Marine Biology 85, 313–322 (1985)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

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

I. Myctophidae

J. Kinzer [1] and K. Schulz [2]

[1] Institut für Meereskunde, Universität Kiel; Düsternbrooker Weg 20, D-2300 Kiel 1, Federal Republic of Germany (FRG)
[2] Biologische Anstalt Helgoland; Notkestraße 31, D-2000 Hamburg 52, Federal Republic of Germany (FRG)

Abstract

Fishes and zooplankton were obtained (March–April 1979 and partly in August 1974) from 45 hauls taken during the day and at night in the central equatorial Atlantic between Latitude 3 °N and 2 °S from the surface to 1 250-m depth, using the RMT 1+8, a combined opening-closing plankton and micronekton trawl. The vertical distribution of 30 myctophid species is described. All species migrate in a diel pattern, *Ceratoscopelus warmingii* and *Lampanyctus photonotus* down to at least 1 250 m. During daytime most species aggregated at 400- to 700-m depth, therefore only partly occupying the depth of the Deep Scattering Layer (400 to 500 m at 15 kHz). The feeding patterns of seven of the most abundant species were compared, with a total of 1 905 stomach contents being analysed. All seven species are regarded as opportunistic predators, which feed predominantly during the night on calanoid copepods. A total of 66 species of calanoid copepods were identified among the prey items, with smaller species definitely being in the minority. Stomachs of *C. warmingii* (700 to 1 250 m depth) and *Lepidophanes guentheri* (500 to 900 m depth) from daytime samples contained copepod species restricted to the upper 150 m of the water column, including *Undinula vulgaris, Nannocalanus minor,* and *Euchaeta marina,* thereby confirming an extended vertical migration of predators. Differences in diet and preferences between species in their total food spectrum are described.

Introduction

In the oceanic environment extensive vertical migrations of myctophids and other mesopelagic fish species have been well documented by many authors (Pearcy and Laurs, 1966; Badcock, 1970; Badcock and Merrett, 1976; Pearcy *et al.,* 1977; Frost and McCrone, 1979; Willis and Pearcy, 1982; Roe and Badcock, 1984), but the role of midwater fish in the marine food web, particularly in tropical oceanic regions, has not been sufficiently investigated.

This study considers the vertical range of distribution of the more abundant myctophid species from the central equatorial Atlantic and their feeding patterns in relation to their diel vertical migrations.

Materials and methods

Individuals were collected during March–April 1979 on RV "Meteor" (cruise 51) in the central equatorial Atlantic, between Lat. 3 °N and 2 °S along longitude 22 °W (Fig. 1). Sampling was done at a speed of 2 kn, using an acoustically operated, opening-closing rectangular midwater trawl (RMT 1+8). This is essentially a twin net consisting of an 8-m² trawl of 4.5-mm mesh size and a 1-m² plankton net of 0.303-mm mesh size. 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).

Altogether 34 hauls were carried out at night between 0- to 200-m depth. Another series of hauls was carried out during the daytime around the depths of the Deep Scattering Layer. Due to the lack of sufficient daytime samples from depths below 200 m, additional samples from RRS "Discovery" (cruise 64, 1974) were investigated. They consisted of two series of hauls collected with the RMT 1+8 in the same area (at Lat. 3 °N and on the equator, Fig. 1), during July 1974. The 14 samples were collected in the daytime between 300- and 1 250-m depth, mostly in 100-m depth intervals and of 2-h duration, except at the deepest level where the haul was of 4-h duration.

Stomach analysis was done from samples preserved in buffered 4% formalin which were later transferred to 70% isopropyl alcohol. The degree of stomach filling from

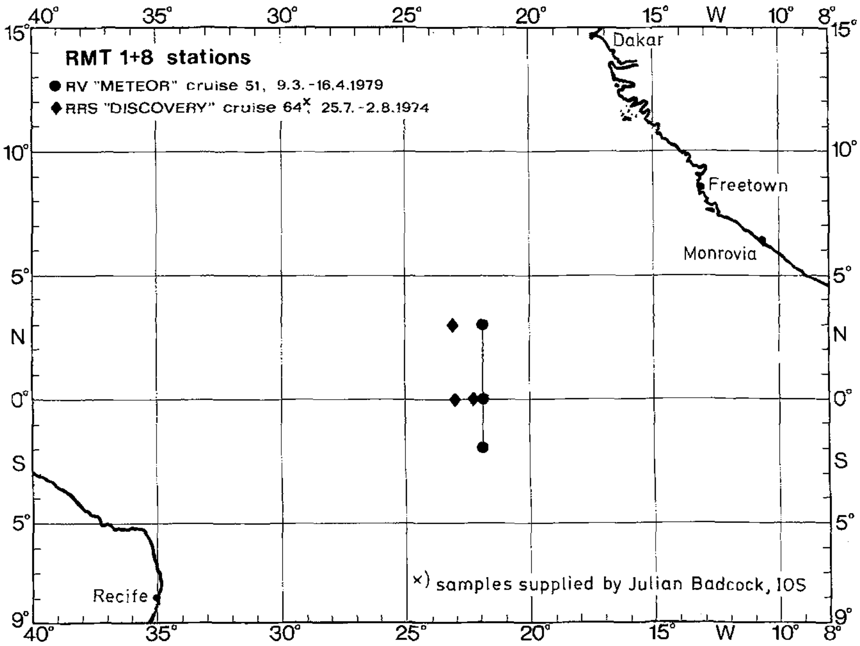

Fig. 1. Locations of RMT 1+8 stations in the central equatorial Atlantic

Table 1. Number of myctophid specimens collected at night with the RMT 1+8 on a transect between 3°N and 2°S in the upper 200 m (RV "Meteor", cruise 51, 1979); ( ) = number of hauls

	3°N	Equator	2°S	Σ
Electrona risso	1 (1)			1
Hygophum macrochir	11 (3)	18 (3)	23 (4)	52
Benthosema suborbitale	5 (2)	1 (1)	5 (2)	11
Diogenichthys atlanticus	7 (5)	2 (1)	22 (4)	31
Myctophum affine		1 (1)		1
Myctophum nitidulum	1 (1)	3 (2)		4
Myctophum asperum	8 (3)	15 (2)	12 (4)	35
Notolychnus valdiviae	71 (4)		49 (4)	120
Diaphus dumerilii	74 (6)	8 (3)	19 (4)	101
Diaphus garmani	4 (1)		1 (1)	5
Diaphus problematicus	1 (1)	1 (1)	3 (1)	5
Diaphus splendidus	6 (2)	3 (2)	2 (2)	11
Diaphus bertelseni			1 (1)	1
Diaphus luetkeni	56 (7)	21 (4)	27 (4)	104
Diaphus lucidus	4 (3)			4
Diaphus fragilis	34 (7)	9 (2)	7 (4)	50
Diaphus vanhoeffeni	1 (1)	9 (3)	2 (2)	12
Diaphus mollis	18 (7)	3 (1)	8 (4)	29
Diaphus brachycephalus	18 (7)	112 (4)	16 (4)	146
Diaphus elucens	1 (1)			1
Lampadena luminosa	4 (2)			4
Lampanyctus isaacsi		1 (1)	1 (1)	2
Lampanyctus photonotus	1 (1)	1 (1)		2
Lampanyctus nobilis		19 (3)		19
Lampanyctus tenuiformis		1 (1)	1 (1)	2
Lampanyctus alatus	63 (9)	43 (5)	146 (4)	252
Lampanyctus taaningi		2 (1)		2
Lepidophanes guentheri	155 (8)	37 (5)	46 (4)	238
Lepidophanes pyrsobolus		2 (1)		2
Bolinichthys supralateralis		1 (1)		1
Bolinichthys photothorax	5 (3)	4 (2)	4 (3)	13
Ceratoscopelus maderensis		5 (1)		5
Ceratoscopelus warmingii	71 (9)	108 (6)		179
Notoscopelus resplendens		2 (2)	1 (1)	3
	620	432	396	1 448

samples collected during the night (0–200 m depth) was classified according to the following scale: 0 = empty, 1 = nearly empty, 2 = half full, 3 = full and 4 = extended stomach.

Besides stomach analysis at higher taxonomic levels, copepods were usually differentiated to genus and where possible to species.

Results

Abundance and vertical distribution

Of the 45 myctophid species described by Nafpaktitis *et al.* (1977) and recently by Hulley (1981) from the Atlantic Tropical Region, 34 species were collected in the 34 hauls at night from 0 to 200 m. Table 1 lists the nighttime distribution of myctophids in the upper 200 m of the water column. Some species seem to occur more frequently at the northern station, such as *Lepidophanes guentheri* (155 individuals in 8 hauls) and *Diaphus dumerilii* (74), but due to the few samples collected at the three stations, this could be merely accidental. *Diaphus brachycephalus* was abundant at the equator (112), while *Lampanyctus alatus* reached a peak at Lat. 2 °S (146). Another dominant species, *Ceratoscopelus warmingii,* was present at the equator and at Lat. 3 °N, but did not occur at Lat. 2 °S. Zoogeographically, the sampling area is well within the Guinean Region as defined by Backus *et al.* (1970), with the warmest Atlantic surface water in April reaching 28 °C (Fig. 2) (Bauerfeind *et al.,* 1984). At a depth of 1 000 to 1 200 m the temperature is 5 °C, and at 800 m 6 °C. Organisms migrating from 800 m or deeper to the upper 100 to 200 m therefore have to tolerate a wide temperature range.

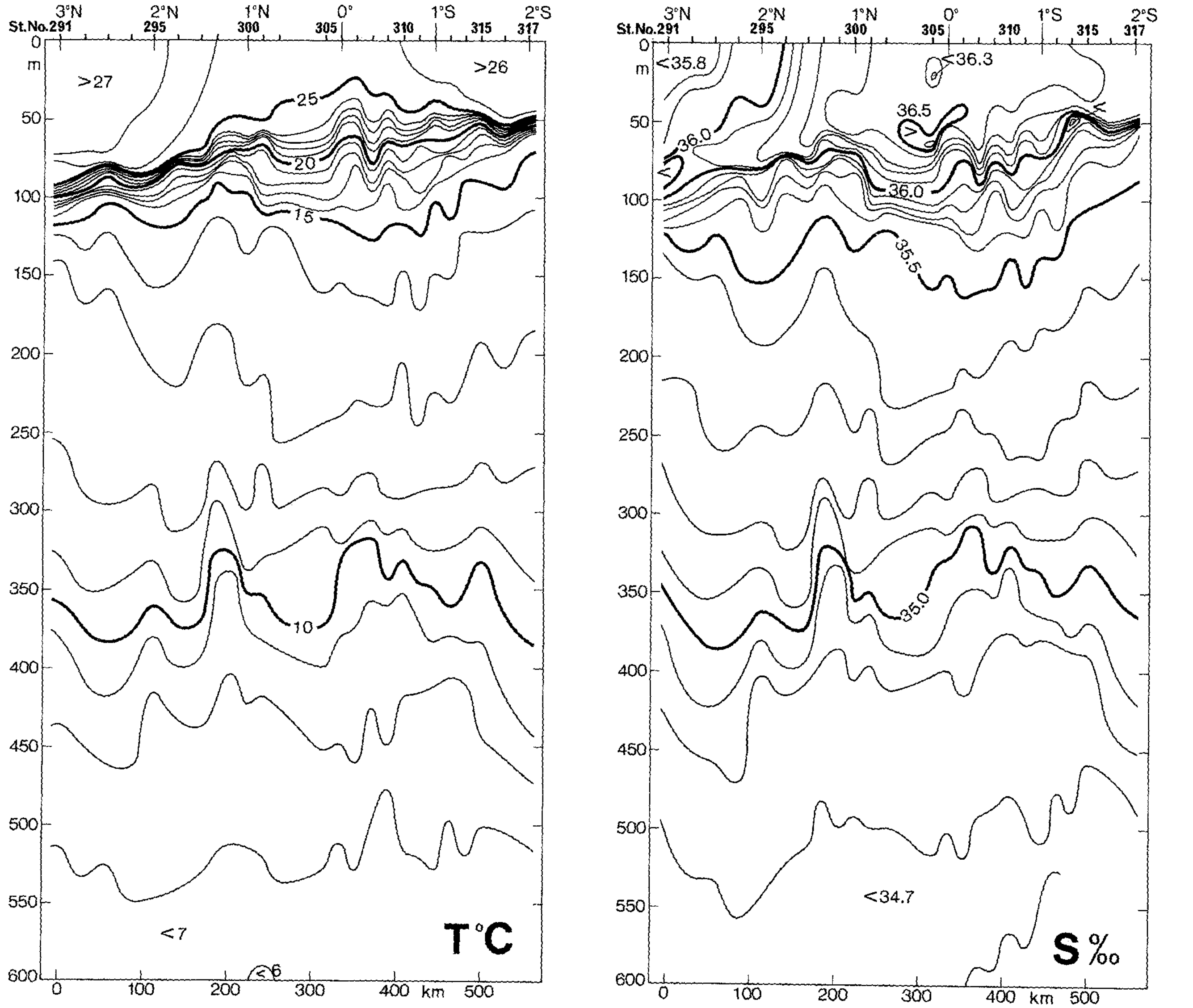

Fig. 2. Isotherms and isohalines for the meridional section in Long. 23°W derived from STD measurements taken at the time of RV "Meteor" sampling program

Table 2 describes the depth distributions of myctophids during the daytime from two series of RMT-8 hauls (totalling 14 positive hauls) from 300 to 1 250 m. Above 300 m, no myctophids were collected during the daytime. Most species occurred between 400- to 600-m depth, with *Benthosema suborbitale, Diogenichthys atlanticus, Myctophum affine* and *M. asperum* being particularly abundant. *Hygophum macrochir* and *Ceratoscopelus warmingii* were collected over the whole column from 400- to 1 250-m depth. *Lobiancha dofleini* is seldom observed in the tropical Atlantic. Only two were caught during the day, and they originated from 400- to 500-m depth.

Of the *Diaphus* species, *D. luetkeni* appeared mostly from 400 to 500 m, with single individuals collected at 500 to 900 m. According to Nafpaktitis *et al.* (1977), this tropical species is a ranking myctophid in the Atlantic Tropical Region with its greatest abundance in the Guinean Province, daytime distribution 375 to 750 m. *D. lucidus* and *D. mollis* were the two other more abundant species collected during daytime.

Two *Lampanyctus* species, *L. photonotus* and *L. nobilis*, contrast with the other myctophid species in their wide depth range between 600 and 1 250 m. This also holds true for *Lepidophanes guentheri* and *Ceratoscopelus warmingii*, which have the broadest depth distribution (400 to 1 250 m). The vertical distribution of *C. warmingii* corresponds with that of other collections (Nafpaktitis *et al.*, 1977). *C. warmingii* has been collected in opening-closing nets in the eastern North Atlantic (Lat. 30 °N, Long. 23 °W) and near Bermuda and the Canary Islands even to depths of 1 500 m (Badcock and Merrett, 1976; Nafpaktitis *et al.*, 1977).

Deep scattering layers

Daytime abundance of myctophids in particular depths has often been correlated with the depth of Deep Scattering Layers (DSL). Myctophids with gas-filled swimbladders are mostly responsible for the cause of

Table 2. Daytime depth distribution of myctophids from RMT 8 samples collected at stations between 3°N, 22°56′W and 0°41′N, 22°49′W during GATE-Expedition of RRS "Discovery", July 1974

Depth (m)	*Electrona risso*	*Hygophum reinhardtii*	*Hygophum macrochir*	*Benthosema suborbitale*	*Diogenichthys atlanticus*	*Myctophum affine*	*Myctophum nitidulum*	*Myctophum asperum*	*Symbolophorus rufinus*	*Centrobranchus nigroocellatus*
300– 400										
400– 500			6	16	6	8		12		1
				20		13				
1 500– 600		1	10	5	84		6		1	
			8		7					
600– 700	1		2							
			8							
700– 800			2							
800– 900			3							
900–1 000			4				2			
1 000–1 250			1							

Depth (m)	*Notolychnus valdiviae*	*Lobianchia dofleini*	*Diaphus dumerilii*	*Diaphus splendidus*	*Diaphus luetkeni*	*Diaphus lucidus*	*Diaphus fragilis*	*Diaphus vanhoeffeni*	*Diaphus mollis*	*Lampadena luminosa*
300– 400			2		4		2		2	
400– 500	198	2	5	1	31	17	2	3	2	
			4		3		1		16	1
1 500– 600					1	3				
						4				
600– 700					1					
700– 800										
800– 900	1				1					
900–1 000										
1 000–1 250										

Depth (m)	*Lampanyctus isaacsi*	*Lampanyctus photonotus*	*Lampanyctus nobilis*	*Lampanyctus tenuiformis*	*Lampanyctus alatus*	*Lepidophanes guentheri*	*Bolinichthys supralateralis*	*Bolinichthys photothorax*	*Ceratoscopelus warmingii*	*Notoscopelus resplendens*
300– 400										
400– 500							1		2	
1 500– 600				3	15	23	5	4	3	
					20	55				
600– 700	16	20	1	5	2	13		5	6	
		2			22	48			27	
700– 800		8	1			4			14	2
		10	3						6	
800– 900		5	1			10			2	
		3	3			3			3	
900–1 000		15				4			6	1
		2							6	
1 000–1 250			14			1			34	2

Table 3. Occurrence of midwater fishes of 8 RMT 1+8 samples collected at 2°S at depths above, within and below DSL-depth (each a 30-min haul)

Station	Depth (m)	No. of specimen	Remarks
45/63	200–350	no fish	above DSL
59	300–350	few sternoptychids	at DSL
61	350–400	few sternoptychids	at DSL
54	350–420	30 myctophids	at DSL
55	400–500	61 myctophids	below DSL
60	400–500	60 myctophids	below DSL
62	400–500	42 myctophids	below DSL

sound scattering at 15 to 30 kHz (Marshall, 1951, 1960; Backus *et al.*, 1968; Baird *et al.*, 1974; Farquhar, 1977). As opening-closing nets and trawls improved and the depth of the DSL was sampled more precisely through the development of telemetering *in-situ* net depth to the ship, it appeared that myctophids were less often responsible for sound scattering. Exceptions possibly occur in areas of mass abundance.

In equatorial waters during cruise 51 of RV "Meteor" we observed at 15 kHz a typical two banded DSL with the main layer between 300 m and a maximum of 450-m depth. A shallower and weaker layer was recorded between 200 and 250 m. With a quick ascent and descent of the layer (average 8 cm s^{-1}) we assumed that it was caused by fish. In a series of 30-min sampling at the DSL and its surrounding depth at Lat. 2 °S we caught about twice as many myctophids just below the DSL than at the depth of the DSL (Table 3).

Above the DSL no mesopelagic species were caught. Also, according to the depth distribution of myctophids from the "Discovery" daytime samples (Table 2), many myctophid species have their maximum distribution between 400 to 500 m. The exceptions are most *Lampanyctus* species (apart from *L. alatus*), *Lepidophanes guentheri* and *Ceratoscopelus warmingii,* which were observed even further down to 1 250 m depth (see above).

Our findings correspond well with the "Discovery" data, since at 300 to 400 m no myctophids, except a few *Diaphus* spp., were caught (Table 2); most myctophid species appeared at 400 to 500 m and below, down to some 700 or 1 000 m.

Food and feeding patterns

Analysis of stomach fullness and stomach content was done on seven of the more abundant myctophid species collected in the upper 200 m at night:

Lampanyctus alatus	252 ind. / 18 hauls
Lepidophanes guentheri	238 ind. / 17 hauls
Ceratoscopelus warmingii	179 ind. / 15 hauls
Diaphus brachycephalus	146 ind. / 13 hauls
Notolychnus valdiviae	120 ind. / 8 hauls
Diaphus lütkeni	104 ind. / 15 hauls
Diaphus dumerilii	101 ind. / 13 hauls

Preliminary analysis was also done on the stomach contents of samples of these species collected during the daytime, with particular emphasis on calanoid copepods as prey organisms. Only *Diaphus brachycephalus* was missing in the daytime hauls, so that no data could be collected on this species.

Because of the relatively large mesh size of the RMT 8 cod end, net feeding of the individuals sampled can be considered negligible.

Ceratoscopelus warmingii. The average size of *C. warmingii* was 34 mm SL in our RMT 8 samples. Of all seven species investigated, this species had the broadest diversity of prey items at all three stations (Fig. 3). At the most northern station appendicularians slightly prevailed by numbers (23%), followed by copepods (22%) and salps (12%), euphausiids and their larvae, fish scales, ostracods, amphipods, gastropods, a few chaetognaths, siphonophores and fish larvae. A wide variety of taxa and sizes of taxa and sizes of prey was also described by Clarke (1978, 1980) from the tropical Pacific.

Comparing the three different locations it seems that most species fed on more appendicularians at Lat. 3 °N, with a steady decrease towards the south. A diet composition, which varies geographically and/or with the season, was also described for this species by Hopkins and Baird (1977).

C. warmingii is the only species in our samples which also feeds on salps. At each of the three stations, salps contributed to their diet (up to 12% at Lat. 3 °N and 2 °S).

Lepidophanes guentheri. This species was second in abundance and the largest species we caught, with an average size of 46 mm SL. At Lat. 3 °N their prey consisted of about 50% copepods, with other food items being appendicularia (13%), euphausiids (10%), ostracods and fish scales (Fig. 3). In contrast to observations by Hopkins and Baird (1977), no siphonophores were found in their stomachs. Also in samples collected during the daytime at 500 to 900 m, copepods and euphausiids dominated.

Diaphus dumerilii. This species is very common and had an average size of 43 mm SL in our catches. It is therefore the largest *Diaphus* species in our collection. At the northern station the diet consisted mostly of copepods and almost 30% appendicularia, except for some ostracods, euphausiids, amphipods, and gastropods (Fig. 3). At the equator station we had only a few *D. dumerilii* in our nets. At Lat. 2 °S the analysis of 22 stomachs revealed a similar diet, except for a higher content of copepods (63%).

Our few daytime collections of *Diaphus dumerilii* from 400 to 600 m contained mostly juveniles about 25 mm SL. Their diet consisted of copepods, ostracods, and gastropods. Digestion was advanced, indicating food uptake only at night. This is in contrast to individuals from off NW Africa with no diurnal feeding pattern. It seems that in areas of upwelling off NW Africa, the behaviour of midwater fish might be different from oceanic regions. This also holds true for *Myctophum punctatum* and *D. holti* in this area which continued feeding during the daytime (Hopkins and Baird, 1977; Kinzer, 1982).

Diaphus luetkeni. This is another abundant tropical myctophid which, because of its smaller mean size (35 mm SL), appears to select smaller prey items. Copepods were the prevailing prey at all three stations (±70% by numbers), supplemented by ostracods, amphipods, euphausiids, and to some extent fish scales (Fig. 3). At the southern station this species also preyed on chaetognaths. As in daytime samples from 400 to 500 m (31 individuals), most prey items [i.e. copepods, a few euphausiids and single amphipods (*Phronima* sp.)] exhibited advanced digestion, and it is thus assumed that *D. luetkeni* feeds at night.

Diaphus brachycephalus. This species was caught only in nighttime samples in 200- to 0-m standard hauls. With an average size of only 28 mm SL, it was the smallest *Diaphus* species in the samples. Copepods and ostracods were the dominant prey organisms (Fig. 3). Compared to the other six myctophid species, *D. brachycephalus* preys preferably on ostracods (20%).

Lampanyctus alatus. L. alatus averaged 41 mm in size, but despite its relatively large size, feeds primarily on copepods (mean value 65%; Fig. 3). Only at the equator were 22% euphausiids found in their stomachs, the remaining prey consisting of ostracods, decapods, appendicularians, siphonophores, fish and fish scales. The advanced state of digestion of the stomach content from daytime samples of 500 to 600 m indicates that they feed predominantly during the night.

Notolychnus valdiviae. The smallest of all myctophids in our samples, *N. valdiviae* had an average SL of only 25 mm. Athough an abundant species, we collected *N. valdiviae* only at Lat. 3 °N and 2 °S. One of the richest daytime hauls from 400 to 500 m yielded 198 individuals (Table 2). As can be expected from their small size, their prey consisted of more than 90% copepods and ostracods, with only a few appendicularians and euphausiids (Fig. 3). Copepods were predominantly medium-sized, and particularly members of the genera *Candacia, Euchaeta* and *Pleuromamma* were obtained. The smallest specimen dissected (15 mm SL) was found to contain copepod prey of at least 2.9 mm total length (*Euchaeta hebes*).

Results of stomach analysis suggest that feeding is restricted to the nighttime, which also corresponds to the findings of Merrett and Roe (1974).

Copepods as prey organisms

In most mesopelagic fishes of the size order of myctophids, particularly copepods are reported as the dominant prey organisms by numbers (see Hopkins and Baird, 1977). This also holds true for myctophids from the present

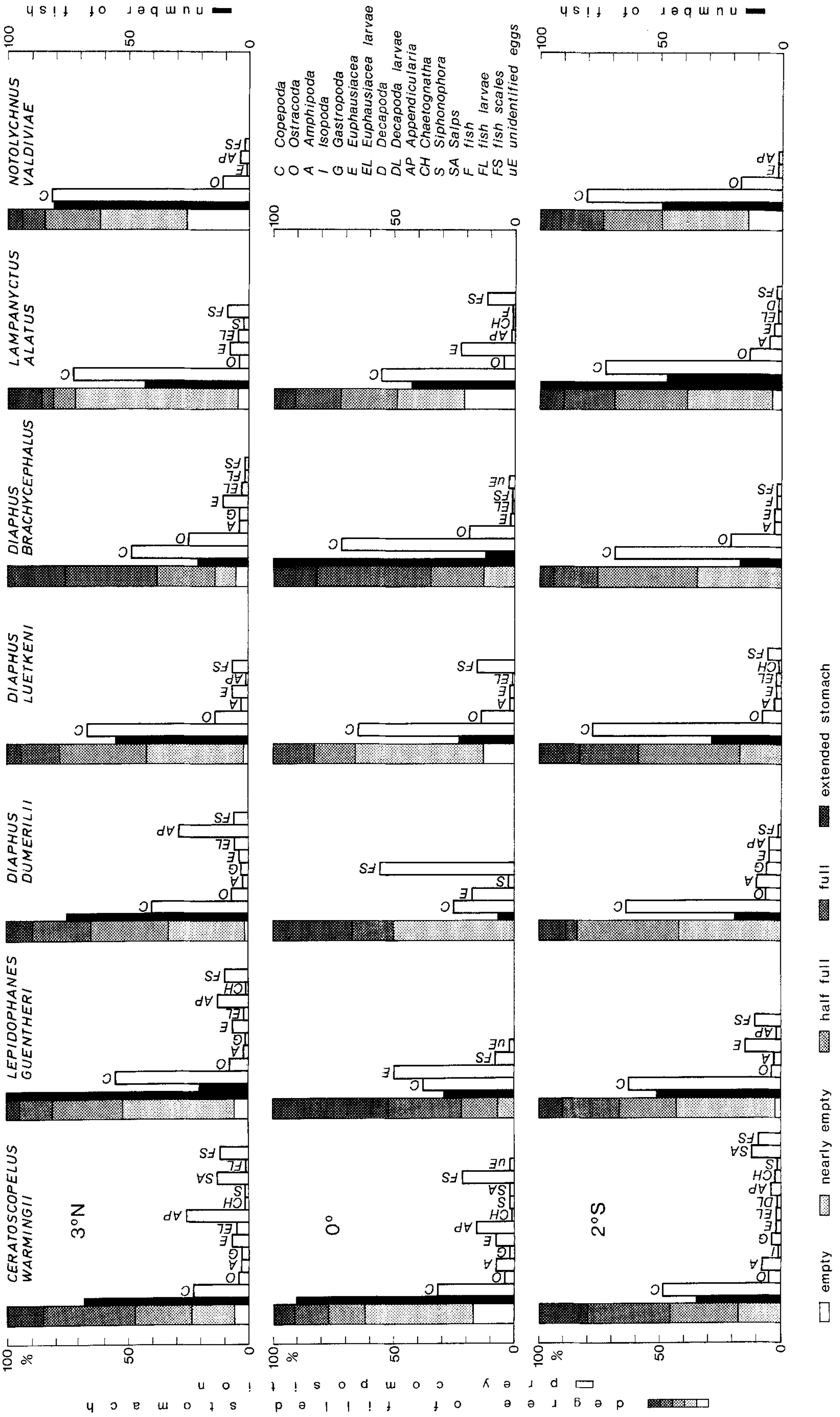

Fig. 3. Percentage of food items in stomach contents and filling stage of stomachs in seven myctophid species (nighttime samples, 0 to 200 m depth)

Table 4. Calanoid copepods in the diet of 7 species of myctophids. Values are percents of total number of calanoid prey. RV "Meteor", cruise 51, 1979, 0–200 m depth, nighttime.
o = species restricted to 0 to 150 m depth; dashes = 0%

Stomach contents Calanoida	*Notolychnus valdiviae* (10 ind., $\overline{SL}$ 17.3 mm, 17 prey)	*Ceratoscopelus warmingii* (15 ind., $\overline{SL}$ 42.4 mm, 58 prey)	*Lepidophanes guentheri* (10 ind., $\overline{SL}$ 53.5 mm, 137 prey)	*Lampanyctus alatus* (10 ind., $\overline{SL}$ 43.3 mm, 93 prey)	*Diaphus brachycephalus* (8 ind., $\overline{SL}$ 29.5 mm, 34 prey)	*Diaphus dummerilii* (11 ind., $\overline{SL}$ 47.9 mm, 102 prey)	*Diaphus luetkeni* (7 ind., $\overline{SL}$ 37.3 mm, 39 prey)	$\bar{x}$
o *Nannocalanus minor*	–	–	5.8	6.5	2.9	3.9	7.7	4.6
o *Undinula vulgaris*	5.9	6.9	4.4	9.7	–	2.9	–	4.8
Neocalanus spp.	5.9	3.4	–	2.2	11.8	13.7	–	4.8
Eucalanus spp.	–	–	0.7	2.2	–	–	–	0.6
Rhincalanus cornutus	–	1.7	1.5	1.1	–	–	–	0.8
Paracalanus aculeatus	–	–	0.7	–	–	–	–	0.2
Clausocalanus spp.	–	3.4	8.0	1.1	–	–	10.3	3.8
Aetideus spp.	–	–	0.7	2.2	–	–	7.7	
Euchirella spp.	5.9	20.7	4.4	8.6	2.9	9.8	2.6	8.1
Undeuchaeta spp.	5.9	–	0.7	–	–	2.0	2.6	
Chirundina streetsi	–	–	0.7	1.1	–	–	–	
Chiridius poppei	5.9	–	–	1.1	–	–	–	
o *Euchaeta marina*	–	10.3	9.5	7.5	–	11.8	7.7	8.5 } 15.4
Euchaeta spp.	23.5	3.4	6.6	16.1	–	2.9	–	6.9 } *Euchaeta*
Scottocalanus spp.	–	3.4	2.2	–	–	5.9	–	2.3 spp.
Lophothrix spp.	–	–	0.7	–	–	2.9	–	
o *Scolecithrix danae*	–	–	–	2.2	20.6	2.9	–	2.5
Pleuromamma spp.	11.8	15.5	19.0	4.3	–	13.7	7.7	12.1
Lucicutia spp.	5.9	1.7	2.6	1.1	–	3.9	5.1	
Heterorhabdus spp.	–	3.4	0.7	–	–	1.0	–	
Arietellus spp.	–	1.7	0.7	–	–	–	–	
o Candacia pachydactyla	–	1.7	1.4	3.2	–	3.9	–	2.1
Candacia spp.	5.9	–	3.6	5.3	14.7	2.9	–	4.0
Calanoida spp.	23.5	22.4	24.8	23.7	47.1	15.7	48.7	26.0
Mean calanoid prey items per stomach	1.7	3.9	10.5	9.3	4.3	9.3	5.6	

study. From analysis of stomach contents of 91 specimens from daytime and 71 from nighttime samples, a total of 66 calanoid copepod species have been identified. Of these, about half of the taxa consisted of large taxa (> 3 mm total length), whereas only ten species were small-sized (< 1.5 mm), suggesting some prey selection against small individuals. The smallest calanoid copepod species to fall as prey measured 0.7 mm (*Clausocalanus pergens*), the maximum size of identifiable (fresh) specimens was about 6 mm in total length (*Euchaeta gracilis*). Since stomach residues (i.e. chitinous structures) of several copepod taxa, including the genera *Undinula, Nannocalanus, Pleuromamma,* and *Candacia,* were often of diagnostic value in species identification, taxa lacking those characters might generally be underestimated in the counts and were mostly classified "Calanoida spp.".

Generally, nighttime samples yielded a higher percentage of copepod prey items that could be identified to genus or species (76%) than daylight hauls (6%). This seems clearly attributable to a different advance in digestion for both day and night.

Vertically several of the copepod species identified are restricted to the upper 150 m of the water column (see Tables 4 and 5). From nighttime samples it appears that numerically most important as myctophid prey were members of the genera *Euchaeta, Euchirella, Pleuromamma,* and *Candacia,* as well as the above-mentioned *Nannocalanus minor* and *Undinula vulgaris.*

Stomach contents of six conspecific myctophids, excluding *Diaphus brachycephalus,* were studied from daytime hauls of RRS "Discovery" with reference to their range of vertical migration (Table 5). The stomachs of

Table 5. Calanoid copepods in the diet of 6 species of myctophids. Values are percents of total number of calanoid prey. RRS "Discovery", cruise 64, 1974, various depths, daytime. o = species restricted to 0 to 150-m depth; dashes = 0%

Stomach contents Calanoida	*Notolychnus valdiviae* 400–500 m (15 ind., $\overline{SL}$ 20.2 mm, 28 prey) 1 haul	*Ceratoscopelus warmingii* 700–1 250 m) (17 ind., $\overline{SL}$ 26.5 mm, 28 prey) 5 hauls	*Lepidophanes guentheri* 500–900 m (36 ind., $\overline{SL}$ 50.1 mm, 186 prey) 9 hauls	*Lampanyctus alatus* 500–800 m (11 ind., $\overline{SL}$ 42.3 mm, 29 prey) 3 hauls	*Diaphus dumerilii* 300–500 m (4 ind., $\overline{SL}$ 46.8 mm, 17 prey) 2 hauls	*Diaphus luetkeni* 300–900 m (8 ind., $\overline{SL}$ 37.0 mm, 31 prey) 4 hauls	$\bar{x}$	
o *Nannocalanus minor*	3.6	7.1	17.7	6.7	–	19.3	13.8	*N. minor*
o *Undinula vulgaris*	3.6	10.7	13.4	6.7	28.3	–	11.6	*U. vulgaris*
Neocalanus spp.	3.6	–	1.1	–	–	–		
Eucalanus spp.	–	–	1.6	–	–	–		
Rhincalanus cornutus	–	3.6	1.6	–	5.9	3.2		
Paracalanus aculeatus	–	10.7	–	–	5.9	3.2		
Clausocalanus spp.	3.6	10.7	–	–	5.9	–		
Aetideus spp.	–	–	–	–	5.9	–		
Euchirella spp.	3.6	–	1.1	3.4	–	6.5		
Undeuchaeta spp.	7.1	–	0.5	–	–	3.2		
Chirundina streetsi	–	–	–	6.7	–	–		
o *Euchaeta marina*	–	3.6	6.5	3.4	–	–	4.1	8.5 *Euchaeta* spp.
Euchaeta spp.	10.7	–	3.2	10.3	–	3.2	4.4	
Scottocalanus spp.	–	–	–	–	–	3.2		
Lophothrix spp.	–	–	0.5	–	–	–		
o *Scolecithrix danae*	–	7.1	1.6	–	5.9	6.5		
Pleuromamma spp.	3.6	17.9	10.2	3.4	5.9	6.5	9.1	*Pleuromamma* spp.
Heterorhabdus spp.	–	–	–	3.4	–	–		
Arietellus spp.	–	–	–	3.4	–	–		
Candacia pachydactyla	7.1	–	5.4	3.4	–	–	4.1	9.1 *Candacia* spp.
Candacia spp.	14.3	–	5.4	6.7	–	–	5.0	
Calanoida spp.	39.3	28.6	30.1	41.4	29.4	48.4	33.5	
Mean calanoid prey items per stomach	1.9	1.7	5.2	2.6	4.3	3.9		

Ceratoscopelus warmingii sampled at 700 to 1 250 m contained a number of surface-restricted copepods (0 to 150 m). These include *Nannocalanus minor, Undinula vulgaris, Paracalanus aculeatus, Euchaeta marina,* and *Scolecithrix danae,* giving evidence for an extended vertical range, partly from depths below 1 000 m. Also the remaining myctophid species obviously fed substantially on these copepod taxa which are of a size range between 1.5 and 3.0 mm, except for the small species *P. aculeatus* as well as *E. marina,* which surpass 3-mm total length. Most of the other copepod taxa identified from the daytime series migrate vertically in a diel pattern within the upper 800 m.

From Tables 4 and 5 it appears that some of the differences observed in diet composition (besides differences in standard length of the predators) might be due to seasonal variations (April/July) or different years of sampling. Regarding mean copepod prey items per stomach from myctophids obtained during day or night, distinctly higher numbers were counted in the latter period, except for *Notolychnus valdiviae,* suggesting preferred nocturnal feeding in these taxa. This is also consistent with the advanced state of digestion of stomach contents as mentioned above.

Discussion

Vertical migration of juvenile and adult *Ceratoscopelus warmingii* has already been observed by Badcock and Merrett (1976) from the eastern North Atlantic, where this species was caught during the daytime at 900 to 1 500 m. Nocturnally they occurred from 25 to 200 m, predominantly at 50 to 100 m. Stomach analysis gave further proof for such a long range vertical migration. The prey showed only a few traces of digestion, and it is therefore assumed that feeding was primarily nocturnal.

Comparing the feeding patterns of the seven myctophid species described above, the diet composition seems more or less similar, with the exception of *Ceratoscopelus warmingii,* a species with a much wider food spectrum including appendicularians, salps and siphonophores. Regarding siphonophores as food of *C. warmingii,* they have also been observed by Clarke (1978, 1980) as prey organisms from samples collected in the Pacific Ocean. In samples from the Gulf of Mexico, Hopkins and Baird (1977) obtained salps and siphonophores constituting up to 25% of food items.

The food spectrum is particularly restricted in *Notolychnus valdiviae* (Fig. 3), the smallest fish species from our net samples. A preference for copepods and ostracods was also described by Merrett and Roe (1974) from the NE Atlantic (Lat. 30 °N, Long. 23 °W) and by Hopkins and Baird (1977). Regional patterns in its diet variability are indicated when comparing the stations between Lat. 2 °S and 3 °N. A later analysis of the simultaneous collected plankton samples of the RMT 1 net should possibly provide evidence with regard to prey availability in this area.

Possibly some selective feeding regarding prey size was observed in *Lampanyctus alatus.* Within an average size of only 41 mm SL, its diet consisted of 10% euphausiids, more than any other species except for the large *Lepidophanes guentheri.* Size selectivity was also observed by Hopkins and Baird (1977) in *L. alatus,* "selecting prey items particularly in between 2–4 mm, while feeding sparsely on the 0.5–0.9 mm size classes despite the latter's much greater relative abundance in surrounding waters". Merrett and Roe (1974) reported highly selective feeding in *Lampanyctus cuprarius* on amphipods.

In the Gulf of Mexico, Hopkins and Baird (1977) observed a preference for euphausiids by *Lepidophanes guentheri* in contrast to the proportional occurrence of euphausiids in the diet of the larger *Ceratoscopelus warmingii* from the same depth level (90 to 100 m). Samyshev and Schetinkin (171) described catches of *L. guentheri* from Deep Scattering Layers off NW-Africa, where euphausiids and copepods were the prevailing food items, and to some extent also decapod larvae (Brachyura). They pointed out that food uptake continued day and night due to vertical migration within the DSL, giving permanent access to their food.

Most species of myctophids are opportunistic predators feeding predominantly in a diel pattern at night. Only in more productive areas, particularly in upwelling zones such as off NW Africa, was continuous feeding during the day observed. This is evident in *Benthosema glaciale* and some other species (Kinzer, 1977, 1982) and in *Diaphus dumerilii* and *Lepidophanes guentheri* (Samyshev and Schetinkin, 1971). *Ceratoscopelus warmingii* from the central Pacific feeds on plankton at night, but takes larger prey, such as *Cyclothone* spp., whenever encountered during the day (Clarke, 1978, 1980).

Large amounts of fish scales, up to 20% of stomach content, were found in *Diaphus dumerilii,* and to a lesser extent in *Lepidophanes guentheri, Lampanyctus alatus, Ceratoscopelus warmingii* and *D. luetkeni.* In areas of upwelling off NW Africa, Kinzer (1982) analysed the scales to originate mostly from myctophids. In *D. holti* the relative abundance of fish scales per food item ranked as high as 50%. Wörner (1975) found fish scales in the stomachs of *Ceratoscopelus maderensis* and *Myctophum punctatum* from neuston net samples. Off NW-Africa *D. holti* collected during the daytime had fed on various crustacean species, but stomachs never contained any fish scales (Kinzer, 1982). It seems probable that they have been mistaken for prey organisms in the dark. Fish scales have been sampled from water bottles quite abundantly from 17 to 83 m^{-3} at 7- to 15-m depths of the Gulf of Mexico (Hopkins and Baird, 1975). In a recent contribution by Sazima (1983), the author has compiled scale-eating habits of a large number of both freshwater and marine fish species, with a few of the taxa feeding predominantly on scales. It was observed that the scales are removed from the body of the fish by attack, but in some lepidophagous fish the scales are gathered as they sink or are collected from the substrate (Sazima, 1983). Whitfield and Blaber (1978) described the marine teleost *Terapon jarbua* (Forsskål) as digesting fish scales, which have a relatively high energy content of 2 cal mg^{-1}. Van Oosten (1957) reported fish scales to consist of 40 to 85% protein, however, their nutritive value has not yet been investigated.

Acknowledgements. We thank J. R. Badcock, Institute of Oceanographic Sciences, Wormley, UK for kindly providing us with the samples of myctophids of the RRS "Discovery" cruise 64, 1974. Our special thanks to Ms. K. Beldzik, Institut für Meereskunde, for dissecting the stomachs, presorting its prey organisms and preparing the drawings. We also wish to thank Dr. N. Merrett, Institute of Oceanographic Sciences, UK, who read the manuscript and provided helpful suggestions and criticisms. This contribution was supported by the German Research Council (DFG).

Literature cited

Backus, R. H., J. E. Craddock, R. L. Haedrich, D. L. Shores, J. M. Teal, A. S. Wing, G. W. Mead and W. D. Clark: *Ceratoscopelus maderensis:* peculiar sound-scattering layer identified with this myctophid fish. Science, N.Y. *160,* 991–993 (1968)

Badcock, J.: The vertical distribution of mesopelagic fishes collected on the SOND cruise. J. mar. biol. Ass. UK *50,* 1 001–1 044 (1970)

Badcock, J. and N. R. Merrett: Midwater fishes in the eastern North Atlantic. – I. Vertical distribution and associated biology in 30°N, 23°W, with developmental notes on certain myctophids. Prog. Oceanogr. *7,* 3–58 (1976)

Baird, R. C., D. F. Wilson, R. C. Beckett and T. L. Hopkins: *Diaphus taaningi* Norman, the principle component of a shallow sound-scattering layer in the Carioca Trench, Venezuela. J. mar. Res. *32*, 301–312 (1974)

Baker, A. de C., M. R. Clarke and M. J. Harris: The NIO combination net (RMT 1+8) and further developments of rectangular midwater trawls. J. mar. biol. Ass. U.K. *53*, 167–184 (1973)

Bauerfeind, E., C. Brockmann, E. Fahrbach, J. Meincke, H.-J. Panitz, G. Rohardt and A. Sy: A compendium of the oceanographic data obtained during "FGGE-Equator '79", cruise No. 51 of RV "METEOR". "Meteor"-Forsch. Ergebn., Reihe A/B, *25*, 1–108 (1984)

Clarke, T. A.: Diel feeding patterns of 16 species of mesopelagic fishes from Hawaiian waters. Fish. Bull., U.S. *76*, 495–513 (1978)

Clarke, T. A.: Diets of fourteen species of vertically migrating mesopelagic fishes in Hawaiian waters. Fish. Bull. U.S. *78*, 619–640 (1980)

Farquhar, G. B.: Biological sound scattering in the oceans: a review. *In:* Oceanic sound scattering prediction, pp 493–528. Ed. by W. R. Anderson and B. J. Zahuranec. New York: Plenum Press 1977

Frost, B. W. and L. E. McCrone: Vertical distribution, diel vertical migration, and abundance of some mesopelagic fishes in the eastern subarctic Pacific Ocean in summer. Fish. Bull., U.S. *76*, 751–770 (1979)

Hopkins, T. L. and R. C. Baird: Net feeding in mesopelagic fishes. Fish. Bull, U.S. *73*, 908–914 (1975)

Hopkins, T. L. and R. C. Baird: Aspects of the feeding ecology of oceanic midwater fishes. *In:* Oceanic sound scattering prediction, pp 325–360. Ed. by W. R. Anderson and B. J. Zahuranec. New York: Plenum Press 1977

Hulley, P. A.: Results of the research cruises of FRV "Walther Herwig" to South America. LVIII. Family Myctophidae (Osteichthyes, Myctophiformes). Arch. Fisch. Wiss. *31*, 1–300 (1981)

Kinzer, J.: Observations on feeding habits of the mesopelagic fish *Benthosema glaciale* (Myctophidae) off NW Africa. *In:* Oceanic sound scattering prediction, pp 381–392. Ed. by W. R. Anderson and B. J. Zahuranec. New York: Plenum Press 1977

Kinzer, J.: The food of four myctophid fish species off Northwest Africa. Rapp. P.-v. Réun. Cons. int. Explor. Mer *180*, 378–383 (1982)

Marshall, N. B.: Bathypelagic fishes as sound scatterers in the ocean. J. mar. Res. *10*, 1–17 (1951)

Marshall, N. B.: Swimbladder structure of deep-sea fishes in relation to their systematics and biology. Discovery Rep. *31*, 1–122 (1960)

Merrett, N. R. and H. S. J. Roe: Patterns and selectivity in the feeding of certain mesopelagic fishes. Mar. Biol. *28*, 115–126 (1974)

Nafpaktitis, B. G., R. H. Backus, J. E. Craddock, R. L. Haedrich, B. H. Robison and C. Karnella: Order Iniomi (Myctiphormes). *In:* Fishes of the Western North Atlantic, Part 7, 299 pp. Ed.-in-Chief Gibbs. New Haven: Allen Press 1977

Pearcy, W. G. and R. M. Laurs: Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-Sea Res. *13*, 153–166 (1966)

Pearcy, W. G., E. E. Krygier, R. Mesecar and F. Ramsey: Vertical distribution and migration of oceanic micronekton off Oregon. Deep Sea Res. *24*, 223–245 (1977)

Roe, H. S. J. and J. Badcock: The diel migrations and distributions within a mesopelagic community in the north-east Atlantic. 5. Vertical migrations and feeding of fish. Prog. Oceanogr. *13*, 389–424 (1984)

Samyshev, E. Z. and S. V. Schetinkin: Feeding patterns of some species of Myctophidae and *Maurolicus muelleri* caught in the sound-dispersing layers in the north-western African area. Ann. Biol. Cons. int. Explor. Mer *28*, 212–214 (1971)

Sazima, I.: Scale eating in characoids and other fishes. Environ. Biol. Fishes *9*, 87–101 (1983)

Van Oosten: The skin and scales. *In:* The physiology of fishes, pp 207–224. Ed. by M. E. Brown. New York: Academic Press 1957

Whitfield, A. K. and S. J. M. Blaber: Scale-eating habits of the marine teleost *Terapon jarbua* (Forskal). J. Fish Biol. *12*, 61–70 (1978)

Willis, J. M. and W. G. Pearcy: Vertical distribution and migration of fishes of the lower mesopelagic zone off Oregon. Mar. Biol. *70*, 87–98 (1982)

Wörner, F. G.: Untersuchungen an drei Myctophiden-Arten *Benthosema glaciale* (Reinhardt, 1837), *Ceratoscopelus maderensis* (Lowe, 1839) und *Myctophum (M.) punctatum* Rafinesque 1810, aus dem nordwestafrikanischen Auftriebsgebiet im Frühjahr 1972. Diss., Univ. Kiel, 1975

Date of final manuscript acceptance: January 22, 1985.
Communicated by O. Kinne, Oldendorf/Luhe