

FEEDING AND VERTICAL MIGRATION OF THE CHAETOGNATH *SAGITTA FRIDERICI* (RITTER-ZAHONY, 1911) IN THE SOUTHERN BENGUELA DURING SPRING 1987, WITH NOTES ON SEASONAL VARIABILITY OF FEEDING ECOLOGY

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The feeding biology and the vertical migration of *Sagitta friderici* were examined over 24 h at two stations in the southern Benguela during spring (October) 1987. Together with studies conducted during summer (February 1991) and winter (May 1984), they serve to allow valuable generalizations of the biology and ecology of this abundant chaetognath. Populations migrate vertically and feed nocturnally, although the timing and the extent of migration vary between studies. *S. friderici* exhibits ontogenetic layering and the cross-shelf distribution of maturity stages differs, suggesting that it is able to take advantage of cross-shelf water movement in order to maintain populations in the nearshore waters of the West Coast. *S. friderici* prey almost exclusively on copepods (cannibalism is rare), and there is a positive relationship between the lengths of predator and prey that is influenced by the size structure of the prey environment. This casts doubt on the validity of a chaetognath species-specific relationship between predator and prey size. *S. friderici* selects its prey on the basis of size, and not species. Daily ration is related linearly to prey density, so reflecting the low density of prey and providing support for theoretical predictions regarding ingestion rates under oceanic conditions. The impact of *S. friderici* predation on the copepod assemblage is generally less than 3% of the standing stock, although it could be much higher under conditions of low copepod biomass and poor secondary production.

Die voedingsbiologie en die vertikale migrasie van *Sagitta friderici* is oor 24 h by twee stasies in die suidelike Benguela gedurende lente (Oktober) 1987 ondersoek. Tesame met studies wat gedurende somer (Februarie 1991) en winter (1 Mei 1984) gedoen is, is dit moontlik om waardevolle veralgemenings oor die biologie en ekologie van hierdie volop chetognaat te maak. Bevolkings migreer vertikaal en vreet snags ofskoon die tydsberekening en die omvang van migrasie tussen studies wissel. *S. friderici* vertoon ontogenetiese laagvorming en die verspreiding van rypeidstadia verskil in die dwarste oor die plat, wat daarop dui dat dit in staat is om waterbeweging oor die breedte van die plat te benut om bevolkings in die aanlandige waters van die Weskus te handhaaf. *S. friderici* maak byna uitsluitlik op kopepodes jag (kannibalisme is skaars), en daar is 'n positiewe verband tussen die lengtes van roofdier en prooi wat beïnvloed word deur die groottestruktuur van die prooi-omgewing. Dit wek onsekerheid oor die geldigheid van 'n verband tussen die groottes van roofdier en prooi wat eie aan elke chetognaatspesie is. *S. friderici* soek sy prooi uit met grootte as grondslag, en nie spesie nie. Daaglikse rantsoen hou lineêre verband met prooidigtheid en weerspieël sodoende die lae digtheid van die prooi en verleen steun aan teoretiese voorspellings aangaande innamekoerse onder oseaniese omstandighede. *S. friderici* verwyder oor die algemeen minder as 3% van die biomassa teenwoordig, ofskoon dit veel meer kan wees as die kopepodebiomassa laag is en sekondêre produksie swak.

Certain zooplankton species in the southern Benguela, such as the euphausiid *Euphausia lucens* and the copepod *Calanoides carinatus*, have been the focus of detailed seasonal distribution, life history and feeding studies (see reviews of Pillar *et al.* 1992, Verheye *et al.* 1992). These crustaceans are considered to be key elements in the pelagic trophic web, because they are relatively large and abundant and feature regularly in the diet of some commercially important fish species (James 1987, Payne *et al.* 1987).

Chaetognaths, on the other hand, have received little attention, despite the fact that they are the most abundant, exclusively carnivorous zooplankton in the region (Gibbons *et al.* 1992) and are capable of dominating the zooplankton biomass under certain circumstances

(Pillar and Barange 1993). Chaetognaths were among the first zooplankton to be used to characterize and track different water masses elsewhere in the world (Russell 1935), and almost all the early local studies (Heydorn 1959, Stone 1969, Masson 1972) focused on their patterns of distribution in relation to water circulation and type. Much of the early work locally was based on regular sampling throughout the year. Biological studies have recently given way to ecological studies (Stuart and Verheye 1991, Gibbons 1992, *in press*), as emphasis has shifted towards understanding the trophic dynamics of the pelagic realm, with particular reference to fish production (e.g. Hutchings 1992). Unlike the earlier studies, however, most recent work has been the result of intensive "one-off" cruises,

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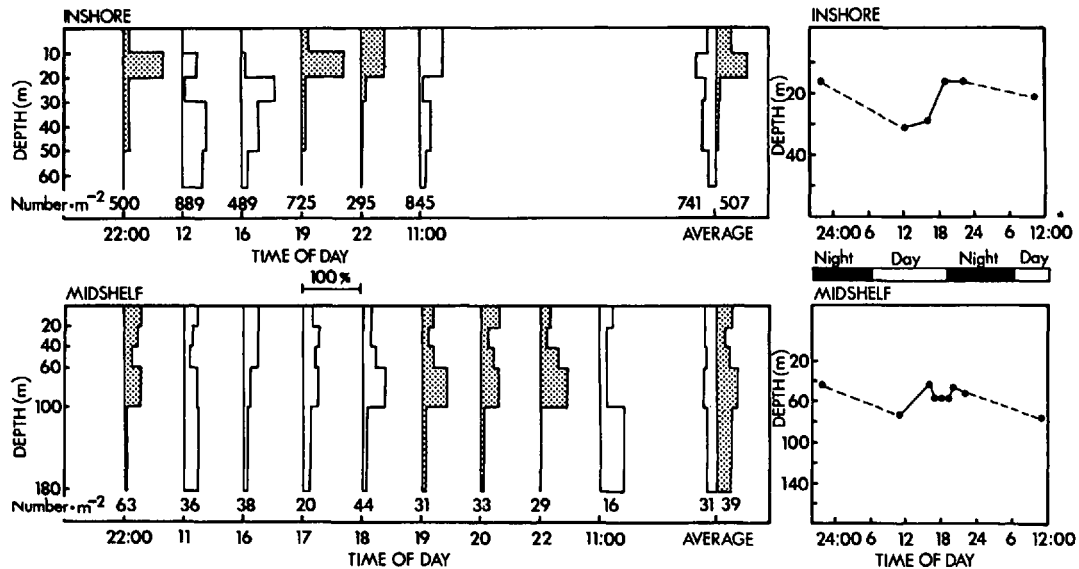


Fig. 1: (a) Vertical distribution of *Sagitta friderici* (% of total) at the inshore and midshelf stations. Hatched plots are night-time samples. The approximate time of sample collection and depth-integrated abundances ($\cdot \text{m}^{-2}$) are indicated below the plots. (b) Diel changes in the mean vertical distribution of *Sagitta friderici* within the water column at the inshore and midshelf stations

and so a true and seasonal picture of the ecology and trophic role of chaetognaths in the Benguela has failed to emerge.

The feeding and vertical migration of the most abundant chaetognath in the southern Benguela, *Sagitta friderici* (also referred to as *Parasagitta friderici*; Bieri 1991), is presented here from data collected at two 24-h anchor-stations in the southern Benguela during October 1987. The results of this spring study are then compared with those generated from similar winter (May 1984, Stuart and Verheye 1991) and summer (February 1991, Gibbons in press) studies. In the absence of extant, published monthly data sets, these separate studies allow for the construction of a fuller description of the biology and ecology of *S. friderici* in the southern Benguela.

MATERIALS AND METHODS

Samples were collected over two 24-h periods in October 1987 at two stations on a transect running seawards from the Olifants River mouth, South Africa ($31^{\circ}37'S$ $18^{\circ}18'E$; Gibbons *et al.* 1991a). The mid-shelf station was located 57 miles from the coast (water depth 190 m) and the inshore station at 5 miles (depth 80 m). At each station, a CTD/rosette cast to the bottom provided continuous profiles of temperature and salinity.

Chaetognath collections from each station were made at intervals over 24 h by means of a 1-m^2 multiple opening-closing rectangular midwater trawl (RMT 1×6) equipped with mesh size of $200 \mu\text{m}$. The net was towed obliquely at 2 knots in five different depth strata, from just above the bottom to the surface (mid-shelf — 190–100 m, 100–60 m, 60–40 m, 40–20 m, 20–0 m; inshore — 80–60 m, 60–40 m, 40–20 m, 20–10 m, 10–0 m). Flow was estimated by means of an electronic flowmeter mounted centrally above the mouth of the net. All zooplankton samples were preserved in buffered (CaCO_3) saline formalin for later processing.

In determining vertical distribution and abundance, all chaetognaths were counted from each sample. When collections were large, subsamples were taken with a Folsom splitter and at least 100 individuals were counted. Data were standardized to numbers per cubic and per square metre using net flowmeter data. The mean vertical position (weighted mean depth, WMD; Roe *et al.* 1984) of chaetognaths in the water column was determined using the method of Pearre (1974):

$$d = \frac{\sum n_i d_i}{\sum n_i} \quad (1)$$

where n_i is the number of individuals per 1 m^3 at that depth range and time and d_i is the midpoint of the depth range.

The total body length (excluding tail fin) of 100

individuals selected randomly from each sample was measured and the stage of maturity determined according to the development of the ovaries (Zo 1973). Stage I animals had no visible ovaries; Stage II had developing ova of different sizes, but no mature ova; Stage III had one or more mature ova.

The diet of *Sagitta friderici* was determined by stomach content analysis. Owing to the time-consuming nature of this process, only animals from the WMD sample for each collection time were examined (Fig. 1). Approximately 100 animals (sample-size dependent) in good condition from each WMD collection were first measured (from the tip of the head to the end of the tail, excluding the tail fin), and the middle and the posterior section of the body were cut out and transferred to glycerine, where the gut and gut contents were squeezed out. The anterior portion of the gut was excluded from the analysis in order to eliminate data contamination by codend feeding. Gut contents were examined at a magnification of 160 for copepod mandibles and chaetognath hooks, which were counted, measured and identified to species. Mandible widths were converted to copepod prosome lengths using the equation provided by Stuart and Verheye (1991), as recalculated from Stuart and Pillar (1990). Chaetognaths without mandibles, but with copepod fragments, were ignored in direct estimates of the number of copepods consumed, but were scored as feeding. In some instances, fewer than 100 individuals were collected, especially at the midshelf station. In those circumstances, as many specimens as possible were examined.

In order to relate the diet of *Sagitta friderici* to the ambient food environment, copepod abundance and distribution were determined over the same time period as chaetognaths were sampled. These data were collected from the upper 80 m at six depths using a diaphragm pump (Peterson *et al.* 1990). Approximately 2 m³ of water was delivered from each depth through a pipe of mouth opening 7.6 cm² and filtered on deck through a mesh of 200 µm. Copepods from below 80 m were sampled from the same RMT collections as the chaetognaths. All copepods were counted by species from 2-ml subsamples taken with a piston pipette (see Peterson *et al.* 1990). The size distribution of copepods from the water column was determined by measuring the prosome lengths of 200 individuals selected randomly from each sample.

The estimation of prey selection by a predator is fraught with difficulties, not least of which is the problem of determining where the predator has been feeding. An attempt has been made to minimize this error by looking only at night-time samples. An attempt has also been made to correct the ambient prey environment (at the depth of chaetognath capture) by incorporating assemblages from prior foraging depths (to the

equivalent of the gut-passage time; Stuart and Verheye 1991). A fuller rationale and description of this methodology is provided by Gibbons *et al.* (1991b) and Gibbons (1992).

The number of prey (ingested) per chaetognath per day (NPCPD) was calculated as described by Stuart and Verheye (1991):

$$I = N_d h_d d / t_D + N_n h_n / t_D \quad (2)$$

where I is the ingestion rate (copepods·chaetognath⁻¹·day⁻¹), N_d and N_n refer to the number of copepods per chaetognath gut during the day and night respectively, h_d and h_n are the number of hours of daylight and darkness respectively, and t_D is the digestion time in hours.

Gut passage times for *S. friderici* were calculated from the general equation relating digestion time to temperature (Stuart and Verheye 1991):

$$t_D = 10.96e^{-0.086T} \quad (3)$$

where T is temperature (°C).

Temperatures at the average population depth at the inshore and midshelf stations were approximately 10 and 12°C respectively. With this information and a knowledge of the densities of predator and prey, it was possible to determine the impact of *Sagitta friderici* on the copepod standing stock (Stuart and Verheye 1991).

To determine day/night differences in vertical distribution, mean day and night time-depths (WMDs) were compared by means of single-factor Kruskal-Wallis analyses. This non-parametric test was also used to examine changes in chaetognath feeding over time. Additionally, Kolmogorov-Smirnov one-sample tests (Sokal and Rohlf 1981, Zar 1984) were performed in order to:

- (i) compare the size distributions of chaetognaths between stations and depths;
- (ii) determine if *S. friderici* selected components of its diet from the ambient prey spectra.

Differences between data were considered significant at the 95% level.

RESULTS AND DISCUSSION

Descriptions of the physical environment at the two stations during October 1987 are provided elsewhere (Peterson *et al.* 1990, Gibbons *et al.* 1991a, Gibbons 1992) and will not be presented here. A more detailed account of the abundance and structure of the copepod assemblage at both stations is presented by Peterson *et*

al. (1990). Copepod densities over the upper 20 m were higher at the inshore station ($8\,607 \cdot \text{m}^{-3}$) than at the midshelf one ($3\,595 \cdot \text{m}^{-3}$). Numbers peaked in the thermocline (10–20 m) inshore and were distributed more evenly throughout the upper 40 m at the midshelf station, but they decreased rapidly with depth (to $620 \cdot \text{m}^{-3}$ at a depth of 100–200 m; Gibbons *et al.* 1991a). Assemblages were dominated numerically by small copepods, of which *Oithona* spp. (0,2–0,8 mm carapace length) and small calanoids (*Paracalanus parvus* and *Ctenocalanus vanus*, 0,4–0,7 mm) were most prevalent (Table 1). *Centropages brachiatus* (0,8–1,2 mm) was the commonest copepod of medium size, although large calanoids, e.g. *Calanus agulhensis* (2–3 mm) and *Calanoides carinatus* (0,5–2,2 mm) were present.

Table 1: Mean relative species composition and size distribution of copepods (prosoma length) in the diet of *Sagitta friderici* and in the water column at the inshore and midshelf station during the nights of 26 and 28 October 1987. Data are rounded up to the nearest whole number. Ambient data are adjusted for depths of prior chaetognath occupation to the equivalent of the gut passage time (see Gibbons *et al.* 1991b, Gibbons 1992)

Prey size-class (mm)	Inshore		Midshelf	
	<i>S. friderici</i>	Water column	<i>S. friderici</i>	Water column
0,2	1	0	0	0
0,3	29	0	14	0
0,4	7	9	8	4
0,5	10	35	13	28
0,6	28	12	15	11
0,7	18	12	16	10
0,8	4	11	13	13
0,9	1	11	7	12
1,0	2	5	10	5
1,1	0	1	4	4
1,2	0	3	0	5
1,3	0	0	0	1
1,4	0	0	0	1
1,5	0	0	0	2
1,6	0	0	0	1
1,7	0	1	0	3
1,8	0	0	0	0
1,9	0	0	0	0
Taxon				
<i>Oithona</i> spp.	28	45	16	11
<i>Ctenocalanus vanus</i>	8	7	12	9
<i>Paracalanus parvus</i>	19	21	23	18
<i>Centropages brachiatus</i>	45	21	44	42
<i>Metridia lucens</i>	0	2	0	4
Large calanoids	0	4	5	16

Distribution and population size structure

Sagitta friderici represented approximately 53% ($624 \cdot \text{m}^{-2}$) and 7% ($35 \cdot \text{m}^{-2}$) of all chaetognaths sampled at the inshore and midshelf stations respectively. Of the balance, *S. tasmanica* represented 41% ($482 \cdot \text{m}^{-2}$) and 85% ($425 \cdot \text{m}^{-2}$) at each station, whereas *S. minima* accounted for 1% ($12 \cdot \text{m}^{-2}$) and 7% ($35 \cdot \text{m}^{-2}$) respectively. Other chaetognaths (e.g. *S. enflata*) were rare. Of the 12 species of chaetognath identified by Heydorn (1959) in the waters of the southern Benguela, the three most abundant were those listed above. Although *S. friderici* was dominant then (as now at the inshore station), *S. tasmanica* was generally less common than *S. minima*. An examination of Heydorn's (1959) data by latitude, however, reveals that *S. tasmanica* was more common than *S. minima* in the region of Lambert's Bay (see Gibbons *in press*), than it was farther south, off the Cape Peninsula.

S. minima is a species of warm water, oceanic areas and its presence nearshore in the Benguela reflects the movement of oceanic and frontal water shorewards during onshore winds. Owing to the narrow continental shelf in the region of the Cape Peninsula (Shannon 1985) and the greater concentrations of oceanic species accumulated at the frontal zone there than farther north (Pagès 1991), the effect of onshore water movement is greater there than it is in St Helena Bay. *S. tasmanica*, by contrast, is a species common in the waters around Antarctica (Pierrot-Bults and Nair 1991) and its low temperature tolerance probably pre-adapts it to the upwelling areas along the coastline of West Africa, where it is common (Thiriot 1978). *S. friderici* is a neritic chaetognath (Pierrot-Bults and Nair 1991) that shows a preference for cool water (Heydorn 1959, Stone 1969, Venter 1969, Masson 1972, Gibbons *in press*), and it was significantly more abundant inshore than in the midshelf region of St Helena Bay (data in Fig. 1).

The size distributions of *Sagitta friderici* at both stations were unimodal around 10 mm total length (*TL*, Fig. 2). Populations inshore were mostly maturing (Stage II) and mature (Stage III) adults, whereas juveniles (Stage I) were more numerous at the midshelf station. Owing to the probable escapement of individuals <4 mm *TL* through the 200- μm mesh of the net (Pearre 1974), immature *S. friderici* may have constituted a greater proportion of the population than indicated here. The presence of immature individuals through winter (Stuart and Verheye 1991), spring (this study) and summer (Gibbons *in press*) suggests that it reproduces throughout the year, a conclusion also reached by Masson (1972). Incomplete coverage through the year and a failure to catch individuals <4 mm *TL* pre-

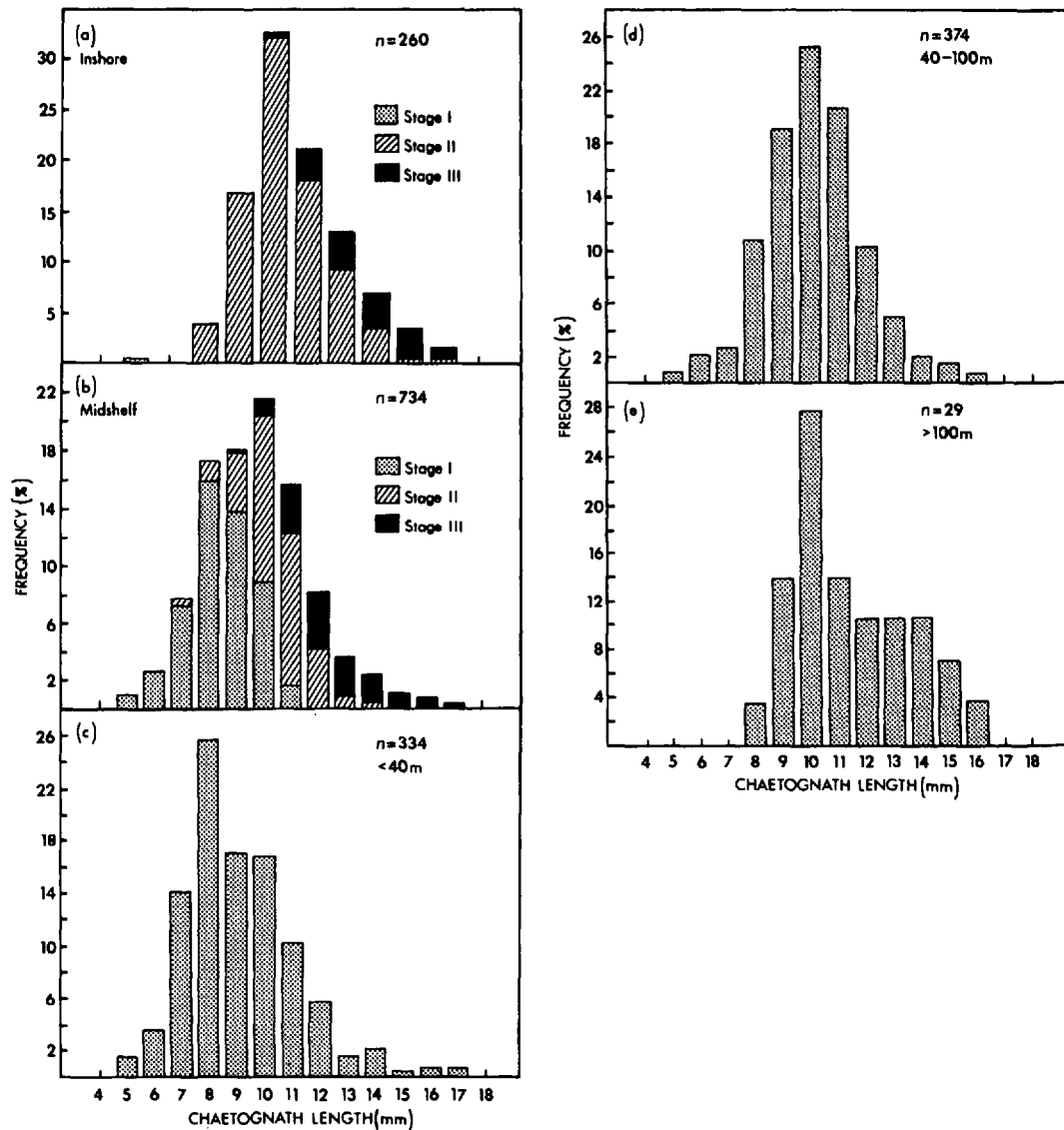


Fig. 2: Length frequency histograms of *Sagitta friderici* populations at (a) the inshore and (b) the midshelf stations, calculated over all depths. The relationship between chaetognath length and the stage of ovarian development is superimposed. Changes in the size structure of the midshelf population with depth are shown in blocks (c) – (e), illustrating ontogenetic layering

vents any conclusions regarding the number of generations per year, but Masson (1972) suggests that there may be at least five, with peaks in spawning during winter and spring.

A greater relative abundance of smaller individuals

over the midshelf than inshore was also reported by Masson (1972), Hopson (1983) and Gibbons (in press), although an unknown number of specimens in the samples of Hopson may have been *S. minima*. Both the euphausiid *Euphausia lucens* (Pillar *et al.* 1989)

and the copepod *Calanoides carinatus* (Verheye *et al.* 1991) display a similar cross-shelf distribution of maturity and size during upwelling conditions. This is thought to be the product of the interaction between ontogenetic layering (whereby younger developmental stages show limited vertical migration and are generally confined to more superficial depths than adults) and wind-driven Ekman transport. The cross-shelf size distribution is dynamic, however, and it is closely linked to the process of upwelling. Therefore, during downwelling and periods of onshore winds, both immature and adult *E. lucens* and *C. carinatus* are concentrated inshore, and the cross-shelf size gradient observed during upwelling breaks down (Pillar *et al.* 1989, Verheye *et al.* 1991).

These patterns in cross-shelf size distribution have been linked to a strategy allowing the maintenance of populations of *E. lucens* and *C. carinatus* within the coastal zone of the Benguela upwelling region (Pillar *et al.* 1989, Verheye *et al.* 1991). Although no active upwelling was observed during both this spring study and the summer investigation of Gibbons (in press), both studies were conducted during the "upwelling season" in the southern Benguela (Shannon 1985), and upwelled water was present on the shelf at both times. Unfortunately, winter samples of *S. friderici* in St Helena Bay are not available for comparative analysis. However, because *S. friderici* also appears to display ontogenetic layering (Stuart and Verheye 1991, Fig. 2c-e), it is possible that populations of this chaetognath are maintained in the nearshore waters of the Benguela by the same mechanism.

Vertical migration

Sagitta friderici appeared to migrate vertically at both stations (Fig. 1). However, the irregular spacing of samples makes it difficult to draw any detailed conclusions regarding the timing of ascent, or the depths of occupation between midnight and the early hours of the afternoon. At the inshore station, the population was shallower by night than by day (Fig. 1). The situation was less clear at the midshelf station and probably reflects both population ascent into the surface waters before the onset of darkness and the very low densities of *S. friderici* (Gibbons in press).

Vertical migration of *S. friderici* has previously been observed in the southern Benguela by both Stuart and Verheye (1991) and Gibbons (in press), and in the western Mediterranean by Pearre (1974, as *S. bipuncta*). There seems to be little consistency in timing or pattern between these studies (some suggest midnight sinking),

although with the exception of the study of Stuart and Verheye (1991), it appears to be a day-night phenomenon. Similar results are common in the chaetognath literature (e.g. Sullivan 1980, Drits and Utkina 1988). However, constancy of pattern need not be expected in diel vertical migration because of the many factors which complicate observations and their interpretation (Pearre 1979). Migration of zooplankton would appear to be an individual rather than a population response (Pearre 1973, Simard *et al.* 1985, Gibbons 1993) and, because most studies (including this one) have examined the population and not the individual, clear conclusions and generalizations cannot be made.

Food and feeding

Copepods constituted almost the entire diet of *Sagitta friderici* at both stations. Cannibalism was rare and occurred only inshore (<1%). A preference for copepods and a low incidence of cannibalism has been reported for *S. friderici* by all previous workers in southern African (Heydorn 1959, Stone 1969, Venter 1969, Lazarus 1974, Stuart and Verheye 1991, Gibbons in press) and Mediterranean (Pearre 1974, 1976) waters. The incidence of cannibalism predicted by Pearre's (1982) Equation 2, which is based on a knowledge of chaetognath head width (0,52 mm at 10 mm TL, Stuart and Verheye 1991) and total chaetognath density, is 46,3% at the inshore station and 20,5% at the midshelf station. The frequency of cannibalism predicted from a knowledge of head width alone (Equation 5 of Pearre 1982) is 12,7%. Pearre (1982) argued that, because head width alone accounted for 66% of the variation in cannibalism within the data set he presented (chaetognath abundance absorbed only 12% of the variability), it was a better predictor of cannibalism than the compound equation. The fact that the current data are significantly smaller than any predicted value suggests a failure to identify chaetognaths within the gut of *S. friderici*. While it is possible that very small chaetognaths were overlooked in the gut (they do not have readily observable hooks) this problem was shared also by the data set used by Pearre (1982) in the construction of his equations, and so it can be ignored. Perhaps, therefore, the discrepancy may lie with the fact that the equations generated by Pearre (1982) fail to take into account the abundance of alternative, copepod prey and are based solely on chaetognath abundance. Moreover, the absence of any good correlation with chaetognath abundance (Pearre 1982) must reflect the variability in the quality of the published abundance data he used, because cannibalism must be dependent

Table II: Frequency of single and multiple prey items in the diet of *Sagitta friderici* at the inshore and midshelf stations during October 1987

Number of prey	Frequency (%)	
	Inshore	Midshelf
1	74,8	85,4
2	14,5	12,5
3	7,3	2,1
4	2,7	0
5	0,8	0

on the density of chaetognath prey. To predict the incidence of cannibalism based on head width alone would ignore the unusual situation where chaetognath prey may be absent.

Both incidence of multiple prey (Table II) and mean number of prey recovered from chaetognaths were generally greater at the inshore than at the midshelf station (Fig. 3). Although this may be due to differences in sample size (Fig. 3), it is not a product of variations in the chaetognath size distributions, because there were no significant regressions between chaetognath length and the number of prey recovered from them (but see Pearre 1974, Stuart and Verheye 1991). These results resemble observations by Gibbons (in press) and may be related to prey density, an issue that will be dealt with later.

Sagitta friderici consumed a relatively wide size range of copepods at both stations. The size distribution of prey consumed at each station was bimodal (Table I), the smaller peak occurring at 0,3 mm prosome length and the larger at 0,6–0,7 mm. The size composition of the diet of *S. friderici* was significantly different from that of the water column ($p < 0,01$). The most abundant size-class of copepod in the food environment (0,5 mm) was largely ignored at both stations and falls in the trough between the two preferred modes. Although it might appear that copepods of 0,3 mm prosome length were being heavily selected for (because of their rarity in the water column), this is probably an artifact of the sampling and reflects the escapement of small copepods through the 200- μ m mesh of the net. However, it has recently been suggested that, whereas there is a positive relationship between copepod prosome length and mandible width, estimates of the former from the latter may vary by 20% (Karlson and Båmstedt 1994). If this were to be adjusted for in Table I, it could be argued that chaetognaths were taking smaller copepods at approximately ambient proportions. Clear interpretation of prey choice by species (Table I) is complicated by the lack of con-

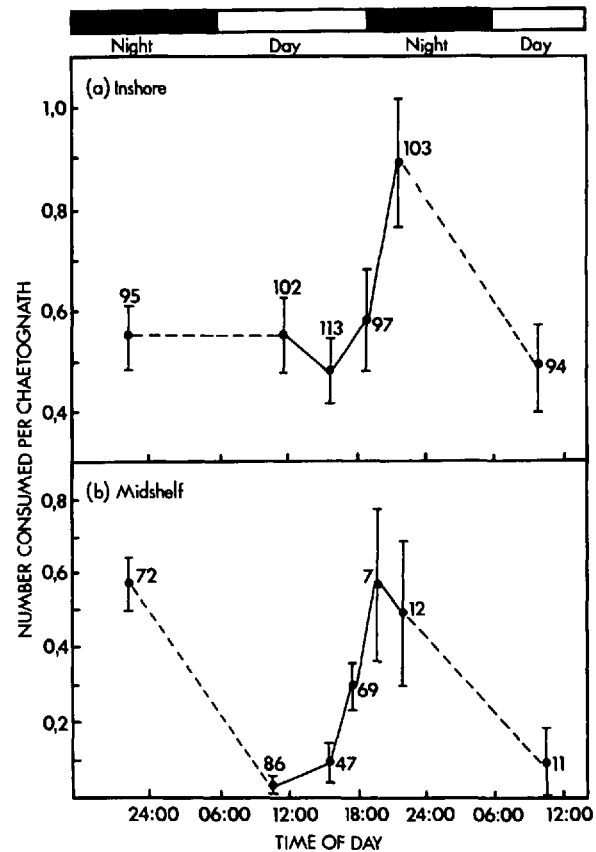


Fig. 3: Mean (SE bars) number of copepods consumed per *Sagitta friderici* at (a) the inshore and (b) the midshelf station during October 1987. The number of chaetognaths examined from each weighted mean depth (see Fig. 1) is indicated

sistency in pattern observed between stations. It would appear, however, that both large calanoids and *Metridia lucens* were taken by *S. friderici* at lower than ambient proportions (Gibbons in press) and that only *Centropages brachiatus* was taken at greater than ambient proportions inshore (Gibbons in press).

Firm conclusions regarding nocturnal prey choice cannot be made from the results presented here, because of a possible mismatch between the depth of prey capture and sample collection. Nevertheless, the prey size data are in general agreement with those obtained by Stuart and Verheye (1991) and Gibbons (in press), despite differences in the prey environment between studies. Taking all these factors into account, it would appear that prey are selected by *Sagitta*

Table III: Mean and (in parentheses) standard error of the prey size of *Sagitta friderici* by length-class. Data are from the inshore and midshelf stations combined

Chaetognath length (mm)	Mean prey length (mm)
8	0,47 (0,06)
9	0,55 (0,04)
10	0,60 (0,02)
11	0,66 (0,03)
12	0,64 (0,04)
13	0,72 (0,05)
14	0,87 (0,11)

friderici on the basis of size and not species, with the dominant species in the preferred size-classes being taken. Although several studies on prey selection by chaetognaths have suggested a selection for particular prey species (e.g. Pearre 1976), it is generally felt that prey are chosen on the basis of size (Feigenbaum 1991). An exception to this may occur with *Centropages brachiatus*, which is often the commonest copepod of medium size, yet is frequently subjected to greater selection pressure than the size-class it occupies (Gibbons *et al.* 1991b, Gibbons 1992, in press).

There was a positive relationship between chaetognath length and prey length (Table III). This relationship is generally viewed as a power curve (Pearre 1980). For the data presented here (Fig. 4) the power relationship is significant ($p < 0,00001$), even though the r^2 value itself is very low (0,048; see also Pearre 1980). There is, however, a good linear agreement ($r^2 = 0,95$) between mean prey size and chaetognath length-class (Table III, Fig. 5). The difference between the significance and clarity of these relationships (Fig. 4, Table III) reflects the fact that chaetognaths do not forage in an optimal manner, and that large chaetognaths catch and ingest both large and small prey, whereas small individuals tend to eat small prey only. (Inevitably, therefore, the average prey size increases in grouped data.) This contrasts with the data presented by Reeve and Walter (1972), who noted that, whereas prey size increased with predator size, small chaetognaths ingested proportionally bigger prey than large chaetognaths. However, the data of Reeve and Walter were derived from laboratory measurements on larvae, which they suggested had higher energy requirements and/or more-elastic head tissues. Reeve and Walter also acknowledged that the range of prey sizes increased with chaetognath size, which led to a relative reduction in the size of preferred prey.

The relationship between chaetognath and prey length as illustrated by Table III appears to be similar to that of Stuart and Verheye (1991), but it seems to

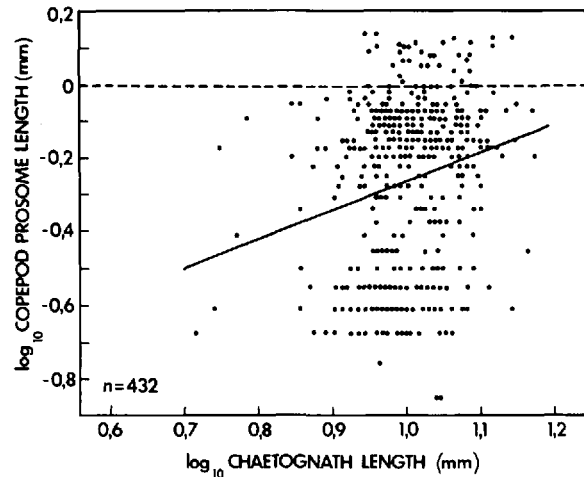


Fig. 4: Relationship between prosome length (PL) of copepod prey and total length (TL) of predatory *Sagitta friderici*. The data are best described by the power curve $PL = 0,004 TL^{0,78}$ ($r^2 = 0,048$; $p < 0,00001$)

differ from that of Gibbons (in press) by being of shallower slope (Fig. 5). Given the typical variance about these regressions (Fig. 4), it can be argued that the plots are identical. Differences between them may, nevertheless, be real and reflect variations in the size range of prey available during each study. In other words, a mixture of very small and very large prey would result in a plot of steep slope, because the chaetognath would capture both, whereas a prey environment of items of small and medium size would result in a plot of shallower slope. These data suggest that size relationships between chaetognaths and copepods may not depend entirely on the chaetognath species itself (as generally suggested by Pearre 1980), but that they must also reflect the size distribution of the prey environment (Rakusa-Suszczewski 1969, Sullivan 1980). Indeed, they cast doubt on the validity and applicability of the relationship between specific chaetognath species and prey size (Pearre 1980).

EFFECTS OF PREY DENSITY

The number of prey recovered from *Sagitta friderici* was generally greater during the night than during the day at both stations (Fig. 3; few conclusions can be reached from the first night of sampling at both stations owing to the paucity of data). During the second night at the inshore station, the mean number of prey per chaetognath was inversely correlated with the depth of sample collection and, in turn, positively related to the ambient copepod density. This was not so clear at

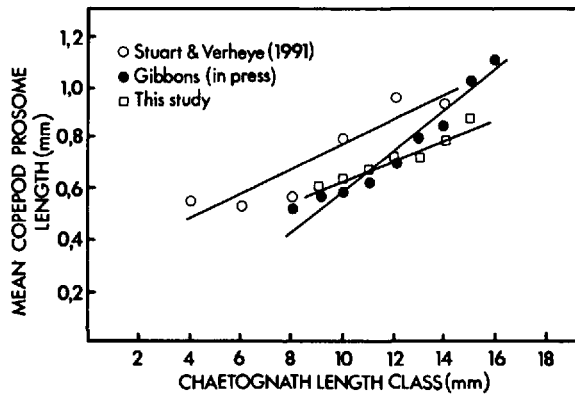


Fig. 5: Predator total length (TL) : prey prosome length (PL) size relationships for *Sagitta friderici*, from the studies of Stuart and Verheye (1991), Gibbons (in press) and this study. Note that prey sizes are means. The data are best described by linear relationships of the form $PL = mTL + c$, where m , c and r^2 for the fits are 0,049, 0,28 and 0,85; 0,07, -0,104 and 0,94; and 0,041, 0,22 and 0,95 for each study respectively

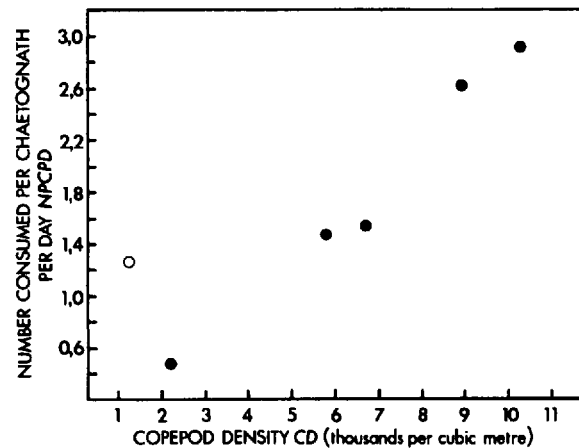


Fig. 6: Relationship between daily ingestion of copepods (NPCPD) by *Sagitta friderici* and copepod density (CD) in the upper 40 m of the water column. Data are from Stuart and Verheye (1991), Gibbons (in press) and this study. The relationship is described by the linear equation $NPCPD = 0,00031 CD - 0,306$ ($r^2 = 0,98$). An equivalent datum from Pearre (1974) from the western Mediterranean Sea is shown as an open circle, but it has not been included in construction of the equation

the midshelf station, and there seemed to be a delayed response between the depth of initial occupation (and copepod density) and the number of prey per chaetognath. This probably reflects both an increased incidence of feeding with nocturnal progression, and the accumulation of prey in the gut. Nocturnal feeding by *S. friderici* was recorded by both Pearre (1974) and Gibbons (in press). It was not observed by Stuart and Verheye (1991), probably because only 25% of the samples analysed were collected during the day.

Laboratory experiments suggest that the number of prey consumed per chaetognath is positively related to prey density (Reeve 1964, 1980, Nagasawa 1984). However, as Feigenbaum and Maris (1984) and Feigenbaum (1991) noted, there is little hard field evidence to support this logic, because the prey present in a chaetognath's gut at any one depth do not necessarily reflect prey capture at that depth. Tracking the number of prey consumed per chaetognath from samples taken from the upper (depth) mode of the population during ascent may provide some evidence of changes in ingestion rate with prey density (Gibbons 1992). However, elevated numbers of prey consumed per chaetognath over time can also reflect prey accumulation resulting from delayed or slow digestion. A plot of daily ingestion (as number of prey per chaetognath per day) against prey abundance (Fig. 6) suggests that there is generally a positive relationship between the two. Although the data used in the construction of this Figure have been recalculated from samples collected at dif-

ferent times of the year, its interpretation need not be confounded by seasonality, because water temperatures were approximately equal during each sampling season.

Published data sets with which to compare Figure 6 are unfortunately rare, despite the relatively large number of seasonal studies on chaetognath feeding (Rakusa-Suszczewski 1969, Øresland 1987, 1990). Kimmerer (1984) noted that an Ivlev function best fitted the seasonal data he collected for *Sagitta enflata* off Hawaii, whereby daily ingestion levelled off at high abundance of prey. However, prey densities observed during the study of Kimmerer (1984) were an order of magnitude greater than those recorded here, and his ingestion data were clustered around the asymptote (Fig. 1 of Kimmerer 1984). In the case of *S. friderici* (Fig. 6), ingestion is linearly proportional to prey density. Such would be expected at low densities of prey, and this is in agreement with the theoretical conclusions reached by Reeve (1980) for chaetognaths feeding under oceanic conditions.

It is estimated that *Sagitta friderici* could consume 0,56 and 0,01% respectively of the copepod standing stock in the upper 20 m at the inshore and midshelf stations. These values compare reasonably well with those obtained by Stuart and Verheye (1991; 2,12% inshore) and Gibbons (in press; 2,9% inshore, 0,03% midshelf) from the same region. As pointed out by

Mironov (1960, as cited by Stuart and Verheye 1991), however, it is not really accurate to compare a rate process (predation) with copepod standing stock; it is more accurate to use copepod production. If a production : biomass ($P:B$) ratio of 5 were to be used for copepods in St Helena Bay (Verheye *et al.* 1992), *S. friderici* would be said to consume approximately 2,5 and 0,5% of copepod production at the inshore and midshelf stations respectively.

The impact obviously varies with densities of both predator and prey and may be greater in winter when mesozooplankton biomass is lowest (Andrews and Hutchings 1980, Verheye *et al.* 1992). Because zooplankton production is also generally lower in winter than spring or summer (H. M. Verheye, Sea Fisheries Research Institute, pers. comm.) as a result of reduced upwelling (Shannon 1985), the accumulated impact of predation may be significantly more than the estimates presented here (see also Sameoto 1987, Øresland 1990). This statement is also likely to be true in areas or patches where the biomass of chaetognaths is greater than that of copepods (Hopson 1983, Fearon *et al.* 1986, Pillar and Barange 1993). Nevertheless, in comparison with macrozooplankton such as the euphausiid *Euphausia lucens* (Pillar *et al.* 1992), the impact of *S. friderici* on copepod populations is small.

CONCLUSIONS

Although the data presented here are patchy, if they are taken in conjunction with results collected from other studies, they permit valuable generalizations to be made regarding the biology and ecology of *Sagitta friderici* in the southern Benguela. For example, the size relationship between predator and prey appears to vary with the size structure of the prey environment. Repetitive studies such as these have also permitted determination of how daily ingestion varies with prey abundance, a field observation that has eluded description until now. It has also allowed conclusions to be drawn from otherwise inconclusive and sparse data. For example, the cross-shelf size distribution coupled with ontogenetic layering suggests a mechanism whereby *S. friderici* may be maintained within the dynamics of the Benguela ecosystem. Finally, it has indicated the generally unimportant role of *S. friderici* as a predator of mesozooplankton in the nearshore waters of the Benguela.

ACKNOWLEDGEMENTS

We thank the officers and crew of the F.R.S. *Africana*

for their assistance during the cruise, and numerous colleagues, especially Mrs S. M. Payne, Ms E. Le Roux and Ms A. Polito (all Sea Fisheries Research Institute — SFRI), who counted the copepod samples, for their help with sampling. Drs L. Hutchings, S. J. Painting, H. M. Verheye (SFRI) and S. Pearre (Dalhousie University, Canada) and Mr C. D. Van der Lingen (SFRI) made valuable comments on an earlier version of the manuscript. Financial assistance was provided by the Benguela Ecology Programme of the Foundation for Research and Development.

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