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The influence of copepod and krill grazing on the species composition of phytoplankton communities from the Scotia-Weddell sea

An experimental approach

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Abstract. The influence of copepods (mainly *Oithona similis*) and krill (*Euphausia superba*) grazing on the species composition of plankton communities in ship-board containers was investigated during the spring and post-spring period in the Scotia-Weddell Sea in the Antarctic ocean. Numbers of grazers were experimentally manipulated in containers with natural phytoplankton assemblages. With natural levels of copepods but no krill a high (700–950 μg C $\cdot l^{-1}$, ca 30 μg chl a $\cdot l^{-1}$) phytoplankton biomass developed. In these cultures large diatoms, e.g. *Corethron criophilum* and chains of *Thalassiosira* sp., made up 80% of total phytoplankton cell carbon at the end of the experiment. In cultures with elevated numbers of copepods (5X or 10X the natural level) phytoplankton biomass was somewhat reduced (ca 23 μg chl a $\cdot l^{-1}$) compared to cultures with natural copepod abundance, but still high. Phytoplankton species composition was on the other hand greatly influenced. Instead of large diatoms these cultures were dominated by *Phaeocystis pouchetii* (70%) together with small *Nitszchia* sp. and *Chaetoceros neogracile* (20%). In containers with krill (both juveniles and adults), but without elevated numbers of copepods, phytoplankton biomass rapidly approached zero. With 10X the in situ level of copepods, krill first preyed on these before *Corethron criophilum* and *Thalassiosira* sp. were grazed. When krill were removed a plankton community dominated by flagellates (60–90%), e.g. *Pyramimonas* sp. and a Cryptophycean species, grazed by an unidentified droplet-shaped heterothrophic flagellate, developed. These flagellates were the same as those which dominated the plankton community in the Weddell Sea after the 'spring bloom'. A similar succession was observed in situ when a krill swarm grazed down a phytoplankton 'bloom' in a few hours. Our experiments show that copepods cannot control phytoplankton biomass in shipboard cultures even at artificially elevated numbers. Krill at concentrations similar to those in natural swarms have a great impact on both phytoplankton biomass and species composition in shipboard cultures. Both copepods and krill may have an impact on phytoplankton species composition and biomass in situ since the rates of phytoplankton cell division were probably artificially increased in shipboard cultures compared to natural conditions, where lower growth rates make phytoplankton more vulnerable to grazing. A similarity between phytoplankton successions in containers and in situ, especially with respect to krill grazing, supports the conclusion that grazing may structure phytoplankton communities in the Scotia-Weddell Sea.

Herbivores may both benefit phytoplankton through increased nutrient regeneration as well as decrease net growth rates through ingestion of algae (Porter 1976; Sterner 1986; Bergquist and Carpenter 1986). Since herbivores are usually selective with respect to the food they ingest the effect of grazing on phytoplankton is size- or

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species-specific. Even if total phytoplankton biomass is not influenced by grazers, there may be marked shifts in phytoplankton community structure. Algae which are avoided by grazers are thus favoured under a heavy grazing pressure, since competition from those algae that are preferred by grazers is reduced.

In Antarctic waters nutrient concentrations are normally high enough that nutrient regeneration through zooplankton should be of less importance than the mortality inflicted upon phytoplankton through grazing. This is, however, true only to the extent that nitrate may be used with the same efficiency as a nitrogen source as ammonium or urea. If phytoplankton net growth rate is primarily grazer controlled in a high-nutrient environment, nutrient limitation of phytoplankton growth rate and resource competition should be of less importance for the structuring of the phytoplankton community, although grazing *per se* does not exclude resource competition, only modifies the outcome (Sommer 1988a). Sommer (1986; 1988b) proposed that competition for silica and nitrate in combination with light may structure phytoplankton communities in Antarctic waters. He (Sommer 1988b) showed that patterns of phytoplankton distribution in the Drake Passage were consistent with effects from species–specific nutrient and light limitation of growth rates, although nutrient limitation of growth rate was never strong.

In temperate marine waters the transition from the spring diatom bloom, with a high proportion of new production *sensu* Eppley and Petersen (1979), to regenerative summer, flagellate dominated, phytoplankton communities, is often thought to be caused by exhaustion of nutrients and sedimentation of the bloom. However, even in Antarctic waters, where at least macronutrient levels are essentially non-limiting for phytoplankton growth all year round (Holm-Hansen et al. 1977; Hayes et al. 1984), there is a succession from dominance of large diatoms to flagellates, often of nanoplanktonic size ($< 20\ \mu m$), with ammonia as the main nitrogen source (Glibert et al. 1982; Teixeira et al. 1986; Weber and El-Sayed 1987).

In Antarctic waters phytoplankton biomass is generally low in spite of extremely high levels of inorganic nutrients. Thus, phytoplankton is not utilizing these nutrients to full extent. Several reasons have been suggested to explain this phenomenon (Cullen 1991), e.g. slow growth rates due to low temperatures (Sakshaug 1989) or limitation by trace metals as iron (cfr. Martin and Fitzwater 1988, Martin and Gordon 1988, Martin et al. 1991, de Baar et al. 1990, Chisholm and Morel 1991), but above all a deep mixing depth, causing light limitation (Sakshaug 1989).

Iron limitation of macronutrient uptake, chlorophyll *a* synthesis and phytoplankton carbon accumulation in shipboard cultures was found during the EPOS leg 2 cruise in the Scotia-Weddell Sea, although even without iron additions a high biomass accumulated in shipboard cultures (de Baar et al. 1989, 1990). The authors concluded that in situ Fe is not the major factor controlling phytoplankton growth. Little is known with respect to species–specific effects of iron limitation on phytoplankton growth in situ. However, Buma et al. (1991) showed that diatoms were favoured by Fe-additions in shipboard cultures with Antarctic water and Chavez et al. (1991) found a similar effect for samples from the equatorial Pacific. According to Helbling et al. (1991) there was a shift from nanoplankton to microplankton after Fe addition to Antarctic pelagic water.

Light, as influenced by a deeply mixed layer, is often thought to be the main factor preventing a buildup of phytoplankton biomass in Antarctic waters (Hayes et al. 1984; Sakshaug and Holm-Hansen 1984; Sakshaug 1989; Sakshaug and Skjoldal 1989, Mitchell et al. 1991). However, during the EPOS leg 2 cruise no deeply mixed layer was found anywhere. According to Veth (1991) the mixed layer was between 15 and 40 m. Smetacek and Veth (1989) in their preliminary conclusions of the expedition results state that "a shallow stratified water column may well be a prerequisite but does not necessarily result in accumulation of phytoplankton biomass. This conclusion is contrary to the general opinion that mixed layer depth is the single most important factor in controlling the occurrence of blooms. Hence, there must be other factors operating in this region that control algal biomass build-up". Buma et al. (1991) likewise concluded that light conditions *per se* were neither a limiting factor for phytoplankton production in situ, nor an explanation for the high phytoplankton biomasses observed in their shipboard cultures.

In Antarctic plankton communities the abundant krill (*Euphausia superba*) is a very efficient grazer (Boyd et al. 1984; Meyer and El-Sayed 1983; Price et al. 1988) and an inverse relation between krill and phytoplankton biomass has been observed (El-Sayed 1984; Priddle et al. 1986). It has also been shown that krill grazing and deep mixing favours flagellates over diatoms (Kopczynska 1992). Copepod grazing has received less attention, but e.g. Schnack (1985) and von Bodungen et al. (1986) have shown substantial copepod grazing in some regions of the Antarctic Ocean. In an environment with extremely low temperatures and supposedly deep mixing depths phytoplankton growth rates are limited by abiotic factors even under a luxuriant nutrient supply. When rates of cell division are low due to low temperatures and low light availability, phytoplankton should be more vulnerable to grazing than when they are living in an optimal environment with respect to abiotic factors. In fact not even the extremely high macronutrient concentrations in Antarctic waters preclude structuring of phytoplankton communities through resource competition. Sommer (1986) has shown that competition for silica and nitrate may regulate diatom abundance because Antarctic diatoms have extremely high nutrient half-saturation values for growth. Thus biotic regulating factors, grazing and resource competition, should not be excluded as regulating factors for Antarctic phytoplankton communities.

Our objective was to study experimentally the regulating effect of copepods and krill on phytoplankton assemblages of nutrient-saturated Antarctic waters. The goal was to get an idea to what extent grazing can potentially play a role in phytoplankton species successions, e.g. the transition from a nitrate-dependent diatom community to a regenerative flagellate community, and if grazing can control phytoplankton biomass. We wanted to study not

only the effects from krill, the 'classical' grazer in Antarctic waters, but also effects from copepod grazing, since in the Antarctic ocean the role of copepods compared to krill for grazing is still unclear (Laws 1985; Miller et al. 1985; Quetin and Ross 1985; von Bodungen 1986; von Bodungen et al. 1986). We were especially interested in the relation between copepods and bloom-forming non-diatoms, as e.g. *Phaeocystis pouchetii*, which is known to occasionally form dense populations in Antarctic waters (El-Sayed 1984; von Bodungen 1986; Sakshaug and Skjoldal 1989) as well as in other polar (Sakshaug and Holm-Hansen 1984) and temperate areas (Lancelot et al. 1987).

Materials and methods

This study was performed during the EPOS (European *Polarstern* Study – a part of the European Science Foundation supported polar science programme) leg 2 expedition to the Scotia and Weddell Seas, Antarctica, with the R/V Polarstern of the Alfred-Wegener-Institute for Polar and Marine Research, Bremerhaven (Hempel et al. 1989). The expedition took place from November 1988 to January 1989, i.e. during the austral spring-summer period, when the sea-ice is receeding southwards. Experiments reported here were performed with water from stations 158 (59°26, 9'S-48°43, 7'W) and 167 (60°30, 2'S-46°59, 7'W), located in the area of the Scotia-Weddell Sea Confluence and Weddell Sea, respectively (Fig. 1 A and B).

Two types of shipboard experimental manipulations were made (Fig. 2A and B): a) addition of copepods to natural phytoplankton assemblages and b) addition of krill to phyto- (and zoo)plankton assemblages. Water with the natural plankton communities was collected from 20 m depth with 30 l Niskin bottles mounted on a CTD Rosette and filtered through a 150 μm nylon net in order to remove copepods.

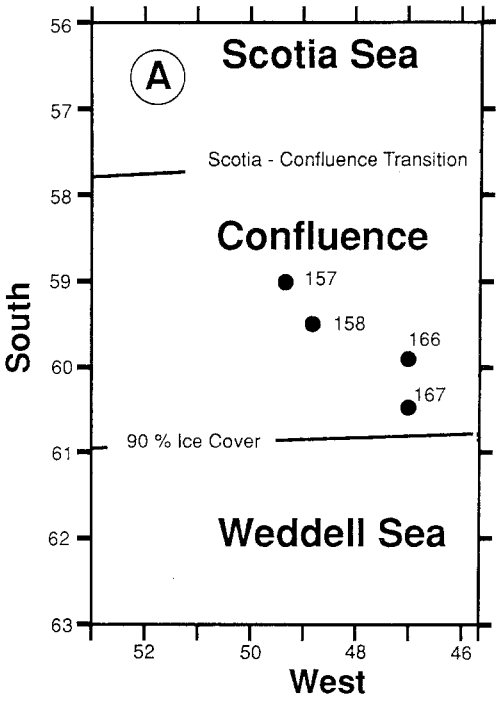
Copepod experiments

Copepods were collected through vertical hauls from 200 m depth to the surface using a small 50 μm mesh size net (station 167). (Our intention was to collect the copepods with a 150 μm mesh size net). This was also done in two initial experiments (with water from two different stations). However, these experiments unexpectedly failed because the copepods died during the course of the experiments due to injury during collection). Before experiments started, copepods were kept in flasks with air bubbling for at least 24 h in order to separate injured animals from the ones in good condition. A sample of the suspended (live) copepods was then counted and numbers approximately corresponding to 1X (=control), 5X and 10X the natural concentration (calculated from net hauls 0–100 m depth; Fransz et al. 1989) were added to the experimental flasks. Copepod experiments were performed in 10 l Pyrex™ bottles (Fig. 2A).

Experimental containers were incubated at a temperature of (0→−1 °C) (in situ≈ −1.0– 1.5 °C at 20 m depth) and a light intensity of 100 $\mu E \cdot m^{-2} \cdot s^{-1}$ with a 16:8 light:dark cycle. Light intensity was approximately saturating for photosynthesis (Tilzer et al. 1985; Lancelot and Mathot 1989). The 1% quanta depth for the three stations varied between approximately 30 and 60 m (Magas and Svansson 1989). At noon light intensity at the surface was typically around 1000 $\mu E \cdot m^{-2} \cdot s^{-1}$. Thus 100 $\mu E \cdot m^{-2} \cdot s^{-1}$ should correspond to a depth of 15–30 m at noon.

Krill experiments

Krill (*Euphausia superba* Dana) juveniles (length 1.85–2.53 cm) were captured with a hand net among sea-ice. They were maintained on



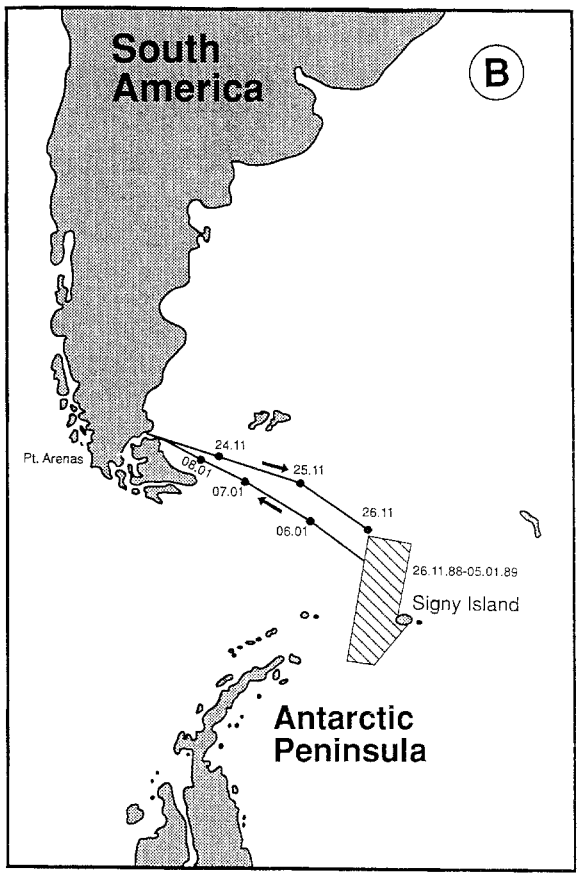


Fig. 1A, B. Sampling area. **A** Redrawn from de Baar et al. 1990. **B** Sampling period and route covered by the EPOS expedition leg 2 redrawn from Buma et al. 1991

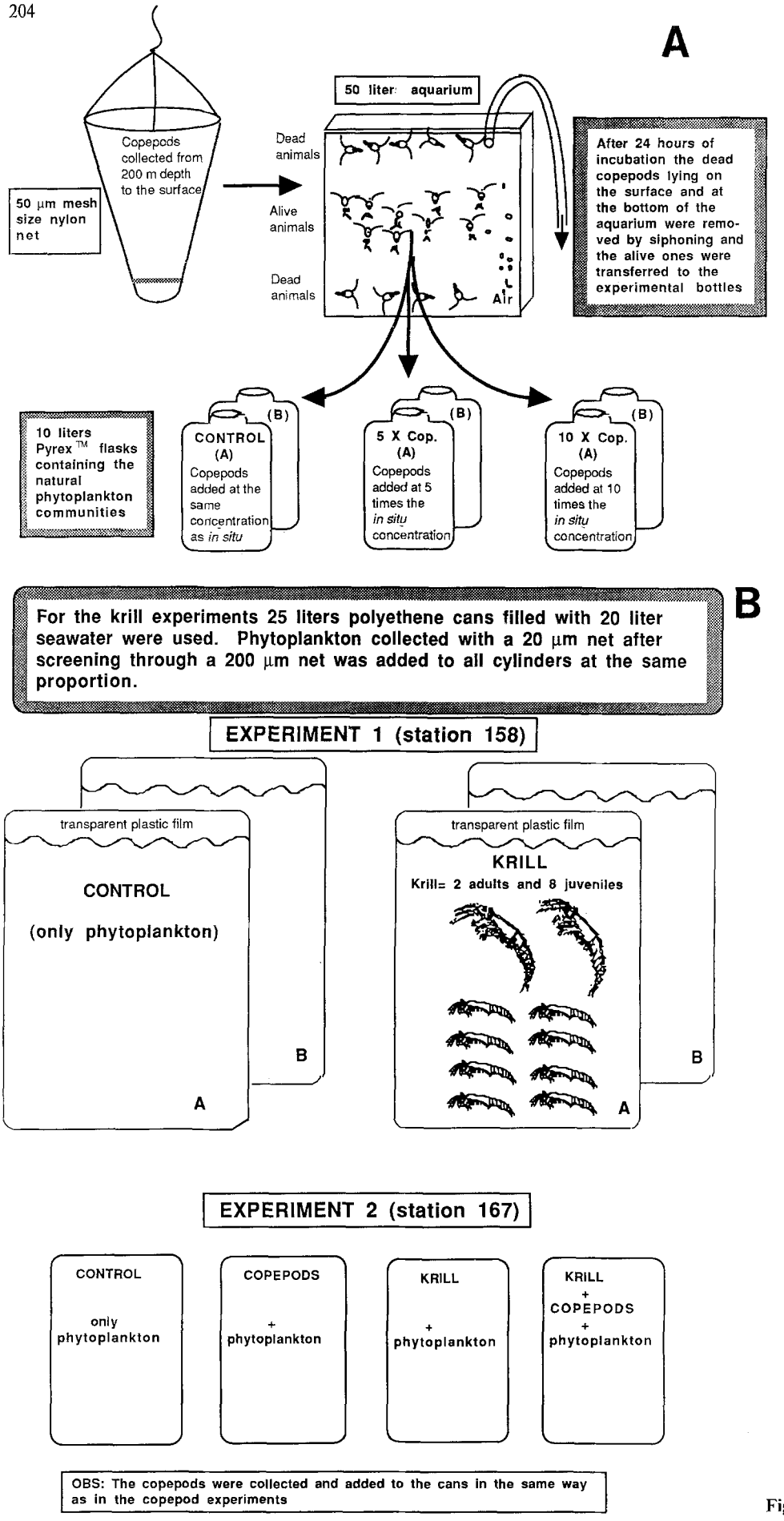


Fig. 2A, B. Experimental set-up

board in a 60 l tank at 0 °C until experiments started. Water in the tank was renewed every 2 days and krill were fed micro-algae liberated by melting blocks of 'brown ice'. Adult krill (length 3.5–4.5 cm) were collected at station 157 (59° 01, 9′ S) and 166 (60° 00, 0′ S) (RMT catch) and kept as juveniles, except that net phytoplankton from the pelagic stations served as food (Cuzin-Roudy and Schalk 1989). Krill were checked for vitality before transfer to the experimental containers.

Krill experiments were performed in 25 l polyethene cans with the top cut off and covered with a transparent plastic film to allow light penetration comparable to the Pyrex™ flasks (Fig. 2B). To the water in the cans phytoplankton collected with a 20 μm plankton net was added, after screening through a 200 μm net, in order to increase the initial phytoplankton density by approximately 20 times and thus simulate 'bloom' conditions. It must be observed that the initial phytoplankton assemblage in this experiment was different from the initial community in the copepod experiment for the same station, due to the addition of net plankton (> 20 μm) to the station 167 'krill' experiment.

Eight juvenile and 2 adult krills were put in 20 l water in the cans. In the first experiment (station 158) one juvenile was substituted on the 5th day of the experiment due to uncompleted moulting. All krill were alive when the experiment was terminated on the 8th day, and some juveniles had moulted. In the second experiment (station 167) 3 females and 1 male were added on the 9th day. All animals were alive when the experiment was terminated on the 11th day. In this experiment we left the krill inside the containers during an additional 5 days compared to the first experiment. Copepod additions in krill experiments were 10X the in situ concentrations. Krill containers were incubated under the same temperature and light conditions as for the copepod experiment.

Samples were taken after manual shaking of the Pyrex™ bottles. The water in the cans (krill experiments) was gently mixed with a Secchi-disc like device made from a petri dish (15 cm diameter) before sampling. There was thus no continuous stirring. Samples were taken for chlorophyll *a* and were divided into three fractions: total, < 20 μm (filtering through a nylon net) and < 3 μm (filtering through a 3 μm Nucleopore filter). The total fraction was used for chemical analysis, species identification and phytoplankton cell counting. Samples were taken daily for the experiments with krill and every 2–3 days for the copepod experiments. In vivo chlorophyll *a* fluorescence was measured on the three size fractions using a Turner model 112 fluorometer. Fluorescence was transformed to chlorophyll *a* through calibration with extracted chlorophyll *a* (Jeffrey and Humphrey 1975) of some samples during the course of the experiments. Chlorophyll *a* together with cell carbon calculated from cell numbers, cell volumes and the formulas in Edler (1979), were used as measures of phytoplankton biomass. Cell counts were done according to the standard Utermöhl method, using a Nikon (model Diaphot-TMD) inverted microscope. Cell numbers differed somewhat when comparing results based on fresh samples counted on board the ship and the same samples counted 6 months later using a Leitz Labovert FS microscope. The heterotrophic 'droplet'-shaped flagellate which could be seen alive with *Pyramimonas* sp. and Cryptophyceans inside could not be identified in samples preserved with the normal Lugol fixation. However, samples had also been preserved with a much higher than normal concentration of Lugol's solution for the counting of ciliates (which were extremely rare). These samples could be used for identification and counting of the sensitive flagellates. Copepods were only counted initially and at the end of the experiments, due to the large volume of water necessary for a quantification. Copepods were counted and biomass estimated (AFDW = ashfree dryweight) as described by Fransz (1988) and Fransz et al. (1989).

Nutrient analyses (NH_4, NO_3, No_2, Si and PO_4) were done in the beginning and at the end of the experiments (for methods see Anon. 1989).

Results

Nutrients

Nutrient levels excluding ammonia (0.3–0.8 μM) were very high for all stations (Table 1). Nitrate varied between 27.5 and 28.2 and phosphate between 1.67 and 1.84 μM. Silica

Table 1. Nutrient concentrations at 20 m depth for the different stations and at the end (and middle for the st. 158 krill experiment) of the experiments. For the mesozooplankton experiment the following treatments were set up: C (control = in situ (1X) level of mesozooplankton), 5X and 10X (= mesozooplankton additions in relation to in situ values). For the krill experiments treatments were: C (control = in situ (1X) level of mesozooplankton, no krill), Z = 10X in situ level of mesozooplankton, *K* = krill addition ($500 \cdot m^{-3}$), *KZ* = krill ($500 \cdot m^{-3}$) + mesozooplankton addition (10X). *ud* = undetectable

St.	Day	T°C	NO_3 μM	NH_4 μM	PO_4 μM	Si μM	Chla $\mu g \cdot l^{-1}$
Mesozooplankton experiment							
167	1	−0.98	27.5	0.41	1.84	78	0.66
C	16		ud	0.12	0.03	5.5	30.7
5X	16		3.6	0.43	0.42	32.3	23.6
10X	16		3.4	0.79	0.53	38.1	23.0
Krill experiments							
158	1	−1.29	28.2	0.91	1.67	69.4	0.67
C	10		2.6	0.13	0.31	35.0	16.4
Z	10		2.5	0.23	0.23	37.0	15.3
K	10		16.1	0.89	0.71	65.3	3.6
KZ	10		18.3	1.01	0.83	58.0	3.6
C	22		ud	0.32	0.21	7.2	22.7
Z	22		ud	0.43	0.19	8.7	21.2
K	22		3.6	1.3	0.24	59.3	17.1
KZ	22		4.2	1.2	0.32	56.7	16.9
167	1	−0.98	27.5	0.41	1.84	78	0.66
C	14		ud	0.31	0.01	6.6	24.1
Z	14		ud	0.61	0.03	8.7	23.6
K	14		17.8	2.4	0.64	60.8	22.2
KZ	14		ud	0.82	0.16	27.7	4.8

values were 69.4 and 78.0 μM (see also Anon. 1989 and van Bennekom et al. 1989).

Copepod impact on phytoplankton

Copepods were in different developmental stages. There were no consistent depth distribution patterns or diurnal changes in distribution (Fransz et al. 1989). Mean copepod biomass for transects from the Weddell Sea (62°S, 49°W) over the Weddel-Scotia Confluence to the Scotia Sea (57°S, 59°W) in the upper 100 m was between a few to over 15 mg AFDW $\cdot$ m^{-3}, with an increasing trend from south to north and with approximately equal biomass in small (< 1 mm) and large (> 1 mm) organisms (Fransz et al. 1989). Corresponding numbers of copepods per m^3 were roughly 500 to 5000, with smaller species and early developmental stages dominating. These values can be compared to the approximately 10 mg AFDW $\cdot$ m^{-3} remaining in the control (= 1X) bottles at the end of the st. 167 copepod experiment.

Additions of copepods corresponding to 5X and 10X the natural (1X = control) concentrations decreased the phytoplankton biomass only slightly, but changed the species composition at station 167 appreciably (Fig. 3). When cultures reached the stationary phase after 10 days of growth phytoplankton biomass remained at around 28 mg chl $a \cdot$ m^{-3} for cultures with the in situ concentration of copepods, but around 22 mg chl $a \cdot$ m^{-3} for cultures with 5X or 10X elevated zooplankton abundance (Table 1). It can be noted that duplicates were very similar with respect to chlorophyll (Fig. 3). For the control treatment only a small part (3.7%) of the chlorophyll was in the fraction < 20 μm and virtually nothing (0.9%) in the picoplankton size class, < 3 μm. The smaller phytoplankton size fractions increased somewhat with elevated numbers of copepods (7.8 – 13.3% and 2.2 – 4.5% for < 20 and < 3 μm, respectively for 5X and 10X copepod treatments), but netplankton (> 20 μm) dominated (C = 95.4, 5X = 90, 10X = 82.2%) in all treatments, although the species composition was very different for control cultures and cultures with elevated copepod numbers.

There was less difference between treatments with respect to total phytoplankton carbon than for chlorophyll (Figs. 3 and 4). Phytoplankton cell carbon was totally dominated by diatoms in the control bottles, and by 'flagellates' in the copepod bottles. In the control bottles, the phytoplankton species dominating in the stationary growth phase was the large diatom *Thalassiosira antarctica*, which contributed more than 80% of the total phytoplankton biomass as cell carbon (Fig. 4). This species was virtually absent in the bottles with extra copepods added. Such a difference was also seen for another large diatom, *Corethron criophilum*, although it's biomass was only approximately 10% of that for *Thalassiosira antarctica*. Small diatoms, *Chaetoceros neogracile* and a 2 μm *Nitzschia* sp., were also found in the control bottle, but were quantitatively not important.

In bottles containing 5X and 10X the natural copepod densities colonies of *Phaeocystis pouchetii* became dominant (70% of the biomass), while they disappeared in the controls (Fig. 4). About 15% of phytoplankton carbon was in small diatoms, especially the 2 μm *Nitzschia* sp. With respect to the group Chryptophyceae and *Pyramimonas* sp. (Buma et al. 1991) there were no obvious differences between treatments. These flagellates, as well as a droplet-shaped heterotrophic flagellate (Buma et al. 1989), were quntitatively not important. Zooplankton biomasses at the end of the experiment were roughly proportional to the initial addition: the mean dry weight (mg $\cdot$ m^{-3}) were 13, 62 and 198 for the 1X, 5X and 10X bottles. The dominating copepod species was the small copepod *Oithona similis* in addition to nauplia.

Phosphate, nitrate and silicate were consumed by the phytoplankton in the control to low levels, while there were appreciable amounts of phosphate and silica left unutilized at the end of the experiment for the 5X and 10X mesozooplankton treatments (Table 1).

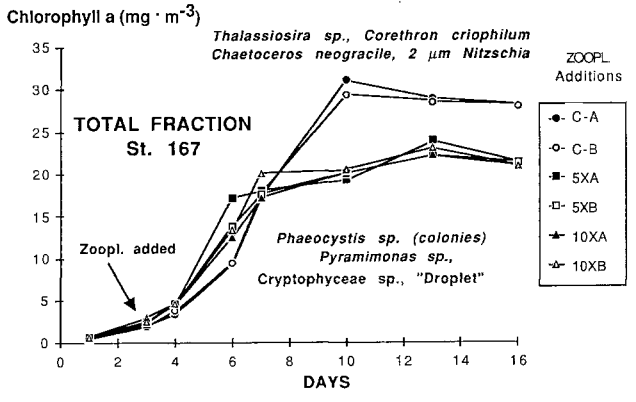


Fig. 3. Biomass (measured as chlorophyll *a*) produced by the natural phytoplankton community from st. 167 in bottles with different concentrations of mesozooplankton (1X = Control = C, 5X and 10X the natural abundance). A and B for each treatment are replicates. Dominant phytoplankton species at the end of the experiment for the different treatments are also indicated

Krill impact on copepods and phytoplankton

Duplicate control treatments in the st. 158 krill experiment were very similar with respect to chlorophyll *a* (Fig. 5). The phytoplankton biomass increased steadily until the 12th day, stabilized during a few days at 20 mg chl $a \cdot$ m^{-3} and then decreased slightly. Duplicate krill containers were practically identical with respect to chlorophyll *a*. In krill containers phytoplankton biomass decreased to less than 1 mg chl $a \cdot$ m^{-3} within 2 days (Fig. 5). On the 5th day we removed the krill, which caused a steady increase in chlorophyll *a* until the termination of the experiment.

The phytoplankton species composition in the krill containers developed quite differently from the control containers. In the controls the large diatoms *Corethron criophilum* and *Chaetoceros neglectum* made up the bulk of the biomass at the end of the experiment (together > 80% of phytoplankton carbon), while in the krill containers, even if the larger diatoms increased somewhat after krill had been removed, a small *Pyramimonas*-species, Crypto-

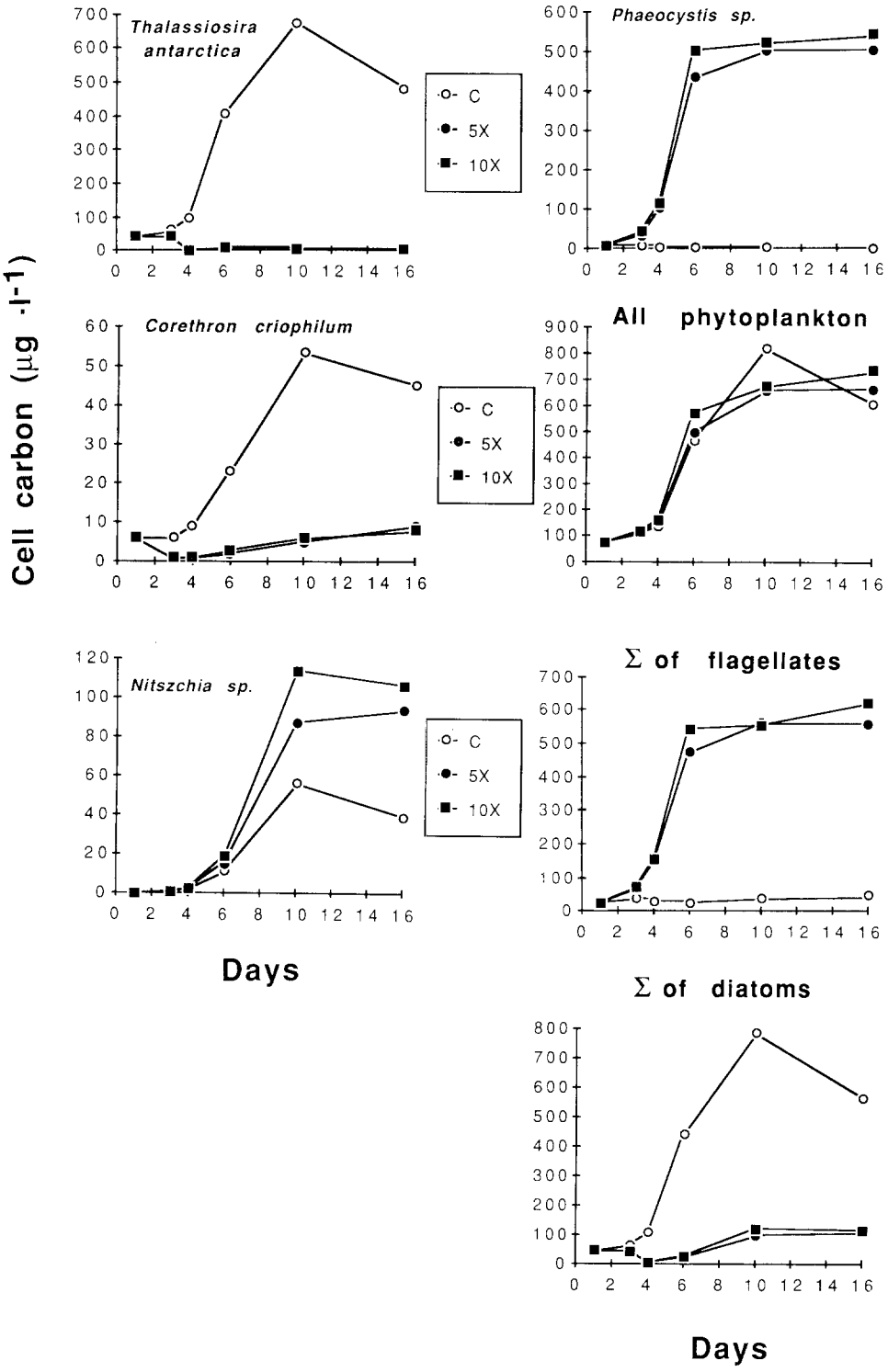


Fig. 4. Cell carbon of different phytoplankton species, total phytoplankton, sum of flagellates, including *Phaeocystis pouchetii*, and sum of diatoms for the st. 167 mesozooplankton experiment. Treatment explanations as in Fig. 3

phycean-species and the heterotrophic 'droplet' flagellate made up some 60% of the biomass (Fig. 6). The community of nanoplanktonic flagellates that developed in the krill containers was basically the same as the community observed in the Weddell Sea during the latter part of the cruise period, the post 'spring-bloom' period (Buma et al. 1989; Buma et al. 1991).

For experiment 2, with water from the most southerly station, 167, the krill addition treatment behaved in the same way as for experiment 1 (station 158). The phytoplankton biomass decreased rapidly to low values (a few mg chl $a \cdot m^{-3}$, Fig. 7). During the first 4 days, when there was still phytoplankton left in the krill container, the growth rate of phytoplankton biomass (based on chloro-

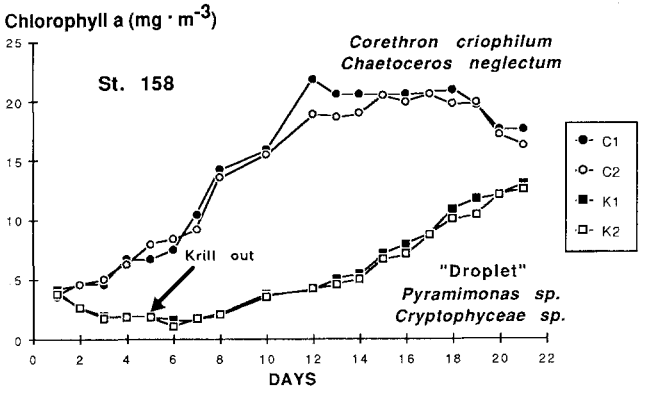


Fig. 5. Phytoplankton biomass (as chlorophyll *a*) in the st. 158 krill experiment. C1, C2 = controls; K1, K2 = krill addition = 8 juveniles + 2 adults. Dominating phytoplankton species during the later part of the experiment also shown

phyll *a*) in the control, copepod, and krill + copepod containers were all around $0.2 \cdot d^{-1}$, while in the krill container the growth rate was negative, $-0.2 \cdot d^{-1}$ (Fig. 8).

The phytoplankton that developed after removal of the krill showed similarities to the phytoplankton community observed in the Weddell Sea during the latter part of the cruise period, the post 'spring bloom' period (Buma et al. 1989, Buma et al. 1991), i.e. dominance of *Pyramimonas* sp., Cryptophycean-species and the heterotrophic 'droplet'-shaped flagellate, that together made up 95% of the phytoplankton carbon in the container (Fig. 9). In the control, copepod, and krill + copepod treatments, the large diatom *Thalassiosira antarctica* dominated the phytoplankton biomass after a few days and at the end of the experiment made up some 90% of the total carbon (Fig. 9).

If krill and control (C and K) containers from the two stations are pooled it can be shown (Mann-Whitney U-

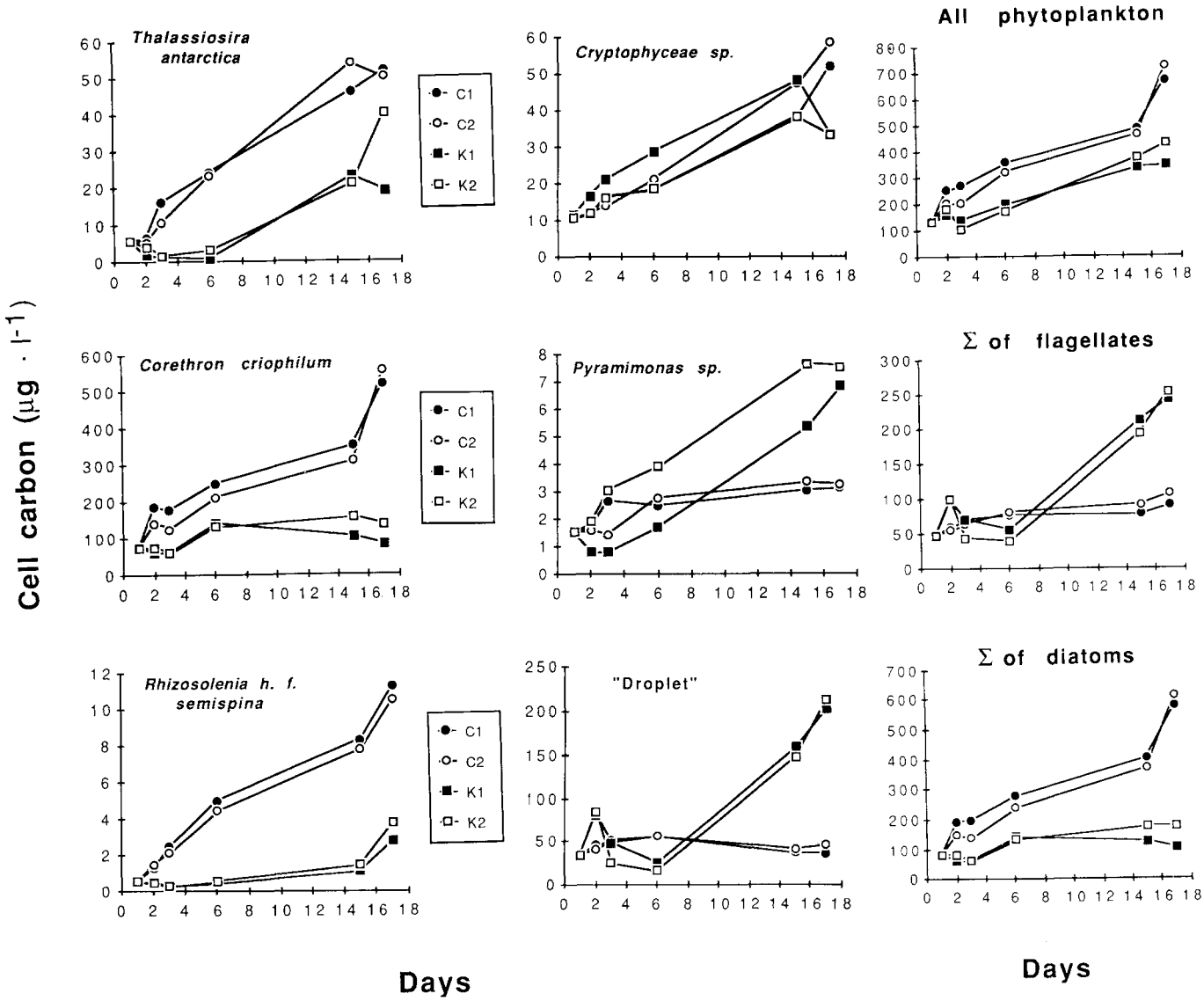


Fig. 6. Cell carbon of different phytoplankton species, total phytoplankton, sum of flagellates, and sum of diatoms in the st. 158 krill experiment. Treatment explanations as in Fig. 5

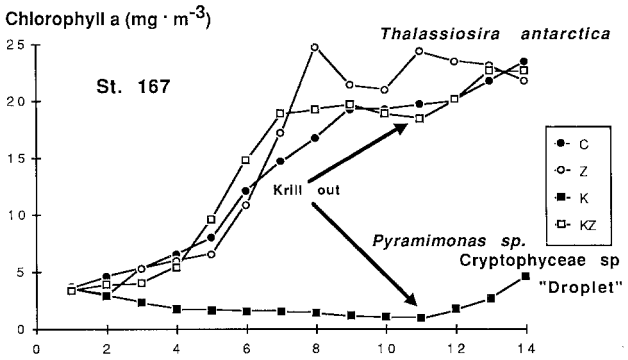


Fig. 7. Phytoplankton biomass (as chlorophyll *a*) in the st. 167 krill experiment. C = control (no krill, natural level of mesozooplankton), Z = 10X mesozooplankton addition, K = krill addition = 8 juveniles + 2 adults, KZ = krill + 10X mesozooplankton addition. Dominating phytoplankton species during the later part of the experiment also shown

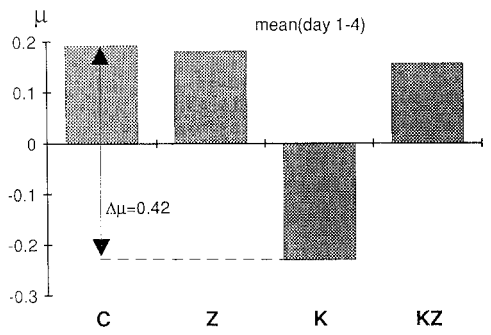


Fig. 8. Phytoplankton growth rate based on chlorophyll *a* development for the first 4 days of experiment (st. 167). Explanation of symbols as in Fig. 7

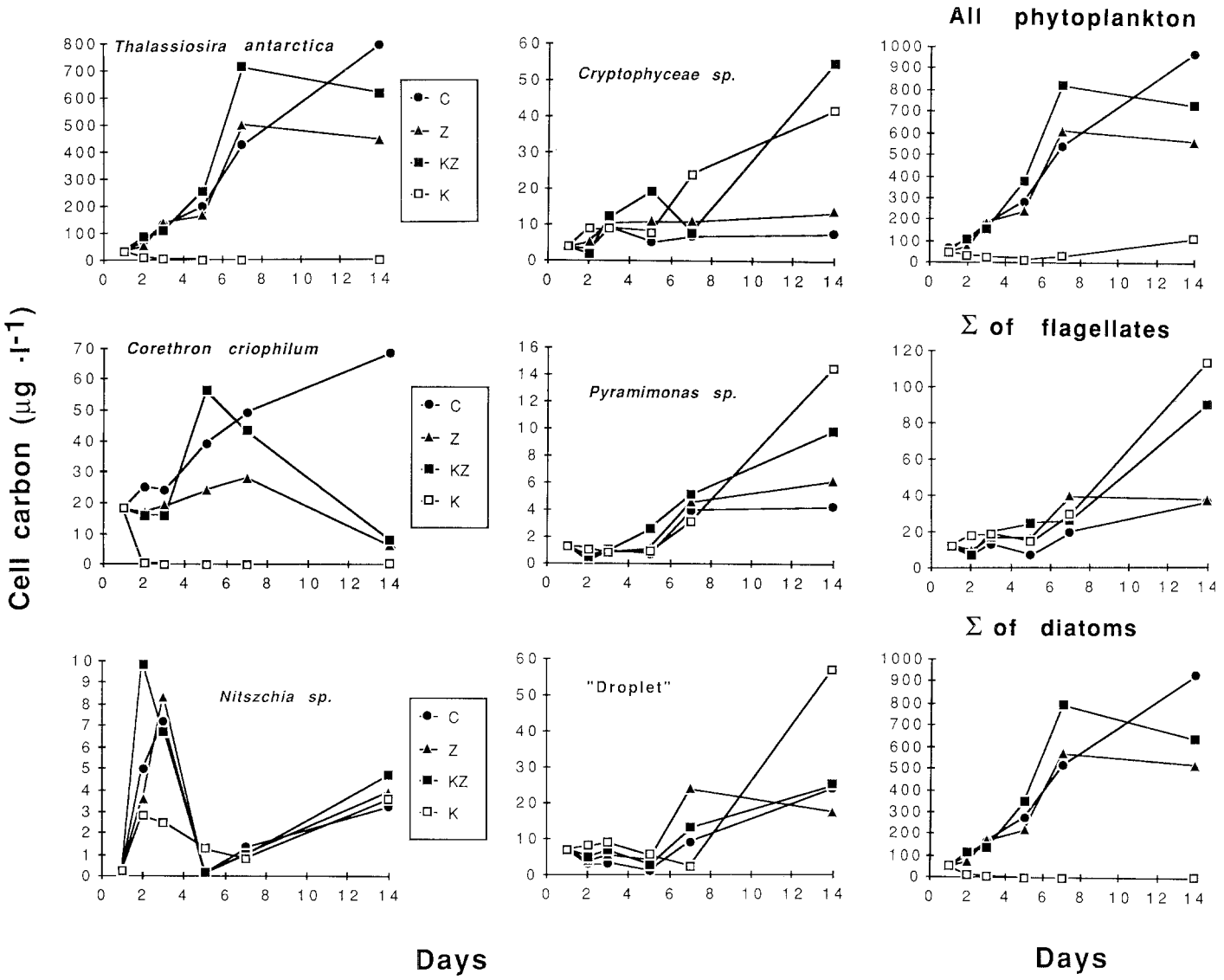


Fig. 9. Cell carbon of different phytoplankton species, total phytoplankton, sum of flagellates, and sum of diatoms for the st. 167 krill experiment. Treatment explanations as in Fig. 7

test) that krill addition caused a significant ($p<0.05$) lowering of total phytoplankton carbon as well as diatom carbon, but that there was no significant ($p>0.5$) krill effect on flagellate carbon.

In the container where krill were added together with copepods, the phytoplankton biomass did not decrease compared to when krill alone was added (Fig. 7). Krill in this container initially preyed selectively on copepods, giving a pale yellow-beige colour to the digestive gland and gut, until there was virtualdy no copepods left. In the container where krill was added without copepods, digestive glands and guts were bright green due to the diet of large diatoms, which were selectively grazed by the krill (Fig. 7).

In the krill experiment 2, in the control bottles, dominating copepods were *Oithona similis*, *Metridia gerlachei*, and *Oncaea* sp., while in the container with 10X copepods *Oithona similis* dominated, followed by *Ctenocalanus citer*, *Metridia gerlachei*, *Oncaea* sp. and *Calanoides acutus*. Copepods were in good condition with high biomasses in the control and 10X copepod containers at the termination of the experiment (dry weight = 38 and 89 mg $\cdot$ m^{-3} for the control and 10X respectively).

In the st. 158 krill experiment most inorganic nitrogen and phosphate had been consumed at the end of the experiment for all treatments (Table 1). A large part of the silicate on the other hand remained in the krill treatments, while most was consumed in the control treatments. In the st. 167 krill experiment nitrate and phosphate were consumed to low levels in the control, as well as in containers with added copepods or copepods plus krill (Table 1). However, with only krill much of the initially available nitrate and silicate remained at the end of the experiment. With both krill and copepods most of the nitrate and phosphate were consumed, but only approximately one third of the silicate, corresponding to the dominance of non-diatoms in this treatment.

Discussion

While phytoplankton biomass was generally low in situ (usually <2 μg chl $a \cdot l^{-1}$, maximum 4.5 μg chl $a \cdot l^{-1}$, Jaques and Panouse 1989, 1991) shipboard cultures showed the capacity for exhaustion of nutrients and the accumulation of very high phytoplankton biomasses (20–30 μg chl $a \cdot l^{-1}$) after ca 2 weeks of incubation. Only with krill additions (500 animals $\cdot$ m^{-3}) could the buildup of phytoplankton biomass be prevented. We used a comparatively high photon flux density in our experiments, 100 μE $\cdot$ m^{-2} $\cdot$ s^{-1}. However, even at one tenth of this value (11 μE $\cdot$ m^{-2} $\cdot$ s^{-1}, corresponding to a depth of 30–60 m at noon) there was almost the same overall growth rate of phytoplankton in shipboard cultures (Granéli unpublished results). In situ, the lowering of the net growth rate due to a deep mixing layer may be more severe, although during the EPOS leg 2 cruise the mixed layer was quite shallow. It is thus less likely that light limitation could be the reason for the low phytoplankton biomass in situ compared to shipboard cultures. If growth rates of phytoplankton in situ were low due to a deep mixed layer or low surface insolation, this would enhance effects from grazing on the biomass and structure of the phytoplankton community. Thus, if clear effects from krill and copepod grazing were seen in our experimental containers, with an optimal light regime and no losses due to sedimentation of algal cells out of the mixed layer, even more marked effects should be expected in situ. However, grazing effects on phytoplankton species composition were pronounced only when the numbers of copepods were artificially raised well above natural average levels (5X or 10X), while krill densities in swarms may be higher than the 500 animals (400 juveniles, 100 adults) $\cdot$ m^{-3} we used in the experimental containers. Johnson et al. (1984) reported an average of 170 animals $\cdot$ m^{-3} in smaller swarms, but large swarms may contain up to over 1000 or even 10000 individuals $\cdot$ m^{-3} (Shulenberger et al. 1984). Since swarms are local phenomena it is not to be expected that krill can uniformly graze down phytoplankton over the whole Antarctic Ocean. However, in the Antarctic Peninsula area Kopczynska (1992) found strong evidence that both deep mixing and krill grazing acts to suppress diatom blooms and cause flagellates to dominate.

It must be pointed out that other species–specific phytoplankton loss factors than grazing, e.g. more rapid sinking of large diatoms compared to small ones or flagellates, could hypothetically in situ produce the same successional patterns as those that were observed in our confined laboratory systems. The absolute, in situ rates of krill and mesozooplankton grazing must be quantified before a final evaluation of the importance of grazing for phytoplankton species successions can be made.

In summary, because light conditions for phytoplankton growth may have been better than in situ, while loss rates due to grazing were exaggerated, we may not be able to say much about the *quantitative* effects of krill and mesozooplankton predation/grazing on Antarctic plankton community regulation. On the other hand we may conclude that at least krill grazing is a plausible *mechanism* for phytoplankton species successions.

Changes in phytoplankton community structure in situ showed a resemblance to what occurred in our experimental containers. During the EPOS leg 2 cruise it was observed that a krill swarm grazed down a diatom dominated 'bloom' within a few hours (Smetacek and Veth 1989). At the same time a cryptophycean flagellate became the dominant autotroph and there was a shift to a low P/R ratio. A similar succession in the plankton community was also observed in situ during the transition from 'spring' to 'summer' in the Weddell Sea (Buma et al. 1989). Jacques and Panouse (1991) found in the Weddell/Scotia Confluence area a rapid change in January from a high biomass netplankton community (4 μg chl $a \cdot l^{-1}$) to a nanoplankton system dominated by various flagellates, especially cryptophyceans, which they interpreted as an effect of krill grazing.

Copepods, even at elevated concentrations, could not prevent the build-up of a phytoplankton 'bloom' in the shipboard cultures, in contrast to krill. However, copepods could change the species composition of 'blooms' markedly, from dominance of large diatoms to the colonial *Phaeocystis pouchetii*. Copepods did not graze this algae,

and thus caused it to bloom instead of the large diatoms preferred by grazers, as has been suggested by Verity and Smayda (1989). A similar copepod (mainly small species) preference for larger diatoms over various types of flagellates, causing the latter to become dominant, has been observed in experiments with grazer manipulations in the Skagerrak (Granéli et al. 1989, 1993; Olsson et al. 1992). In the North Sea *Phaeocystis pouchetii* blooms to high cell concentrations and Lancelot et al. (1987) has suggested that this species is grazed only when cells are in small size colonies. Colony formation may be enhanced by phosphorus limitation (Veldhuis and Admiraal 1987), but this is not likely to happen in Antarctic waters. Thus colony formation may instead be seen as an anti-grazer adaptation.

Our results from the experiment with water from station 158 showed that krill grazed selectively first on the large diatoms leaving the small Cryptophycean-species sp. and *Pyramimonas* sp. to grow undisturbed. Meyer and El-Sayed (1983) working experimentally on the grazing selectivity of krill on phytoplankton, found that krill filtered solitary cells with less than 20 μm in diameter much slower than larger diatoms and chain forming species. Thus food selectivity was size dependent, as was also found by Quetin and Ross (1985). Based on extensive studies of phytoplankton biomass and species composition, krill abundance and mixing depth Kopczynska (1992) concluded that krill prefer feeding on diatoms, but are less efficient grazers on microflagellates (< 20 μm). We found that krill behaved in a similar manner when the food source was dominated by phytoplankton (as in the st. 158 experiment). However, if copepods were abundant krill did prefer to prey first on these. Feeding on copepods, with a clearance rate three times as high as for phytoplankton, has previously been observed by Price et al. (1988). These authors also noted that krill ingestion rate of copepods was independent of phytoplankton concentration, showing that krill selectively ingested copepods. Only when copepods had been eliminated in the st. 167 experiment did krill start to graze on diatoms, suggesting that food selectivity is not only size related, but also depends on food quality. The protein- and lipid-rich copepods were probably a better quality food than diatoms of similar size. The diatom that dominated in this experiment was the chain forming *Thalassiosira antarctica*, which is of a size comparable to some of the copepods. Predation on copepods may also be necessary during winter, when no phytoplankton is available, although average copepod abundance even during summer in Antarctic waters may be too low to meet the minimal metabolic requirements of krill (Price et al. 1988). That krill during winter switches to predatory feeding has recently been supported by studies made during the fourth RACER expedition to an area west of the Antarctic peninsula during the Antarctic winter (Öresland pers. comm.). Krill may thus regulate both an important grazer component (copepods) as well as graze directly on phytoplankton (cfr. Price et al. 1988). This is important not only with respect to energy transfer in the food chain, but also for plankton community structure, since krill and copepod grazing in our experiments caused different phytoplankton successions. Krill may be a 'keystone' species, similar to the likewise omnivorous *Mysis*-species of many temperate lakes, which may play important roles in structuring limnetic food webs (Grossnickle 1982). The difference between Antarctic and temperate waters with respect to the regulation of phytoplankton communities during the spring and early summer period may be related to large overwintering stocks of krill in Antarctic waters, which may rapidly graze down blooms, while in temperate waters the development of grazers (e.g. copepods) is out of phase with phytoplankton development at this time of the year (e.g. Fransz and Gieskes 1984).

Krill grazing could be responsible for the shift from a netplankton dominated phytoplankton community based on nitrate as nitrogen source, to a nano- and picoplankton community based on regenerated nitrogen and with a large heterotrophic component in the form of a 'microbial loop'. Also copepods could structure the phytoplankton community, e.g. by consuming diatoms and thus indirectly favouring other algae, e.g. the grazing-resistant colony-forming type of *Phaeocystis pouchetii*, sometimes observed as blooms in Antarctic waters. However, the actual effect of selective copepod grazing in situ is still unclear since copepod grazing studies have not been made under in situ conditions.

We suggest that grazing by both copepods and krill (as has earlier been proposed e.g. by Meyer and El-Sayed 1983) may have noticeable effects on Antarctic phytoplankton biomass, community structure and species successions. This conclusion was also reached by Buma et al. (1991) based on their results from Fe enrichment experiments during the EPOS leg 2 cruise. However, we certainly do not want to advocate grazing as the *only* structuring force; in situ there is a complicated, hierarchical interplay between several abiotic and biotic regulating mechanisms (Frost 1991). It must also be stressed that results from our as well as other laboratory or ship-board experiments with Antarctic water (cfr. de Baar et al. 1990) need to be compared to in situ processes. There is still no final answer to the question why nutrients are not fully utilized by phytoplankton in the Southern Ocean as well as other high nutrient–low chlorophyll areas (Cullen 1991; Frost 1991), a phenomenon referred to as the "Antarctic Paradox" by Tréguer and Jacques (1986). Finally it is important to note that our results refer to the Scotia-Weddell Confluence area, where biological activity, including phytoplankton and krill biomasses, is elevated compared to the bulk of the Southern Ocean (Nelson et al. 1987).

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