Diel vertical migration and feeding of *Sagitta friderici* and *Sagitta tasmanica* in the southern Benguela upwelling region, with a comment on the structure of the guild of primary carnivores

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ABSTRACT: Diel vertical migration of the 2 most common chaetognaths (*Sagitta friderici* and *S. tasmanica*) in the southern Benguela was investigated at two 72 h stations during summer 1991. Feeding was examined over 24 h windows in these data sets. Both species exhibited diel vertical migration, although this was not obvious from changes in the mean depth occupied by night and day. Both species fed maximally at night in the upper layers before moving to deeper water to digest their food. Their diets were composed almost exclusively of copepods, and size preferences were exhibited by each species. The chaetognaths were segregated along a number of niche axes: viz. depth, time of maximal feeding and diet itself. It is suggested that competition between chaetognaths may have been high during periods of prolonged quiescence and mismatch, and that resource partitioning in a persistent guild has evolved to mitigate this. This alters the concept of zooplankton communities in upwelling regions as being exclusively physically structured. Although comparisons between the diets of chaetognaths and of the other first-order carnivore, *Euphausia lucens*, reveal similar partitioning of copepod prey, this structure cannot be interpreted in terms of historic competition but rather reflects differential mechanisms of resource acquisition.

KEY WORDS: Chaetognatha · Feeding · Diel vertical migration · Resource partitioning · Zooplankton community structure · Southern Benguela upwelling region

INTRODUCTION

Chaetognaths are generally the most numerous and conspicuous carnivores in samples of marine zooplankton and on average constitute 30 % of zooplankton biomass (Reeve 1970). Previously considered as voracious, they are now known to be quite selective predators with little direct effect on zooplankton standing stocks (see references in Feigenbaum & Maris 1984, Feigenbaum 1991), except under conditions of low environmental productivity (Kimmerer 1984, Øresland 1990). Because copepods make up the bulk of chaetognaths' diet (Feigenbaum & Maris 1984), they

can be considered to constitute one of the most important 'primary carnivores' in pelagic marine ecosystems (microheterotrophs excepted). Chaetognaths, in turn, fall prey to just about all other pelagic carnivores, including fish (e.g. James 1987).

Three species of chaetognath are to be found in the inshore waters of the southern Benguela, all of which can be classified as either epi- or shallow mesopelagic. *Sagitta friderici* (or *Parasagitta friderici*, see Bieri 1991) is typically the most abundant (Heydorn 1959) and can at times make up 90 % of chaetognath numbers (Venter 1969). It is a cold-water, neritic species that has a somewhat disjoint distribution, occurring all the way up the west coasts of both the American and African continents (Pierrot-Bults & Nair 1991). The other common species, *Sagitta tasmanica* (= *Serratosagitta tas-*

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manica), is generally less numerous than *S. friderici* in the southern Benguela, but is abundant in the northern Benguela (Venter 1969). It has a circumantarctic distribution, generally occurring at latitudes higher than 40° S, although its range does extend northward up the Atlantic coast of Africa to south of the bulge (Pierrot-Bults & Nair 1991). There is a northern hemisphere population of *S. tasmanica* centred on the NE Atlantic which extends as far south as the upwelling region along the north African coast (Thiriot 1978), and another has recently been identified in the Middle Atlantic Bight (Grant 1991). The least abundant of the 3 locally common species, *Sagitta minima* (= *Mesosagitta minima*), is a circumglobal, warmwater oceanic species which is largely confined to latitudes between 40° N and 40° S (Pierrot-Bults & Nair 1991). It is usually found at the shelf edge in the southern Benguela and occurs inshore under periods of blue water intrusion (Heydorn 1959).

Earlier studies of *Sagitta friderici* and *S. tasmanica* have concentrated on their diet and diel vertical migration (DVM) (Stuart & Verheye 1991, Gibbons 1992, Gibbons & Stuart in press) in isolation of each other. Direct comparative studies have not been made and it has not been possible to make any comments on the structure of the guild of first-order carnivores. Here, the diel vertical migration and feeding of both species of chaetognath are compared at 2 stations in the southern Benguela upwelling region and these in turn are compared with the facultative carnivore *Euphausia lucens*.

MATERIALS AND METHODS

Sample collection. During February 1991, 2 stations along a transect running off the Olifants River mouth, South Africa (31° 37' S, 18° 18' E) were intensively sampled over 72 h. The inner station (inshore) was in 65 m of water and was 2 nautical miles from the coast. It was sampled between 22:00 h on 16 February and 23:00 h on 19 February 1991. The other station (midshelf) was situated in 255 m of water and was 62 nautical miles from the coast. It was sampled between 10:00 h on 20 February and 23:00 h on 22 February 1991.

At each station, a conductivity-temperature-depth rosette sampler was cast to the bottom every 6 h to provide profiles of temperature and salinity. Water samples taken at 10 m intervals in the upper 100 m were analysed immediately for chlorophyll *a*. Zooplankton samples were collected using a 200 μm mesh 1 m² multiple opening-closing rectangular midwater trawl (RMT 1 × 6), which was towed obliquely at 2 knots over 5 depth strata from just above the bottom to the sur-

face. These strata were approximately 65–50, 50–30, 30–20, 20–10, 10–0 m at the inshore station, and 250–100, 100–60, 60–40, 40–20 and 20–0 m at the midshelf station. Flow was estimated by means of an electronic flowmeter mounted above the mouth of the net, and 100 % filtration efficiency was assumed for the tows, which were of short duration for each net. On retrieval, the contents of each net were preserved in 4 % buffered ($CaCO_3$) saline formalin for examination in the laboratory. Zooplankton were collected every ca 2 h throughout the night (ca 20:00 to 06:00 h) and every ca 4 h during the day. Gear failure at 03:00 h on 19 February 1991, however, meant that sampling was suspended for 6 h.

Sample processing. In determining vertical distribution and abundance, all chaetognaths were counted from each sample. When collections were large, subsamples were taken using a Folsom splitter and a minimum of 50 individuals were counted. Data were standardised to numbers per m³ and per m² using net flowmeter data.

The total body length (excluding tail fin) of 50 randomly selected individuals from each sample was measured and the stage of maturity determined according to the development of the ovaries (Thomson 1947).

Copepod consumption by both species of chaetognath was determined over a single 24 h period at each station (17 to 18 February 1991 inshore and 20 to 21 February 1991 at the midshelf station) following the method described by Gibbons (1992). In short, the hind guts of 50 measured individuals of each species from each sampling time and depth were dissected out and broken open in glycerine on glass slides. The contents were examined at 160× magnification for copepod mandibles, which were counted, measured and identified to species. Samples with fewer than 20 individuals were ignored: when 20 to 50 individuals were collected, the whole sample was analysed if possible. In each sample the proportion of the population containing food in their guts, the food containing ratio (FCR = no. chaetognaths containing food/total no. chaetognaths × 100), was calculated as was the mean number of prey items per chaetognath (NPC = total no. prey items/total no. chaetognaths). Copepod mandible widths were converted to copepod prosome lengths and widths using the equations in Stuart & Pillar (1990) and Stuart & Verheye (1991).

In order to relate the diet of chaetognaths to the ambient food environment, copepod abundances and distribution were determined over the same two 24 h periods. These data will not be presented or discussed in detail, as they only represent selected portions of the larger 72 h data sets, which are yet to be fully analysed and will be published elsewhere. All copepods were counted by species from 2 ml subsamples taken with a

piston pipette (see Peterson et al. 1990) from each depth stratum at every other sampling interval (3 day, 3 night). All developmental stages are here lumped together, because while there is undoubtedly a correlation between the dimensions of copepod mandibles (recovered from chaetognath guts) and developmental stage, it is not at present available.

The estimation of prey selection by a predator in a 3-dimensional environment is fraught with difficulties, not least of which is the problem of determining where the predator has been feeding (see approaches taken by Pearre 1973, 1974, Stuart & Verheye 1991, Gibbons 1992). In this study no attempt has been made to tie together migration paths and distances over the gut passage time with changes in the ambient prey field over those distances (as Gibbons 1992). Rather, comparisons have been made using a weighted estimate of diet at night, i.e. the proportional composition of the diet at any depth has been weighted by the proportion of the chaetognath population at that depth, and the total summed over the depth ranges.

Statistical analysis. To determine day/night differences in vertical distribution both between and within species, mean day and night time depths were compared using single-factor Kruskal Wallis analyses (Zar 1984). This non-parametric statistical test was also used to examine day/night differences in abundance, and to determine changes in chaetognath feeding over time as well as to assess the significance of depth on gut-contents (NPC). Kolmogorov-Smirnov 1- and 2-sample tests (Sokal & Rohlf 1981, Zar 1984) were performed on selected data in order to (1) compare the size distributions of chaetognath 'populations' between stations and depths, (2) determine whether either species of chaetognath selected components of its diet from the ambient prey spectra, and (3) compare the size distributions of prey eaten between the 2 chaetognaths. Null hypotheses were (respectively) that (1) populations have the same size distribution irrespective of station and depth, (2) each prey species and size class of prey occurs in the diet of each chaetognath species at the same proportion as it occurs in the water column and (3) that the diet by prey size of both species of chaetognath were the same. Differences between data were considered significant at the 95 % level.

RESULTS

Fuller descriptions of the physical environment at the 2 stations during February 1991 are provided by Gibbons (1993). In short, a pronounced thermocline existed between 5 and 25 m at the inshore station, where chlorophyll maxima were observed between 10 and 20 m. At the midshelf station, by contrast, the thermocline was weak and the chlorophyll concentration decreased from the surface. Surface chlorophyll levels at the inshore station (13.31 to 55.04 μg l^{-1}) were an order of magnitude greater than at the midshelf station (1.46 to 4.57 μg l^{-1})

Copepods: abundance and distribution

Probably owing to the combination of adult and copepodite data, there was little difference in the vertical distribution of copepods between sampling intervals at night. All the nocturnal collections are thus considered together as replicates. Likewise with the diurnal samples, so that the data are considered here in terms of day and night only. A fuller description and figure can be found in Gibbons (1993).

Although copepods were more or less evenly distributed throughout the water column at the inshore station, densities were highest in the upper 20 m (day, 26 617 m^{-3}; night, 7391 m^{-3}) and reached minimum values between 50 and 65 m (day, 3378 m^{-3}; night, 3832 m^{-3}). *Oithona* spp. dominated the copepod assemblage throughout the water column (Table 1) and reached maximum densities in the upper 20 m (day, 21 260 m^{-3}). *Metridia lucens* was more common at depth than near the surface, while *Centropages brachiatus* was mostly restricted to the upper 20 m (1048 m^{-3}) and occurred at very low densities below 50 m (night, 7.1 m^{-3}).

Copepods were less abundant at the midshelf station, and total densities decreased markedly from the upper 20 m (day, 9114 m^{-3}; night, 9216 m^{-3}) to a minimum at between 100 and 250 m (day, 83 m^{-3}; night, 160 m^{-3}). *Oithona* spp. were less common at the midshelf than the inshore station, and communities in both the surface and deep-water layers were dominated by small calanoids (*Paracalanus* spp. and *Ctenocalanus vanus*) (Table 1). *Metridia lucens* was again more common in deep than shallow water layers, where it comprised 27 % of total copepods between 100 and 250 m. *Centropages brachiatus* and large calanoids (*Calanoides carinatus* and *Calanus agulhensis*) were mostly confined to the upper 20 m (4553 m^{-3} and 1142 m^{-3}, respectively) and represented < 5 % of the copepods between 100 and 250 m (5.8 and 1.5 m^{-3} respectively).

The shallow distribution of *Centropages brachiatus* makes it a useful tracer of surface feeding chaetognaths (as Pearre 1973, Gibbons 1993).

Sagitta friderici

Sagitta friderici comprised approximately 53 % of chaetognaths at the inshore station and 8 % of those at

Table 1. *Sagitta friderici* and *S. tasmanica*. Distribution of copepod species (% of numbers) in ambient food environment and chaetognath guts in surface and deep-water layers. Nocturnal samples combined; total unity not required since species not eaten (e.g. *Rhincalanus nasutus*) not included. *Sf: S. friderici; St: S. tasmanica; –*: too few data

| Taxon	Inshore			Midshelf		
	Ambient	*Sf* gut	*St* gut	Ambient	*Sf* gut	*St* gut
		0–20 m depth			0–20 m depth	
Oithona spp.	41.0	29.1	17.6	12.2	12.1	0
Small calanoids	28.9	42.8	76.5	46.1	9.8	5.5
Centropages brachiatus	10.7	21.1	0	33.9	65.1	92.4
Metridia lucens	4.5	0.6	0	0.4	0	0
Large calanoids	3.7	6.4	5.9	7.3	13.0	2.1
		50–65 m depth			100–250 m depth	
Oithona spp.	58.4	23.6	10.7	18.1	–	3.2
Small calanoids	27.1	50.0	85.7	51.0	–	6.4
Centropages brachiatus	0.3	13.2	0	3.2	–	71.3
Metridia lucens	12.3	5.3	0	26.9	–	0
Large calanoids	1.7	7.9	3.6	0.8	–	19.1
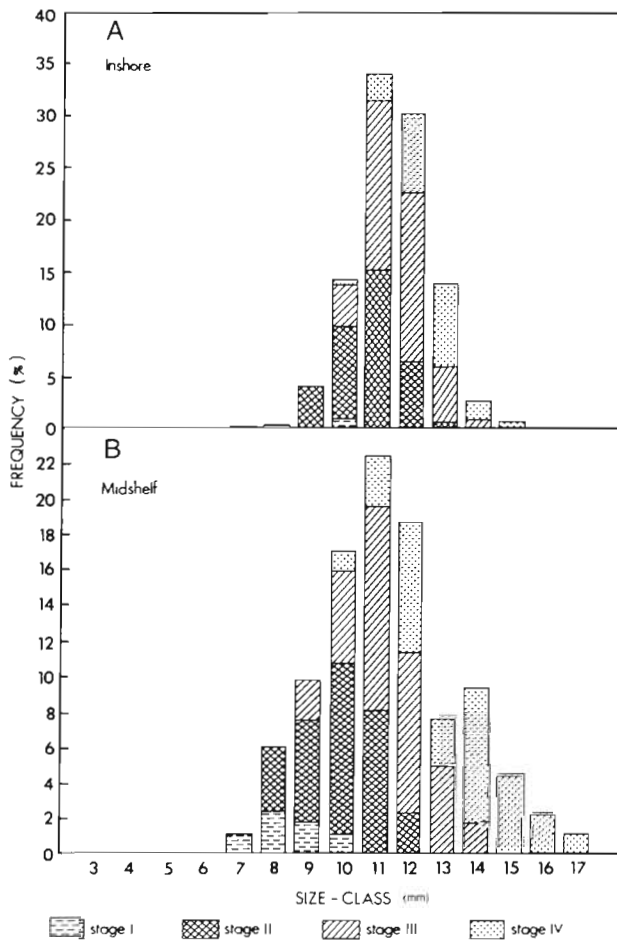
Fig. 1. *Sagitta friderici*. Length:frequency (as percent) plots of populations at the (A) inshore and (B) midshelf stations. The relationship between chaetognath length and the stage of ovarian development is superimposed

the midshelf station during the period of this study. *S. tasmanica* represented 43 % and 39 % at each station respectively, and the balance was made up largely by *S. minima*.

Populations of *Sagitta friderici* at both the inshore and midshelf stations exhibited a similar unimodal size-frequency distribution, with adults reaching a maximum size of approximately 17 mm (Fig. 1). These distributions resemble those presented by Stuart & Verheye (1991) and Gibbons & Stuart (in press). There was no significant difference in the size structure of samples with depth at either station (p > 0.05) and this did not change over time.

Sagitta friderici was generally much more abundant at the inshore than midshelf station (see depth-integrated abundances in Fig. 2), which is hardly surprising considering the neritic nature of this species (Pierrot-Bults & Nair 1991). There were no significant differences in chaetognath abundance over the diel cycle at either of the 2 stations, indicating that individuals were not migrating beyond the sampling depth. Although this should make for easy interpretation of net-collected samples, examination of the vertical profiles presented in Fig. 2 would suggest that DVM is anything but clear at either station. And certainly, there was no significant difference in the mean depth occupied by daytime (30.95 ± 2.44 m inshore, 16.59 ± 2.38 m midshelf) or night-time populations (23.53 ± 1.63 m and 18.06 ± 2.59 m respectively) (p < 0.01). If the vertical distribution of *S. friderici* between 17 and 18 February at the inshore station is examined in more detail (Fig. 3A), however, it is clear that the population was not static. Indeed, there was a pronounced movement into the surface 20 m at both dusk and dawn indicative of
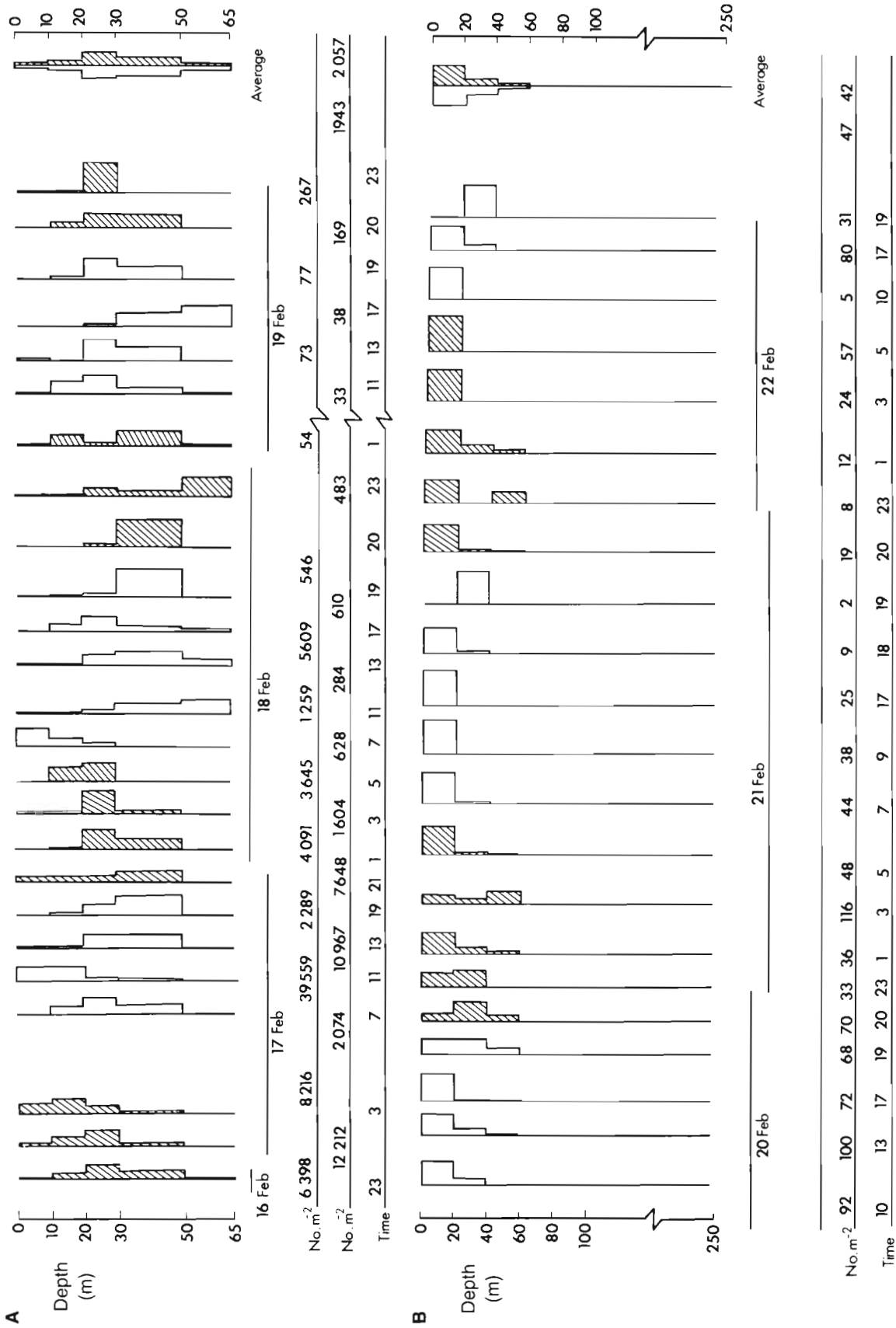
Fig. 2. *Sagitta friderici*. Vertical distribution (% of total) at the (A) inshore and (B) midshelf stations. Hatched plots sampled at night. The approximate time of sample collection is indicated. Numbers below plots are depth-integrated abundances (m²); diurnal average at the inshore station excludes the very high estimate of abundance made at 11:00 h on 17 February
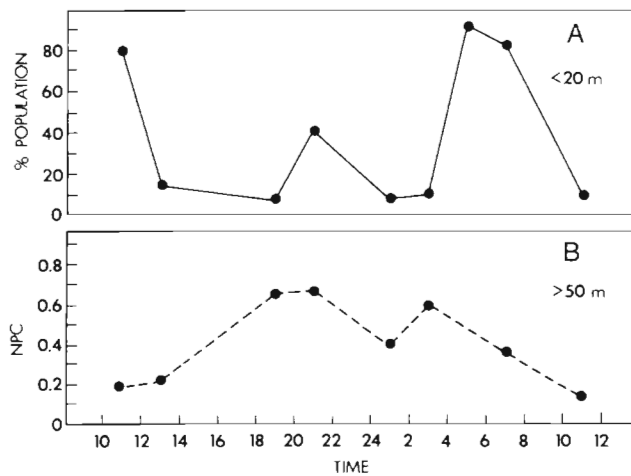
Fig. 3. (A) Proportion of *Sagitta friderici* in the upper 20 m at the inshore station between 17 and 18 February 1991 (B) Mean number of copepods per chaetognath collected from deep water (> 50 m) over the same period

Table 2. *Sagitta friderici* and *S. tasmanica.* Mean (SE) prey size (mm) by length class. Data are from the inshore and mid-shelf stations combined

Chaetognath length (mm)	S. friderici	S. tasmanica
7	0.284 (–)	
8	0.538 (0.041)	0.548 (0.063)
9	0.573 (0.006)	0.562 (0.071)
10	0.586 (0.019)	0.620 (0.065)
11	0.646 (0.016)	0.776 (0.091)
12	0.702 (0.017)	0.719 (0.063)
13	0.805 (0.027)	1.022 (0.095)
14	0.844 (0.046)	1.030 (0.042)
15	1.022 (0.113)	1.038 (0.020)
16	1.111 (0.227)	1.073 (0.019)
17		1.066 (0.024)

Table 3. *Sagitta friderici* (*Sf*) and *S. tasmanica* (*St*). Frequency (%) of multiple prey items in chaetognath diets at the inshore and midshelf stations

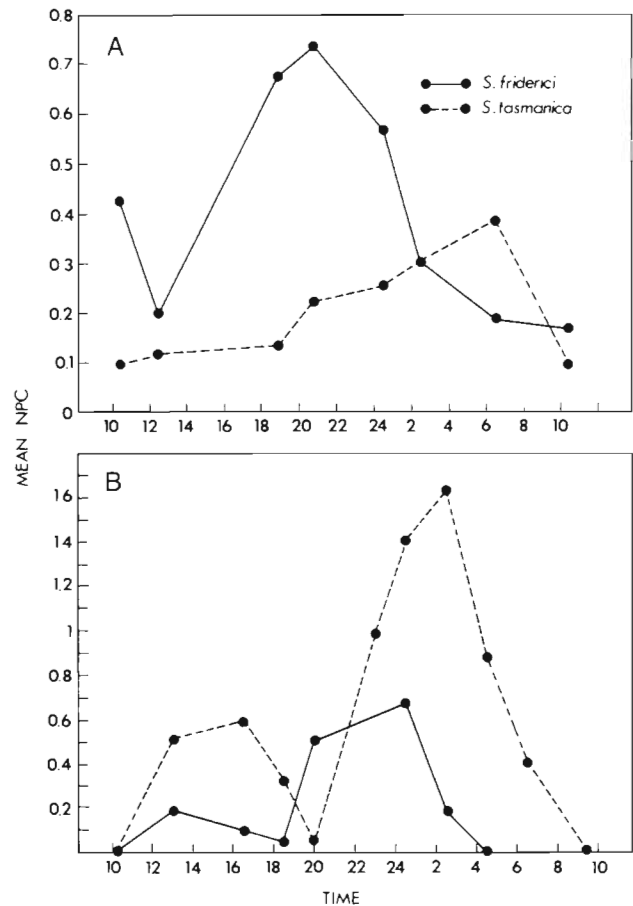| No. of prey	Inshore		Midshelf	
	Sf	St	Sf	St
1	65.9	94.3	87.3	61.9
2	19.9	4.7	9.9	18.6
3	7.1	1.0	2.8	9.8
4	3.2	–	–	5.2
5	2.4	–	–	2.3
6	1.0	–	–	1.0
7	0.2	–	–	0.5
8	–	–	–	0.5
9	0.2	–	–	0.3

Fig. 4. *Sagitta frederici* and *S. tasmanica.* Mean number of copepods per chaetognath (NPC) at the (A) inshore and (B) midshelf stations during 17 to 18 February 1991. These data are calculated as the product of means at each depth strata by proportion of the population at each strata (thus no error bars)

midnight sinking (see also Stuart & Verheye 1991). No clear patterns of movement were observed at the midshelf station, either because densities were too low or the sampling scales were of the wrong resolution.

Copepods formed over 98% of the diet of *Sagitta friderici* and cannibalism occurred in only 6 of the 2817 specimens examined at the inshore station. Cannibalism was not observed at the midshelf station possibly because too few animals (186) were examined. This generally low incidence of cannibalism is in agreement with the observations of Stuart & Verheye (1991) and Gibbons & Stuart (in press). There was no relationship between the number of prey eaten and chaetognath length but there was a positive correlation between the lengths of predator and prey (Table 2). The mean number of copepods eaten by chaetognaths at the inshore station was greater than that at the midshelf station,

Table 4. *Sagitta friderici* and *S. tasmanica*. Mean number (SE) of prey items per chaetognath (NPC) per depth stratum, by day and night. All data per stratum are averaged (day and night separately). •NPC at dusk and dawn significantly different from those at other diurnal sampling intervals (see Fig. 3). –: too few data

Depth stratum	S. friderici Day	S. friderici Night	S. tasmanica Day	S. tasmanica Night
Inshore				
0–20 m	0.299 (0.053)	0.632 (0.053)	0.286 (0.125)	0.449 (0.077)
20–50 m	0.213 (0.057)	0.437 (0.067)	– –	0.169 (0.043)
50–65 m	0.320• (0.038)	0.382 (0.058)	0.189 (0.019)	0.238 (0.024)
Midshelf				
0–40 m	0.139 (0.058)	0.663 (0.081)	0.522 (0.083)	1.378 (0.101)
40–100 m	0.050 (0.050)	0.489 (0.080)	0.368 (0.045)	1.056 (0.106)
100–250 m	–	–	0.400 (0.244)	0.562 (0.085)

Table 5. *Sagitta friderici* and *S. tasmanica*. Size (prosome length) and species distribution of copepods in diets, and in the water column at the inshore station during the night of 17 to 18 February 1991. Data are the sum of the size distributions at each (sampled) depth stratum multiplied by the proportion of the population occupying that stratum

Size class (mm)	S. friderici	S. tasmanica	Ambient
0.1	0.02	0	0
0.2	0.54	3.39	0
0.3	16.04	1.23	0.60
0.4	5.45	7.29	1.35
0.5	8.06	11.24	29.28
0.6	10.17	14.10	19.87
0.7	21.02	46.31	16.34
0.8	10.55	9.59	12.86
0.9	3.89	0.62	2.63
1.0	4.56	0	1.73
1.1	1.09	0	1.45
1.2	2.26	2.80	1.92
1.3	1.02	0	2.85
1.4	2.11	0	1.10
1.5	1.15	0	0.80
1.6	2.00	0	1.60
1.7	1.96	0	1.73
1.8	4.69	0	1.69
1.9	2.57	0.62	0.87
2.0	1.46	2.80	0.53
2.1	0.49	0	0.63
2.2	0.02	0	0.09
Taxon			
Oithona spp.	20.38	10.35	51.70
Small calanoids	40.17	80.35	32.60
Centropages brachiatus	18.45	0	4.40
Metridia lucens	1.08	0	7.60
Large calanoids	19.92	9.30	3.70
N	1180	134	

with up to 9 prey items being recovered from a single individual. Single prey items otherwise accounted for 66 % and 87 % of the diet of *S. friderici* at each station respectively (Table 3).

Sagitta friderici had the remains of prey in its gut throughout the 24 h periods of detailed investigation at both stations (Fig. 4). And, despite the absence of any statistically clear DVM, the number of prey recovered from chaetognath guts was higher during the night (0.51 ± 0.03 per chaetognath inshore, 0.59 ± 0.06 midshelf) than during the day (0.29 ± 0.03 inshore, 0.11 ± 0.04 midshelf). While there was no correlation between the number of prey per chaetognath and the depth of sample collection during the day (and at night at the midshelf station; Table 4), individuals sampled in the upper 20 m of the inshore station at night had more prey in their guts than those collected in deep water (Table 4). Interestingly though, more copepods were recovered from chaetognath guts at dawn and dusk from *S. friderici* in deep water than at other times during the hours of daylight at the inshore station (Fig. 3B), and this is in agreement with the movement of superficially feeding individuals into deep water (Fig. 3A).

Sagitta friderici ate a wide size range of copepods at both stations (0.3 to 2.2 mm prosome length, inshore; 0.3 to 1.4 mm, midshelf). At both stations the size distribution of copepods consumed was bimodal (Tables 5 & 6): the smaller peak occurring at 0.3 mm prosome length and the larger at between 0.7 mm (inshore) and 1.0 mm (midshelf). The most abundant size class(es) of copepods in the water column was largely ignored at

both stations, and falls in the trough between the 2 preferred modes. While it might appear that copepods of 0.3 mm length were strongly selected for (because of their rarity in the water column), this result is likely to be artifactual and reflect the escapement of (such) small copepods through the 200 μm mesh of the net (see e.g. Pillar 1984). Inshore, copepods of the larger prosome length class preferred by *S. friderici* belonged almost exclusively to 'small calanoids', and at the midshelf station to *Centropages brachiatus*. Small calanoids were taken at approximately ambient proportions inshore (Table 5) both by species and size class (0.6 to 0.8 mm prosome length). On the other hand, *C. brachiatus* (the species) occurred at significantly greater proportions in the diet of *S. friderici* than it did in the water column, at both stations (Tables 5 & 6) but the size class (0.8 to 1.3 mm prosome length) was preferred only at the midshelf station. This reflects the

Table 6. *Sagitta friderici* and *S. tasmanica*. Size (prosome length) and species distribution of copepods in chaetognath diets, and in the water column at the midshelf station during the night of 20 to 21 February 1991. Data are the sum of the size distributions at each (sampled) depth stratum multiplied by the proportion of the population occupying that stratum

Size class (mm)	S. friderici	S. tasmanica	Ambient
0.1	0	0	0
0.2	0	0	0
0.3	6.88	0.16	0
0.4	2.94	0	2.93
0.5	0	1.15	28.85
0.6	1.01	0.51	11.95
0.7	3.48	3.11	25.81
0.8	7.42	4.25	16.78
0.9	22.64	7.88	4.14
1.0	23.57	29.56	5.75
1.1	9.43	19.56	4.66
1.2	12.29	18.29	0.71
1.3	5.41	5.32	0.75
1.4	2.47	1.60	0.73
1.5	0	0.63	1.03
1.6	0	0.83	0
1.7	0	0.79	0.02
1.8	0	1.29	0
1.9	0	2.44	0
2.0	0	1.76	0
2.1	0	0	0
2.2	0	0.65	0
Taxon			
Oithona spp.	9.84	0.79	14.41
Small calanoids	9.35	5.29	42.89
Centropages brachiatus	68.55	81.00	32.92
Metridia lucens	0	0.32	2.03
Large calanoids	12.26	12.60	7.75
N	76	546	

fact that *C. brachiatus* dominated the ambient size class at the midshelf station whereas *Metridia lucens* dominated inshore (but was taken at much lower than ambient proportions).

The elevated presence of *Centropages brachiatus* in the diet of *Sagitta friderici* was noticeable at all depths sampled (although only the upper- and lower-most layers are shown in Table 1). Because of the surface-living nature of this copepod (De Decker 1984), its relatively high abundance in the chaetognaths collected from deep water suggests one of two things. Either some *S. friderici* were feeding at shallower depths, or *S. friderici* were feeding in water deeper than 50 m but individual chaetognaths were very strongly selecting for the species *C. brachiatus*. The former is in keeping with the evidence presented above regarding DVM and feeding (see also Pearre 1973).

Sagitta tasmanica

The size range and frequency distribution of *Sagitta tasmanica* at the 2 stations were markedly different from each other (Fig. 5) (as Gibbons 1992[1]). The modal size of the population inshore was 7 to 9 mm, while at the midshelf station it was 14 to 15 mm. At the inshore (but not midshelf) station there was also a shift in the size distribution of the population with increasing depth (Fig. 5), to include a greater proportion of smaller individuals. This ontogenetic layering was also partially observed by Gibbons (1992).

Sagitta tasmanica was generally more abundant at the inshore than midshelf station. There were no significant differences in chaetognath abundance over the diel cycle at either station (Fig. 6) indicating that, as with *S. friderici*, few individuals were migrating to beyond the deepest depth sampled. Despite this, DVM was not clear at either station (Fig. 6) and there were no significant differences in the mean depth occupied during the day (41.36 ± 2.12 m inshore, 47.15 ± 9.06 m midshelf) or night (37.29 ± 2.74 m, 46.34 ± 7.25 m respectively) (p < 0.01). On more detailed inspection, however, it is clear that populations at both stations did not remain static (Fig. 7). The bulk of the *S. tasmanica* population inshore was situated in the middle and deeper layers of the water column, but individuals moved progressively into the upper 20 m during the night, to peak at just before dawn (Fig. 7A). Populations at the midshelf station (Fig. 7C), by contrast, were to be found in the upper 40 m throughout the 24 h. *S. tasmanica* 'peaked' in the upper 40 m at noon and moved to gradually deeper depths with nocturnal progression, before moving back to the surface the following day.

Copepods formed over 99% of the diet of *Sagitta tasmanica*, and cannibalism occurred in only 3 of the 1120 specimens examined at the inshore station and in 1 of the 825 individuals at the midshelf station. There was no relationship between the number of prey eaten and chaetognath length (p > 0.05), but there was a positive correlation between the size of predator and prey (Table 2, p < 0.01). The mean number of copepods eaten by chaetognaths at the midshelf station was greater than that at the inshore station (as Gibbons 1992) with up to 9 prey items being recovered from a single individual (Table 3). Single prey items otherwise accounted for

[1] It should be pointed out that the size distributions of *Sagitta tasmanica* presented in Gibbons (1992; Fig. 3, p. 254) were based on individuals whose lengths were over-measured by a factor of 1.2. Thus the modal size of offshore populations was not 18 to 20 mm as stated but rather 15 to 17 mm. Likewise the modal length of the inshore population was not 14 to 16 but 11 to 13. The maximum size attained was not 24 mm but 20 mm. None of the relationships presented are otherwise affected
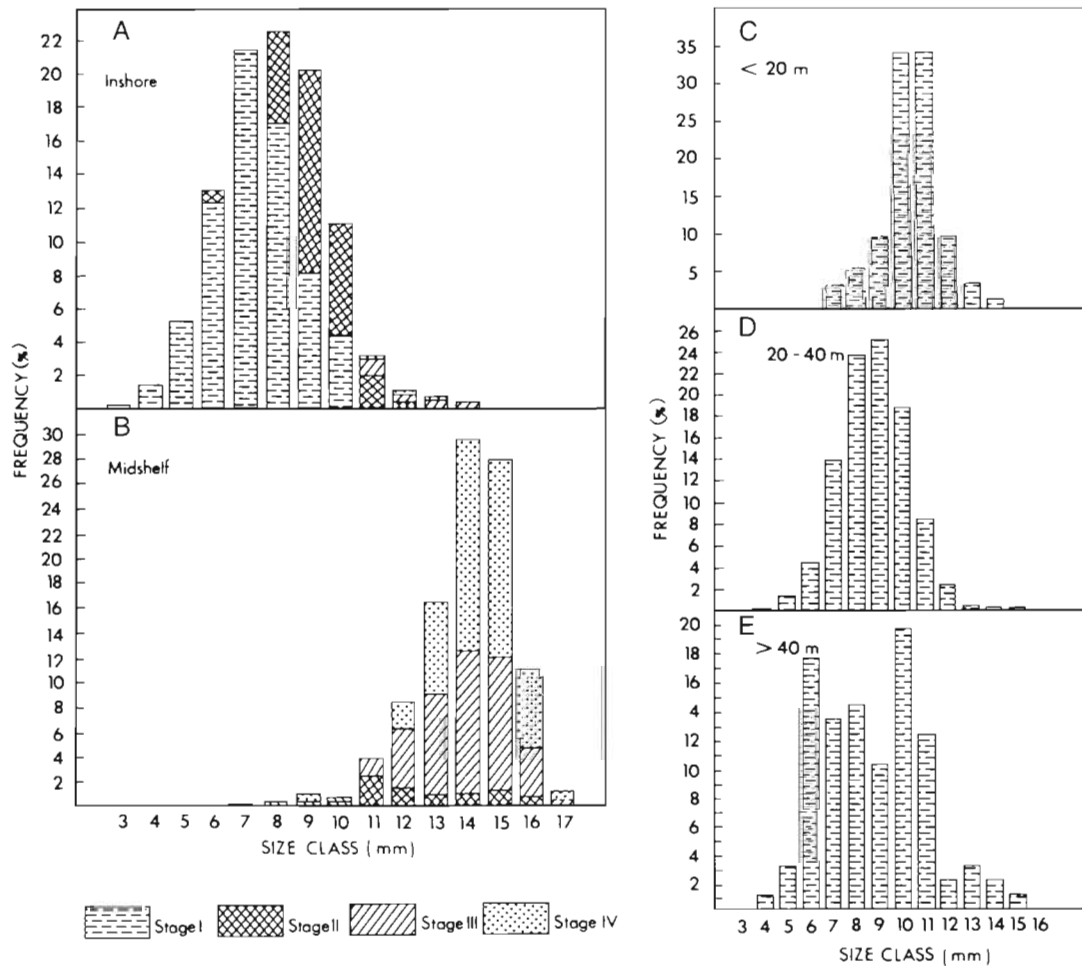
Fig. 5. *Sagitta tasmanica*. Length:frequency (as percent) plots of populations at the (A) inshore and (B) midshelf stations. (C, D, E) Changes in the size structure of the inshore population with depth. The relationship between chaetognath length and the stage of ovarian development is superimposed in (A) and (B)

94 % and 62 % of the diet of *S. tasmanica* at the inshore and midshelf stations respectively (Table 3).

Although *Sagitta tasmanica* had the remains of copepods in its gut throughout the 24 h of detailed study at both stations (Fig. 4), the mean number of copepods recovered from each chaetognath was higher during the night (0.25 ± 0.02 inshore, 1.08 ± 0.06 midshelf) than during the day (0.19 ± 0.02 inshore, 0.41 ± 0.04 midshelf). There were no significant differences in the numbers of copepods eaten by chaetognaths from the different depth strata sampled by day (Table 4), but significantly more prey were recovered from individuals collected in the surface than deep water at night, at both stations (Table 4). Just as the average number of copepods recovered from chaetognath guts generally increased with nocturnal progression (Fig. 4), so too did the number recovered from individuals in deep water (Fig. 7). In both instances this trend would appear to reflect the movement of *S. tasmanica* from the copepod-rich surface waters into the deeper layers (Fig. 7).

Sagitta tasmanica ate a relatively broad size range of prey at both stations (0.1 to 2.0 mm prosome length inshore, 0.3 to 2.2 mm midshelf). The incorporation of large prey into the diet of chaetognaths at the midshelf station may be attributed to the larger individual size of chaetognaths at that station. Unlike the size distribution of prey consumed by *S. friderici*, that observed for *S. tasmanica* (Tables 5 & 6) was unimodal and peaked at 0.7 mm prosome length inshore and between 0.9 and 1.2 mm at the midshelf station. Again, the larger size of preferred copepod at the midshelf station can be partly attributed to the larger chaetognath size at the midshelf station. At the inshore station copepods belonging to the modal size class were mostly small calanoids, which were heavily selected for (by size and species) (Tables 5 & 6), whilst at the midshelf station they were almost exclusively *Centropages brachiatus* (as Gibbons 1992), which were also heavily selected for, by species and size. The presence of *C. brachiatus* at disproportionate levels (rela-
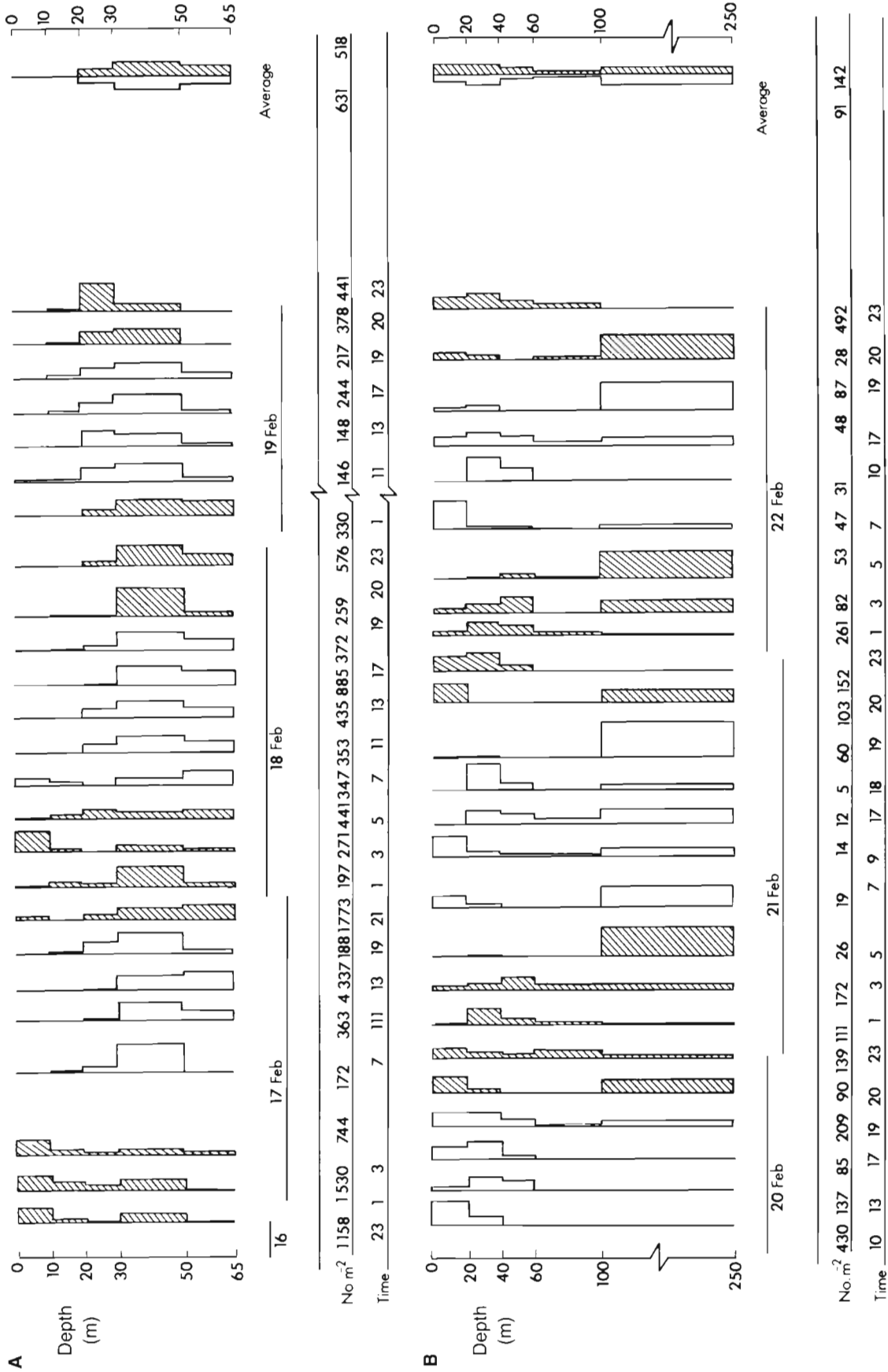
Fig. 6. *Sagitta tasmanica*. Vertical distribution (% of total) at the (A) inshore and (B) midshelf stations. Hatched plots sampled at night. The approximate time of sample collection is indicated. Numbers below plots are depth-integrated abundances (m^{-2})
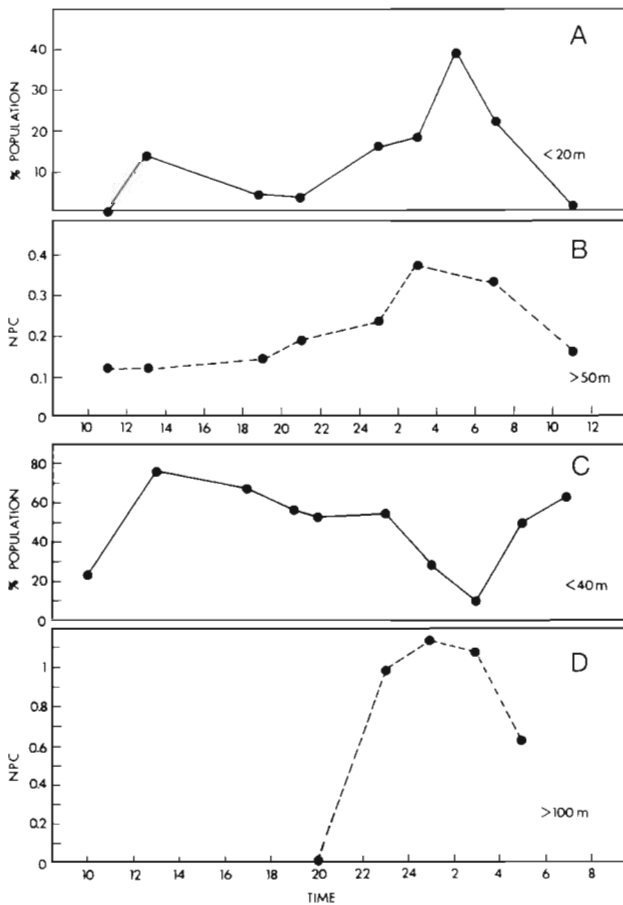
Fig. 7. (A, C) Proportion of *Sagitta tasmanica* in the upper (A) 20 m at the inshore station between 17 and 18 February 1991, and (C) 40 m at the midshelf station between 20 and 21 February 1991. (B, D) Mean number of copepods recovered from chaetognath guts in deep water at the (B) inshore and (D) midshelf stations over the same periods

tive to the water column) in the guts of deep collected *S. tasmanica* at night (Table 1) indicates prior feeding at more superficial depths, and supports the evidence presented earlier on vertical migration.

DISCUSSION

There was no significant difference in the mean depth occupied during the day or night by either *Sagitta friderici* or *S. tasmanica*. Although this suggests that neither chaetognath displayed DVM, the mean depth occupied by day (or night) conveys no information on changes in distribution throughout the day (or night), and masks such variable processes as midnight-sinking (Simard et al. 1985). Even by following changes in mean depth it is possible to miss the more subtle, asynchronous migrations of individuals

within populations (e.g. Pearre 1973, Gibbons 1993). By using tracers of surface feeding (in this case total copepods and *Centropages brachiatus*), however, it is clear that each species of chaetognath was exhibiting DVM. And much of their populations occurred in the surface waters at some stage during the night. Otherwise there was no constancy of pattern between species or station, and little agreement with previous accounts. For example, Stuart & Verheye (1991) also observed *S. friderici* to exhibit midnight-sinking at an inshore station in St Helena Bay (South Africa) during winter. In contrast to this study, on the other hand, Gibbons (1992) observed *S. tasmanica* during spring in the midshelf region of the southern Benguela to exhibit very pronounced and rapid movement from deep water to the surface at dusk. It must be stressed that such constancy of pattern should not be expected in DVM because of the very many factors which complicate observations and their interpretation (Pearre 1979). What does appear to be consistent between observations, however, is that *S. friderici* occurs at shallower depths than *S. tasmanica*, throughout 24 h and over many km of the continental shelf ($p < 0.01$).

Greater prey recoveries were made from both species of chaetognath obtained from the surface than from deep water at night. This suggests that individuals were feeding at the copepod maxima, and when considered with the generally greater densities of chaetognaths in the surface at night, explains the nocturnal feeding rhythms observed. Peaks in copepod recoveries from chaetognaths in deep water were generally made after those in the surface, suggesting the subsequent downward movement of individuals to deeper water to digest their food (as Pearre 1973). Nocturnal feeding by chaetognaths is frequently observed (Szyper 1978, Sullivan 1980, Sameoto 1987), even in the absence of clear DVM (e.g. Pearre 1974, but see also Pearre 1973), and appears to vary seasonally and with changes in the ambient food environment (Rakusa-Suszczewski 1969, Øresland 1987). Of interest here too is an apparent segregation in feeding intensity between the species. Feeding maxima were observed earlier in the night for *Sagitta friderici* (as also Stuart & Verheye 1991) than they were for *S. tasmanica*.

The diets of both species of chaetognath were comprised almost exclusively of copepods, which is no surprise considering copepods were the dominant ambient prey type. Such is the norm for chaetognaths (see review of Feigenbaum & Maris 1984). Nor is the observation that prey size increases with predator size anything new (Reeve & Walter 1972, Pearre 1980). There is generally a positive relationship both between predator size and prey size, and between predator size and prey size range, which results in a specific (Pearre

1980) window of 'preferred' prey size. Changes in the size of this window reflect not only changes in the size structure of the chaetognath population, however, but also in the ambient prey spectra (and its estimation). Interpretations of size 'selection' are not easy, as the absence of a prey size class in the diet of a chaetognath may simply reflect the absence or rarity of that size class in the water column (Feigenbaum 1979 in Pearre 1980) rather than any response to that size class as such. Thus it is possible to interpret the shift in size of the preferred prey eaten by *Sagitta tasmanica* from the inshore to the midshelf station in terms of both a shift in chaetognath and prey size. That there is a specific change in preferred prey eaten by *S. tasmanica* (small calanoids were strongly selected for inshore but against at the midshelf station) reflects the change in species-size class structure of the water column. The larger size of *S. tasmanica* (midshelf) than *S. friderici* is similarly reflected in the larger size of preferred prey (as Rakusa-Suszczewski 1969).

Guild structure and resource partitioning

In 'climax' marine ecosystems, such as the North Pacific Gyre, samples of zooplankton separated by many hundreds of kilometres and taken many months apart show a striking degree of similarity (McGowan & Walker 1979, 1985), in terms of both their high diversity and their near constant structure. Congeneric species and guild-members show pronounced partitioning of vertical space and trophic resources (Ambler & Miller 1987, Hopkins et al. 1989, Flock & Hopkins 1992, Hopkins & Gartner 1992). Because oceanic biomass across the trophic spectra is low, such behaviours mitigate against interspecific competition, and have evolved primarily as a result of prolonged environmental stability. Zooplankton assemblages in upwelling areas, by contrast, are characterised by low diversity (De Decker 1984, Pillar et al. 1992, Verheye et al. 1992). There is often little similarity between samples separated by a few kilometres and taken only days apart (McGowan & Walker 1985). The reason for this is that upwelling areas are oceanographically dynamic and exhibit significant physical heterogeneity (references in Richards 1981, Payne et al. 1987, 1992). Few species have the necessary adaptations to persist, although those that do so may be abundant (e.g. Pillar et al. 1992, Verheye et al. 1992).

In the light of the physical dynamics of upwelling ecosystems and their high productivity, it is perhaps thought that the evolution of interspecific behaviours allowing co-existence has been unnecessary; i.e. in contrast to climax systems, zooplankton assemblages are structured by physical rather than biological

processes. From the data presented here and that collected elsewhere (Fig. 8), however, it would appear that *Sagitta friderici* and *S. tasmanica* are segregated along a number of niche axes in the southern Benguela upwelling region. And this is reminiscent of resource partitioning (Schoener 1974, 1986, Longhurst 1985). Traditionally, emphasis in studies of resource partitioning is placed on sibling species (Schoener 1986). There have been a number of ecological studies on sympatric species of chaetognaths which explored differences in diet (Rakusa-Suszczewski 1969, Stone 1969, Pearre 1974, 1976, Sullivan 1980, Øresland 1987, 1990) and vertical distribution (Russell 1933, Pearre 1974, Sullivan 1980, Sameoto 1987).[2] Yet, with the exception of a comment by Rakusa-Suszczewski (1969, p. 229) none of these authors have attempted to interpret their findings in terms of community structure. The reason for this may be the difficulty of imagining any meaningful interaction between few species in a large, 3-dimensional environment that may be fluctuating in a stochastic manner, and in which food is generally considered abundant. But how valid are these reasons and is it possible to interpret the results presented here in terms of resource partitioning?

Despite the productivity of pulsed upwelling regions (Cushing 1971) there is a significant mismatch in time and space between primary and secondary production, which is reflected in a 'relatively' low copepod biomass and fish production (Hutchings 1992). The net result is that much phytoplankton production enters sedimentary and micro-heterotrophic pathways rather than mesozooplankton (Brown et al. 1991, Hutchings et al. 1991). Furthermore, large areas of the southern Benguela upwelling region are dominated by nano-phytoplankton for much of the year (Hutchings 1992). During prolonged periods of quiescence and mismatch, and in areas dominated by nano-phytoplankton, copepod production can be depressed (Verheye et al. 1992) and copepod starvation may ensue (Attwood & Peterson 1989). By implication then, copepods (of any one size class) may at times be scarce, and this could have resulted in intense interspecific competition for a common prey size.

If we accept that food may have been, and can be, limiting then the evolution of partitioning behaviours amongst chaetognaths requires both a persistence to guild structure and sufficient time. The diversity and abundance in nearshore assemblages tend to be re-

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[2]The segregation of feeding time has also been observed (e.g. Roger 1973), yet this need not reflect resource partitioning and may simply be the result of differential digestion time and hence the accumulation of prey. Alternatively, it may reflect the movement of a migrating prey field, if guild members are vertically segregated (as Barange et al. 1991)
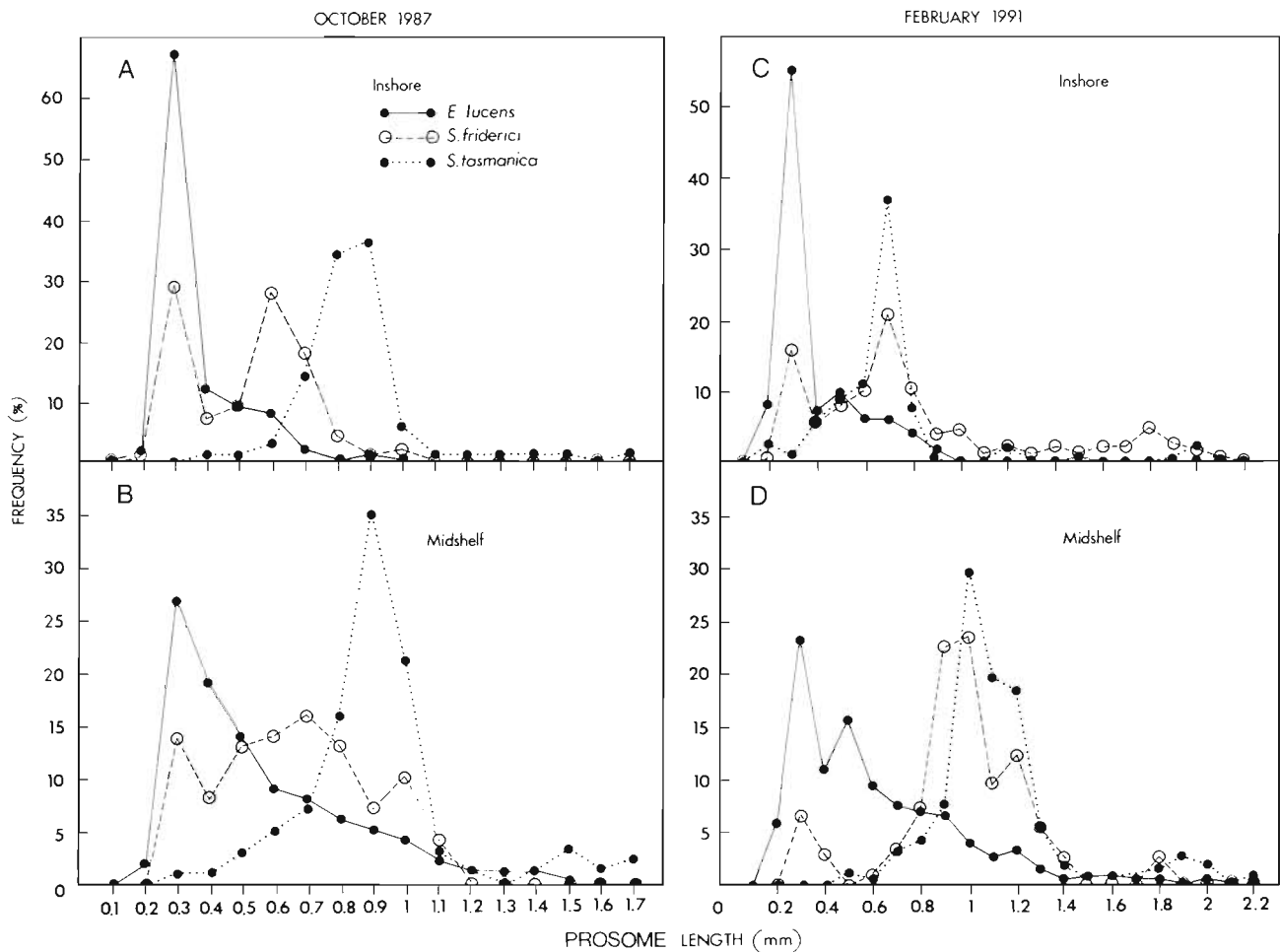
Fig. 8. Size-frequency distribution of copepods recovered from *Sagitta friderici, S. tasmanica* and *Euphausia lucens* collected in St Helena Bay during (A, B) October 1987 and (C, D) February 1991. Data in (C) and (D) from Gibbons (1993) (*E. lucens*) and in (A) and (B) from Gibbons (1992) (*S. tasmanica*), Gibbons & Stuart (in press) (*S. friderici*) and Gibbons et al. (1991b) (*E. lucens*)

duced during active upwelling, because surface water is moved offshore by Ekman transport, and it is replaced by newly upwelled water of low species richness. During relaxation and onshore water flow, on the other hand, there is a concomitant increase in species richness as neritic assemblages are supplemented with oceanic species. Despite this difference, however, nearshore zooplankton communities are still identifiable irrespective of the state of upwelling (Macpherson 1991, Pagés et al 1991, Pagés 1992). There are several reasons for this. Oceanic water tends to supplement the nearshore assemblage with rare species during relaxation. Neritic species are not necessarily lost from the system during upwelling, and are often returned during wind reversals (Pagés et al. 1991, Pagés 1992). And the upwelled water itself contains the dominant species characteristic of the nearshore region, i.e. those forms which perform (ontogenic) vertical migration to take advantage of the various long-shore and cross shelf water movements in their

population maintenance (Hutchings 1988, Pillar et al. 1992, Verheye et al. 1992). Thus there is an underlying persistence to the 'core' structure of nearshore assemblages irrespective of the state of upwelling. While shelf-upwelling ecosystems are generally considered to be young ecosystems (geologically), it is thought that the Benguela ecosystem evolved at some time between the Late Miocene and Early Pliocene (Shannon 1985). During the ice-age of the Late Pleistocene in the southern Benguela, the area falling within the 200 m isobath was approximately 32 % bigger than it is today (Miller 1990, Hutchings 1992). The offshore bathymetry would have been steeper than it is at present and this may have led to more intense upwelling. As both *Sagitta friderici* and *S. tasmanica*, however, are essentially cold water species they are likely to have been abundant (then as now). Rates of evolutionary change are not known for zooplankton, but it would appear that there may have been several million years of 'persistent'

structure which may have allowed partitioning to evolve between 'core' members.

Competition, per se, is very difficult to demonstrate (see e.g. Underwood 1986) and one is more often than not left with patterns on which to base conclusions (but see Connor & Simberloff 1984, Gilpin & Diamond 1984). This is a especially a problem in the pelagic environment, because of the difficulties involved in detailed experimentation, and more so in the marine than in the limnetic (e.g. DeMott 1989). For example, it is not possible to observe the behaviours of the different species in the southern Benguela in isolation from each other, as they appear to co-occur throughout the nearshore area. However, no attempt is made here to suggest that these species are currently competing with each other. Rather, it is suggested that historic processes of competition may have led to the regular partitioning of resources currently observed. Hutchinsonian Ratios (1:1.3) (Hutchinson 1959) are frequently used by limnetic (Hutchinson 1967) and terrestrial (Toft 1985) ecologists to infer resource partitioning from size differences between guild members or congeners. Their application to the marine pelagic has met with limited success, especially with regard to herbivorous copepods, as size and food selection are not necessarily related (Mullin 1967). Food and size do appear to be related in the Chaetognatha, both interspecifically and ontogenically (Pearre 1980). It should be noted too, that the cross-shelf distributions of *Sagitta friderici* and *S. tasmanica* differ: large *S. friderici* (11.5 mm) and small *S. tasmanica* (8 mm) inshore and small *S. friderici* (11 mm) and large *S. tasmanica* (14.5 mm) in the midshelf region (as also Gibbons & Stuart in press). Size ratios between the two are approximately 1:1.3 which would suggest that Hutchinsonian Ratios may be applicable to chaetognaths.

Alternative explanations for biological pattern of this type include reproductive isolation, predation and resource specialisation (Longhurst 1985, Schoener 1986). As it is thought that the 2 species of chaetognath are from different species-complexes or genera (Bieri 1991) the former can possibly be discounted (but see Kapp 1993). Although predators on zooplankton are as diverse in their feeding mode as they are in their taxonomy, most are opportunistic, size selective filter- or particulate-feeders (e.g. James & Findlay 1989, Hopkins & Gartner 1992, van der Lingen 1994). Few specialise in prey by species so predation can be disregarded as an explanation for the observed pattern. Likewise, as both species of chaetognath have the same method of prey capture and the same sensors (Bone & Goto 1991) at their disposal for detecting prey, resource specialisation can also be discounted. These results, if interpreted as evidence of resource partitioning, suggest that there may be more biological structure to the zooplankton communities of physically driven upwelling ecosystems than previously thought.

No discussion of trophic partitioning amongst primary carnivores in the southern Benguela would be complete without reference to the krill *Euphausia lucens*. This euphausiid represents approximately 50% of total zooplankton biomass in the region (Pillar et al. 1992). It is a facultative carnivore whose diet is a reflection of the quantitative and qualitative food environment (Pillar et al. 1992). When chlorophyll concentrations are low, or phytoplankton is of a poor quality *E. lucens* places a pronounced emphasis on carnivory to meet metabolic demands (Stuart 1989, Stuart & Pillar 1990, Gibbons et al. 1991a, b, Stuart & Huggett 1992). When feeding carnivorously, krill prey almost exclusively on copepods, so that lateral carbon transfer within the guild is negligible (Gibbons et al. 1992). Cnidarians and ctenophores, and amphipods and decapods are not included amongst primary carnivores because they are not always present in samples and they occupy a trophic guild above that of chaetognaths and euphausiids. A comparison of the diets of the 2 chaetognaths with *E. lucens* (Fig. 8) reveals minimal trophic overlap, because krill feed almost entirely on small copepods. Although it is tempting to interpret these results (under conditions of low chlorophyll) in terms of resource partitioning, chaetognaths are specialist carnivores (Feigenbaum & Maris 1984) whilst euphausiids of the genus *Euphausia* appear to be primarily filter-feeding herbivores (Roger 1973) whose feeding appendages can also be used to catch small, slow-moving prey (Mauchline & Fisher 1969). Thus, although euphausiids in multispecies assemblages may partition copepod food resources (Barange et al. 1991, Roger 1973, 1975), the apportionment of prey with chaetognaths must be seen in light of resource specialisation.

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