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Feeding of the carnivorous copepod *Euchaeta antarctica* in Antarctic waters

Vidar Øresland

Department of Zoology, Stockholm University, S-106 91 Stockholm, Sweden

ABSTRACT: Copepod *Euchaeta antarctica* stages V and VI were caught during 24 h sampling programmes in March 1989 at a coastal station in Gerlache Strait, Antarctic Peninsula, and in January 1990 at an oceanic station in the north Weddell Sea. Gut content analyses showed that copepods made up 80 to 90 % of all food items by number *Metridia gerlachei, Calanoides acutus, Euchaeta* spp., other large copepods, *Oncaea* spp., *Oithona* spp. and other small copepods were the main prey of *E. antarctica* (V, VI). Large copepods were probably more important as food (on a dry-weight basis) than small copepods. Mean number of prey per *E. antarctica* (V, VI) was 0.9 and 1.1 at the coastal and the oceanic station, respectively. Copepodids at stage V contained more prey items (1.3) than adult females (0.5) at the coastal station in March. A sample from South Georgia showed that *E. antarctica* feeds during winter *E. antarctica* individuals were not eating continuously since, in all areas, over 30 % of them had empty guts. The parasitic dinoflagellate *Blastodinium* sp. was found in the gut of 6.6 % of *E. antarctica* at the oceanic station. This infection did not affect the number of food items found in their guts.

INTRODUCTION

Feeding of carnivorous zooplankton and their importance as a structuring force on zooplankton communities in coastal waters have received considerable interest during the last 2 decades (e.g. Greve 1981, Feigenbaum & Maris 1984, Ohman 1986, Miller & Daan 1989). There have been few studies, however, in open oceanic areas and fewer still in Antarctic waters. Hopkins (1985a, b) showed that chaetognaths and the copepod *Euchaeta antarctica* were among the most common macrozooplankton predators in the planktonic food web in Gerlache Strait (64° 05′ S, 61° 50′ W), Antarctic Peninsula, during the austral fall (March–April). Øresland (1990) studied the feeding and predation impact of the chaetognath species in the same area from December to March, and Yen (1986, 1991) carried out laboratory studies on the feeding of *E. antarctica* (also from Gerlache Strait) during the austral summer. *E. antarctica* is common in all sectors of the Antarctic Ocean and occurs also north of the Antarctic Convergence in the Atlantic, Pacific and Indian Oceans (Fontaine 1988). The studies by Hopkins (1985a, b) and Yen (1986, 1991) suggest that the species may be of great importance in the zooplankton community but more detailed information of its feeding based on field collections is still lacking.

In this study the natural diet and the mean occurrence of prey during 24 h in *Euchaeta antarctica* were studied through gut content analyses on field samples collected during summer at a coastal and an oceanic station. A sample from South Georgia was also analyzed to investigate winter feeding. The occurrence of the dinoflagellate parasite *Blastodinium* sp. and its effect on the feeding behaviour of *E. antarctica* are also reported.

METHODS

Euchaeta antarctica for gut content analyses were collected from the upper 1000 m of the water column during 24 h sampling programmes in: Croker Passage, Gerlache Strait, Antarctic Peninsula (64° 05.8′ S, 61° 50,4′ W, coastal station) and north of eastern Weddell Sea (60° 01.4′ S, 12° 38.4′ W, oceanic station, Fig. 1). For logistic reasons, it was only possible to obtain samples during one 24 h period at each station. At the coastal station, 9 double oblique plankton hauls were taken between 12 and 13 March 1989. A ring net (0.7 m diameter, 500 µm mesh size) was used during the first 8 hauls and a WP2-90 µm net was used during the last haul. Sampling speed of the net (depending on ship and wire speed) was 0.5 to 1 m s^{-1}. Mean bottom

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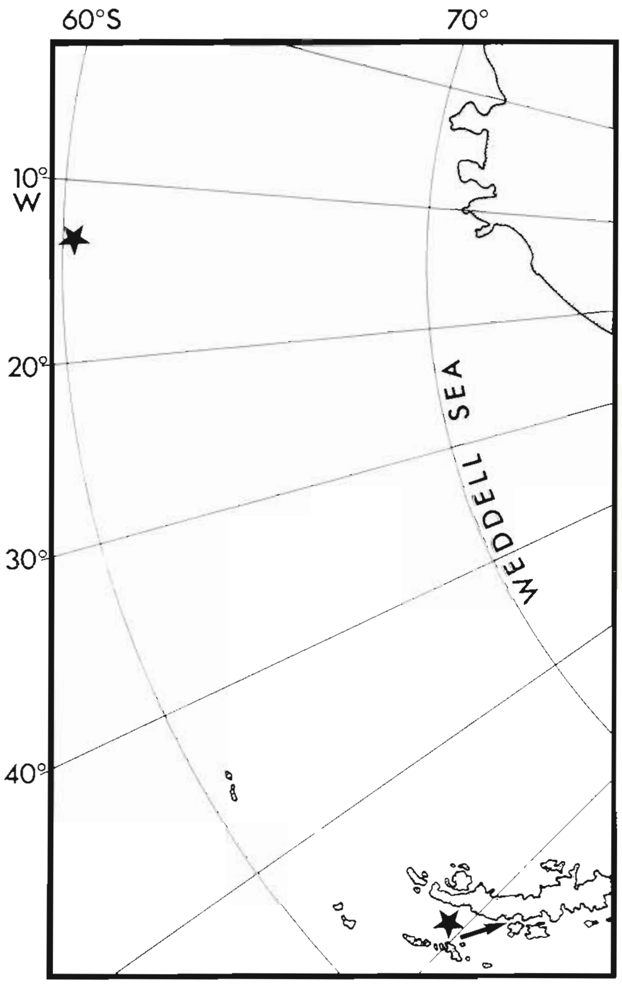

Fig. 1. Location of coastal and oceanic station (stars)

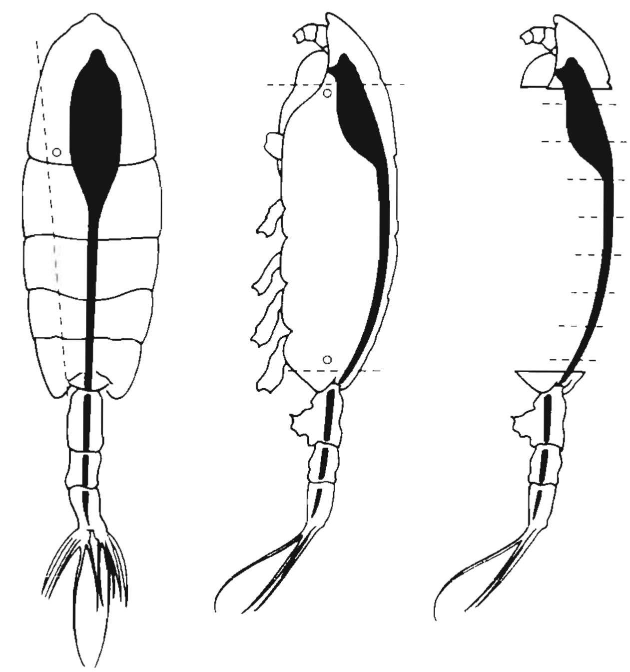

Fig. 2. *Euchaeta antarctica*. Dissection details. Dashed lines: cuts using a microscalpel; circle: position of tungsten needle during cutting

depth was 1214 m, mean sampling depth 983 m. Mean sampling time was 59 min. At the oceanic station, 9 double oblique plankton hauls were taken between 10 and 11 January 1990. Two ring nets (1 m diameter, 200 μm mesh size) were employed simultaneously on the wire separated by 20 m. Sampling speed was ca 1 m s^{-1}, bottom depth ca 2400 m, and mean sampling depth was 1017 m. Mean sampling time was 119 min. Sampling depths at both stations were estimated from length of wire out and angle, and are therefore not accurate. Below 50 m depth the temperature ranged from ca −1 to 0 °C at the coastal station, and from −1.5 to 0.5 °C at the oceanic station (data from CTD casts made during sampling periods).

All zooplankton samples were fixed in 4 % formaldehyde in seawater buffered with borax. All *Euchaeta antarctica* stages V and VI at the oceanic station were sorted alive (due to high occurrence of phytoplankton) and preserved within ca 20 min of the net coming on board. All *E. antarctica* stages V and VI from the coastal station were sorted and placed in a fresh formaldehyde solution within 3 mo of initial preservation. The remaining zooplankton from both stations could not be counted due to the poor state of preservation caused by formaldehyde which had been polymerized after exposure to low temperature (beyond control of the author). The *Euchaeta* specimens were, however, well preserved when analysed.

The copepods were placed on a soft piece of plastic in a Petri dish and covered with water. Prosome length of *Euchaeta antarctica* was measured in 0.1 mm intervals under a stereomicroscope, using an eyepiece micrometer. The copepods were then dissected under the stereomicroscope using an insect pin (sharpened and formed under a stereomicroscope to the shape of a 3 mm long microscalpel) and needles made of tungsten wire (0.1 to 0.3 mm in diameter) sharpened in melted $NaNO_2$. The gut, with the attached anterior end of the prosome and the urosome, was dissected out in one piece and the gut was then transferred to a few drops of polyvinyl-lactophenol on a microscope slide (Fig. 2). The anterior end of the prosome and the urosome were removed, and the gut cut into 5 to 10 small pieces after which the gut contents could easily be removed. The part of the gut found in the urosome was not analysed. Analysis of gut contents was inferred from identification of prey mandibles or other identifiable prey parts observed through an inverted microscope.

Mean number of prey per copepod and mean percentage of *Euchaeta antarctica* without food during the

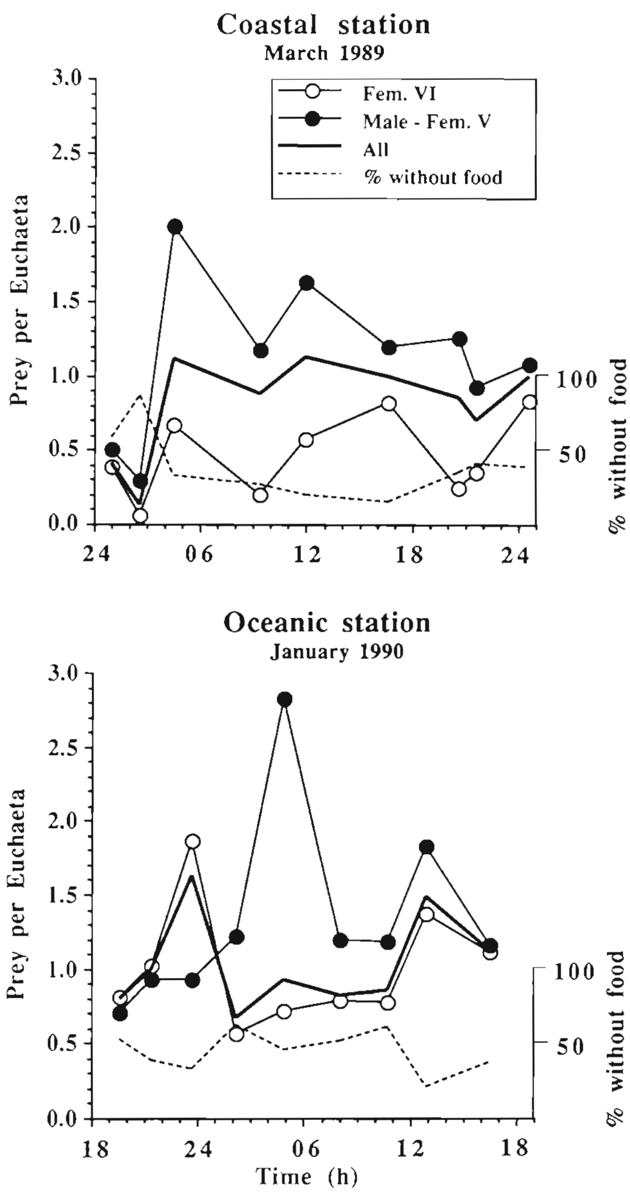

Fig. 3. *Euchaeta antarctica*. Number of prey per individual during 24 h sampling periods at coastal and oceanic station. Number of *E. antarctica* and food items on which the curves are based are given in Tables 2 & 3

sampling periods were estimated by calculating the mean height of the curves in Fig. 3 using a MOP-videoplan image analyzer (Kontron Electronics). This method limits bias in estimates due to uneven distribution of data points by time. In order to help evaluate differences in mean number of prey between adult females and stage V's for the 24 h periods (Fig. 3), and to reduce variance due to dependence on time, their temporal mean values were subtracted (paired observation at each sampling occasion), and tested for difference from zero (Dixon & Massey 1969, p. 121).

A sample of adult *Euchaeta antarctica* females, taken over the South Georgia shelf on 13 August 1983 between 10 and 185 m (see Ward & Wood 1988), was provided by Peter Ward, British Antarctic Survey. Thirty specimens were analysed for gut contents in order to obtain preliminary data on their feeding during winter. The dinoflagellate parasite *Blastodinium* sp. was identified using Sewell (1951) and references given in the 'Discussion' section.

RESULTS

Size and developmental stage of *Euchaeta antarctica* may be important factors affecting prey preference and feeding rates. Females at stage VI (adults) are much larger than adult males and specimens at stage V (Table 1). There was little or no difference between stations, when mean length of both sexes and stages were compared. However, both sexes and stages had a wider size range at the coastal station, which was sampled 2 mo later than the oceanic station.

None of the adult males (stage VI) examined were feeding at either the coastal or oceanic station. The gut was present (but thin), and the mandibles and mandibular teeth were reduced in size (mandible width was ca 0.10 mm). Adult males are therefore not included in any of the following feeding data.

Percentage distributions of the different prey categories found in adult females, and males and females at stage V, are shown in Table 2 (coastal station) and Table 3 (oceanic station). The category of large copepods included all copepods with a mandible width ≥ 0.07 mm and comprised stages III–IV of *Euchaeta* spp., stages III–V of *Calanoides acutus*, possibly some *Calanus propinquus*, and unidentified copepods. *Metridia* spp. stages III–VI (mandible width ≥ 0.06 mm) are shown separately from other large copepods since

Table 1. *Euchaeta antarctica*. Prosome lengths (mm) of individuals from coastal (March 1989) and oceanic (January 1990) station

Station/ Stage	n	Mean	Min	Max	Range	SE
Coastal station						
Female VI	110	6.96	5.5	7.8	2.3	0.0381
Female V	48	5.08	4.1	5.6	1.5	0.0444
Male VI	103	5.36	4.2	6.3	2.1	0.0319
Male V	61	4.86	4.1	5.8	1.7	0.0429
Oceanic station						
Female VI	440	6.88	5.9	7.5	1.6	0.0116
Female V	17	5.13	4.8	5.5	0.7	0.0490
Male VI	47	5.20	4.8	5.6	0.8	0.0433
Male V	80	5.06	4.7	5.4	0.7	0.0179

Table 2. *Euchaeta antarctica*. Percentage prey as a function of sex and developmental stage at the coastal station

Prey categories	Females VI	Female V	Male V	All V	All VI + V
Large cop.	17	5	6	6	9
Metridia spp.	32	23	30	27	28
Small cop.	21	47	44	46	39
Crustaceans	17	15	14	15	15
Polychaetes	0	3	3	3	2
Other	13	7	2	4	6
n *Euchaeta*	110	50	64	114	224
n Prey	47	60	63	123	170

The category 'large copepods' includes all copepods with a mandible width ≥ 0.07 mm. *Metridia* spp. have a mandible width ≥ 0.06 mm. 'Small cop.' include all other copepodids. See text for further explanations

Table 3. *Euchaeta antarctica*. Percentage prey as function of sex and developmental stage at the oceanic station. For further details consult footnote to Table 2

Prey categories	Females VI	Female V	Male V	All V	All VI + V
Large cop.	14	9	10	10	13
Metridia spp.	41	9	43	40	41
Small cop.	32	36	43	42	35
Crustaceans	4	9	2	2	4
Polychaetes	2	18	2	3	2
Other	7	18	1	2	6
n *Euchaeta*	449	17	80	97	546
n Prey	429	11	110	121	550

they were so numerous. Most were *M. gerlachei*, which was the dominant species of the genus in both areas. Small copepods consisted of *Oncaea* spp., *Oithona* spp., some small *Metridia* and *Euchaeta*, and unidentified copepods. Crustacea consisted of unidentified crustaceans of which the majority were the remains of large and small copepods whose size could not be determined (mandibles not found). Only 1 krill larva (unidentified species at calyptopis stage 2) was taken at each station. Some of the polychaetes were identified as *Pelagobia longicirrata*. The remaining food category consisted of unidentified items, a few pellets containing phytoplankton, and 2 chaetognaths (oceanic station).

Copepods were the predominant prey of all *Euchaeta antarctica* comprising at least 77 and 88 % of all prey items at the coastal and oceanic station, respectively (Tables 2 & 3). These are conservative estimates since the food category 'crustacea' also contained unidentified copepods. It is notable that *Metridia* spp. was more common as prey than other large copepods at both stations when all *E. antarctica* are considered. Together, *Metridia* spp. and other large copepods equalled or predominated over small copepods. At both stations the gut content of stage VI females comprised the highest proportion of large copepods and the lowest proportion of small copepods. Adult females also took the largest individual copepod prey items, *Calanoides acutus* at stage V (mandible width 0.17 and 0.18 mm) at the coastal and oceanic station, respectively. Of the large copepods, only 1 *C. acutus* was positively identified from the coastal station. At the oceanic station 37 *C. acutus* (of which some may have been *Calanus propinquus*) were found. Only 5 and 3 large *Euchaeta* spp. were found at the coastal and oceanic station, respectively. *Oncaea* spp. and *Oithona* spp. were not counted separately.

A significant difference ($p < 0.01$) was found in the number of prey items between adult females and individuals at stage V at the coastal station, but not at the oceanic station ($p > 0.05$) (Fig. 3). The mean number of prey (mean height of the curves in Fig. 3) of adult females, stage V individuals, and all *Euchaeta* was 0.5, 1.3, and 0.9, respectively, for the coastal station, and 1.0, 1.4 and 1.1, respectively, for the oceanic station. It is notable that the adult females in January at the oceanic station contained twice as many food items as adult females in March at the coastal station (see 'Discussion'). Interpretation of diel feeding patterns based on the shape of the curves should be avoided due to the large (1000 m) depth interval sampled (see 'Discussion').

It is important to know the frequency of multiple prey (Table 4) since the effect of individual prey on digestion time may be more obscure if several prey items are present in the gut. The frequency of multiple prey and the high occurrence of specimens with empty guts (Fig. 3) may reflect a variation in prey encounter rate and show that feeding in the natural environment is not continuous. This should be considered when doing short-term laboratory feeding experiments. Multiple prey were more common at the oceanic station. A maximum of 3 copepods (1 *Calanoides acutus* and 2 *Metridia* sp.) were found in a single adult female at the coastal station and 7 copepods (1 large copepod, 3 *Metridia* sp. and 3 *Oncaea* sp.) at the oceanic station. On average, 33 and 44 % (calculated from curves in Fig. 3) of all *Euchaeta antarctica* (adult males excluded) had empty guts, at the coastal and oceanic station, respectively.

The 30 adult female *Euchaeta antarctica* from South Georgia (taken in winter) contained on average 0.8 prey per individual. The 24 prey items consisted of: 8 large copepods, 3 *Metridia* sp., 7 small copepods, 4 crustaceans and 2 unidentified items. The largest prey

Table 4. *Euchaeta antarctica*. Percentage, in 4 different prey categories, of prey items found singly or together with 1, 2, 3 or more other prey (not necessarily of the same category) at stages V and VI

No. prey items	Coastal station				Oceanic station			
	Large cop.	*Met.*	Small cop.	Other	Large cop.	*Met.*	Small cop.	Other
Single	73	46	56	80	38	17	34	76
+ 1	7	40	39	17	28	24	21	11
+ 2	20	15	5	2	15	28	29	10
+ ≥3					19	32	16	3
n	15	48	66	41	72	225	190	63

cop. = copepod; *Met.* = *Metridia* spp.; Other = other prey; n = number of items within each prey category

item was a *Calanus acutus* at stage V with a mandible width of 0.20 mm. Only 3 cases of double prey ingestion were found, and 33 % had empty guts. These adult females had a prosome length between 6.8 and 7.8 mm and a mean length of 7.33 mm; the majority of these specimens had well developed ova and/or egg sacs.

The occurrence of the parasitic dinoflagellate *Blastodinium* sp., found inside the guts of *Euchaeta antarctica* from the oceanic station, was recorded in order to evaluate their possible impact on *E. antarctica* feeding behaviour. *E. antarctica* from the coastal station was not analysed for parasites. They were all at the diploblastic or polyblastic stage (e.g. Corkett & McLaren 1978). Only 1 *Blastodinium* sp. was found in each specimen. The parasite is ca 2.5 to 3.5 mm long, occupies most of the gut and is easily observed right through the copepod prosome. The 36 infested specimens (6.6 % of all *E. antarctica*, adult males excluded) did not show any apparent changes in external morphology. Although only 36 *Blastodinium* sp. were found it is notable that 59 % (n = 10) of all female V individuals were infected. Only 4.9 % (n = 22) of female VI stages and 5.0 % (n = 4) of male V stages were infected. No male VI stages were infected. Infected and uninfected *E. antarctica* contained on average 1.1 and 1.0 food items per individual, respectively.

DISCUSSION

Methods

Diel variation in feeding itself was not focussed upon in this study but the 1000 m deep plankton hauls had to be taken both day and night since a possible diel variation would affect the estimates of number of prey taken. *Euchaeta antarctica* living at different depths may have different prey encounter rates, diel feeding patterns, diet and feeding rates. Therefore, if one wishes to compare gut content data with prey occurrence in deep waters, or investigate diel feeding patterns, samples taken at different depth intervals are needed. The use of ring nets (multiple nets were not available) allows only for 2 different sampling strategies during a 24 h period: either sampling different fractions of the water column a few times, or sampling the whole water column many times. Oblique hauls through the upper 1000 m of the water column were chosen since sampling several depth intervals would give relatively few animals in each haul and only about 3 to 4 samples from each depth interval.

No fresh and undigested prey items were found in any *Euchaeta antarctica*, suggesting that feeding inside the net did not occur. Hauling and handling time will affect the number of prey items found due to digestion prior to preservation. Whether gut contents of *E. antarctica* are lost during hauling, handling and preservation due to egestion has not yet been investigated. Yen (1985) observed no loss of gut content after exposing *E. elongata* with full guts to formaldehyde in the laboratory. Incomplete mastication of prey may be another potential source of bias. In laboratory studies on *E. norwegica* prey were not always eaten entirely; this was explained by high prey concentrations (Båmstedt & Holt 1978).

Feeding

The predominance of copepods in the diet of *Euchaeta antarctica* is in accordance with earlier studies on *Euchaeta* species (e.g. Båmstedt & Holt 1978, Yen 1983, 1985, 1986, 1991, Hopkins 1985b, Hopkins & Torres 1988). The large size range of copepod prey items in this study (including the winter sample) is notable, ranging from small specimens of *Oncaea* and *Oithona* to large *Calanoides acutus* at stage V It is not surprising that adult males did not feed since their mandibles and mandibular teeth are reduced in size.

The gut contents of *Euchaeta antarctica* included a high proportion of large copepods and *Metridia* sp.; this indicates that they may be much more important as food than small copepods. This should be true even allowing for increased digestion times, since the large copepods (*Metridia* included) have a ca 5 to 15 times higher dry weight (Øresland 1990). However, no detailed estimates can be made until digestion times for different food items and more detailed dry-weight data are available. The importance of *Metridia* sp. as a food item is supported by Yen's (1986, 1991) study in which feeding experiments indicated that preferred prey of adult female *E. antarctica* during summer were ca 1.2 mm in prosome length. This size corresponds e.g. to *Metridia* at stage IV. Similarly large-sized copepods were found to be important in the diet of *Eukrohnia hamata* (Øresland 1990) except in December when small copepods predominated.

That adult females contained fewer food items than individuals at stage V at the coastal station (Fig. 3) may not necessarily mean that they ingest proportionally less food by weight. The larger females may take larger prey items (Table 2). Adult females at the oceanic station contained twice as many food items as females at the coastal station. There were no major differences in prey category proportions, predator size and water temperature which could affect overall digestion time. Therefore, this difference in gut contents may possibly reflect a real difference in food intake, which could indicate a somewhat lower energy requirement in March.

The mean number of prey for all *Euchaeta antarctica* (0.9 and 1.1 for the coastal and oceanic station, respectively) is about 4 to 10 times higher than that found for *Eukrohnia hamata* (0.10 to 0.26 from December through March) in Gerlache Strait (Øresland 1990). This difference in gut content indicates that *E. antarctica* has a higher feeding rate than *E. hamata* (0.3 to 0.7 copepods d^{-1}, Øresland 1990) even allowing longer digestion times for *E. antarctica*. When laboratory-determined digestion times for different prey categories of *E. antarctica* at stages V and VI become available, it will be possible to calculate and compare feeding rates using the data in Tables 2 to 4 and those obtained from Fig. 3. It will then also be possible to compare such feeding rates with feeding rates of *E. antarctica* estimated in laboratory experiments.

The South Georgia data show that *Euchaeta antarctica* continues to eat during winter in contrast to what was suggested for the Gerlache Strait area by Yen (1991). However, more winter data are needed if any differences in summer and winter feeding are to be understood for different areas in the Southern Ocean. The fact that *E. antarctica* is feeding during winter may, together with predation by chaetognaths, have an important cumulative effect on prey population dynamics during the long winter in the Southern Ocean, when prey production is minimal.

Parasitism and feeding

Blastodinida mainly parasitize marine protists and metazoans like copepods, siphonophores, appendicularians, jelly-fish, thaliaceans, annelids and fishes (Cachon & Cachon 1987). *Blastodinium* sp. infection in *Euchaeta antarctica* has to my knowledge not been reported previously. According to Corkett & McLaren (1978) host infection takes place by ingestion of the dinospores or cysts with the host's food. Absence of parasites in adult males may therefore be due to the fact that they were not feeding. It is not known during which period of the year infection occurs, nor is anything known about the life span of *Blastodinium* in Antarctic waters. It is therefore not possible to explain the differences in percentage infection between copepodite stages in this rather limited material.

The occurrence of *Blastodinium* sp. did not affect the number of food items found in the gut. It is, however, not known if digestion times and feeding rates of the host are affected by this parasite. Ianora et al. (1990) found numerous, apparently functional, chloroplasts in the cytoplasm of *Blastodinium*. Ianora et al. (1990) reported (referring to Pasternack et al. 1984) that photosynthetic activity in *Blastodinium* might contribute up to 50 % of the nutritional requirements of the parasite. However, according to Cachon & Cachon (1987) there are various intermediary stages between autotrophy and complete heterotrophy in this genus. Different negative effects on the reproductive biology of their hosts were reported, e.g. sexual castration (Cachon & Cachon 1987) and sex reserval (Cattley 1948). Ianora et al. (1990), however, found no sexual castration or abnormal ovaries.

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