

Feeding and predation impact of the chaetognath *Eukrohnia hamata* in Gerlache Strait, Antarctic Peninsula

Vidar Øresland

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

ABSTRACT: Chaetognaths *Eukrohnia hamata*, *Sagitta marri*, *S. gazellae* and *S. maxima* were caught monthly, from December 1986 through March 1987, during 24 h sampling programmes. *E. hamata* made up 94 % of all chaetognaths by number and 2 to 7 % of zooplankton wet weight. Gut content analyses showed that *Euchaeta*, spp., *Calanoides acutus*, *Metridia gerlachei*, *Microcalanus pygmaeus*, *Oncaea*, spp., *Oithona*, spp. and appendicularians were the main prey of *E. hamata*. A feeding rate of 0.8 appendicularians d^{-1} in January could not explain a drastic reduction of the appendicularian population in February. Feeding rates for copepods varied from 0.3 to 0.7 prey d^{-1} , being highest in December and March. *E. hamata* consumed between 5 and 11 % of its own dry weight in copepods d^{-1} . Large copepods were more important (on a dry weight basis) than small copepods as food for *E. hamata*. It is suggested that even if the daily impact of *E. hamata* predation is low, it may have an important cumulative effect on copepod populations during the long winter period, when prey production is minimal.

INTRODUCTION

Antarctic food web literature is dominated by studies on krill and vertebrates. Much less attention has been given to the planktonic part of the food web (krill excluded), although it constitutes an important part of Antarctic life. Hopkins (1985a, b) examined the zooplankton and micronekton community and characterized the principal features of the food web in Gerlache Strait, Antarctic Peninsula, in the austral fall. However, detailed information on diel feeding behaviour, seasonal changes in diet and feeding rates, as well as estimates of predatory influence on prey populations, is still lacking for Antarctic carnivorous zooplankton.

Chaetognaths are dominant zooplankton predators in all oceans, including Antarctic waters. Among the macrozooplankton, they are often second only to copepods in abundance and biomass. Chaetognaths are generally believed to have a considerable influence on their prey populations, of which copepods seem to be most important (for review, see Feigenbaum & Maris 1984). Only limited information on the diet of chaetognaths from Antarctic waters is available (David 1955, Hopkins 1985b, Hopkins & Torres 1989). The most abundant

chaetognath species in Antarctic waters are *Eukrohnia hamata* (often comprising 90 to 95 % of all chaetognaths), *Sagitta gazellae* and *S. marri* (David 1955, 1956, 1958, 1965, Timonin 1968, Dinofrio 1973, James 1979, Alvarino et al. 1983a, b, Hagen 1985). In this study the feeding of these chaetognaths is compared, and some speculations concerning the predation impact of *E. hamata* on its prey populations are considered.

METHODS

Zooplankton were collected hourly, from RV 'Polar Duke', in Hughes Bay, Gerlache Strait (Fig. 1) during 24 h sampling programmes on 22 to 23 December 1986, and 26 to 27 January, 28 February (sampling stopped after 9 h due to bad weather conditions) and 20 to 21 March 1987. A 4.5 m long ring net with 1 m opening diameter and 300 μm mesh size was used. Double oblique hauls of 25 to 50 min duration were made from near (< 100 m) the bottom to the surface. Sampling depth was estimated from wire angle and wire length. Bottom depth varied between 270 and 500 m. Net speed was 1 to 1.5 $m s^{-1}$. Sampling was not quantitative since no flowmeter was used, and numbers of organ-

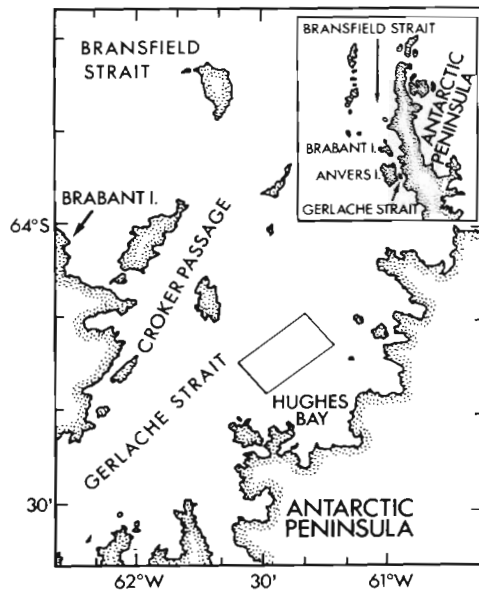


Fig. 1. Sampling area in Hughes Bay, Gerlache Strait

isms are presented as percentage values and as numbers per net haul. All samples were immediately preserved in 4 % formaldehyde in seawater, buffered with borax. STD or CTD casts were made on all sampling occasions and hydrographic data are presented in Niiler et al. (1990). Below 50 m depth there was little variation in temperature (generally from -1 to 0 °C).

All chaetognaths were sorted out from the samples, and appeared to be in good condition (the body, gut, and most of the fins were intact). They were measured in 1 mm size intervals under a stereomicroscope. Body length was measured from the anterior tip of the head to the end of the tail, excluding the tail fin. Maturity stages of *Eukrohnia hamata* were classified according to the development of the ovaries as follows; Stage 1, ovaries rudimentary or not visible; Stage 2, short and thin ovaries, ova hardly visible; Stage 3, ova easily visible, tail segment always full and opaque. This is a modification of the maturity stage system used by David (1955) for *Sagitta gazellae*. Stage 3 includes David's Stages 3 and 4. His Stage 5 (spawned individuals) was not found in this study.

Analysis of chaetognath gut content was inferred from identification of prey mandibles or other hard or special prey parts and followed the same procedure as in Øresland (1987). Feeding in the net was not regarded as important in this study since the frequency of food items in the forward part of the gut was always low (see also Pearre 1973, Feigenbaum 1982, Øresland 1987, Sameoto 1987).

The remaining zooplankton was subsampled, using a Folsom splitter (McEwen et al. 1954) and Kott's plank-

ton splitter (Kott 1953), and all specimens were counted. Identifications of zooplankton were made mainly according to Mackintosh (1934), Vervoort (1951, 1957), David (1956), Alvarinho (1962), Ramirez & Dinofrio (1976), and Park (1978). The wet weight of the preserved samples (total or subsamples, and animals > 15 mm long removed) was determined after free water was removed by vacuum through a glass micro-fibre filter until the water ceased to drip from the funnel. All chaetognaths were weighed separately, and their wet weight compared to the weight of the remaining zooplankton.

The average individual dry weight of small copepods, large copepods and *Eukrohnia hamata* in December through March was estimated by weighing 100, 50 and 30 specimens respectively from each month on a microbalance. All specimens were sorted out at random and dried at 60 °C for 48 h. The dry weight data are used when calculating the daily consumption of small and large copepods and consumption in relation to *E. hamata* body weight.

Calculation of the daily feeding rate, on each prey category, followed the same procedure as in Øresland (1987) using the equation (Bajkov 1935):

$$FR = \frac{\text{mean NPC} \times 24}{DT}$$

where FR = daily feeding rate (no. prey d^{-1}) (each category of prey is estimated separately); mean NPC = mean number of a certain prey category per chaetognath during a 24 h period; DT = digestion time (h) for a certain category. Multiplication by 24 gives the daily feeding rate. See Feigenbaum & Maris (1984) for a discussion of the equation.

In order to obtain mean NPC values for different prey categories, the numbers of prey per chaetognath (NPC) obtained from different samples during the 24 h sampling periods were plotted for *Eukrohnia hamata* (Fig. 3). Unidentified and unusual prey categories, comprising 8 % of all food items, were excluded. The mean height of the curve connecting the NPC data is equal to the mean NPC. The mean height was calculated by taking 5 photocopies of each curve which were cut out and weighed on a microbalance. The mean weight of each curve was then divided by the weight of a known area of the same paper and also divided by the length of the x-axis enclosed by the curve. This length corresponds to the time duration of sampling. The mean heights were also calculated using a MOP-Videoplan image analyzer (Kontron Electronics), which gave the same results as the weighing method. Since no data are available on the digestion time of Antarctic chaetognaths, data on *Sagitta elegans* from the Swedish west coast (Øresland 1987) were used when calculating feeding rates (see below).

RESULTS

Eukrohnia hamata was by far the most common chaetognath in this study. The relative occurrences of *E. hamata*, *Sagitta marri* and *S. gazellae* were quite constant and ranged between 93 and 95 %, 3 and 7 % and 0 and 3 % respectively (minimum and maximum mean values of the 4 sampling series). A few (maximum 18) *S. maxima* were caught during each sampling series. The percentage wet weight of *E. hamata* was 7.2, 3.0, 1.9 and 2.5 % of that of the 300 µm net zooplankton, from December through March. Fig. 2 shows no large change in the size frequency distribution of *E. hamata* which could affect feeding behaviour in this study. However, a slight increase in length of individuals at Stage I from December through March is perhaps indicated. The median of all *E. hamata* was constant at 16 mm from December through February and increased to 18 mm in March. Size classes consisting of individuals making up less than 1 % of the sample size are not shown. No individual was shorter than 5 mm. Maximum length of *E. hamata* was 31 mm (not shown), found in January and March. There were no great shifts in stage distribution. A few Stage 3 individuals (not shown) were found also in December and January. No spermatophores (= sperm clusters) or marsupial sacs (Alvariño 1968), were found on Stage 3 specimens.

The variety of food items within the different species (Table 1) reflects to some degree the number of

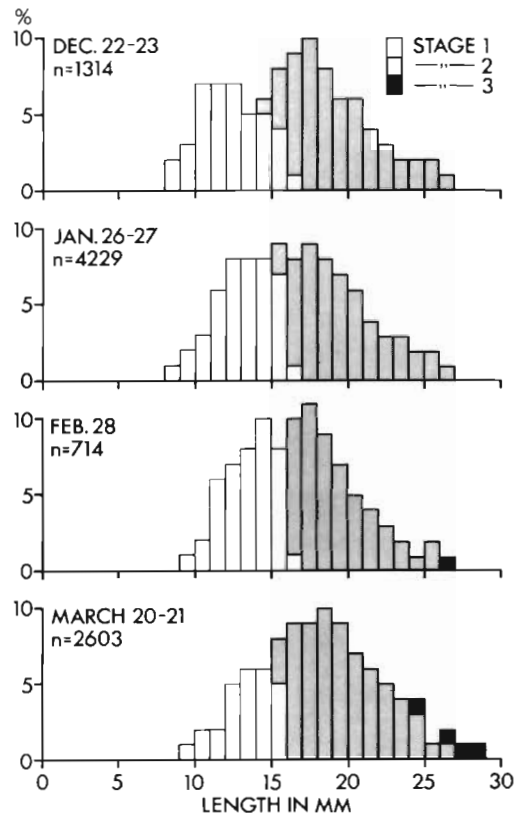


Fig. 2. *Eukrohnia hamata*. Length-frequency and maturity stage distribution in Hughes Bay, 1986-87

Table 1. *Eukrohnia hamata* and *Sagitta* spp. Food items found in chaetognaths from December 1986 through March 1987

Food item	Chaetognath			
	<i>E. hamata</i>	<i>S. marri</i>	<i>S. gazellae</i>	<i>S. maxima</i>
<i>Rhincalanus gigas</i>	•		•	
<i>Euchaeta antarctica</i>	•			
<i>Euchaeta</i> spp.	•			•
<i>Calanoides acutus</i>	•	•	•	
<i>Metridia gerlachei</i>	•	•	•	•
<i>Scolecithricella</i> spp.	•			
<i>Microcalanus pygmaeus</i>	•			
<i>Oithona</i> spp.	•			
<i>Oncaea</i> spp.	•	•	•	
Unident. copepodids	•	•	•	
Copepod nauplii	•	•		
Unident. crustaceans	•	•	•	
Euphausiid larvae	•		•	
Appendicularians	•			•
<i>Sagitta marri</i>		•	•	
Unident. chaetognaths	•			•
Polychaetes		•	•	•
Unident. non-crustaceans	•	•	•	
No. of food items	1870	89	41	7
No. of chaetognaths	8860	388	157	35
No. food/No. chaetogn.	0.21	0.23	0.26	0.20

chaetognaths analyzed. Copepods were the most common food item found in all the chaetognath species. An interesting difference between species is that *Eukrohnia hamata* contained many appendicularians (shown below) while *Sagitta marri* and *S. gazellae* only had 2 and none, respectively. Another notable difference is that polychaetes (mainly *Pelagobia longicirrata*) made up 34 % of the food items of all *S. gazellae* but only 3 and 0 % of the food items of *S. marri* and *E. hamata*, respectively. Most polychaetes found in *S. gazellae* (11 out of 14) were found in March. Two

and 4 krill larvae (calyptopis stages) were found in *E. hamata* and *S. gazellae*, respectively. Only a single chaetognath prey item was taken by each chaetognath species. The similarity between species in number of prey per chaetognath is notable. The few *S. maxima* contained no unusual prey.

NPC (number of prey per chaetognath) curves for *Eukrohnia hamata* are shown in Fig. 3. The copepod *Metridia gerlachei* (Stages III to VI) constituted 31, 35, 39 and 52 % of all large copepods found in *E. hamata* from December through March. The corresponding

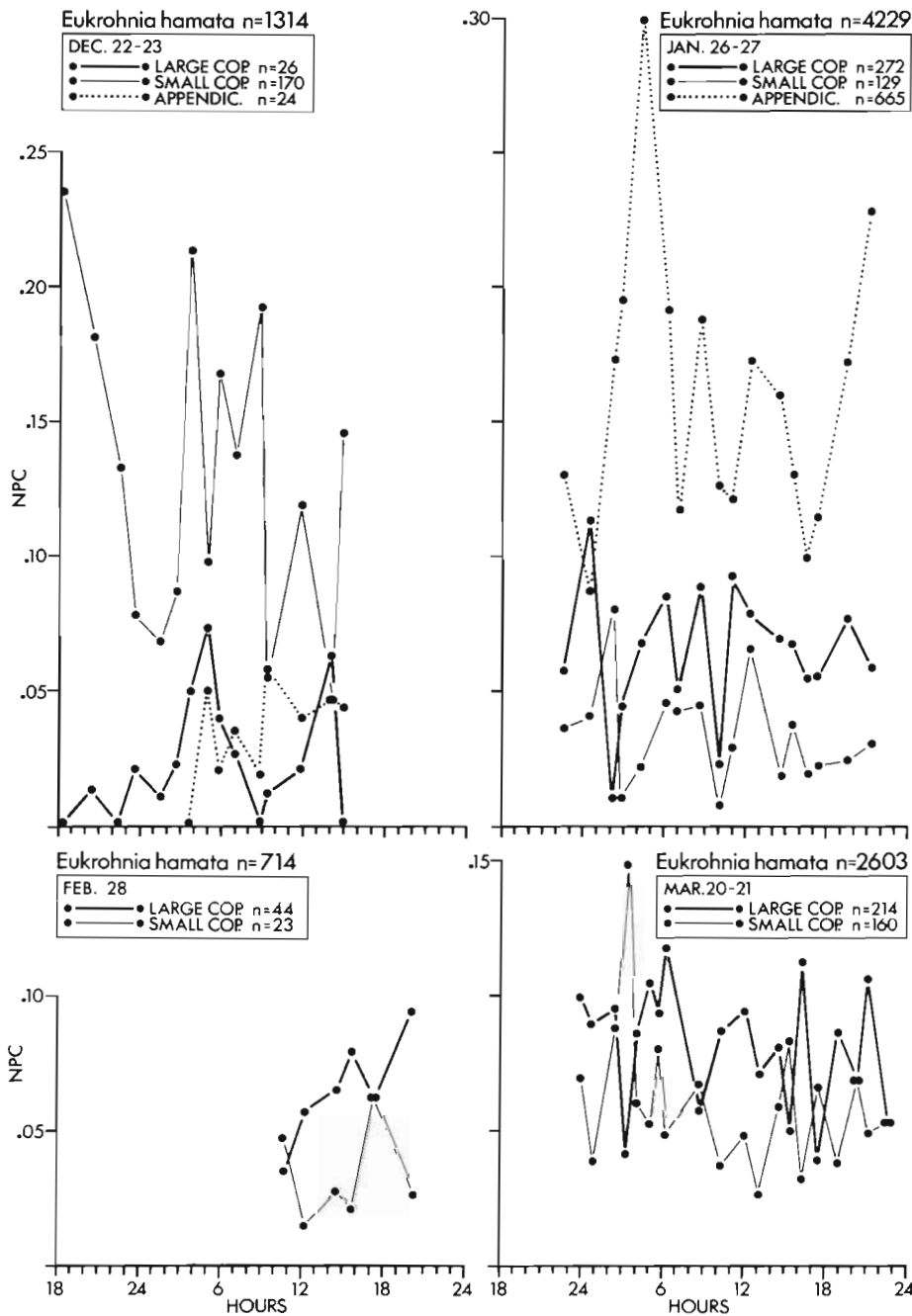


Fig. 3. *Eukrohnia hamata*. Number of prey per chaetognath (NPC) during 24 h for different prey categories in Hughes Bay, 1986-87. Large copepods include copepodids with mandible width > 0.06 mm, including *Metridia gerlachei* III as the smallest size within the category. Small copepods are all other copepods with mandible width ≤ 0.06 mm

values for *Euchaeta*, spp. (Stages III to V) were 42, 43, 23 and 8 %, and for *Calanoides acutus* (Stages III to VI) they were 4, 21, 27 and 40 %. It is notable that no adult *Euchaeta* spp. was taken. Only a single appendicularian was taken in February and none was taken in March. The NPC curves also give some indications of the variation in feeding intensity during the 24 h sampling periods.

Table 2 shows the mean NPC and the daily feeding rate (FR = no. prey taken daily) of *Eukrohnia hamata* for the 3 major prey categories. January had the highest total FR value due to the consumption of appendicularians. If only copepods are considered the total FR in December was double that in January and February, due to feeding on small copepods. On a dry weight basis, however, large copepods comprised 48, 86, 94 and 92 % of all copepod biomass consumed from December through March, indicating the importance of large copepods as food for *E. hamata*. *E. hamata* consumed 5, 7, 8 and 11 % of its own biomass in copepods d⁻¹ from December through March. The FR calculations are assumed here not to be affected, through longer digestion time, by whether the prey occurred alone or together with other prey. The occurrence of multiple prey in *E. hamata* was low, varying between 1 % (January) and 7 % (March), and more than 2 prey items were never found together.

Small copepods were probably seriously underestimated by the 300 µm net (see 'Discussion'). The percentage occurrence of prey categories in the water column shown in Fig. 4 should therefore be interpreted

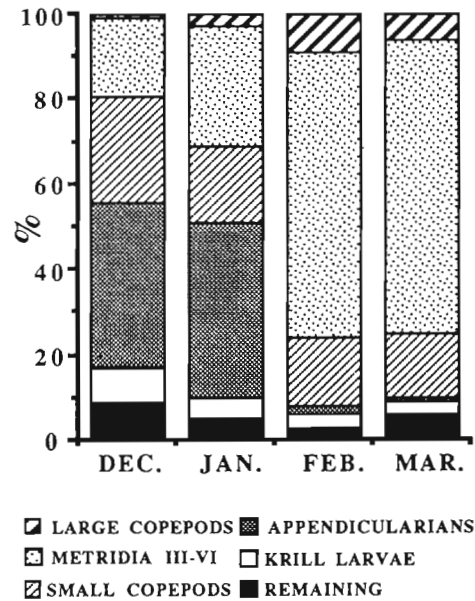


Fig. 4. Percentage occurrence of prey categories caught in a 300 µm plankton net in Hughes Bay, 1986-87. Large copepods include copepodids in Stages III to VI of *Calanoides* and *Euchaeta* spp. or similar sized copepods. Small copepods include all copepodids I and II and copepods such as *Oncaea*, *Oithona* and *Microcalanus* spp.

with caution. *Metridia* Stages III to VI were so common that they are shown specifically. The notable increase of *Metridia* Stages III to VI and large copepods and the decrease of appendicularians in February and March are reflected in diet and FR shown in Table 2. Table 3

Table 2. *Eukrohnia hamata*. Mean number of prey items per chaetognath (mean NPC) during 24 h, based on curves shown in Fig. 3. Daily feeding rates (FR) are shown within brackets. Assumed digestion time for large copepods is 9.33 h and for small copepods and appendicularians 4.90 h (from Øresland 1987)

	1986 22-23 Dec	1987 26-27 Jan	1987 28 Feb	1987 20-21 Mar
Median length <i>E. hamata</i> (mm)	16	16	16	18
Food items				
Large copepods ^a	0.02 (0.05)	0.07 (0.18)	0.07 (0.18)	0.08 (0.21)
Small copepods	0.13 (0.64)	0.03 (0.15)	0.03 (0.15)	0.06 (0.29)
Appendicularians	0.02 (0.10)	0.16 (0.78)	^b ^b	^b ^b
Total	0.17 (0.79)	0.26 (1.11)	0.10 (0.33)	0.14 (0.50)
No. of food items	220	1066	67	374
No. of analyzed <i>E. hamata</i>	1314	4229	714	2603

^a Large copepods include all copepods with a mandible width > 0.06 mm, and *Metridia* III. Small copepods include all other copepodids
^b Only one appendicularian was taken in February and none was taken in March

Table 3. Daily proportion (%) of prey standing crop taken by *Eukrohnia hamata* in Hughes Bay, 1986–87

	December	January	February	March
Large copepods	0.06	0.06	0.03	0.05
Small copepods ^a	0.58	0.10	0.12	0.34
Appendicularians	0.06	0.21	c	c
Standing crop ^b				
No. <i>E. hamata</i>	88	249	119	130
No. large copepods	7931	69840	70000	55255
No. small copepods ^a	9707	38720	14880	11200
No. appendicularians	13930	92160	1600	1307
No. of net hauls	15	17	6	20

^a Number of small copepods was probably underestimated by the 300 µm net resulting in an overestimation of the predation impact

^b Mean number of *E. hamata* and prey organisms per net haul

^c Only one appendicularian was taken in February and none was taken in March

shows the daily percentage proportion of the prey standing crop taken by *Eukrohnia hamata*. These data were calculated by multiplying FR (Table 2) by 100 × number of *E. hamata* (Table 3) and then dividing by number of 'available' prey (Table 3).

DISCUSSION

Knowledge of the size distributions of predators is important since size often sets the limit for what prey a predator may be able to take. Further, size distribution and maturity stage data give information about life span, breeding periods and periods of growth, which are important to consider when food requirement and feeding are to be understood. The length of the life span and the breeding periods are unknown or uncertain for all chaetognaths in Antarctic waters, due to lack of information on size and maturity status during most of the year.

It is known that the large individuals of *Eukrohnia hamata* in Antarctic waters occur deeper than small individuals (Hagen 1985). Consequently, the proportion of individuals in Stage 3 and spawned individuals, if they existed in the area during this period, may have been underestimated due to occurrence below sampling depth and even occurrence close to the bottom. The total lack of *E. hamata* shorter than 5 mm may perhaps have been due to mesh size (300 µm) of net. These limited data give little support for a major breeding peak of *E. hamata* during summer, but breeding at a low level cannot be excluded. The small changes in size distribution during summer indicate a life span longer than 1 yr. In Korsfjorden, Norway, *E. hamata* appeared to have a life span of 2 yr with breeding at a maximum during spring and fall and at a low level during summer (Sands 1980). A 2 yr life

span in Arctic waters was suggested by Kramp (1939), Bogorov (1940) and Sameoto (1987).

Diet

It was no surprise that copepods were the main food for these Antarctic chaetognaths since copepods are known to be the main food for chaetognaths in general, as well as making up the main part of zooplankton (krill excluded from this discussion). Hopkins (1985a) found that *Metridia gerlachei*, *Calanoides acutus* and *Euchaeta antarctica* comprised 74 % of zooplankton biomass (dry weight) and that small species and *M. gerlachei* were the most numerous copepods in March–April in Croker Passage, Gerlache Strait. Sullivan (1980) found that especially small copepods were common in the gut content of *Eukrohnia hamata* in the subarctic Pacific. David (1955), Hopkins (1985b) and Hopkins & Torres (1989) reported copepods as most frequent prey (of a total of 45, 20 and 33 food items found, respectively) in some Antarctic chaetognaths.

It is difficult to explain the fact that appendicularians were almost exclusively taken by *Eukrohnia hamata* and polychaetes almost exclusively taken by *Sagitta gazellae*. It is not possible to relate vertical distribution to diet in this study, due to the sampling method used. According to Hagen (1985) the chaetognaths showed no diel migration and the 3 chaetognath species had an overlapping vertical distribution. *E. hamata* and *S. gazellae* showed a wide depth range. *S. marri* was usually found deeper than 200 m, perhaps explaining why it took few appendicularians, which inhabit the upper 100 or 200 m. The size of appendicularians should not pose a problem for any of the chaetognath species, which all have overlapping size distribution. The polychaete *Pelagobia longicirrata* was taken both

by the largest and the smallest chaetognath species but not by the medium-sized *E. hamata*. Øresland (1987) reported a similar difference in diet between chaetognath species in Gullmarsfjorden, Sweden, where *S. setosa* fed on appendicularians and the deeper living *S. elegans* did not. Feigenbaum (1982), on the other hand, reported a sharp increase in ingestion of appendicularians from 1 to 10 March by *S. elegans* in Vineyard Sound, Massachusetts, USA, an area where the species occurs in the surface layer. Perhaps all of these differences in diet are due to different encounter rates of prey but this would have to be investigated on a space and time scale important to the chaetognaths.

Predation on chaetognaths does not seem to be important in *Eukrohnia hamata* during this time of the year and the data for the other chaetognath species are too limited to permit any conclusions. It should be noted, however, that cannibalism and predation on small prey populations may have a drastic effect even at what for normal food categories might be considered a low feeding rate (see Øresland 1987). David (1955) found as much as 13 % chaetognaths (by number) in the gut of *Sagitta gazellae*. Sullivan (1980) found only 4 prey chaetognaths in *E. hamata*.

Feeding rates

The estimates of mean NPC and DT are equally important when calculating FR, and the possible bias in these estimates should be considered and compared in relation to the desired reliability level of the FR calculations. The diel variation in feeding indicates the importance of 24 h sampling programmes if reasonable estimates of mean NPC for different food categories are to be obtained for that period. However, for a period of 1 mo or longer, a single 24 h sampling period may not be representative enough, especially during periods with large changes in food species composition. The calculated FR may be biased due to the use of DT data from another chaetognath species and from a somewhat higher temperature (*Sagitta elegans* at 6 °C; Øresland 1987). The use of data from organisms living at a higher temperature would overestimate FR and the predation impact. However this needs to be verified experimentally.

The only other DT estimate at low temperature (*Sagitta elegans* at 0 °C) is 10.2 h for copepods (Feigenbaum 1982). However, the estimates in Øresland (1987) were chosen since they indicate an important difference between DT of small and large copepods. Furthermore, the size of the chaetognaths in the DT experiments in Øresland (1987) was more similar to *Eukrohnia hamata* in this study. The FR estimates on appendicularians in this study could be biased by the

assumption that appendicularians only appeared as single prey in the gut and by the assumption that DT for appendicularians is equal to that of small copepods. Shelbourne (1962) reported that *Oikopleura dioica* in the North Sea usually contained 2 or 3 pellets. This indicates that multiple appendicularian prey were not common in this study, since no chaetognath contained more than 3 appendicularian fecal pellets.

The FR of *Eukrohnia hamata* for copepods ranges from 0.3 to 0.7 prey items d^{-1} , rather similar to the FR range (0.2 to 1.0) of *Sagitta elegans* on the Swedish west coast (Øresland 1987), which is a species of similar size and which takes similar sized prey. *E. hamata* consumed between 5 and 11 % of its own dry weight in copepods d^{-1} . The few available estimates on other species ranges between < 1 and 40 % (Feigenbaum & Maris 1984). Differences between the estimates are difficult to interpret since they were obtained using different methods and assumptions. Low temperature and absence of diel vertical migration should decrease food requirement of *E. hamata*. Food is available throughout the year and a build up of food reserves for the winter period does not seem to occur. The gut of *E. hamata* contains an oil droplet whose function is obscure. The small size of the oil droplet does not indicate a winter storage function. Buoyancy control and/or food storage for occasional use are more probable functions. Many chaetognaths have an ambush feeding behaviour (Feigenbaum & Maris 1984) which should reduce food requirement.

Predation impact

The daily predation on large copepods ranged from 0.03 to 0.06 % (by number) and on small copepods it ranged from 0.10 to 0.58 % of respective standing crop. However, the estimates of predation on small copepods should be regarded as overestimates since the occurrence of small copepods in the sea was underestimated by the 300 μm net (Sullivan 1980, Hopkins 1985a). Sameoto (1987) calculated that chaetognaths (mainly *Eukrohnia hamata* and *Sagitta maxima*) were major predators on copepods, consuming between 1.2 and 1.3 % (by number) of the copepod standing crop d^{-1} . Oil from oil-rich prey can remain in the gut to some degree after the faecal pellet has been dropped (Øresland 1987). However, the oil in the slightly expanded middle part of the gut, especially in larger individuals, occurs independently of food presence in the gut. Therefore, oil in *E. hamata* should not necessarily be interpreted as food remains in gut content analyses (as was done by Sameoto 1987). In this study the proportion of *E. hamata* to zooplankton wet weight ranged from 2 to 7%. Sameoto (1987) reported that in August, as much as 5 to

17 % of the zooplankton biomass (wet weight) consisted of chaetognaths in Baffin Bay, western Greenland.

Life spans and productivity of prey organisms are important when predation impact is considered. Calculations on predation impact using standing crop are of limited value during periods of high productivity, and will always overestimate predation. However, in Antarctic waters the period of high production is probably limited to a few months for most prey species of *Eukrohnia hamata*. Unfortunately, there are no productivity estimates for the common prey species of *E. hamata* in Antarctic waters. Knowledge of the life spans and the breeding periods of the Antarctic copepods is limited (especially for small copepods). Marin (1988) reported a life span of 1 yr for *Calanoides acutus* and *Calanus propinquus* and 1 to 2 yr for *Rhincalanus gigas*. Most common copepods do not reproduce during winter, and growth is probably limited during this long period, although the winter season may be more biologically active than previously presumed (Marin 1988). A rough calculation, 0.05 multiplied by 240 (d), estimates that *E. hamata* can reduce copepod populations by about 12 % from March to October (assuming a daily predation of 0.05 % of standing crop, no production, and the all other factors remain constant). Øresland (1987) found that *Sagitta elegans* continued to feed (on large copepods only) during winter. The feeding rate (dry weight) was approximately equal in winter and summer (see Table 3 in Øresland 1987) assuming that the dry weights of large copepods were 5 times higher than that of small ones. In this study the dry weights of large copepods were between 5 and 15 times those of small ones.

Appendicularians were not regarded as important food for *Eukrohnia hamata* in this study due to their low biomass. Chaetognath predation cannot itself explain the strong decrease in appendicularian abundance in February. The proportion of appendicularian standing crop taken daily in January was 0.21 %. A rough calculation shows that the appendicularians would be reduced by about 6 % in 30 d, assuming no production and all other factors constant. The food of appendicularians consists of small phytoplankton and protozoan organisms (Raymont 1983). Therefore, the decrease in appendicularian abundance might possibly be related to the general decrease in phytoplankton biomass and production found in February (see Holm-Hansen & Mitchell 1990).

CONCLUSIONS

Copepods are the main food of chaetognaths in Antarctic waters. Large copepods are more important (on a dry weight basis) than small copepods as food for *Eukrohnia hamata* (they are equally important in

December). *E. hamata* is not responsible for the decrease in appendicularian abundance in February. It is suggested that a low but continuous predation impact on copepods during the long winter, when little production takes place, may affect prey population dynamics. Such a predation effect during winter would of course be strengthened if other planktonic predators than chaetognaths, such as the common predatory copepods of the genus *Euchaeta*, eat during winter.

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