Flødevigen rapportser. 1, 1988. ISSN 0333-2594

SOME ASPECTS OF THE FEEDING ECOLOGY OF MYCTOPHIDS IN THE WATERS OFF CENTRAL EAST AFRICA

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ABSTRACT

Alwis, A. de and Gjøsæter, J. 1988. Some aspects of the feeding ecology of myctophids in the waters off Central East Africa. Flødevigen rapportser. 1, 1988: 17-53.

Analyses of the degree of filling and the state of digestion of four species (*Diaphus watasei, Benthosema fibulatum, Myctophum brachygnatum* and *Diaphus garmani*) revealed that all but *D. watasei* were cyclic feeders feeding at or near the surface during the night. *Diaphus wataswe* was an acyclic feeder feeding close to the bottom.

Prey analysis of 14 myctophid species showed that crustacea, mainly copepods, was the main food. Molluscs and bivalve larvae, larvaceans and salps, chaetognaths and polychaetes were also eaten. For *Diaphus watasei*, euphasiids, squids (family Onychoteuthidae), fish and fish larvae (family Myctophidae), contributed a great deal.

All but three species were opportunistic feeders. *Diaphus nielseni, Diaphus jenseni* (both feeding specifically on copepods) and *Myctophum brachygnatum* (feeding specifically on molluscs and bivalve larvae) were selective feeders.

The myctophids showed food partitioning by feeding at different depths, on selected sizes and selected taxa. Ontogenetical resource partitioning was also observed. They were visually oriented predators and the maximum prey size seemed to be determined by the size of the jaw. They seemed to catch individual prey items and swallow them whole.

INTRODUCTION

The mesopelagic zone is inhabited by a fish fauna with high species diversity and also often a surprisingly high biomass (Clark 1978, Gjøsæter and Kawaguchi 1980). In recent years, research on different aspects of the feeding ecology of mesopelagic fish has been carried out to see how the fish manage such a successful survival in this habitat where food is rather scarce.

Diel vertical migration of myctophids and other mesopelagic fishes has been well documented (i.e. Badcock 1970, Badcock and Merrett 1976). It is also reported that most of the fishes are nocturnal feeders feeding in the epipelagic zone (Holton 1969, Gjøsæter 1973, Merrett and Roe 1974, Clark 1978, Gorelova 1974, 1978).

Many mesopelagic fishes seem to be opportunistic feeders, feeding on any prey of suitable size. This is obviously an advantageous habit in a food poor environment (Hartmann and Weikert 1969, Merrett and Roe 1974). Zooplankton is reported to be the most common prey, of which crustaceans play the most imortant role (Collard 1970, Nakamura 1970, Clarke 1973, Gorelova 1974, Hopkins and Baird 1973).

Mesopelagic fish seem to reduce competition by partitioning the food among themselves in several ways. Some species are selective feeders, preferring a specific prey type or size disproportionate to the abundance of prey items in the environment (Samyshev and Schetinkin 1973, Hopkins and Baird 1973). More opportunistic species may minimize competition by feeding at different depths and by showing ontogenetical differences where larger fish take larger prey than do the smaller fish (Marshall 1954, Clarke 1973, 1978, Hopkins and Baird 1973, Merrett and Roe 1974, Tyler and Pearcy 1975).

It is believed that myctophids are visual feeders (Hopkins and Baird 1973, Clarke 1980). Observations have also been made that the minimum and maximum prey sizes of these fishes are determined by gill-raker distances and jaw-sizes respectively (Samyshev and Schetinkin 1973, Ebeling and Cailliet 1974, Clarke 1980). Clarke (1980) found that the diet of myctophids was related to morphological features of the species, especially lens diameter and gill raker spaces.

Myctophid species obtained by R/V "Dr. Fridtjof Nansen" from the Kenya/Tanzania area in 1982 was used in the present paper to study some aspects of the feeding ecology of the mesopelagic fish fauna. The aspects looked into were the diet composition and daily ratio, feeding periodicity, resource partitioning and the importance of different morphological characters in feeding.

MATERIALS

The materials for this study were collected by R/V "Dr. Fridtjof Nansen" along the Tanzanian coast between 5° and 10°S during June-July and November-December, 1982, and off Kenya between 2° and 3°S during November-December, 1982. Sampling was made with a pelagic fish trawl with an opening of about 40x15 m, and with a shrimp trawl with an opening of about 40x6 m. In both trawls the mesh size in the cod end was about 20 mm (stretched mesh). Details of the sampling stations are given in Appendices 1 and 2. More details of the research vessel and the equipment used and the sampling procedure are given in Iversen et al. (1984).

Random samples of the myctophids were preserved in 5% formaldehyde after capture and were brought to the Department of Fisheries Biology of the University of Bergen, Norway, where the identification and further studies of stomach content analyses were carried out.

A total of 1385 fish of the family Myctophidae were investigated. These fish consisted of seven genera: *Diaphus* (6 species: *D. nielseni, D. jenseni, D. watasei, D. thiollierei, D. perspicillatus* and *D. garmani*), *Benthosema* (3 species: *B. pterotum, B. fibulatum, B. suborbitale*), *Myctophum* (2 species: *M. brachygnatum, M. obtusirostrum*), *Symbolophorus* (1 species: *S. evermanni*), *Triphotorus* (1 species: *T.microchir*), *Ceratoscopelus* (1 species: *C. warmingi*) and *Lampanyctus* (1 species: not identified to the species).

METHODS

Fishes were rinsed with fresh water. The standard length of each fish was measured to the nearest millimeter and the stomach (anterior end of the exophagus to the pyloric constriction) was removed and placed in a small petri dish. The stomach was carefully opened using a dissecting blade and a pair of forceps, under a binocular dissecting microscope and the con-tents were placed in a few drops of water. The opened stomach was flushed with fresh water to ensure that all the adhering materials went into the petri dish. The presence or absence of prey items in the mouth and the forepart of the oesophagus was recorded but was not included in the data. The contents in the petri dish were separated carefully and were examined under a binocular microscope and measured to the neares 0.1 mm using an ocular meter. Most prey items were identified only to major taxa (usually order). Fish, fish larvae, squids and octopods were identified to their family. The following measurements were used for the prey items: copepods - prosome length, ostracods, amphipods - maximum carapace length, fish - standard length, all other prey - total length.

The degree of stomach filling was determined according to the following scale:

Degree of filling		Description
0.	Empty	Empty
I.	Little or some content	Up to about 30% filling
II.	Half full	Approx. 30-70% filling
III.	Full	Approx. 70-100% filling, but stomach wall retained its normal thickness

The state of digestion of the stomach contents was determined using the scale:

State of digestion		Description
I.	Newly ingested	Almost all items show no digestion or very slight digestion.
II.	Slightly digested	The stomach contents uniformly lightly digested or less than approx. 30% of contents is partly digested, the rest little or not digested.
III.	Partly digested	The stomach contents uniformly partly digested but still recognizable or about 30-70% of the content is much digested, the rest little or not digested.
IV.	Much digested	All or most of the contents are much digested and not in an identifiable state.

To analyse the difference in diet between species and between samples a log-likelihood ratio test was used as described by Crow (1982).

The diversity of the stomach contents was estimated using Shannon's diversity index (Zar 1974):

$$H = \frac{n \log n - \sum_{i=1}^{k} f_i \log f_i}{n}$$

where K is the number of categories
n is the sample size
f_i is the number of observations in category i.

The dry weight of the stomach contents and of the fish was obtained by drying at 80°C to a constant weight (1-2 days for stomach contents and 2-7 days for the fish). The major prey groups were dried separately, while the rest were taken together.

Daily ratio was estimated for four species (*Diaphus watasei, D. garmani, Brenthosema fibulatum* and *Myctophus brachygnatum*) which had more than 10 full stomachs. The method given in Gorelova (1983) was used:

$$\frac{R_d}{W} = \frac{Y_t}{Y_m} \cdot \frac{12Y}{T} \cdot 100$$

R_d - quantity of food consumed by the fish in a day (mg)
Y - mean stomach filling index of all fish
Y_m - mean filling index for all fish with predominant freshly swallowed prey items (here taken as fish with half full or full stomach)
Y_f - mean filling index for the fish with stomach contents
W - average weight of fish (mg)
T - digesting time

Filling indices were calculated as the ratio of dry weight of the stomach contents (mg) to the dry weight of fish. Time of digestion was calculated using the formulas of Tseitlin (1980):

$$T = 84.1\ W^{0.31}\ Y_m^{0.31}\ \exp. 0.0806\ (20 - t)$$

t - average temperature of the environment (t was taken as 22°C)
W - average weight of fish (gm)

For *D. watasei* staying in colder water than the other species the following formula was used:

$$T = 57.9\ W^{0.182}\ Y^{0.62}\ \exp.\ 0.0806\ (20 - t)$$

t - used in these calculations was 18°C.

To investigate the relationship between morphological characters and feeding pattern, the methods given by Clarke (1980) were followed. Four morphological characters were examined.

1. The pre-maxillary length was taken as a measure of gape because direct measurement of the size of gape is difficult to obtain without knowing the angle to which the mouth is opened while feeding.

2. The diameter of lens was taken as a measure of visual ability.

3. The average distance between gill-rakers on the lower branch of the first arch was taken as a measure of minimum particle size.

These three morphological characters were expressed as linear functions of standard lengths determined by least square regression (Fig. 1-3.

4. Lengths of the raker bearing segments of the firsh arch and the length of the gill-raker at the joint between the upper and lower branches of the arch were taken assuming that the product of these measurements is proportional to the filtering area of the gill-raker. This area was expressed by linear regression of its logarithms to standard length (Fig. 4).

All measurements were made to the nearest 0.1 mm. Pre-maxillary lengths were measured using a vernier caliper and the others using an ocular meter.

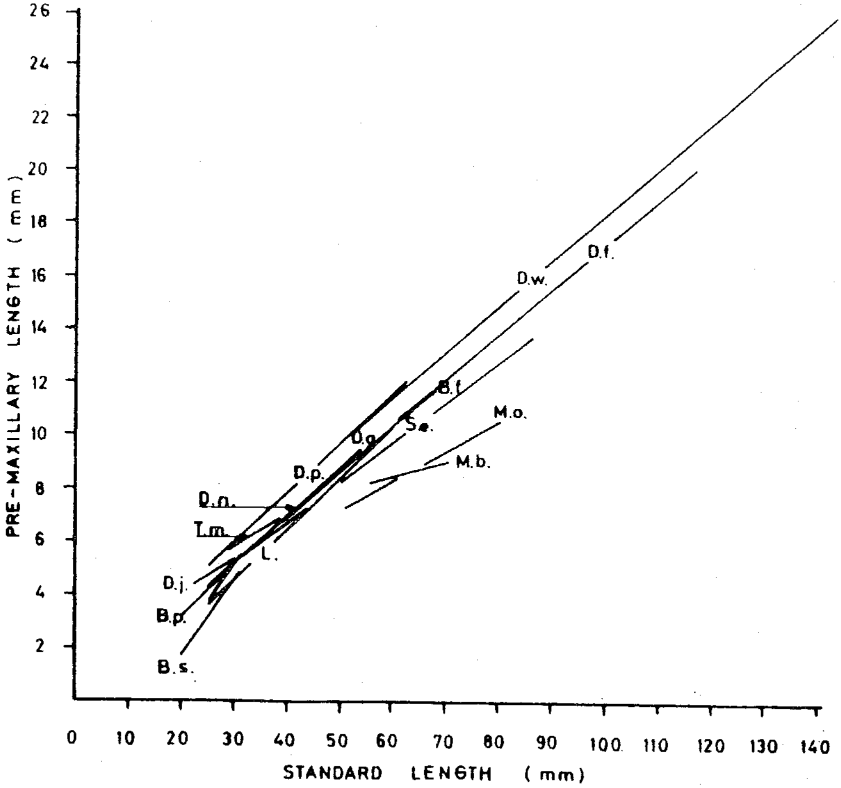


Fig. 1. Relationship between standard length and pre-maxillary length for 14 myctophids. Lines are drawn from equations determined by least square regression. Coefficients of determination (r^2) exceeded 0.8 for all but *D. jenseni* (0.68), *B. fibulatum* (0.34), *D. nielseni* (0.73) and *M. brachygnatum* (0.38). Abbreviations stand for the genus and species name as given below and the number of fish studied from each species is given in parentheses.

D.n. - Diaphus nielseni (40)
D.j. - Diaphus jenseni (40)
D.w. - Diaphus watasei (330)
D.t. - Diaphus thiollierei (81)
D.p. - Diaphus perspicillatus (40)
D.g. - Diaphus garmani (209)
P.p. - Benthosema pterotum (52)
B.f. - Benthosema fibulatum (166)
B.s. - Benthosema suborbitale (36)
M.b. - Myctophum brachygnatum (131)
M.o. - Myctophum obtusirostrum (43)
S.e. - Symbolophorus evermanni (86)
T.m. - Triphoturus microchir (31)
L. - Lampanyctus sp. (57)

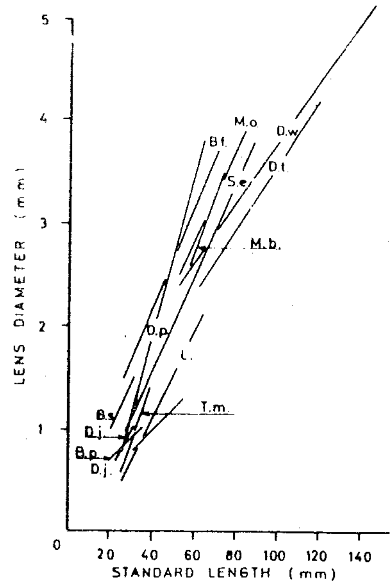


Fig. 2. Relationship between standard length and lens diameter for 14 myctophids. Lines are drawn from equations determined by least square regression. Coefficients of determination (r^2) exceeded 0.8 for all but *D. garmani* (0.64), *M. brachygnatum* (0.67) and *D. thiollierei* (0.73). Names of fish species and the number studied are as in Fig. 1.

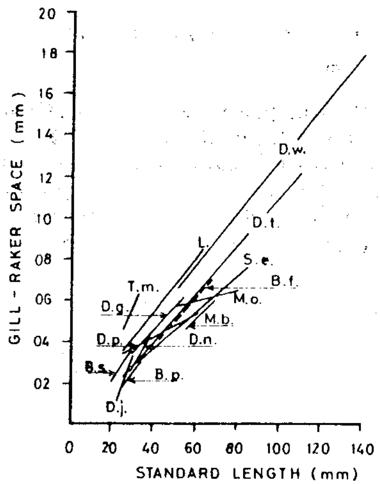


Fig. 3. Relationship between standard length and gill-raker space for 14 myctophids. Lines are drawn from equations determined by least square regression. Coefficients of determination (r^2) exceeded 0.8 for all but *D. garmani* (0.45), *T. microchir* (0.67), *D. nielseni* (0.69), *B. suborbitale* (0.66), *M. brachygnatum* (0.4) and *M. obtusirostrum* (0.23). Names of fish species and the number studied are as in Fig. 1.

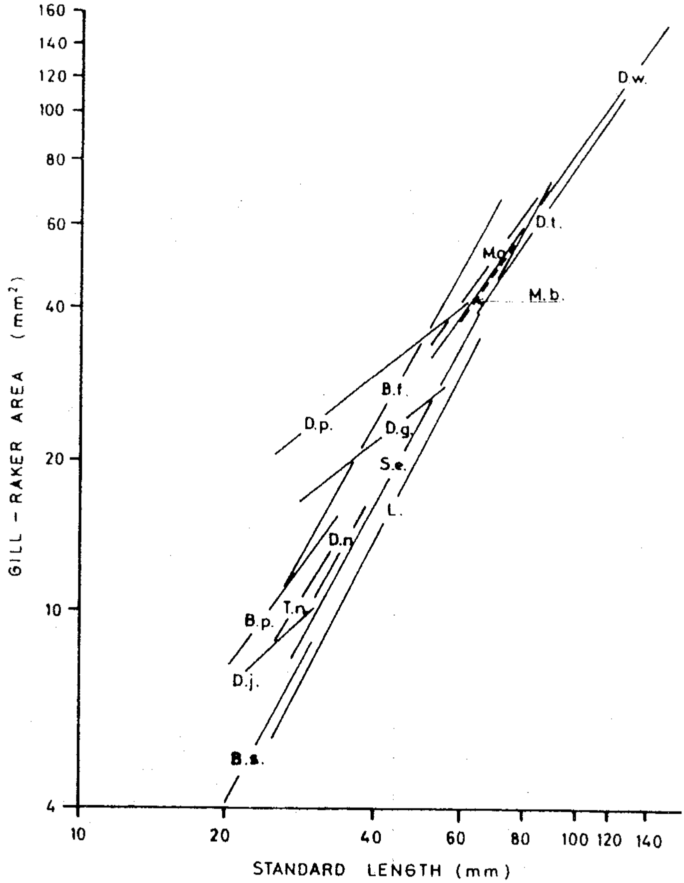


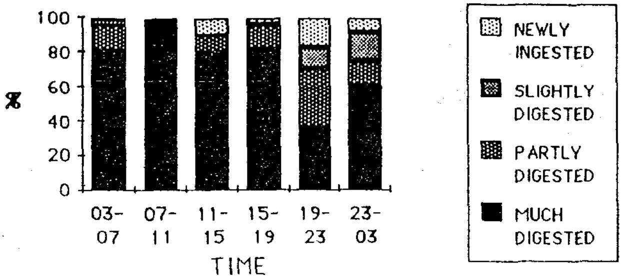
Fig. 4. Relationship between standard length and gill-raker area (On logarithmic scale) for 14 myctophids. Lines are drawn from equations determined by least square regression of the logarithms of the data. Coefficients of determination (r^2) exceeded 0.8 for all but *D. garmani* (0.34) and *T. microchir* (0.26). Names of fish species and the number studied are as in Fig. 1.

RESULTS

Diaphus watasei

This species was the largest of all the 15 species studied (size range 50-140 mm). Pre-maxillary lengths (9.9-26.1 mm) and gill-raker distances (0.66-1.8 mm) were large while lens diameters (2.4-5.2 mm) and gill-raker areas (31.62-154.88 mm^2) were average compared ot those of the other species (Fig. 1-4).

D. watasei seem to have fed during both night and day as newly ingested food was observed throughout the diel cycle (Fig. 5). The highest percentage of newly ingested prey items was found between 1900-2300 h indicating that the fish apparently fed most intensively before midnight. The degree of stomach filling did not vary much over the diel period.



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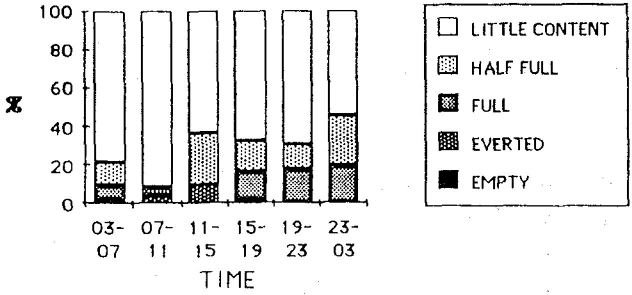

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Fig. 5. Degree of stomach filling (a) and state of digestion (b) for *Diaphus watasei*.

Their prey consisted of crustaceans (copepods, euphausiids, crustacean larvae, decapod shrimp, amphipods, ostracods), molluscs, squids and octopods, fish and fish larvae (Fig. 6). For this species, copepods were only important for the smallest specimens. Euphausiids, squids, fish and fish larva were eaten frequently. All squids were identified as members of the family Onychoteuthidae and all octopods were from the amily Octo-

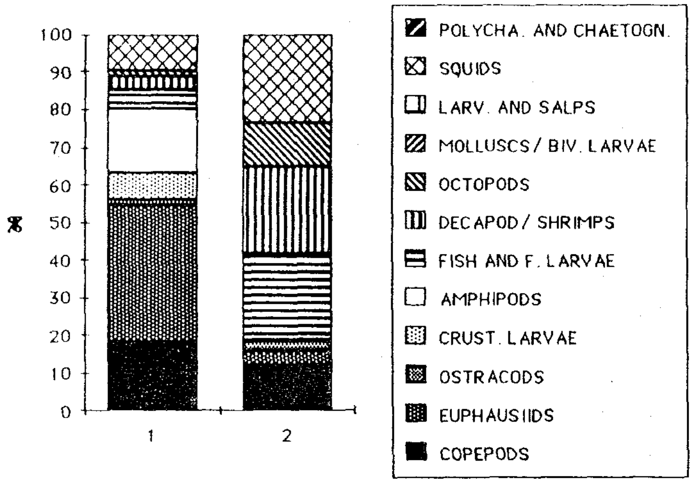


Fig. 6. Percentage composition of prey items in *Diaphus watasei* at two different seasons. Symbols for prey, 1) June-July, 2) November-December.

podidae. All fish and fish larvae were of the family Myctophidae. *D. watasei* showed a high prey species diversity (Shannon's diversity H=0.86) (Table 1).

The diet varied with the season and the variation was significant for major prey items (Table 2). During June/July, euphausiids and ampipods were the two main components in the diet while in November/December, squids, fish and fish larvae, decapod shrimp and octopods played a main role.

Fish taken at different depths also showed a variation in diet composition (Fig. 7). The most important difference was the presence of amphipods and the absence of squids and octopods in the stomach of fish taken from 101-150 m depth range. The main contribution at 401-450 m depth range was squid, whereas it was less important at other depths.

For fish of size 51-80 mm copepods were important (Fig. 8). Fish above this size range apparently did not feed on copepods at all while they had mostly fed on bigger prey items such as fish, squids and euphausiids (Fig. 8).

Table 1

Daily ratio and time of digestion (For explanation see text).

Species	Length group (mm)	Y_m / Y_f	Time of food digestion (hours)	Average weight of fish (g)	Daily ratio (% of body weight) For fish feeding at 1 - 100 m	For fish feeding at >100 m
M. brachygnatum	51-60	1.00	4	0.795	2.64	
	61-70	1.10	5	0.898	2.90	
B. fibulatum	51-60	1.40	4	0.545	3.78	
D. garmani	31-40	1.09	4.72	0.173	5.49	
	41-50	1.10	5.67	0.239	6.21	
D. watasei	71-80	1.42	6.20	1.220		3.98
	91-100	1.14	8.40	3.027		3.76
	101-110	1.18	9.13	4.156		3.46
	111-120	1.53	13.54	6.530		3.79
	121-130	1.38	11.25	9.100		3.09

Table 2

Relationships of morphological characters, feeding selectivity, Shannon's diversity index and sizes of food items in different fish species.

Species	Size range of fish (mm)	Size of prey items Min. (mm)	Max. (mm)	Type of feeding index (H)	Shannon's diversity
D. watasei	50-140	0.60	60	n-s	0.86
C. warmingi	28-60	0.40	30	n-s	0.75
S. evermanni	25-87	1.60	20	n-s	0.45
M. brachygnatum	55-70	0.40	20	s	0.34
D. garmani	30-53	0.40	18	n-s	0.64
D. thiollierei	60-110	0.80	17	n-s	0.65
Lampanyctus sp.	25-62	0.40	15	n-s	0.32
B. fibulatum	25-67	0.40	12	n-s	0.52
D. perspicillatus	25-60	0.40	12	n-s	0.32
B. suborbitale	20-30	0.40	10	n-s	0.47
M. obtusirostrum	50-80	0.40	10	n-s	0.62
D. jenseni	22-30	0.40	2.75	s	n c
D. nielseni	30-38	0.40	2.25	s	0.02
I. microchir	25-32	0.40	1.80	n-s	0.23
B. pterotum	25-33	0.40	1.60	n-s	0.41

Species	Range of lens diam. (mm)		Range of pre-maxil. length (mm)		Range of gill-raker distance (mm)		Range of gill-raker area (mm)	
	min.	max.	min.	max.	min.	max.	min.	max.
D. watasei	2.40	5.20	9.90	26.10	0.66	1.80	31.62	154.88
C. warmingi	not measured		not measured		not measured		not measured	
S. evermanni	1.0	3.80	4.80	13.80	0.25	0.75	8.13	72.44
M. brachygnatum	2.60	3.50	8.30	9.10	0.46	0.60	38.02	57.70
D. garmani	0.80	1.30	4.80	9.50	0.34	0.60	16.59	28.18
D. thiollierei	2.40	4.20	10.70	20.30	0.62	1.22	38.02	109.65
Lampanyctus sp.	0.60	2.10	3.70	10.90	0.35	0.85	5.49	35.48
B. fibulatum	1.50	3.70	4.40	11.80	0.22	0.70	10.72	67.61
D. perspicillatus	0.80	3.80	5.20	11.80	0.33	0.53	20.42	42.66
B. suborbitale	1.00	1.50	1.70	4.70	0.21	0.37	4.07	8.71
M. obtusirostrum	2.50	3.90	7.30	10.70	0.57	0.64	33.88	69.18
D. jenseni	0.70	1.02	4.40	5.40	0.10	0.33	7.59	10.23
D. nielseni	1.00	1.40	5.90	6.90	0.28	0.42	10.72	16.60
I. microchir	0.50	1.00	3.80	5.80	0.46	0.63	8.70	13.18
B. pterotum	0.70	1.00	3.20	5.90	0.18	0.30	20.42	42.66

n-s = non-selective, s = selective, n c = not calculated

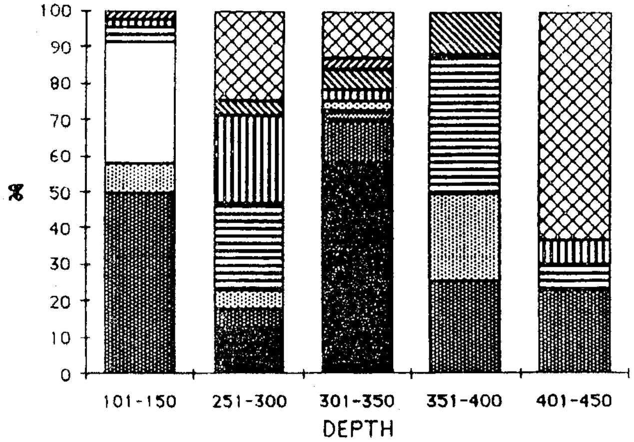


Fig. 7. Percentage composition of prey items in *Diaphus watasei* at different depths. Symbols for prey items as in Fig. 6.

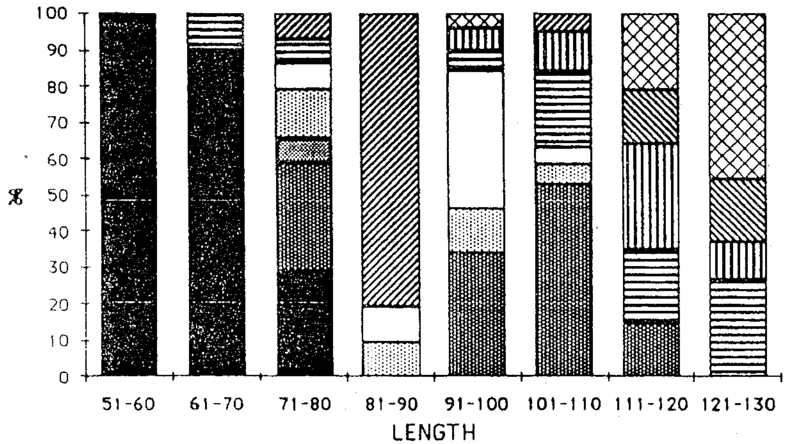


Fig. 8. Percentage composition of prey items in different length groups of *Diaphus watasei*. Symbols for prey items as in Fig. 6.

D. watasei took larger prey items than any of the other species (Fig. 9). Mean length of copepods showed an increasing trend with the increasing fish size and so did the euphausiids (Fig. 10, 11). All length groups of *D. watasei* had taken larger euphausiids than similar length groups of other fish species.

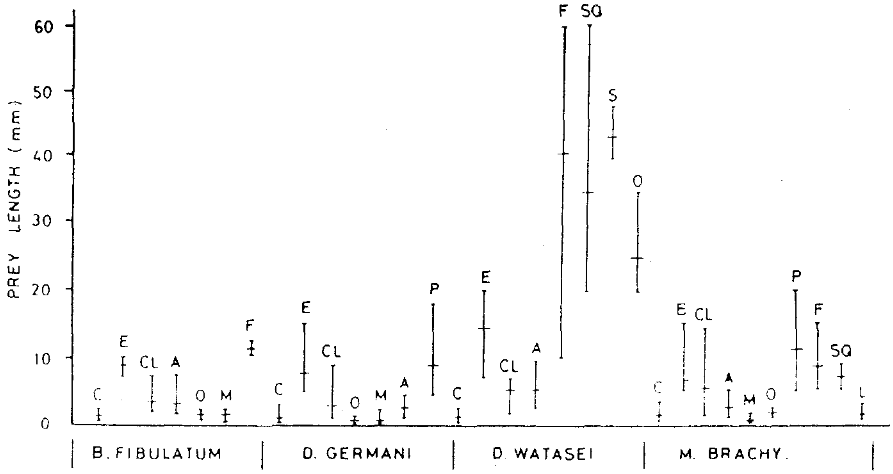


Fig. 9. Length ranges (vertical line) and mean lengths (horizontal bars) of various prey items found in the stomachs of different myctophid species. Abbreviation on top of vertical lines for prey items stand for: C - copepods, E - euphausiids, M - molluscs and bivalve larvae, CL - crustacean larvae, A - amphipods, F - fish and fish larvae, O - ostracods, SQ - squids, S - shrimps, L - larvaceans and salps.

Estimated time of food digestion for these fishes varied from 6-14 h depending on the size group (Table 1). The daily ratio was estimated to be between 3% and 4% of the body weight for all size groups.

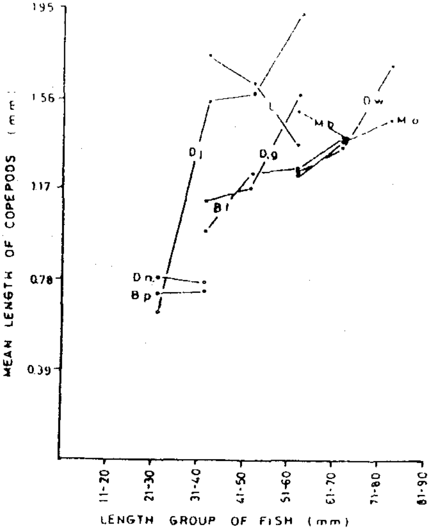


Fig. 10. Relationship between mean length of copepods and the length of fish for different fish species. Abbreviations for different fish species as in Fig. 1

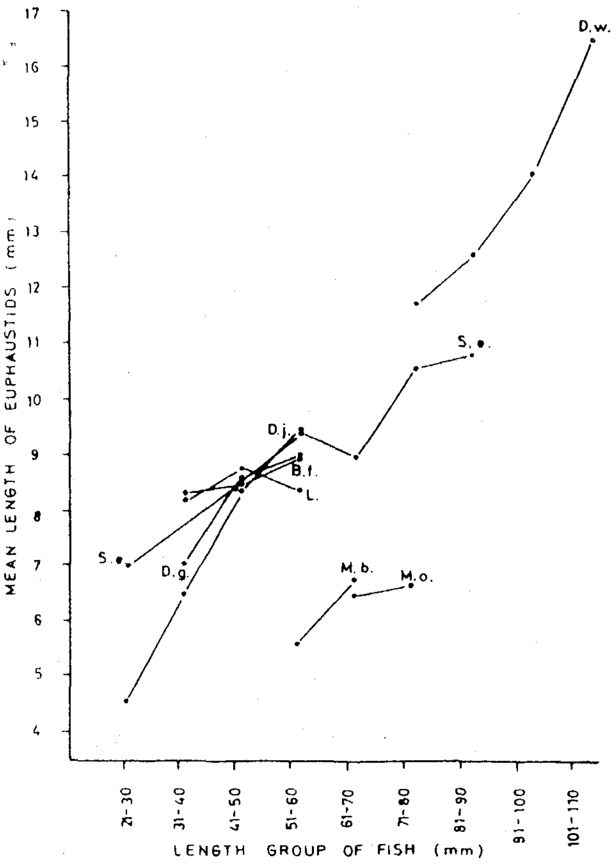
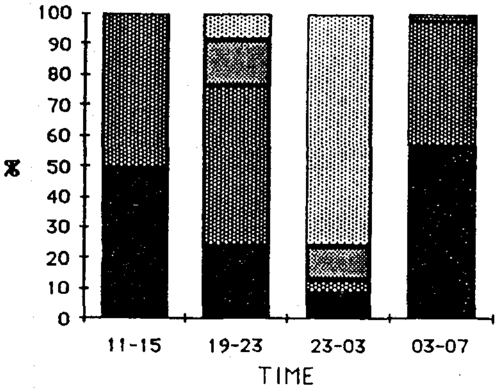


Fig. 11. Relationship between mean length of eupahusiids and the length of fish for different fish species. Abbreviations for different fish species as in Fig. 1.

Diaphus garmani

The size range of this species was between 30-53 mm. Pre-maxillary sizes (4.8-9.5 mm), gill-raker areas (16.6-28.2 mm^2) and gill-raker distances (0.3-0.6 mm) were average while the lens diameters were comparatively small (0.8-1.3 mm) (Fig. 1-4).

Newly ingested food items were found at 1900-2300 and 2300-0300 h with the highest percentage during the latter period (Fig. 12). The percentage of half full and full stomachs also increased during this period.



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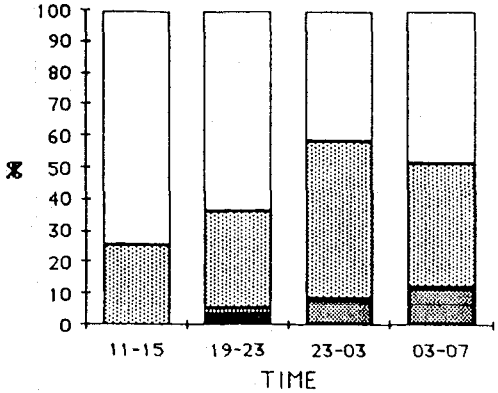

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Fig. 12. Degree of stomach filling (a) and state of digestion (b) for *diaphus garmani*.

No newly ingested food items were found in 0300-0700 and 1100-1500 hr samples and most of the stomach contents were partly or much digested.

This species seems to have fed on a wide range of crustaceans (copepods, crustacean larvae, euphausiids, amphipods, ostracods) and other prey items like molluscs, bivalve larvae, fish and fish larvae (of family Myctophidae), larvaceans and salps, chaetognaths and polychaetes. Nearly 40% of the total prey items were copepods and the contribution by ostracods was also considerable (32%) (Fig. 13). This species showed a

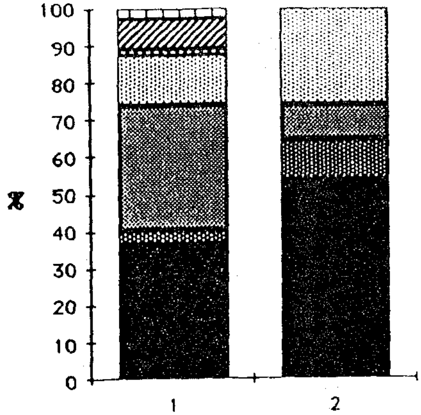


Fig. 13. Percentage composition of prey items in *Diaphus garmani* at two different seasons. 1) June July, 2) November-December.

high prey species diversity (Table 2) and a significant difference in the diet from that of the other three main species (Table 1). *D. garmani* showed a statistically significant seasonal variation in the diet (Fig 13 and Table 2). Stomach contents also differed with different depths (Fig. 14).

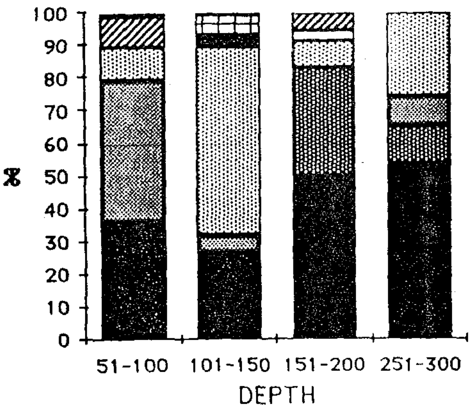


Fig. 14. Percentage composition of prey items in *Diaphus garmani* at different depths. Symbols as in Fig. 6.

The size range of the prey was average.

The ontogenetical difference shown by this fish species was similar to *Diaphus watasei*. They were found to ingest more large organisms such as

Table 3

Contingency tables for three Myctophid species to compare their principal forage items during two seasons.

D. watasei

Prey	Season I	II	Ni	Gi
Euphausiids	34	1	35	17.34
Squids	10	7	17	1.0
Fish/fish larvae	4	7	11	5.38
Decapod shrimps	4	7	11	5.38
Nj	52	22	74=N	
Gj	7.92	21.18		29.10

B. fibulatum

Copepods	140	86	22.6	6.57
Euphausiids	8	4	12	0.05
Crustacean larvae	51	4	55	17.42
Amphipods	22	1	23	9.91
Nj	221	95	316=N	
Gj	7.81	26.14		33.9

D. garmani

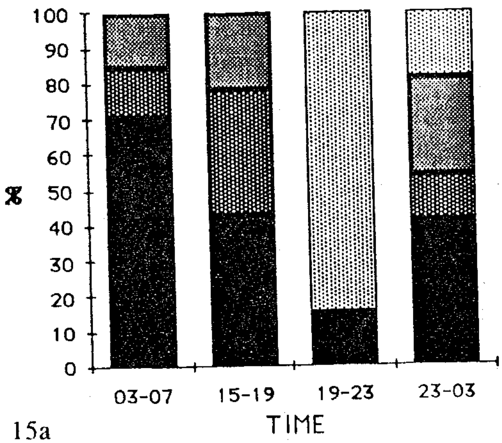
Copepods	234	38	272	2.24
Euphausiids	23	8	31	5.25
Crustacean larvae	86	18	104	3.64
Ostracods	222	6	228	22.83
Nj	565	70	635=N	
Gj	3.29	30.66		33.96

euphausiids, as the fish length increased. Large fish also took larger individuals of copepods, crustacean larvae and euphausiids (Fig. 10, 11, 19).

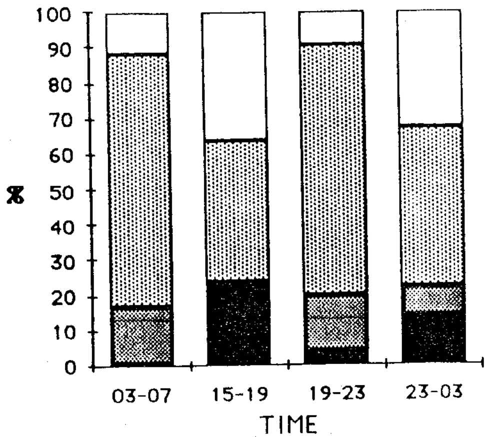
Benthosema fibulatum

The size range of this species was 25-67 mm. They had average premaxillary lengths (4.4-11.8 mm) and gill-raker spaces (0.2-0.7 mm) and comparatively large lens diameters (1.5-3.7 mm) and gill-raker areas (10.7-67.6 mm^2) (Fig. 1-4).

The highest percentage of newly ingested food was observed during 1900-2300 h (Fig. 15), but newly ingested food was also found between



15a



15b

Fig. 15. Degree of stomach filling (a) and state of digestion (b) for *Benthosema fibulatum*

2300 and 0300 h. The highest percentage of much digested stomach contents was found during 0300-0700 h. The stomach filling was lowest during the afternoon (1500-1900 h). The data suggest that feeding is most intensive during early night.

B. fibulatum also had foraged on a wide variety of items quite similar to *Diaphus garmani*. But the numerical importance of copepods was higher for *B. fibulatum* (65%). Crustacean larvae were also of some importance (16%).

Contribution by other items was small (Fig. 16). The prey species diversity was high (Shannon's diversity index H=0.52) (Table 2) and the composition is significantly different from the other three main species

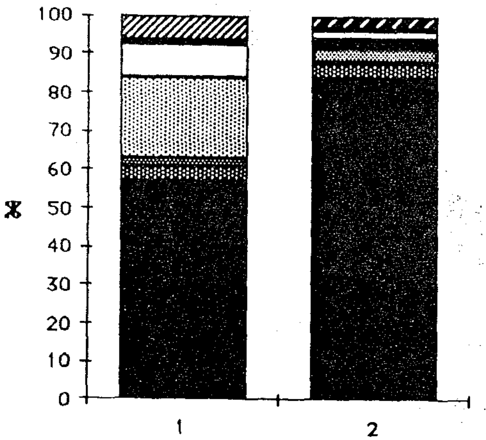


Fig. 16. Percentage composition of prey items in *Benthosema fibulatur*. 1) June-July, 2) November-December. Symbols as in Fig. 6.

(Table 4). Seasonal and depth variations were also observed in the composition of diet and the former was significantly different (Fig. 16, 17 and Table 3). The prey size preferred by the species was average (between 0.4-12 mm) (Fig. 9), and the larger length groups preyed upon larger prey than the small ones (Fig. 18, 10, 11, 19). The estimated time of food diges-tion was 4 h for fish of size range 51-60 mm and the daily ratio was 3.8% of body weight (Table 1).

Table 4

Contingency table analysis for stomach content data for four important Myctophid species.

Prey Predator	*D. watasei*	*D. garmani*	*B. fibulatum*	*M. brachygnatum*	Ni	Gi
Copepods	22	272	226	537	1057	578.54
Euphausiids	35	31	12	24	102	240.10
Crustacean larvae	8	104	55	32	199	413.89
Amphipods	16	3	23	22	64	133.01
Ostracods	1	228	12	8	249	909.25
Molluscs/ bivalve larvae	2	50	14	4515	4581	1331.85
Fish/fish larvae	11	3	2	20	36	48.96
Nj	95	691	344	5158	6288=N	
Gj	385.91	1579.37	815.51	873.26		3655.60

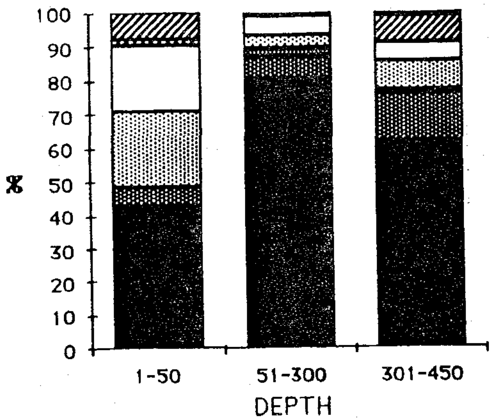


Fig. 17. Percentage composition of prey items in *Benthosema fibulatum* at different depths. Symbols as in Fig. 6.

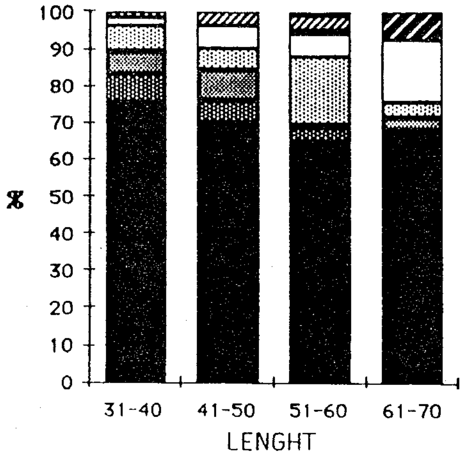


Fig. 18. Percentage composition of prey items in different length groups of *Benthosema fibulatum*.

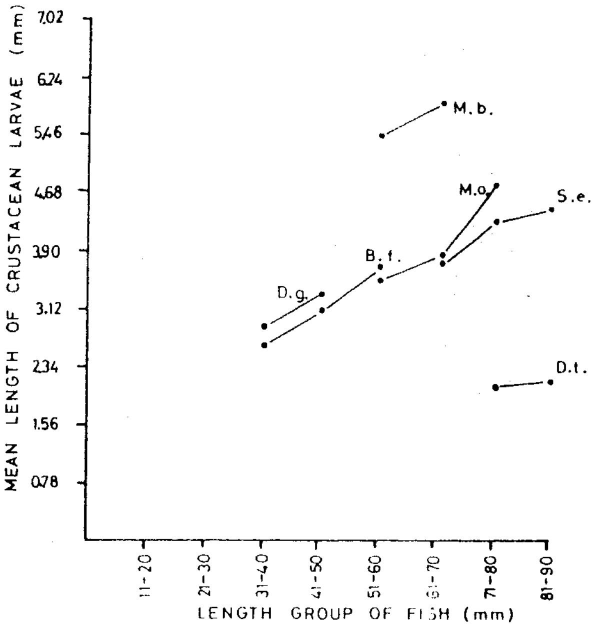


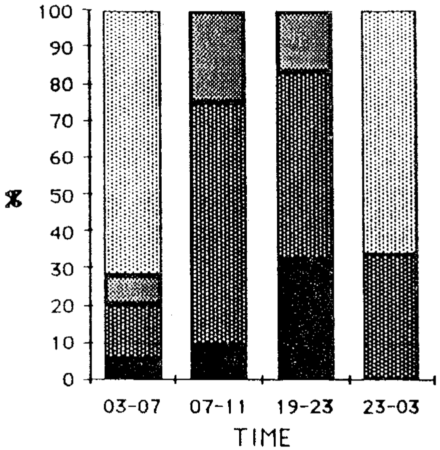
Fig. 19. Relationship between mean length of crustacean larvae and the length of fish for different fish species. Abbreviations for different fish species as in Fig. 1.

Myctophum brachygnatum

Fish sizes ranged from 55-70 mm. Pre-maxillary lengths (8.3-9.1 mm) and gill-raker distances (0.5-0.6 mm) were very low compared with the other species. Lens diameters were very high (2.6-3.5 mm) and gill-raker areas were average (38.0-53.7 mm^2) (Fig. 1-4).

M. brachygnatum had a high percentage of newly ingested food during the period 2300-0700 h and the percentage of full stomachs increased from mid-night till early morning (from 2300-0300 to 0300-0700 h) (Fig. 20). This indicates that intensive feeding took place during night time.

More than 75% of the diet consisted of molluscs and bivalve larvae (mainly the latter). Larvaceans and salps ranked second in importance (9%) (Fig. 21). This species had a lower prey species diversity (H=0.34) than the three species mentioned above (Table 2), and the composition was significantly different from those species (Table 4). The prey size range for the species was average (Fig. 9). Sizes of crustacean larvae and euphau-siids taken increased with increasing fish size (Fig. 11, 19).



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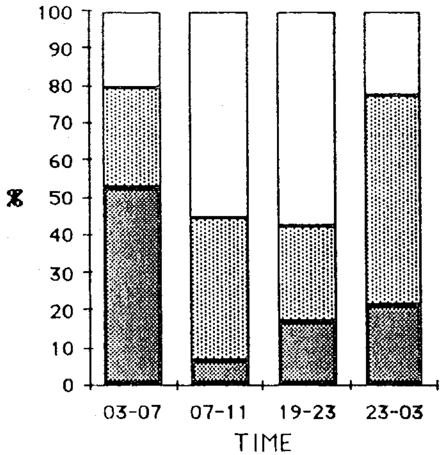

20b

Fig. 20. Degree of stomach filling (a) and state of digestion (b) for *Myctophum brachygnatum*.

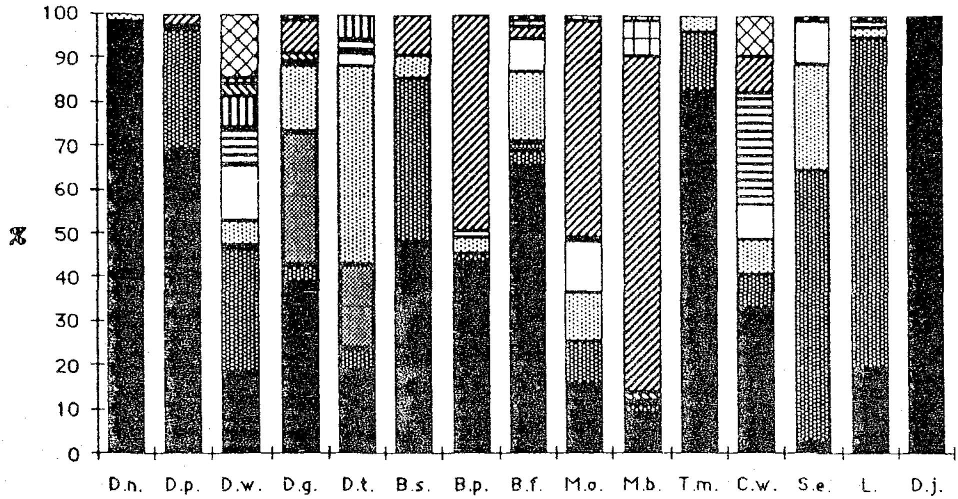

Fig. 21. Percentage composition of prey items in various species. Abbreviations of species names as in Fig. 1. Symbols of prey items as in Fig. 6.

M. brachygnatum was only caught during November/December and seasonal variation in feeding could not be studied.

Fish taken from the surface layers (1-50 m) had a very high percentage of molluscs and bivalve, and those taken from deeper layers (251-300 m) had more copepods although a statistical comparison was impossible as the sample taken from deeper depths was very small.

Myctophum obtusirostrum

Fish sizes ranged from 50-80 mm. They had large lens diameters (2.5-3.9 mm), average gill-raker distances (0.57-0.64 mm) and gill-raker areas (33.9-69.2 mm^2) with comparatively short pre-maxillaries (7.3-10.7 mm) (Fig. 1-4). Gill-raker distance of the species did not vary much with the increasing standard lengths.

As for *M. brachygnatum*, molluscs and bivalve larvae were important (50%), and so were copepods, euphausiids and crustacean larvae (Fig. 21). This species showed a high prey species diversity (Table 2). Molluscs were the main component during November/December while copepods and crustacean larvae were important in June/July. The prey size range was average. Sizes of prey items (copepods, crustacean larvae and auphausiids) increased with increasing fish sizes (Fig. 10, 11, 19).

Symbolophorus evermanni

Standard lengths of this fish ranged from 25-87 mm. Gill-raker distances were low (0.3-0.8 mm). Other morphological characters were average (pre-maxillary lengths 4.8-13.8 mm; lens diameters 1-3.8 mm; gill-raker areas 8.1-72.4 mm^2) (Fig.1-4).

The diet mainly consisted of crustaceans (copepods, euphausiids, crustacean larvae and amphipods). A very high percentage of the diet consisted of euphausiids (62%). Copepods were of minor importance (Fig. 21). The prey species diversity was average compared with other species (Table 2). Euphausiids were the main forage item and copepods were not taken at all during November/December. During June/July crustacean larvae were the most important. As in most other species, the prey sizes increased with the fish size,(Fig. 11, 19). The minimum prey size of this species was the highest of all species (Table 2).

Benthosema suborbitale

This species represented fish sizes between 20-30 mm. Lens diameters were high (1-1.5 mm) and so were the gill-raker distances (0.2-0.4 mm). Pre-maxillary sizes (1.7-4.7 mm) and gill-raker areas (4.1-8.7 mm^2) were both low (Fig. 1-4).

More than 90% of the diet were crustaceans (copepods, euphausiids and crustacean larvae). 9% of the diet were molluscs and bivalve larvae (Fig. 21). The prey species diversity was average (H=0.47). The number of specimens was too low to analyse seasonal variation in feeding. Prey size range was average for this species.

Triphoturus microchir

The size range of fish caught was 25-32 mm. This species had the highest gill-raker distances (0.5-0.6 mm) and one of the lowest lens diameters (0.5-1 mm). Pre-maxillary sizes (3.8-5.8 mm) and gill-raker areas (8.7-13.2 mm^2) were average (Fig. 1-4).

This species had fed on crustaceans which consisted of copepods (83%), euphausiids (13%) and crustacean larvae (4%) (Fig. 21). The prey species diversity was fairly low (H=0.23). No great variation was observed in different seasons. The size of the prey eaten was very small.

Lampanyctus sp

Fish size ranged from 25-62 mm. This species had very low gill-raker areas (5.5-35.5 mm^2) and lens diameters (0.6-2.1 mm), high gill-raker distances (0.4-0.9 mm) and average sized pre-maxillaries (3.7-10.9 mm) (Fig. 1-4).

Lampanyctus had fed mainly upon euphausiids (75%). Copepods were also of some importance. Crustacean larvae, amphipods, fish and fish larvae (of family Myctophidae) were the other items eaten (Fig. 21). Prey species diversity of the species was low (H=0.32). In November/December 100% of the diet was euphausiids. In June/July they had taken a variety of items. Prey size range was average.

Diaphus nielseni

Fish sizes ranged from 30-38 mm. All morphological characters were average (pre-maxillary lengths 5.9-6.9 mm; lens diameters 1.0-1.4 mm; gill-raker distances 0.3-0.4 mm and the gill-raker area 10.7-16.6 mm^2) (Fig. 1-4).

99% of the food were copepods and crustacean larvae were only 1% (Fig. 21). Species diversity was very low (H=0.02). The size range of food items was also very low.

Diaphus jenseni

The size range of fish caught was 22-30 mm. Gill-raker distances of the species were very low (0.1-1.3 mm). Gill-raker areas (7.6-10.2 mm^2), lens diameters (0.7-1.0 mm) and pre-maxillary sizes (4.4-5.4 mm) were ave-rage compared to the other species (Fig. 1-4).

100% of the prey items were copepods (Fig. 21). The length range of the prey items was very low.

Diaphus perspicillatus

Fish sizes ranged from 25-60 mm. This species had very large pre-maxillaries (5.2-11.8 mm) and big lenses (0.8-3.8 mm). Gill-raker distances (0.3-0.5 mm) were average and gill-raker areas (20.4-42.7 mm^2) were large (Fig. 1-4).

Crustaceans were the main component of the food (copepods, euphausiids and ostracods). Copepods were about 68% of the diet (Fig 21). The prey species diversity was comparatively low (H=0.32). The prey size range was average.

Diaphus thiollierie

Fish sizes were between 60-110 mm. The lens diameters (2.4-4.2 mm) were smaller than average for the fish size. All other morphological features were average (pre-maxillaries 10.7-20.3 mm, gill-raker distances 0.6-1.2 mm and gill-raker areas 38.0-109.7 mm^2) (Fig. 1-4).

The fish had eaten a wide variety of food. Crustaceans made up more than 95% which included copepods, euphausiids, crustacean larvae, ostracods, decapod shrimps and amphipods, of which crustacean larvae were the most important (Fig. 21). This species showed a very high prey species diversity (H=0.65). The prey size range for this group was average. Crustacean larvae sizes increased with increasing fish sizes (Fig. 19).

Benthosema pterotum

Fish sizes ranged from 25-33 mm. Gill-raker distances were very low (0.2-0.3 mm). Pre-maxillary lengths (3.2-5.9 mm), lens diameters (0.7-1 mm) and gill-raker areas (20.4-42.7 mm^2) were average (Fig. 1-4).

51% of the prey consisted of crustaceans (copepods 44%, euphausiids 2%, crustacean larvae 4% and amphipods 1%) and 49% of molluscs and bivalves (Fig. 21). The prey species diversity was average (Table 2).

Ceratoscopelus warmingi

Fish sizes ranged from 28-60 mm. Food consisted of crustaceans (copepods, euphausiids and crustacean larvae), molluscs and bivalve larvae, squids, fish and fish larvae. Copepods comprised 33% of their diet and fish and fish larvae contributed 26% (Fig. 21). All squids observed belonged to the family Onychoteuthidae and fish and fish larvae to the family Myctophidae. The prey species diversity was very high (H=0.75). The prey size range was generally high.

DISCUSSION

Feeding behaviour

1. Composition of diet

Net-feeding is considered to be one of the important sources of error in diet analysis of midwater fish (Lancraft and Robinson 1979, Sazima 1983). The trawl used in this study (high opening shrimp and fish trawls for demersal trawling and a large commercial trawl for pelagic trawling) had a 20-21 mm mesh size in the cod end (Iversen et al. 1984). Most of the prey items in the diet of all species studied were in the range of 0.4-20 mm (Fig. 9). Therefore it is not likely that such small prey items could be retained in the cod end for the fish to feed on. Nevertheless, there is a probability that larger prey items may be retained in the cod end. In *Diaphus watasei*, three of the fish had three fresh specimens of myctophid species of *Diaphus garmani* and two fish had two fresh specimens of squids of the family Onychotheuthidae in the forepart of their esophagus. It is possible that these were taken in the cod end. However, these were not included in the analysis.

Regurgitation of food due to stress is another probable factor that affects diet analysis. There were three fish of the species *Diaphus watasei* with everted stomachs which is evidence of regurgitation. Anyhow, the evaluation of regurgitation is not possible. Neither regurgitation nor net feeding was observed in any of the other species, hence it can be assumed that the stomach contents reflect the normal diet for all but *D. watasei* in which these two factors might have changed the real composition of diet, although the significance of the change cannot be evaluated.

Trawl nets used in this survey did not have a closing device. Therefore the contamination of fish at different depths could have taken place. This may have led to erroneous results in aspects like diet variation at different depths and feeding chronology.

The dominant prey of the 15 myctophid species investigated were zooplankton. All but two species had a wide spectrum of prey items in the diet. *Diaphus jenseni* had fed exclusively on copepods and 99% of the diet of *Diaphus nielseni* also were copepods (Fig. 6, 13, 16, 21). Although *Myctophum brachygnatum* had taken a variety of food items, the principal diet was molluscs and bivalve larvae (mainly bivalve larvae)(75%) and larvaceans and salps (9%). The most abundant zooplankton of the other species were crustaceans, such as copepods (>75% calanoid copepods), amphipods, ostracods and larval forms of crustaceans. Molluscs, bivalve larvae, larvaceans, salps, chaetognaths and polychaetes were the other zooplankton species which were important for some of the fish species. Some larger species like *Diaphus watasei* and *Ceratoscopelus warmingi* were found to ingest bigger organisms like decapod shrimp, fish and fish larvae (of family Myctophidae) and oceanic squids (of family Onychoteuthidae) (Fig. 6, 21).

Myctophids are generally considered to be opportunistic feeders. Most of the investigations carried out on myctophids suggest that this group ingest whatever prey of suitable size is available to them. It has also been hypothesised that this suitable size is determined by various mophological and behavioural parameters of fish (Ebeling and Cailliet 1974, Clarke 1980).

Diet composition of *Diaphus nielseni*, *D. jensensi* and *Myctophum brachygnatum* is clearly different from the diet of the other species and probably do not reflect the zooplankton composition of the environment. These three species were caught with other species from surface layers (1-50 m) at dawn (0300 h) (Appendix 1). A few *M. brachygnatum* were caught at deeper depths as well. *D. nielseni* and *D. jenseni* were apparently selecting copepods and *M. brachygnatum* was specifically feeding on molluscs, bivalve larvae end larvaceans and salps. As these three species were recorded only during one season, a seasonal comparison was not possible to confirm their selective feeding. Neither was a regional comparison possible.

Selective feeding of myctophids has been reported several times (Paxton 1967, Harmann and Weikert 1969, Samyshev and Schetinkin 1973, Gorelova 1975).

Some authors connect such homogenetic prey composition in the stomachs with the patchy distribution of prey items (Collard 1970, McCrone 1981). However, by compiling other data and their own observations, Hopkins (1977) concluded that preferential or selective feeding exists among mesopelagic fish which may result from complex morphological, physiological and behavioural factors of both predators and prey items. Imsand (1981) based upon his studies on two *Triphoturus* species the hypothesis that in the short term a predator can be operating as an opportunist but in the long term its effect can be that of a specialist.

2. *Resource partitioning*

Feeding at different depths in the water column has been considered as the most obvious and general form of resource partitioning (Hopkins 1977). As the composition of zooplankton also vary with depth (Kinzer 1969, Roe 1974, Weikert 1982), it can be expected that fish feeding at different depths consume different types of food (Fig. 7, 14, 17). Prey composition differed with depths. As no opening/closing device was available in the trawl there was a possibility that the samples were mixed at different depths while trawling, and the data therefore are uncertain. *Diaphus watasei* which had fed on benthic octopods of the family Octopodidae, seems to be the only species that takes food from the bottom.

Prey size selectivity is another method of resource partitioning. This can be achieved both ontogenetically and interspecifically. Ontogenetical size variation is quite prominent in almost all species studied (Fig. 8, 10, 11, 19), and there are also differences in the most frequently taken prey size between species.

Resource partitioning by choosing specific taxa is evidenced in *D. nielseni* and *D. jenseni*. These two species fed mainly on copepods which would not have been the only prey at the time of their feeding as other species taken together with these two had a variety of prey items. The diet of *Myctophum brachygnatum* also indicate selective feeding.

3. *Morphological characters and feeding behaviour*

Visual systems of myctophids are highly adapted for the low light intensities of the midwater environment (Marshall 1979). A visually oriented feeding mode has been observed in many studies of midwater fish (Hopkins and Baird 1973, Clarke 1980). It is also assumed that the fish who possess larger lenses have an ability to detect a broader range of food items (both in size and taxa). This is well characterized by three of the species which had larger lenses than the others (namely *Myctophum brachygnatum, M. obtusirostrum* and *Benthosema fibulatum*). Vision is not the only character that determines the type and size of food. Hopkins and Baird (1973) found that the feeding pattern of *Sternoptyx diaphana* was consistent with morphological features such as prominent eyes, relatively small nasal rosettes, narrow rigid body plan, modestly sized vertically oriented mouth with small curved teeth, few spinose gill-rakers along with a small tooth plate on the branchial arches and a photophore and pigmented pattern maximizing invisibility. Clarke (1980) concluded that the difference in lens size and gill-raker space was most obviously and frequently correlated with differences in diet and the preference in the myctophids he examined. It has been shown that the minimum size of prey is determined by the gill-raker distance of the predator while the maximum prey size is determined by the jaw size of the predator (Yasuda 1960a, b, Ebeling and Cailliet 1974). The importance of mouth size for mesopelagic fish as well as other fish species has also been supported by several authors (Ebeling 1962, Hunter 1980).

The maximum prey sizes are always larger for species which possess larger pre-maxillary lengths (Table 2). For instance *Diaphus watasei* had the highest recorded maximum prey size as well as the highest recorded pre-maxillary size. Other species with large pre-maxillary sizes also took relatively large prey (*D. thioherie* and *Symbolophorus evermanni*). Those who had relatively small pre-maxillaries also had relatively low maximum prey sizes (i.e. *Benthosema pterotum* and *D. jenseni*). This agrees with the assumption that pre-maxillary size determines the maximum prey size.

The minimum prey size taken by most species was 0.4 mm whereas the minimum gill-raker distance of most species was less than the minimum prey size (Table 2). If fish make use of the gill-rakers to retain and concentrate small prey items as suggested by Ebeling and Cailliet (1974) and Clarke (1980), it should be expected to find minimum prey sizes corresponding to the distances between the gill-rakers of the predator. No such observation was made here. On the contrary, the minimum prey size for most species was constant and higher than the minimum gill-raker space. This could be an indication that these fishes do not simply filter their food, but select individual animals by sight. This is further confirmed by the lack of correlation of dietery pattern with differences in gill-raker areas.

4. Feeding chronology

Samples not being preserved immediately after capture may be one of the main practical problems encountered in this study. This may lead to biased estimates of state of digestion. Interpretation of feeding periodicity from the presence or absence of fresh and/or digested food is also difficult without knowing the digestion rate of mesopelagic fish (Hopkins 1977). It can be expected that different prey items have different digestion rates. For instance, a hard shelled mollusc may have more resistance to digestion than a soft-bodied larvacean and salp. This could bias results on both prey content analysis as well as interpretations on feeding periodicity.

In view of these difficulties it is impossible to draw firm conclusions on feeding periodicity. The data available suggest, however, an acyclic feeding pattern for *Diaphus watasei* and a nocturnal feeding pattern for *Myctophum prachygnatum, Benthosema fibulatum* and *Diaphus garmani.* Adults of *D. watasei* usually live on or near the bottom depths ranging from 100-550 m (Nafpaktitis 1978). The results show that they had been feeding in the 140-450 m range (Fig. 7). Probably the bottom layer where they live generally has enough food so they do not migrate to surface layers where food is rich at night. The other species took most of their food at night near the surface.

Acyclic feeding behaviour had been reported previously for other *Diaphus* species like *D. dumerillig* and *D. taaningi* (Samyshev and Schetinkin 1973), while night-morning feeding had been reported for *D. theta* (Tyler and Pearcy 1975). Other studies carried out for several species of *Benthosema, Diaphus* and *Myctophum* report the principal feeding period to be night (Gjøsæter 1973, Gorelova 1974, Baird et al. 1975, Clarke 1978, McCrone 1981).

The present calculation suggests that the daily ratio is a constant proportion of the body weight. Hopkins (1977) also concluded this after reviewing other studies. Hopkins' (1985) results of the daily ratio of *Lampanyctus alatus* (2.4-4.4%) and Clarke's (1978) results of *L. steinbecki* and *Hygophum proximum* (2.8%) are in general agreement with the results of the present study. Daily ratios calculated by Legand and Rivaton (1969) and Baird et al. (1975) for other mesopelagic fishes are lower than the values given above. Legand and Rivaton (1969) found that the food of myctophids with full stomachs was approximately 1% of their body weight. In the latter study the value obtained for *Diaphus taaningi* was 0.8% of the body weight. None of the methods used in the studies were direct.

Gorelova (1983), using the same method as in the present study, found that the myctophids she studied had a daily ratio between 4% and 16.9% and a digestion time of 5 h for juveniles and 7 h for adults.

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