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Benthic feeding by krill, *Euphausia superba* Dana, in coastal waters off West Antarctica and in Admiralty Bay, South Shetland Islands

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Abstract Diatoms in the food of krill caught in the summer in coastal waters close to the South Shetland Islands and in the summer and three winters in Admiralty Bay, King George Island were investigated. The diatoms were used as indicators of sources of krill food. Principal component analysis divided the diatom taxa into two groups, one being pelagic diatoms and from the food of krill in coastal waters, and the other being benthic diatoms and taxa from the food of krill in Admiralty Bay. All pelagic taxa of diatoms were consumed by krill. In the summer in coastal waters, benthic diatoms in krill food originated from the sublittoral. In the summer in Admiralty Bay, besides phytoplankton, diatoms were noted from the sublittoral and littoral in the food of krill. However, in the winter mostly sublittoral and epiphytic diatoms were present in krill food.

Introduction

Krill graze on phytoplankton during summer (Quetin and Ross 1991). In the Antarctic, the growing season of phytoplankton is about 120–150 days (El-Sayed and Fryxell 1993). In winter the amount of phytoplankton is low, both in coastal waters (Clarke and Leakey 1996) and in the open ocean (Garrison et al. 1991), and the sources of krill food during that period are still unclear.

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In winter, krill stomachs are much less full, indicating decreased feeding in that period (Morris and Priddle 1984; Lancraft et al. 1991). However, krill food intake is sufficient to enable it to moult (Morris and Priddle 1984), undergo ovarian development (Mauchline and Fisher 1969) and grow (Stepnik 1982). The winter food for krill may be of sea-ice community origin (Spiridonov et al. 1985; Smetacek et al. 1990). Other possible sources of krill food in winter are detritus (Kawaguchi et al. 1986) or metazoa (Nordhausen et al. 1992; Huntley et al. 1994; Nishino and Kawamura 1994).

Diatoms, which dominate Antarctic Ocean phytoplankton in periods of blooms (Clarke and Leakey 1996), in pack ice (Garrison et al. 1986) and in benthos (Gilbert 1991), are also very important as indicatory species. They are the only group of producers that can be identified down to species level and counted in various assemblages with sufficient precision to enable the comparison of their taxa and assemblages (Garrison et al. 1986). This feature of diatoms was used to investigate krill food sources.

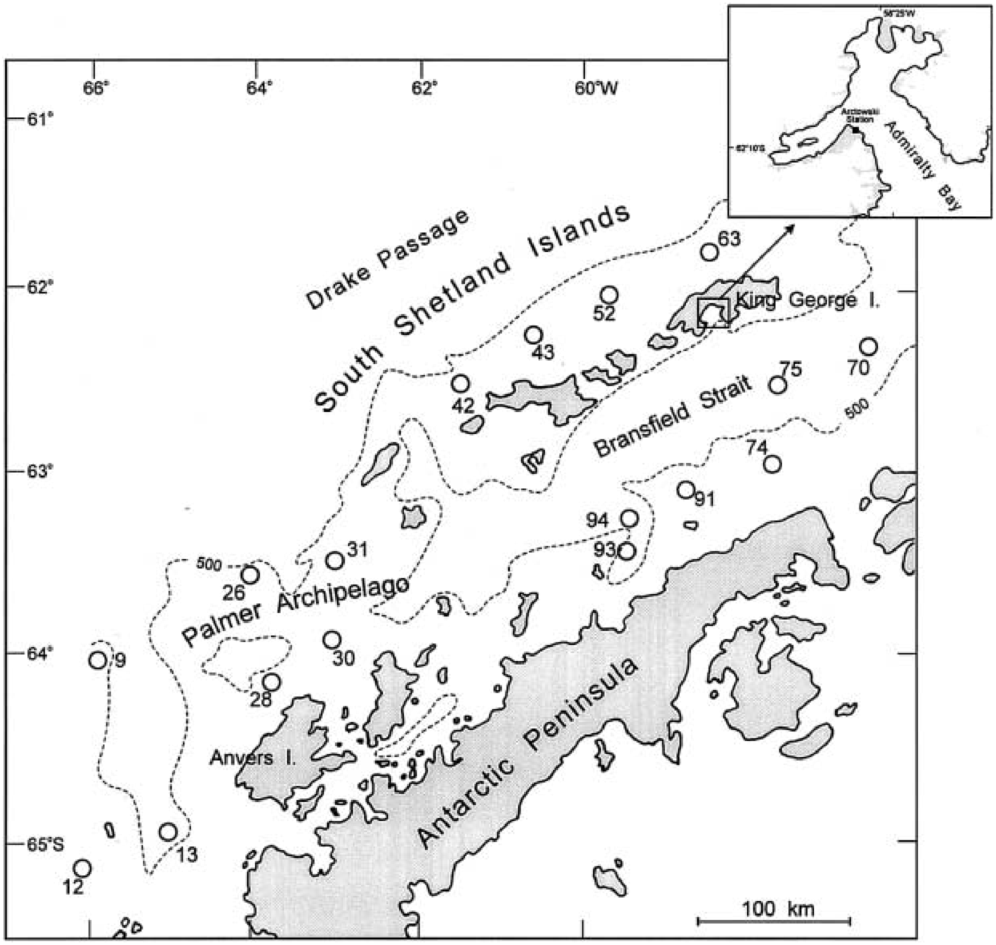
The aim of the present study was the qualitative analysis of diatoms from the food of *Euphausia superba* collected in coastal waters off West Antarctica in one summer, and from those in Admiralty Bay collected in one summer and three winters. The results of the analysis served to determine habitats that constitute sources of krill food in various regions and seasons.

Materials and methods

Specimens of *E. superba* from coastal waters were subsampled from commercial catches or Bongo net hauls from the r/v *Profesor Siedlecki* in the course of the BIOMASS-FIBEX Expedition. The food content of 72 krill specimens taken from 17 sites in the Bransfield Strait and the southern part of the Drake Passage in the period from 16 February to 11 March 1981 was analysed (Fig. 1). Diatom taxa occurring in krill stomachs of the region were listed by Ligowski (1982).

In Admiralty Bay, King George Island, South Shetland Islands krill were caught with a frame net of 1 × 0.6 m from the *Dziunia*

Fig. 1 Map of study area with stations sampled for krill



fishing cutter during the Polish Academy of Sciences expeditions to Arctowski Station. The food content of 20 krill specimens collected in February 1978, 32 specimens from 8 samples in 1984, 8 specimens from 2 samples in 1985 and 12 specimens from 3 samples in 1986, was analyzed.

Stomachs were extracted after dissecting the carapace. The stomach content was transferred to a drop of distilled water on a microscopic cover glass. The dried stomach content was moistened with 96% ethanol and embedded in Pleurax, a synthetic resin with a high refractive index. The contents of stomachs were studied using a MBB-1A (LOMO, Leningrad) optical microscope with ×60 and ×100 oil immersion apochromatic objectives, and an Amplival (Carl Zeiss Jena) microscope with a ×100 oil immersion planachromatic objective and Nomarski differential interference contrast (DIC). The qualitative composition was determined by identifying all the diatoms that occurred in the prepared stomachs. Frustules of larger or more delicate diatoms that occurred in the stomachs were crushed, in which case a sum of fragments that would constitute a single cell was subjectively estimated.

Admiralty Bay and the adjacent ocean are regions in which diatom diversities in the water column, pack ice and benthos are known. These data enabled the classification of taxa identified in krill food as originating from either plankton or benthos. Taxa commonly found in pack ice were classified as planktonic species. All taxa living on various substrates, e.g. epiphytes, were considered benthic. According to Tischler's (1976) classification, accidental species, i.e. occurring with a frequency $<25\%$, and constant species, with a frequency $>50\%$ of collected samples, were distinguished. Data on diatom occurrence in natural habitats were employed to compare diatom taxa from various habitats with the diatom taxa found in krill food. The comparison was carried out using principal component analysis (PCA).

Results

One hundred and five diatom taxa were recorded in *E. superba* stomachs; 60 of them were considered planktonic and 42 benthic, while the habitats of 3 taxa were indeterminable (Table 1). Fifty-three planktonic and 27 benthic diatom taxa were identified in krill caught in coastal waters. In krill caught in Admiralty Bay in the summer, 39 diatom taxa were planktonic and 33 benthic; in the krill caught in the same bay in winter, 30 diatom taxa were planktonic and 29 benthic. Thirty-six diatom taxa were constant both in coastal waters and in Admiralty Bay, of which 17 were pelagic and 17 benthic.

Actinocyclus actinochilus, *Chaetoceros* spp., *Corethron pennatum*, *Coscinodiscus* spp. and species of the genus *Fragilariopsis* were most frequently found in krill stomachs from coastal waters. Krill from coastal waters also contained a considerable number of benthic species, of which the epiphytic taxon of *Coccconeis costata* and sublittoral bottom taxa of *Paralia sol* were the most

Table 1 Diatoms found in the stomach contents of *Euphausia superba* in coastal waters off West Antarctica and in Admiralty Bay (*P* planktonic taxa; *B* benthic taxa; *IV* in 75–100% of samples, *III* in 50–75% of samples; *II* in 25–50% of samples; *I* in 1–25% of samples; *bold* letters indicate taxa stable in food of krill in at least one studied area)

Taxa	Habitat	Frequency in studied area		
		Coastal waters	Admiralty Bay	
			Summer	Winter
***Achnanthes charcotii* M. Peragallo**	**B**		**IV**	**I**
***A. groenlandica* Grunow in Cleve et Grunow**	**B**		**III**	
Achnanthes spp.	B	I	I	II
***Actinocyclus actinochilus* (Ehrenberg) Simonsen**	**P**	**IV**	**III**	**III**
Actinocyclus sp.	P	I		
Amphiprora spp.	P	I		
***Amphora* spp.**	**B**	**I**	**III**	**I**
Anaulus spp.	B			I
Arachnodiscus ehrenbergii Bailey	B		I	
Asteromphalus hookerii Ehrenberg	P	I		
A. hyalinus Karsten	P	I		
A. parvulus Karsten	P	I		
Azpeitia tabularis (Grunow) Fryxell et Sims	P	I	I	
Chaetoceros atlanticus Cleve	P	I		
Ch. bulbosus' complex	P	I		
Ch. concavicornis Mangin	P	I		
***Ch. criophilus* Castracane**	**P**	**I**	**III**	**I**
Ch. dichaeta Ehrenberg	P	I	I	
Ch. neglectus Karsten	P	I		
Chaetoceros resting spores	B			I
***Chaetoceros* spp.**	**P**	**IV**	**I**	
Cocconeis antiqua v. *tenuistriata* Van Heurck	B	I	II	I
***C. costata* Gregory**	**B**	**III**	**IV**	**IV**
C. costata v. *hexagona* Grunow	B	I		I
***C. costata* v. *kerguelensis* Cleve**	**B**		**IV**	
***C. decipiens* Cleve**	**B**	**I**	**IV**	
C. distans var. *bahusiensis* Cleve-Euler	B	I	I	
C. fasciolata (Ehrenberg) Brown	B	I	I	I
C. gautierii Van Heurck	B		I	I
C. illustris Schmidt	B		I	I
***C. infirmata* Manguin**	**B**	**I**	**IV**	**II**
***C. melchiori* Frenguelli et Orlando**	**B**	**I**	**III**	**I**
***C. orbicularis* Frenguelli et Orlando**	**B**	**I**	**IV**	**II**
***Cocconeis* spp.**	**B**	**I**	**IV**	
***Corethron pennatum* (Grunow) Ostenfeld**	**P**	**IV**	**II**	**I**
Coscinodiscus bouvet Karsten	P	I	I	
C. oculoides Karsten	P	I	I	I
***Coscinodiscus* sp.1**	**P**	**IV**	**III**	**III**
Coscinodiscus sp.2	P	I	I	
Dactyliosolen antarcticus Castracane	P	I	I	I
Diploneis spp.	P			I
Entopyla ocellata (Arn.) Grunow	B	I	I	I
Eucampia antarctica (Castracane) Mangin	P	II	I	I
***Fragilariopsis curta* (Van Heurck) Hustedt**	**P**	**IV**	**IV**	**I**
***F. cylindrus* (Grunow) Krieger**	**P**	**IV**	**I**	**I**
***F. kerguelensis* (O'Meara) Hustedt**	**P**	**IV**	**III**	**IV**
***F. oliquecostata* (Van Heurck) Heiden**	**P**	**IV**	**I**	**I**
***F. rhombica* (O'Meara) Hustedt**	**P**	**III**	**III**	**II**
F. ritscherii Hustedt	P	I		I
***F. sublinearis* (Van Heurck) Heiden**	**P**	**III**	**II**	
F. vanheurckii (M. Peragallo) Hustedt	P	I	I	I
Fragilariopsis spp.	P		I	
Gomphonema sp.	B	II	II	I
***Gomphonemopsis littoralis* (Hendey) Medlin**	**B**		**IV**	
Grammatophora angulosa Ehrenberg	B	I	I	I
Grammatophora sp.	B	I		
Haslea trompii (Cleve) Simonsen	P	I		
Isthmia enervis Ehrenberg	B			
***Licmophora gracilis* (Ehrenberg) Grunow**	**B**		**III**	I
***L. juergensii* Agardh**	**B**		**III**	**I**
Licmophora spp.	B	I	II	I

Table 1 (*continued*)

Taxa	Habitat	Frequency in studied area		
		Coastal waters	Admiralty Bay	
			Summer	Winter
Manguinea fusiformis (Manguin) Paddock	P	I		
M. rigida (M. Peragallo) Paddock	P	I		
***Navicula directa* (M. Smith) Ralfs**	**P-B**	**I**	**III**	**I**
***N. glaciei* Van Heurck**	**P-B**	**III**	**IV**	**I**
N. jejunoides Van Heurck	P-B	I	I	
N. marnieri Manguin	B	I		I
N. rhombica v. *adeliae* Frenguelli	B		I	I
Navicula spp.	P	I	I	I
Nitzschia adeliana v. *maior* Manguin	P			I
***Nitzschia/Fragilariopsis* spp.**	**P**	**IV**	**II**	
Odontella spp.	B	II	II	
***Paralia sol* (Ehrenberg) Crawford**	**B**	**II**	**III**	**III**
Pinnularia quadratarea (M. Schmidt) Cleve	B	I	I	
Pleurosigma spp.	B	I	I	
Porosira pseudodonticulata (Hustedt) Jousé	P	I	I	
Proboscia alata (Brightwell) Sundström	P	I	I	
P. inermis (Castracane) Jordan et Ligowski	P	I		
P. truncata (Karsten) Nöthig et Ligowski	P	I		
***Pseudogomphonema kamtschaticum* (Grunow) Medlin**	**B**	**I**	**IV**	**II**
Pseudo-nitzschia turgidula (Hustedt) Hasle	P		I	I
Pseudonitzschia spp.	P	I	I	I
Rhabdonema sp.	B			I
Rhizosolenia antennata (Ehrenberg) Brown	P		I	
Rh. antennata f. *semispina* Sundström	P		I	I
Rhizosolenia spp.	P	I	I	I
***Rhoicosphenia* spp.**	**B**	**I**	**III**	**I**
Rouxia sp.	B	I		
Stellarima microtrias (Ehrenberg) Hasle et Sims	P	I	I	I
Synedropsis sp.	P	I		I
Thalassionema bacillare (Heiden) Kolbe	P	I		
***T. nitzschioides* (Grunow) Mereschkowsky**	**P**	**III**	**III**	**I**
***Thalassiosira antarctica* Comber**	**P**	**I**	**III**	**I**
***Th. gracilis* (Karsten) Hustedt**	**P**	**III**	**II**	**II**
Th. gracilis v. *expecta* (VanLandingh.) G. Fryxell et Hasle	P	I	I	I
Th. lentiginosa (Janisch) G. Fryxell	P	II	I	II
Th. oliverana (O'Meara) Makarova et Nikolaev	P	I	I	
Th. perpusilla Kozlova	P	I		
Th. ritscherii (Hustedt) Hasle	P	I	I	
Thalassiosira resting spores	B			I
***Thalassiosira* spp.**	**P**	**III**		**I**
***Thalassiothrix antarctica* Schimper ex Karsten**	**P**	**III**	**III**	**II**
***Trachyneis aspera* (Ehrenberg) Cleve**	**B**	**I**	**III**	**III**
Trigonium spp.	B	I	II	I
Tropidoneis spp.	P		I	

abundant. The most frequent benthic taxa in krill stomachs from Admiralty Bay were epiphytic species of the genus *Cocconeis*, mainly *Cocconeis costata* and species from sublittoral, *P. sol* and *Trachyneis aspera*. In the summer the frequency of occurrence of benthic species originating from the bay's littoral, such as *Achnanthes charcotii*, *Achnanthes groenlandica*, *Gomphonemopsis littoralis*, *Pseudogomphonema kamtschaticum*, or species of the genus *Licmophora*, increased.

Using principal component analysis of the percentage frequency of all the diatom taxa identified in the various natural habitats and food types of krill, the sites were divided into two groups. One of them contained the diatoms of krill food from coastal waters and diatoms from the pelagic zone, including planktonic and sympagic diatoms, while the other contained diatoms of krill from Admiralty Bay and diatom taxa from benthic habitats: littoral, sublittoral and epiphytes (Fig. 2a). A similar division into site groups occurs when considering only constant species, i.e. those occurring in over 50% of all samples in a given habitat (Fig. 2b).

In some krill stomachs, fragments of setae from thoracic legs of krill were found.

In krill winter food in Admiralty Bay, large amounts of detritus, mineral particles and, also, rare spicules of sponges were noted alongside benthic diatoms. Among detritus that was impossible to identify, epiphytic diatoms frequently occurred, which suggests macroalgal origin. Fragments recognisable as macroalgae were encountered in small quantities in May and August samples.

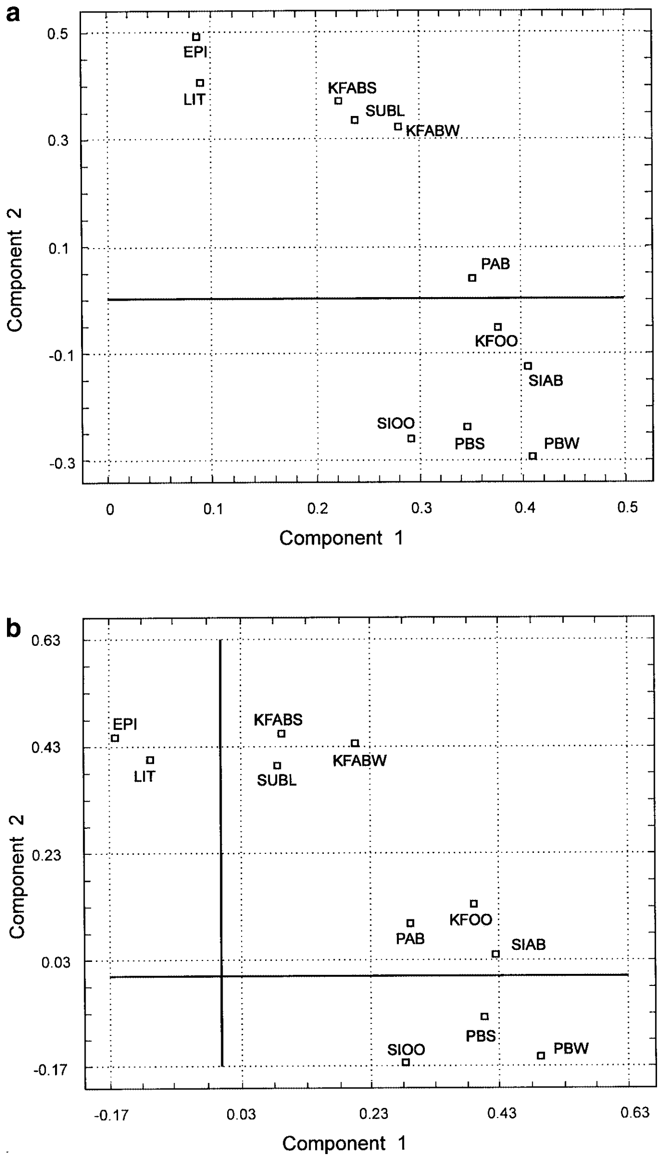


Fig. 2 Principal component analysis (PCA) using the percentage **a** of all diatom taxa, **b** of constant diatom taxa in: *PWS* plankton in the Weddell Sea, *PBS* plankton in the Bellingshausen Sea, *PAB* plankton of Admiralty Bay, *SIOO* sea ice of the open ocean, *SIAB* sea ice of Admiralty Bay, *SUBL* sublittoral, *LIT* littoral, *EPI* epiphytes, *KFOO* food of krill from coastal waters in summer, *KFABS* food of krill from Admiralty Bay in summer, *KFABW* food of krill from Admiralty Bay in winter

Discussion

Diatoms (Bacillariophyta), in addition to their role in primary production in the Antarctic marine ecosystem, are also useful as indicatory species because of their siliceous frustules. Diatoms live in every habitat accessible to krill: water column, sea ice and benthos. Finding diatoms from various habitats in krill gut contents indicates, not only that they constitute food for krill, but also implies krill are feeding on other material from that habitat.

The relatively precise data on diatom taxa eaten by krill and in what numbers, enabled the author to compare them with diatom communities of natural habitats.

In the food of krill, planktonic diatom taxa were present which are sometimes regarded as taxa avoided by krill, for example, genera *Chaetoceros*, *Dactyliosolen*, *Rhizosolenia* and *Tropidoneis* (Opalinski et al. 1997; Perissinotto et al. 1997). Small fragments of fragile frustules of these pelagic diatoms were probably not visible when using methods applied by Opalinski et al. (1997) and Perissinotto et al. (1997) for identification of krill gut content, namely water mounts and dry microscopic objectives.

A division into site groups as a result of the PCA analysis indicates the main krill food sources. The analysis also indicates that diatoms were consumed by krill mainly from the pelagic zone in coastal waters, and from the sea bottom and from macroalgae, besides the pelagic zone, in Admiralty Bay.

Krill from coastal waters, in the stomachs of which benthic diatoms occurred, were caught in sites located close to the Antarctic Peninsula, Palmer Archipelago and the South Shetland Islands. No benthic diatoms were observed in net phytoplankton collections made at the same time and close to the krill sampling sites (Kopczynska and Ligowski 1982). Benthic diatoms contributing to krill food in summer in coastal waters are diatoms originating from the sublittoral. It appears that shelf waters are regions in which krill may exploit food originating from the bottom.

A higher number of benthic diatom taxa occurred in krill collected from Admiralty Bay than in those from coastal waters. Resting spores of the typical planktonic diatoms of *Thalassiosira* and *Chaetoceros*, which were frequently found on the sublittoral bottom, were included among benthic diatoms. Benthic species growing on macroalgae and the bottom may get into the water column and occur with a high number of species and abundance there. In Admiralty Bay, Ligowski (1986) noted 30 diatom taxa typical of benthic communities among 161 identified taxa in net phytoplankton collected from March to May and in October and November. In summer phytoplankton in Admiralty Bay, only single cells of benthic diatoms were reported by Kopczynska (1993). During the summer period, benthic diatoms occurred more frequently in krill food than in phytoplankton.

The critical period for krill is winter. "It is during the winter that difficulties occur for the krill and for the scientist who wonders what krill eat". (Boyd et al. 1984) In that period krill feed, both to grow and moult (Stepnik 1982; Morris and Priddle 1984; McClatchie 1988). Various strategies of krill survival in winter are used (Quetin and Ross 1991). They include body shrinkage, lipid utilisation, exploiting food of various habitats, and a lower metabolic rate.

In winter in Admiralty Bay, benthic species, such as *Paralia sol*, *Trachyneis aspera* and the epiphyte *Cocconeis costata*, account for many of the diatoms in krill stomachs. During this season no benthic species are found in the upper water column of Admiralty Bay (Kopczynska 1993, 1996). Presumably the sea ice covering the whole or part of Admiralty Bay in winter prevents wind-driven mixing.

In summer in Admiralty Bay, food was also composed of diatoms from the sublittoral and littoral, besides phytoplanktonic diatoms, while in winter it was mainly sublittoral and epiphytic diatoms. The absence in the water column of benthic diatoms, and their simultaneous presence in krill food indicate near-bottom or on-bottom foraging of *E. superba* in Admiralty Bay in winter. Besides diatoms, large amounts of formless detritus, among which epiphytic diatoms were frequently discernible, suggest that the detritus in krill food may originate from macrophytes. The digestive enzymes in krill serve mainly to digest the polysaccharide chrysolaminaran (Turkiewicz 1995), which is the main reserve material of diatoms (Hoek et al. 1995), but an analysis of *E. superba* digestive enzymes also proved the presence of *b*-1,4-xylanases, enabling it to digest macroalgae (Turkiewicz 1995).

In winter, krill were distributed deeper than in the summer (Lascara et al. 1999), being found in layers near to the bottom (Kawaguchi et al. 1986). The possibility of krill exploiting benthic food in winter was suggested by Holm-Hansen and Huntley (1984). Kawaguchi et al. (1986) observed that krill change their habitat to the benthopelagic during winter under the coastal fast ice. Their study was based on observations of the filling and coloration of krill stomachs without any direct analysis of consumed food except for fragmentary substances and sand.

Benthic diatoms in Admiralty Bay grow down to a depth of 150 m (Ligowski 1993). Krill usually occur at a depth of 100–200 m (Siegel 1985; Godlewska 1996), but have been recorded at depths of even 400–450 m in the Weddell Sea (Gutt and Siegel 1994), 500 m in the Bransfield Strait and 1000 m in the Drake Passage (Marin et al. 1991). Thus, the whole bottom area that is colonised by benthic diatoms may be penetrated by krill.

Benthic microalgae of the Antarctic sublittoral consist exclusively of diatoms, develop all year round and their biomass rapidly increases in spring, before the phytoplankton bloom (Dayton et al. 1986; Gilbert 1991). The spring bloom of littoral benthic diatoms also occurs earlier than that of phytoplankton. At similar geographical latitudes (60–64°S), their growth after winter occurred in early October (Krebs 1983; Ligowski 1993), while the phytoplankton bloom was noticeable as late as November or even December (Krebs 1983; Ligowski 1986; Clarke and Leakey 1996).

Epiphytic diatoms reach a density of 200,000 cells/cm^2 (Thomas and Jiang 1986), or even 2,000,000 cells/cm^2 of macroalgae (R. Ligowski, unpublished data). In Admiralty Bay, macroalgae occur down to a depth of 90–100 m and cover 35% of the bay bottom (Zielinski 1990). They are a substrate of huge surface area, which is colonised by diatoms all year round (Ligowski 1993).

In Admiralty Bay, sympagic diatoms were absent in krill winter food despite their occurrence in pack sea ice in Admiralty Bay, sometimes at high densities, from as early as mid-June to the middle of October (Ligowski 1987).

Benthic food, including diatoms, proved to be an important element for krill caught in the coastal region of West Antarctica both in summer and winter, particularly in winter and in sites with scarce phytoplankton. In the period of sparse winter phytoplankton growth, krill consume epiphytic and sublittoral diatoms and other benthic organic matter.

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