ bloom. Apparently, large meso- and macrozooplankton densities and feeding activities were insufficient to exert either positive (via faecal pellets) or negative (via reducing suspended phytoplankton concentration) effects on sedimentation (Sarnelle 1999). As a consequence of the classical mismatch between phytoplank-

Table 7. Comparison of abundance and grazing impact of most important herbivorous zooplankton species during pre-drogue, drogue and post-drogue surveys in the top 300 m water column. Pre- and post-drogue data were extracted from Froneman et al. (1997). Underlined values are significantly different (p-values are provided) from each other (1-way ANOVA with a post-hoc comparisons using Tukey's test for unequal n)

Period	Abundance (ind. m^{-3})		Grazing impact (mg pig. m^{-2} d^{-1})	
	Range	Mean (±SD)	Range	Mean (±SD)
Pre-drogue (n = 8)	2.5–12.5	5.5 ± 3.3	0.07–0.61	0.34 ± 0.18
Drogue (n = 3)	12.1–19.8	14.7 ± 4.4	0.61–1.05	0.78 ± 0.24
Post-drogue (n = 4)	5.5–16.4	11.0 ± 4.9	0.66–2.15	1.19 ± 0.66
p-value	0.0353		0.0208	

ton production and zooplankton grazing in the MIZ, the most important mechanism of the downward POC flux was algal sinking. This scenario may be true during the pre-bloom period (sinking of ice algae) and is likely to persist during the post-bloom period as well (massive sinking of ice-edge blooms). Finally, the results of this study clearly demonstrate the importance of the upper layer for the vertical flux regulation in the Antarctic MIZ. This is similar to processes described in the MIZ of the Barents Sea (Andreassen & Wassmann 1998), where the bulk of the organic carbon was retained and probably re-mineralized through microbial food and classical webs in the upper euphotic and aphotic zones. This calls for a re-evaluation of the importance of micro- versus mesozooplankton grazing in the dynamics of the Antarctic marine ecosystem.

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