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Vertical distribution and feeding patterns of midwater fish in the central equatorial Atlantic
II. Sternoptychidae

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Abstract

The vertical distribution of seven sternoptychid species was examined from RMT 1+8 samples collected aboard R.V. "Meteor" in March-April 1979 and from Royal Research Ship R.R.S. "Discovery" in July 1974 in the central equatorial Atlantic. During daytime sternoptychids occupied depths between 200 and 1 250 m, with *Sternoptyx pseudobscura* living deepest, centering between 800 and 900 m, and *Argyropelecus sladeni* most shallow, aggregating predominantly at 300 and 400 m. They are all considered limited or partial migrants, ascending only some 100 and 200 m towards the surface at night. Only *A. sladeni* was observed to enter the epipelagic zone (0 and 200 m). – Feeding patterns were investigated from stomach content analyses of *Sternoptyx diaphana, S. pseudobscura, Argyropelecus sladeni* and *A. affinis*. Additional stomach contents were analysed from samples of *S. diaphana, A. hemigymnus* and *A. olfersi* collected in June 1985 from F.R.V. "Walther Herwig" in the temperate NE Atlantic at 46 °N, 17 °W by means of the Engel Trawl. The food spectrum of the six species is generally described, and additional dietary evidence regarding calanoid copepod prey is provided for four of these taxa. All sternoptychid species investigated were planktivorous, feeding predominantly on copepods and ostracods, except for the largest size class, which preyed heavily on euphausiids and amphipods. The relationship of predator size towards prey type and prey size is analysed for both *Sternoptyx* species. Of these, *S. pseudobscura* in particular exhibits taxonomic selectivity towards polychaete prey. The diet of both species of *Sternoptyx* included a number of epipelagic or even neustonic calanoid copepod species which contributed more than 50% of the total copepod population by numbers. So far it is not known how the predators find access to prey organisms of the upper 200 m, as netfeeding is considered unlikely. Cyclopoid copepods of the genus *Sapphirina* were observed as dietary component particular of *S. diaphana*.

Introduction

Most investigations on the feeding ecology of mesopelagic fish in the oceanic environment have been focused on myctophids (Gjösaeter 1973, Tyler and Pearcy 1975, Hopkins and Baird 1977, Clarke 1978, Gorelova 1978, Kinzer 1982, Kinzer and Schulz 1985). Except for gonostomatids, myctophids are probably the most abundant fishes, migrating in a diel pattern in the upper 1 000 m of the water column, thereby accelerating vertical transport of organic matter to the depths.

Though not as abundant as myctophids, sternoptychids usually rank third in abundance, sharing the same environment to a maximum depth of 1 500 m. They are generally considered to be non-migrators except for some species which exhibit a slight diurnal vertical shift of 100 to 200 m (Baird 1971, Hopkins and Baird 1985). Compared to a large number of studies on the feeding strategies of myctophids, our knowledge of the trophic ecology of sternoptychids is still relatively scarce (Hopkins and Baird 1973, 1977, 1985, Merrett and Roe 1974, Roe and Badcock 1984). In a recent investigation Howell and Krueger (1987) reported on the life history of the dominant sternoptychids from the subtropical North Atlantic.

The present study describes the daytime vertical distribution patterns of some of the dominant sternoptychid species from the central equatorial Atlantic and the results of stomach content analyses. Some additional observations on the food of three sternoptychid species from the temperate eastern North Atlantic at 46 °N, 17 °W are included.

Materials and methods

The material was collected during March and April 1979 on cruise 51 of R.V. "Meteor" in the central equatorial Atlantic between Lat. 3 °N and 2 °S along Longitude 22 °W (see Fig. 1 in Kinzer and Schulz 1985). All samples were obtained using the RMT 8, a frontal opening-closing midwater trawl of

8 m^2 mouth area and mesh size of 4.5 mm. The net is combined with a simultaneously fishing 1 m^2 plankton net of 303 μm mesh size as the RMT 1+8 combination net. The opening and closing of the two nets were controlled by a net monitor which acoustically telemetered in situ measurements of the depth of the net, temperature, speed and distance fished (Baker et al. 1973). The preservation techniques and analyses of stomach contents are described by Kinzer and Schulz (1985).

From 67 samples collected by R.V. "Meteor" between the surface and 1 125 m depth, 23 hauls were positive, yielding a total of 272 sternoptychid fishes: 139 *Sternoptyx diaphana*, 17 *S. pseudobscura*, 37 *Argyropelecus affinis*, 61 *A. sladeni*, and 18 *A. hemigymnus*. Due to repeated malfunctioning of the RMT 8 closing mechanism additional samples from R.R.S. "Discovery" were included in diet analyses, kindly supplied by J. Badcock, Institute of Oceanographic Sciences, Wormley, Surrey, UK. These samples were collected with the RMT 1+8 in July 1974 aboard R.R.S. "Discovery", Cruise 64, from the same area on the equator and at Lat. 3°N along Longitude 23°W (see Fig. 1, Kinzer and Schulz 1985) in two vertical distribution series from the surface to 1 500 m depth during daytime. The upper 1 000 m of the water column was sampled in 100 m contiguous strata, and deeper, below that depth in 250 m bands. Each stratum of the upper 1 000 m was sampled for 2 h, and those fished deeper for 4 h. Only RMT eight samples were examined.

Additional samples of sternoptychids were collected in June 1985 in the eastern temperate North Atlantic off NW Spain at 46°N, 17°W from F.R.V. "Walther Herwig" using the Engel Trawl, which was towed at daytime to a maximum depth of 1 300 m. A total of 43 individuals of *S. diaphana*, 10 *S. pseudobscura*, 265 *A. hemigymnus* and 54 *A. olfersi* were obtained from three trawl tows. Micronekton collections were preserved in buffered 4% formalin in seawater solution. The dissected stomachs were subsequently transfered to 70% isopropyl alcohol (Kinzer and Schulz 1985).

Table 1. Depth distribution during daytime of seven sternoptychid species collected with the RMT 8 in two vertical series in central equatorial Atlantic (R.R.S. "Discovery", Cruise 64, 1974)

Depth (m)	Sternoptyx diaphana	Sternoptyx pseudobscura	Sternoptyx pseudodiaphana	Argyropelecus affinis	Argyropelecus gigas	Argyropelecus hemigymnus	Argyropelecus sladeni
200–300	8	0	0	0	0	0	10
300–400	3	0	0	2	1	39	53
400–500	12	2	0	52	5	11	0
500–600	315	11	2	4	0	1	1
600–700	468	24	6	0	0	1	1
700–800	175	48	5	0	0	0	0
800–900	77	62	1	0	0	0	0
900–1 000	15	19	0	0	0	0	0
1 000–1 250	0	2	0	0	0	0	0
1 250–1 500	0	0	0	0	0	0	0

Stomachs were removed by dissection of the pigmented distensible region posterior to the oesophagus. Food in the mouth or oesophagus was not included in the analyses. The prey organisms from the stomachs were counted and identified as far as possible, with particular emphasis on calanoid species. Prey with intact bodies were measured to the nearest 0.1 mm using an ocular micrometer. Regarding different prey taxa, the following measurements were taken: total length of copepods; carapace length of ostracods; tip of rostrum to tip of telson of euphausiids; the anterior end of the eyes to the tip of uropods (or telson) of amphipods. Chaetognaths were measured in total length. Since polychaetes, particularly alciopids, were mostly too fragmentary for measuring, only their heads were counted.

Before removing the contents of the stomachs, a rough assessment of its fullness was made using the following arbitrary scale: empty, nearly empty, half full, full and extended stomach.

Results

Abundance and vertical distribution

A total of 67 hauls (R.V. "Meteor") in the central equatorial Atlantic yielded eight species of sternoptychids, including the contribution made from R.R.S. "Discovery" data. *Sternoptyx diaphana* was by far the most abundant species, followed by *Argyropelecus sladeni, S. pseudobscura, A. affinis* and *A. hemigymnus*. Relatively few specimens of *S. pseudodiaphana* (14) and *A. gigas* (6) were caught. Furthermore, two individuals of *A. aculeatus* were collected, one specimen at 3°N (100 to 200 m at night) the other at the equator during the day (400 to 500 m depth). This is consistent with observations of Baird (1971) stating that this species is a rare inhabitant of the tropical Atlantic.

The pattern of vertical distribution during daytime is shown in Table 1 as compiled from two R.R.S. "Discovery" vertical distribution series of RMT 8 hauls. Above 200 m and below 1 250 m depth no sternoptychids were caught. *Sternoptyx diaphana* was predominantly taken between 500 and 800 m, with few post-larvae of 8 mm SL obtained in the 200 to 400 m horizon. The deepest living sternoptychid was *S. pseudobscura*, and was most abundant between 700 and 900 m depth. The vertical distribution of *S. diaphana* is very similiar to that reported for this species in the eastern Gulf of Mexico around 27°N, 86°W. On the other hand *S. pseudobscura* from that region was most common at about 900 m and therefore occurred somewhat deeper there than in the equatorial Atlantic (Hopkins and Baird 1985).

All the four *Argyropelecus* spp. obtained in the area of investigation have a rather shallow daytime distribution, primarily between 300 and 500 m depth (Table 1). Of these *A. affinis* occurred deepest, between 400 and 500 m, which agrees with the data presented by Baird (1971), while *A. sladeni* was the shallowest living species observed at 300 to 400 m. The remaining members of the genus, *A. hemigymnus* and *A. gigas*, were most common between 300 and

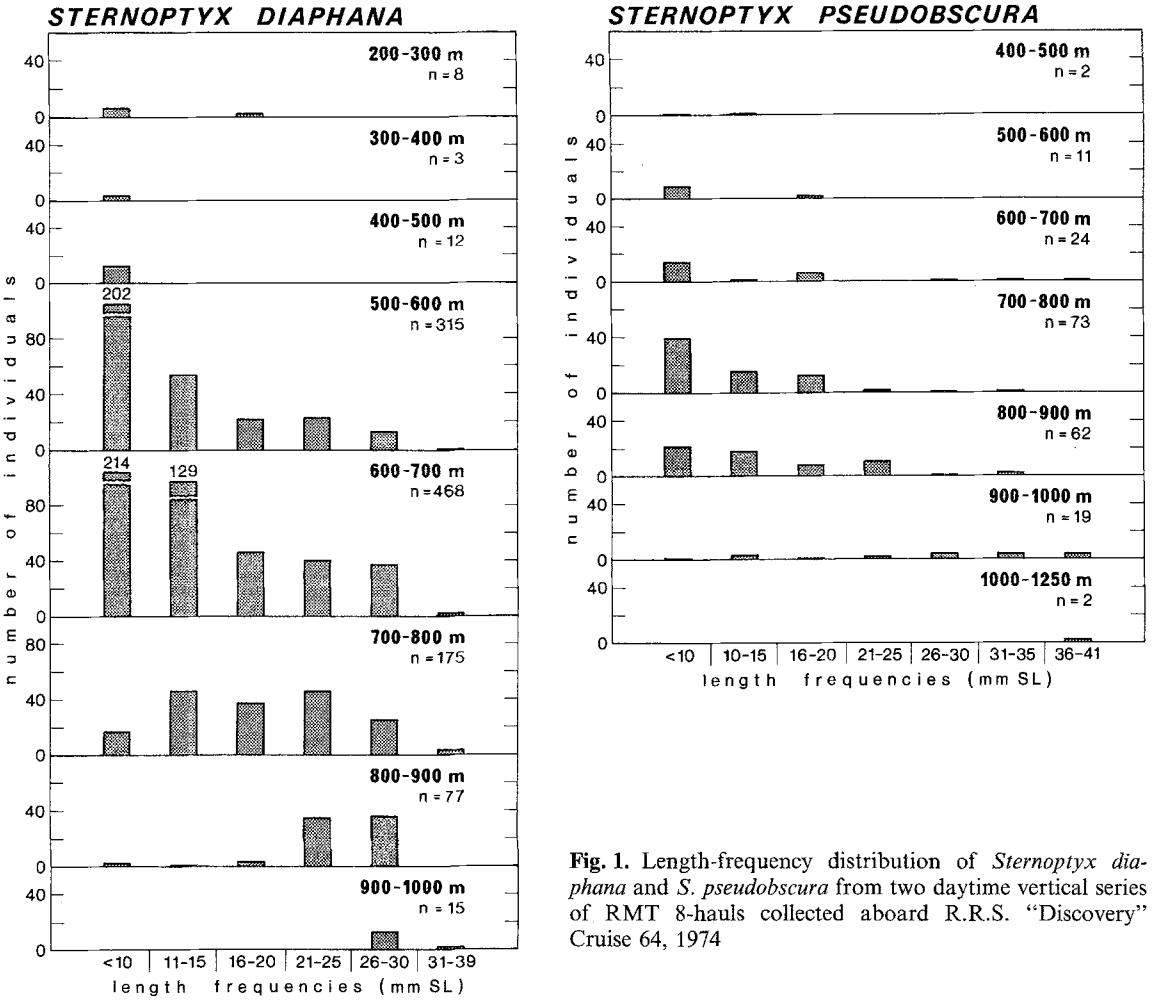

Fig. 1. Length-frequency distribution of *Sternoptyx diaphana* and *S. pseudobscura* from two daytime vertical series of RMT 8-hauls collected aboard R.R.S. "Discovery" Cruise 64, 1974

500 m depth during the day. In the R.V. "Meteor" collections, *A. aculeatus* and *A. sladeni* were the only species sampled between 100 and 200 m during the night, with a maximum catch of eight *A. sladeni* in one haul (22 to 56 mm SL). In all, only three individuals of *A. aculeatus* were caught between 100 and 200 m depth at night. Size frequencies of *S. diaphana* and *S. pseudobscura* obtained at different depths are shown Fig. 1. In *S. diaphana*, individuals of the smallest size-group of 7 to 10 mm SL predominated, with 11 to 15 mm specimens being second in abundance. Individuals of both size groups were found mostly at 500 to 700 m depth and largest specimens (>20 mm SL) were encountered below 500 m only. Depths below 800 m were dominated by maximum sized individuals (>20 mm SL), with >26 mm SL specimens exclusively occupying the 900 to 1 000 m zone. A similar depth-size relationship of *Sternoptyx diaphana* has been reported from the subtropical North Atlantic at 32°N, 64°W by Howell and Krueger (1987) and by Hopkins and Baird (1985) from the Gulf of Mexico.

Of *Sternoptyx pseudobscura* the smallest and also dominant size class of 7 to 10 mm SL was found between 500 and 900 m. The relatively few large individuals of 36 to 41 mm SL only occurred at the greatest depth sampled, 900 to 1 250 m. According to Baird (1971) and Hopkins and Baird (1985) *S. pseudobscura* is the deepest living member of the genus and has mostly been encountered between 800 and 1 500 m depth.

Deep scattering layers

A typical two-banded Deep Scattering Layer (DSL) was recorded at a frequency of 15 kHz within the equatorial area of investigation, its main layer occurring at a depth of 300 to 450 m (Kinzer and Schulz 1985). Midwater fishes such as myctophids possessing gas-filled swimbladders and because they migrate in a diel pattern, have usually been considered as the causative sound scattering organisms (Marshall 1951, Farquhar 1977).

The analyses of RMT 8-samples collected from R.V. "Meteor" at the depth of the DSL (with sampling depths of 300 to 350 m, 350 to 400 m and 350 to 420 m), revealed only few *Argyropelecus hemigymnus, A. affinis* and *A. sladeni*, averaging 3 to 5 specimens per 30-min. haul. Although sternoptychids possess a well-developed gas-filled swimbladder (Brooks 1977, Marshall 1960) they are usually considered too rare to be responsible for sonic backscattering. So far only Bradbury et al. (1970), using a 11 kHz echosounder,

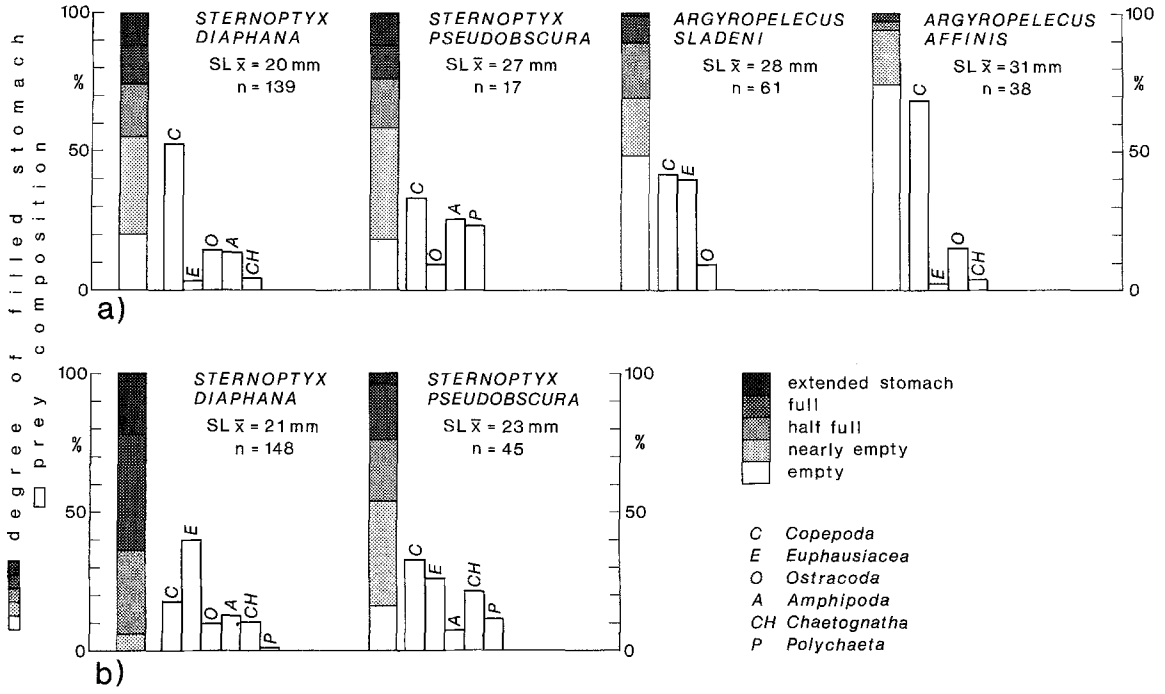

Fig. 2. Percentage of prey items and degree of filling stage of stomachs from four sternoptychid species collected between 100 to 1 250 m depth in central equatorial Atlantic. (a) R.V. "Meteor", 1979 (b) R.R.S. "Discovery", 1974

reported *A. sladeni, A. hemigymnus, A. affinis* and *Sternoptyx diaphana* at the depth of the DSL at 350 to 500 m from the equatorial Indian Ocean and presumed that they were sound scatterers.

Although RMT 8-hauls from R.R.S. "Discovery" fished in the DSL, were of 2 h duration and yielded a maximum of 37 *Argyropelecus hemigymnus*, 24 *A. sladeni*, 2 *A. affinis* and one *A. gigas* per catch, sternoptychids are considered to be too few to contribute significantly to sound scattering.

Food and feeding patterns

The diet composition and degree of stomach fullness of four of the prevailing sternoptychid species from the central equatorial Atlantic are presented in Fig. 2. *Sternoptyx* spp. have been treated separately (Fig. 2a and b) because samples of different years were examined.

Sternoptyx diaphana. Among the collected sternoptychids, this species was smallest in size ($\bar{x}=20$ mm SL) but was most abundant in the R.V. "Meteor"-samples. A total of 139 stomachs from 19 hauls were analysed and an additional 148 stomachs from R.R.S. "Discovery"-samples. As can be seen from Fig. 2a, more than 50% of food items were copepods. Of these, 8% consisted of epipelagic specimens of the genus *Sapphirina* (Cyclopoida) which were found in stomachs collected down to depths of 800 to 900 m. Besides copepods, other prey taxa included ostracods, mostly representatives of the genus *Conchoecia*, and amphipods, both contributing about 15% each. About two-thirds of the amphipods were phronimids of 2 to 5 mm total length. In addition to the relatively few euphausiids and chaetognaths ingested (each less than 5% of total prey), stomachs of *Sternoptyx diaphana* contained single decapod larvae, pteropods, polychaetes, appendicularians and fish larvae.

The prey of *Sternoptyx diaphana* collected from R.R.S. "Discovery" were proportionately different from that of the "Meteor"-specimens. Euphausiids were dominant and comprised 40% of the diet, while copepods (18%) were less important. *Sapphirina* spp. appeared as prey in specimens taken at all depths between 500 and 900 m, but were predominant at 600 to 800 m depth, although rather infrequently, with only 1.2% of the total copepod population. Other food items were found in comparable numbers to the "Meteor"-samples. Additionally, a few polychaetes, heteropods, appendicularians and fragments of salps occurred.

Furthermore, 43 stomach contents of *Sternoptyx diaphana* ($\bar{x}=26$ mm SL) included in dietary analyses from open trawl samples of F.R.V. "Walther Herwig" in the northeastern Atlantic at 46°N, 17°W have been analysed. As can be seen from Fig. 3, the prey spectrum is similar to that found in the equatorial Atlantic, although proportionally amphipods (40%) were much better represented. Hyperiid amphipods measured 4.3 to 8.4 mm. Ostracods and chaetognaths were relatively rare prey items, and yet rarer were decapod and fish larvae.

Sternoptyx pseudobscura. Only 17 specimens averaging 27 mm SL were collected from "Meteor"-samples. Apart from a slight dominance of copepods (30%), amphipods and polychaetes prevailed in the diet, with ostracods (9%) being relatively infrequent. Other single food items consisted of euphausiids, chaetognaths, heteropods and fish larvae.

As with *Sternoptyx diaphana*, the 45 "Discovery"-samples of *S. pseudobscura* ($\bar{x}=23$ mm SL) had a different di-

Table 2. Ontogenetic change in diet composition and prey type of two *Sternoptyx* species collected aboard R.R.S. "Discovery", 1974. Values give total number of prey found in stomachs. Number of fishes examined in parentheses. Polychaeta not included

Predator (SL in mm)	Prey type	Copepoda	Ostracoda	Amphipoda	Decapoda	Chaetognatha	Euphausiacea	fish larvae
Sternoptyx diaphana								
		<2.0 mm						
10–14 (19)		30	14	2				
15–19 (30)		14	32	3				
20–24 (43)		12	21	2				
25–29 (50)		6	15	3				
30–34 (6)			1					
		62	83	10				
		Σ=155						
		2.0–4.9 mm						
10–14 (19)		28		1				
15–19 (30)		32	5	20				
20–24 (43)		27	8	27		1	1	
25–29 (50)		14	18	35	1		3	2
30–34 (6)			2	3				
		101	33	86	1	1	4	2
		Σ=228						
		5.0–9.9 mm						
10–14 (19)					4	10		
15–19 (30)				4	2	6	182	1
20–24 (43)				6		3	418	2
25–29 (50)				1	1		130	
30–34 (6)				11	7	36	732	3
		Σ=789						
		10.0–20.0 mm						
10–14 (19)						5		
15–19 (30)						4		
20–24 (43)				3			21	
25–29 (50)							26	
30–34 (6)				2			186	
				9		38	233	
		Σ=17						
Sternoptyx pseudobscura								
		<2.0 mm						
10–14 (4)		21	1					
15–19 (13)		5						
20–24 (8)		8	1					
25–29 (9)		3	1					
30–34 (6)		3						
		40	3					
		Σ=43						
		2.0–4.9 mm						
10–14 (4)		3						
15–19 (13)		5						
20–24 (8)		6	1					
25–29 (9)		7	2	5				
30–34 (6)		1						
		22	3	5				
		Σ=30						
		5.0–9.9 mm						
10–14 (4)								
15–19 (13)								
20–24 (8)				3				
25–29 (9)		1		1		29		
30–34 (6)				2				
		1		9		38	233	
		Σ=281						
		10.0–20.0 mm						
10–14 (4)								
15–19 (13)								
20–24 (8)								
25–29 (9)						2		
30–34 (6)						2		1
						4		1
		Σ=5						

etary composition. Compared with the "Meteor"-samples, next to copepods (30%), *S. pseudobscura* preyed primarily on euphausiids (26%) and chaetognaths (21.7%), while polychaetes (11.8%) and amphipods (7.2%) were less abundant. Among the amphipod prey, members of the families Hyperiidae and Phronimidae predominated. Surprisingly, ostracods were almost completely missing from the diet, with only six specimens encountered.

Table 2 presents the diet composition of the different size classes of *Sternoptyx diaphana* and *S. pseudobscura* with reference to prey type and size. Within the first two size-classes of *S. diaphana*, copepods were the prevalent food items in the diet, with ostracods ranking second and appearing to be equally abundant in all size groups except the largest. In general, larger predators ingested additionally larger and heavier prey organisms, particularly amphipods and euphausiids. Other relatively large prey taxa, such as chaetognaths, were found to be eaten also by the smaller size classes of both *Sternoptyx* spp. Since specimens of *S. diaphana* prevailed within the 20 to 29 mm size categories most food items identified were relatively large (5.0 to 9.9 mm), consisting predominantly of euphausiids. Hopkins and Baird (1973) found that 50% of food items of a size <9.9 mm, with maximum prey numbers within the >4.9 mm-category were mostly composed of copepods, amphipods and ostracods.

Considering the size preference of prey type among specimens of *Sternoptyx pseudobscura*, copepods prevailed within the smallest size class of the predators. Like *S. diaphana*, euphausiids were preyed on exclusively by size classes >20 mm SL. Polychaetes, mostly of the families Alciopidae and Tomopteridae, were an important component in the food of *S. pseudobscura*, but less so in *S. diaphana*. Unfortunately, due to frequent fragmentation and/or advanced stage of digestion polychaete specimens could not be classified by size and were thus excluded from Table 2. All size-classes of both *Sternoptyx* spp. fed on polychaetes, the smallest *S. diaphana* and *S. pseudobscura* predators measuring 11 mm SL. The largest intact polychaete ingested by an individual of *S. diaphana* of only 25 mm SL measured 90 mm in length.

Argyropelecus sladeni. This was the best sampled *Argyropelecus* spp. collected most abundantly from R.V. "Meteor". About half the specimens had everted stomachs due to expansion of the swimbladder. Thus, only 61 stomachs were available for diet analysis. Copepods and euphausiids prevailed, in almost equal proportions (42.3 and 39.7%) with ostracods ranking third (9%). Other single prey items identified were amphipods, mostly phronimids, decapod larvae and chaetognaths. Larger specimens of *A. sladeni* fed almost exclusively on euphausiids. A single specimen of 50 mm SL, collected at 100 to 200 m depth, was found to have ingested a total of 37 euphausiids (6 to 9 mm). However, its stomach appeared only half full.

Argyropelecus affinis. As also observed in *A. sladeni*, ca ½ of the 76 *A. affinis* specimens sampled had their stomachs

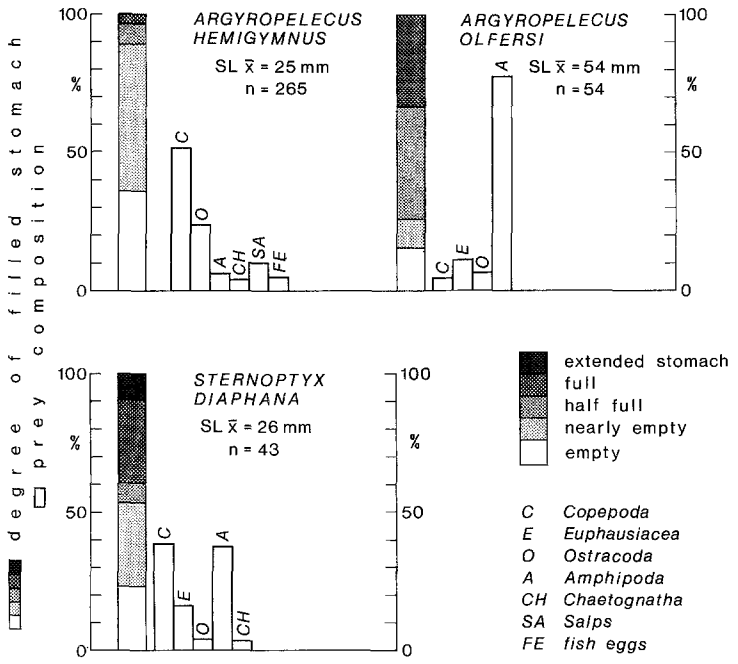

Fig. 3. Percentage of prey items and filling stage of stomachs of three sternoptychid species collected between 0 and 1 500 m depth in eastern North Atlantic at 46°N, 17°W. (F.R.V. "Walther Herwig", June 1985)

everted. Thus only a reduced number of stomach contents (38) could be analysed. Although the largest sternoptychid species from equatorial samples ($\bar{x} = 31$ mm SL), copepods (70%) prevailed as prey, ostracods ranked second (16%). Only a few chaetognaths, euphausiids and fish larvae were recorded.

Argyropelecus hemigymnus. Among the sternoptychids collected from F.R.V. "Walther Herwig" in the northeastern Atlantic, *A. hemigymnus* was by far the most abundant species. Their average size was 25 mm SL. A total of 265 stomachs were analysed. As with other *Argyropelecus* spp., a small number of specimens had everted stomachs. The diet composition and degree of stomach fullness of *A. hemigymnus* and *A. olfersi* are shown in Fig. 3. Copepods (50%) and ostracods (20%) were the prevailing food organisms. This dietary preference corresponds closely to the findings of both Merrett and Roe (1974) and Hopkins and Baird (1985) as compiled froms six oceanic areas, whereas Roe and Badcock (1984) observed selective feeding on chaetognaths, particularly by the larger size groups (21 to 35 mm), in the temperate northeastern Atlantic at 44°N, 13°W. However, *A. hemigymnus* from the "Walther Herwig"-collection had fed frequently on salps (10%), a phenomenon not found in any of the other sternoptychid species. Up to four salps were found in a single stomach (a fish of 22 mm SL). Ingested fish eggs made up 6% of the food items, and remarkably, euphausiids were completely missing.

Argyropelecus olfersi. This species had an average SL of 54 mm, with the maximum size sampled reaching 78 mm SL. Stomachs from 54 specimens were included in the diet study. The large size of this species was reflected in its food proportion as 78% of the prey items consisted of amphipods measuring up to 14 mm total length (Fig. 3). Only relatively few individuals of euphausiids (12%), ostracods and copepods were recorded. Other single food items comprised pteropods, siphonophores, chaetognaths and fishes. Among the fish prey was one *Argyropelecus* sp. of 20 mm SL, and the largest ingested fish was 30 mm SL. Almost 10% of the captured individuals of *A. olfersi* had everted stomachs.

Copepods as prey organisms

Copepods, primarily calanoids, usually comprise the major prey items of younger fish of a given species, while larger crustaceans (euphausiids etc.) as well as molluscs or fishes become increasingly important in diet with further fish growth (Hopkins and Baird 1977, 1985). This was also evident from our collections.

A limited number of stomachs of *Argyropelecus affinis, A. sladeni, S. diaphana* and *S. pseudobscura* were analysed for calanoid copepod prey. Calanoid copepods taken as prey ranged in size between 1.5 and 6.5 mm TL as analysed from 69 stomachs of both *Sternoptyx* spp. Obviously there was a positive selection for medium-sized to large prey organisms since small specimens (<1.5 mm) were absent from the stomachs, although they are abundant constituents of the plankton community. Members of the genus *Argyropelecus, A. affinis* and *A. sladeni* were found, with total lengths of copepod prey reaching a minimum of only 1 mm (e.g., *Clausocalanus furcatus*). However, these small dietary items were rare. Regarding the predator-food size relationship, there was clear evidence for an increase of maximum size of copepod prey with increasing standard length of the fish, e.g., the smallest size-class of *S. diaphana* (11 to 12 mm SL), fed upon calanoids attaining 3.2 mm total length, while fishes >23 mm SL ingested copepods of up to 6.5 mm.

Table 3 lists a total of 48 calanoid copepod species of 28 genera that have been identified from the stomachs of four

Table 3. Calanoid copepods in diet of four species of sternoptychid fishes from central equatorial Atlantic. Frequency of dietary items for each predatory species is given

Prey species	*Argyropelecus affinis* 6 fish	*Argyropelecus sladeni* 23 fish	*Sternoptyx diaphana* 59 fish	*Sternoptyx pseudobscura* 10 fish
Aetideus acutus	2	2	–	–
Aetideus giesbrechti	–	1	–	–
Arietellus sp.	–	–	1	–
Candacia bipinnata	–	–	1	1
Candacia curta	–	–	11	5
Candacia pachydactyla[b]	–	3	33	11
Candacia varicans	–	–	2	–
Candacia spp.	1	3	9	–
Centropages violaceus[b]	–	–	1	–
Clausocalanus furcatus[a]	1	8	–	–
Clausocalanus mastigophorus[a]	–	1	3	–
Clausocalanus sp.	2	–	–	–
Eucalanus sewelli	–	–	13	4
Eucalanus subtenuis	–	–	1	–
Eucalanus spp.	2	–	4	–
Euchaeta acuta	1	–	1	–
Euchaeta gracilis	–	–	1	–
Euchaeta hebes	–	–	8	–
Euchaeta marina[a]	1	–	87	–
Euchaeta media	–	2	–	–
Euchaeta spinosa	–	–	1	1
Euchaeta spp.	3	5	9	4
Euchirella messinensis	1	–	–	–
Euchirella pulchra	1	–	–	–
Euchirella rostrata	–	–	5	–
Euchirella splendens	–	2	2	–
Gaetanus miles	–	1	–	–
Gaidius sp.	–	1	–	–
Heterorhabdus sp.	1	1	–	–
Heterostylites longicornis	–	1	–	–
Labidocera acutifrons[c]	–	–	–	1
Lucicutia gemina	7	–	–	–
Lucicutia magna	2	–	–	–
Metridia sp.	–	–	1	–
Nannocalanus minor[a]	–	8	9	–
Neocalanus gracilis	–	4	21	1
Neocalanus robustior	–	–	9	3
Neocalanus spp.	–	–	2	–
Paracandacia simplex	–	–	9	1
Pleuromamma abdominalis	1	7	–	–
Pleuromamma borealis	–	13	–	–
Pleuromamma quadrungulata	–	1	–	–
Pleuromamma xiphias	1	–	–	–
Pleuromamma spp.	–	3	–	–
Pontellopsis perspicax[c]	–	–	3	–
Rhincalanus cornutus	–	6	1	–
Scaphocalanus sp.	–	1	–	–
Scolecithricella sp.	–	1	–	–
Scolecithrix danae[a]	–	5	31	33
Scottocalanus securifrons	–	2	–	–
Scottocalanus thomasi	–	1	–	–
Scottocalanus sp.	1	–	–	–
Spinocalanus sp.	1	–	–	–
Undeuchaeta plumosa	–	–	2	–
Undinula vulgaris[a]	2	1	27	1
Calanoida (unident.)	5	24	36	–

[a] Species restricted to the upper 200 to 250 m
[b] Species confined to the upper 100 m
[c] Species of neustonic habitat

sternoptychid species, with most taxa being characteristic of the upper mesopelagic zone. However, a number of species recorded as dietary items are inhabitants of epipelagic or even neustonic habitats, as was confirmed by K. Hülsemann (personal communication) who made discrete vertical analyses of the copepod population of the upper 500 m from the same cruise (R.V. "Meteor" Cruise 51). Differences in feeding behaviour among the predatory species were more or less marked with regard to copepod prey. *Argyropelecus sladeni* fed heavily on the genus *Pleuromamma*, mesopelagic during daytime, with additional few candaciids or euchaetids being found in their stomachs. *A. affinis* contained a relatively high number of specimens of the genus *Lucicutia* which is considered mesopelagic as well.

Both members of the genus *Sternoptyx* were found to have ingested large numbers of candaciids additional to *Scolecithrix danae*, the latter being the principal copepod of the *S. pseudobscura* diet. Of the candaciids, *Candacia pachydactyla* was the most prevalent prey species that is typically limited to the upper 100 m of the water column. Euchaetids played a major role in the diet of *S. diaphana*, with *Euchaeta marina*, a representative of the upper 250 m, comprising one-fourth of the total calanoid copepod prey, at least. Only small numbers of this family were recorded from *S. pseudobscura*, and *E. marina* was entirely missing. Additional species of the near-surface plankton (0 to 250 m depth) that contributed significantly to the food of the sternoptychids, particularly of *S. diaphana*, were *Nannocalanus minor* and *Undinula vulgaris*. Copepod taxa other than calanoids were relatively rare food items except cyclopoid copepods of the genus *Sapphirina* that made up to 8% of the total copepods of *S. diaphana* prey.

Discussion

In contrast to myctophids, with most species performing a pronounced diel vertical migration, the sternoptychid species move only some 100 to 200 m towards the surface and of the species sampled here, only *Argyropelecus sladeni* entered the upper 200 m of the water column during the night. Data on differences in vertical distribution are reported by Badcock and Baird (1980) for *Sternoptyx* spp. They state that the depth of maximum abundance varies geographically, and is often correlated with temperature and light regime.

During the day populations of *Sternoptyx diaphana* and *S. pseudobscura* from the equatorial Atlantic mainly shared identical depth levels, thus utilising the same plankton resources. However, the latter species showed some taxonomic selectivity towards polychaete prey, a phenomenon also reported, from both the Gulf of Guinea and the Gulf of Mexico (Hopkins and Baird 1977, 1985). Possible means of capturing alciopid polychaetes of such tremendous size – polychaetes from R.V. "Meteor"-collections were up to four times the size of their predators – were discussed by these authors (1985) who suggested that such elongate prey items

might be ingested by suction. According to the same authors (1977) relatively large individuals of the species *Argyropelecus aculeatus* of 13 to 60 mm SL also feed on polychaetes.

Our results suggest that the four sternoptychid species studied from the central equatorial Atlantic feed opportunistically on zooplankton. The discrepancy in prey composition between *Sternoptyx diaphana* and *S. pseudobscura* collected from R.V. "Meteor" and R.R.S. "Discovery" might be due to a different plankton composition in both years (Fig. 1). In 1974 both species preyed preferably o euphausiids while, in 1979, stomachs of *S. diaphana* contained mostly copepods and those of *S. pseudobscura* additional amphipods and polychaetes. Hopkins and Baird (1985) observed taxonomic selectivity in *S. diaphana*, because stomachs they examined contained proportionally more ostracods and hyperiid amphipods than simultaneously collected plankton samples from the same depth strata. Taxonomic feeding selectivity has also been described by Merrett and Roe (1974) for *Argyropelecus aculeatus* which selected for ostracods and against calanoid copepods. Regional differences in the diets of sternoptychids have been observed by Hopkins and Baird (1973, 1977, 1985) as the stomachs of larger *S. diaphana*, collected in six different regions, also contained a higher percentage of amphipods. *S. diaphana* from "Walther Herwig" samples collected in the NE Atlantic also fed intensively on amphipods (40% of prey composition, Fig. 2). The average size of the predators (26 mm SL) there was greater than that of the specimens sampled from the equatorial population.

The present collections reveal a surprisingly high fraction of epipelagic copepods in the diet of both *Sternoptyx* spp. Relatively more individuals of these taxa were ingested by these deep-living predators than by the shallower *Argyropelecus* spp. Only 25% of the calanoid copepod prey of *Argyropelecus sladeni*, the shallowest-living sternoptychid from this survey, were composed of species restricted to the upper 250 m, but this fraction reached more than 50% in both *Sternoptyx* spp. It is worth noting that nearly all of these epipelagic copepod species were also reported as an important dietary component of sternoptychids from the Gulf of Mexico (Hopkins and Baird 1985). Moreover, as in the Gulf, *S. diaphana* and *S. pseudobscura* fed on some pontellid copepods in the equatorial Atlantic that are characteristic of the surface layer, namely *Pontellopsis perspicax* and *Labidocera acutifrons*. The latter species was even shown by these authors to be the principal copepod in the diet of *S. pseudobscura* which contrasts with our collections, yielding only a single specimen from a total of 10 stomachs. In addition, three individuals of *S. diaphana* each contained a single specimen of *P. perspicax*., Questions on how these predators might have found access to their vertically segregated prey are thus raised. Based on our results or the literature, (Badcock and Baird 1980), neither member of the genus *Sternoptyx* has been encountered at epipelagic depths. Moreover, due to the large mesh size of the RMT 8 (4.5 mm) net feeding seems unlikely to occur, although it has been reported on a small scale in *S. diaphana* (Lancraft and Robison, 1980). Furthermore, there was no indication of any secondary feeding which might have occurred by means of a primary predator that escaped our attention in subsequent stomach analysis. In addition, in the Gulf of Mexico, Hopkins and Baird (1985) found no evidence of downwelling of near-surface water to depths occupied by *Sternoptyx* spp. Summarizing, these authors were unable to present a probable explanation for the large amount of copepod prey typical of surface or subsurface levels.

Besides calanoids, stomachs of *Sternoptyx* spp. contained considerable numbers of the epipelagic cyclopoid copepods of the genus *Sapphirina*, which constituted up to 8% of the total copepod prey within the stomachs of *S. diaphana*, but did not exceed 1.5% in the diet of *S. pseudobscura*. With regard to prey of the genus *Sapphirina*, Hopkins and Baird (1985) obtained similar results from their investigations in the eastern Gulf of Mexico, where both *Sternoptyx* spp. occur even deeper, with *S. diaphana* centering at 700 m and *S. pseudobscura* around 900 m depth. As in our samples, only *S. diaphana* was observed to have preyed heavily on the genus *Sapphirina*, whereas stomachs of *S. pseudobscura* contained few individuals. Since the same arguments as given above militate against direct feeding on free-swimming individuals, Hopkins and Baird (1985) discussed observations made by Heron (1973), who reported *Sapphirina angusta* from inside *Thalia democratica* salps, feeding on "all accessible internal structures of the host". As Hopkins and Baird (1985) found salps only rarely in the digestive tracts of *S. diaphana*, they suggested a "free swimming period for these crustaceans and/or browsing by hatchetfishes while the prey is external on the host". This interpretation would be consistent with our results showing evidence of fragments of some salps inside the stomachs of *S. diaphana*.

Sternoptyx diaphana from the temperate northeastern Atlantic did not feed on salps or other gelatinous organisms, contrary to *Argyropelecus hemigymnus* that was found to forage quite heavily on salps (10% of total prey items, Fig. 3). Among the vertical migrating myctophids from the equatorial Atlantic only *Ceratoscopelus warmingii* was found to prey also on salps, amounting to 12% of total number of prey items, although *Sapphirina angusta* has never been observed in their stomachs (Kinzer and Schulz, 1985). Other information on gelatinous organisms (siphonophores, tunicates, etc.) has been presented by Hopkins and Baird (1977) who reported these taxa to constitute up to 24% of total prey items in *C. warmingii* stomachs from the Caribbean Sea and Gulf of Mexico, however, only few *Sapphirina angusta* (1.3%) were noted. In contrast to *Sternoptyx* spp. *C. warmingii* was foraging predominantly in the surface layer at night, and therefore, probably preying on free swimming *Sapphirina angusta* copepods.

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