Prey composition and feeding rate of *Sagitta elegans* var. *arctica* (chaetognatha) in the Barents Sea in early summer

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Sagitta elegans var. *arctica*, the dominant and locally abundant chaetognath in the Barents sea, was collected from the upper 50 m in Arctic water masses during an ice edge bloom in early summer 1983. In situ sampling was made along a transect at discrete depths with a 375 µm mesh net mounted on a plankton pump. Prey composition and feeding rate were estimated from gut content analyses on preserved specimens combined with data on digestion times from previous studies. No diel variations were found in feeding activity. The diet reflected the composition of available prey in the zooplankton and consisted mainly of nauplii, small copepods (early stages of *Calanus*, *Pseudocalanus*, *Oithona*) and appendicularians. Prey usually occurred as a single item in the gut.

Mean prey body width related to chaetognath head width yielded a power curve, with a large amount of scatter, showing that chaetognaths in the Barents Sea can use a wide spectrum of prey sizes. Similarly, maximum prey body width was related to chaetognath head width as a power curve, reflecting the existence of an upper prey size limitation due to the chaetognath mouth size. The highest abundance of *S. elegans* (5 specimens m^{-3}), and the most intense feeding activity, were found within or beneath the maximum zooplankton biomass. Further, distribution and feeding were affected by light intensity, salinity, and the population structure of *S. elegans* var. *arctica*.

Estimated feeding rates ranged between 0.30 and 1.05 prey items per chaetognath day^{-1}. This corresponds to an ingestion of 8–54 µg AFDW day^{-1}, and a consumption of 0.08–0.22% of the zooplankton standing stock day^{-1}. From these rates, the calculated yearly ingestion by *S. elegans* var. *arctica* was 3% of the annually secondary production.

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Introduction

Chaetognaths are supposed to be important predators in copepod communities (review of feeding given by Feigenbaum & Maris 1984), and gut content analyses from field samples have shown that chaetognaths may consume a significant part of the herbivore standing stock and/or production (Sameoto 1973; Kotori 1976; Davis 1984; Williams & Collins 1985). The diet often reflects what is available in the zooplankton (Pearre 1973; Sullivan 1980), and due to prey size selection (Reeve & Walter 1972; Pearre 1980; Kimmerer 1984; Greene 1986) chaetognaths may also have a considerable influence on size structure within lower trophic levels. Feeding and vertical migration are usually coupled processes and have therefore often been studied together (reviewed in Alvariño 1965). Both field and laboratory studies suggest that factors such as temperature, light, salinity, density, maturity stage and prey abundance play major roles in regulating vertical distribution and feeding (Harder 1968; Rakusa-Susczewski 1969; Jacobsen 1971; Pearre 1973; Szyper 1978; Feigenbaum 1979; Sullivan 1980).

Considered to be the cold-water variant of *S. elegans* Verrill, the chaetognath *Sagitta elegans* var. *arctica* Aurivillus was the dominant chaetognath species in the study area in the Barents Sea during the period of investigation. North of the Polar Front in the Barents Sea, the water column stabilises during spring as a result of ice melting. A short-lived phytoplankton bloom at the ice edge gives rise to spawning and the development of zooplankton (Marshall 1958; Rey & Loeng 1985; Rey et al. 1987) which, in turn, may be preyed upon by *S. elegans* var. *arctica*. Feeding in *S. elegans* at low temperature has previously been studied at the western side of the Atlantic (Sameoto 1972, 1973, 1987; Pearre 1973, 1981; Feigenbaum 1982). Almost all studies on feeding are from bays or semi-enclosed bodies of water, and so far no studies have been published on chaetognath feeding in Arctic open-ocean areas, where the temperature is close to the freezing point. The objective of this study was to define the prey population of *S. elegans* var. *arctica* and relate this to the individual size of the chaetognath. In addition the predation rate was related to the environmental conditions, and an energy budget was defined to evaluate the impact of the chaetognaths on the zooplankton community. This work was conducted in conjunction with the Norwegian Research Program for Marine Arctic ecology (Pro Mare) and in partial fulfillment toward a Cand. Scient. degree at the Department of Fisheries and Marine Biology, University of Bergen, Norway.

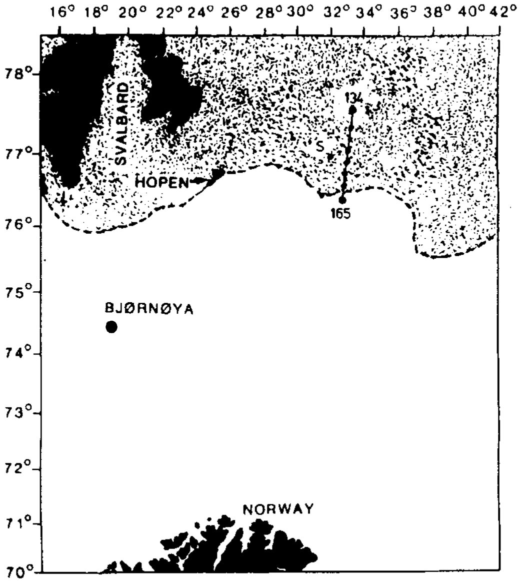

Fig. 1. Map of the Barents Sea showing the position of the transect (heavy line), and the station where samples were taken during a 24 hour period (S). Dotted line: approximate position of the ice edge May–June 1983.

Materials and methods

Sampling stations were located in the Arctic waters east of Svalbard and north of the ice edge, along a transect extending from 76°40'N to 77°35'N (Fig. 1). Zooplankton were sampled from the upper 50 m between 27 May and 13 June, 1983, during a cruise in the Barents Sea on R/V LANCE. A submersible plankton pump (0.9 m opening diameter; Solemdal & Ellertsen 1984), fitted with a 375 μm mesh net, was pumped for one minute at 4 to 7 discrete depths (Table 1). Due to its high capacity ($2.3\,m^3 \cdot s^{-1}$ capacity; Hassel pers. comm.), low water velocity ($1.5\,m \cdot s^{-1}$) and filtration in situ, this pump is suitable for providing qualitative sampling of zooplankton of good quality. Technical specifications and performance characteristics are described in Solemdal & Ellertsen (1984). At each station, preliminary results on the vertical distribution of phytoplankton were given by an in situ fluorescence profile (Q-Instruments, Denmark). The actual zooplankton sampling depths were chosen on the basis of this information. Vertical profiles of salinity and temperature were obtained by using a Neil-Brown MK III CTD, and subsurface light extinction was measured with a Lambda LI-185 quantum meter and an underwater quantum sensor.

A Folsom plankton splitter was used for subsampling zooplankton samples (Motoda 1959). One half was immediately preserved in 4% buffered formaldehyde, and the other half was fractionated by pouring the sample through 250, 500, and 1000 μm sieves. These fractions were used for zooplankton biomass estimations by drying the samples at 80°C over night, weighing them and then combusting them in a furnace at 500°C for 24 hours. The weight lost from dry to ashed material (ash free dry weight, AFDW) was used as a measure of zooplankton biomass.

All chaetognaths were removed from the preserved subsample. Samples with many *S. elegans* were subsampled a second time with the Folsom splitter, yielding a subsample of one quarter of the total sample. The chaetognaths were counted and examined under a Wild M5A dissecting microscope. Body length was measured to the nearest mm from the top of the head to the end of the tail (excluding the tail fin) by placing a piece of graph paper with 1 mm grid under a petri dish. Head widths were measured with the chaeta in closed position using an occular micrometer, and a regression equation of head width versus body length was established (Fig. 2) from measurements of 175 specimens.

Since *S. elegans* is a protandric hermaphrodite with continuous development from juvenile to

Table 1. Sampling depths at stations along the transect.

Sampling depth (m)	134 77°35'N	137 77°19'N	158 77°00'N	160 76°55'N	162 76°50'N	164 76°45'N	165 76°40'N
5	X	X	X	X	X	X	X
15	X	X	X	X	X	X	X
20							X
25			X	X	X	X	X
30	X	X					X
35							X
40			X	X	X	X	X
50	X	X					X

mature stage, classification into developmental stages is highly subjective. The criteria used here are primarily based on the ripening of the ovaries, which are more readily seen than the male gonads (Russell 1932; McLaren 1969):

Stage I Ovaries invisible or very small. No sperm cells visible in the tail.

Stage II Ovaries visible, but eggs small and uniform.

Stage III Well-developed ovaries with some eggs larger than others, seminal vesicles conspicuous.

Chaetognaths can lay several batches of eggs over a protracted period (Dallot 1968; Ghirardelli 1968; Reeve & Cosper 1975; Nagasawa 1984). The release of eggs causes shrinkage of the ovaries (Dallot 1968) and presents problems in differentiating Stage II from Stage III, where eggs have been released (spent). In this study, spent individuals, which were recognised as large specimens with unusually small ovaries in spite of well-developed seminal vesicles, were classified as Stage III.

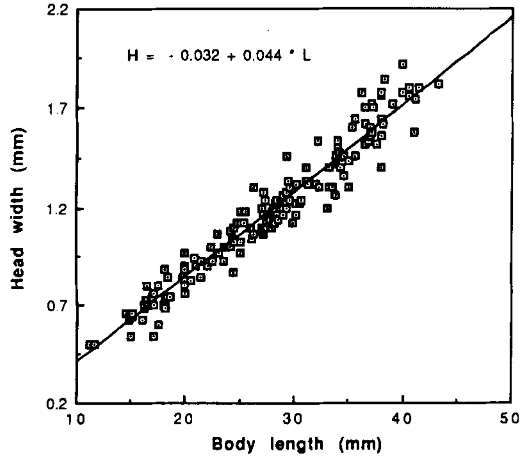

Fig. 2. Sagitta elegans var. *arctica*. Barents Sea. Head width (H, in mm) versus body length (L, in mm).

Specimens with prey in the gut were separated and the position of the prey item in the gut was noted. Cod-end feeding is usually considered to be a source of error in gut content analyses (Reeve et al. 1975; Sullivan 1980). After passing the propeller of the pump, however, it is not likely that the chaetognaths continue to feed in the cod end. Besides, at the low temperature of the Arctic water (below 0°C), the time for swallowing and digestion by *S. elegans* var. *arctica* is prolonged (Feigenbaum 1982). Therefore, only prey items that had not been completely swallowed (less than 0.2% of the total prey found) were excluded from the feeding-rate analyses. Prey items were dissected, using needles made of tungsten-wire sharpened in melted $NaNO_2$ (Øresland 1987), and were then divided into three groups according to the degree of digestion (Nagasawa & Marumo 1972, 1976; Pearre 1973; Feigenbaum 1979):

Group 1. Prey intact and situated in the anterior half of the gut.

Group 2. Prey partly digested but with the shape still recognisable.

Group 3. Prey with shape that is difficult to identify, and often not visible through the body wall, situated in the posterior part of the gut.

Groups 1 and 2 were used as indicators of actively feeding chaetognaths (Pearre 1973). Body widths of prey items in Group 1 were measured in order to relate prey size to chaetognath head width. Head width is considered to be more closely related to prey size than body

Table 2. Shape and size of mandibulae blade in copepods, used for identification of gut content in *Sagitta elegans*, Barents Sea. A. *Calanus* spp., B. *Pseudocalanus* sp., C. *Oithona* sp., D. Harpacticoida.

Species	Width (µm) of mandibulae blade
Calanus spp. I	<70 µm
C. finmarchicus II–III *C. glacialis* II–III *C. hyperboreus* II	75–122 µm
C. finmarchicus IV–V *C. glacialis* IV *C. hyperboreus* III	122–160 µm
C. finmarchicus VI	160–180 µm
C. glacialis V *C. hyperboreus* IV	180–197 µm
C. glacialis VI	197–217 µm
C. hyperboreus V	236–270 µm
C. hyperboreus VI	>279 µm
Pseudocalanus	62–77 µm
Oithona	25 µm
Harpacticoida	42 µm


A


B


C


D

length (Reeve & Walter 1972; Pearre 1974, 1980, 1981). However, head width may underestimate the functional mouth size, since the mouth opening expands considerably during swallowing (Reeve & Walter 1972; Sullivan 1980; Pearre 1980).

Gut contents in Groups 2 and 3, which could not be identified by their shape, were placed in a drop of polyvinyl-lactophenol on a microscope slide. Staining with lignin-red was used to facilitate the detection of copepod remains. The mandible pairs of copepods, were counted and the width of the mandible blades measured in a microscope. Identifications of the copepod species and developmental stage were made with the help of shape and size of the mandible (Table 2). Here, mandible blades have been dissected from copepods of known species and stage, measured, and grouped into size-classes. The three species of *Calanus* found in the Arctic water of the Barents Sea (*C. finmarchicus*, *C. glacialis* and *C. hyperboreus*) had similarly shaped mandibulas. Mandible widths made it possible to differ among stages within the same species; however, the mandible width of a certain copepodite stage overlapped in size with different stages of other *Calanus* species. *Calanus* prey could thus only be relegated to size groups (Table 2). The presence of appendicularians was determined on the basis of their fecal pellets, which resist digestion (Shelbourne 1962).

Daily feeding rates were calculated from the equation of Bajkov (1935):

$$FR = \frac{NPC\,(24)}{DT}$$

where FR = daily feeding rate expressed as number of prey per day, DT = digestion time in hours, and NPC = number of prey per chaetognath, as determined from gut-content analysis. Preliminary observations in this study of *S. elegans* collected with food in their guts showed a maximum

Table 3. Data sources for copepod ash free dry weights (µg) used in the present study.

Species	µg AFDW	Reference
nauplii (NI–NVI)	0.7	µgC in *C. helgolandicus* 3NI–NVI; Paffenhöfer (1971) C = 54% of DW; AFDW = 93% of DW; Båmstedt (1986)
Calanus spp. I	11.2	Eilertsen et al. (1989)
C. glac II *C. hyperb* II	31.6	Eilertsen et al. (1989)
C. glac III	61.3	Båmstedt & Tande (1985)
C. hyperb III	142.3	Conover & Corner (1968)
C. finm IV	53.0	Båmstedt et al. (1990)
C. glac IV	253.1	Båmstedt & Tande (1985)
C. hyperb IV	358.1	Conover & Corner (1968)
C. finm V	161.8	Båmstedt et al. (1990)
C. glac V	578.9	Båmstedt & Tande (1985)
C. hyperb V	2156.9	Ikeda & Skjoldal (1989)
C. finm VI	356.0	Ikeda & Skjoldal (1989)
C. glac VI	899.8	Båmstedt & Tande (1985)
C. hyperb VI	3693.3	Ikeda & Skjoldal (1989)
Pseudocalanus IV–VI	9.7	Kosbokova (1980); Laurence (1974) 91.5% AFDW
Oithona	2.8	Båmstedt et al. (1990)
Oikopleura (0.85–0.91 mm)	4.3	Gorsky et al. (1987)
Unidentified prey		average AFDW of prey items were calculated in each sample and used as estimate for unidentified prey AFDW

gut-clearing time of 12.5 hours. Based on the equation by Pearre (1981, subsequently corrected in Pearre 1982) and a mean temperature of −1.5°C in the upper 50 m, a digestion time of 11.8 hours was estimated. In accordance with these two estimated values, an approximate DT of 12 hours was used in all calculations of feeding rate. A single value was used for all stations as temperature varied less than 0.5°C. DT is regarded as independent of chaetognath size or type of food (Kuhlmann 1977; Szyper 1978; Feigenbaum 1979; Sullivan 1980).

Ash-free dry weights (AFDW) of prey were obtained from data from previous studies (Table 3). When no specific data were available, a factor of 93% (Båmstedt 1986) was used to convert DW to AFDW. In cases of overlapping mandible sizes of *Calanus* species or stages, a median dry weight value was calculated.

The regression of *S. elegans* dry weight versus body length was obtained using 55 newly captured individuals which were rinsed in distilled water. Individual dry weights were determined as described above and data were fit to a power curve (Fig. 3). Average values of abundance and feeding rates for each station were presented as integrated values from 0 to 40 or 50 m, calculated by integrating over each depth interval. In order

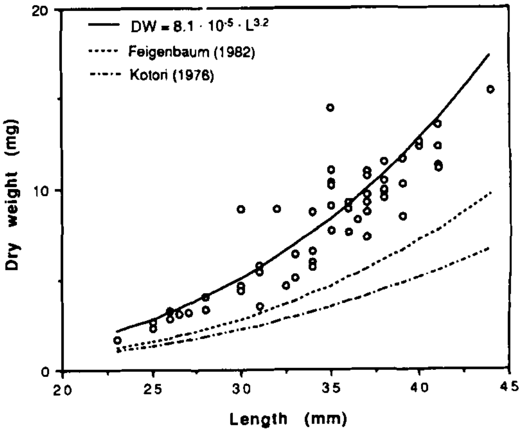

Fig. 3. Body dry weight (DW, in mg) versus body length (L, in mm) for *Sagitta elegans* var. *arctica*, Barents Sea (—— this study), *S. elegans*, Bering Sea (–·–·– Korori 1976) and *S. elegans*, Vineyard Sound (------ Feigenbaum 1982).

to avoid bias due to variable sampling intervals, the relative prey composition of *S. elegans* was based on the summed gut contents from all depths. Significance tests on the regression equations were performed, using a t-test on the correlation coefficients, where z-transformations were used for sampling sizes larger than 50 (Sokal & Rohlf 1981). All data on zooplankton biomass, hydrography (salinity and temperature) and light, were kindly provided by the Institute of Marine Research, Bergen.

Results

Diel variations

The Diel variation in the feeding activity of *S. elegans* is revealed by mapping the average number of prey per chaetognath (NPC) collected from 0–50 m during day and night (Fig. 4). By summing the gut content over all sampled chaetognaths, within-depth variations due to vertical migration are minimised. In July, the Arctic experiences a 24 hour light period. During sampling, the level of the surface illumination varied between 696 (noon) and 96 (midnight) µE $m^{-2} \cdot s^{-1}$ (Fig. 4). The highest average NPC occurred during low illumination. However, the average "Night" NPC (0.223 ± 0.390, n = 3), when surface irradiation was less than 400 µE $m^{-2} \cdot s^{-1}$, did not differ significantly from the average "Day"-NPC (0.091 ± 0.125, n = 3; $P > 0.05$, t-test Sokal & Rohlf 1981).

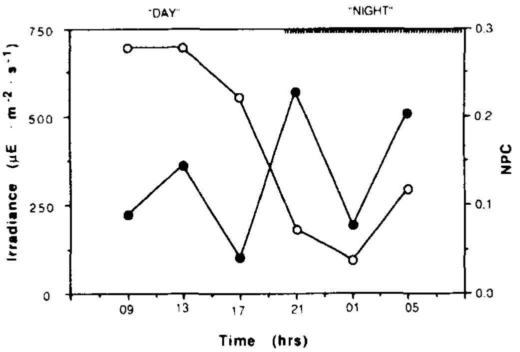

Fig. 4. Sagitta elegans var. *arctica*, Barents Sea, May–June 1983. Average number of prey per chaetognath (NPC, based on all sampling depths) during a 24-hour period ●. The corresponding light curve for surface illumination is indicated ○), and "night" is defined as the period with surface illumination <400 µE $m^{-2} \cdot s^{-1}$.

Gut content

Of the 3014 *S. elegans* analysed, 35.7% contained food. Among these, 6% contained multiple prey (never more than 3 items), mostly represented by small species such as *Oithona* or copepod nauplii. Copepods dominated the diet for all chaetognaths, representing up to 99.9% of the total number of prey items found (Table 4). *Oikopleura* sp. (*Tunicata: Larvacea*), the only non-copepod prey detected, was sparsely represented (0.1%).

Breakdown of the relative occurrence of each prey type of *S. elegans* for the three maturity

Table 4. Gut content of *Sagitta elegans* var. *arctica*, Barents Sea, May/June 1983. Percentage of prey items in terms of number and AFDW.

Prey	Prey width	Typical abundance (no. per m³) in plankton	Proportion in diet % No.	% AFDW
nauplii	0.2–0.3	800–4600	21.2	0.2
Calanus spp. I	0.3–0.4	40–400	7.1	1.0
C. finm II–III; *C. glac* II–III; *C. hyperb* II	0.4–0.6	30–500	7.6	4.6
C. finm IV–V; *C. glac IV*; *C. hyperb* III	0.6–0.8	100–400	18.4	36.7
C. finm VI	0.8–0.9	3.0–30	3.9	18.3
C. glac V; *C. hyperb* IV	0.9–1.1	5–50	2.3	14.1
C. glac VI	1.2–1.4	1.0–10	0.8	9.1
C. hyperb V	1.6–1.8	0–13	0.3	7.2
Pseudocalanus	0.3–0.4	50–1000	22.8	2.9
Oithona	0.2	10–500	9.15	0.3
Oikopleura	0.4	0–2	0.2	0.0
Harpacticoida		0–0.5	0.1	0.0
unidentified prey			6.2	5.5

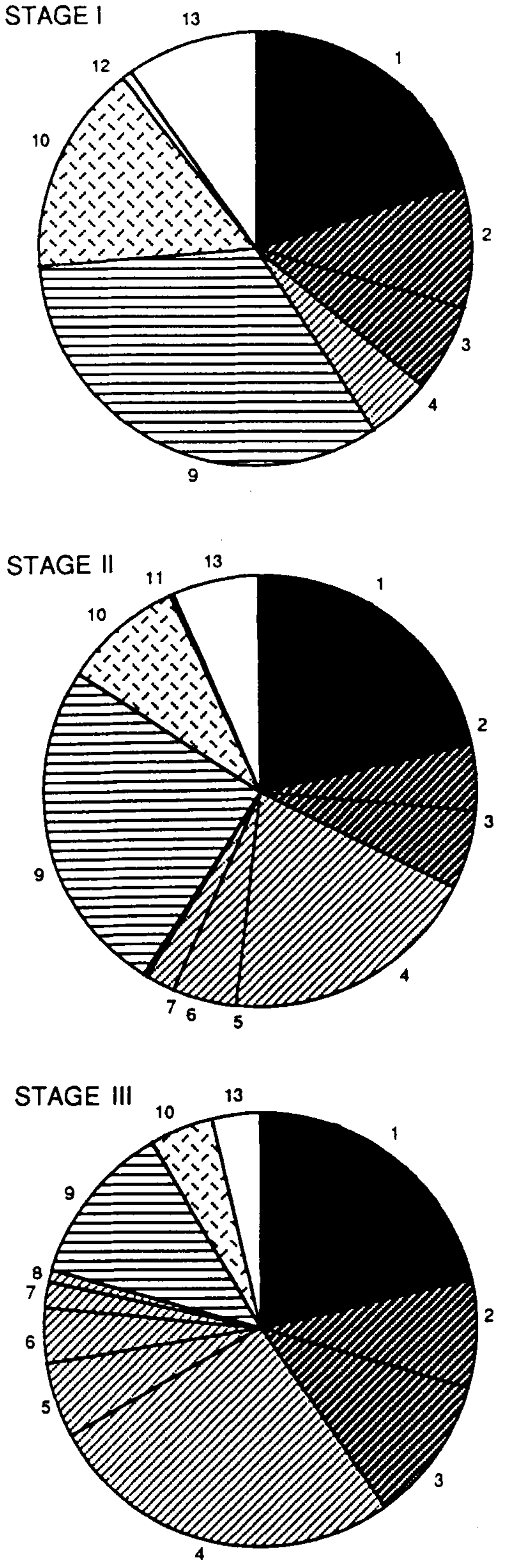

Fig. 5. Sagitta elegans var. *arctica*, Barents Sea, May–June 1983. Proportions of prey items found in the guts of Stages I, II, and III.

stages (Fig. 5) reveals a diet consisting mainly of 5 copepod species: *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Pseudocalanus* sp. and *Oithona* sp., but small prey items, such as copepod nauplii, *Calanus* spp. C-I, *Oithona* sp. and *Pseudocalanus* sp., were the most abundant prey types. These were especially frequent in the diet of juvenile *S. elegans*, constituting 78 and 61% of the prey items in Stages I and II (Fig. 5), whereof 33 and 25% were represented by *Pseudocalanus* sp. alone. In fully mature *S. elegans* (Stage III) the number of prey types was higher than in earlier stages. Smaller prey forms constituted 46% of the prey, while the larger copepodites of *Calanus* spp. were more frequently found than in juvenile *S. elegans* (Fig. 5). *Pseudocalanus* sp. dominated in the diet, although the dominance was less pronounced (12%) than in juvenile *S. elegans*.

In terms of the biomass, the numerous small prey items (*Oithona* sp., *Pseudocalanus* sp. and copepod nauplii) contributed 3.4% of the gut contents of *Sagitta elegans*, while 85% of the biomass was contributed by larger copepods (*C. hyperboreus* IV–V and *C. finmarchicus/glacialis* V–VI, Table 4). The proportion of unidentified prey (6% of total items) was highest in juvenile *S. elegans*. This was due to the smaller average prey size and the resultingly greater problems of identification.

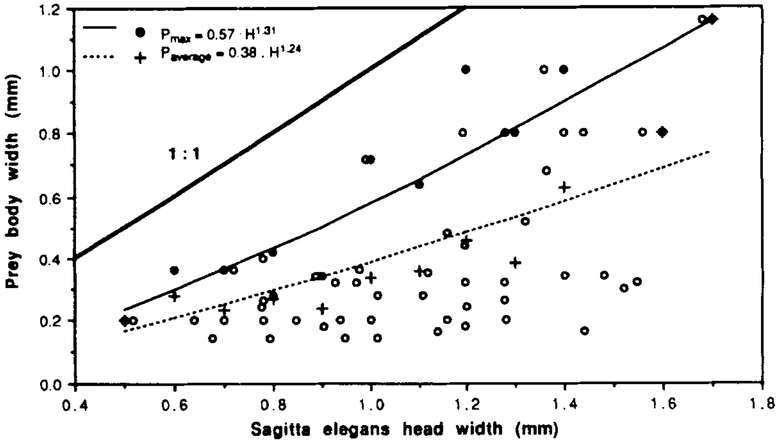

Fig. 6. Sagitta elegans var. *arctica*, Barents Sea. Prey body width (P, ○) versus chaetognath head width (H). Mean prey body width and maximum prey body width versus chaetognath head width, fitted to power curves. Bold line shows 1:1 ratio.

Prey size in relation to predator size

Prey size and the size range of prey increased with increasing head width of *S. elegans* (Fig. 6). In order to detect any functional relationship between chaetognath size and prey size, chaetognath head widths were divided into size classes of 0.1 mm. Regressions were calculated within each size class between 1) maximum and average prey body width and 2) the average chaetognath head width. Both relationships were best described by power curves (Fig. 6).

Feeding and prey abundance

Feeding activity (as NPC) versus the corresponding zooplankton abundance (as mg ash-free dry weight·m^{-3}) revealed no statistically significant regression (linear regression, $P > 0.05$) when all stations and depths were included. For each depth of sampling a regression analysis between NPC and zooplankton abundance was performed. The analysis revealed a tendency of higher NPC at higher zooplankton abundance, although the relationships were not statistically significant ($P > 0.05$).

Transect

Moving from north to south along the transect, the surface temperature increased from −1.7 to −1.2°C, whereas the temperature below 30 m varied little (Fig. 7A). The stations north of 76°45'N (134–164) were situated in ice-covered waters, although the ice cover was not dense. Reduction of salinity due to ice melting caused the strong pycnocline around 20 m in the southernmost stations (Fig. 7B and C). The variation in surface illumination between the stations (due to cloudiness and time of day) was low, with the exception of Station 137, where the irradiation was considerably higher.

The highest concentrations of *S. elegans* (78 specimens·m^{-2}) were found near the ice edge at station 162, and the proportion of mature *S. elegans* increased from 12 to 63% towards the south (Fig. 8A). A large number of eggs were found in the surface sample from Station 165. The two southernmost stations (164 and 165) had a considerable number of spent individuals.

Zooplankton abundances along the transect are reported in Gjøsæter et al. (1983). The biomass in the upper 50 m ranged from 1.9 to 6.9 g AFDW·m^{-2} at Stations 137 and 162, and showed the same pattern as *S. elegans* with elevated values near the ice edge (Fig. 8B). The zooplankton biomass north of the ice edge was dominated by *C. glacialis, C. hyperboreus, Metridia longa* and *Pseudocalanus* sp. The northernmost stations had a high number of older developmental stages of overwintered copepods, whereas copepod nauplii and early developmental stages dominated the *Calanus* population at station 165 (Gjøsæter et al. 1983).

The highest abundance of *S. elegans* (never exceeding 5 specimens m^{-3}) was found within or beneath the maxima for zooplankton biomass (Figs. 9, 10A, and 11A). Very few chaetognaths were found above the pycnocline at 20 m in the southern part of the transect (Figs. 9 and 11A).

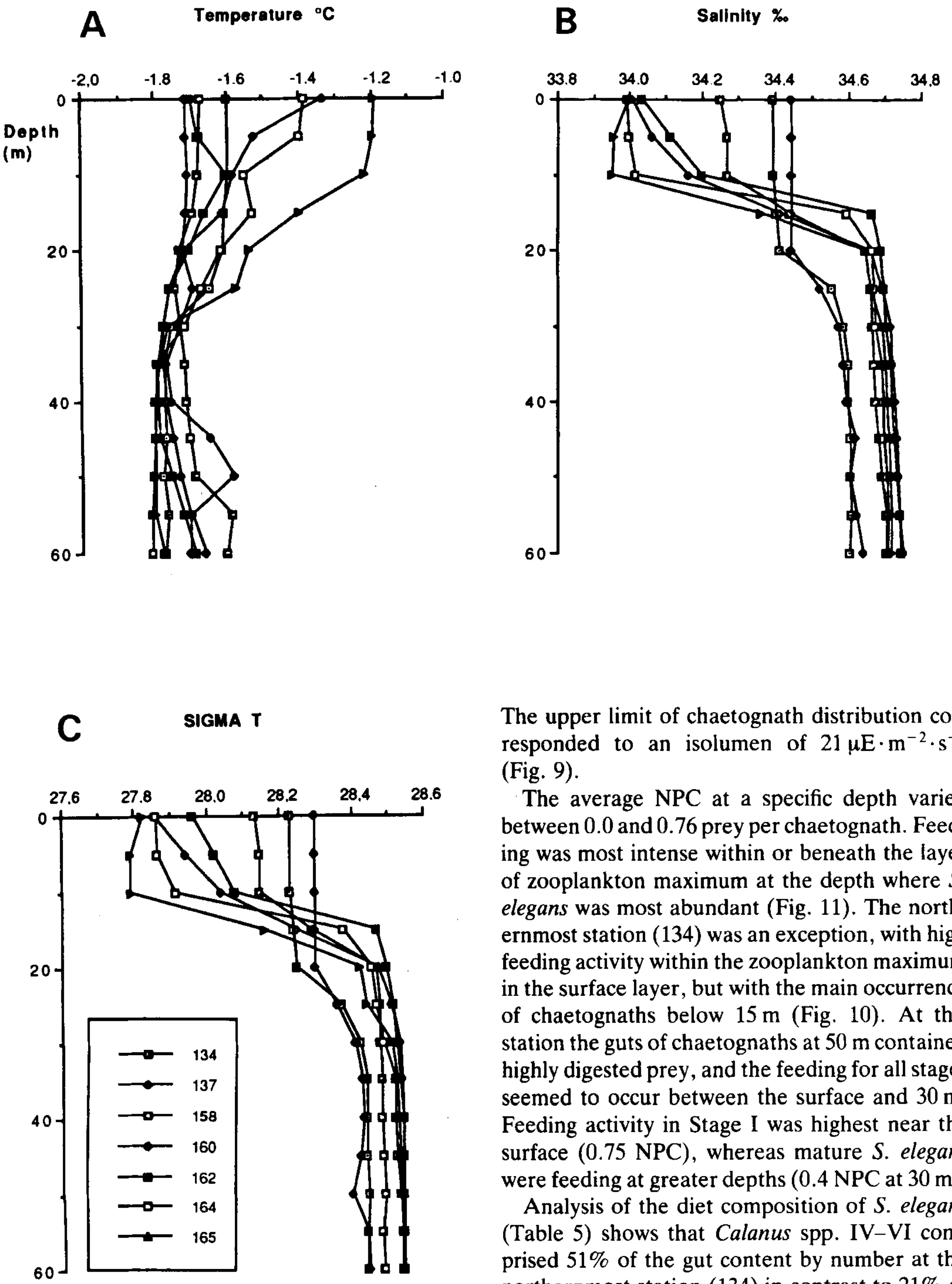

Fig. 7. Barents Sea, May–June 1983. Vertical profiles of hydrographical parameters along the N–S transect, extending from 77°35′N (Station 134, —□—) to 76°40′N (Station 165, —▲—). A. Temperature, °C; B. Salinity, ‰; C. Density, Sigma-t. All data from The Institute of Marine Research, Bergen.

The upper limit of chaetognath distribution corresponded to an isolumen of 21 $\mu E \cdot m^{-2} \cdot s^{-1}$ (Fig. 9).

The average NPC at a specific depth varied between 0.0 and 0.76 prey per chaetognath. Feeding was most intense within or beneath the layer of zooplankton maximum at the depth where *S. elegans* was most abundant (Fig. 11). The northernmost station (134) was an exception, with high feeding activity within the zooplankton maximum in the surface layer, but with the main occurrence of chaetognaths below 15 m (Fig. 10). At this station the guts of chaetognaths at 50 m contained highly digested prey, and the feeding for all stages seemed to occur between the surface and 30 m. Feeding activity in Stage I was highest near the surface (0.75 NPC), whereas mature *S. elegans* were feeding at greater depths (0.4 NPC at 30 m).

Analysis of the diet composition of *S. elegans* (Table 5) shows that *Calanus* spp. IV–VI comprised 51% of the gut content by number at the northernmost station (134) in contrast to 21% at the southermost station (165). The proportion of younger *Calanus* stages (nauplii, *Calanus* spp. C-I, II, III) was 28% and 55% of the diet at Stations 134 and 165. Nauplii were not found in the chaetognath guts at Station 134. The proportions of

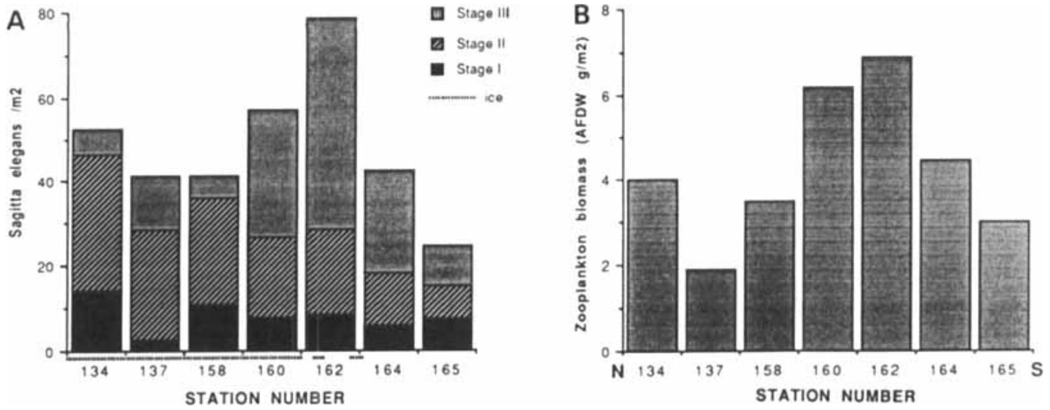

Fig. 8. Barents Sea, May-June 1983. N-S transect, extending from 77°35'N (Station 134) to 76°40'N (Station 165). A. *Sagitta elegans* (abundances integrated from 0 to 50 m: no. per m^2); B. Zooplankton biomass (From 375 µm Judaytow, 0-50 m: g AFDW m^{-2}.

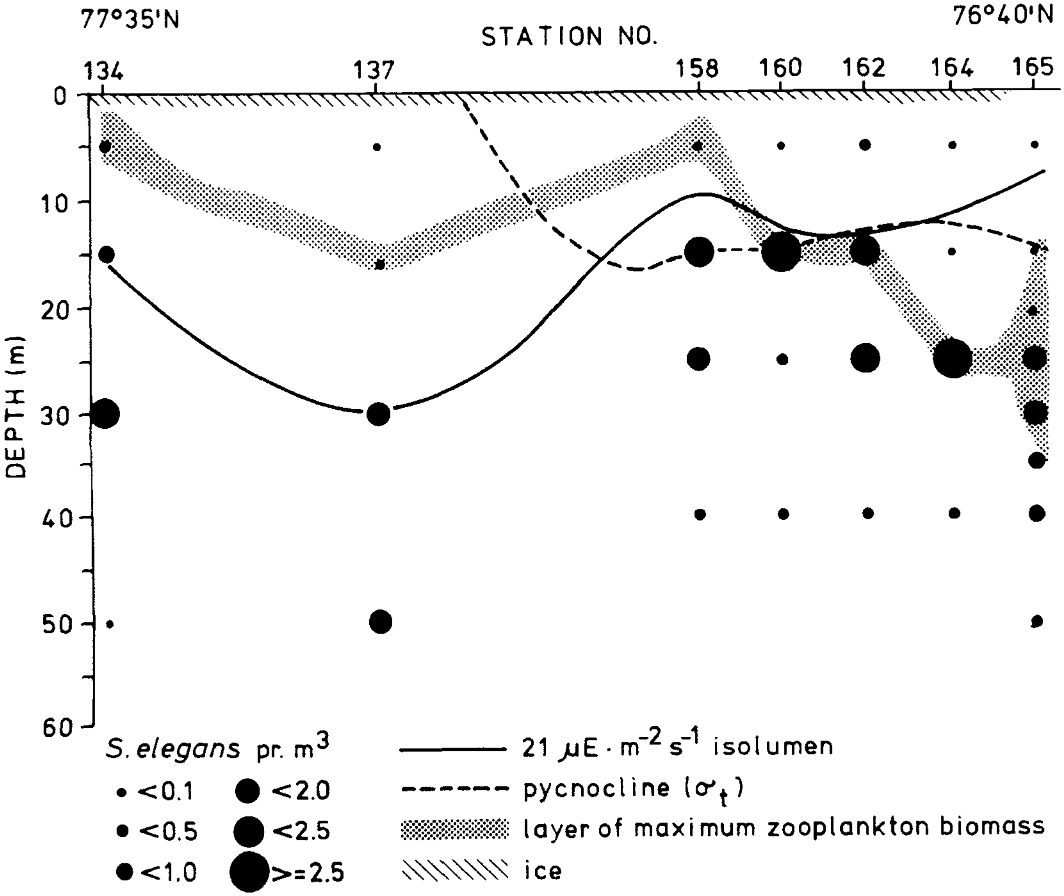

Fig. 9. Barents Sea, May-June 1983. N-S transect, extending from 77°35'N (Station 134) to 76°40'N (Station 165). Sampling depths are marked by solid circles, the size of which indicates the number of *Sagitta elegans* per m^3 (see figure legend); Isolumen of 21 µE m^{-2} · s^{-1} (solid line), pycnocline (broken line), and the layer of maximum zooplankton biomass (shaded area). Ice-cover indicated by slanted lines.

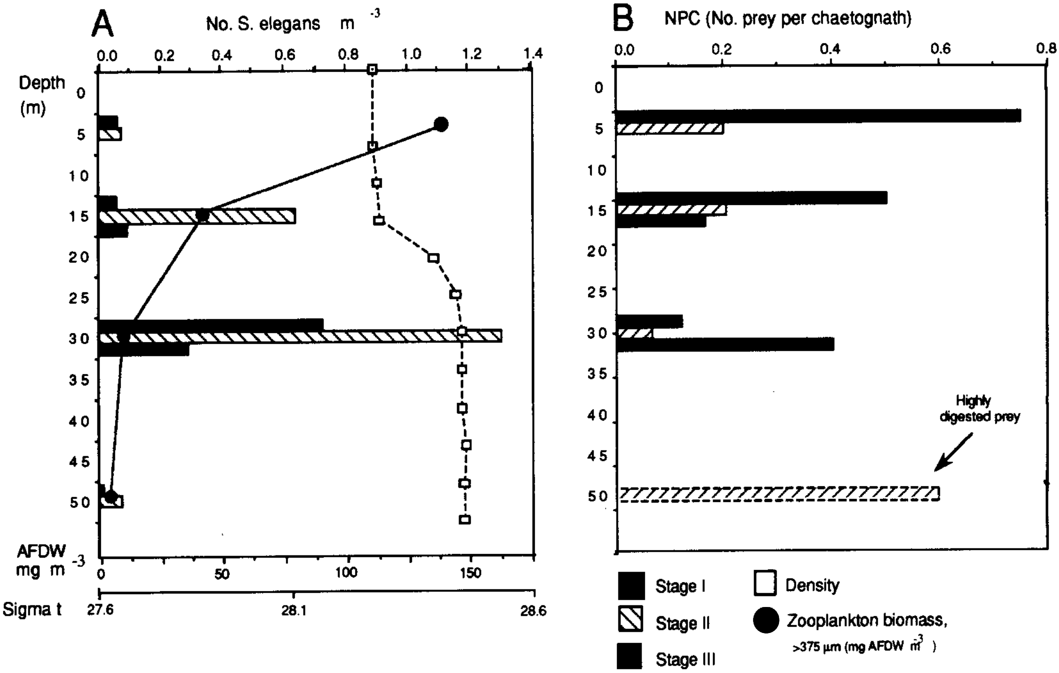

Fig. 10. Station 134, 77°35′N. Barents Sea, May–June 1983. A. Vertical distribution of *Sagitta elegans* (No. per m^3). Stage I = ■, Stage II = ▨, and Stage III = ▣). Vertical distribution of zooplankton biomass (mg AFDW m^{-3}, solid line) and density profile (Sigma T, broken line); B. Vertical profile of feeding activity (NPC) in *S. elegans*. Symbols as in 10A.

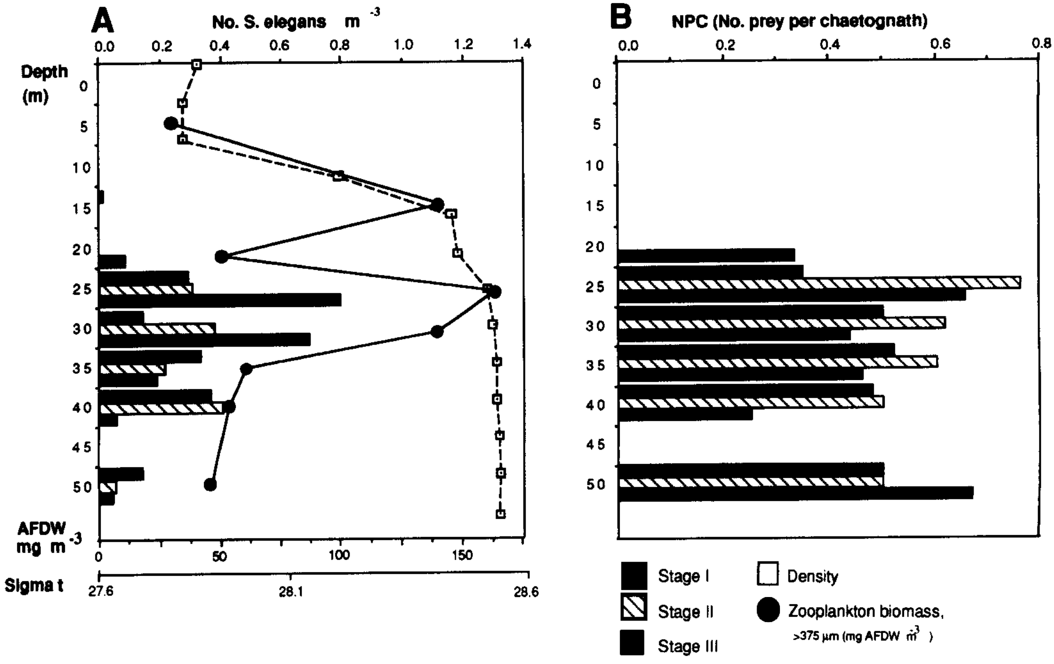

Fig. 11. Station 165, 76°40′N, Barents Sea, May–June 1983. A. Vertical distribution of *Sagitta elegans* (No. per m^3). Vertical distribution of zooplankton biomass (mg AFDW M^{-3}, solid line) and density profile (Sigma T, broken line); B. Vertical profile of feeding activity (NPC) in *S. elegans*. Symbols as in 10A.

Table 5. Composition (%) of *Sagitta elegans* diet and of the zooplankton at the northernmost (134) and southernmost (165) stations.

Species	Station 134 % gut	zoopl	Station 165 % gut	zool
nauplii	0	—	30.1	—
Calanus spp. I	12.8	0.42	16.3	12.8
C. finm II–III *C. glacialis* II–III *C. hyperboreus* II	15.4	1.98	9.0	20.6
C. finmarchicus IV–V *C. glacialis* IV *C. hyperboreus* III	33.3	35.4	16.9	36.6
C. finm VI	10.3	0.09	3.0	4.6
C. glac V *C. hyperboreus* IV	0	5.2	1.2	7.3
C. glacialis VI	2.6	0.26	0	1.4
C. hyperboreus V	5.1	0.21	0	0.9
Pseudocalanus sp.	5.1	55.8	7.83	14.9
Oithona sp.	0	—	1.2	—
Oikopleura sp.	2.6	—	0	—
unidentified	12.8	—	10.2	—

small copepod species such as *Oithona* sp. and *Pseudocalanus* sp. were highest at the southernmost station. The diet of *S. elegans* reflected the composition of the zooplankton. The proportions of the different copepods in the zooplankton given in Table 5 are incomplete, especially for small-sized prey, due to the coarse mesh-size used in sampling. However, the northernmost station (134) contained a high number of older developmental stages of overwintered copepods (*Calanus* spp. IV–VI made up 95% of the *Calanus* population, Table 5). Copepod nauplii and early developmental stages dominated the *Calanus* population at Station 165 (Gjøsæter et al. 1983), thus *Calanus* spp. C-I, II, III comprised 2.4 and 33% of the zooplankton at Stations 134 and 165 (Table 5).

By using a digestion time of 12 hours, and an average number of *S. elegans* m^{-3} (0–40 or 50 m) at each station, the average feeding rate was estimated to be between 0.30 and 1.05 prey per chaetognath day^{-1} (Table 6). The values tended to increase towards the south, and they did not differ among the three stages. In terms of ash-free dry weight, however, adult *S. elegans* possessed a considerably higher feeding rate than did the

Table 6. Barents Sea, May–June 1983. Feeding rates integrated over depth, as number of prey and μg AFDW day^{-1} per *Sagitta elegans*.

Station	Depth	Number of prey eaten/day per *Sagitta* I	II	III	average	μg AFDW eaten/day per *Sagitta* I	II	III	average
134	0–50 m	0.33	0.23	0.72	0.31	21.9	44.2	428.3	83.2
137	0–50 m	0.29	0.31	0.27	0.30	0.9	1.5	23.2	8.0
158	0–40 m	0.88	0.88	0.69	0.85	8.6	51.7	66.5	43.9
160	0–40 m	0.91	0.83	0.53	0.67	4.5	48.5	59.6	49.5
162	0–40 m	0.56	0.69	0.46	0.53	10.3	52.6	38.7	39.4
164	0–40 m	1.13	0.84	1.05	1.00	18.7	55.6	60.1	53.7
165	0–50 m	0.92	1.19	1.05	1.05	19.5	29.9	90.4	50.0

Table 7. Percentage of the zooplankton standing stock (AFDW) removed per day by *Sagitta elegans*, Barents Sea, May–June 1983.

Station	Total (>375 μm)	Percentage of the standing stock (AFDW) removed per day <1000 μm	1000–2000 μm	[>2000 μm]*
134	0.22	0.02	0.21	2.84
137	0.08	0.04	0.19	0.00
158	0.10	0.03	0.16	0.35
160	0.16	0.03	0.22	0.80
162	0.15	0.04	0.23	0.16
164	0.11	0.06	0.19	0.00
165	0.07	0.02	0.14	0.00

* Based on one or two prey items only.

juveniles. Stage III ranged from 23 to 428 μg per chaetognath per day, compared with 0.9–30 μg and 1.5–56 μg per day for Stages I and II.

The proportion of zooplankton standing stock removed by *S. elegans* per day, varied between 0.07 and 0.22% of the zooplankton biomass, which mainly affected the 1000–2000 μm fraction (Table 7).

Discussion

Digestion time

Laboratory experiments on *Sagitta hispida* (Reeve 1980) have shown increased DT with prey size and number of food items for a given size of predator. Szyper (1978) reported that DT for *S. enflata* did not depend on the size of the predator, since larger chaetognaths (which take larger prey) also had a greater capacity of digestion than did small chaetognaths. No significant relation was found by Feigenbaum (1982) between DT and length in *S. elegans*, nor between DT and prey weight. By using a single value for DT, as was done here for *S. elegans*, differences in digestibility of various sizes of prey would lead to an underestimation of FR for small as opposed to large prey items and an overestimation of FR for multiple prey as opposed to single prey. As no digestion time was directly measured for *S. elegans* var. *arctica* in this study, the calculated feeding rates should be interpreted with caution. However, the striking similarity between the calculated value of DT using Pearre's (1981) equation (11.8 h) and the longest time to defecation observed on specimens in the laboratory in the present study (12.5 h) support the validity of using a DT of 12 h.

Type and size of prey

The dominance of nauplii, *Oithona* sp. and *Pseudocalanus* sp. in the diet of *S. elegans* in the Barents Sea is in accordance with results from several other areas (Reeve 1966, 1980; McLaren 1969; Reeve & Walter 1972). This does not necessarily indicate selection for these species but rather reflects the high abundance of these three prey types in the zooplankton; it is an effect of co-occurrence (Pearre 1973). Such a lack of strict selectivity was found by Sullivan (1980), and several others have shown a preference for size rather than species (Rakusa-Suszczewski 1969; Reeve & Walter 1972; Kimmerer 1984).

The coarse mesh-size used (375 μm) has certainly resulted in incomplete sampling of small chaetognaths. Nor was the prey of these chaetognaths sampled, since juvenile chaetognaths probably feed on nauplia-sized prey. Both small chaetognaths as well as nauplia-sized prey are, however, potential prey for larger chaetognaths in the sample. Thus, it is most likely that the composition in the recorded prey abundance available for the chaetognaths is biased. Because of this, no attempts were made to estimate the selectivity of *S. elegans*. Skjoldal et al. (1987) found a retention efficiency of 56 and 98% for *Calanus finmarchicus* Stages I and II on a 375 μm mesh screen. A considerable proportion of copepodite Stages I–III of *Pseudocalanus* sp. were also shown to pass through the net. Although the abundances reported in this study of potential prey for *S. elegans* must be considered as underestimations, comparisons between gut content and zooplankton composition at stations 134 and 165 (Table 5) show a reflection of the zooplankton composition in the diet of *S. elegans*. A high proportion of older development stages of *Calanus* spp. in the north and of young stages in the south is found both in the zooplankton and in the chaetognath guts. However, despite a high proportion of *Pseudocalanus* sp. in the zooplankton at station 134 (56%), small prey species (*Oithona* sp. and *Pseudocalanus* sp.) in the diet of *S. elegans* were most frequent at the southern station (165). Since Station 165 contained a high proportion of juvenile *S. elegans*, this may be an effect of prey size limitation or selection or both.

As shown in this study, larger chaetognaths tended to catch prey of larger sizes (see Fig. 6). The large amount of scatter, increasing with chaetognath size, demonstrates that *S. elegans* in the Barents Sea can use a wide spectrum of prey sizes. Small prey items such as nauplii are taken by all stages of *S. elegans*, whereas larger copepodites are only taken by larger chaetognaths. Maximum prey size is governed by the size of the mouth opening (Feigenbaum & Maris 1984) and prey widths have often been found to exceed the chaetognath head width since the mouth opening expands considerably during swallowing (Reeve & Walter 1972; Sullivan 1980; Pearre 1980). Elasticity of the head tissue decreases with age (Reeve & Walter 1972). Consequently, smaller chaetognaths can take larger prey sizes in relation to their head widths than larger ones can. A relationship between predator size (H) and maximum prey size (P_{max}) should therefore result in a non-linear function, e.g. a power curve ($H = aP^b$) with a slope (b) <1. The relationship between mean prey body width ($P_{average}$) and chaetognath head width (H) reflects the size preference and selection by *S. elegans*. Pearre (1980) found the best prediction of prey size for *S. elegans* in Bedford Basin, Canada, to be a power curve with the slope (b) of 0.756. The power curve found by Reeve & Walter (1972) was explained by the decreased elasticity of the head tissue with age and/or greater requirements of the young for food. Feigenbaum (1979) found the weight of mean prey of *S. enflata* in the Gulf Stream did not change with chaetognath size, which may be due to the absence of large prey in the study area (Pearre 1980).

The maximum and average prey sizes within each size class of *S. elegans* in this study resulted in the power curves shown in Fig. 6. The regression for maximum prey size could reflect an upper prey-size limitation due to mouth size. No adult *C. hyperboreus* were found among the prey items in chaetognath guts, which suggests that they may be larger than the maximum size of prey for *S. elegans* var. *arctica*. However, since prey widths were always considerably smaller than chaetognath head widths (curve lying below the 1:1 slope in Fig. 6), predator evasion may be a more important factor than size alone as a modifying agent reducing the predation. Both regressions have slopes >1, which possibly reflected the availability of large prey in the Barents Sea, and large *S. elegans* var. *arctica* in the Barents Sea may have greater ability to catch large prey. The large confidence limits of the slopes (1.31 ± 1.12 and 1.24 ± 1.87 for maximum prey size and average prey size respectively), are, however, not statistically different from 1.0 or from the curve for *S. elegans* in Bedford Basin (Pearre 1980). Failure to record small prey items, such as *Oithona* sp., would tend to overestimate the slopes in Fig. 6. Narrow range of chaetognath head width (0.5–1.7 mm), the absence of small chaetognaths (none <15 mm), and the large range of prey sizes make the regression uncertain. Conclusions concerning prey size selection in *S. elegans* var. *arctica* are therefore highly speculative.

The absence of evidence for cannibalism in these data is in contrast with the cost/benefit calculations of Pearre (1982), who considered cannibalism or predation on chaetognath-sized objects to be energetically necessary for the existence of large predators. Assuming a maximal density of three chaetognaths per cubic metre, and a mean head width of 1.1 mm, the expected cannibalism calculated from his equation (2) would be 60% of the diet items. Thus, it seems that it is not merely the chaetognath abundance which is determining the proportion of cannibalism, but rather the abundance of chaetognaths relative to other prey in the zooplankton. Cannibalistic behaviour may be beneficial only when alternative large prey are rare (Kimmerer 1984). In the Barents Sea, copepod prey seems to be abundant enough to fulfill the energy needs of the chaetognaths. Compared to other chaetognath species, the occurrence of cannibalism in *S. elegans* has been reported to be low (Feigenbaum & Maris 1984; Øresland 1987). The abundance of small chaetognaths were probably underestimated due to the coarse mesh size used for sampling (the smallest chaetognath found was 12 mm). It cannot be excluded, however, that absence of cannibalism is due to low abundance of small individuals in the zooplankton.

The average weight of prey ingested (calculated from feeding rates in Table 6) was higher in Stage III (161 µg $prey^{-1}$) than in juveniles (18.4 µg $prey^{-1}$). This suggests a strategy in Stage III *S. elegans* to take few larger prey, while juveniles constitute their diet of smaller prey taken more frequently. A few large feedings are energetically advantageous provided that large prey require proportionately less energy to consume (Paloheimo & Dickie 1966; Emlen 1973; Kerr 1978); this argument pertains, however, only when large prey are sufficiently abundant (Sullivan 1980). Furthermore, while the energy content and the encounter rate increase with increasing prey size, the susceptibility, and thereby the vulnerability, of the prey tend to decrease (Greene 1986). This probably explains why the larger prey, such as older copepodite stages of *Calanus* spp. were almost lacking in the diet of *S. elegans* from the Barents Sea.

Chaetognaths are defined as raptorial, ambush predators, dependent on prey movements before initiating encounters and possessing a short attacking distance (Feigenbaum & Reeve 1977). The high abundance of *Oithonia* sp. in the diet may be the result of the flapping movements of this prey. In addition, the peripheral escape zone of *Oithona* (the minimum distance needed to avoid capture) is found to be wide (Fleminger & Clutter 1965), making the prey easy to detect and catch. In contrast, gut content analyses on 10–40 mm herring larvae (a visual predator) from the Georges Bank region, although showing prey composition similar to that of *S. elegans*, revealed relatively lower proportions of the transparent *Oithona* (Cohen & Lough 1983).

Distribution and feeding

The vertical distribution and feeding of *S. elegans* seems to be affected by four major factors:

1. *Prey abundance.* – According to the model described by Rey et al. (1987) and Skjoldal & Rey (1989), a phytoplankton bloom is associated with the increase in light and water stability around the retreating ice edge. Thus, the successional time axis in the plankton development coincides with the N–S gradient. Zooplankton abundance along the transect (Gjøsæter et al. 1983) showed the characteristic ice edge development, i.e. a zooplankton maximum of overwintered copepods in the surface layer of the northernmost stations, and a displacement of the maximum deeper down in the more developed bloom further south (Fig. 9). The vertical distribution of chaetognaths was associated with the zooplankton maxima, as most clearly seen at the southern stations (160–165). Here the main occurrence was found within or close beneath the zooplankton maximum, where feeding was usually most intense (Fig. 11). Similarly, Sullivan (1980) found that *S. elegans* stayed and fed near the thermocline, where the highest biomass of total zooplankton was situated, but no relationship was found between feeding rate and prey abundance when the latter ranged between 100 and 1500 prey m^{-3}.

Reeve (1980) found increased feeding with increasing food concentration for *Sagitta elegans* in the laboratory, until satiation was reached at 60,000 copepods m^{-3}. However, as chaetognaths do not feed as readily in the laboratory, they may require the inducement of higher prey densities for maximum consumption (Feigenbaum & Maris 1984). Drits (1981) found a logarithmic relationship between the proportion of *S. enflata* containing food and the concentration of prey in the zooplankton. Generally, however, attempts to correlate feeding in nature with zooplankton availability have been unsuccessful (Mironov 1960; Nagasawa & Marumo 1972), and the results from the present data are no exception. The abundance of suitable prey experienced by *S. elegans* along the transect varied between 260 and 1800 prey items m^{-3} within the layer of zooplankton maximum. The lack of a significant correlation between NPC and prey abundance may be explained in three ways: 1) *S. elegans* does not feed at the depths it is caught in, i.e. migration between different prey concentrations (Pearre 1973); 2) the chaetognaths in nature depend on localized patches of high prey density, which we are unable to estimate (Sullivan 1980); and 3) *S. elegans* var. *arctica* is not food-limited. The latter is supported by the calculation of the energy budget, as shown below.

2. *Salinity.* – The stability of the upper 50 m is mainly determined by the salinity, and a well-developed pycnocline was found only near the ice edge (station 158–165). The maximum prey abundance was usually closely associated with the pycnocline, where the highest chlorophyll *a* values were also found. The effect of reduced salinity on the vertical distribution of *S. elegans* was demonstrated at Station 158 (Fig. 10) where few chaetognaths occurred above the pycnocline at 15 m (salinity < 24‰), despite the high abundance of prey. Studies on *S. elegans* from the Bristol Channel have shown that the chaetognath can tolerate salinities between 22 and 35‰ (Williams & Collins 1985). However, steep salinity and density gradients may affect the vertical distribution of some zooplankters (Furnstin 1938; Banse 1964; Harder 1968; Pearre 1970).

3. *Light.* – The close agreement between the 21 $\mu E\ m^{-2} \cdot s^{-1}$ isolume and the upper limit of chaetognath occurrence was especially evident at Station 137, where the illumination was high (Fig. 9). The effect was a deeper distribution of both prey and predator, and the feeding activity was markedly reduced (Table 6). The value is conspicuously close to the critical surface light intensity of 24 $\mu E\ m^{-2} \cdot s^{-1}$ for feeding onset found in Canadian arctic copepods (Head et al. 1985). Results from Station 134 (Fig. 10) indicate that light affects the distribution rather than the feeding activity. The few *S. elegans* from above 15 m had a high NPC value, and chaetognaths from below 15 m had a more digested state of the gut content suggesting that chaetognaths feed in the surface water where prey is abundant, and then

swim downwards. Although this is in agreement with the theory that satiated specimens of *S. elegans* should swim downwards (Pearre 1973), it is in opposition to the inhibiting effect of light on feeding as reported by the same author.

4. *Maturity stage*. – Jacobsen (1971) attributed seasonal changes in the vertical distribution of *S. elegans* from Oslofjorden, Norway, to the seasonal changes in size (and thus maturity stage). Diel vertical migration of chaetognaths has often been explained as an adaptation for avoiding visually directed predators (Pearre 1973) and is often more pronounced in mature specimens (Russel 1931; Pearre 1973; Terazaki & Marumo 1979; Sullivan 1980; Lough & Trites 1989). Such an ontogenetically differentiated pattern may be governed by the prevailing light conditions. For example, mature specimens, which are more visible to predators due to their size and developed gonads, were found to feed deer than juveniles at Station 134 (Fig. 10). However, the predatory effect on the vertical distribution requires data on temporal and vertical abundance of potential predators of *S. elegans*.

Diel variation in feeding

Diel variations in chaetognath feeding rates, with a higher NPC during night, are commonly reported from gut content analysis on the highly migratory *S. elegans* (e.g. Rakusa-Susczewski 1969; Szyper 1978; Feigenbaum 1982), and feeding is often considered to be inhibited by light (Pearre 1973). Nevertheless, Mironov (1960) and Feigenbaum (1979) did not find statistically significant diel variations in feeding activity. Such observations might reflect individual non-synchronous cycles due to state of satiation (Pearre 1973). The present results do not indicate any cyclic feeding behaviour of *S. elegans*, although the species seems to be affected by light, as evidenced by very restricted occurrence above 10 m. However, due to the long digestion time and the lack of data on vertical migration, it is impossible to evaluate any diel rhythm in feeding of the chaetognath. This study has therefore considered feeding to be constant during the 24-hour day, and calculations of the feeding rate in this study are based on a single NPC value.

During sampling in the present investigation, the surface light intensity always exceeded 96 μE m$^{-2}\cdot$s^{-1}, well above the triggering value for feeding onset of 24 μE m$^{-2}\cdot$s^{-1}, reported by Head et al. (1985) for zooplankton in the Canadian Arctic. During the Arctic summer, diel migration (Båmstedt 1984; Longhurst et al. 1984; Eilertsen et al. 1989; Hansen et al. 1990) and feeding rhythms (Båmstedt 1984) in zooplankton have been found to be suppressed, although the results diverge somewhat. Head et al. (1985) reported a diel cycle in the feeding rhythm of herbivorous zooplankton from the Canadian Arctic, despite the absence of a vertical migration behaviour. An increase in chaetognath feeding often corresponds to a well-developed diel vertical migration of potential prey (Rakusa-Susczewski 1969). The bulk in zooplankton biomass in the present investigation was observed between 5 and 15 m during the whole 24-hour period, i.e. there was no significant vertical migration. The chaetognaths should therefore be in constant contact with their prey by avoiding vertical migration, and the resulting continuous or intermittent feeding might be a logical adaptation to this situation. However, information thut would enable an evaluation of any migratory behaviour of the chaetognaths in the Barents Sea requires further investigations with frequent sampling from the entire water column.

Energy budget considerations

The calculated feeding rates in this investigation appear to agree with results from previous studies at higher temperatures, in which laboratory measurements on digestion time were combined with gut content analyses. Feigenbaum (1982) reported that *S. elegans* (3.5–20.5 mm) consumed 0.5–1.1 prey per day in Vineyard Sound, Massachusetts, at 0°C, when a DT of 10.2 hours was used. Applying a digestion time of 9.3 hours, Øresland (1987) calculated the predation rate to 0.2–1.0 prey items d^{-1} for 11–28 mm *S. elegans* at 6°C in Gullmarsfjorden, Sweden. Feeding experiments in the laboratory generally reveal higher values for *S. elegans*; Kuhlman (1977) measured 2.5 prey d^{-1} at 15°C and Reeve (1980) measured 4 prey d^{-1} at 13°C.

Mean specific daily ration (SDR) is the DW of prey intake as a proportion of predator body DW. AFDWs of prey in the three maturity stages in Table 6 were converted to dry weight (DW = 1.08 AFDW) and averaged for all stations. By applying the length–dry weight regression in Fig. 3, SDRs were calculated for the median size

Table 8. Energy budget for *Sagitta elegans*, Barents Sea, May–June 1983. Caloric-demand calculations are based on respiration rates from Sameoto (1972), using the median size in each maturity stage.

		I 15 mm	II 25 mm	III 32 mm
A	DW (mg)[1]	0.47	2.41	5.31
B	WW (mg)[2]	5.9	30.1	66.4
C	RR, 1.5°C (µl 0 ind 24 h)[3]	9.9	24.7	38.5
D	Caloric demand/ind for maintenance[4;5]	0.07	0.16	0.26
E	Energy cont/ind (Cal)[6]	1.70	8.22	17.60
F	Energy-specific caloric demand (D/E)	0.039	0.020	0.015
G	Mean FR (mgDW ind^{-1} 24 h^{-1})[7]	0.013	0.044	0.118
H	Mean SDR (DW) = diet (G/A)[1]	0.027	0.018	0.022
I	Mean SDR (Cal) = diet (G*5.25/E)[8]	0.040	0.028	0.035
J	demand/diet (% Cal) (F/I)	96.5	71.6	41.3

[1] *From equation in Fig. 3.*

[2] *Conversion factor of 12.5:1 (Sameoto 1972)*

[3] *Respiration regression at 1.5°C (Sameoto 1972)*

[4] 1 ml O = 4.8 cal (Sameoto 1972)

[5] *Assimilation efficiency of 72% (Sameoto 1972)*

[6] *Calorific content of chaetognaths from Shushkina & Musayeva (1980)*

[7] *Averages for all stations by using integrated values of abundances and feeding rates*

[8] *1 mg dry wt of copepod = 5.25 cal (22 J) (Båmstedt 1986)*

within each maturity stage of *S. elegans* (Table 8). Specific daily ration ranged between 0.018 and 0.027; the highest values were found in Stage I, which is in accordance with higher energy needs in juveniles (Szyper 1978; Feigenbaum 1979, 1982; Canino & Grant 1984). The results were somewhat lower than published daily rations for *S. elegans* (Feigenbaum 1982: 0.006–0.465; Pearre 1981: 0.0011–0.15), possibly due to a temperature effect. However, Davis (1984) calculated an even lower SDR (<0.008) for chaetognaths in a model of the copepod population of the Georges Bank. The specific daily ration of the chaetognaths is an indicator of their impact as predators (Feigenbaum 1979). Whether sufficient energy is allowed for growth depends on the magnitude of the metabolic processes, e.g. respiration (Pearre 1981). The metabolic data has been compiled in this study to set up an energy budget for the three maturity stages of *S. elegans* var. *arctica* (Table 8). It must be emphasised that the variable origin of the data makes the results rather precarious; they can, however, be considered suitable for inter-stage comparisons. Respiration demands (41–97% of ingested energy per day) indicate that *S. elegans* were feeding in excess of their basal requirements. Sameoto (1973) estimated annual respiration of *S. elegans* in Bedford Basin to be 75.3% of the ingested energy. Small *S. elegans* (6.5 mm) from Vineyard Sound consumed 60% more than their estimated metabolic requirements at 0°C, while large individuals were simply maintaining themselves (Feigenbaum 1982). Mature *S. elegans* from Bedford Basin did not meet their metabolic needs during the spawning season in July, while juveniles experienced deficit during December (Pearre 1981). Calculations from this study indicate that a higher proportion of the ingested energy is used for respiration in juveniles (97%) than in larger specimens (72 and 41% in Stages II and III). Excretion losses were not included in the calculations, but low nitrogen excretion was reported by Ikeda & Skjoldal (1989) for an early summer period.

Significance of chaetognath predation

In spite of low feeding rates, previously published results show that chaetognaths may be of great importance as predators on copepods. Reeve (1970) suggested that chaetognaths, with an estimated biomass equal to 30% of the copepods in the world ocean, are the primary carnivores in the marine environment. Sameoto (1973) estimated consumption by *S. elegans* in St. Margaret's Bay, and Bedford Basin, Nova Scotia, as 2.2–3.3% and 36% of the annual secondary production and concluded that chaetognaths were the most important predators on copepods in the latter area. During summer *S. elegans* in the Bering Sea removed daily 0.2% of the zooplankton standing stock, equivalent to 10% of the secondary production (Kotori 1976). In a model of the copepod population dynamics on Georges Bank, Davis (1984) found that *S. elegans*, together with *Pleurobrachia* (Ctenophora) and *Centropages* (Copepoda), could control the copepod population. In the Bristol Channel a biomass of 6.35 mg C m^{-3} of *S. elegans* was enough to cause a significant decline in the copepod standing stock in late summer (Williams & Collins 1985).

The calculated proportion of total zooplankton removed per day by *S. elegans* in the Barents Sea (0.08–0.22%, see Table 7) mainly affected the 1000–2000 µm sized-fraction, and on an annual basis the extrapolated proportions would reach considerable dimensions. However, due to the sample technique, smaller *S. elegans* are probably underestimated. Presumably, this would lead to an underestimation of feeding on smaller-sized fractions as well as the overall impact. On the other hand, the addition of a large biomass of smaller *S. elegans* would also lead to a correspondingly higher estimate of the total prey abundance. Besides, we neither know the annual *production* of zooplankton, nor the seasonal stability of the predation rate of chaetognaths in the Barents Sea, so we cannot draw any definite conclusions about the impact of chaetognaths here. A very rough estimation of secondary production is given by applying a conversion factor of 10% from primary production (Skjoldal & Rey 1989). The annual primary production in the Barents Sea is estimated to 70 g C m^{-2} (Rey et al. 1987). Using the data on abundance (Fig. 8A) and feeding rates (Table 6) of *S. elegans* and a carbon content of high latitude copepods of 54.7% (Båmstedt 1986), and integrating over one year, we find that 3% of the secondary production in the Barents Sea is consumed by *S. elegans*. The calculations are highly approximative, and more precise and extended data on digestion time, predator abundance, and prey abundance are required before any final conclusion can be made.

The ctenophore *Mertensia ovum* were found to consume 0.7% per day of the zooplankton biomass in the Barents Sea (Swanberg & Båmstedt 1991 this volume) which is 2.5 times higher than the maximum daily consumption by *S. elegans* (see Table 7). Thus, *S. elegans* var. *arctica* may not be the most important predator among the invertebrates in this area. However, at low food densities, chaetognaths are at a competitive advantage compared to ctenophores (Reeve et al. 1980). Thus, the values obtained here, indicate that predation by *S. elegans* var. *arctica* locally could be of consideration in areas of high chaetognath abundance.

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