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Feeding ecology of Spinocalanus *antarcticus*, a mesopelagic copepod with a looped gut

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Abstract *Spinocalanus antarcticus*, an abundant mesopelagic copepod in polar seas, has a greatly elongated and looped midgut, contrary to most other copepod species. The total gut length is 1.77, 1.86 and 1.90 times the total body length in adult females, CV and CIV, respectively. Gross morphology of the midgut is similar in all copepodite stages and adults. It is described here from specimens collected in the Arctic Ocean. In stratified samples from the deep Amundsen and Makarov Basins *S. antarcticus* showed a clear preference for the depth layer between 100 and 500 m. Generally, the guts were packed with material, but most of it was impossible to identify. In most specimens the digestive tract was filled with undefined detritus particles ("detritus balls"). They were almost spherical, heterogeneous organic aggregates of 40–100 µm diameter, with small clay-sized mineral flakes imbedded. Mineral particles in the size range of 1–10 µm were found in large quantities in the guts of many specimens. Cysts of Chrysophycea and dinoflagellates and fragments of dinoflagellates, diatoms, tintinnids and radiolarians, as well as skeletons of silicoflagellates, were rather rare; some animal remnants were also found. A high carbon/nitrogen ratio (8.9) and very high lipid content (54% of dry weight) indicated a very good nutritional state. The adaptive significance and possible feeding strategy of this deep-water copepod is discussed.

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Introduction

Primary production in the ice-covered Arctic Ocean is based on a poor and short phytoplankton bloom. A considerable part of the available organic matter is converted into fecal material and debris by herbivorous plankton already within the euphotic zone, before it sinks to depth. As a consequence, the waters below are ruled by a weak and pulsed short seasonal input of organic matter. The mesopelagic zooplankton community established there is dominated by copepods. It shows a much lower biomass and higher species diversity than the community of the epipelagic realm above (Kosobokova and Hirche 2000). The question arises how this community covers its energy demands.

Knowledge on feeding ecology, composition of food, quantitative food uptake and feeding rates of meso- and bathypelagic copepods is poor. What is known is that below the epipelagic zone carnivorous and omnivorous feeding modes prevail, and the share of omnivory increases with depth (Arashkevich 1969). Data on feeding of omnivorous/detritivorous deep-water copepods are especially rare (Arashkevich 1969; Harding 1974; Hopkins 1985; Gowing and Wishner 1986, 1992, 1998; Steinberg 1995). Experimental studies on feeding of deep-water detritivorous copepods are also quite few (Arashkevich 1975). Mostly gut contents were analyzed, but they often consisted only of material hardly identifiable by light microscopy (Arashkevich 1969; Harding 1974; Gowing and Wishner 1986). The importance of marine snow as potential food source has been proposed (Lampitt et al. 1993); however, it is not clear whether the materials of marine snow, containing many digestion-resistant forms, are actually available for assimilation (Silver and Alldredge 1981) or whether animals can survive at the low particle concentrations at depth (Jackson and Burd 2002). Flux feeding proposed recently by Jackson and Burd (2002) could provide an advantageous strategy for detritivores at depth, in contrast to an active search for food through volume filtration. This strategy includes feeding on falling particles with rates proportional to the vertical flux rather than to particle concentration (Jackson and Burd 2002) and may allow organisms to conserve energy. However, the specific chemical nature of constituents of marine snow suggests that especially effective digestive systems are needed to enable deep-water detritivores to benefit from this potential food source (Silver and Alldredge 1981).

The gut morphology and ultrastructure presumably is of great importance for effective utilization of food by detritivores in the food-limited environment of the deep sea. Gross gut morphology and histology have been extensively studied for many free-living epipelagic copepod species (Lowe 1935; Park 1966; Yoshikoshi 1975; Arnaud et al. 1978, 1980; Boxshall 1985, 1992). In general, their alimentary canal typically consists of a short ectodermal foregut (the esophagus), an endodermal midgut and a short ectodermal hindgut (Boxshall 1992). The midgut is the most extensive part of the digestive tract. It stretches out from the esophagus to near the end of the urosome and is lined with different types of epithelium cells for which different functions (absorption, digestion and excretion) have been proposed (Arnaud et al. 1980). Based mostly on investigations of epipelagic species it is widely accepted that the copepod midgut is an almost straight tube, sometimes slightly folded between the middle and posterior zones (Arnaud et al. 1980). The major differences between species concerned the number of midgut regions, cell types that compose the midgut epithelium, presence or absence of an anterior midgut diverticulum, and the posterior zone in a dorsal or ventral position (Arnaud et al. 1978, 1980; Hallberg and Hirche 1980; Musko 1983, 1988). Remarkable deviations from this ‘‘regular’’ gut type were observed in copepods, to our knowledge, only twice. Vinogradov (1972, his Fig. 75) presented a drawing of a greatly elongated gut in the abyssopelagic copepod *Chiridiella* sp. collected between 7000 and 8000 m in the Kurilo-Kamchatka Trench. This gut was twisted into a broad loop. Later, Nishida et al. (1991) observed an elongated and looped gut in *Lophothrix frontalis* Giesbrecht from ca. 1000 m depth in Sagami Bay, Central Japan Sea. In both species, elongation of the midgut was considered an adaptation for better assimilation of the food available in the bathy- and abyssopelagic realms (Vinogradov 1972; Nishida et al. 1991).

During the course of our zooplankton investigations in the Arctic Ocean we discovered a conspicuous, strongly elongated and looped gut in a member of the deep-water copepod family Spinocalanidae, *Spinocalanus antarcticus*, a common and abundant inhabitant of the mid-water layers of the Arctic Ocean (Harding 1966; Kosobokova 1989; Kosobokova and Hirche 2000). Here we present a description of the gross gut morphology and discuss its adaptive value, and examine the possible feeding strategy of this deep-water copepod using results of a qualitative analysis of the gut content, lipid composition and C/N ratio.

Materials and methods

Abundance and distribution

Zooplankton were collected during the expeditions ARK XI/1 (July–August 1995) and ARK XII (August 1996) of R.V. ‘‘Polarstern’’ to the Arctic Ocean (Table 1; Fig. 1). Stage composition and distribution of *Spinocalanus antarcticus* were studied from samples collected with a multinet (0.25 m^2 mouth opening, 150 μm mesh size). Ten stratified samples were taken in two successive vertical hauls from the bottom and 300 m to the surface at each station. Depth intervals were bottom–1800–1000–750(500)–300–0 m for the deep casts and 300–200–100–50–25–0 m for the shallow casts. Samples were preserved in 4% hexamin-buffered formalin. In 1995, sampling was carried out at five stations in the deep Amundsen and Makarov Basins at 81°N. In 1996, four stations were sampled north of 82°30′ (Fig. 1).

All individuals of *S. antarcticus* were sorted out of the multinet samples, and copepodite stages were counted separately. Prosome length was measured from the tip of the cephalosome to the distal lateral end of the last thoracic segment. Total body length was measured from the tip of the cephalosome to the end of the furcal rami under a Wild dissection microscope at a magnification of 25× or 32×.

Gut morphology

To study the gross morphology of the alimentary canal, between five and ten individuals of each stage from copepodite I (CI) to adults were stained in bengal rose for 6–14 h and then transferred to glycerol to clear the tissues. The gut morphology was examined under a light microscope on intact animals. The gut length was measured from the anterior of the midgut to the posterior of the anus on dissected guts.

Specimens from formalin samples were rinsed in Sørensen buffer and embedded in epoxyresin (Araldit CY212). After hardening, blocks were cut with glass knifes in 5 μm slides and mounted on microscope mounting slides. Photographs were taken under a Zeiss Axiophot invert microscope (50×). Intestinal mineral particles were investigated and mineralogically identified by EDAX analysis (X-ray disperse analysis). X-ray analysis was carried out on a Philips SEM 515 combined with the ‘‘Econ IV Detector’’. Analysis and depiction of the signal were done on a semi-automatic EDAX computer (PV9900 Super Quant).

Gut content

Gut content was examined in five to ten individuals of CIV to CVI taken at random from each sample at stns 47 (ARK XI/1) and 80

Table 1. Zooplankton station list (*Mn* multinet; *Bo* bongo net)

Station	Date	Depth (m)	Time (GMT)	Sampling gear
ARK XI/1				
47	20 Aug 1995	3830	17:19	Mn
49	22 Aug 1995	2700	08:56	Mn
51a	23 Aug 1995	1750	18:31	Mn
52	24 Aug 1995	1290	15:17	Mn
55	25 Aug 1995	1690	16:39	Mn
57	27 Aug 1995	2640	06:19	Mn
ARK XII				
48	07 Aug 1996	3863	03:05	Mn
55	09 Aug 1996	4427	07:59	Mn
72	14 Aug 1996	3923	21:26	Mn
76	17 Aug 1996	1958	05:40	Mn
80	19 Aug 1996	3854	05:09	Bo
82	20 Aug 1996	3857	17:55	Bo
99	01 Sep 1996	3004	21:27	Bo

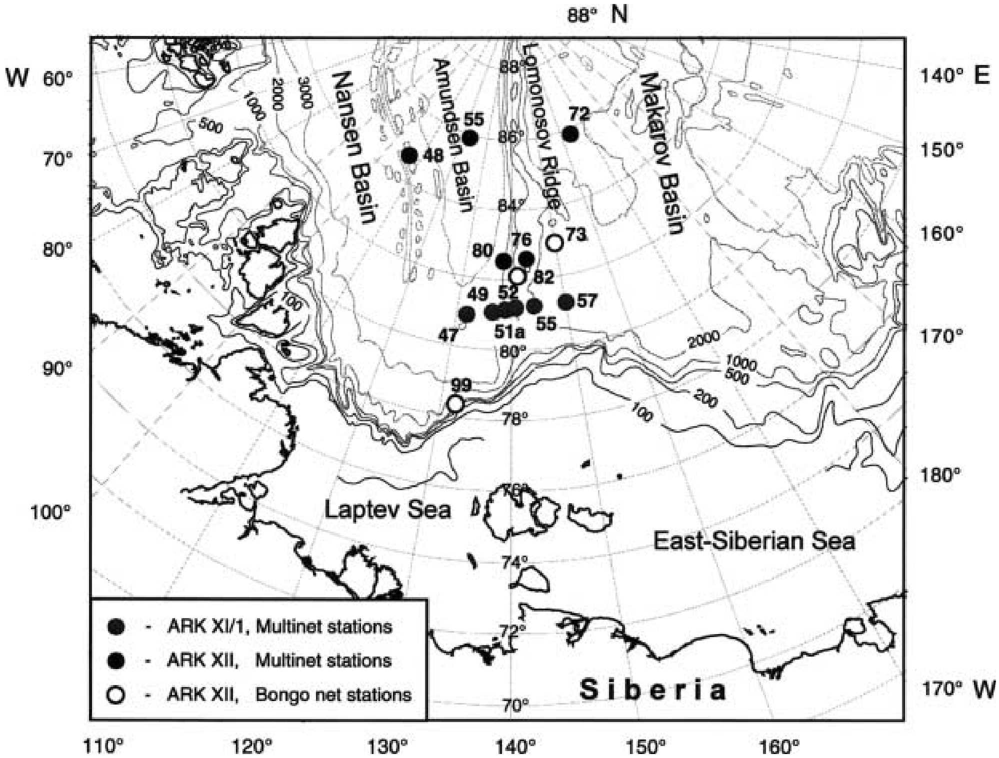

Fig. 1. Zooplankton sampling locations in the eastern Nansen and Makarov Basins, Arctic Ocean

(ARK XII). Copepods were dissected in 100% glycerol with a micro-scalpel under a stereo-microscope. To avoid contamination of the gut content with body tissues, the complete digestive tracts were carefully removed from the animals after cutting off the abdomen and opening the thorax. The midgut was transferred into a drop of polyvinyl lactophenol (PVLP), the gut content was taken out, mounted in PVLP and examined under a Zeiss Axioscope with differential interference contrast (DIC) and phase contrast (Ph) at magnifications of 200×, 400× and 1000×. For comparison, seston particles from each multinet catch were also examined with light microscopy at a magnification of 200×.

Lipids, carbon and nitrogen

Samples for lipid analysis were collected during ARK XII with a bongo net (0.28 m^2 mouth opening, 300 µm mesh size) from 0–1500 and 0–2000 m depth at stns 73, 82 and 99 (Fig. 1). Female *S. antarcticus* were sorted out immediately after capture and incubated in filtered seawater from several hours up to 2 days until defecation was completed. For each lipid analysis, five to ten females were transferred to glass tubes containing dichloromethane:methanol (2:1 by volume) with 0.01% buthylhydroxytoluene and stored at –80°C. Lipid content and composition were determined according to Kattner and Fricke (1986) and Kattner et al. (1989); fatty acids were identified from retention times.

For carbon and nitrogen measurements from eight to ten CV and female *S. antarcticus* were pooled in tin caps and stored at –30°C. They were dried for 2 days at 60°C and then analyzed for total organic carbon and nitrogen by combustion at 1050°C using a Heraeus C/N elemental analyzer.

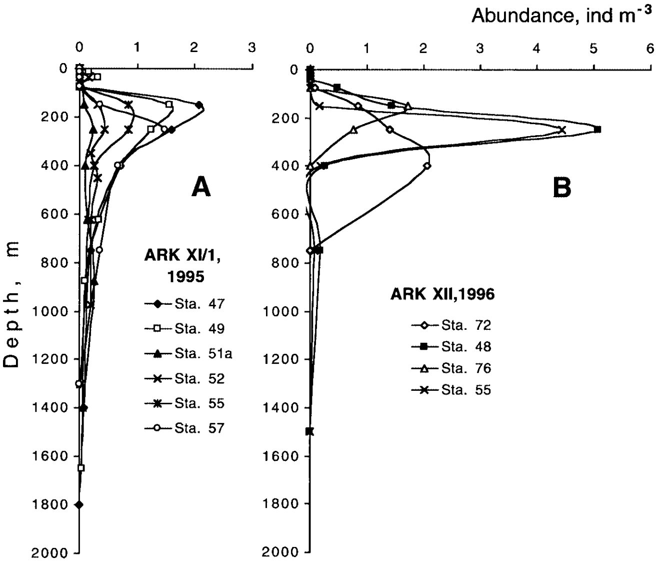

Fig. 2A, B. *Spinocalanus antarcticus*. Vertical distribution of the *S. antarcticus* population (ind. m^{-3}) in the study area in 1995 (**A**) and 1996 (**B**)

Results

Stage composition and vertical distribution

All stages from CI to adult females and males were present in the population of *Spinocalanus antarcticus* in the study area. The species demonstrated a clear preference for the depth layer between 100 and 500 m (70–99%), with abundance varying from 20 to 500 ind. per 100 m^3, and occurred seldom above 100 and below 500 m ($<$ 50 ind. per 100 m^3, Fig. 2). The presence of a few specimens in the samples from the upper 100 m layer might be an artifact resulting from contamination of nets during the first, deep cast in the interval bottom–300 m (see "Materials and methods"). In general, the patterns of the vertical distribution were similar at most stations except stn 72 (ARK XII) and showed maxima between 100 and 300 m (Fig. 2A, B). At stn 72 the population occupied greater depths and demonstrated a deeper maximum in the interval between 300 and 500 m (Fig. 2B). Comparison between day and night stations did not show a correlation between positions of maximum abundance and time of the day (Table 1).

The vertical distribution of developmental stages showed that adults were the deep-living stages in the population (Fig. 3). The youngest copepodites, CI and CII, had their maximum abundance at almost the same depth as adult females, while the CIII maximum was shifted to the upper layers and CIV demonstrated a preference for the uppermost part of the species depth range (Fig. 3).

Gross morphology of midgut and fecal pellets

The gross morphology of the midgut of *S. antarcticus* was similar in all copepodite stages and adults from the Arctic Ocean and in specimens from Antarctic waters kindly provided by Dr. S. Schiel. It is therefore described here only for the adult female (Fig. 4). The midgut makes up the greatest part of the alimentary canal. Its first wide and sac-shaped portion (P1) is located on the ventral side of the prosome. In the third thoracic segment the midgut narrows and bends dorso-laterally, extending to the anterior part of the prosome along its left dorsal side almost up to the esophagus (P2). There it bends again and proceeds to the posterior of the abdomen (P3). In P3, fecal pellet formation takes place. The total gut length is 1.77, 1.86 and 1.9 times the total body length in adult females, CV and CIV, respectively (Table 2).

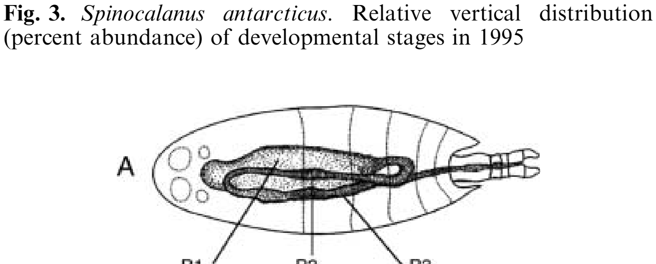

Fig. 3. *Spinocalanus antarcticus*. Relative vertical distribution (percent abundance) of developmental stages in 1995

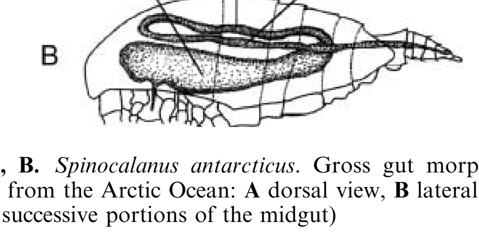

Fig. 4A, B. *Spinocalanus antarcticus*. Gross gut morphology of females from the Arctic Ocean: **A** dorsal view, **B** lateral view (*P1*, *P2*, *P3* successive portions of the midgut)

The fecal pellets of adult females were ca. 2000 µm long, ca. 80 µm wide and usually as long as P3. Both tips were symmetrically narrowed. There was no difference in shape between the front and back ends of a pellet. The color in the transmission light was greenish, while under reflected light greenish to whitish. Under the light microscope, the content of the pellets appeared as densely packed material formed by evenly distributed granules of similar size.

Gut content

A total of 103 (94%) specimens out of 110 *S. antarcticus* CIV to CVI examined had food in their guts. Individuals with filled guts were present over the entire depth range of the species. Generally, the guts were packed with material, but most of it was impossible to identify (Fig. 5A–C). Table 3 presents the number of individuals with particular food items in the guts and shows the relative spectrum of organic particles in the guts.

In most specimens both P1 and P2 of the digestive tract were filled with undefined detritus particles ("detritus balls") (Fig. 5D; Table 3). They were almost spherical heterogeneous organic aggregates of 40–100 µm diameter, with small clay-sized mineral flakes imbedded (Fig. 5E, F). They did not have an outer membrane, but had a smooth outline, and strongly resembled the "detritus balls" found in copepod guts by Harding (1974, his plate IV, D). Nothing comparable by size and/or morphology, however, was found either in seston samples from the study area, or in the guts of five other mesopelagic copepods examined in parallel (*Aetideopsis rostrata*, *Chiridius obtusifrons*, *Gaetanus tenuispinus*, *G. brevispinus*, *Scaphocalanus acrocephalus*) (Scherzinger, unpublished data).

In a few specimens fragments of dinoflagellates (*Gonyaulax* spp., *Peridinium* spp.) were found (Table 3) as well as almost amorphous round structures with two flagella; the latter were classified as an unidentified dinoflagellate species after finding intact specimens with the same flagellum morphology in the guts. In a few guts skeletons of silicoflagellates, fragments of tintinnids and radiolarians (50–70 µm) and remnants of ciliates, recognized from membranes with numerous cilia, were also found. All these items are pooled under "protozoans" in Table 3. Diatoms were quite rare and were found mostly as fragments of small-sized cells (20–25 µm). Animal remnants in the guts included fragments of cuticula, maxillipeds of copepods and bristles. At least 30% of the animal remnants were not recognizable. Cysts of Chrysophycea (5–14 µm diameter) and dinoflagellates (50 µm) were also observed (Fig. 5B; Table 3). Sometimes,

Table 2. *Spinocalanus antarcticus*. Length of prosome, total body and gut (mm; ±SD) of copepodite stages CIV and CV and adult females

Stage	*n*	Total length	Prosome length	Gut length	Gut/Total length
CIV	7	1.50 ± 0.08	1.21 ± 0.04	2.85 ± 0.14	1.90 ± 0.08
CV	3	1.96 ± 0.25	1.55 ± 0.16	3.63 ± 0.58	1.86 ± 0.20
Female	8	2.67 ± 0.11	2.12 ± 0.06	4.72 ± 0.24	1.77 ± 0.12

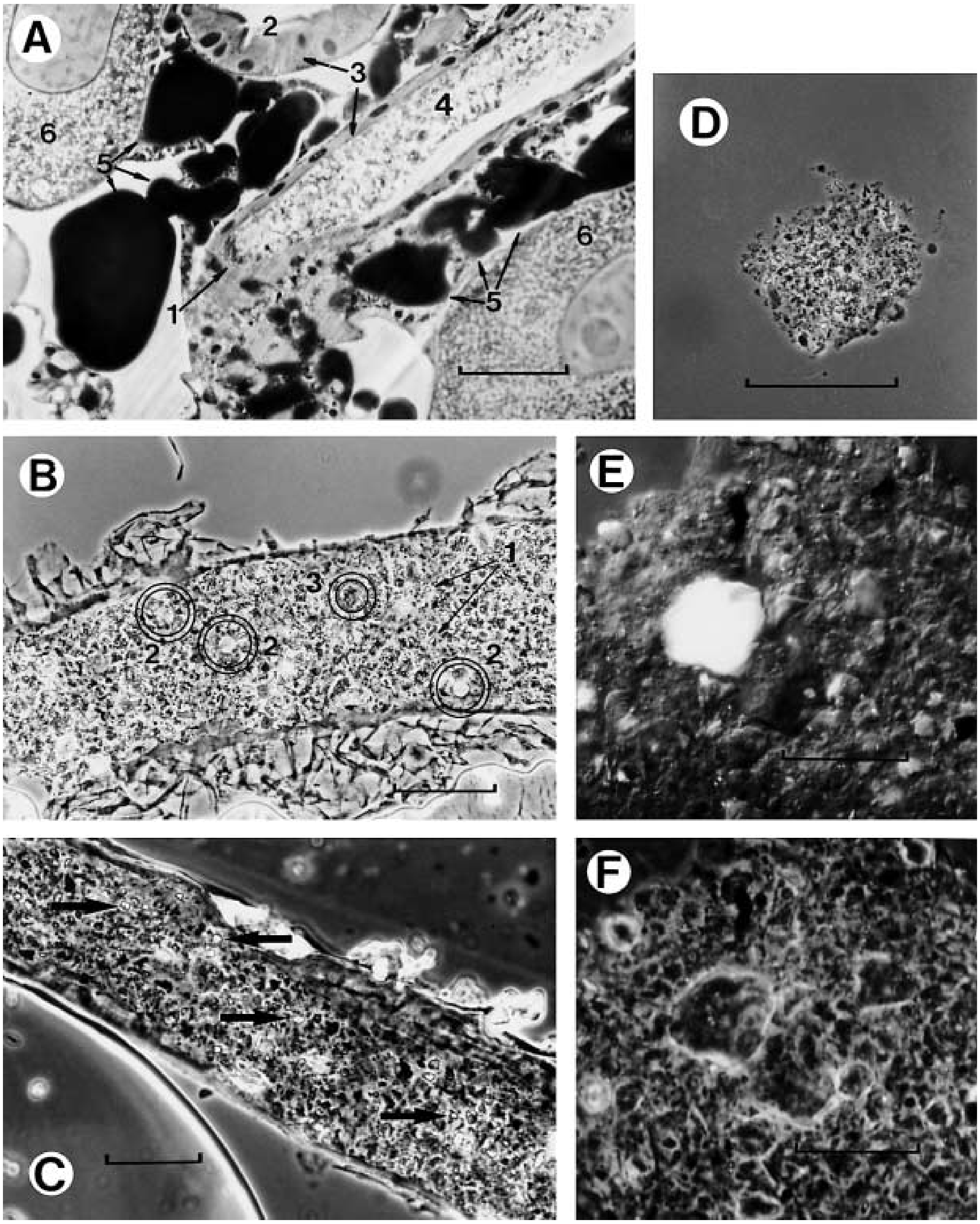

Fig. 5A–F. *Spinocalanus antarcticus*. Sections through the midgut and gut contents. **A** Section through the cephalothorax (*1* longitudinal section through the midgut; *2* cross section through the midgut; *3* gut epithelium; *4* gut content; *5* lipid drops; *6* oocytes with nuclei) (*scale bar*: 30 µm). **B** Longitudinal section through the midgut P2 (*1* mineral particles; *2* cysts; *3* detritus) (*scale bar*: 40 µm). **C** Longitudinal section through the midgut P2 (*arrows* mineral particles) (*scale bar*: 30 µm). **D** A "detritus ball" with mineral particles imbedded (*scale bar*: 100 µm). **E** Mineral particles imbedded in the gut content (*scale bar*: 50 µm). The big white particle is silty quartz, photograph taken under differential interference contrast; **F** the same as E under phase contrast

bright-red or ruby-red, almost triangular particles of uncertain origin were registered; they could have been mineral particles or remains of appendicularians.

Mineral particles in the size range of 1–10 µm were found in large quantities in the guts of many *S. antarcticus* specimens (Fig. 5B–F; Table 3). Of the specimens with full guts, 26% did not contain any recognizable food items, but only mineral particles and "detritus balls".

Carbon and nitrogen content

Carbon content of females varied between 40.8 and 76.7 µg ind.$^{-1}$ (mean 56.6) and between 39.4 and 46.4 µg ind.$^{-1}$ (mean 42.4) in CVs (Table 4). The average C/N ratios for female (8.6) and CV (8.2) *S. antarcticus* were very high and similar to that of well-fed, predominantly herbivorous *Calanus glacialis* (9.1) collected simultaneously.

Table 3. *Spinocalanus antarcticus*. Occurrence frequencies (*OC*, percent of animals with a particular item in the gut) and numerical frequencies (*NF*, average percent contribution of a particular item to the gut content in all guts analyzed) of gut contents in 103 specimens in stages CIV–CVI

Gut content	OC	NF	Size range, μm
"Detritus balls"	82	62	50–100(150)
Mineral particles	100		1–50
Protozoans (tintinnids, radiolarians, ciliates, silicoflagellates, dinoflagellates)	32	7	50–70
Diatoms	2	3	20–25
Animal remnants	8	4	
Cysts	13	20	5–50
Pellets	0	0	
Red particles	50	4	< 5
Indeterminate organics	28		

Table 4. *Spinocalanus antarcticus*. Mean organic carbon and nitrogen content (μg), and C/N ratio of females and CVs (*n* number of specimens per measurement)

Developmental stage	*n*	Carbon	Nitrogen	C/N
Female	13	76.7	8.9	8.62
	1	40.8	4.7	8.72
	8	52.4	6.1	8.54
CV	10	46.4	5.7	8.20
	8	39.4	4.8	8.19

Lipid composition

Lipid reserves are stored by *S. antarcticus* in numerous small and transparent droplets distributed all over the prosome, but with higher concentrations and larger size in the vicinity of the digestive tract (Fig. 5A). The lipid composition was characterized by domination of the 18:1(*n*-9) fatty acid (37%), which is usually considered indicative of a carnivorous diet (Graeve et al. 1997) (Table 5). On the other hand, the concentrations of 16:1(*n*-7) and 18:1(*n*-7), typical biomarkers for diatoms (Graeve et al. 1994, 1997), were 15% and 6%, respectively. Concentrations of 20:1(*n*-9) and 22:1(*n*-11), which are typical components of body lipids synthesized by herbivorous calanoids (Hopkins et al. 1993) were relatively low, 8% and 2.5%, respectively. The presence of the 17:0 fatty acid (6%) indicates sulfate-reducing and other anaerobic bacteria (Napolitano 1998).

Table 5. *Spinocalanus antarcticus*. Fatty acid composition (± SD) and wax ester content from the total lipid extract, and percent dry weight of female (average for ten specimens) (assuming dry weight = 2.5×carbon content)

	Content (mass %)
Fatty acids	
14:0	0.69 ± 0.08
16:0	3.10 ± 0.18
16:1(*n*-7)	14.48 ± 0.59
16:1(*n*-5)	0.57 ± 0.03
16:2	0:64 ± 0.04
16:3	0.41 ± 0.03
16:4	0.02 ± 0.00
17:0	5.73 ± 1.16
18:0	1.06 ± 0.03
18:1(*n*-9)	36.66 ± 1.20
18:1(*n*-7)	5.88 ± 0.55
18:2(*n*-6)	2.81 ± 0.21
18:3(*n*-3)	0.85 ± 0.10
18:4	1.76 ± 0.65
20:1(*n*-11)	1.61 ± 0.20
20:1(*n*-9)	8.13 ± 1.23
20:5(*n*-3)	4.37 ± 0.62
22:1(*n*-11)	2.46 ± 0.42
22:1(*n*-9)	3.39 ± 0.31
22:6	4.23 ± 0.36
Wax esters	83.5
Lipids (% dry wt)	54

Discussion

Spinocalanus antarcticus is a typical bipolar, deep-water calanoid copepod, common and rather abundant both in the Arctic and Antarctic (Damkaer 1975; Schiel 1998). The spinocalanids have a wide vertical range with an upper depth limit at about 100 m, which according to Damkaer (1975) gives them a potential for a wide, in some species a world-wide, distribution in the relatively uniform and interconnected deep-ocean water masses. In temperate waters, their maximum is generally found between 750 and 1000 m (Arashkevich 1969; Vinogradov 1972), where they contribute from 10% to 40% to zooplankton biomass. At abyssopelagic depths between 6000 and 8000 m in the Kurilo-Kamchatka Trench the genus *Spinocalanus* numerically dominates among other copepods (Vinogradov 1972). In the Arctic Ocean most spinocalanids (three species of the genus *Spinocalanus* and three of *Mimocalanus*) occupy depths below 500 m and have maxima below 1000 m (Damkaer 1975; Kosobokova 1989; Kosobokova and Hirche 2000). Two other species, *Spinocalanus longicornis* and *S. antarcticus*, are shallower dwelling, predominantly occupying the layers between 100 and 500 m (Kosobokova and Hirche 2000). In the Greenland Sea *S. antarcticus* was found between 300 and 2000 m, with maximum concentrations below 500 m (Hirche, unpublished data). In Antarctic waters it was found between 100 and 1000 m (sampling was restricted to 1000 m), with maximum numbers between 200 and 300 m in summer and between 500 and 1000 m in winter (Schiel 1998). Differences in the distribution of particular developmental stages observed during the present study may indicate ontogenetic migration. Deepest occurrence of the adults and youngest copepodites (CI and CII) and shallower occurrence of CIV suggest reproduction at depth and gradual ascent in the course of development from CI to CIV. Between-station variability of the vertical distribution of *S. antarcticus* within the study area (Fig. 2A, B) may be related to the circulation and distribution of Atlantic water in the Arctic Ocean (Kosobokova and Hirche 2000). A comparison of distribution at day and night stations indicates that this species did not undergo diel vertical migrations in the Arctic Basin in late summer, which excludes the possibility of its feeding in the upper layers.

The feeding habits of the spinocalanids are poorly studied, especially those of species inhabiting the Arctic Ocean. A detailed comparison of the morphology of mouth appendages in the Calanoida led Arashkevich (1969) to the conclusion that spinocalanids have a mixed feeding mode in comparison with typical filter feeders and raptorial feeders. Their plumed setae on maxilliped II allow filtering of fine particles, while strong opal teeth on the mandible allow them to tear up larger objects obtained when grasping. The mouth appendages of *S. antarcticus* were described by Damkaer (1975). They do not deviate strongly from other *Spinocalanus* species (Arashkevich 1969; Damkaer 1975). According to their gut content, spinocalanids have been considered as predominantly detritivorous (Arashkevich 1969; Harding 1974). Arashkevich (1969) described the gut content of *S. similis* from the Kurilo-Kamchatka Trench as a "greenish non-shaped mass". Harding (1974) reported that the major content of the guts of six other deep-water *Spinocalanus* species from 1000 to 4000 m was formed by detrital remnants, while a considerable variety of other particles (bacteria, pigmented cells, diatoms, dinoflagellates, coccoliths, cysts, tintinnids, silicoflagellates, radiolarians, copepod remnants) composed less than 5% of the gut contents. Sometimes, *Spinocalanus* species have been shown to have large amounts of mineral particles of 1–10 μm diameter in their guts (Harding 1974).

The spectrum of particles observed in the guts of *S. antarcticus* during the present study (Table 3) largely coincides with earlier observations on other *Spinocalanus* species (Harding 1974; Hopkins 1985). A new observation for this species is the frequent presence of detrital balls (Fig. 5D), which have been found before in a number of other deep-sea copepods (Harding 1974); this may indicate a preference for the flux-feeding strategy suggested by Jackson and Burd (2002). The frequent abundance of these detrital balls and mineral particles seems to be specific for this species. The gut content characterizes *S. antarcticus* as an omnivore/detritivore with indiscriminate filtration of all materials available in its habitat, a "generalist" in terms of Gowing and Wishner (1986). This is also supported by the fatty acid composition, which points to utilization of a combined plant and animal diet (Table 5).

While the gut content of *S. antarcticus* is similar to other spinocalanids and many other detritivores (Harding 1974; Hopkins 1985; Gowing and Wishner 1986), its gut morphology, looped and almost twice the body length, represents an outstanding example of deviation from the "regular" gut type of most free-living copepods (Lowe 1935; Park 1966; Yoshikoshi 1975; Arnaud et al. 1978, 1980; Boxshall 1985, 1992). This certainly poses questions on the advantage of the specific gut anatomy and on the specific food sources from which the species could potentially benefit.

Both a high C/N ratio and lipid content (Tables 4, 5) of *S. antarcticus* strongly suggest effective utilization of the food resources available in its habitat and quite a strong adaptation of this species to storing energy in the form of lipids. While C/N ratio and lipid content are quite similar between *S. antarcticus* and the predominantly herbivorous *Calanus glacialis*, the source of the reserves is obviously different. Earlier Harding (1974) showed from staining of the gut contents of congeners that they are quite efficient in utilizing protein. Carbohydrates, in contrast, were incompletely utilized and were found in fecal pellets (Harding 1974). Gut elongation could allow a higher degree of utilization of organic material, especially the carbohydrate components of detritus, due to longer retention time and enlargement of the surface area for absorption. The numerous detrital balls found during our study could be leftovers of intensive digestion. Thus, ultrastructural examination of the looped midgut of the copepod *Lophothrix frontalis* showed that the entire posterior zone, equal to nearly two-thirds of the total gut length, was lined with epithelium cells with an absorptive function (Nishida et al. 1991). The authors regarded the numerous lipid droplets in the epithelium as indication of active absorption in this zone. In *S. antarcticus* lipid droplets were also most numerous in vicinity of the gut.

The particles sinking to the deep sea include marine snow, fecal pellets, plankton cells and animal remnants (Silver and Alldredge 1981; Silver et al. 1984; Karl and Knauer 1984; Alldredge and Silver 1988; Lampitt et al. 1993; Heissenberger et al. 1996). Non-living detrital sources such as marine snow are known to be metabolic centers in the deep sea where associated bacterial and algal forms convert non-living material to regenerated production (Silver and Alldredge 1981; Alldredge et al. 1986; Alldredge and Silver 1988; Simon et al. 1990; Turley and Mackie 1994; Long and Azam 1996). The organic carbon content of marine snow has been reported to exceed that of surrounding waters by several orders of magnitude (Silver and Alldredge 1981; Alldredge and Silver 1988). At least three-fourths of the biomass in these microenvironments consists of phytoplankton represented by pico-sized coccoid cyanobacteria and green algae (< 2 μm), as well as larger size fraction diatoms, while other biogenic materials in marine snow consist of heterotrophic bacteria (Silver and Alldredge 1981).

Although a wide variety of planktonic organisms including copepods, ostracods, euphausiids, amphipods, salps, doliolids and fish have been found to feed on marine snow (Alldredge 1976; Lampitt et al. 1993; Steinberg 1995; Walters and Shanks 1996; Green and Dagg 1997; Gowing and Wishner 1998) and although its carbon value may be high, the nature of the materials in it indicates that a relatively small proportion of the carbon may actually be available for assimilation by regular detritivores (Silver and Alldredge 1981). The cyanobacteria and picoplankton-sized eukaryotic algae in marine snow, for example, have been shown to be resistant to digestion and to persist intact in both the gut and fecal pellets of copepods and some other animal groups (Silver and Bruland 1981; Johnson et al. 1982; Gowing and Wishner 1986; Lampitt et al. 1993). However, more recent investigations indicated that they might also serve as a food source (O'Neil 1998; Turner et al. 1998; Engstroem et al. 2000) or supplement the copepod diet (Schmidt and Jonasdottir 1997). Silver and Alldredge (1981) suggested that the presence of the carbon-rich systems of marine snow in the deep sea, where food resources are otherwise restricted, might have resulted in the evolution of especially efficient digestive systems in deep-water detritivores. In this context, the considerably elongated guts in *S. antarcticus* and two other copepods described before, *Chiridiella* sp. (Vinogradov 1972) and *Lophothrix frontalis* (Nishida et al. 1991), may represent an example of such a digestive system. Moreover, Biddanda and Pomeroy (1988) have shown that natural assemblages of marine bacteria, which colonize fresh diatom detritus, living diatoms (Smith et al. 1995) and marine snow (Smith et al. 1992), express very high levels of hydrolytic ectoenzymes and can dissolve the silica of diatom cell walls (Bidle and Azam 1999). During the long passage through the looped gut of *S. antarcticus* such assemblages could support digestion in a similar fashion to the symbiotic flora in the guts of mammalian ruminantia. This would also explain the almost complete absence of diatom frustules in the guts of *S. antarcticus*.

Especially in the ice-covered Arctic and Antarctic waters, where mineral particles are quite important components of the matter sinking all-year round from the ice sheet (Hargrave et al. 1994), bacteria could be a very specific food source. Two types of aggregates could be generally distinguished in settled material: inorganic aggregates, composed only of mineral particles without visible binding agents, and organic aggregates, which contain both biogenetic and mineral particles bound in an organic matrix (Hargrave et al. 1994). Organic aggregates contain mineral particles of a narrower size range (mostly <10 μm) than inorganic aggregates (>10–60 μm). The size of the mineral particles observed in *S. antarcticus* guts fits well with the size range found in prior studies. The ingestion of bacteria attached to the surfaces of mineral particles sinking in the water column has also been proposed by Harding (1974). This scheme would be in accordance with the presence of the 17:0 fatty acid in *S. antarcticus*, a biomarker for bacterioplankton (Napolitano 1998).

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