Protozoans as a food source for Antarctic krill, *Euphausia superba*: Complementary insights from stomach content, fatty acids, and stable isotopes

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Abstract

We studied the diet of Antarctic krill, *Euphausia superba*, at five stations across the southwest Atlantic sector in summer 2003 by analyzing stomach content, fatty acids, and stable isotopes on the same individuals. Our aim was to examine what each method could contribute to our understanding of krill nutrition and whether differences seen in growth rates were linked to their food. All three methods indicated clear regional differences in diet, but small ontogenetic and sex-related differences. Overall, diatoms were the most abundant item in the stomach, but at three of the stations, tintinnids, large dinoflagellates, and other armored flagellates dominated the identifiable biomass. Copepod remains were rare. Fatty acids profiles gave additional information about feeding on weakly silicified diatoms and athecate heterotrophic dinoflagellates, with the latter being the main food source at one of the stations. Two independent indices of carnivory, $\delta^{15}N$ and the fatty acid ratio 18:1(n-9)/18:1(n-7), were correlated among krill from the same swarm, suggesting consistent differences in diet between individuals. An internal index of trophic position, (i.e., $\delta^{15}N_{\text{glutamic acid}}$-$\delta^{15}N_{\text{phenylalanine}}$) underlined the importance of heterotrophic food for the nutrition of krill, even in summer. Highest growth rates of krill were found during a diatom bloom and coincided with a mixed diet, large digestive gland, and fast stomach passage. However, even in a nonbloom, flagellate-dominated system, krill were able to sustain medium growth rates when feeding on heterotrophic dinoflagellates. Each method supplied specific information on krill nutrition, and the true picture is only revealed when the various methods are used together.

Studies of trophic relationships are central to our understanding of ecosystems. On one hand, they shed light onto the feeding ecology of individual species. On the other hand, they indicate general paths of nutrient and energy transfer through the food web. At the base of pelagic food webs are various algal groups and microbes whose importance for sustaining higher trophic levels changes, both regionally and during phytoplankton succession (Kiørboe 1993). Those qualitative and quantitative differences in diet are reflected in the biochemical composition and physiology of grazers and secondary consumers (St. John and Lund 1996).

A range of methods has been used to study trophic relationships, with each having strengths and drawbacks. Stomach content analysis is the most direct approach, with food particles examined under the microscope. However, items differ in their digestibility and therefore recognition, and results only represent the recently ingested food. Feeding incubations give insights into food selectivity and ingestion rates, but might suffer from perturbation of complex natural food assemblages by confinement. The use of bioindicators, which get passed on from food sources to the consumer, is an alternative approach. Some fatty acids are specific to certain algal groups or to copepods (Dalsgaard et al. 2003), whereas stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) vary with nutrient source and physiology of primary producers and trophic level of consumers (Michener and Schell 1994). Such bioindicators integrate information on diet over days to months (e.g., Fry and Arnold 1982; Alonzo et al. 2005*b*),

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but separation of food sources is often not straightforward. Thus, each method is sensitive to a different timescale and aspect of the diet, potentially biasing the study. This could explain why results on trophic relationships are often conflicting (Båmstedt 2000).

Antarctic krill, *Euphausia superba*, illustrates the problems surrounding the various methods of studying diet. Krill is a major species in the Southern Ocean because of its high biomass and importance as prey for fish, bird, and marine mammals. Its diet has been studied for more than 70 yr, and results vary. Morphologically, krill is adapted for eating phytoplankton (Kils 1983; Ullrich et al. 1991). This has been supported by early analyses of the stomach content describing the abundant and easily recognizable diatoms as their main food items (Barkley 1940). More recently, attention has also been paid to the enumeration of protozoans and copepod mandibles (Hopkins 1985; Atkinson et al. 2002).

Fatty acid analyses have shown high contents of phytoplankton indicators in *E. superba* compared to other Antarctic euphausiids (Falk-Petersen et al. 2000; Phleger et al. 2002), supporting their reliance on phytoplankton. The indication of heterotrophic food sources via fatty acids is more complicated (Dalsgaard et al. 2003). Feeding on zooplankton has been invoked by Cripps et al. (1999), but the fatty acid ratio they used has since been questioned (Stübing and Hagen 2003). However, stable nitrogen isotope ratios also point to truly omnivorous feeding in krill (Rau et al. 1991; Schmidt et al. 2004), and laboratory experiments underline their ability to select for ciliates and copepods when offered in mixtures with phytoplankton (Price et al. 1988; Atkinson and Snÿder 1997). Although the omnivorous character of krill is well accepted by now, the importance of heterotrophic organisms on a day-to-day basis and at times of low phytoplankton abundance has rarely been quantified (Perissinotto et al. 2000).

Therefore, dietary methods should not just reveal the broad trophic position of an animal, they should also be sensitive to small-scale differences in diet. Those specific diets represent a link between the current food environment and an animal's constitution and performance. To be able to detect changes in diet, bioindicators have to be specific to several food sources, and influences of other factors such as developmental stage or sex should be minor. The value of fatty acids as trophic indicators for krill has been questioned (Hagen et al. 2001); in some studies, krill reflected little of the variability in dietary fatty acid composition in the field (Cripps and Hill 1998) or laboratory (Virtue et al. 1993; Stübing et al. 2003). Feeding experiments have shown that some of the common fatty acids used as trophic indicators are not assimilated or immediately catabolized in krill (Stübing et al. 2003), whereas others are synthesized de novo (Alonzo et al. 2005*a*). However, in other studies, distinct fatty acid signatures have been induced by diet, especially when the lipid content was moderate (Stübing et al. 2003; Alonzo et al. 2005*a*). The application of stable isotopes as a trophic indicator is also problematic in krill. The slow turnover of nitrogen and carbon in older developmental stages can confound the trophic signal with those of a temporally or spatially changing food-web baseline (Schmidt et al. 2003).

Here, we used stomach content, fatty acid, and stable isotope analyses simultaneously to examine the diet of *Euphausia superba*. Individuals were sampled during a cruise in the southwest Atlantic sector in summer 2003, which was characterized by highly variable concentrations of phytoplankton and large differences in krill growth rates (Atkinson et al. 2006). The summer is krill's main period for growth, reproduction, and buildup of lipid stores (Hagen et al. 2001), and therefore it is important to understand how variability in quantity and quality of food links to growth rates. The aim of this study is to find out (1) which are the main food sources for krill in summer, (2) whether the three methods are sensitive to local differences in krill diet, and (3) whether the observed differences in growth rates can be explained by differences in diet.

Methods

Sampling—During a survey aboard RRS *James Clark Ross* in January–February 2003, krill were collected with a rectangular midwater trawl (RMT8) at 24 stations across the Scotia Sea and near South Georgia. Some of the krill were immediately frozen, and others were used to measure their natural growth rates (Atkinson et al. 2006). In the vicinity of each krill haul, potential food sources were obtained from water samples and plankton netting (details in Atkinson et al. 2006). For this study, we used freshly frozen krill from five of those stations, which covered a wide spectrum of krill growth and phytoplankton abundance (Fig. 1). Our Sta. 1, 2, 3, 4, and 5 match sites 40, 36, 34, 24, and 21 of Atkinson et al. (2006, their table 1).

Dissection of krill—Krill were stored at −80°C until treatment in the laboratory. Wet mass was measured immediately after removal from the freezer. For dissection, krill were placed on ice. First, the exoskeleton was removed and the stomach was taken out. To calculate the mass of the stomach content, the stomach was weighed, emptied into a water sample, briefly blotted dry, and reweighed. The digestive gland, the size of which might indicate the recent nutritional condition of krill (Shin 2000), was transferred into a preweighed glass vial. Thereafter, the gut was removed and also emptied into a water sample. The third and fourth abdominal segments were dissected and each transferred into a preweighed glass vial. Abdominal segments and the digestive gland were freeze-dried for 24 h and the vials reweighed. Finally, sex and maturity stage of the krill were determined following Makarov and Denys (1981).

Microscopic analyses of stomach and gut content—The two water samples with the stomach and gut content were gently mixed in a whirly-mixer, transferred into Utermöhl counting receptacles, and settled for at least 2 h. The samples were analyzed on the same day, no preservative was added. First, rare items such as large diatoms, tintinnids, thecate dinoflagellates, and copepod or krill remains were counted by scanning the complete receptacles

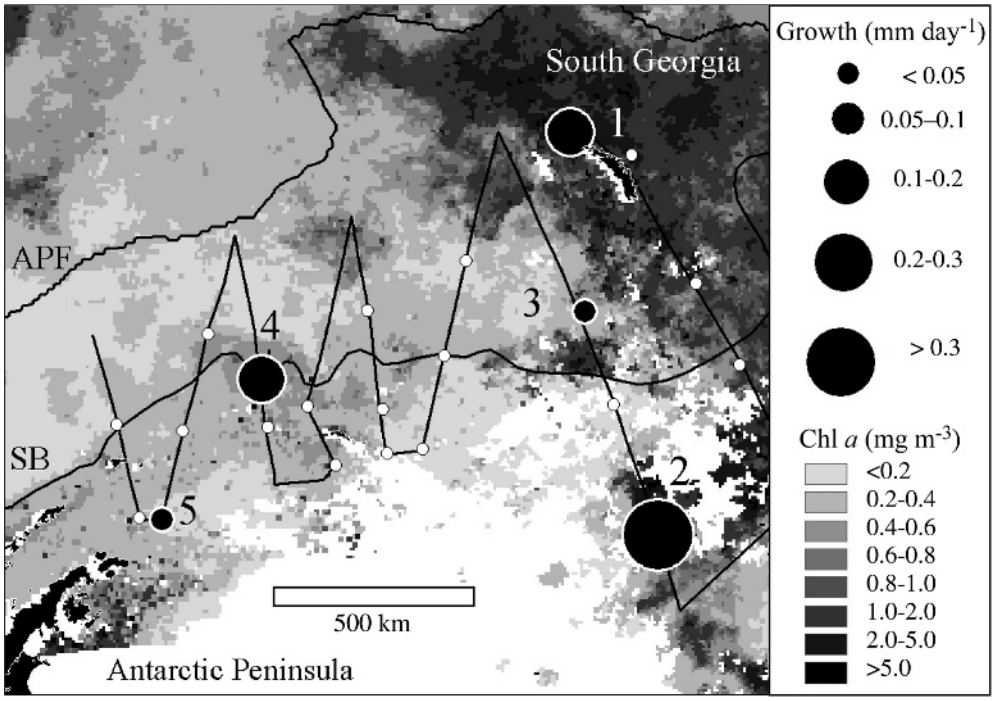

Fig. 1. Map of the investigation area. Open and solid circles mark stations sampled for growth rate measurements on krill (Atkinson et al. 2006). The size of the solid circles indicates the growth rates of krill (mm d^{-1}, normalized to 40-mm body length) for those stations where individuals were additionally analyzed for stomach content, fatty acids, and stable isotopes (present study). Regional differences in phytoplankton abundance are illustrated by a composite SeaWiFS image from December 2002 to February 2003 (areas of absent data are white). Fronts plotted are the historical positions of the Antarctic Polar Front (APF) and the Southern Boundary of the Antarctic Circumpolar Current (SB).

at ×200 magnification. Common small diatoms and other thecate flagellates were enumerated from the stomach sample only by scanning two perpendicular transects across the whole diameter of the receptacle at ×200 magnification. For each station, the dimensions of different food items were measured and their biovolume was calculated following Archer et al. (1996) and Kang et al. (2001) for diatoms and dinoflagellates, and Buck et al. (1992) and Thompson (2001) for tintinnids. The ratio of tintinnids and large dinoflagellates in stomach versus gut was used as an indicator of stomach passage, assuming that higher numbers in the gut result from a fast stomach throughput and incomplete digestion.

Fatty acid analysis—After freeze-drying and weighing, the lipids of the digestive gland and fourth abdominal segment were extracted in chloroform : methanol (2:1, v:v). Fatty acid methyl esters (FAMEs) were prepared from aliquots of total lipid after the addition of an internal standard (21:0) to each aliquot. FAMEs were generated by transesterification of lipid samples in methanol containing 1.5% sulfuric acid at 50°C for 16 h (Christie 1982). FAMEs were then purified by thin layer chromatography by a hexane : diethyl ether : acetic acid solvent system (90 : 10 : 1, v : v : v) and analyzed with a Thermo Finnigan Trace 2000 gas chromatograph (GC). The GC was equipped with on-column injection, installed with a ZBWAX column (30 m × 0.32 mm), and hydrogen was used as the carrier gas. FAMEs were detected by flame ionization and identified by comparing retention time data with those obtained from standard mixtures.

Isotopic analysis of bulk nitrogen and carbon—To examine the isotopic composition of the particulate organic matter (POM), 2–4 L of water from 20 m depth were filtered onto a GF/F filter and frozen at −80°C. Back in the laboratory, these filters were dried at 60°C for 24 h and packed into tin capsules. The third abdominal segment of each krill was ground in an agate mortar after freeze-drying and weighing. Carbon and nitrogen stable isotope ratios in both POM and krill tissue were then analyzed with a CHN analyzer (Thermo Finnigan CE 1108) combined with a mass spectrometer (Finnigan Delta S) via a Conflow II open split interface. Calibration for the total carbon and nitrogen determination was done with an acetanilide standard. All isotope abundances are expressed in δ notation as: δX (‰) $= ((R_{sample}/R_{standard}) - 1) \times 10^3$, where X is ^{13}C or ^{15}N, and R is $^{13}C : {}^{12}C$ or $^{15}N : {}^{14}N$. PeeDee Belemnite carbonate (NBS 21 and 22) and atmospheric nitrogen (IAEA-N1, -N2, -N3) were used as the standards for carbon and nitrogen, respectively. A laboratory internal standard (Peptone, Merck) was run for every sixth sample. The peptone standard indicated an analytical error associated with the isotope measurements of less than

Table 1. Biochemical composition of POM and abundance of important plankton organisms at krill sampling stations.

	Sta. 1	Sta. 2	Sta. 3	Sta. 4	Sta. 5
Chl *a* (μg L^{-1})*	5.4	0.84	0.09	0.66	0.17
Chl *a*, 0.2–2 μm (%)*	9	11	41	44	66
Chl *a*, 2–12 μm (%)*	9	27	33	55	30
Chl *a*, >12 μm (%)*	82	62	26	1	4
Total fatty acids (μg L^{-1})	153	79	38	44	31
Σ diatoms (% of total FA)	31	40	21	17	12
Σ dinoflagellates (% of total FA)	20	15	21	28	23
Σ prymnesiophytes (% of total FA)	10	8	14	14	13
C : N ratio	7.0	6.6	8.9	6.7	9.3
Nanoflagellates (ind. mL^{-1})†	496	654	315	1,191	273
Heterotrophic dinoflagellates >20 μm (ind. mL^{-1})†	63	35	16	19	8
Diatoms (ind. mL^{-1})†	335	470	11	0.2	21
Diatoms >100 μm (ind. mL^{-1})	3	1	0.4	0.06	0.07
Corethron spp. (% of diatoms >100 μm)	0.2	5	10	95	95
Large tintinnids (ind. m^{-3})	493	257	33	4	16
Copepods (ind. m^{-3})	2,662	556	625	418	453

Samples for Chl *a* were taken at 6.5-m depth, those for fatty acids, C, and N and small plankton counts at 20-m depth. Fatty acids characteristic for diatoms, dinoflagellates or prymnesiophytes were summarized according to Dalsgaard et al. (2003). Diatoms = Σ (16:1(n-7),16:4(n-1),20:5(n-3)); dinoflagellates = Σ (18:5(n-3),22:6(n-3)); prymnesiophytes = Σ (18:1(n-9),18:4(n-3)). Large diatoms or diatom chains, large tintinnids, and copepods were counted from 100-μm net samples of the whole water column.

* Original data in Korb et al. (2005).

† Original data in Atkinson et al. (2006).

$\pm$0.2‰ for both isotopes. Two to three replicates were analyzed from each sample.

Isotopic analysis of amino acid nitrogen—For isotopic analysis of individual amino acids, one sample per station was prepared by pooling equal amounts of the ground third abdominal segment from all krill of the station, regardless of their sex and developmental stage. In addition, two specimens from Sta. 2 were analyzed individually. Amino acids were prepared for gas chromatography/combustion/isotope ratio mass spectrometry (GC/C/IRMS) analysis by acid hydrolysis of samples and derivatization to N-pivaloyl-i-propyl (NPP) amino acid esters (Metges and Petzke 1997). In brief, about 1 mg of protein was hydrolyzed with ultrapure 6 mol L^{-1} HCl for 24 h at 110°C. Amino acids were purified by cation exchange chromatography (Dowex 50WX8, Na^+ form, 200–400 mesh, elution with 4 mol NH_4OH L^{-1}), dried under N_2 at 60°C, and esterified with acetylchlorid and isopropanol. The product was dried under N_2 and dissolved in pyridine. Pivaloylchloride was added for acylation.

The stable isotopic composition of nitrogen in NPP derivatives of amino acids were analyzed by GC/C/IRMS using a Finnigan delta S isotope ratio mass spectrometer (Therma Electron) interfaced to a Hewlett-Packard 5890 gas chromatograph. An Ultra 2 column (50 m $\times$ 0.32 mm internal diameter, 0.52-μm film thickness) with helium as carrier gas (1 mL min^{-1}) was used to separate amino acid esters. The injector temperature was 280°C, and the following oven temperature gradient was used: 70°C, held 1 min; 70–220°C, ramp 3°C per minute; 220–300°C, ramp 10°C per minute, held for 8 min at 300°C. Autosampler injections (CTC A200S; CTC Analytics) were done splitless and contained 0.5 μL of sample. Measured ratios of ^{15}N and ^{14}N were derived from mass-to-charge ratios (*m*/*z*) 29 to *m*/*z* 28 ion current signals of the mass spectrometer, and the standard gas used was calibrated against the international standard AIR (ambient inhalable reservoir).

Each sample run was preceded by two pulses of reference N_2 and followed by three pulses of reference N_2, whose isotopic composition was calibrated against a variety of organic standards (peptone, histidine, and acetanilide) by continuous-flow isotope ratio mass spectrometry with a Carlo Erba NA 2100 elemental analyzer interfaced with a Micromass Optima mass spectrometer.

Statistics—Multiple comparisons of means were carried out with a Tukey test. Station-specific equations of linear regression between the amount of an individual fatty acid and the total lipid content were compared by analysis of covariance. Principal component analysis (PCA) was performed to identify those fatty acids that account for most of the variance between krill from the five stations. For correlation analysis between individual $\delta^{15}N$ and concomitant physiological and biochemical parameters, linear correlation coefficients (r^2) were calculated. Differences were considered significant when $p < 0.05$.

Results

Characterization of the ambient water—The five stations clearly differed in plankton abundance and composition (Table 1, Fig. 1). Station 1 was rich in potential food organisms: high concentrations of chlorophyll *a* (Chl *a*), deriving mainly from cells >12 μm, and high abundances of tintinnids and copepods. Cell counts and fatty acid composition of the POM suggest that diatoms dominated the phytoplankton. At Sta. 2, there was less Chl *a*, but also

a dominance of diatoms (>12 μm). Other stations had low to moderate Chl *a* concentrations and a very high proportion of small phytoplankton (<12 μm). Small flagellates (cryptophytes, single-cell *Phaeocystis* sp., and heterotrophic dinoflagellates) were especially common at Sta. 4, as indicated by cell numbers and fatty acid profiles.

Digestive gland, stomach content, and food passage—The size of the digestive gland varied between developmental stages and sampling locations (Table 2). When accounting for differences in body mass, male krill had significantly smaller digestive glands than juveniles and females at Sta. 3, 4, and 5 (Tukey test, $p < 0.05$; the single subadult male from Sta. 3 was not included in the test) and juveniles had smaller digestive glands than females at Sta. 3 (Tukey test, $p < 0.05$), but there were no sex-related differences at Sta. 1. Regional differences were most pronounced for subadult males, whose digestive glands were more than twice as large at Sta. 2 as at other stations (Tukey test, $p < 0.05$, the single subadult male at Sta. 3 was not included in the test). Adult females had largest digestive glands at Sta. 4 and adult males at Sta. 1 (Tukey test, $p < 0.05$).

The relative mass of the stomach content was often variable, even within the same station and development stage, which restricted statistical comparisons. However, krill from Sta. 2 and 5 showed generally lower values than individuals from Sta. 3 and 4. There were no consistent differences between males and females.

The stomach contained usually a large proportion of unidentifiable material, either greenish-black fluff (Sta. 1) or strongly macerated debris (Sta. 2, 3, 4, and 5), and a smaller part of recognizable items. Individuals from the same school had similar stomach contents, but there were clear differences between stations (Table 2, Fig. 2). Krill from Sta. 1 were characterized by a large range of identifiable food items, including various thecate dinoflagellates (*Protoperidinium* spp. and *Dinophysis* spp.) and tintinnids (*Salpingella* spp., *Codonellopsis* spp., and *Cymatocylis* spp.). Heterotrophs formed the biggest fraction of the total identifiable volume because of the high numbers and large dimensions of some species (e.g., *Protoperidinium antarcticum* and *Cymatocylis calciformis*). Other important items were small-celled diatoms from the genera *Thalassionema* and *Eucampia*.

At Sta. 2, most food items in the stomachs were identifiable and of diatom origin. Important were small pennate diatoms such as *Pseudonitzschia* spp. and various species of *Fragilariopsis*. Large pennate diatoms (e.g., *Rhizosolenia* spp., *Thalassiothrix* spp.) and discoid diatoms of various sizes also contributed significantly to the total volume. Dinoflagellates, even though relatively high in numbers, were small in size and therefore of minor importance for the total identified volume. Sta. 3 was similar to Sta. 2 in that small diatoms were the most numerous items in krill stomachs, but the digestion of the material was more advanced at Sta. 3. Typical for this station were small (~15 μm) discoid diatoms and pennate diatoms such as *Thalassionema* sp. and *Fragilariopsis kerguelensis*. Heterotrophic items were rare.

Krill stomach contents at Sta. 5 and particularly Sta. 4 were characterized by very few recognizable items but a lot of small debris most likely of diatom origin. Some individuals from Sta. 4 showed high abundances of a small, unidentified flagellate, and all individuals were rich in the autotrophic dinoflagellate *Prorocentrum* spp., causing autotrophic flagellates to represent the largest part of the total identified volume. The rest derived from small diatoms of the genera *Pseudonitzschia*, *Thalassionema*, and *Fragilariopsis* and a few tintinnids (mainly *Codonellopsis* spp.). Most individuals from Sta. 5 had high numbers of a relatively large tintinnid, *Cymatocylis convallaria*, causing tintinnids to dominate the total identified volume. Other important items were small diatoms such as *Thalassionema* sp. and a large (~40 μm) discoid diatom.

At all stations, there was very little indication of krill feeding on copepods, and low but consistent numbers of mandibles and appendages have only been found at Sta. 1. At maximum, there were five mandibles per stomach. The largest mandible had a width of 100 μm. The majority were 20–30 μm wide and derived from the cyclopoid *Oithona* spp. In contrast to copepod remains, krill setae and setulae were regularly found in stomachs. Some individuals at Sta. 4 and 5 showed very high numbers of setae (up to 370 bits) and loose setulae (up to 14,000).

Krill from various stations also differed in the processing of food. This is illustrated not only by the different degree of diatom maceration (low at Sta. 2 and high at Sta. 3, 4, and 5), but also by the ratios of tintinnids and heterotrophic dinoflagellates in stomach versus gut. Individuals from Sta. 2 had about half as many tintinnids and heterotrophic dinoflagellates in their stomachs than in their guts. A ratio of 1–2 was common for krill from Sta. 1, while individuals from Sta. 3, 4, and 5 clearly had more items in the stomach than in the gut. The differences between stations were significant for both tintinnids and heterotrophic dinoflagellates at Sta. 2 (Tukey test, $p < 0.05$) and for tintinnids at Sta. 1 (Tukey test, $p < 0.05$). This suggests that food passage through the stomach was fast for krill at Sta. 1 and particularly at Sta. 2, but slower at Sta. 3, 4, and 5.

Total lipid content and fatty acid profiles—Krill lipid content ranged from 3% to 35% of dry mass depending on tissue, sex/maturity stage, and station (Table 3). The lipid content of the digestive gland exceeded that of the abdominal muscle by a factor of ~1.8 in lipid-rich krill and by a factor of ~1.5 in krill with less lipid. If various stages cooccurred at the same station, adult males often had lower lipid levels than females, but subadult males had higher values than females (Tukey test, $p < 0.05$). However, those differences between sex/maturity stages were smaller than the site-to-site variability in lipid content: individuals from Sta. 1 and 2 showed significantly higher values than those from Sta. 3, 4, and 5 (Tukey test, $p < 0.001$).

Dominant fatty acids were the saturated (SFA) 14:0 and 16:0, the long-chain polyunsaturated (PUFA) 20:5(n-3) and 22:6(n-3), and the monounsaturated fatty acids (MUFA) 18:1(n-9) and 18:1(n-7) (Table 3). Variability in the proportion of those fatty acids, except for 18:1(n-7), is closely linked with the total lipid content of krill (e.g., in muscle,

Table 2. *Euphausia superba*, total wet mass (g, means ± SD), dry mass of digestive gland (mg g^{-1} total wet mass), wet mass of the stomach content (mg g^{-1} total wet mass), number of identified food items in the stomach (items ind. $^{-1}$) and indices of stomach passage (ratio of tintinnids and large dinoflagellates in stomach vs. gut) of krill from different stations.

	Sta. 1					Sta. 2	Sta. 3					Sta. 4				Sta. 5	
	MS1 (n=5)	MS3 (n=3)	FS (n=2)	MA2 (n=3)	FA4 (n=3)	MS2 (n=8)	Juv (n=3)	MS2 (n=1)	FA2/3 (n=5)	MA2 (n=3)	FA4 (n=2)	Juv (n=1)	FA2/3 (n=4)	MA2 (n=5)	FA3/4 (n=4)	MS2 (n=5)	FA1 (n=3)
Total wet mass	0.7±0.0	1.5±0.1	1.0±0.1	1.4±0.2	2.0±0.2	0.6±0.1	0.5±0.0	1.3	1.0±0.1	1.5±0.1	1.5±0.3	0.6	0.7±0.2	1.1±0.3	1.2±0.2	0.5±0.1	0.5±0.0
Digestive gland	15.6±1.3	16.0±2.6	14.1±7.2	15.2±2.4	14.1±7.4	35.4±6.6	11.2±0.6	28.3	19.2±2.4	6.4±0.8	16.0±2.6	19.7	25.8±5.8	10.3±3.5	20.0±5.0	12.7±2.6	17.2±2.5
Stomach content	2.7±1.6	1.8±1.1	2.0±1.1	1.7±0.4	1.2±0.6	1.5±0.3	2.1±0.8	1.6	2.1±0.6	1.9±0.3	2.0±0.8	3.1	2.5±0.6	2.0±0.4	2.0±0.2	1.7±1.5	1.4±0.9
Flagellates small																	
unidentified	0	0	0	0	0	0	0	0	0	0	0	8.9T	3.4T±2.8T	1.1T±1.8T	757±790	0	0
Diatoms																	
small discoid	0	0	0	0	0	5.4T±3.3T	5.6T±3.4T	14.9T	12.3T±5.0T	23.9T±8.2T	20.5T±7.9T	39	100±86	129±55	160±39	191±26	323±56
small pennate	16T±8.3T	19T±14T	20T±17T	30T±17T	23T±13T	46T±27T	7.0T±3.9T	12T	19T±6.8T	32T±7.6T	37T±7.9T	24T	24T±3.2T	17T±7.0T	21T±3.2T	20T±2.5T	21T±1.7T
Fragilariopsis spp.	73±48	42±19	52±36	308±157	208±123	29T±18T	863±275	2.5T	2.1T±0.7T	3.6T±0.2T	3.2T±1.5T	3.3T	2.6T±1.3T	1.6T±0.7	2.5T±1.4T	0	0
Eucampia sp.	861±399	1.2T±1.2T	1.0T±0.4T	4.1T±2.1T	4.0T±3.0T	0	0	0	0	0	0	0	0	0	0	0	0
large discoid	0	0	0	0	0	238±60	36±12	29	54±18	89±31	73±20	0	0	0	0	207±50	223±79
large spiny	36±72	111±204	34±13	230±277	260±326	1.1T±0.4	498±266	561	2.4T±1.7T	4.3T±1.9T	4.5T±2.8T	47	62±12	213±119	154±87	226±200	257±160
Dinoflagellates																	
Prorocentrum spp.	1.4T±1.3T	1.6T±1.2T	1.0T±0.5T	2.0T±0.9T	2.2T±1.9T	785±359	338±112	1,086	652±182	394±14	729±171	2.0T	3.0T±1.1T	3.6T±1.7T	3.6T±0.3	314±181	225±157
Dinophysis spp.	23±14	38±17	17±10	12±20	28±15	6±6	4±5	4	11±15	7±2	6±5	0	0	0	0	0	0
Protoperidinium spp.	94±39	152±63	69±63	258±130	233±118	74±40	6±6	15	9±6	9±6	10±7	0	2±3	9±8	6±6	0	1±1
Tintinnids																	
Salpingella spp.	153±58	166±95	134±110	204±126	288±139	0	0	0	0	0	0	0	0	0	0	0	0
Codonellopsis spp.	16±9	33±22	23±19	54±32	56±22	2±2	3±1	5	7±3	5±3	9±3	8	11±4	13±5	10±1	2±3	3±5
Cymatocylis spp.	20±13	49±23	12±14	59±38	63±30	4±5	1±1	5	6±3	4±3	5±2	0	0±1	3±3	3±5	35±41	45±53
Copepods																	
mandibles	1±1	1±2	1±1	2±3	1±2	1±1	0	1	0	1±2	0±1	0	0	0	0	0	0
appendages	6±9	11±6	10±13	8±11	8±7	1±1	0	0	0	0	1±2	0	0	0	0	0	0
Krill																	
setae	3±3	11±7	5±3	15±8	11±21	5±4	4±6	1	4±3	8±4	8±6	0	5±4	85±160	11±9	33±54	103±116
setulae	124±83	198±59	236±192	40±117	60±105	99±105	84±22	35	116±45	133±91	103±77	249	186±155	3.2T±5.9T	395±315	243±207	1.1T±1.6T
Index stomach pass.																	
Tintinnids	4.1±1.9	3.3±1.5	1.2±1.1	1.5±0.1	1.5±0.9	0.5±0.4	2.7±1.5	2.5	6.8±4.3	8.7±5.0	7.9±8.0	1.6	3.6±3.7	8.9±3.1	6.5±2.7	3.8±3.7	6.7±6.4
Dinoflagellates	2.1±1.1	1.9±1.1	0.8±0.7	0.9±0.1	1.3±0.4	0.6±0.2	1.5±0.5	3.8	1.4±0.6	2.0±2.4	2.2±0.9	-	-	3.0±2.0	-	-	-

Krill were divided by their sex and increasing sexual maturity according to Makarov and Denys (1981): juveniles (Juv), subadult males (MS1–3), subadult females (FS), adult males (MA1–2), and adult females (FA1–5). Discoid diatoms include *Coscinodiscus* spp., *Thalassiosira* spp., and *Asteromphalus* spp. The threshold between "small" and "large" discoid diatoms was a 40-μm diameter. Small pennate diatoms are complete or broken *Thalassionema* sp. and *Pseudonitzschia* spp. Large spiny diatoms include bits of *Thalassiothrix* sp., *Rhizosolenia* spp., *Corethron* spp., and *Chaetoceros* spp. n, number of krill analyzed, $T = \times 10^3$.

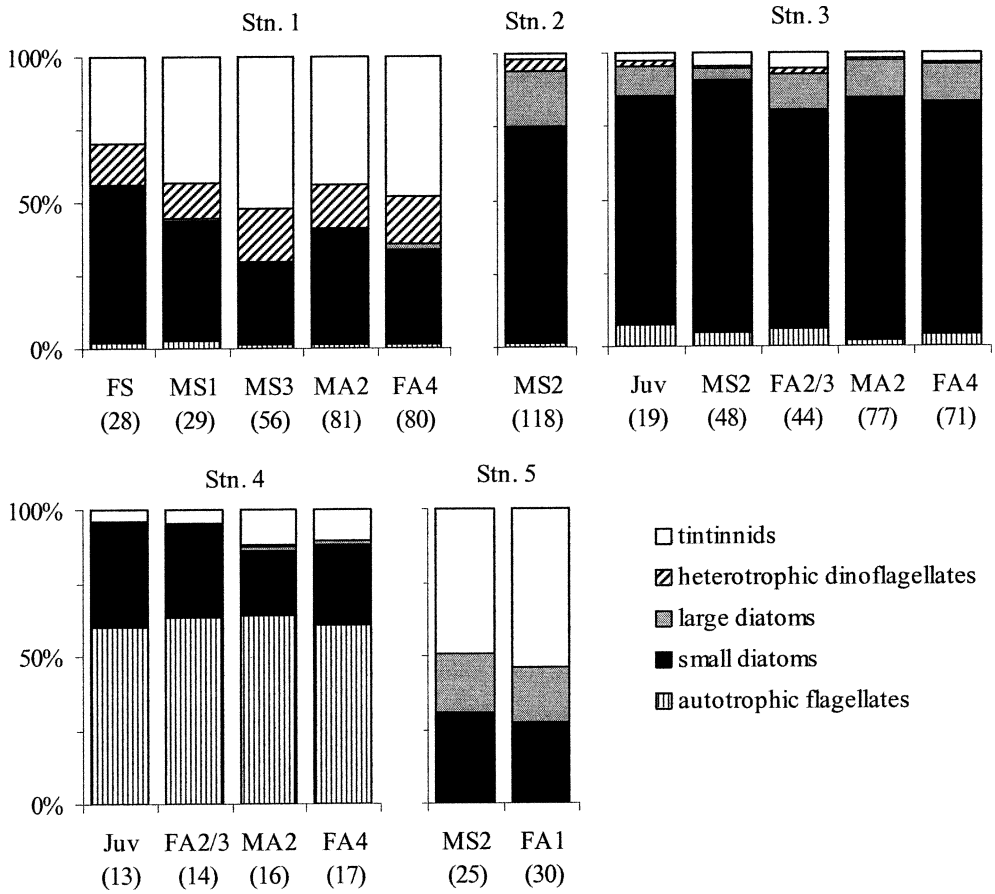

Fig. 2. *Euphausia superba*. Contribution of different plankton groups to the total volume of identifiable stomach items (except for copepod remains and krill molts). Values of total volume ($\times 10^6$ μm^3) are given in brackets underneath the plot. Maturity stages and sample size as in Table 2.

$r^2 = 0.83$ for 14:0 and $r^2 = 0.85$ for 22:6(n-3), Table 3). Lipid-rich individuals were characterized by a high percentage of saturated fatty acids, whereas PUFAs were dominant in krill with low lipid content. Krill also contained substantial proportions of indicator fatty acids typical for microalgae, up to 12% of 16:1(n-7) and up to 8% of 18:4(n-3).

To reveal site-specific differences in krill nutrition, we used the absolute amount of individual fatty acids (mg g^{-1} dry mass) rather than their proportion (% of total fatty acids) and compared only among stations where krill had similar lipid content (Fig. 3, Table 4). Lipid-rich krill were common at Sta. 1 and 2. Individuals from Sta. 1 were characterized by higher concentrations of the diatom indicator, 16:1(n-7), and the product of its in vivo elongation, 18:1(n-7) (significant differences in intercepts of trendlines, $p < 0.001$), as well as of the copepod indicator, Σ (20:1(n-9); 22:1(n-11); 22:1(n-9)) ($p < 0.001$). In contrast, krill from Sta. 2 had higher concentrations of the flagellate indicator, 18:4(n-3) ($p < 0.01$) and another diatom indicator, 16:4(n-1) ($p < 0.05$). Other fatty acids differed in only one of the two tissues or in neither.

Krill with lower lipid content were sampled at Sta. 3, 4, and 5. Individuals from Sta. 4 had the lowest concentration of the diatom indicator, 16:1(n-7) ($p < 0.05$), but highest concentrations of the flagellate indicators, 18:4(n-3) and 22:6(n-3) ($p < 0.01$). Krill from Sta. 3 were richest in 18:1(n-7) ($p < 0.05$), but depleted in 18:4(n-3) ($p < 0.01$).

A two-dimensional plot of fatty acid ratios summarizes the results of krill feeding on diatoms versus flagellates (Fig. 4). Krill from Sta. 1 had highest ratios of 16:1(n-7)/18:4(n-3) and 20:5(n-3)/22:6(n-3), whereas krill from Sta. 4 had lowest ratios and those from Sta. 3 and 5 were intermediate (Tukey-test, $p < 0.05$). Individuals from Sta. 2 associated with those from Sta. 1 in the 20:5(n-3)/22:6(n-3) ratio, but had significantly lower values in the 16:1(n-7)/18:4(n-3) ratio (Tukey test, $p < 0.001$). Calibration with values deriving from laboratory experiments (Alonzo et al. 2005*a*) suggests that krill from Sta. 1 was feeding mainly on diatoms and those from Sta. 4 mainly on flagellates, whereas krill from the other three locations had a mixed diet. Those spatial differences in diet were reflected in the fatty acids ratios of both digestive gland and muscle, and overrode differences between sex or maturity stages.

A similar separation of the five stations was enabled by PCA (Table 5, Fig. 5). Together, the first three principal components (PCs) account for 96% of variance. The first PC reflects the differences in total fatty acid content,

Table 3. *Euphausia superba*, total lipid (% dry mass, means ± SD), total fatty acids (mg g^{-1} lipid), and fatty acid composition (%). The last column indicates the relationship between percent fatty acid and total lipid.

Digestive gland

	Sta. 1					Sta. 2	Sta. 3					Sta. 4				Sta. 5		Fatty acid to total lipid (r^2)
	MS1 (n=5)	MS3 (n=3)	FS (n=2)	MA2 (n=3)	FA4 (n=3)	MS2 (n=8)	Juv. (n=3)	MS2 (n=1)	FA2/3 (n=5)	MA2 (n=3)	FA4 (n=2)	Juv. (n=1)	FA2/3 (n=4)	MA2 (n=5)	FA3/4 (n=4)	MS2 (n=5)	FA1 (n=3)	
Total lipid	24.0±4.0	29.3±3.9	27.7±8.9	15.2±4.3	21.1±0.3	24.7±3.2	14.4±2.4	26.5	9.4±1.5	5.4±3.2	13.5±2.2	6.2	9.2±2.9	5.6±1.1	10.6±2.3	9.4±1.9	6.9±2.3	
Total fatty acids	734±50	739±32	701±31	546±90	695±50	658±58	536±25	710	558±55	429±68	733±78	600	650±48	531±118	579±44	546±36	590±37	
14:0	12.0±0.6	13.0±1.0	12.3±0.8	6.4±2.1	9.9±0.9	11.5±0.7	9.2±1.4	11.0	6.3±1.0	3.8±0.2	8.9±1.2	6.1	5.4±1.5	3.6±0.5	5.0±1.2	5.2±2.0	4.2±1.7	0.79*
16:0	14.8±1.9	23.5±0.9	22.8±0.1	18.4±3.5	22.3±0.3	22.6±0.6	21.2±0.9	23.1	18.9±0.7	14.6±0.0	22.2±1.2	19.2	19.9±1.2	17.5±0.5	18.7±0.8	18.2±0.9	17.2±0.7	0.66*
16:1(n-7)	10.6±0.4	10.5±1.0	11.3±0.8	5.7±2.7	9.2±1.1	8.8±0.8	7.6±1.2	8.8	4.9±0.7	2.7±0.4	8.5±1.6	2.5	2.4±0.1	0.8±0.3	2.0±0.7	4.1±1.5	3.3±0.9	0.72*
16:2(n-4)	2.6±0.3	2.5±0.0	2.5±0.4	1.6±1.1	3.5±0.3	1.6±0.1	1.8±0.3	2.1	2.0±0.4	0.5±0.1	3.0±0.5	1.6	1.5±0.4	0.4±0.2	2.0±0.5	2.0±0.7	1.6±0.9	0.21*
16:4(n-1)	0.4±0.1	0.5±0.2	0.4±0.2	0.5±0.4	0.6±0.2	0.7±0.2	0.4±0.1	0.6	0.3±0.1	0.1±0.1	0.4±0.1	0.3	0.2±0.0	0.0±0.0	0.2±0.1	0.4±0.3	0.2±0.3	0.31*
18:0	1.6±0.2	1.4±0.2	1.1±0.0	1.2±0.1	1.2±0.3	1.6±0.2	1.1±0.2	1.6	0.5±0.1	1.3±0.0	1.2±0.1	1.3	0.8±0.3	1.0±0.1	0.6±0.0	0.7±0.1	0.5±0.1	0.44*
18:1(n-9)	11.5±1.0	13.0±1.5	12.2±0.8	5.7±1.9	11.8±0.7	12.1±0.6	8.7±1.4	11.3	6.1±0.8	4.1±0.3	11.5±1.1	7.6	7.4±1.5	4.2±0.5	7.1±0.9	5.9±1.7	6.2±1.9	0.65*
18:1(n-7)	7.2±0.3	7.3±0.2	7.6±0.3	8.4±0.8	8.6±0.7	6.4±0.4	8.6±0.7	7.6	11.9±0.6	7.6±0.3	9.1±0.9	4.8	7.8±1.0	4.3±0.6	8.7±1.0	8.7±0.4	9.2±0.6	0.03
18:2(n-6)	1.1±0.2	1.1±0.1	1.4±0.0	1.9±0.8	1.2±0.2	1.8±0.1	2.2±0.3	1.4	2.7±0.2	2.9±0.2	1.7±0.6	1.9	1.9±0.1	2.1±0.1	2.1±0.1	2.6±0.6	3.1±0.4	0.47*
18:3(n-6)	0.2±0.1	0.2±0.0	0.3±0.0	0.2±0.0	0.2±0.0	0.3±0.0	0.3±0.0	0.2	0.3±0.0	0.3±0.1	0.2±0.1	0.2	0.2±0.0	0.1±0.2	0.2±0.0	0.2±0.0	0.2±0.1	0.09*
18:3(n-3)	0.3±0.0	0.3±0.0	0.3±0.0	0.6±0.3	0.3±0.1	0.5±0.0	0.7±0.1	0.4	1.0±0.1	1.0±0.1	0.6±0.2	2.5	3.0±0.1	3.0±0.3	3.3±0.4	2.1±0.8	2.2±0.5	0.59*
18:4(n-3)	0.9±0.1	0.8±0.3	0.6±0.0	1.4±0.0	0.9±0.2	2.0±0.3	1.6±0.2	1.4	1.7±0.4	1.4±0.0	1.2±0.3	8.6	5.9±1.3	5.6±1.4	4.9±0.7	4.0±1.6	3.9±1.3	0.41*
20:1(n-9)	1.3±0.1	1.4±0.1	1.4±0.1	0.9±0.4	1.3±0.2	1.2±0.2	0.8±0.1	1.3	0.5±0.1	0.6±0.1	1.1±0.0	1.8	1.1±0.1	1.4±0.4	0.9±0.2	0.8±0.2	0.8±0.2	0.18*
20:1(n-7)	0.3±0.0	0.4±0.0	0.4±0.1	0.3±0.2	0.4±0.1	0.2±0.0	0.2±0.1	0.4	0.5±0.0	0.2±0.0	0.4±0.1	0.1	0.3±0.1	0.3±0.2	0.6±0.1	0.1±0.1	0.1±0.1	0.02
20:4(n-6)	0.3±0.1	0.3±0.1	0.4±0.0	0.6±0.3	0.3±0.0	0.6±0.1	0.5±0.1	0.4	0.6±0.1	1.1±0.0	0.3±0.1	0.4	0.4±0.1	0.5±0.1	0.4±0.1	0.3±0.1	0.4±0.1	0.07
20:4(n-3)	0.2±0.1	0.3±0.1	0.3±0.0	0.6±0.3	0.4±0.0	0.6±0.1	0.7±0.1	0.4	0.9±0.1	1.0±0.0	0.5±0.2	0.5	0.7±0.1	0.9±0.2	0.8±0.1	0.7±0.2	0.8±0.2	0.55*
20:5(n-3)	16.8±1.6	16.3±2.7	16.4±0.7	29.4±2.2	18.9±2.1	19.4±1.1	21.2±1.9	18.9	25.0±1.8	31.9±0.0	18.4±1.3	18.5	21.2±2.4	23.7±1.6	22.3±2.0	26.9±3.6	25.8±2.6	0.47*
22:1(n-11)	1.2±0.0	1.2±0.1	1.2±0.0	0.7±0.6	1.0±0.5	0.8±0.1	0.6±0.1	1.1	0.3±0.1	0.2±0.3	0.6±0.2	0.2	0.1±0.1	0.1±0.1	0.1±0.2	0.3±0.2	0.3±0.1	0.64*
22:1(n-9)	0.2±0.0	0.2±0.0	0.2±0.0	0.1±0.1	0.1±0.1	0.0±0.1	0.1±0.1	0.1	0.0±0.1	0.0±0.0	0.0±0.0	0.1	0.2±0.0	0.0±0.0	0.1±0.1	0.2±0.1	0.2±0.1	0.04
22:6(n-3)	5.3±0.3	4.7±0.5	5.8±1.1	13.5±7.8	6.4±1.2	5.9±0.5	10.1±1.8	6.3	12.8±1.4	21.8±0.7	8.5±1.8	18.7	17.0±1.6	26.7±2.2	17.1±2.5	14.1±3.7	17.4±4.6	0.79*
Others	1.2±0.1	1.2±0.1	1.3±0.2	2.0±1.1	1.6±0.3	1.4±0.1	2.3±0.5	1.5	2.7±0.2	3.0±0.1	1.6±0.3	3.1	2.8±0.3	3.8±0.2	3.2±0.3	2.4±0.2	2.4±0.3	

Table 3. Continued.

Muscle	Sta. 1					Sta. 2	Sta. 3					Sta. 4				Sta. 5		Fatty acid to total lipid (r^2)
	MS1 (n=5)	MS3 (n=3)	FS (n=2)	MA2 (n=3)	FA4 (n=3)	MS2 (n=8)	Juv. (n=3)	MS2 (n=1)	FA2/3 (n=5)	MA2 (n=3)	FA4 (n=2)	Juv. (n=1)	FA2/3 (n=4)	MA2 (n=5)	FA3/4 (n=4)	MS2 (n=5)	FA1 (n=3)	
Total lipid	14.1±1.3	17.1±0.9	15.1±1.7	10.4±3.1	11.4±1.7	14.8±3.2	11.6±1.6	14.4	6.3±1.0	4.2±0.2	8.6±0.6	5.1	6.9±1.6	3.9±0.6	5.7±1.2	6.6±1.9	6.1±1.2	
Total fatty acids	772±26	790±10	771±13	727±61	735±54	735±24	677±68	743	578±42	464±15	652±35	586	579±76	558±63	598±99	502±11	515±27	
14:0	11.6±0.9	12.6±0.8	12.2 ±0.2	9.5±0.9	9.0±1.0	10.9±0.7	10.8±0.9	10.8	6.2±0.8	1.9±0.3	6.7±0.4	3.1	4.7±1.9	3.0±1.6	4.1±2.0	5.0±2.1	3.4±1.2	0.83*
16:0	24.6±0.8	24.0±1.2	24.0±0.6	22.2±1.0	22.3±0.3	23.1±0.5	23.9±0.0	23.4	21.8±0.6	20.7±0.7	22.5±0.2	25.3	22.8±2.8	21.7±1.0	21.6±0.5	21.6±0.6	21.2±0.3	0.61*
16:1(n-7)	11.0±0.5	10.2±0.7	11.2±0.0	8.4±0.6	8.6±1.4	8.3±0.6	9.2±1.0	8.8	5.3±0.6	2.1±0.4	7.0±0.9	2.8	2.9±0.4	1.8±0.8	2.5±0.7	4.4±1.0	3.4±0.9	0.79*
16:2(n-4)	2.6±0.3	2.3±0.1	2.3±0.3	2.6±0.4	3.3±0.3	1.6±0.2	2.2±0.3	2.1	2.2±0.2	0.3±0.1	2.6±0.1	1.4	1.5±0.5	0.8±0.9	1.5±1.2	1.6±0.6	1.3±0.4	0.20*
16:4(n-1)	0.4±0.1	0.4±0.2	0.4±0.1	0.7±0.3	0.5±0.2	0.7±0.2	0.5±0.1	0.6	0.2±0.1	0.0±0.0	0.4±0.0	0.2	0.1±0.2	0.0±0.1	0.1±0.1	0.4±0.3	0.1±0.1	0.41*
18:0	1.4±0.1	1.4±0.2	1.3±0.2	1.6±0.3	1.3±0.3	1.6±0.1	1.2±0.2	1.3	0.6±0.1	0.9±0.1	1.1±0.2	4.5	3.0±3.6	1.0±0.5	0.8±0.1	1.2±0.3	1.8±0.9	0.19*
18:1(n-9)	12.5±0.7	13.4±1.4	13.7±2.5	10.1±1.4	12.3±0.9	12.6±0.7	11.2±1.0	13.2	8.8±0.9	12.4±0.6	11.6±0.1	11.3	9.5±1.1	9.1±1.0	10.3±1.3	9.4±1.8	11.7±3.2	0.37*
18:1(n-7)	6.6±0.2	6.9±0.3	7.0±0.8	7.1±0.2	7.8±0.5	6.0±0.4	7.2±0.4	7.0	10.0±0.5	6.3±0.1	8.9±0.8	5.1	7.2±1.2	5.9±1.9	7.4±1.1	7.0±0.5	7.0±0.9	0.04
18:2(n-6)	1.2±0.2	1.2±0.1	1.5±0.1	1.6±0.3	1.3±0.2	1.8±0.1	2.0±0.3	1.5	2.9±0.2	3.1±0.1	1.9±0.4	2.5	2.6±0.1	3.0±0.4	2.8±0.2	2.8±0.5	2.9±0.2	0.72*
18:3(n-6)	0.2±0.1	0.2±0.1	0.4±0.1	0.2±0.1	0.2±0.0	0.3±0.0	0.3±0.0	0.2	0.2±0.0	0.1±0.1	0.2±0.1	0.0	0.2±0.2	0.0±0.1	0.1±0.1	0.1±0.1	0.1±0.1	0.41*
18:3(n-3)	0.3±0.0	0.3±0.1	0.2±0.0	0.3±0.1	0.4±0.1	0.6±0.0	0.6±0.1	0.5	1.0±0.2	0.7±0.1	0.6±0.1	1.9	2.7±0.1	2.5±0.5	2.7±0.9	1.5±0.7	1.4±0.7	0.56*
18:4(n-3)	0.7±0.2	0.8±0.3	0.5±0.1	0.9±0.2	0.9±0.2	2.1±0.3	1.2±0.2	1.5	1.4±0.4	0.5±0.0	1.0±0.1	4.4	4.0±1.2	2.7±0.8	2.9±1.4	2.0±0.6	2.2±1.0	0.13*
20:1(n-9)	1.2±0.1	1.3±0.1	1.4±0.1	1.2±0.2	1.1±0.3	1.1±0.1	0.8±0.1	1.2	0.5±0.2	0.3±0.0	0.9±0.1	0.9	0.6±0.1	0.6±0.2	0.5±0.2	0.5±0.1	0.5±0.2	0.67*
20:1(n-7)	0.3±0.0	0.3±0.0	0.4±0.1	0.3±0.1	0.3±0.1	0.2±0.0	0.2±0.0	0.3	0.4±0.0	0.0±0.0	0.3±0.1	0.0	0.1±0.1	0.0±0.1	0.1±0.1	0.0±0.1	0.0±0.0	0.25*
20:4(n-6)	0.3±0.1	0.4±0.1	0.5±0.0	0.6±0.1	0.4±0.1	0.5±0.1	0.4±0.0	0.3	0.5±0.0	1.3±0.2	0.5±0.1	0.6	0.5±0.2	0.6±0.2	0.6±0.3	0.7±0.2	0.8±0.4	0.39*
20:4(n-3)	0.3±0.0	0.3±0.1	0.3±0.1	0.3±0.1	0.3±0.1	0.5±0.1	0.5±0.0	0.4	0.6±0.1	0.4±0.0	0.5±0.1	0.4	0.4±0.3	0.5±0.1	0.6±0.1	0.5±0.1	0.4±0.2	0.23*
20:5(n-3)	16.1±0.9	16.0±2.2	14.9±1.3	21.4±1.9	18.6±1.3	18.3±1.2	16.7±0.8	17.0	19.6±0.9	20.5±1.5	18.9±0.2	15.4	17.7±2.9	20.2±1.6	19.3±2.6	22.2±2.3	20.2±2.4	0.37*
22:1(n-11)	1.0±0.1	1.0±0.1	1.1±0.1	0.8±0.2	0.7±0.3	0.6±0.1	0.5±0.1	1.0	0.2±0.1	0.0±0.0	0.4±0.1	0.0	0.0±0.0	0.0±0.1	0.0±0.1	0.1±0.1	0.0±0.0	0.73*
22:1(n-9)	0.1±0.1	0.1±0.0	0.0±0.0	0.0±0.1	0.0±0.1	0.0±0	0.0±0.0	0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0	0.0±0.1	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.17*
22:6(n-3)	6.4±0.3	5.9±1.0	6.0±0.7	8.8±2.4	9.2±1.5	7.8±0.7	8.8±1.1	7.9	15.1±1.5	27.8±2.4	12.4±0.1	18.6	17.5±3.3	24.4±5.0	20.2±5.7	17.5±2.8	20.5±2.7	0.85*
Others	1.3±0.2	1.0±0.2	1.2±0.1	1.4±0.1	1.5±0.2	1.4±0.2	1.7±0.2	0.9	2.4±0.4	0.9±0.1	1.6±0.1	1.8	1.9±0.5	2.0±0.6	2.0±0.5	1.3±0.3	1.1±0.5	

* $p < 0.05$.

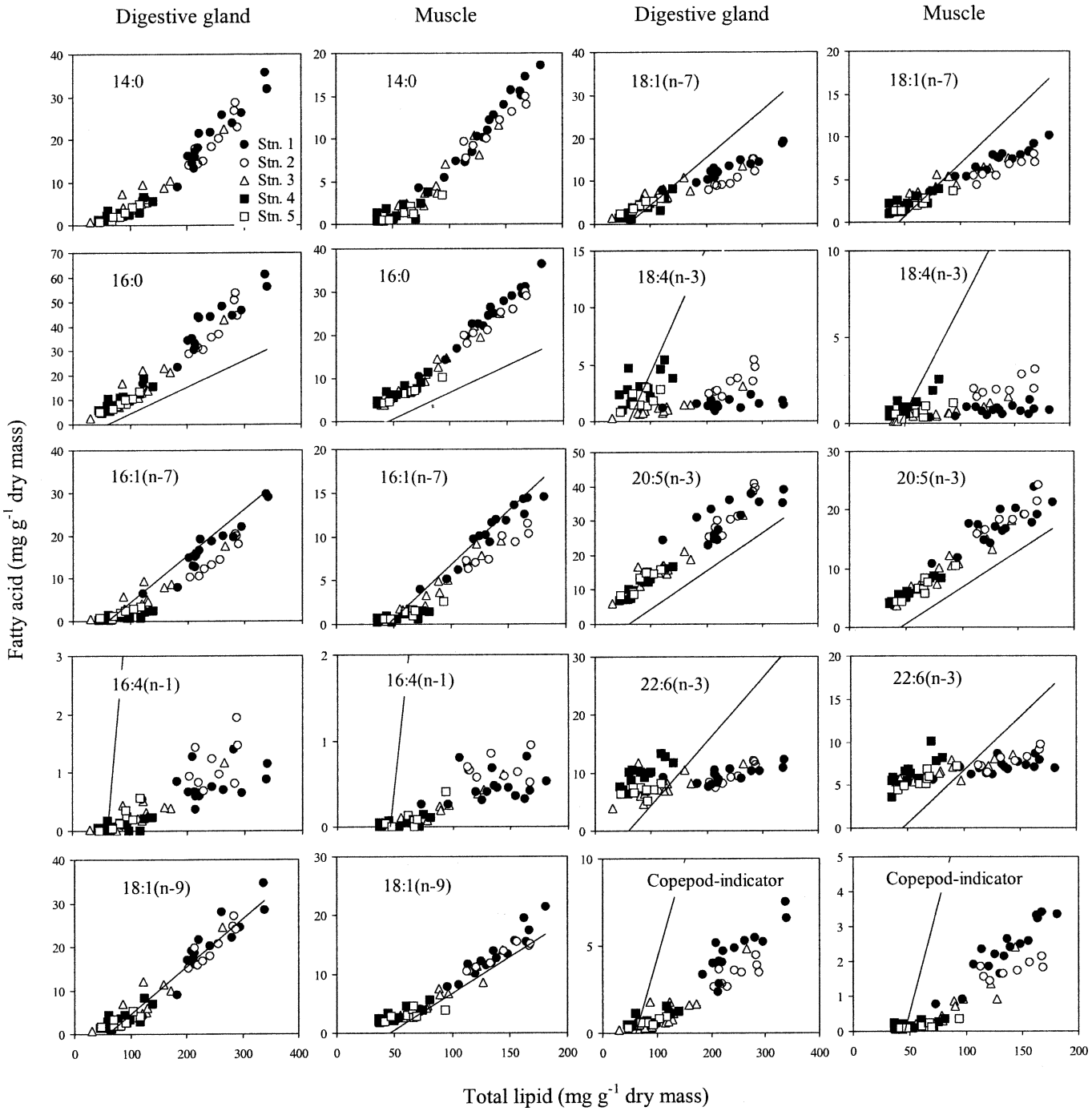

Fig. 3. *Euphausia superba*. Concentration of indicator fatty acids in relation to total lipid. A detailed look reveals station-specific differences in the content of individual fatty acid when comparing specimens with similar amount of total lipid (statistical results in Table 4). An overall look suggests differences in the dynamic of various fatty acids. Cross-plot comparison is enabled by including the data of the first fatty acid, 14:0, in each of the following plots (solid line, $r^2 = 0.95$). In krill, 14:0 is mainly abundant in triacylglycerol, and therefore indicates the increase of this storage lipid with raising total lipid content (Hagen et al. 2001). Copepod indicator = Σ (20:1(n-9); 22:1(n-11); 22:1(n-9)).

showing similar low loadings for all fatty acids. Therefore, on axis 1, krill with high fatty acid content (Sta. 1 and 2) are displaced from those with low fatty acid content (Sta. 3, 4, and 5). In the second PC, the flagellate indicators, 18:4(n-3) and 22:6(n-3) show high loadings, separating stations with krill feeding on flagellates (Sta. 2 from 1, and Sta. 4 from 3 and 5) on axis 2. In the third PC there is additional high loading for the diatom indicator

Table 4. Comparison of regressions between the amount of individual fatty acids and the total lipid content (Fig. 3) for pairs of stations where krill had similar lipid content.

Indicator fatty acid	Sta. 1 vs. Sta. 2		Sta. 3 vs. Sta. 4		Sta. 3 vs. Sta. 5		Sta. 4 vs. Sta. 5	
	D	M	D	M	D	M	D	M
14:0		1				3		
16:0		1				3		4
16:1(n-7)	1	1	3	3		3	5	5
16:4(n-1)	2	2					5	
18:1(n-9)								
18:1(n-7)	1	1	3		3	3		
18:4(n-3)	2	2	4	4	5	5	4	4
20:5(n-3)							5	
22:6(n-3)		2	4	4			4	4
Copepod indicator	1	1						

Numbers refer to the station with the higher intercept if differences were significant by analysis of covariance ($p < 0.05$). D, digestive gland; M, muscle.

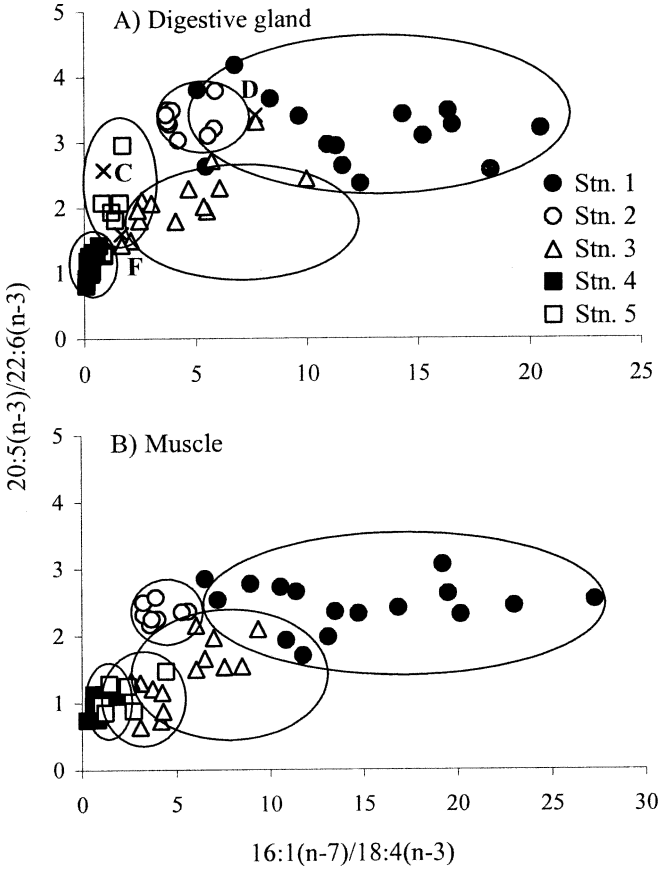

Fig. 4. *Euphausia superba*. (A) Digestive gland. (B) Muscle ratios of 20:5(n-3)/22:6(n-3) versus 16:1(n-7)/18:4(n-3) for all individual krill. Crosses marked by capital letters indicate average ratios of krill after 3 weeks' feeding on monospecific algae in the laboratory. D, diatoms; C, cryptomonads; F, dinoflagellates (original data in Alonzo et al. 2005*a*, table 6).

Table 5. Principal component (PC) analysis. Loading of indicator fatty acids from the digestive gland in PC 1, 2, and 3. The analysis was based on the amount of the fatty acids expressed as mg g^{-1} dry mass.*

	PC-1 (77%)	PC-2 (14%)	PC-3 (6%)
14:0	−0.357	0.059	−0.023
16:0	−0.359	0.037	−0.037
16:1(n-7)	−0.352	0.143	−0.093
16:4(n-1)	−0.316	−0.026	0.555
18:1(n-9)	−0.356	0.055	0.004
18:1(n-7)	−0.346	0.114	−0.143
18:4(n-3)	−0.087	−0.743	0.470
20:5(n-3)	−0.349	−0.018	0.076
22:6(n-3)	−0.155	−0.629	−0.649
Copepod indicator	−0.347	0.094	−0.115

* Copepod indicator = Σ (20:1(n-9); 22:1(n-11); 22:1(n-9)).

16:4(n-1), which again separates Sta. 2 from 1 (axis 3 not presented).

Stable nitrogen and carbon isotopes—Bulk $\delta^{13}C$ and $\delta^{15}N$ were similar for development stages and sexes from the same catch, but varied between stations (Table 6). For trophic-level interpretations, we used the $\delta^{15}N$ values. Those were highest at Sta. 1 and lowest at Sta. 3, 4, and 5 (Tukey test, $p < 0.05$). However, bulk $\delta^{15}N$ of krill alone are not sufficient to infer absolute or relative differences in their trophic positions without appropriate isotopic baselines (Post 2002). In a first approach, we related the $\delta^{15}N$ of krill to those of simultaneously sampled POM. The offsets ranged from 0.6‰ at Sta. 5 to 4.9‰ at Sta. 3 (Fig. 6). Two of the values were clearly below 3–4‰, by which consumers are typically enriched relative to their diet (Michener and Schell 1994), suggesting a fundamental problem with this approach.

Alternatively, the analysis of individual amino acids provides an internal index to trophic position, $\Delta\delta^{15}N_{glu\text{-}phe}$

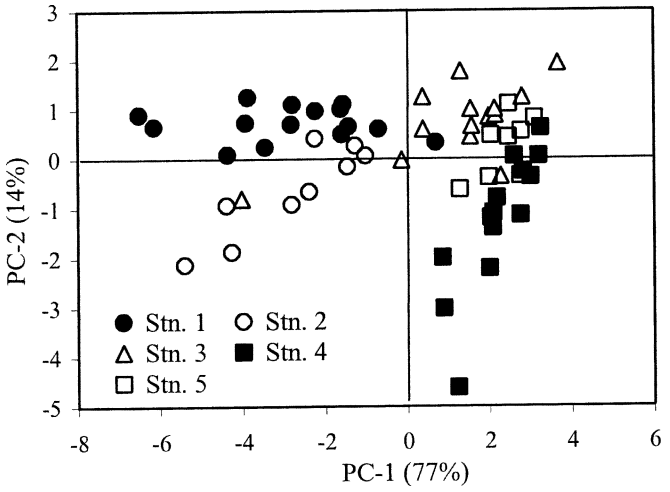

Fig. 5. *Euphausia superba*. Principal component analysis describing fatty acid profiles of the digestive glands (mg g^{-1} dry mass). Projection of individuals from different stations on PC1–PC2 plane.

Table 6. *Euphausia superba*, carbon and nitrogen isotope values in muscle tissue (‰, mean ± SD).

	Sta. 1					Sta. 2		Sta. 3				Sta. 4				Sta. 5	
	MS1 (n=5)	MS3 (n=3)	FS (n=2)	MA2 (n=3)	FA4 (n=3)	MS2 (n=8)	Juv (n=3)	MS2 (n=1)	FA2/3 (n=5)	MA2 (n=3)	FA4 (n=2)	Juv (n=1)	FA2/3 (n=4)	MA2 (n=5)	FA3/4 (n=4)	MS2 (n=5)	FA1 (n=3)
δ^{13}C	−20.4±0.4	−22.2±1.7	−19.6±0.5	−21.0±0.3	−21.0±1.5	−26.4±1.0	−25.2±0.4	−25.6	−26.3±0.5	−26.0±0.5	−25.3±0.8	−27.2	−27.6±1.1	−26.6±1	−27.7±0.6	−27.7±0.8	−26.7±0.8
δ^{15}N	5.4±0.6	5.7±0.5	5.6±0.2	5.3±0.3	5.2±0.8	4.5±0.2	3.4±0.3	3.7	3.0±0.2	3.5±0.3	3.2±0.3	3.3	3.5±0.2	3.4±0.3	4.0±0.5	3.2±0.5	3.9±0.4

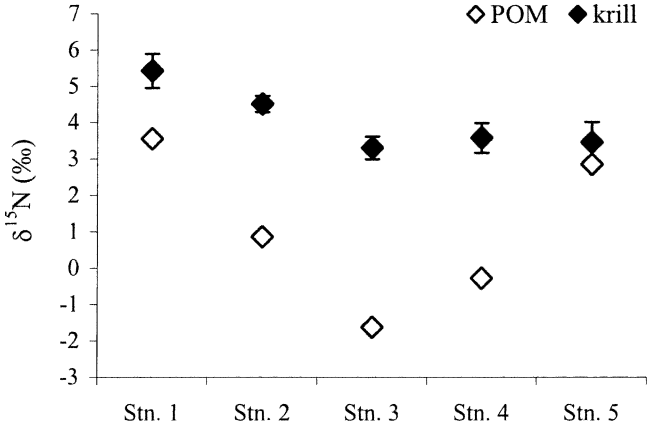

Fig. 6. *Euphausia superba*. Offset in δ^{15}N between krill and simultaneously sampled particulate organic matter (POM).

(McClelland and Montoya 2002). This approach benefits from the fact that some amino acids (e.g., phenylalanine) are not fractionated in the food web and therefore preserve isotopic information about the food web baseline directly in the consumer. Other amino acids (e.g., glutamic acid) change by ~7‰ between diet and consumer and are thus more sensitive indicators of trophic enrichment than the bulk δ^{15}N (McClelland and Montoya 2002). In this study, the δ^{15}N of individual amino acids varied between –15.2‰ and +15.6‰ (Table 7). Some amino acids showed consistently high (e.g., glutamic acid, alanine, aspartic acid) or low (e.g., glycine) δ^{15}N values, whereas others varied between stations (e.g., valine). The δ^{15}N of phenylalanine ranged from −2.2‰ to −1.1‰. Highest values were found at Sta. 1 and 5 and lowest values at Sta. 3 and 4, which resembles the pattern seen in bulk δ^{15}N of POM. The $\Delta\delta^{15}N_{glu\text{-}phe}$ values indicate that krill fed omnivorously at all stations, but that the heterotrophic component was largest at Sta. 1, 2, and 4 (Fig. 7).

Discussion

Each of the three methods—stomach content analysis, fatty acid analysis, and stable isotope measurements—was sensitive to regional differences in the diet of krill. Below, we first discuss the results and methodological problems for each approach separately. Second, we merge the findings from the three approaches to crystallize the main outcome of this study and to illustrate the unique contribution of each method. Finally, we link our information on food sources to simultaneously measured growth rates (Atkinson et al. 2006), which can be seen as an indicator of krill's benefit from the diet.

Stomach content—Barkley (1940) did the pioneering work on stomach content of Antarctic krill. Even though his identifications were restricted mainly to diatoms, the regional coverage, the number of krill analyzed (~1,550 ind. compiled into 172 samples) and the thoroughness of the analysis are exceptional. Barkley's main results were that (1) regional differences in the stomach content of krill reflect changes in the plankton of the water column,

Table 7. *Euphausia superba*, δ^{15}N of individual amino acid (‰).

Amino acid	Sta. 1	Sta. 2	Sta. 3	Sta. 4	Sta. 5
Alanine	15.1±0.5	15.4±0.7	12.6±0.6	14.6±0.3	14.8±0.3
Aspartic acid	11.0±0.3	9.8±0.3	9.0±0.5	10.0±0.2	10.2±0.1
Glutamic acid	15.6±0.4	14.6±0.6	12.9±0.1	13.8±0.1	13.7±0.2
Glycine	−3.8±0.3	−3.9±0.4	−5.7±0.8	−4.8±0.4	−4.1±0.6
Histidine	−1.9±1.2	−4.9±2.6	−3.9±1.0	−0.4±0.4	−0.4±0.9
Isoleucine	3.8±1.3	3.3±0.8	2.8±1.6	4.8±1.4	7.0±0.9
Leucine	9.1±1.2	8.8±0.7	8.3±1.0	10.5±0.3	11.0±0.5
Lysine	0.5±0.5	−3.5±2.1	−1.1±0.4	0.9±0.1	−0.2±0.7
Methionine	−1.7±0.9	−3.9±1.2	−2.9±0.9	−2.8±0.5	−1.7±0.2
Phenylalanine	−1.2±0.7	−1.7±1.0	−2.0±0.7	−2.2±0.7	−1.1±0.4
Proline	5.5±1.0	4.8±1.3	6.6±0.7	9.5±0.5	9.8±0.4
Serine	−1.4±0.2	−1.1±0.6	−3.0±0.3	−2.4±0.4	−1.5±0.2
Threonine	−1.2±0.8	−3.3±1.0	−4.1±0.8	−6.1±1.1	−6.5±0.8
Tyrosine	4.8±0.4	3.9±1.2	3.0±0.3	3.9±0.4	4.3±0.3
Valine	−14.1±1.3	−15.2±1.8	−13.4±2.0	−6.2±1.6	−0.8±0.5

For each station, individuals were pooled into one sample, two derivates were prepared, and each derivate was analyzed three times (mean ± SD). Aspartic acid includes asparagines; glutamic acid includes glutamine.

(2) large (4–6 cm) and small (1–4 cm) krill do not differ in their diet, (3) the prominent food items are small, smooth diatoms including genera *Fragilariopsis*, *Coscinodiscus*, *Actinocyclus*, *Distephanus*, *Asteromphalus*, and *Biddulphia*, and (4) large, spiny diatoms such as *Corethron* spp. and *Chaetoceros* spp. are less suitable. Some of these findings have since been debated, but they are supported by our results, as we discuss below.

Regional differences in krill's stomach content were also observed in the present study. Near South Georgia (Sta. 1), stomachs contained high numbers of *Eucampia antarctica*, a species that characteristically blooms in coastal regions (e.g., Garibotti et al. 2003). By contrast, krill from the ice edge (Sta. 2) were feeding on *Fragilariopsis kerguelensis, F. curta*, *Pseudonitzschia* spp., and some discoid diatoms, which typify marginal ice-edge blooms (e.g., Kang et al. 2001). Stations from the central and western Scotia Sea had lower Chl *a* concentrations and higher proportions of small phytoplankton. The stomach content was characterized by small discoid diatoms (Sta. 3), strongly macerated diatom debris with few intact cells (Sta. 4), or broken frustules of large discoid diatoms (Sta. 5). Likewise, Barkley (1940) reported empty stomachs or the dominance of *Coscinodiscus* spp. for some krill samples, while *Fragilariopsis* spp. were usually the most abundant diatoms in the stomachs.

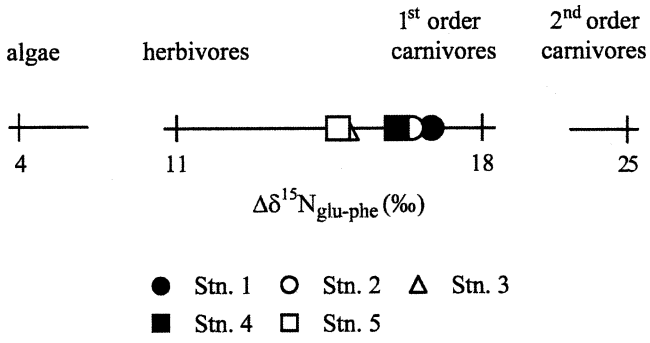

Fig. 7. *Euphausia superba*. Values of $\Delta\delta^{15}N_{glu\text{-}phe}$ in krill from different stations are represented on a scale of trophic positions. According to McClelland and Montoya (2002), phytoplankton has a $\Delta\delta^{15}N_{glu\text{-}phe}$ value of 4‰, and there is a 7‰ increment for each trophic level.

Body mass and sex had only minor effects on the diet of krill. Younger developmental stages had often less material in their stomachs than older stages, but the appearance of characteristic diatom species and the proportion of various food categories were similar within one school.

More debated is Barkley's (1940) conclusion that krill avoid feeding on large spiny diatoms. Feeding experiments show a preference for large diatoms, including the genera *Chaetoceros* and *Corethron* (Meyer and El-Sayed 1983; Granéli et al. 1993), but field studies on gut content have suggested their rejection (Hopkins and Torres 1989; Perissinotto et al. 1997). We found krill feeding on *Rhizosolenia* spp. (distinctive by their terminal spine) at Sta. 2, where a mixture of diatom species was available. In contrast, krill stomachs contained very little fresh diatom material at Sta. 4 and 5, even though *Corethron* spp. was highly abundant in the water column (Table 1). This suggests that *Corethron* spp. alone did not trigger feeding.

Hopkins and coworkers were first to describe the consistent appearance of proto- and metazoan remains from krill stomachs and therefore to illustrate their omnivory (Hopkins 1985; Hopkins and Torres 1989; Lancraft et al. 1991; Hopkins et al. 1993*a*,*b*). Those studies were carried out from autumn to spring in the Scotia and Weddell Seas, and showed krill regularly feeding on tintinnids, dinoflagellates, radiolarians, silicoflagellates, invertebrate eggs, coelenterates, copepods, and euphausiid debris in addition to diatoms. Other authors have since confirmed these food sources for krill (e.g., Buck et al. 1992; Nishino and Kawamura 1994; Perissinotto et al. 1997). However, most of these studies do not allow a quantitative comparison of identified autotrophs versus heterotrophs, e.g., diatoms and protozoan or metazoan. This is because (1) the occurrence of various food categories was recorded, but items were not counted,

(2) only small, common items were counted reliably, or (3) all items were counted, but numbers have not been transferred to an index of biomass.

Our analysis enables a quantitative assessment of items preserved in the stomach because we scanned subsamples for common items, the complete sample for rare items, and included morphometric measurements to estimate their volumes. Some krill stomachs contained up to 400 tintinnids and 350 heterotrophic dinoflagellates, but numerically, protozoans never contributed more than 2% to the total. Their importance only appears when taking differences in dimension into account: at three of the stations, protozoans accounted for 5–15% of the total identified volume and at two stations for 40–70%. Even though volumes can only be a rough indicator of assimilated matter and soft items were not included in these calculations, the data strongly suggest that protozoans are important for krill nutrition in summer.

In addition to phytoplankton and protozoans, we found occasionally thousands of krill setulae in the stomachs of *Euphausia superba*, while the number of copepod remains was consistently low regardless of their concentration in the water column (Table 1). Even though krill has been seen to feed on copepods in the field (Hopkins et al. 1993*a*; Nishino and Kawamura 1994; Atkinson et al. 2002), it was never in such high amounts as observed in laboratory experiments (Price et al. 1988; Granéli et al. 1993; Huntley et al. 1994). Even though *E. superba* is able to feed raptorially, in situ, it is not so prevalent as for some other euphausiids: adult *Meganyctiphanes norvegica* (~0.5 g wet mass), for instance, can contain up to 150 mandibles per stomach with a maximum width of 170 μm (unpubl. data; Båmstedt and Karlson 1998), whereas the larger *E. superba* (~1.5 g wet mass) contained maximally five mandibles with a width of up to 100 μm (present study; Atkinson et al. 2002).

This difference between the two species holds true also for their feeding on euphausiids. Debris of euphausiid molts has been found in the stomachs of *E. superba*, but no eye fragments, i.e., ommatidia (present study; Hopkins et al. 1993*b*), whereas *M. norvegica* contained numerous ommatidia indicating their feeding on whole individuals (unpubl. data; Mauchline 1980). In general, it seems that *E. superba*'s ingestion of molt debris is related to the amount of phytoplankton available, as Hopkins (1985) suggested for various zooplankton and micronekton species. At Sta. 4 and 5, krill had relatively little fresh diatom material in their stomachs, but some individuals contained large numbers of setae and loose setulae. Such ingestion of molts might support the energy and nutrient budget when other sources are rare.

Fatty acids—Fatty acid analyses of freshly caught krill have shown compositional differences between developmental stages and sexes (Clarke 1980; Virtue et al. 1996; Stübing et al. 2003), between seasons and years (Hagen et al. 2001; Phleger et al. 2002) as well as between regions (Mayzaud 1997). However, site-to-site comparisons of fatty acid profiles of POM and krill, to reveal their feeding habits, are rare (Cripps et al. 1999). Cripps et al. (1999) found krill feeding on diatoms when large diatoms were abundant and to consume zooplankton or starve when the algal biomass was low and small cells were dominant.

Our results agree with those of Cripps et al. (1999) in two important aspects. First, fatty acids profiles of krill can indeed reflect distinct food regimes in the field. Second, the effect of different diets can be seen despite differences due to sex or maturity stage. However, unlike Cripps et al. (1999) who stated that krill was not feeding on flagellates even when they were prominent, we found local dominance of flagellates versus diatoms to be clearly reflected in the fatty acids of krill. In an intensive diatom bloom, krill had highest ratios of diatom versus flagellate indicators (Sta. 1), whereas ratios were lowest when phytoplankton was less abundant and dominated by flagellates (Sta. 4). Krill from other stations had intermediate ratios, feeding on neither diatoms nor flagellates to a large extent (Sta. 3 and 5) or substantially on both (Sta. 2).

In this study, PCA labeled the flagellate indicators 18:4(n-3) and 22:6(n-3) as most important in separating krill from various stations. Likewise, Hagen et al. (2001) found seasonal changes in the algal community to be accompanied by differences in the fatty acid profile of krill, especially in 18:4(n-3). Stübing et al. (2003) recommended the use of 18:4(n-3) as a trophic indicator, as it is a non-essential fatty acid and rapidly metabolized when not replaced from the diet. In contrast, 22:6(n-3) is essential for structure and function of biomembranes and therefore efficiently retained in the organism, which could limit its suitability as a trophic indicator (Stübing et al. 2003). Nevertheless, we found significant differences in the concentration of 22:6(n-3), even for krill with similar amounts of total lipid. Individuals from Sta. 4 had about one-third more 22:6(n-3) in the digestive gland than those from Sta. 3 and 5, which suggest some accumulation of 22:6(n-3) when abundant in the diet. We conclude that the high amounts of 22:6(n-3) derived mainly from the ingestion of dinoflagellates, which have usually higher proportions of 22:6(n-3) than cryptophytes or prymnesiophytes (Dalsgaard et al. 2003). Microscopic analysis of a water sample confirmed high numbers of small heterotrophic dinoflagellates at Sta. 4 (Table 1).

Local differences were also found for the concentration of the diatom indicators 16:1(n-7) and 16:4(n-1) in krill. Comparing the two stations rich in diatoms, one indicator showed higher values in krill from Sta. 1, while the other was higher at Sta. 2. This illustrates that the amount of certain indicator-fatty acids in the diet might vary with phytoplankton taxonomy and conditions (Virtue et al. 1993). Nevertheless, the high 16:1(n-7)/18:4(n-3) ratios and the generally high amounts of 16:4(n-1) suggest that krill relied on diatoms at both sampling sites. Likewise, a study from the Indian sector of the Southern Ocean pointed to the importance of 16:1(n-7) and 16:4(n-1) for separating krill with different feeding history (Mayzaud 1997).

Krill also varied in their content of C_{20} and C_{22} monounsaturated fatty acids, characteristic of copepods such as *Calanoides acutus*, *Calanus propinquus* and *Oithona similis* (Dalsgaard et al. 2003). This would suggest that individuals from Sta. 1 consumed more copepods than those from Sta. 2. However, application of these carnivory

indicators is controversial. On one hand, laboratory experiments have shown that the proportion of those fatty acids increases when krill are feeding on copepods instead of algae (Stübing et al. 2003). On the other hand, their generally low amounts in krill (< 2% of total fatty acids), suggest their poor assimilation from food or fast catabolism, and thus limited suitability for quantitative evaluation (Stübing et al. 2003). An ultimate test would be a calibration experiment relating the amount of 20:1 and 22:1 fatty acids in the diet to those accumulated in krill.

These site-to-site differences, observed for a variety of indicator-fatty acids, contrast with the suggestion that krill maintain a specific fatty acid pattern independent of their food (Hagen et al. 2001; Stübing et al. 2003). Krill fatty acids obviously reflect changes in diet in some studies (Cripps et al. 1999; Alonzo et al. 2005*a*) but not in others (Cripps and Hill 1998; Stübing et al. 2003). Explanations for a weak influence of diet on krill fatty acid profiles are the loss of information by analyzing lipids in whole krill (Alonzo et al. 2005*a*) or low feeding activity and the buffering effect of large quantities of storage lipids (Stübing et al. 2003). Below we examine our results in the context of these arguments.

Alonzo et al. (2005*a*) observed marked changes in the fatty acid composition of the digestive gland but not in the remaining body, and proposed the digestive gland to be the major repository of trophic signals in krill. However, we found fatty acids in digestive gland and muscle to show the effects of diet in a very similar manner. Also, the argument of storage lipids buffering the incorporation of trophic signals (Stübing et al. 2003) seems not to hold in general: krill of Sta. 1 and Sta. 2 showed significant differences in their fatty acid composition even when the lipid content was high. More likely, seasonal differences in krill's physiology enabled reflection of trophic signals in our study but not in that, for example, of Stübing et al. (2003). We sampled krill in summer when individuals were feeding and growing rapidly (Atkinson et al. 2006), allowing the incorporation of fatty acids from the diet. In contrast, Stübing et al. (2003) studied krill already adjusted to winter conditions, with low feeding rates not supporting further lipid accumulation. Indeed, laboratory experiments have suggested that the strength of dietary signals in krill depends mainly on their feeding rates (Alonzo et al. 2005*a*).

Even though high lipid content does not necessarily hinder the accumulation of trophic indicators, our results suggest that the fatty acid profile of krill is to some extent affected by the total lipid content (Fig. 2). First, lipid-poor individuals miss out on those indicator-fatty acids that are mainly incorporated in triacylglycerols, but rarely in phospholipids (Hagen et al. 2001; Stübing et al. 2003). As primary depot lipid, triacylglycerols become only accumulated in krill at lipid levels >5 % of dry mass (Hagen et al. 1996). This explains why fatty acids such as 16:1(n-7) and 16:4(n-1) were not present in individuals with low lipid content (this study; Hagen et al. 2001).

Second, the accumulation of individual fatty acids differed: some increased sharply with lipid content (e.g., 16:0, 20:5(n-3)), while others increased moderately (e.g., 18:1(n-7)) or were rather independent of lipid content (e.g., 22:6(n-3)). Probably the nature of these relationships reflects differences in the dynamics of various fatty acids rather than a different diet. Kattner and Hagen (1998) and Hagen et al. (2001) also plotted the concentration of individual fatty acids versus the total amount of lipids, and found, as in this study, steeper slopes for 16:0 than 14:0, for 18:1(n-9) than 18:1(n-7) and for 20:5(n-3) than 22:6(n-3). It has been hypothesized that the concentration of 22:6(n-3) is tightly regulated in copepods, euphausiids and fish to realize special properties related to the animals' mobility (e.g., Scott et al. 2002).

A clear demonstration of the different dynamics of various fatty acids is only possible when lipid-poor and lipid-rich krill have been raised on the same algae, e.g., by offering different concentrations. The resulting curve of fatty acid concentration versus total lipid content would enable us to separate effects of lipid content from those of diet. Without this, comparisons should be restricted to individuals with similar lipid content (Stübing et al. 2003). Differences in fatty acid ratios should be backed up with absolute amounts of fatty acids and interpreted with care.

Stable isotopes—An appropriate measurement of the isotopic baseline is essential for sensing small differences in trophic position. These could be external references like simultaneously sampled POM or well-studied herbivores (Gurney et al. 2001, Post 2002), or internal references inherent in some amino acids (McClelland and Montoya 2002).

In this study, the δ^{15}N of POM was not suitable as an isotopic baseline for krill. Within 5 weeks of sampling across the Scotia Sea and at South Georgia, the δ^{15}N of POM varied by ~10‰, but those of krill by only ~2‰ (present study and unpubl. data). Such differences in the range of δ^{15}N have been found previously for POM and krill, and might reflect their integration times (Rau et al. 1992; Schmidt et al. 2003). The δ^{15}N of phytoplankton-dominated POM can respond to rapid variations in the primary nitrogen source or conditions for fractionation (Post 2002), while krill's isotopic equilibration with a new diet can take several weeks (Frazer et al. 1997; Schmidt et al. 2003). Even copepods might not be a sufficient reference for krill, as they are more sensitive to changes in δ^{15}N of primary producers than adult krill (Schmidt et al. 2003).

As an alternative approach, we analyzed δ^{15}N values of individual amino acids. The basic assumption is that some amino acids do not change their isotope signature when passing through the food web (e.g., phenylalanine), while others become strongly fractionated (e.g., glutamic acid). Their relationship supplies an internal index of trophic position, $\Delta\delta^{15}N_{glu\text{-}phe} = \delta^{15}N_{glu} - \delta^{15}N_{phe}$ (McClelland and Montoya 2002). Applied to our data, the index confirmed krill's omnivory, but also indicated regional differences in the importance of heterotrophic food. At two of the stations, the $\Delta\delta^{15}N_{glu\text{-}phe}$ were similar to values previously found in male and female krill (~14.5‰, Schmidt et al. 2004), while values at the remaining stations were ~1–2‰ higher.

In conclusion, the $\Delta\delta^{15}N_{glu\text{-}phe}$ index seems to be a sensitive tool for trophic studies, enabling us to distinguish about one-third of a trophic level difference between krill schools in the Scotia Sea. However, distinction between various heterotrophic food sources is not

possible from $\delta^{15}N$ values. Excretion of isotopically light nitrogen, the main process causing food web enrichment in $\delta^{15}N$, is common to metazoans (Wada et al. 1987) and protozoans (Hoch et al. 1996). Similar to zooplankton, exponentially growing flagellates and ciliates show a 3‰ to 5‰ difference in $\delta^{15}N$ between excreted ammonium and biomass (Hoch et al. 1996). Thus, krill feeding on herbivorous protozoans or herbivorous copepods might have similar $\delta^{15}N$ offsets from the baseline.

Comparison between methods—One aim of our study was to compare the results from different dietary methods. This can be a problem under dynamic and advective field conditions, because each method integrates food source information over different timescales. However, we found the methods to match well across the five stations and to give a similar overall result, indicating a substantial contribution of heterotrophic food to the diet of krill in summer. This broad agreement might reflect the specific conditions of our study. Firstly, in the weeks before and during the survey, there was a consistent large-scale pattern of phytoplankton distribution with low Chl *a* western and central areas and blooms in the east (unpubl. SeaWiFS data). Secondly, high feeding activity and growth potential of the krill supported a rapid incorporation of new food indicators.

However, the methods differ not only in their integration time, but also in their sensitivity to particular food items and in the complexity of data interpretation. Stomach content and fatty acids, for instance, are sensitive to different types of heterotrophic food. The nutritional importance of tintinnids and large thecate dinoflagellates was revealed by microscopic analysis, that of athecate heterotrophic dinoflagellates by their fatty acids. Regarding feeding on diatoms, both methods showed similar regional trends, with high amounts at Sta. 2 and lower amounts at Sta. 3, 4, and 5. Station 1 was an exception, as tissues had a high content of diatom-indicating fatty acids, but relatively few diatoms were seen in the stomach. Possibly, iron-replete conditions at South Georgia favored weakly silicified diatoms (Smetacek et al. 2004), which are hard to distinguish in the stomach. The "green mush," regularly found in krill from Sta. 1, supports this interpretation. Thus, the results of stomach content and fatty acids analysis were complementary for heterotrophic food sources, and supportive in terms of feeding on diatoms.

The $\Delta\delta^{15}N_{glu\text{-}phe}$ values were clearly higher than expected from purely herbivorous feeding and thus support the other two methods on the importance of heterotrophs. However, more detailed data interpretation could be misleading without additional information from other approaches. For example, if taken alone, the high $\Delta\delta^{15}N_{glu\text{-}phe}$ might suggest that herbivory was minor in krill. This contradicts the other two methods. A possible explanation is that some of the heterotrophic food organisms were themselves omnivorous or carnivorous, causing high $\Delta\delta^{15}N_{glu\text{-}phe}$ even when phytoplankton was an important food source. This might be especially relevant for krill feeding within microbial food webs, which are often characterized by numerous trophic linkages (e.g., Stoecker et al. 1995).

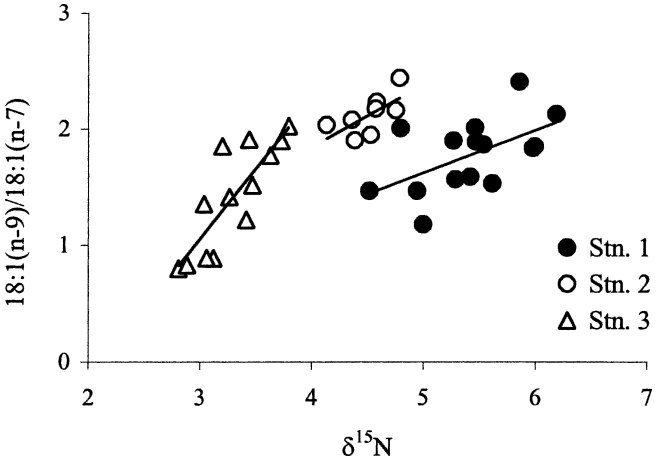

Fig. 8. *Euphausia superba*. Individual differences in the fatty acid ratio 18:1(n-9)/18:1(n-7) and $\delta^{15}N$ values. The relationship is significant positive for all three stations ($p < 0.05$, linear regression).

The $\Delta\delta^{15}N_{glu\text{-}phe}$ is not specific to any particular heterotrophic food source and distinction between copepods and protozoans is only possible from stomach content analysis. Here we suggest high $\Delta\delta^{15}N_{glu\text{-}phe}$ to reflect mainly feeding on protozoans, as copepod remains were rare. The highest $\Delta\delta^{15}N_{glu\text{-}phe}$ cooccurred with a high abundance of tintinnids and thecate dinoflagellates at Sta. 1, and with the ingestion of athecate dinoflagellates at Sta. 2 and 4.

To compare isotope and fatty acid indices directly, we related the $\delta^{15}N$ of individual krill to their fatty acid ratio 18:1(n-9)/18:1(n-7). The ratio 18:1(n-9)/18:1(n-7) is frequently used to estimate the degree of carnivorous versus herbivorous feeding (Dalsgaard et al. 2003). The basic assumption is that 18:1(n-7) represents feeding on phytoplankton, while metazoan and some protozoans contain more 18:1(n-9) (Falk-Petersen et al. 2000; Broglio et al. 2003). At three of the stations, there was a positive correlation between $\delta^{15}N$ and the fatty acid index of carnivory (Fig. 8), while relationships with maturity stage, mass, lipid content, other fatty acids or their ratios were not significant for more than one station (data not presented). This result has two important implications. Firstly, the repeated positive relationships between independent $\delta^{15}N$ and 18:1(n-9)/18:1(n-7) values raises general confidence in their application as trophic indicators. Secondly, it suggests that individual krill from the same school had different feeding histories.

Profound differences in feeding history within a school are intriguing. They could be related to different origins of krill if schools disperse and form rapidly (e.g., Hamner and Hamner 2000). Alternatively, they could indicate individual differences in trophic level if krill remain within the same school (e.g., Clarke and Morris 1983). Our data support the latter because at all three stations, there was a continuum of 18:1(n-9)/18:1(n-7) versus $\delta^{15}N$ values instead of clustered points, which suggests a spectrum of diets within a school rather than two recently merged schools. Further, even in a school of subadult males with very similar body mass, lipid content and

Table 8. *Euphausia superba*, growth rates, uptake of various food sources, and processing of food at different stations.

	Sta. 1	Sta. 2	Sta. 3	Sta. 4	Sta. 5
Growth rates (mm d^{-1})	0.120	0.306	0.039	0.101	0.048
Small flagellates—a, b	Low	High	Low	High	Medium
Diatoms—a, b	High	High	Medium	Low	Low
Large dinoflagellates—a	High	Medium	Low	Low	Low
Tintinnids—a	High	Low	Low	Low	Medium
Copepods—a	Low	Low	Low	Low	Low
Krill molts—a	Low	Low	Low	Medium	Medium
Heterotrophs—c	High	High	Medium	High	Medium
Index of stomach passage	Medium	Low	High	High	High
Weight of digestive gland	Low	High	Low	Medium	Low

Growth rates given in Atkinson et al. (2006) have been normalized for 40-mm body length. Original data have been transferred into relative criteria, "low," "medium," and "high" to simplify presentation. Letters indicate the applied method on which the estimates were based on (a) stomach content analysis, (b) fatty acid analysis, and (c) stable isotope measurements.

size of digestive gland (Sta. 2), two individuals differed by 0.6‰ in $\delta^{15}N$, 1.7‰ in $\Delta\delta^{15}N_{glu\text{-}phe}$, 0.2 in 18:1(n-9)/18:1(n-7) and 20 tintinnids in their stomachs. Thus, intra-school variability in diet was distinguished by the application of multiple dietary methods.

In conclusion, our study shows that no method is necessarily better than another as all of them deliver specific information. Microscopic analysis of the stomach content enables the identification of organisms with hard structures to species or genus level and gives additional information on their size and degree of digestion. This might provide insights on feeding habitat and behavior. In contrast, fatty acids and $\delta^{15}N$ indicate broad taxonomic groups or trophic level. However, being sensitive also to delicate food items, these bioindicators are useful to evaluate the importance of diatoms versus dinoflagellates or autotrophic versus heterotrophic food. A combination of those methods is a powerful tool for studying trophic interactions.

Linking diet to growth rates—Growth rates are an indicator of the net benefit an organism obtains in a specific environment. Despite this, few studies have related in situ growth rates of *Euphausia superba* to their nutritional history, either indicated by ambient phytoplankton communities (Ross et al. 2000, Atkinson et al. 2006) or by krill's content of specific fatty acids (Pond et al. 2005). These studies all stress the importance of diatom blooms for high growth rates in krill. Here we link, for the first time, the food environment to detailed information on krill diet and growth rates (Tables 1 and 7). The results suggest that the notion of diatom blooms promoting krill growth is actually more complex. Firstly, rapidly growing krill in a diatom bloom (Sta. 2) contained also a strong heterotrophic component to their diet, secondly, diatom blooms near the retreating ice edge (Sta. 2) and in coastal waters (Sta. 1) did not support the same high growth rates, and thirdly, feeding on a flagellate-dominated community also enabled krill to sustain medium growth rates (Sta. 4).

These findings can be explained in the context of food quality and trophic upgrading by protozoans. Both Sta. 1 and 2 were characterized by a diatom bloom and krill was feeding on a mixed diet including diatoms as well as various protozoans. However, growth rates were very high at Sta. 2, but only moderate at Sta. 1. Slower stomach passage and small digestive glands at Sta. 1 point to lower feeding rates and less intensive synthesis of digestive enzymes and subsequent uptake of nutrients (Table 8). These differences in processing of food suggest that the contrasting growth rates were at least partly related to nutrition.

At Sta. 4, growth rates of krill were also lower than at Sta. 2, but overall among the highest rates measured at the 24 stations of the survey (Atkinson et al. 2006). This is surprising, because almost all Chl *a* was in the small size fractions and the total concentration was only moderate ($\sim$0.6 μg Chl *a* L^{-1}). Cryptophytes and single-cell prymnesiophytes were the main autotrophs, but spindle-shaped heterotrophic dinoflagellates of 10–15 μm outnumbered similar-sized autotrophs by a factor of $\sim$7. High amounts of flagellate-indicating fatty acids in krill suggest that they were feeding on this community. Thus, whereas Ross et al. (2000) observed diatoms to be superior food to prymnesiophytes and cryptophytes, we found that a flagellate-dominated assemblage supported krill feeding and growth in a similar manner to a diatom-dominated system.

Station 5 was also flagellate dominated, but the Chl *a* concentration and the proportion of heterotrophic dinoflagellates were lower than at Sta. 4. Krill contained lower levels of flagellate-indicating fatty acids and had lower growth rates than at Sta. 4. This suggests that the presence of heterotrophic dinoflagellates plays an important role for the benefit krill obtain from flagellate-dominated assemblages. Some autotrophic flagellates may be of low food quality for krill because of their small size and deficiency in essential fatty acids (Ross et al. 2000). As intermediate prey, heterotrophic dinoflagellates can upgrade the quality of these autotrophs, being larger and enriched in essential fatty acids such as 22:6(n-3) (Tang and Taal 2005).

In a model of krill transport across the Scotia Sea, Fach et al. (2002) found that subadult and adult krill did not grow to the size seen at South Georgia when feeding only on phytoplankton and ice algae. The authors suggested that heterotrophic food might contribute substantially to the growth of krill (Fach et al. 2002). Our study supports this and further indicates that protozoans, rather than

copepods or other euphausiids, are the main heterotrophic food source for krill in summer.

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