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Interannual and seasonal variability in short-term grazing impact of *Euphausia superba* in nearshore and offshore waters west of the Antarctic Peninsula

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Abstract

Our focus in this paper is the interaction between macrozooplanktonic grazers and primary producers, and the interannual and seasonal variability in the Palmer Long-Term Ecological Research (Palmer LTER) study region from Anvers Island to Adelaide Island. Short-term grazing estimates are calculated by integrating (1) theoretical and experimental estimates of ingestion rates in response to the standing stock of phytoplankton, and (2) field measurements of phytoplankton standing stock and grazer biomass. Field data come from three austral summer cruises (January/February of 1993, 1994, and 1995) and one sequence of seasonal cruises (summer, fall and winter 1993). The relative and absolute abundance of the dominant macrozooplankton grazers, *Euphausia superba* and *Salpa thompsoni*, varied by at least an order of magnitude on the spatial and temporal scales observed. Mean grazing rates ranged from 0.4 to 9.0 μg chlorophyll m^{-2} h^{-1} for the Antarctic krill and salp populations over the three summer cruises. This leads to variability in the flow of carbon from the primary producers through the grazers on the same scales. Temporal and spatial variability in grazing impact and faecal pellet production are high.

Résumé

Le centre d'intérêt de cet article est l'interaction entre les brouteurs macroplanctoniques et les producteurs primaires, ainsi que la veriabilité interannuelle et saisonnière dans la zone d'étude du Projet Palmer de Recherche Écologique à Long Terme (Palmer LTER), entre l'Ile Anvers et l'Ile Adélaïde. Les estimations de broutage à court terme sont obtenues en intégrant: (1) des estimations théoriques et expérimentales de taux d'ingestion en réponse au stock disponible de phytoplancton, et (2) des mesures in situ du stock de phytoplancton et de la biomasse des brouteurs. Les données de terrain proviennent de trois campagnes en été austral (janvier–février 1993, 1994 et 1995) et d'une séquence de campagnes saisonnières (été, automne et hiver 1993). Les abondances absolue et relative des brouteurs macroplanctoniques dominants,

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Euphausia superba et *Salpa thompsoni*, varient d'au moins un ordre de grandeurs aux échelles spatiale et temporelle des observations. Sur trois campagnes estivales, les taux de broutage moyen varient de 0.4 à 0.9 μg chlorophyll m^{-2} h^{-1} pour les populations de krill antarctique et de salpes. Il en découle une variablité à la même échelle du flux de carbone des producteurs primaires aux brouteurs. La variabilité spatiale et temporelle de l'impact du broutage et de la production de pelotes fécales est forte.

Keywords: Interannual; Seasonal; Grazing; *Euphausia superba*

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1. Introduction

A primary objective of the Palmer Long-Term Ecological Research project (LTER) is to investigate seasonal and interannnual variability in the pelagic marine ecosystem west of the Antarctic Peninsula, particularly in relation to the timing and magnitude of the seasonal sea–ice cycle. To help meet this objective, at the inception of the Palmer LTER a sampling grid was established with fixed geographic station locations (Waters and Smith, 1992) that would be occupied repeatedly over decadal time scales. The mesoscale grid extends alongshore from the southern Bransfield Strait to south of Adelaide Island and 200 km offshore. Over the past several years repetitive sampling of the same grid locations (Fig. 1) has provided a data base that allows us to discuss the dominant macrozooplanktonic grazers and their effect on both the magnitude and variability in grazing impact and carbon flux.

In the Southern Ocean, temporal variability in particulate flux is extreme, and is correlated with the seasonal ice cover and primary production cycles (Honjo, 1990). The relative impact of micro-, meso-, and macrozooplankton grazers on primary production and particulate flux has yet to be tested (Anderson, 1993). However, in the coastal continental shelf areas within the Palmer LTER region, macrozooplankton often dominate the zooplankton assemblage, and their role as grazers and producers of particulate matter may be important.

Two macrozooplankton grazers with the potential to influence vertical flux are the Antarctic krill, *Euphausia superba*, and the salp, *Salpa thompsoni*. Both occur in high densities in the Antarctic Peninsula region, but their distributions and periods of high abundance do not often overlap (reviewed in Ross et al., 1996). Both produce faecal pellets with high sinking rates (Honjo, 1990). Sediment traps in the area are sometimes filled with krill faecal pellets, suggesting that in certain regions and times, krill are the dominant source of sinking particles (Wefer et al., 1988). In addition, salps are able to consume nearly the full range of phytoplankton, and aid in the conversion of small, nonsinking particles into larger, denser sinking particles (Michaels and Silver, 1988). In contrast to salps, krill consume larger phytoplankton cells more efficiently than smaller cells (Quetin and Ross, 1985), although there may be an upper size limit for effective ingestion (Boyd et al., 1984).

In this study we calculate grazing impact and carbon flux for stations sampled consistently during three seasons in 1993 and during the austral summer for three consecutive years (1993, 1994, 1995). The results are discussed in terms of the levels and patterns of variability among seasons and years, distribution of impacts within the grid area, and causes of the magnitude of change and variability seen among years.

2. Materials and methods

2.1. Research cruises

This study examines results from five cruises: austral summer, January/early February, 1993, 1994, 1995; fall, March–May, 1993; and late winter, August–September, 1993. Stations along four transect lines (600, 500, 400 and 300 lines), encompassing an area of 60,000 km^2, from Anvers Island to Adelaide Island (Fig. 1), were sampled during all cruises. Palmer LTER standard alongshore transects are 100 km apart, and standard stations on transects are spaced 20 km apart from the coast to 200 km offshore. Because the same stations were visited during sequential cruises, we have been able to document seasonal (1993, $n = 31$ stations in common) and interannual variability ($n = 32$ stations in

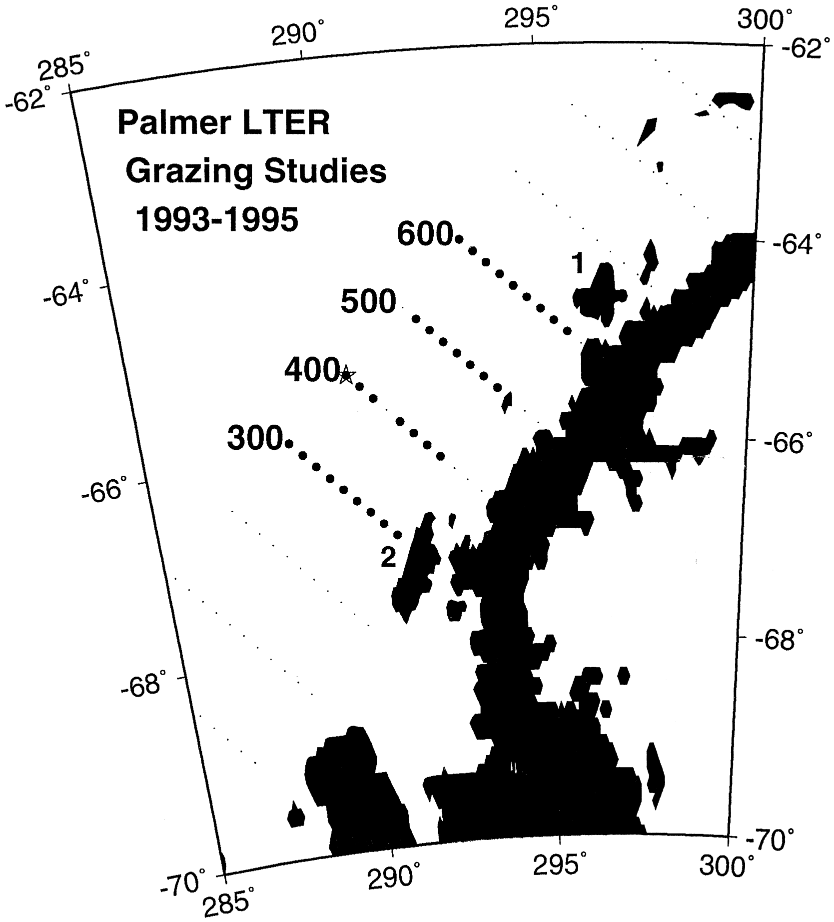

Fig. 1. Location in the LTER grid of station samples analyzed for seasonal (∗) and interannual (∗ plus star) variability. Other stations in the LTER grid are shown (•). Islands are identified as: 1—Anvers, 2—Adelaide.

common) in this region. Ice cover limited geographical sampling range in August/September 1993, as net tows could not be done on the inshore stations of the 300 and 400 lines. Data on krill and salp abundance and phytoplankton standing stock (Smith et al. b, this volume) were collected concurrently. Primary production was estimated with a bio-optical model for the same cruises (Smith et al. a, this volume). Data on phytoplankton abundance throughout the 1992–1993 season at Station E, a time series station near Palmer Station on Anvers Island, were from Smith et al. b, this volume. In this study, chlorophyll a concentrations were used as a proxy measure for phytoplankton abundance. Consequently, species composition and size distribution within the phytoplankton community were not considered.

2.2. Macrozooplankton grazer distribution and abundance

Macrozooplankton were collected at each station with a 2-m square fixed-frame net (700 μm mesh, 500 μm mesh cod end). The net was rigged with a General Oceanics flowmeter to measure volume filtered, and a time–depth recorder to record maximum depth of tow. Standard tows were oblique from the surface to 120 m and lasted for approximately 30 min at a ship speed of 3.5 km h^{-1}. When flow meters did not operate properly (January 93 and 2 weeks of March 93), volume filtered was estimated from tow duration and the relationship between tow duration and volume filtered found in January 1994.

Trawl contents were analyzed for macrozooplankton abundance either on board or from preserved subsamples. Total wet volumes of Antarctic krill (*E. superba*) and *S. thompsoni* were measured separately with a graduated cylinder. For grazing estimates, wet volume of krill was converted to wet weight with a density of 1 g cm^{-3} based on data from Ross and Quetin (unpublished), and the effect of size on the functional response curve assumed negligible. For salp grazing estimates, numbers of zooids within defined size categories were estimated from numbers of zooids in a subsample. Zooid size categories (total length, oral–atrial distance) included: 10–20 mm, 20–30 mm, 30–40 mm, and >40 mm. Stage 0–1 solitary zooids with eleoblasts were generally <10 mm, and were not included in the grazing estimates since they are still primarily dependent on the eleoblast for nutrition (Foxton, 1966).

2.3. Grazing model for Antarctic krill

Grazing rates as a function of phytoplankton concentration were measured in laboratory experiments at Palmer Station during two austral summers, 1990–1991 and 1991–1992. Experiments were run for two sequential 6-hour periods. During the first 6 h (control period), the experimental tub contained no krill. During this time krill were acclimated in other tubs to experimental conditions. After the 6-h control period krill were transferred from the acclimation to the experimental tubs and allowed to graze the following 6 h. The experimental tubs (50-l volume) were sampled for chlorophyll a concentration at 2-h intervals throughout the control and experimental periods. Five replicate water samples from each sampling period were analyzed for chlorophyll a as described by Smith et al. (1981). Fourteen to eighteen krill (average wet weight 0.5 mg) were used in each experiment.

The results of these experiments were used to formulate functional response curves for *E. superba* that describe the relationship between ingestion and chlorophyll a concentration. Two potential models for a functional response curve were fitted to the data from these 15 experiments (Fig. 2a). Data from 12 experiments with either of two phytoplankton

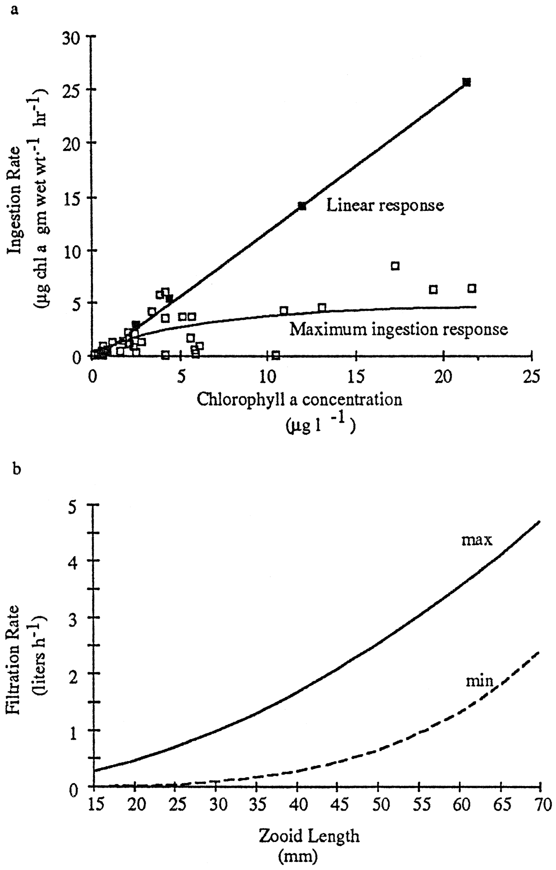

Fig. 2. (a) Functional response relationships for Antarctic krill, *E. superba*. Experiments: food, *Thalassiosira antarcticum*, nine experiments, and *Phaeocystis* sp. colonies (185-μm average diameter), six experiments; experimental volumes about 50 l (Price et al., 1988). Grazing rates for each 2-h experimental period (μg chlorophyll a g^{-1}, wet weight, h^{-1}) were calculated as in Marin et al. (1986). In all cases, C_0 (initial concentration) was less than C_c, the critical concentration for maximum ingestion. With a few exceptions, the algal growth rate was 0. Linear functional response (solid squares, *T. antarcticum*, three experiments, 1991–1992): ingestion $= 1.218 \times$(chlorophyll a, μg l^{-1}) $- 0.435$ ($r^2 = 0.999$). Maximum rate functional response curve (open squares *T. antarcticum*, six experiments in 1990–1991 and all *Phaeocystis* sp. experiments.): ingestion $= 1.257 \times \ln$(chlorophyll a, μg l^{-1}) $+$ 830 ($r^2 = 0.444$). (b) Maximum and minimum filtration rates as a function of zooid length assumed for *S. thompsoni* from literature relationships for *Pegea confederata*. (1) $\log(F_{\mathrm{max}})$ (ml h^{-1}) $=$ $1.843 \times \log$(zooid length) $+ 0.271$, and (2) $\log(F_{\mathrm{min}})$ (ml h^{-1}) $=$ $3.85 \times \log$ (zooid length) $- 3.724$.

species, *T. antarcticum* or *Phaeocystis* sp., fit a maximum ingestion rate model ($r^2 = 0.444$). Among-experiment variability (three 2-h periods) in ingestion rate was high, particularly at low concentrations. The three experiments on *T. antarcticum* in 1991–1992 (nine ingestion rate estimates), yielded data that fit a linear model well ($r^2 = 0.999$). The linear functional response curve supports experiments reported by Price et al. (1988) where maximum ingestion rates by *E. superba* were not achieved even at phytoplankton concentrations of 10–12 μg chlorophyll a l^{-1}, and also by McClatchie (1988), who report a similar linear model for grazing by *Thysanoessa raschii*. In addition, the two functional response curves for estimated grazing impact (Fig. 2a) coincide within the environmental ranges of chlorophyll a concentrations found in this study, generally between 0 and 4 μg chlorophyll a l^{-1}. Thus, to calculate the grazing impact of krill we used the linear model of ingestion exclusively throughout subsequent analysis of the data:

$$\begin{aligned}&\text{Ingestion}\left(\mu\text{g chlorophyll a g wet wt}^{-1}\ \text{h}^{-1}\right)\\&\quad=1.218\left(\mu\text{g chlorophyll a l}^{-1}\right)\\&\qquad-0.435\qquad(r^2=0.999).\end{aligned}$$

For each station, grazing impact was estimated from ingestion rate as calculated from the linear functional response curve and with field data on chlorophyll a concentrations (average in top 50 m, Smith et al. b, this volume), krill wet weight, and the depth of the water column sampled:

$$\begin{aligned}&\text{Grazing impact, }\mu\text{g chlorophyll a m}^{-2}\ \text{h}^{-1}\\&\quad=\left(\text{krill, g wet wt m}^{-3}\right)\\&\qquad\times\left(\mu\text{g chlorophyll a g wet wt}^{-1}\ \text{h}^{-1}\right)\\&\qquad\times(120\ \text{m}).\end{aligned}$$

2.4. Grazing model for *S. thompsoni*

Salps are nonselective feeders with respect to both size and type of particles (Harbison and McAlister, 1979; Kremer and Madin, 1992; Madin, 1974). Unlike many crustaceans, filtration rate for salps is dependent on body size and not phytoplankton concentration. Since no information on grazing rates from *S. thompsoni* is available, maximum and minimum filtration rates were calculated with relationships between total length and filtration rate for *P. confederata*, a slow-swimming oceanic salp that ranges in size from 20–70 mm, the same size range as *S. thompsoni*. This approach is supported by recent data on *S. thompsoni* in the Southern Ocean. Ingestion rates of salps calculated with the 'maximum rate' equation and ambient chlorophyll are comparable to maximum ingestion rates recently obtained for *S. thompsoni* based on pigment analysis techniques (Perissinotto and Pakhomov, this volume). In addition, ingestion rates for salps based on the 'minimum rate' equation are close to the average ingestion rates obtained by (Perissinotto and Pakhomov, this volume). Maximum rates used (Eq. (1)) assumed no temperature response and were calculated with the relationship found at ambient temperatures in the south Atlantic with a pigment analysis technique (Madin and Cetta, 1984) (Fig. 2b):

$$\begin{aligned}\log(F_{\max})\ (\text{ml h}^{-1}) &= 1.843\log(\text{zooid length})\\ &\quad+0.271 \qquad (1)\end{aligned}$$

Minimum rates (Eq. (2)) were derived by applying a temperature response to laboratory experiments of Harbison and Gilmer (1976) at 25°–29°C. A Q_{10} (the factor by which measured response changes with a temperature change of 10°C) of 2 was applied to the equation of Harbison and Gilmer for high filtration rates for a temperature decrease of 23°C. In this resulting relationship (Eq. (2)), minimum rates were lower for small zooids, and a factor of 3 lower for the largest salps (Fig. 2b):

$$\begin{aligned}\log(F_{\min})\ (\text{ml h}^{-1}) &= 3.85\log(\text{zooid length})\\ &\quad-3.724 \qquad (2)\end{aligned}$$

Filtration rates for each size category of salps found at a station were calculated from these relationships, multiplied by the number of salps and the average chlorophyll a concentration in the top 50 m at that station to estimate grazing impact:

$$\text{Grazing impact}\left(\mu\text{g chlorophyll a m}^{-2}\ \text{h}^{-1}\right) = \left(\text{number zooids m}^{-3}\right) \times \left(\text{l h}^{-1}\right) \times \left(\mu\text{g chlorophyll a l}^{-1}\right) \times \left(120\,\text{m}\right).$$

Grazing impacts for each size category of salps were summed to calculate the total grazing impact at a station. The grazing impact of salps was only analyzed for the March 1993 and January 1994 cruises. These were the only cruises with more than incidental catches of salps, > 18 ml 1000 m^{-3}.

2.5. Egestion rates

Faecal pellet production for both macrozooplanktonic grazers was estimated with (1) grazing impact as described above, (2) an assumed 85% assimilation efficiency, and (3) a carbon:chlorophyll a ratio of 50 (Mitchell and Holm-Hansen, 1991). Carbon assimilation efficiencies of 85% have been measured for *Euphausia pacifica* (Ross, 1982) and for *E. superba* (Quetin and Ross, unpublished data). Assimilation efficiencies for salps, including *S. thompsoni*, are unknown, so we assume the same assimilation efficiency for both grazers. We estimate a maximal faecal pellet flux by assuming all faecal pellets will sink.

2.6. Percentage of net primary production grazed

In addition to calculating grazing impact as an hourly rate of chlorophyll a loss, we also calculated the percentage of net primary production (%NPP) grazed by both krill and salps. NPP values were obtained from (Smith et al. a, this volume). Grazing impact values in the equation are described above.

$$\%\text{NPP} = 100 \times \left(\text{Grazing impact, } \mu\text{g chlorophyll a m}^{-2}\ \text{day}^{-1}\right) \times \left(50\ \text{C:chlorophyll a}^{-1}\right) / \left(\text{NPP, } \mu\text{g C m}^{-2}\ \text{day}^{-1}\right)$$

Also, a krill energetics model, using a krill ration of 281 μg chlorophyll a krill^{-1} day^{-1} (Ross and Quetin, 1986) and based on an average krill of 600 mg wet weight, was used to calculate %NPP grazed:

$$\%\text{NPP} = 100 \times \left(281\,\mu\text{g chlorophyll a krill}^{-1}\ \text{day}^{-1}\right) \times \left(50\ \text{C chlorophyll a}^{-1}\right) \times \left(\text{krill density, g m}^{-2}\right) / \left(\left(0.6\ \text{g krill}^{-1}\right) \times \left(\text{NPP, } \mu\text{g C m}^{-2}\ \text{day}^{-1}\right)\right)$$

The average percentage of net primary production grazed (%NPP) was calculated for ‘inner’ stations (up to 100 km offshore from the Antarctic Peninsula) and ‘outer’ stations (from 100 to 200 km offshore of the Antarctic Peninsula).

3. Results

3.1. Seasonal variability

During 1993 krill concentrations in the Palmer LTER region differed by a factor of 6 between January to March, with similar concentrations in March and August (Fig. 3). Salps were present only

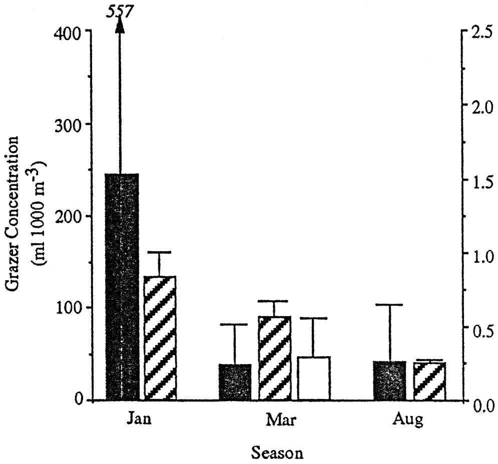

Fig. 3. Seasonal variability in grazer concentration (ml 1000 m^{-3}) and chlorophyll a concentration (μg l^{-1}, bar with diagonal stripes) throughout 1993, with 95% confidence intervals. Grazers: krill, black bars; salps, white bars. $N = 31$ matched stations for January and March, $N = 27$ in August.

in March, but the total concentration of grazers still did not reach January levels. Chlorophyll a concentrations in the water column decreased from January to August, but by a factor of 3 (Smith et al. b, this volume) (Fig. 3).

Seasonal grazing impact showed high variability with maximal impact in January and zero impact in August (Fig. 4, Table 1). Although krill volumes in March 1993 and August 1993 were not very different, in August 1993 grazing impact was zero throughout the grid because the average chlorophyll a concentrations, 0.24 μg chlorophyll a l^{-1}, were less than the threshold for ingestion, 0.36 μg chlorophyll a l^{-1}, in the linear model (Figs. 2a and 3). The range in estimated grazing impact also decreases, with fewer high values in March 1993 than in January 1993 (Table 1). Grazing impact throughout the Palmer LTER grid is not homogeneous in any season, and is higher onshore and south for krill, and offshore and north for salps (Fig. 4). The coefficient of variation in krill grazing rate is greater in March 1993 than in January 1993 due to fewer zero estimates in January (Table 1).

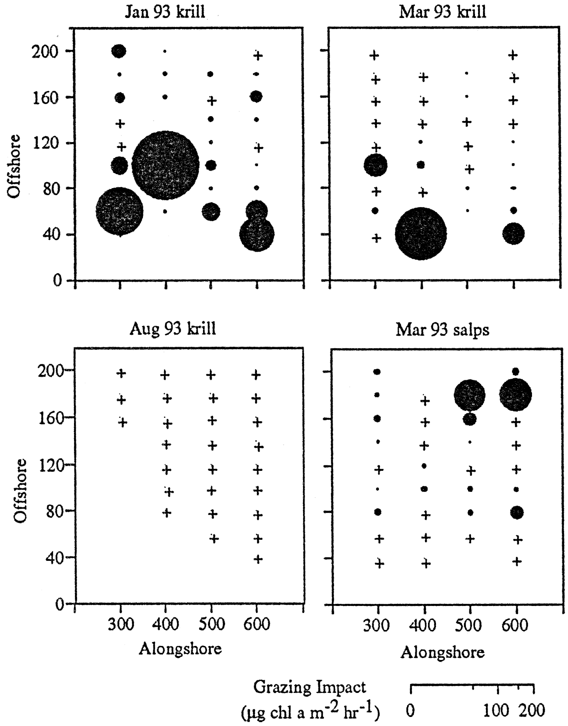

Fig. 4. Distribution of krill and salp grazing impact during the 1993 series of cruises. Axis values correspond to LTER grid locations. The size of the bubble is an index of grazing impact (μg chlorophyll m^{-2} h^{-1}). (+) indicates stations with zero grazing impact.

Table 1
Seasonal and interannual variation in macrozooplankton grazing rates on five cruises in the Palmer LTER study region, 1993–1995

Grazing rate	Jan 1993	Mar 1993	Aug 1993	Jan 1994	Jan 1995
KR					
mean	9.01	1.06	0.00	2.32	0.42
sd	26.95	3.62		3.80	0.72
CV%	299%	342%		164%	171%
SA (max)					
mean		2.32		5.66	
sd		6.94		9.14	
CV%		300%		162%	
SA (min)					
mean		0.11		1.27	
sd		0.34		2.19	
CV%		317%		173%	
Total grazing pressure (krill plus salps)					
KR–SA (max)					
mean	9.01	3.38	0.0	7.97	0.42
sd	26.95	7.51		10.02	0.72
CV%	299%	222%		126%	171%
KR–SA (min)					
mean		1.17		3.58	
sd		3.61		4.53	
CV%		309%		127%	

Mean, standard deviation (sd), and coefficient of variation (CV %) of short-term grazing estimates (μg chlorophyll a m^{-2} h^{-1}) for Antarctic krill (KR, linear functional response curve) and salps (SA, maximum and minimum estimates).

A plot of cumulative grazing impact in the area (sum of 31 matched stations in the grid, going from the lowest to highest in rank order) illustrates seasonal differences in both total grazing impact and the relative influence of individual stations (Fig. 5). If all stations experienced equal grazing impacts, the cumulative line would be linear. The greater the degree of concavity, the greater the influence of a few stations. For the cruises in 1993, grazing impact was negligible in over half the stations in January and March, and all stations in August, and a few high stations dominated the total impact (Fig. 4). For

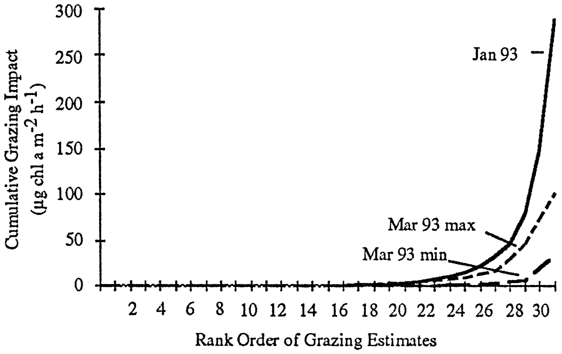

Fig. 5. Cumulative grazing impact of both krill and salps with rank order of grazing impact estimates, i.e., the cumulative sum of the grazing impact estimates from low to high. August is not plotted because grazing was 0. Maximum (dotted line) and minimum (dashed line) cumulative grazing impact curves for March indicate the sum of krill and salp grazing with the maximum and minimum models of filtration rate for salps respectively.

March, the difference in the maximum and minimum salp estimates is a factor of 3 (Table 1), but the maximum cumulative impact is still only about one-third of the estimate for the previous January (Fig. 5).

Temporal variability within a single spring/summer season is also high (Fig. 6), as illustrated with estimates of grazing impact calculated at Station E in the 1992–1993 season. Short term grazing impact ranged from 0–120 μg chlorophyll m^{-2} h^{-1}, with peaks in December and February. Rates at Station E during January, i.e., during the January 1993 cruise, were among the lowest of the season.

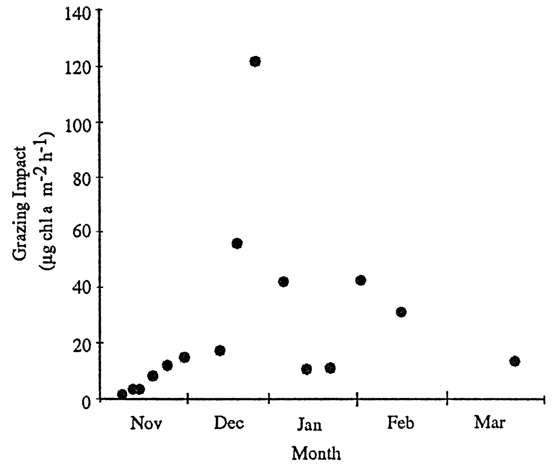

Fig. 6. Grazing impact (μg chlorophyll m^{-2} h^{-1}) at a time series station during 1992–1993, calculated with krill densities at station 600.040 in January, 1993, and weekly estimates of chlorophyll standing stock from Station E of the Palmer nearshore grid (Smith et al. b, this volume). Station 600.040 was chosen for its proximity to the nearshore grid.

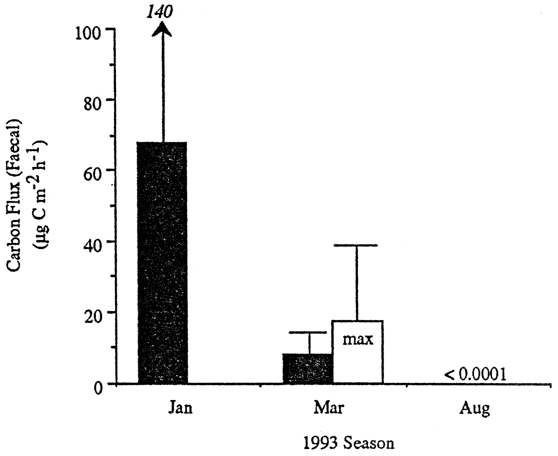

Fig. 7. Seasonal variability in carbon flux (μg carbon m^{-2} h^{-1}) from the upper 120 m of the water column derived from faecal pellet production during 1993, with 95% confidence intervals. Black bars are krill. White bars are salps. $N = 31$.

Based on our assumptions, seasonal variability in estimated carbon flux from faecal pellet production during the cruises follows the pattern seen in grazing impact—highest in January, both krill and salps contributing to total flux in March, and negligible flux in August/September (Fig. 7). Similarly faecal pellet production during the spring/summer seasons (1992–1993) follows the pattern of grazing impact shown in Fig. 6.

3.2. Interannual variability

Interannual variability in grazing impact and carbon flux was examined for three successive January cruises. Abundance of Antarctic krill, expressed as sample volume, varied by a factor larger than 20 among years, whereas chlorophyll a concentrations varied by less than a factor of 2 (Fig. 8). Only in January 1994 were both krill and salps present, with a combined volume about two-thirds that of January 1993. Grazer volume varied more than chlorophyll a

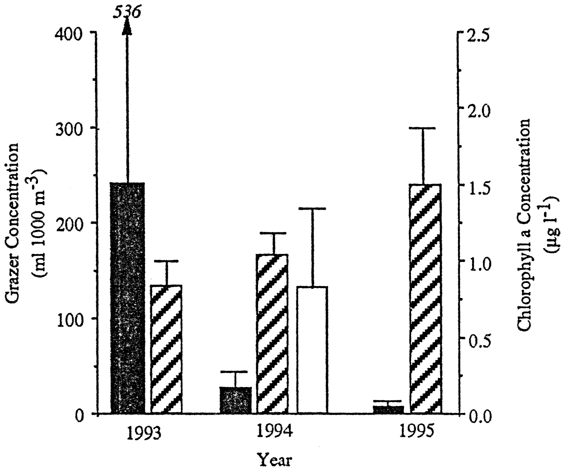

Fig. 8. Interannual variability in grazer concentration (ml 1000 m^{-3}) and chlorophyll a concentration (µg l^{-1}, bar with diagonal stripes) for January/February cruises from 1993–1995, with 95% confidence intervals. Grazers: krill, black bars; salps,white bars. $N = 32$.

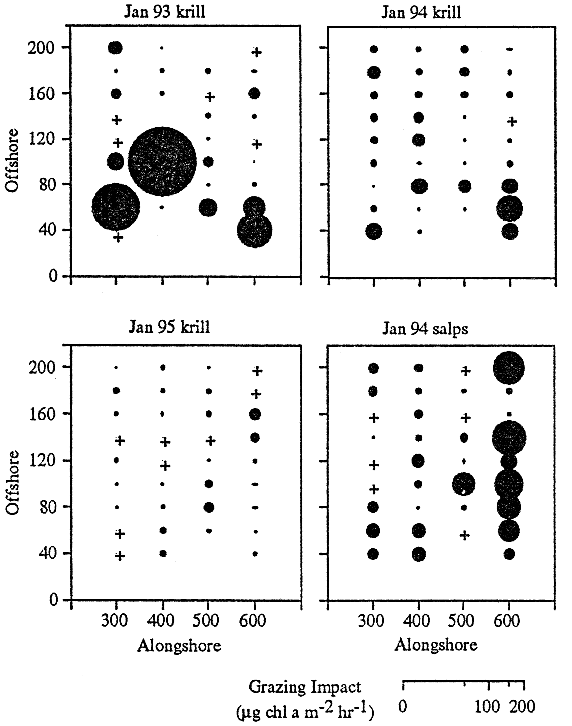

Fig. 9. Distribution of krill and salp grazing impact during three successive January cruises, 1993–1995. Axis values correspond to LTER grid locations. The size of the bubble is an index of grazing impact (µg chlorophyll a m^{-2} h^{-1}). (+) indicates stations with zero grazing impact.

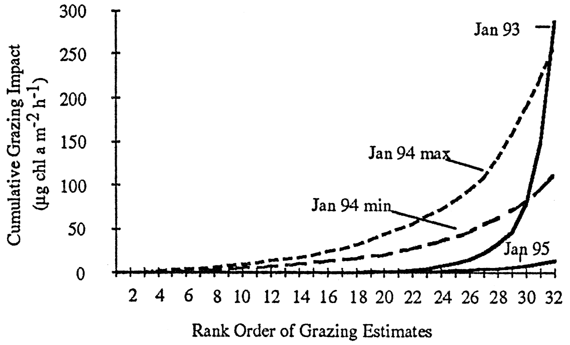

Fig. 10. Cumulative grazing impact of both krill and salps for three January/February cruises, 1993–1995, with rank order of grazing estimates, i.e., the cumulative sum of the grazing impact estimates from low to high. Maximum (dotted line) and minimum (dashed line) cumulative grazing impact curves for January 1994 indicate the sum of krill and salp grazing with the maximum and minimum models of filtration rate for salps respectively.

concentration, and decreased as chlorophyll a concentrations increased.

The distribution and magnitude of estimated krill and salp grazing impact within the Palmer LTER region varied in several aspects. Grazing impact and associated flux were much greater during January 1993 than in January 1995, and intermediate in January 1994. In January 1994, grazers included both krill and salps, with both occurring at multiple

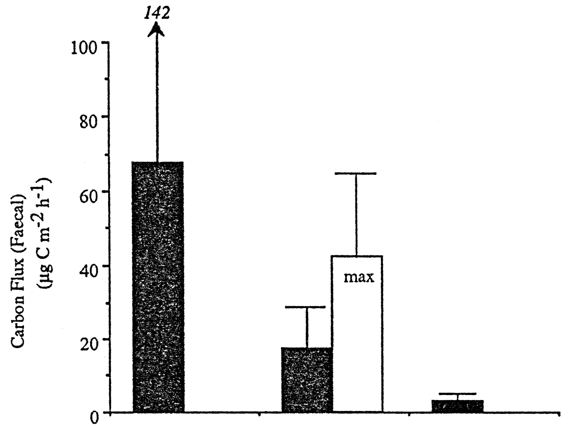

Fig. 11. Interannual variability in carbon flux (µg C m^{-2} h^{-1}) from the upper 120 m of the water column derived from faecal pellet production estimates in January, 1993–95, with 95% confidence intervlas. Dark bars are krill. Light bars are salps. $N = 32$.

Table 2
Percent net primary production (NPP) grazed, based on grazing models for krill and salps, and an energetic model for krill

Range	Krill (grazed)	Krill (energetic)	Salp (max grazed)	Salp (min grazed)
Jan 1993	0–55	0–4265	na	na
Inner stations	6.0 (15)	421 (1147)		
Outer stations	0.4 (0.9)	38 (102)		
Jan 1994	0–4.2	0–127	0–7.8	0–2.4
Inner stations	1.0 (1.3)	23 (37)	1.6 (2.0)	0.2 (0.2)
Outer stations	0.4 (0.4)	14 (16)	1.4 (2.4)	0.2 (0.3)
Jan 1995	0–0.6	0–36	na	na
Inner stations	0.1 (0.1)	0.7 (0.9)		
Outer stations	0.1 (0.2)	7.9 (11)		
Mar 1993	0–76	0–3910	0–37	0–0.013
Inner stations	2.6 (5.9)	228 (517)	0.6 (1.1)	0.0 (0)
Outer stations	0.0 (0)	5.3 (12)	4.4 (10)	0.0 (0)
Aug 1993	0	0–15,465	na	na
Inner stations	0.0 (0)	1763 (5139)		
Outer stations	0.0 (0)	325 (1112)		

Range for all stations, and average and standard deviation (in parentheses) for inner and outer stations, are given for each cruise.
na = no salps.

stations (Fig. 9). In January 1994 and 1995, the distribution of the grazing impact was more homogeneous than in 1993, with much lower coefficients of variation (Table 1). There were 6–8 stations with no krill grazing in both 1993 and 1995, but only 1 in 1994 (Fig. 9). A greater range appears to be associated with higher average impacts.

January 1993 was a year with high variability (300%) in station estimates of grazing impact (Fig. 10). The steep curve reflects the distribution, with many low and a few high grazing impact stations. Although both January 1993 and 1995 show low impacts at about two-thirds of the stations, the cumulative impacts are over an order of magnitude apart. In January 1994, the shallower slope indicated that a higher proportion of the stations contributed measurably to the cumulative impact, whether calculated with the salp minimum or salp maximum equations. The cumulative impact for both krill and salp maximum was close to that for krill alone in January 1993.

As we saw for seasonal carbon flux, the interannual variability in carbon flux from faecal pellet production mimicked grazing impact (Fig. 11). For example, krill and salp maximum together generate nearly as much carbon flux as krill alone in January 1993. January 1995, however, had low grazing impact and carbon flux, the result of low krill volume and no salps.

3.3. Percentage of net primary production grazed

The %NPP grazed calculated from the grazing models for krill and salps was 6% or less in all areas for all cruises (Table 2). For all cruises except January 1995, the average %NPP grazed by krill was greater at the inner stations. Our estimates from the krill energetic model of %NPP grazed for January 94 and 95 were 23% and 0.7%, respectively, in contrast to estimates for January 93 of 421% (Table 2).

4. Discussion

During the series of cruises over the past several years, we have documented striking variability in short-term grazing impacts by macrozooplankton. There was a substantial decrease from summer to winter, and between January 1993 and January 1995, within the area sampled regularly by the Palmer LTER. In addition, clear spatial variability was observed, with high grazing impacts found at only a few stations during the time periods sampled.

Other major patterns were seen in the nature of grazing impact. For example, either krill or a mixture of salps and krill dominate the macrozooplanktonic grazer community. To date we have not within the Palmer LTER region experienced a situation where salps dominate the macrozooplanktonic grazer community, unlike in regions to the north such as around Elephant Island (Ross et al., 1996). Also, there is a tendency for high grazing impact from krill to occur in onshore and southern parts of the region, and if salps are present, for higher rates to occur at offshore stations and northern transects. However, during January 1994, krill and salps co-occurred at many stations, making the pattern less clear.

Variability in grazing impact can stem from either variations in grazer biomass, chlorophyll a concentration, or both. A contour plot of grazing impact with varying conditions of chlorophyll a concentrations and krill biomass illustrates the relative importance of the two major factors (Fig. 11). In this study, while average krill abundance changed more than an order of magnitude in both seasonal and interannual comparisons, average chlorophyll a concentrations varied by factors of < 3. Thus, the interannual difference in grazing impact was primarily due to changes in grazer biomass. Seasonal differences were due to both a decrease in krill abundance and a seasonal decline in chlorophyll a concentration below the feeding threshold.

In contrast to these cruise results, grazing impact in one location can increase several fold with the same abundance levels of krill under bloom conditions. While high levels of phytoplankton were not common during the January cruises, chlorophyll a levels of up to 10 $\mu g\ l^{-1}$ were found in samples from the nearshore stations of the Palmer grid earlier in the season (Smith et al. b, this volume). Grazing impact at these stations follows phytoplankton levels throughout the season near Palmer (Fig. 6), and is an order of magnitude higher during the December bloom than during January. This pattern emphasizes the importance of understanding where cruise results belong in the seasonal succession of events.

The biological response of krill to ambient food levels suggests that there will be short-term variability in both grazing impact and vertical flux. The time/space variability found in sediment traps moored in the Palmer LTER region in 1992–1993 is on the same scales found in this study (Karl et al., 1994). Highest flux was in November/December, coinciding with blooms detected on the nearshore grid which would result in relatively high grazing impact with a constant krill population (Fig. 12). Also, among-trap variability was high, consistent with the spatial patchiness of grazing impact found in this study.

Our values of krill grazing impact are probably underestimates. Grazing rates obtained in laboratory experiments are likely lower than actual field ingestion rates, due to experimental container effects (Price et al., 1988) and animal handling. In addition, grazing impact calculations are based on average concentrations of both krill and phytoplankton, and there is evidence that euphausiids are capable of actively locating and concentrating in small scale phytoplank-

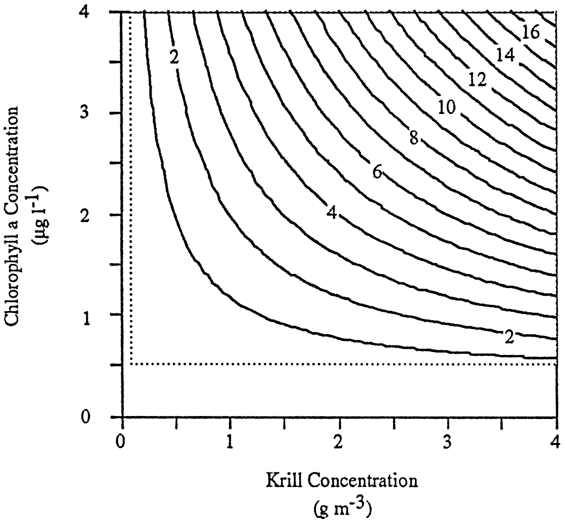

Fig. 12. Contours of grazing impact (μg chlorophyll a $m^{-2}\ h^{-1}$) as a function of chlorophyll a concentration and krill concentration, linear model (Fig. 2a). Dotted line indicates threshold concentrations below which grazing impact is zero.

ton patches (Price, 1989). This behavior would increase grazing impact as a result of grazing in areas of increased phytoplankton abundance.

To further refine our approach and flux calculation, additional experiments measuring assimilation efficiency and differences in faecal pellet sinking rates for different phytoplankton types are needed for both grazers. Also needed are experiments at lower phytoplankton concentrations to confirm the threshold for ingestion. Better estimates of krill abundance and size distribution, combined with the weight dependence of ingestion rate, would also improve these short-term grazing impact and carbon flux estimates. However, such refinements would primarily affect the estimates of absolute grazing impact, not the patterns of seasonal and interannual variability we observed.

In addition to calculating grazing impact as an hourly rate of chlorophyll loss, we have also calculated the percentage of net primary production (%NPP) grazed for both krill and salps (Table 2). %NPP grazed by krill is estimated both from the linear grazing equation and from energetic requirements of krill for metabolism and modest growth (Ross and Quetin, 1986). For all cruises except January 1995, the %NPP grazed by krill was greater at the inner stations.

Calculations of %NPP based on grazing rates provide a short-term measure of impacts in the area. Since each station was only occupied for a few hours, without a time history of both the chlorophyll a concentrations and grazer abundance, the data cannot be used to calculate estimates on longer time scales. However, it is grazing impacts on these short time scales that are essential for understanding the balance between growth and the various loss factors (grazing, sinking and advection) that drive changes in phytoplankton stock at any specific location.

The %NPP estimates for krill based on energetics depend upon average daily requirements for an entire season, and can be used to show whether primary production in a region is adequate to support the krill population. Previous estimates of %NPP grazed by krill based on energetics were 2.5–3.5% NPP during January–March 1981 in the Scotia Sea (Holm-Hansen and Huntley, 1984), and 3% during February–March 1981 in the Southern Indian Ocean (Miller et al., 1985). Their numbers suggest that plenty of food was available for the krill, even when the krill's preference for larger cells was taken into account (Holm-Hansen and Huntley, 1984). Our estimates for January 1994 and January 1995, 23% and 0.7% respectively, also indicate that phytoplankton resources were adequate. In contrast, average %NPP grazed for January 1993, 421%, indicates phytoplankton resources in the region during this time were inadequate to meet energetic needs. However, the energetic approach is based upon annual requirements averaged over the season, and does not incorporate the known response of the grazers to varying food concentrations throughout the season. January 1993 was a time of low phytoplankton levels during the austral summer of 1992–1993, and thus estimated grazing rates were low. Phytoplankton levels during that year peaked in December (Fig. 6), and higher grazing during spring may have balanced the low January levels.

West of the Antarctic Peninsula, 97% of the flux occurs in December and January, with faecal pellets a significant fraction (Wefer et al., 1988). The effect of herbivorous zooplankton on vertical particulate carbon flux depends upon the amount of primary production consumed, the phytoplankton assemblage, and the identity and abundance of the grazers. Grazing by protozoans on small phytoplankton cells is clearly important in oceanic areas where small cells dominate, but the resulting small faecal pellets sink slowly and will contribute little to flux. The role of copepods (mesozooplankton) is less clear, and variable. Schnack et al. (1985) found copepod grazing was 55% of daily primary production in the Drake Passage, but only 1% of daily primary production close to the Antarctic Peninsula in austral spring. Our results show that grazing by macrozooplankton, and its impact on carbon flux west of the Antarctic Peninsula, varies on large temporal and spatial scales.

In summary, this study documents strong spatial, interannual and seasonal variability in grazing impact, vertical flux, and %NPP grazed for both krill and salps. The high degree of seasonal variability underscores the importance of monitoring changes in grazer and phytoplankton biomass throughout the season, while the striking interannual variability suggests that a long term approach will be an important part of understanding the mechanisms underlying these patterns.

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References

Anderson, R.F., 1993. U.S. joint global ocean flux study: Southern Ocean process study science plan. U.S. JGOFS Planning Report No. 17. Woods Hole Oceanographic Institution, MA, 67 pp.

Boyd, C.M., Heyraud, M., Boyd, C.N., 1984. Feeding of the Antarctic krill *Euphausia superba*. J. Crust. Biol. 4, 123–141, Spec. No. 1.

Foxton, P., 1966. The distribution and life-history of *Salpa thompsoni* Foxton with observations on a related species, *Salpa gerlachei* Foxton. Discovery Rep. 32, 1–116.

Harbison, G.R., Gilmer, R.W., 1976. The feeding rates of the pelagic tunicate *Pegea confederata* and two other salps. Limnol. Oceanogr. 21 (4), 517–528.

Harbison, G.R., McAlister, V.L., 1979. The filter-feeding rates and particle retention efficiencies of three species of *Cyclosalpa* (Tunicata, Thaliacea). Limnol. Oceanogr. 24 (5), 875–892.

Holm-Hansen, O., Huntley, M., 1984. Feeding requirements of krill in relation to food sources. J. Crust. Biol. 4, 156–173, Spec. No. 1.

Honjo, S., 1990. Particle fluxes and modern sedimentation in the polar oceans. In: Smith, Jr., W.O. (Ed.), Polar Oceanography, Part B: Chemistry, Biology, and Geology. Academic Press, San Diego, CA, pp. 687–739.

Karl, D.M., Asper, V., Dore, J., Houlihan, T., Hebel, D., 1994. The Palmer-LTER sediment trap array experiment: initial results. Ant. J. U.S. 29 (5), 222–224.

Kremer, P., Madin, L.P., 1992. Particle retention efficiency of salps. J. Plankton Res. 14 (7), 1009–1015.

Madin, L.P., 1974. Field observation on the feeding behavior of salps (Tunicata: Thaliacea). Mar. Biol. 25, 143–147.

Madin, L.P., Cetta, C.M., 1984. The use of gut fluorescence to estimate grazing by oceanic salps. J. Plankton Res. 6 (3), 475–491.

Marin, V., Huntley, M.E., Frost, B., 1986. Measuring feeding rates of pelagic herbivores: analysis of experimental design and methods. Mar. Biol. 93, 49–58.

McClatchie, S., 1988. Functional response of the euphausiid *Thysanoessa raschii* grazing on small diatoms and toxic dinoflagellates. J. Marine Res. 46, 631–646.

Michaels, A.F., Silver, M.W., 1988. Primary production, sinking fluxes and the microbial food web. Deep-Sea Res. 35 (4), 473–490.

Miller, D.G.M., Hampton, I., Henry, J., Abrams, R.W., Cooper, J., 1985. The relationship between krill food requirements and phytoplankton production in a sector of the southern Indian Ocean. In: Siegfried, W.R., Condy, P.R., Laws, R.M. (Eds.), Antarctic Nutrient Cycles and Food Webs, Springer-Verlag, Berlin, pp. 362–371.

Mitchell, B.G., Holm-Hansen, O., 1991. Observations and modeling of the Antarctic phytoplankton crop in relation to mixing depth. Deep-Sea Res. 38 (8/9A), 981–1007.

Perissinotto, R., Pakhomov, E.A., The trophic role of the tunicate *Salpa thompsoni* in the Southern Ocean carbon flux, this volume.

Price, H.J., Boyd, K.R., Boyd, C.M., 1988. Omnivorous feeding behavior of the Antarctic krill *Euphausia superba*. Mar. Biol. 97, 67–77.

Price, H., 1989. Swimming behavior of krill in response to algal patches: a mesocosm study. Limnol. Oceanogr. 34 (4), 649–659.

Quetin, L.B., Ross, R.M., 1985. Feeding by *Euphausia superba*: does size matter? In: Siegfried, W.R., Condy, P.R., Laws, R.M. (Eds.), Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Berlin, pp. 372–377.

Ross, R.M., 1982. Energetics of *Euphausia pacifica*: II. Complete carbon and nitrogen budgets over its life span. Mar. Biol. 68, 15–23.

Ross, R.M., Quetin, L.B., 1986. How productive are antarctic krill?. BioScience 36, 264–269.

Ross, R.M., Quetin, L.B., Lascara, C.M., 1996. Distribution of Antarctic krill and dominant zooplankton west of the Antarctic Peninsula. In: Ross, R.M., Hofmann, E.E., Quetin, L.B. (Eds.), Foundations for Ecological Research West of the Antarctic Peninsula. American Geophysical Union, Washington, DC, Antarctic Research Series, Vol. 70, pp. 199–217.

Schnack, S.B., Smetacek, V., Bodungen, V.B., Stegmann, P., 1985. Utilization of phytoplankton by copepods in Antarctic waters during spring. In: Gray, J.S., Christiansen, M.E. (Eds.), Marine Biology of Polar Regions and Effects of Stress on Marine Organisms. Wiley, Chichester, pp. 65–81.

Smith, R.C., Baker, K.F., Dustan, P., 1981. Fluorometer techniques for measurement of oceanic chlorophyll in the support of remote sensing. SIO Technical Report 81-17. Scripps Institute of Oceanography, La Jolla, CA.

Smith, R.C., Baker, K.S., Byers, M.L., Stammerjohn, S.E., a. Primary productivity of the Palmer Long Term Ecological Research area and the Southern Ocean, this volume.

Smith, R.C., Baker, K.S., Vernet, M., b. Seasonal and interannual phytoplankton biomass to the west of the Antarctic Peninsula, this volume.

Waters, K.J., Smith, R.C., 1992. Palmer LTER: A sampling grid for the Palmer LTER program. Ant. J. U.S. 27 (5), 236–239.

Wefer, G., Fischer, G., Füetterer, D., Gersonde, R., 1988. Seasonal particle flux in the Bransfield Strait, Antarctica. Deep-Sea Res. 35 (6), 891–898.