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In situ grazing rates and daily ration of Antarctic krill *Euphausia superba* feeding on phytoplankton at the Antarctic Polar Front and the Marginal Ice Zone

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ABSTRACT: Measurements of krill gut pigment content, evacuation rates and digestive efficiency were obtained during January 1993 in the Atlantic sector of the Southern Ocean, between the Antarctic Marginal Ice Zone (MIZ) and the Polar Front Zone (PFZ). These were combined with net and acoustically derived abundance and biomass data to estimate the *in situ* grazing of *Euphausia superba* on the phytoplankton assemblages. Individual ingestion rates of krill were 1.5 to 3 times higher than rates previously obtained with *in vitro* incubations. Gut pigment levels and evacuation rates varied in the range of 0.01 to 10 µg chlorophyll *a* equivalents (chl *a* equiv.) ind.$^{-1}$ and 0.10 to 0.31 h^{-1}, respectively. Pigment losses to non-fluorescing products during digestion were very high, in the range of 67 to 90% of the total pigment ingested, indicating that some of the gut pigment levels previously obtained without correction for digestive losses may have been underestimated by up to an order of magnitude. Krill population impact on the phytoplankton stock exhibited a large variability, in the range of 0.0014 to 2.68% of total integrated chlorophyll *a* and 0.023 to 50.8% of primary production consumed per day. The largest variations in impact levels were associated with the method used to estimate krill abundance and biomass, with net derived estimates being much lower (by as much as 2 orders of magnitude) than those obtained from acoustic data. Daily carbon rations obtained from our measurements of pigment ingestion rates are among the lowest recorded for *E. superba* during the summer season and, with 1 exception, ranged between 0.15 and 1.68% of body carbon per day. A daily ration of ~13% body carbon was recorded only at 1 station in the MIZ which exhibited a dense phytoplankton bloom of ~3.5 µg chl l^{-1}. On the basis of the energetic requirements of the summer krill population, it is suggested that throughout the PFZ and the MIZ *E. superba* must consume a much larger proportion of heterotrophic carbon than previously supposed. Gut content analysis suggests that this is achieved by predation on meso- and microzooplankton.

KEY WORDS: Antarctic krill · *Euphausia superba* · Grazing rates · Daily ration · Southern Ocean

INTRODUCTION

Biomass of krill *Euphausia superba* in Antarctic waters generally accounts for ~50% of the total zooplankton stock (Holdgate 1967, Holm-Hansen & Huntley 1984). The grazing impact of this species on the phytoplankton of the Southern Ocean is expected to be substantial and to represent a major pathway in the vertical transport of particulate organic carbon to the deep ocean via production of large faecal pellets and diurnal vertical migration (Tanoue & Hara 1986, Smetacek et al. 1990, Cadée et al. 1992). Krill food consumption has generally been estimated indirectly, by adding together the energy required for production, respiration, excretion and other energetic costs (Clarke & Morris 1983, Price et al. 1988, Huntley et al. 1994). Until very recently, the only direct estimates were obtained from *in vitro* incubations (Antezana et al. 1982, Boyd et al. 1984, Schnack 1985). However, due to bottle containment effects, there are indications that rate measurements derived in this way may have been systematically biased and misinterpreted, even when flow-through systems have been used (Morris 1984, Price et al. 1988).

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The gut fluorescence method is at present the most widely used technique for the measurement of *in situ* feeding rates of zooplankton on phytoplankton. In the case of the Antarctic krill, this method has been recently employed to investigate qualitative aspects of its feeding activity, such as diurnal rhythms and swarm grazing behaviour (Morris & Ricketts 1984, Priddle et al. 1990). In only a few instances (Quetin et al. 1987, Daly 1990, Drits & Pasternak 1993) have both gut pigment content (G) and evacuation rate (k) been measured and combined to estimate ingestion rates of adults (summer and fall) and furcilia larvae (winter). In all these studies, however, gut evacuation rates were determined by measuring the decline in gut pigments in non-feeding krill, kept in filtered seawater for periods of 6 to 24 h. When not feeding, euphausiids can retain food in their guts for periods of up to 2 d (Lasker 1966, Willason & Cox 1987). Thus, accurate evacuation rates can be obtained only when krill are incubated under continuous feeding conditions (Willason & Cox 1987, Perissinotto 1992, Perissinotto & Pakhomov 1996, Pakhomov et al. 1997).

Furthermore, it is now clear that the gut fluorescence method requires that the proportion of ingested chlorophyll *a* that is destroyed or broken down to non-fluorescent end products be measured in conjunction with the other grazing parameters. This is because losses often reach levels ≥50% of the total pigment ingested (Conover et al. 1986, Lopez et al. 1988, Penry & Frost 1991, Mayzaud & Razouls 1992, Perissinotto & Pakhomov 1996). In this study, measurements of gut pigment content, evacuation rate and pigment degradation are combined in an attempt to provide estimates of *in situ* grazing rates and daily rations in Antarctic krill.

MATERIALS AND METHODS

All samples and measurements were taken in January 1993 in the Atlantic sector of the Southern Ocean along the Greenwich Meridian, between the SANAE (South African National Antarctic Expedition) station, on the Antarctic continent, and the Antarctic Polar Front (APF). This formed part of the second cruise of the South African Antarctic Marine Ecosystem Study (SAAMES II) aboard the SA 'Agulhas' along the WOCE SR2 line. Conductivity, temperature and depth (CTD) profiles were obtained at regular intervals of ~10' latitude using a Neil Brown MK III probe. At each station, samples for analysis of nutrients and photosynthetic pigments were collected with 8 l Niskin bottles mounted on a 12 bottle rosette system (General Oceanics).

Chlorophyll *a* and phaeopigment concentrations were measured in 200 to 1000 ml aliquots taken from the Niskin samples at standard depths of 0, 20, 30, 50, 75, 100, 125, 150, 200, 250 and 300 m. Generally, pigment fractionation into pico (<2 µm), nano (2 to 20 µm) and micro (>20 µm) size classes was carried out only on the surface samples (0 m). For this purpose, Whatman GF/F, 2.0 µm Nuclepore and 20 µm Nitex filters were used in a multiple serial filtration manifold. Pigments were extracted for ~24 h in polyethylene tubes with 8 ml of 90% acetone and concentrations measured with a Turner Designs fluorometer.

Daily primary production rates were measured at 5 out of the 14 grazing stations by 24 h dawn-to-dawn, *in situ*-simulated deck incubations (JGOFS 1990). Water was obtained from the 100, 50, 25, 10, 5 and 1% subsurface light-depths and pre-filtered through a 200 µm mesh to remove grazers. For each light level, 3 replicate polycarbonate bottles were inoculated with 25 to 50 µCi of $NaH^{14}CO_3$ (Amersham) and incubated on deck for 24 h in running surface seawater to maintain ambient temperature. The specific activity was obtained by removing and filtering aliquots from each productivity bottle. Filters were then placed in liquid scintillation vials with 10 ml fluor and their radioactivity was measured on board using a Beckman scintillation counter.

Quantitative microphytoplankton (>20 µm) samples were collected from the upper surface layer (~5 m) using a 20 µm mesh filtration unit connected to a shipboard pump (Iwaki Magnet Pump) operated at a flow rate of ~5 l min^{-1} (Berman & Kimor 1983). A constant volume of 20 l was filtered at each station, cells were rinsed off the filter and preserved in 2% hexamine-buffered formalin solution. The major phytoplankton taxa in aliquots retained by the filter were counted using an inverted microscope, after sedimentation in 10 ml chambers (Hasle 1978). The aim of this was to provide an indication of the species composition of the larger phytoplankton in the area.

Krill biomass was determined from net tows (RMT-8 and 500 µm Bongo nets) and acoustically, using a SIMRAD EK500 sounder operated at a frequency of 120 kHz (SIMRAD 1991). The output parameter of the sounder echo-integrator was S_A (m^2/nm^2), the mean backscattering area per unit of horizontal area. This was converted to mean volume backscattering strength, S_V, using the relation (SIMRAD 1991):

$$S_V = 10\log_{10}\{S_A/[4\pi r_0^2(1852\ \mathrm{m/nm})^2(r_2 - r_1)]\}$$

Where r_0 = reference range for backscattering strength (1 m) and r_1 and r_2 are the upper and lower depths of the layer (in m), respectively. The coefficient S_V is related to the density (ρ) of scatterers (ind. m^{-3}) through the equation (Stanton et al. 1987):

$$S_V = 10\log\rho + TS, \text{ and thus: } \rho = 10\exp(S_V - TS)0.1$$

TS is the average target strength of krill and was derived from the length, L (in mm), of the individuals

collected in the net hauls (Greene et al. 1991, SC-CAMLR 1991):

$$TS = 34.85\log L - 127.45$$

Krill were collected at 14 stations along the SANAE-APF transect. Generally, 1 oblique Bongo tow to a depth of 300 m was carried out at each station to investigate the spatial variation in krill biomass and grazing activity. In the vicinity of the APF (Stn WR-22), Bongo tows were repeated at 2.5 h intervals for a 24 h period. One sample from each net tow was preserved with 4% buffered formalin for abundance and length/weight analysis, while the second sample was used for measurements of G and k. For the analysis of the gut pigment content, fresh krill were picked from a 2 l PVC cod-end and put into 10 ml polypropylene tubes (1 individual per tube) where pigments were extracted with pure methanol for 6 to 12 h (Simard et al. 1985). After centrifugation (5000 rpm, ~1740 × g), the pigment content of the methanol extract was measured with a Turner 111 fluorometer, before and after acidification.

Total pigment content was obtained using the formulas of Strickland & Parsons (1968) as modified by Conover et al. (1986). It must be noted, however, that recent work by Head & Harris (1992) and Welshmayer (1994) has shown that the wide-band pass filters generally used in fluorometry may result in an overestimation of the concentration of chlorophyll degradation products. In this study, chlorophyll *a* and phaeopigment concentrations were added together and expressed in units of chlorophyll *a* equivalents (chl *a* equiv.) (Conover et al. 1986). Three to 10 replicate individuals were used for pigment extraction and measurement from each tow.

During the gut evacuation experiments, freshly collected krill were incubated in filtered seawater to which non-fluorescent charcoal powder was added to keep the animals under continuous feeding conditions (Willason & Cox 1987, Perissinotto 1992, Perissinotto & Pakhomov 1996). The role of charcoal particles is to displace previously ingested food. The duration of these incubations ranged from 2–4 h for juveniles (length = 1.5 to 2.5 cm) to 12–24 h for adults (length = 4 to 5 cm) and the decline in gut content was monitored at intervals of 10 to 15 min for the first hour and 1 to 4 h thereafter. Gut evacuation rates (h^{-1}) were derived from the slope of the regression of the natural logarithm of gut pigments versus time (Dam & Peterson 1988). Altogether, 5 gut evacuation experiments were carried out along the transect, 3 with adults and 2 with juvenile krill.

Loss of pigments to non-fluorescent end-products by absorbtion/destruction was estimated at the 24 h station (WR-22) situated in the vicinity of the APF. Five independent measurements of pigment loss were made on this occasion. In each experiment, krill were first allowed to empty their gut of pigments for 24 h in filtered seawater with charcoal particles. Single individuals were then incubated for 1 to 2 h in 1 l bottles with naturally occurring phytoplankton concentrations. A 2-compartment pigment budget approach was employed by comparing the decrease in pigment content of grazing bottles with the increase in gut pigment levels of krill incubated in these bottles (Lopez et al. 1988, Mayzaud & Razouls 1992, Perissinotto 1992). Calculations of the fractional loss of pigment were made using the equation of Perissinotto (1992) and values were expressed as percent digestion efficiency. Krill daily ingestion rates (I) were estimated from the relation (Wang & Conover 1986, Perissinotto 1992):

$$I = kG/(1 - b')$$

where b' is a non-dimensional index of the loss of pigment during digestion. As estimates of k and b' were not available for all stations, average values for these parameters were used when no direct measurements were made. Also, when extrapolating hourly ingestion rates to daily rates, differences in feeding activity between dark and light periods were taken into account. Daytime levels were multiplied by an average of 2.03 (night/day ratio derived from the 24 h station) to derive nighttime rates.

The gut contents of adult krill from 6 stations along the SANAE-APF transect were analysed for identifiable items. As the main aim of this analysis was to test the hypothesis that krill would ingest a substantial proportion of zooplankton in the absence of a rich phytoplankton stock, only krill from north of 60° S (Stn WR-13) to the southern edge of the APF (Stn WR-22) were selected. This is the area where the lowest chlorophyll *a* levels were recorded during the transect. Altogether, 28 guts from preserved krill were removed and the identifiable items in their contents counted under an inverted microscope at 400× magnification.

RESULTS

Hydrology and phytoplankton production

During January 1993, the presence of the APF was identified from salinity, and especially temperature profiles (Fig. 1; 2°C isotherm intersects the 200 m depth) at a latitude of 50° 49' S. The pack ice had retreated close to the continental shelf and its outer edge was located at a latitude of 69° 10' S. The seasonal marginal ice zone (MIZ) in this area usually attains its maximum winter expansion at a latitude of ~60° S (Comiso et al. 1993).

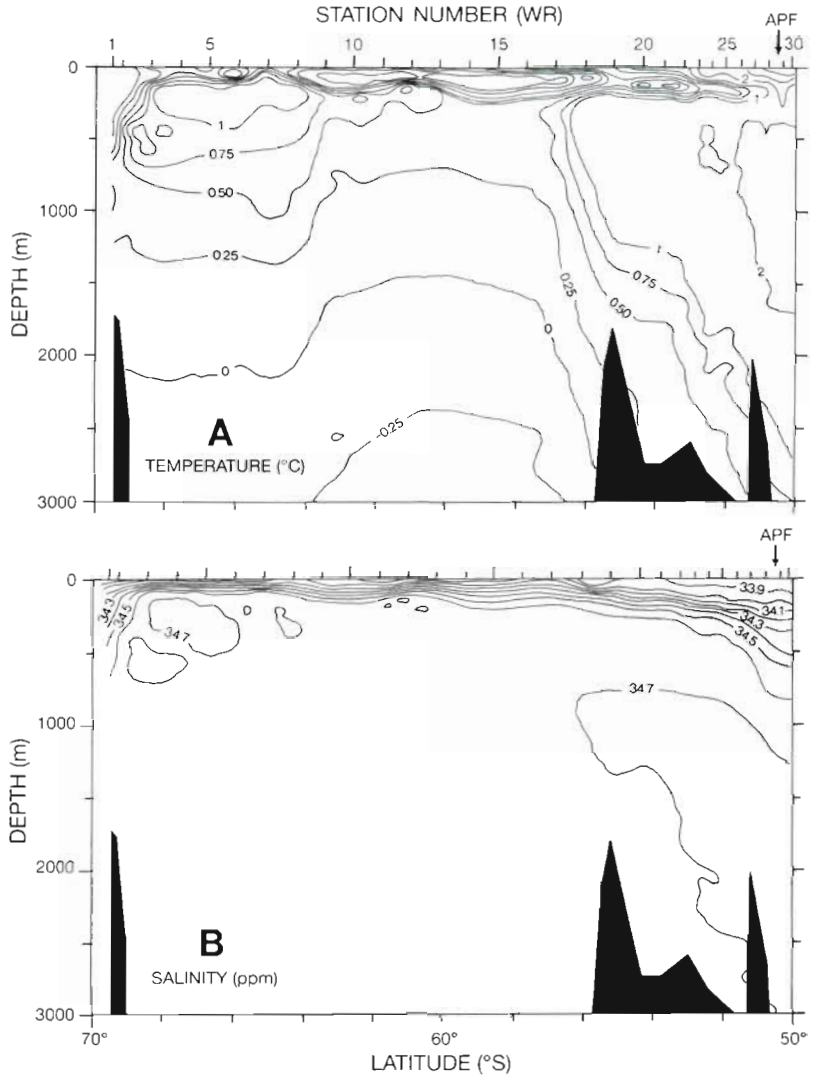

Fig. 1. Vertical distribution of (A) temperature and (B) salinity along the SANAE-APF transect during January 1993. SANAE: South African National Antarctic Expedition; APF: Antarctic Polar Front

Chlorophyll *a* concentration was highest at the edge of the pack ice (Stn WR-2; Fig 2), where a subsurface (10 m) maximum of 3.5 µg l^{-1} was recorded. To the north of this bloom, levels remained relatively high, 1.0 to 1.5 µg l^{-1}, as far as ~60° S but dropped dramatically thereafter to 0.1–0.5 µg l^{-1} (Fig. 2). A sharp increase occurred when the APF was approached at 50° S. Here, chlorophyll *a* concentrations attained again levels of ~1.0 µg l^{-1} (Fig. 2).

In terms of size and taxonomic composition, the relatively rich phytoplankton community south of 60° S was dominated by diatoms of the micro size class (Fig. 3). Here, chain-forming *Nitzschia* spp., *Fragilaria kerguelensis*, *Chaetoceros* spp. and *Corethron criophilum* accounted for 57 to 87% of the total microphytoplankton (Table 1). In the region of the APF, where a second peak in phytoplankton biomass was recorded at Stns WR-26 to WR-30 (Figs. 2 & 3), the nano size class accounted for the largest proportion of the total stock and *Nitzschia* spp. and *C. criophilum* constituted 65 to 87% of the microphytoplankton (Table 1). Between the APF and 60° S, biomass was dominated at first by the pico (Stns WR-19 to WR-25) and then again by the nano size class (Stns WR-13 to WR-18; Fig. 3). In this area, *Nitzschia* spp. was generally still the largest contributor to microphytoplankton abundance but *Chaetoceros* spp., particularly *C. dichaeta* and *C. criophilus*, and *Rhizosolenia alata f.*

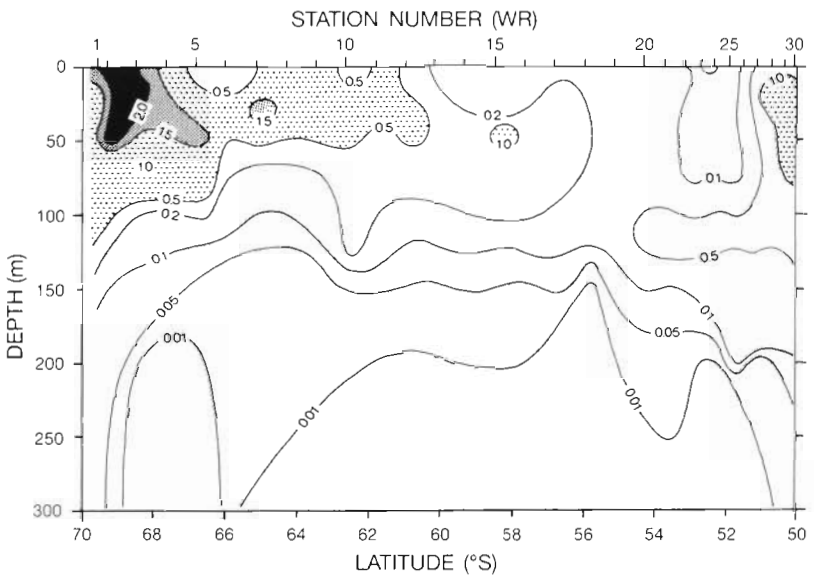

Fig. 2. Vertical distribution of chlorophyll *a* (µg chl *a* l^{-1}) in the upper 300 m layer of the SANAE-APF transect, January 1993

inermis and *R. hebetata f. semispina* were represented in much higher proportions than in the other areas. *C. criophilus* dominated the stock at Stns WR-20 to WR-22, with 69 to 84% of the total (Table 1).

Phytoplankton production rates were highest in the MIZ and at the APF, where daily levels integrated to the euphotic depth reached peaks of 500 to 1200 mg C m^{-2} d^{-1} (Laubscher et al. in press). Lowest rates were recorded in the area between the APF and 60° S (≤200 mg C m^{-2} d^{-1}), in conjunction with the lowest chlorophyll *a* concentrations and diatom abundances.

Krill distribution and biomass

Biomass and abundance levels derived from net tows ranged from minima of ~50 mg dry weight (DW) m^{-2} and ~0.6 ind. m^{-2} to maxima of ~6200 mg DW m^{-2} and ~110 ind. m^{-2}, respectively (Fig. 4). Highest levels occurred between 60° S and the APF, and at the edge of the pack ice.

Acoustic estimates of krill density were consistently higher than net estimates, although the distribution patterns derived from the 2 techniques were very similar (Fig. 4). Maximum levels of acoustic abundances were ~400 ind. m^{-2}, i.e. 4 times higher than the figure obtained from the net tows, while minima were ~10 ind. m^{-2}, i.e. 2 orders of magnitude higher than net estimates. Similarly, biomass levels derived from backscattering energy were 1.1 to 46.6 times (mean = 16.1 ± 13.8 SD) higher than net estimates (Fig. 4). Maximum and minimum acoustic biomass values were ~22 000 and 400 mg DW m^{-2}, respectively.

A diurnal rhythm in vertical migration was observed at the 24 h fixed station in the vicinity of the APF (Stn WR-22; Fig. 5A). Here, krill backscattering area (S_A) was most intense in the upper 25 m during nighttime (~20:00 to 04:00 h GMT) but peaked in the 50 to 200 m depth layer during the day (Fig. 5A).

Krill grazing dynamics

Along the SANAE-APF transect, krill gut pigment content (G) varied markedly, with highest levels recorded at the edge of the pack ice and in the vicinity of the APF (Fig. 6). In the pack ice, maximum individual G values were ~10 µg chl *a* equiv. $ind.^{-1}$, an order of magnitude higher than maxima elsewhere along the transect. The lowest gut pigment levels (~10 to 20 ng chl *a* equiv. $ind.^{-1}$) were found in the area of the seasonal advance and retreat of sea ice, between 60° and 68° S (Fig. 6). Gut pigment content exhibited a clear spatial covariance ($p < 0.05$) with chlorophyll *a* concentration (both surface and depth-integrated), which accounted for ~35 to 60% (r^2) of its total variance. When considering the various size classes separately, microphytoplankton chlorophyll *a* concentration explained the largest proportion (60.6%) of the total variance associated with G. Generally, the highest average gut pigment levels were recorded at stations (Stns WR-2, WR-19, WR-20 and W-24) where microphytoplankton abundance was largely domi-

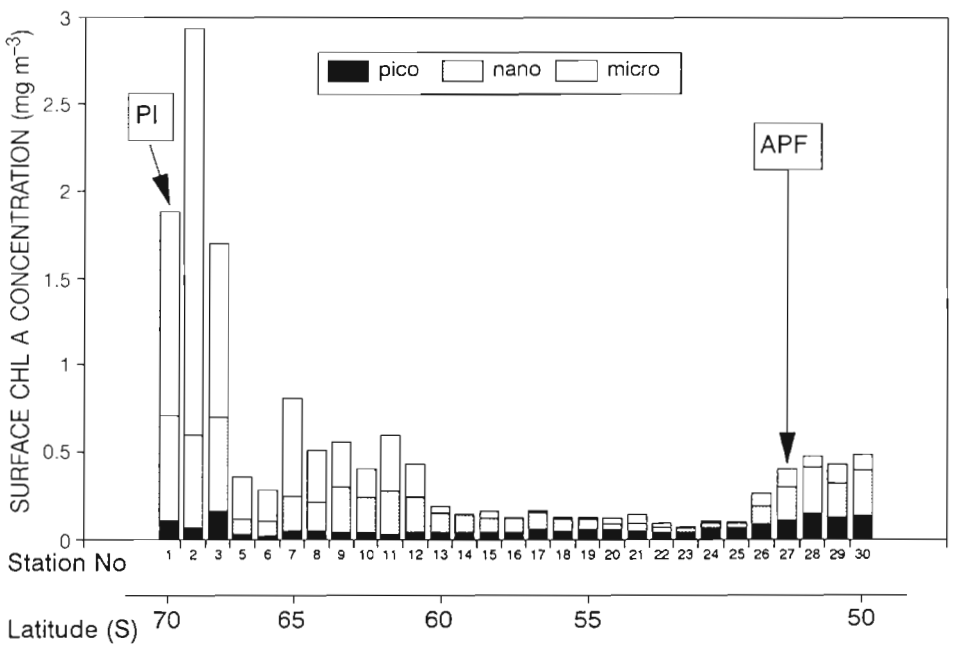

Fig. 3. Relative contribution of the micro-, nano- and picophytoplankton size classes to total chlorophyll *a* concentration in the surface layer (~5 m) of the SANAE-APF transect, January 1993. PI: pack ice

Table 1. Microphytoplankton (≥20 µm) species composition and abundance south of the Antarctic Polar Front. Only species contributing ≥5% to the total stock are listed. C.f.: chain-forming. Abundances are expressed as $\times 10^3$ cells l^{-1}

Stn no. (WR)	Lat.	No. of species	Abund.	Species composition and percent contribution
1	69° 24′	30	21.2	*Nitzschia* sp. (c.f.) (32%), *Chaetoceros* sp. (17%), *Eucampia antarctica* (10%), *Thalassiosira* spp. (9%), *Corethron criophilum* (8%)
2	69° 09′	22	15.0	*Nitzschia* sp. (c.f.) (47%), *Corethron criophilum* (36%)
3	68° 19′	27	38.8	*Nitzschia* sp. (c.f.) (63%), *Chaetoceros dichaeta* (15%), *Thalassiothrix longissima v. antarctica* (5%)
4	67° 30′	25	12.2	*Chaetoceros dichaeta* (37%), *Nitzschia* sp. (c.f.) (15%), *Corethron criophilum* (9%), *Nitzschia seriata* gr. (7%), *Chaetoceros criophilus* (6%)
5	66° 40′	23	11.9	*Chaetoceros dichaeta* (39%), *Corethron criophilum* (20%), *Chaetoceros flexuosus* (17%)
6	65° 50′	28	14.2	*Nitzschia* sp. (c.f.) (58%), *Chaetoceros dichaeta* (14%), *Rhizosolenia hebetata f. semispina* (5%)
7	65° 00′	30	51.0	*Nitzschia* sp. (c.f.) (45%), *Fragilaria kerguelensis* (14%), *Chaetoceros dichaeta* (12%), *Corethron criophilum* (7%), *Chaetoceros atlanticus* (5%)
8	64° 10′	24	57.6	*Nitzschia* sp. (c.f.) (44%), *Fragilaria kerguelensis* (43%)
9	63° 20′	35	10.7	*Nitzschia* sp. (c.f.) (50%), *Asteromphalus heptactis* (10%), *Fragilaria kerguelensis* (8%), *Rhizosolenia hebetata f. semispina* (5%)
10	62° 30′	26	17.1	*Nitzschia* sp. (c.f.) (46%), *Guinardia flaccida* (34%), *Fragilaria kerguelensis* (13%), *Asteromphalus heptactis* (5%)
11	61° 39′	29	31.2	*Nitzschia* sp. (c.f.) (61%), *Chaetoceros flexuosus* (7%), *Fragilaria kerguelensis* (7%)
12	60° 50′	28	20.1	*Nitzschia* sp. (c.f.) (35%), *Chaetoceros dichaeta* (23%), *Guinardia flaccida* (7%), *Nitzschia closterium* (5%)
13	60° 00′	30	10.6	*Nitzschia* sp. (c.f.) (41%), *Guinardia flaccida* (12%), *Chaetoceros dichaeta* (11%), *Fragilaria kerguelensis* (5%), *Chaetoceros criophilus* (5%)
14	59° 10′	27	4.91	*Nitzschia* sp. (c.f.) (48%), *Rhizosolenia alata f. inermis* (10%), *Chaetoceros dichaeta* (7%), *Asteromphalus heptactis* (5%), *Chaetoceros criophilus* (5%)
15	58° 20′	26	3.19	*Nitzschia* sp. (c.f.) (31%), *Rhizosolenia alata f. inermis* (20%), *Chaetoceros dichaeta* (8%), *Chaetoceros criophilum* (6%), *Asteromphalus heptactis* (6%), *Thalassiosira* spp. (6%)
16	57° 30′	25	2.13	*Nitzschia* sp. (c.f.) (43%), *Rhizosolenia alata f. inermis* (20%), *Chaetoceros criophilus* (10%), *Chaetoceros dichaeta* (6%)
17	56° 40′	22	2.03	*Nitzschia* sp. (c.f.) (42%), *Rhizosolenia alata f. inermis* (25%), *Rhizosolenia alata* (6%)
18	55° 50′	19	0.72	*Nitzschia* sp. (c.f.) (41%), *Chaetoceros criophilus* (24%), *Rhizosolenia alata f. inermis* (9%), *Chaetoceros dichaeta* (5%), *Thalassiosira antarctica* (5%)
19	55° 00′	19	0.81	*Nitzschia* sp. (c.f.) (57%), *Chaetoceros criophilus* (16%), *Thalassiosira* spp. (5%), *Corethron criophilum* (5%)
20	54° 10′	16	1.65	*Chaetoceros criophilus* (69%), *Nitzschia* sp. (c.f.) (10%)
21	53° 35′	13	1.95	*Chaetoceros criophilus* (69%), *Nitzschia* sp. (c.f.) (7%), *Rhizosolenia alata f. inermis* (5%), *Chaetoceros dichaeta* (5%)
22	52° 59′	10	2.31	*Chaetoceros criophilus* (84%), *Nitzschia* sp. (c.f.) (5%)
23	52° 34′	20	0.43	*Nitzschia* sp. (c.f.) (76%), *Chaetoceros criophilus* (14%)
24	52° 10′	17	0.48	*Nitzschia* sp. (c.f.) (74%), *Rhizosolenia hebetata f. semispina* (12%)
25	51° 45′	16	0.48	*Nitzschia* sp. (c.f.) (65%), *Rhizosolenia hebetata f. semispina* (17%), *Rhizosolenia alata f. inermis* (8%)
26	51° 20′	32	1.37	*Nitzschia* sp. (c.f.) (63%), *Corethron criophilum* (6%)
27	50° 56′	26	4.73	*Nitzschia* sp. (c.f.) (45%), *Corethron criophilum* (24%), *Chaetoceros peruvianus* (11%), *Chaetoceros dichaeta* (6%)
28	50° 30′	20	9.00	*Nitzschia* sp. (c.f.) (75%), *Corethron criophilum* (12%)
29	50° 06′	27	3.15	*Nitzschia* sp. (c.f.) (43%), *Corethron criophilum* (22%), *Chaetoceros peruvianus* (5%), *Nitzschia seriata* gr. (5%)
30	49° 41′	23	3.48	*Nitzschia* sp. (c.f.) (39%), *Corethron criophilum* (33%), *Rhizosolenia alata f. inermis* (5%), *Nitzschia seriata* gr. (5%)

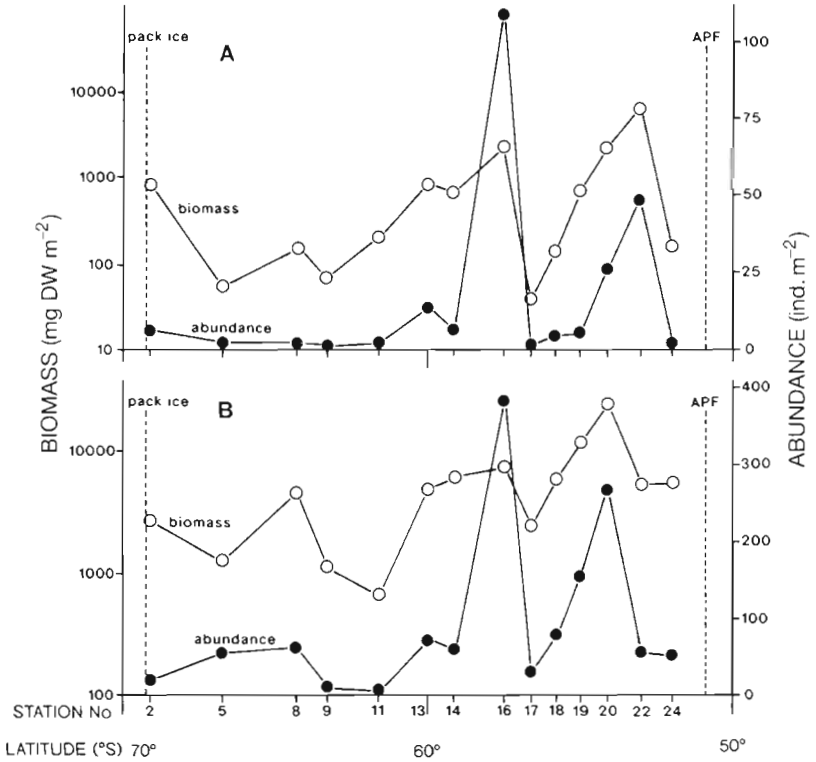

Fig. 4. *Euphausia superba*. Estimates of krill abundance and biomass along the SANAE-APF transect obtained from (A) RMT-8/Bongo net tows and from (B) 120 kHz acoustic backscattering intensity

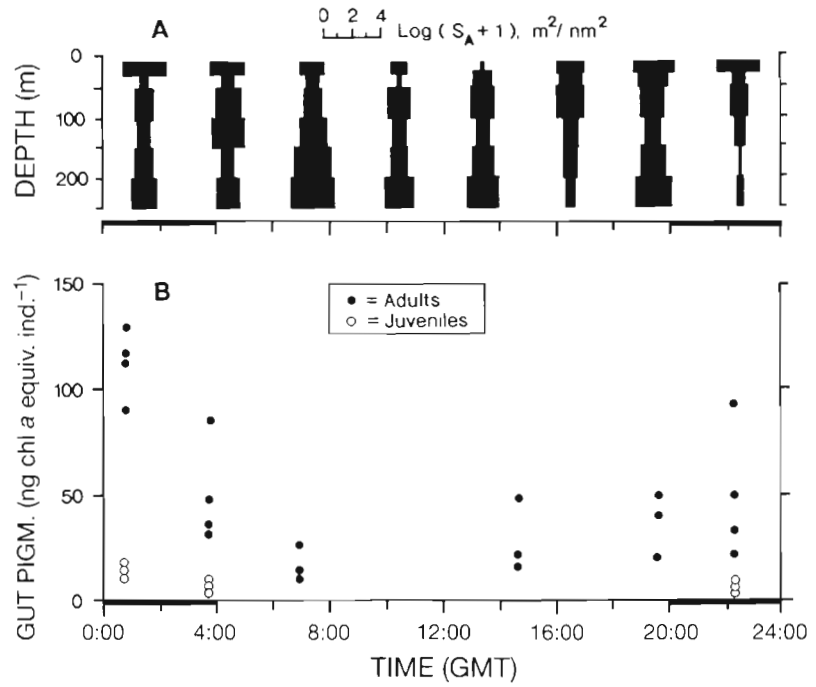

Fig. 5. *Euphausia superba*. Relationship between krill diurnal migrations as derived from (A) acoustic data and (B) gut pigment contents at Stn WR-22, to the south of the APF (28–29 January 1993)

nated by 2 groups of diatoms: chain-forming *Nitzschia* spp. and *Corethron criophilum* (Table 1). It must be pointed out, however, that microphytoplankton abundances at these stations were among the lowest of the transect. On the other hand, stations with the lowest krill gut contents were often dominated by *Chaetoceros dichaeta* (Stn WR-5) or *Chaeotoceros criophilus* (Stn WR-22), or had a substantial proportion of *Chaetoceros* spp. and *Rhizosolenia* spp. cells (>25%, Stns WR-14 and WR-18; Table 1). Diurnal variations in gut pigments were monitored at the 24 h station (Stn WR-22, Fig. 5B). For adults, the pattern observed was the same as for krill vertical migration. Mean nighttime G levels (63.5 ± 39.2 SD) were ~2 times higher than daytime ones (31.3 ± 11.5 SD), although no statistical differences were found between the 2 periods (t-test, $p > 0.05$). No data were available for juveniles during the day.

In all 5 gut evacuation experiments a negative exponential model provided the best fit to the decline in gut pigment content over time (Fig. 7). Gut evacuation rates, k, ranged from 0.10 to 0.17 h^{-1} in adult krill (~4.5 cm length) and from 0.22 to 0.31 h^{-1} in juveniles (~2 cm length) (Table 2). The corresponding gut turnover times, $1/k$, were, therefore, 5.9 to 9.9 h for adults (Fig. 7A) and 3.2 to 4.5 h for juveniles (Fig. 7B). Neither k nor $1/k$ appeared to be related to *in situ* chlorophyll *a* concentration but both parameters covaried with the initial gut pigment content in the case of both adults and juveniles (Table 2).

Levels of gut pigment degradation were very high and ~67 to 90% of the total pigment ingested by krill was not recovered in their guts (Table 3). An average factor of 0.191 (i.e. $1 - b'$) of degradation efficiency was, therefore, used in the calculation of ingestion rates, I.

Individual ingestion rates were highest at the edge of the pack ice (~90 µg chl *a* equiv. ind.$^{-1}$ d^{-1}) and just to the south of the APF, between 52° and 55° S (2 to 3 µg chl *a* equiv. ind.$^{-1}$ d^{-1}; Fig. 6B). Lowest rates were again recorded in

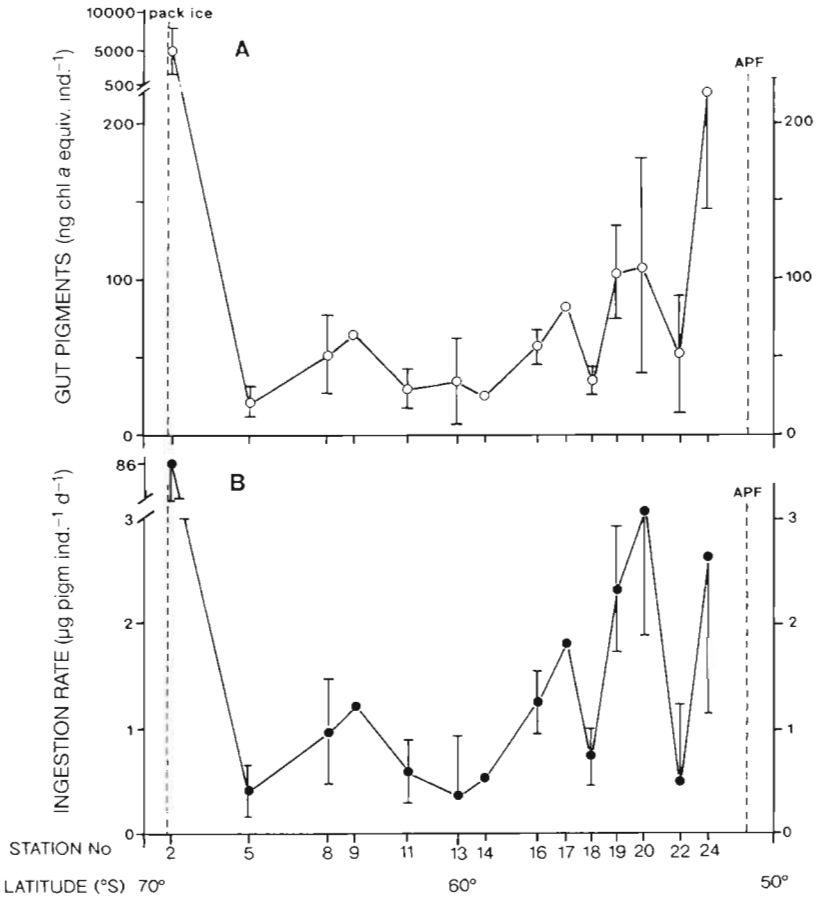

Fig. 6. *Euphausia superba*. Spatial distribution of krill (A) gut pigment content and (B) ingestion rates along the SANAE-APF transect during January 1993. Error bars represent standard deviations from the mean

the region of the seasonal ice retreat, from 59° to 67° S, where on average krill ingested 1 µg chl *a* equiv. ind.$^{-1}$ d^{-1}. When extrapolated to the entire krill population estimated from net tows, the grazing impact of *Euphausia superba* ranged from a minimum value of <1 µg chl *a* equiv. d^{-1} at Stn WR-9 to a maximum of ~570 µg chl *a* equiv. d^{-1} at Stn WR-2 at the edge of the pack ice (Table 4). Using the empirical equation of Hewes et al. (1990), $C = 80chl^{0.6}$, to convert chlorophyll *a* concentration into autotrophic carbon, the range of daily carbon consumption was estimated at ~0.1 to 30 mg C d^{-1} (Table 4). These rates are equivalent to 0.0014–0.42% of total 300 m integrated chlorophyll *a* and 0.023–14.4% of primary production consumed per day (Table 4). However, when krill biomass levels derived from acoustic backscattering energy rather than net tows were considered, population grazing impact varied from ~5 to 1600 µg chl *a* equiv. d^{-1}, or from ~0.5 to 150 mg C d^{-1} (Table 4). These are equivalent to consumption rates of 0.01 to 2.68% and 0.45 to 50.8% of the total chlorophyll *a* and primary production, respectively.

The main food items that could be identified in the gut contents of adult krill were subdivided in 4 groups: microphytoplankton, microzooplankton, mesozooplankton fragments and round bodies of unknown origin (Table 5). With 1 exception (Stn WR-19), microphytoplankton cells and chains dominated gut contents, accounting for 35 to 65% of the total number of recognizable particles. The most important taxa in this group were *Nitzschia* spp., *Fragilaria kerguelensis* and *Thalassiosira* spp., while taxa such as *Chaetoceros* spp. and *Rhizosolenia* spp., which often dominated the microphytoplankton stock in the water column (Table 1), were almost absent from krill guts. Microzooplankton, particularly aloricate ciliates, were also very abundant, constituting ~18 to 47% of the total identifiable fraction, and even dominated in krill guts from Stn WR-19 (Table 5). Mesozooplankton fragments accounted for only ~11 to 31% of total particles by number, but many of them were very large and represented a substantial proportion of the total volume of material ingested.

Table 2. *Euphausia superba*. Gut clearance parameters for juvenile and adult krill and their relationships with ambient chlorophyll *a* (chl *a*) concentration and initial gut pigment content, $G(t_0)$. Chl *a* values were integrated over the upper 300 m layer

Krill stage	Stn no.	Time (GMT)	Gut evacuation k (h^{-1})	Gut turnover $1/k$ (h)	Initial chl *a* (mg chl *a* m^{-2})	$G(t_0)$ (ng chl *a* equiv. ind.$^{-1}$)
Adults	WR-14	10:39 h	0.126	7.94	36.9	64.34
(4–5 cm)	WR-20	15:21 h	0.170	5.87	30.7	107.02
	WR-22/7	22:09 h	0.101	9.88	25.7	48.40
Juveniles	WR-16	08:21 h	0.308	3.24	33.0	57.72
(1.5–2.5 cm)	WR-22/8	00:40 h	0.220	4.55	25.5	12.65

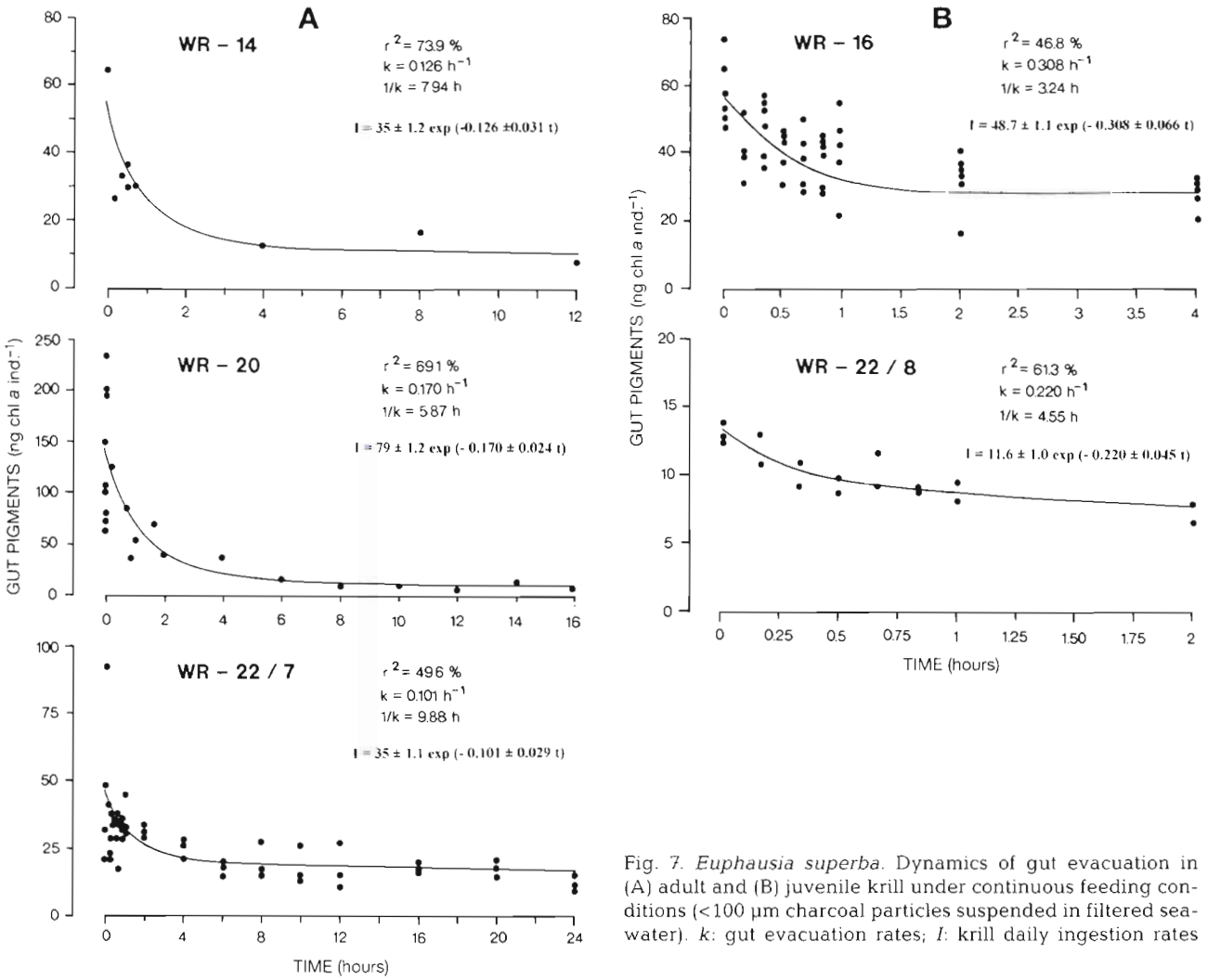

Fig. 7. *Euphausia superba*. Dynamics of gut evacuation in (A) adult and (B) juvenile krill under continuous feeding conditions (<100 µm charcoal particles suspended in filtered seawater). *k*: gut evacuation rates; *I*: krill daily ingestion rates

DISCUSSION

The adaptation of the gut fluorescence technique (Mackas & Bohrer 1976) used in this study provides a rapid and simple method for measuring *in situ* grazing rates of krill on the phytoplankton stock. When applying this method, there are usually 2 major problems that may severely affect the calculation of individual rates and population impact. These are related to an accurate determination of the gut clearance rate (Dagg & Grill 1980, Huntley et al. 1987, Penry & Frost 1990, Tseytlin et al. 1991) and the level of gut pigment degradation to non-fluorescent end products (Conover et al. 1986, Kiørboe & Tiselius 1987, Lopez et al. 1988, Head 1992, Mayzaud & Razouls 1992).

The gut clearance rate (k) and its inverse value, the gut turnover time ($1/k$), are usually determined as loss of gut pigments after the transfer of previously feeding krill to filtered seawater. This is based on the assumption that starvation does not dramatically affect the dynamics of gut evacuation. The assumption is reasonable for copepods, at least during short-term incubations (Ellis & Small 1989, Peterson et al. 1990). However, evacuation rates can be substantially

Table 3. *Euphausia superba*. Estimation of the digestion efficiency for adult krill collected at Stn WR-22 in the vicinity of the Antarctic Polar Front (28–29 January 1993)

Exp no.	Pigment ingested (ng chl *a* equiv. ind.$^{-1}$)	Pigment recovered (ng chl *a* equiv. ind.$^{-1}$)	Digestion efficiency (%)
1	33.6 ± 4.06	3.33 ± 2.15	90.1 ± 6.39
2	24.2 ± 4.24	4.15 ± 0.29	82.9 ± 1.20
3	25.2 ± 3.53	5.97 ± 3.10	76.4 ± 12.3
4	36.1 ± 3.36	4.36 ± 0.94	87.9 ± 2.61
5	27.9 ± 5.13	9.18 ± 1.14	67.0 ± 4.09

Table 4. *Euphausia superba*. Daily estimates of chlorophyll and autotrophic carbon consumption by the krill population along the SANAE-APF transect. Chl-Ing and C-Ing represent the rates of chlorophyll *a* (chl *a*) and carbon ingestion, respectively. Estimates of krill biomass were derived both from data of net tows (N) and from acoustic backscattering (A)

Stn no.	Chl-Ing (N) (µg chl *a* equiv. d^{-1})	Chl-Ing (A) (µg chl *a* equiv. d^{-1})	C-Ing (N) (mg C d^{-1})	C-Ing (A) (mg C d^{-1})	(N)/(A) (%)	% chl *a* (N)	% chl *a* (A)	% prod. (N)	% prod. (A)
WR-2	573.8	1619	29.81	84.14	35.43	0.281	0.871	No data	No data
WR-5	1.03	23.38	0.124	2.802	4.405	0.001	0.032	0.023	0.455
WR-8	2.24	59.08	0.233	6.145	3.791	0.005	0.133	No data	No data
WR-9	0.87	14.68	0.088	1.479	5.926	0.002	0.028	No data	No data
WR-11	1.53	5.35	0.149	0.522	28.59	0.003	0.010	No data	No data
WR-13	4.98	26.71	0.790	4.235	18.64	0.014	0.075	No data	No data
WR-14	3.75	32.21	0.664	5.703	11.64	0.010	0.087	0.294	2.532
WR-16	139.2	489.8	24.73	87.04	28.42	0.420	1.484	14.42	50.76
WR-17	1.09	53.96	0.172	8.497	2.020	0.003	0.159	No data	No data
WR-18	4.04	62.40	0.759	11.74	6.474	0.009	0.275	0.490	6.505
WR-19	13.94	362.7	2.485	64.64	3.843	0.087	1.246	No data	No data
WR-20	80.76	823.3	14.70	149.9	9.809	0.262	2.682	No data	No data
WR-22	25.10	28.13	5.109	5.726	89.23	0.127	0.112	2.280	1.940
WR-24	4.76	143.3	0.934	28.13	3.324	0.018	0.555	No data	No data

underestimated in the case of non-feeding euphausiids as these tend to retain food in their guts for long periods, up to 2 d (Willason & Cox 1987). Thus, our incubations to determine the gut evacuation rate of *Euphausia superba* were carried out in filtered seawater to which non-fluorescent charcoal particles had been added, in concentrations equivalent to the ambient seston wet weight (Perissinotto & Pakhomov 1996).

The other important factor to take into account in the calculation of krill grazing rates is the loss of fluorescing pigments during digestion. Losses may range from 1 to 99% of the total pigment ingested (Conover et al. 1986, Kiørboe & Tiselius 1987) and may be affected by ambient food concentrations and digestive acclimation processes (Mayzaud & Razouls 1992). Our experimental protocol involved a series of 5 replicated measurements of *in situ* gut pigment degradation, or digestion efficiency, of *Euphausia superba*. The values obtained were consistently high, with 67 to 90% degradation levels, indicating that grazing rates obtained from gut pigment concentrations which are not corrected for digestive losses may be underestimated by nearly 1 order of magnitude.

The estimates of individual grazing rates presented in this study are, therefore, among the most realistic obtained to date, as they incorporate all the major variables affecting the measurement of krill grazing *in situ* (Quetin et al. 1987, Daly 1990, Priddle et al. 1990), i.e. gut pigment content, gut evacuation rate and digestion efficiency. However, when scaling up to the impact of the summer krill population on the total phytoplankton stock (Table 4), the figures obtained are largely dependent on the accuracy of the abundance estimates. In this respect, it is worth recalling that the estimates of daily phytoplankton consumption by krill obtained using net abundance data are up to 2 orders of magnitude lower than those obtained using acoustic data (Table 4). This difference is probably due to net avoidance by krill, which is particularly effective in daylight conditions (Holm-Hansen & Huntley 1984, Mathew 1988, Nordhausen 1994). It is now widely accepted that net catches can only provide some lower limits on the abundance of krill (Miller & Hampton 1989). On the other hand, recent developments in the use of acoustic backscattering, and in particular the refinement of the target-strength and temperature calibrations, have dramatically improved the quality of abundance data obtained from this source (Everson et al. 1990, Greene et al. 1991, Hewitt & Demer 1991).

The individual rates of phytoplankton consumption obtained for krill in this study range from a minimum of 0.37 to a maximum of 86 µg chl *a* equiv. $ind.^{-1}$ d^{-1} (or 0.05 to 4.45 mg C $ind.^{-1}$ d^{-1}). When the results of previous feeding studies are standardized to the same units, the ingestion rates estimated from our *in situ* approach are generally 1.5 to 3 times higher than those obtained with *in vitro* incubations (Antezana et al. 1982, Meyer & El Sayed 1983, Schnack 1985, Price et al. 1988) and within the range of values obtained by Quetin et al. (1987) and by Pakhomov et al. (1997) with their adaptation of the gut fluorescence technique. This has important implications for carbon cycling in the Southern Ocean and for the energy budget of the Antarctic krill.

On a meso- and macroscale, only a minor portion (<10%) of the total phytoplankton production of the Southern Ocean is generally considered to be directly channelled to Antarctic krill by grazing (Holm-Hansen & Huntley 1984, Drits & Semenova 1989, Drits & Pasternak 1993). Only occasionally, and in the pres-

Table 5. *Euphausia superba*. Average abundances of identifiable items in the gut contents of krill at stations along the SANAE-APF transect of January 1993. Values in parentheses represent standard error of the mean

Food item	WR-13 (n = 5)	WR-14 (n = 3)	WR-16 (n = 5)	WR-19 (n = 5)	WR-20 (n = 5)	WR-22 (n = 5)
Microphytoplankton						
Chaetoceros constrictus	–	–	–	1.4 (1.40)	–	–
C. criophilus	–	–	0.8 (0.58)	–	–	0.2 (0.20)
Coscinodiscus spp.	–	–	3.8 (2.42)	–	0.2 (0.20)	–
Coretheron criophilum	–	–	–	–	0.2 (0.20)	–
Cylindrotheca closterium	–	–	0.8 (0.80)	–	–	–
Fragilaria kerguelensis	21.2 (4.90)	17.3 (9.78)	37.4 (15.67)	9.8 (5.85)	9.6 (6.13)	4.7 (2.34)
Guinardia flaccida	–	–	–	–	4.8 (3.10)	–
Nitzschia spp. (cells)	3.6 (1.47)	3.6 (1.86)	22.2 (10.86)	4.4 (1.94)	3.0 (1.77)	3.4 (1.57)
Nitzschia spp. (chains)	28.8 (6.17)	6.0 (3.06)	19.4 (7.96)	8.0 (4.18)	6.2 (3.39)	6.8 (2.34)
N. pelagica	–	–	–	–	0.2 (0.20)	–
Rhizosolenia spp.	–	0.3 (0.33)	3.0 (1.22)	1.0 (0.78)	–	1.6 (1.37)
Thalassiosira spp.	5.8 (1.94)	5.0 (0.88)	1.2 (0.74)	9.6 (3.94)	8.4 (2.96)	3.0 (0.63)
Distephanus speculum	–	–	0.8 (0.58)	–	–	–
Ceratium spp.	0.8 (0.59)	3.7 (0.88)	2.2 (0.81)	3.4 (1.70)	0.4 (0.25)	0.8 (0.38)
Exuviaella spp.	–	–	–	–	–	0.8 (0.58)
Microzooplankton						
Amphidinium spp.	–	2.3 (1.86)	1.4 (0.75)	3.4 (2.56)	2.2 (1.50)	–
Amphisolenia spp.	–	–	–	2.8 (0.20)	2.0 (1.38)	0.4 (0.14)
Dinophysis spp.	–	–	2.8 (1.72)	0.8 (0.38)	1.4 (0.51)	–
Procentrum spp.	–	–	1.6 (1.37)	0.2 (0.20)	0.4 (0.25)	–
Peridinium spp.	1.4 (0.51)	1.7 (0.88)	0.4 (0.41)	2.8 (2.56)	1.6 (0.87)	0.5 (0.25)
Strombidium spp. (?)	0.8 (0.59)	–	1.4 (0.51)	–	–	–
Tintinnopsis campanula	–	–	–	0.2 (0.20)	–	–
Tintinnids	1.6 (0.51)	0.7 (0.77)	5.0 (1.93)	9.6 (5.31)	7.4 (2.77)	1.6 (0.40)
Aloricate ciliates	12.6 (1.81)	15.7 (2.03)	44.8 (13.09)	30.8 (9.31)	17.2 (6.06)	9.0 (1.25)
Mesozooplankton						
Crustacean fragments (large)	5.4 (0.93)	11.7 (1.45)	4.4 (1.78)	5.0 (1.35)	2.6 (0.68)	5.6 (0.40)
Crustacean appendages	6.8 (2.84)	3.7 (1.86)	7.8 (2.64)	10.2 (3.65)	4.8 (4.08)	6.2 (1.66)
Polychaete setae	3.8 (0.86)	4.7 (2.91)	5.6 (2.42)	3.6 (1.03)	3.2 (1.12)	3.6 (1.56)
Unidentified round bodies	–	0.3 (0.33)	0.6 (0.40)	0.6 (0.60)	1.6 (0.82)	2.0 (0.55)
Total items identified	92.6	93.1	167.4	107.6	77.4	50.2

ence of very large swarms, have higher rates of consumption been estimated (i.e. 45% of total primary production; von Bodungen 1986). Our results show that at 4 out of the 14 stations investigated krill were grazing over 10% of the local production (Table 4). The impact was highest at Stn WR-16, where ~51% of the total production was consumed.

Throughout the transect, gut pigment levels were directly related to the concentration of ambient chlorophyll *a* and in particular to the portion retained by 20 µm filters, the micro size class. Although this size class dominated the phytoplankton stock at all stations located in the region of the seasonal ice retreat (approx. south of 60° S), krill gut pigment levels and grazing impact were not consistently high in this area (Fig 6, Table 4). This implies that, although krill may preferentially select the micro size class, the taxonomic composition of this phytoplankton group may also be an important factor determining their feeding activity. The highest gut pigment contents were generally associated with the dominance of chain-forming *Nitzschia* spp. or *Corethron criophilum* in the diatom assemblage. With some exceptions, the lowest levels were recorded at stations dominated by *Chaetoceros dichaeta*, *Chaetoceros criophilus* or by a mixture of *Chaetoceros* spp. and *Rhizosolenia* spp. (Table 1). Both *Nitzschia* spp. and *C. criophilum* have commonly been found in the stomach contents of *Euphausia superba* and are regarded as staple food items in its diet (Marr 1962, Kawamura 1981, Schnack 1985, Miller & Hampton 1989, Daly 1990). In our study, *Nitzschia* spp. cells and chains generally dominated the microphytoplankton component of krill gut contents whereas *C. criophilum* did not occur at the stations where krill were collected for gut content analysis. The genera *Chaetoceros* and *Rhizosolenia* are usually poorly represented in the gut contents of krill and, although Meyer & El Sayed (1983) found that krill incubated in glass aquaria could consume these diatoms efficiently, some studies have concluded that they are actually rejected or avoided (Nemoto 1968, Kawamura 1981, Marchant & Nash 1986, Maciejewska & Opalinski 1993, Opalinski et al. 1997). Our analysis of krill gut contents supports this conclusion as both *Chaetoceros* spp. and *Rhi-*

zosolenia spp. were generally not ingested, even when they occurred in large concentrations in the water column (Table 5).

Other studies have concluded that swarms of krill may locally consume 60 to 80% (Holm-Hansen & Huntley 1984) or even >100% (Samyshev 1985) of the total phytoplankton production. However, these conclusions were based on indirect estimates of the energetic requirements of krill and on the assumption that all krill carbon demands are met through an herbivorous diet, at least during the summer season. We believe that this is incorrect and suggest that, even during summer, krill consume a substantial portion of meso- and microzooplankton. Evidence for this can be found through a survey of the results of krill gut content analysis and by considering the daily carbon rations obtained in our study.

Crustaceans and protozoans have consistently been found in the stomach contents of krill, during both winter and summer (Marr 1962, Hopkins 1985, Marchant & Nash 1986, Daly 1990, Huntley et al. 1994, Nishino & Kawamura 1994). Also, grazing experiments have shown that krill can feed very efficiently on copepods, especially when these occur in high densities during summer (Price et al. 1988). During the EPOS study, conducted in spring-summer 1988–1989, Graneli et al. (1993) found that when krill were incubated in a mixture of naturally occurring phytoplankton and copepods they would prey selectively on the zooplankton until they had virtually eliminated them, and only then would krill start consuming algal cells. These authors suggested that this was probably due to the high protein and lipid content of copepods, which would make them a better quality food relative to diatoms of similar size (Graneli et al. 1993). The results of our analysis of krill stomachs confirm the importance of micro- and mesozooplankton organisms in its diet. At 3 out of the 6 stations examined, bodies and fragments of these organisms constituted over 50% of the total recognizable fraction of the gut contents (Table 5). This shows that *Euphausia superba* is a true omnivore and, even during summer, supplements its algal diet with a large heterotrophic carbon component.

Table 6. *Euphausia superba* Dana. Estimates of the daily ration in the Antarctic krill

Daily ration	Conditions, food, method	Source
2.9–8.7[a], mean 5.0	Calculated from energy budget	Chekunova & Rynkova (1974)
0.02–1.66[b] (30–50 mm)	Estimated from ingestion rates and calculated from energy budget of Clarke & Morris (1983)	Antezana et al. (1982)
2.9–3.9[b] (19–35 mm) 1.1–1.5[b] (35–55 mm)	Estimated from *in vitro* filtration rates with a culture of *Dunaliella* as food	Kato et al. (1982)
5.0–6.0[c]	Calculated from energy budget	Clarke & Morris (1983)
0.86–5.63[b] mean 2.0	Estimated with radiocarbon method using cultures of phytoplankton and detritus from flagellates as food	Samyshev & Lushov (1983)
2.3–9.0[b]	Estimated from *in vitro* ingestion rates with net phytoplankton, furcilia of *E. superba* and infusoria as food	Boyd et al. (1984)
2.6–17.1[b] (30–35 mm) 0.8–2.4[b] (40–45 mm) 0.9–3.2[b] (50–55 mm)	Estimated from *in vitro* ingestion rates with net phytoplankton as food	Schnack (1985)
17–28[d]	Estimated from faecal pellet evacuation rates using net phytoplankton as food	Clarke et al. (1988)
8.5[b]	Calculated from energy budget	Price et al. (1988)
0.53–5.81[b]	Estimated from filtration rates using zooplankton and *Artemia* nauplii as food	Krylov (1989)
0.93–2.72[d] 5.0–7.3[d]	Estimated from *in situ* gut pigment contents Estimated from *in vitro* gut pigment contents	Ponomareva & Kuznetsova (1989)
0.31–5.76[b]	Estimated from gut evacuation and ingestion rates	Drits & Semenova (1989)
2–52[a] (furcilia 3–6), realistically 10	Estimated from gut evacuation rates	Daly (1990)
19.7[b] (calyptopis 1–2) 4.4[b] (furcilia 4–5)	Estimated from *in situ* and *in vitro* filtration rates using net phytoplankton as food	Huntley & Brinton (1991)
0.05[b] (38–55 mm)	Estimated from gut evacuation and ingestion rates	Drits & Pasternak (1993)
0.8–3.67[b] (20–40 mm)	Estimated from physiological model	Huntley et al. (1994)

[a]Percentage of wet body weight
[b]Percentage of body carbon
[c]Percentage of body weight (through kJ equivalent)
[d]Percentage of dry body weight

This is supported by the low daily carbon rations obtained from our measurements of carbon-specific ingestion rates for krill grazing on phytoplankton. Daily rations can be calculated from krill length (L) measurements using the empirical equations of Kato et al. (1982) for the conversion into dry weight units, $DW = 1.208\exp(0.104L)$, and of Ikeda & Bruce (1986) for the conversion into carbon units, C = 42.6 – 47.1% DW. The resulting figures show that at all stations situated to the north of the pack ice (from Stn WR-5 to Stn WR-24) krill carbon rations, based on chorophyll alone, were very low, in the range 0.15 to 1.68% of body carbon per day. A high daily ration, in excess of 13% of body carbon, was recorded only at Stn WR-2, at the edge of the pack ice, which exhibited a phytoplankton bloom with chlorophyll *a* concentrations of ~3.5 µg chl *a* l^{-1} (Fig. 2). With this exception the daily rations obtained in this study, which are derived from a purely autotrophic food source, are among the lowest recorded for *Euphausia superba* during the summer season (Table 6). It is widely accepted that krill requires a ration of ~0.80 to 2.8% per day to meet its basic metabolic demands (Clarke et al. 1988, Daly 1990, Huntley et al. 1994). These do not include the energetic costs for growth, molting and reproduction. When all these and a high metabolic activity are taken into consideration, then krill daily ration generally ranges between ~5 and 15% of body carbon (Table 6). This is the typical situation observed in the spring and summer, when spawning takes place and growth efficiency is maximum.

It is thus clear that only the ration recorded at Stn WR-2 was sufficiently high for krill to obtain all their energetic requirements exclusively from a phytoplankton diet. Elsewhere along the transect, most of the energetic demands of the krill population were apparently met by using a heterotrophic source of carbon such as meso- and microzooplankton.

We suggest, therefore, that although Antarctic krill can still be regarded as essentially herbivorous in the presence of dense phytoplankton blooms, through most of its distribution range in the summer it may consume a larger proportion of zooplankton than previously supposed. Some of the previous estimates of the energy budget of krill during its reproductive season have not allowed for sufficient energy input except at unrealistically high phytoplankton concentrations. A substantial utilization of heterotrophic carbon through predation on zooplankton may provide a solution to the balance of its energy budget. It is clear from our study that, even when krill ingestion rates are corrected for evacuation rates and pigment destruction in the gut, phytoplankton accounts for a small fraction of the daily ration of krill. There is an urgent need, therefore, to place more emphasis on characterising and quantifying the feeding of krill on non-algal prey.

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