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# Feeding ecology of the lanternfish *Benthosema pterotum* from the Indian Ocean

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## Abstract

The feeding ecology of lanternfish *Benthosema pterotum* (Alcock) from the north Arabian Sea, Mozambique and the Bay of Bengal was studied. Samples were collected on cruises carried out by R.V. "Dr. Fridtjof Nansen" during the period 1978 to 1983. A wide variety of zooplankton organisms were identified in the diet of *B. pterotum* with crustaceans dominating the diet. Copepods constituted ca. 40 to 90% of the diet. Dry weight analyses of the stomach contents from the Gulf of Oman in February 1983 showed copepods to be 35 to 55% in weight (average in samples). Ontogenetic differences were observed in the diet. Prey size increased as the fish length increased, but the largest fish did not exclude the smaller prey organisms from their diet. Regional variation in diet was also shown in *B. pterotum*. The degree of filling and the state of digestion of stomach contents revealed that this species feeds intensively at night in the epipelagic layer. All copepods identified were epipelagic species, providing additional evidence of diurnal pattern in the feeding chronology of *B. pterotum*. Identification of copepods from the Gulf of Oman in February 1983, revealed that herbivorous species dominated in biomass. Quantitative analyses show that *B. pterotum* probably have a daily food intake of ca. 4.5% of the body weight.

## Introduction

Mesopelagic fishes are one of the most promising unconventional fishery resources in the world. Among mesopelagic fishes myctophids occur throughout the world oceans and are principal components of the midwater fauna. In recent years many studies have been directed towards investigating aspects of their biology and ecology.

Feeding patterns of tropical and sub-tropical myctophids have been studied by Legand and Rivaton (1969), Clarke (1978, 1980), Kinzer (1982) and Gorelova (1983). These studies reveal that these fish are carnivorous, although recent studies by Robison (1984) show that *Ceratoscopelus warmingii* can also feed on phytoplankton. The role of midwater fish in the marine food web, particularly in tropical oceanic regions, has not been sufficiently investigated (Kinzer and Schulz 1985).

Most mesopelagic fish perform diel vertical migrations, staying in deeper waters at day time and coming to the epipelagic zone at night. Attempts have been made to investigate the diel periodicity in feeding of migratory and non-migratory myctophids (Baird et al. 1975, Kinzer 1977, Clarke 1978, McCrone 1981). Some authors suggest that these migrations are primarily for feeding purposes (Marshall 1979) while others (McLaren 1963) suggest it is to avoid or minimize predation or as a cause of saving energy while resting in the cooler deeper waters.

Studies on the trophic position of mesopelagic fishes (Legand and Rivaton 1969, Baird et al. 1975, Hopkins and Baird 1977) and of quantitative aspects of feeding such as food requirement, food digestion rates (Clarke 1978, Tseitlin 1980, Gorelova 1983) are quite limited.

A large part of the material was collected from the north Arabian Sea where one species of fish, *Benthosema pterotum* (Alcock), of the family Myctophidae, is known to dominate the mesopelagic fish community (Gjøsæter 1981a). The objectives of this study were to determine the feeding habits of this species in different geographic regions, ontogenetical variation in the diet, and to document their diel feeding behaviour. Attempts were also made to obtain a general view of some quantitative aspects of feeding such as the daily ration, food consumption compared to primary production, and of its trophic position.

## Materials and methods

This study is based on material from the Gulf of Oman (1979, 1983), Mozambique (1978) and the Bay of Bengal (1979). Specimens were collected by R.V. "Dr. Fridtjof Nansen", mostly using a pelagic trawl with estimated mouth area of 250 $m^2$. The mesh size in the front part of the trawl was ca. 200 mm (streched) decreasing to 9 mm in the cod end. Towing procedure and sampling stations are similar to those described by Dalpadado (1985). The material was preserved in 4% formaldehyde in seawater. Standard length of specimens were measured and the stomach (anterior end of oesophagus to the pyloric valve) was removed, opened and the contents were carefully teased apart. The prey items were usually assigned to the higher taxa, but in some fishes copepods were identified to genera or species.

The length of the prey organisms where possible was measured with an ocular micrometer to the nearest 0.01 mm. Prosome length of copepods, carapace length of amphipods, ostracods, euphausiids and other larger Crustacea were measured. Total length was recorded for all other prey organisms. All identifiable prey were counted. Some prey items such as chaetognaths, larvaceans, gastropods and polychaetes were rarely found intact in the stomachs. Their presence was inferred from identifiable parts such as hooks of chaetognaths and chaetae from polychaetes. In some samples therefore no attempt was made to estimate the number or the length of these prey. Only their presence or absence was noted.

In some specimens from the 1983 Gulf of Oman samples, dry weights of the stomach contents and fishes (with gonad) were taken. The major prey groups were weighed separately while the rest were weighed together in another batch. The stomach contents were dried at 80 °C for 24 h; fish were dried at the same temperature for about 48 h. The weight of stomach contents after a second period in the drying oven indicated that errors were not more than $\pm 0.02$ mg. For the fishes the errors were less than 1%.

In all specimens, the stomach fullness and the degree of food digestion were classified according to the following scales modified from Gjøsæter (1973) and Dalpadado (1983).

| *Degree of filling* | | *Description* |
|---|---|---|
| 0 | Empty | empty |
| I | Little contents | Up to 30% filling |
| II | Half full | Ca. 30 to 70% filling |
| III | Full | Approx. 70 to 100% filling, stomach wall retains its normal tickness |
| IV | Distended | Stomach is expanded, and the stomach wall appears thin and smooth |

| *State of prey digestion* | | *Description* |
|---|---|---|
| I | Newly ingested | Almost all items show no digestion or very slight digestion. |
| II | Slightly digested | The contents uniformly slightly digested or less than ca. 30% of the contents, partly digested, the rest little or not digested. |
| III | Partly digested | The stomach contents uniformly partly digested but still recognizable or ca. 30 to 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 stage. |

A Log-likelihood ratio test was performed to test the significance of diurnal and ontogenetical variation in diet. Details of the methods used are described by Crow (1982).

## Results

### Prey types

*Benthosema pterotum* prey on a wide variety of zooplankton organisms, including copepods, amphipods, euphausiids, ostracods, chaetognaths, larvaceans, molluscs, polychaetes, fish and others (Fig. 1). Crustaceans dominated the diet in all areas examined. Among crustaceans, copepods were the most important food item constituting up to 35 to 55% in weight (Fig. 2). These figures are averages for samples; individual variations were much wider.

Copepods were identified into genera or species in the stomach contents of 48 fishes caught in the Gulf of Oman in February 1983. The cyclopoid copepod *Corycaeus* sp. was numerically the most abundant of the identifiable specimens. Another cyclopoid copepod, *Oncaea* sp., was also regularly observed in stomach contents.

These cyclopoid copepods were small-sized, with a prosome length of ca. 0.64 mm or less and the biomass of the stomach contents of *Benthosema pterotum* consisted mainly of larger calanoid species (pro length 0.8 to 2.5 mm), of which the dominant species were:
*Acartia danae, Candacia* sp., *Centropages furcatus, Clausocalanus* sp., *Eucalanus tenuis, Euchaeta marina, Labidocera acuta, Lucicutia* sp., *Mecynocera* sp., *Nanocalanus minor, Pleuromamma* sp., *Pontellina plumata, Temora discaudata.*

A relatively high number of juvenile calanoids were not identified. Harpacticoid copepods were observed in small numbers, mainly *Microsetella* sp. and *Miracia minor*.

Fishes of the families Trichiuridae, Paralepididae and Gonostomatidae were occasionally preyed upon by *Benthosema pterotum*. Due to the state of digestion these fishes could not be identified to genera/species.

Among fishes with fish scales in their stomachs there seems to be a trend that the proportion of scales decreases with increasing total weight of stomach contents (Fig. 3).

### Regional differences in the diet

Frequency of occurrence of different prey types from the Gulf of Oman, Bay of Bengal, Mozambique, and the Red Sea (Dalpadado and Gjøsæter 1987) indicates that *Bentho-*

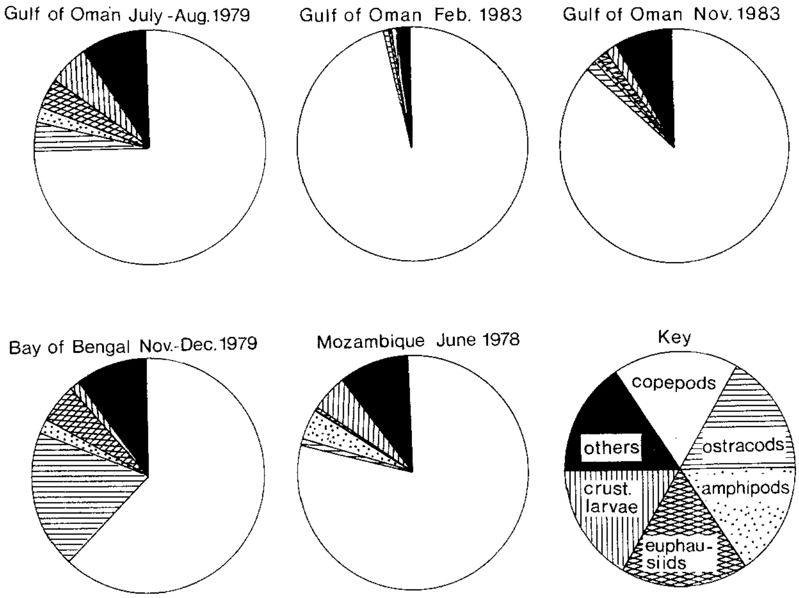



**Fig. 1.** *Benthosema pterotum.* Percentage frequencies of dominant prey items taken from different regions

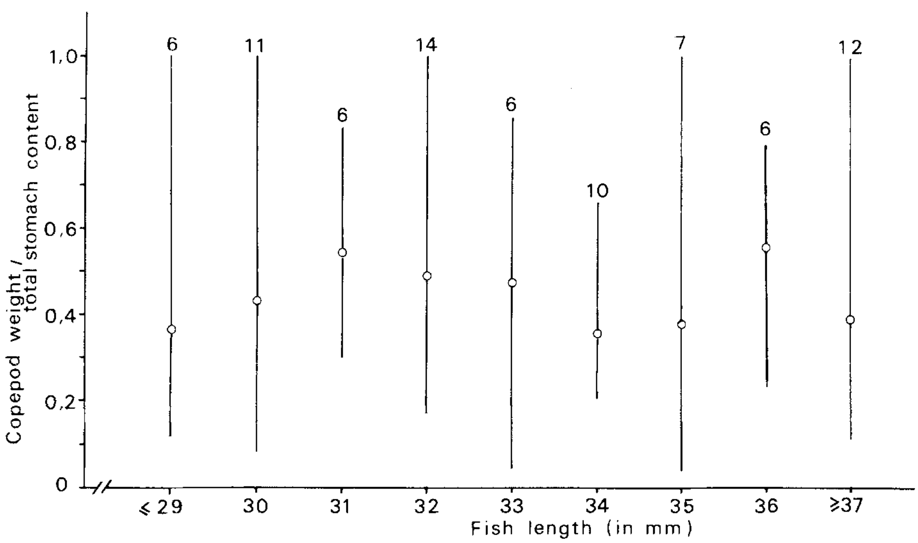



**Fig. 2.** *Benthosema pterotum.* Copepod weight as a proportion of total weight of stomach contents against fish size from Gulf of Oman, Feb. 1983. Circles = mean, vertical bars = range, and number of fish on top of bars

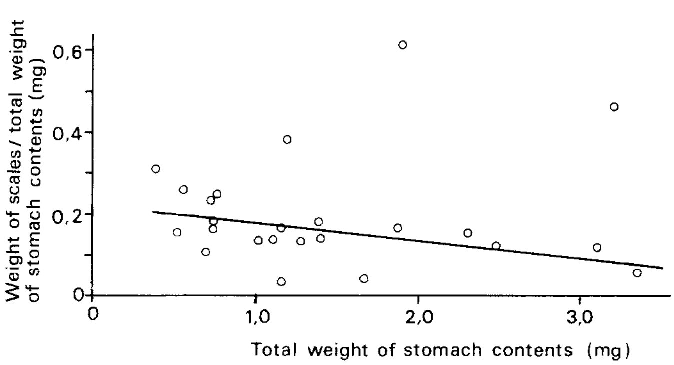



**Fig. 3.** *Benthosema pterotum.* Proportion of fish scales in stomach contents of fish vs total weight of stomach contents from the Gulf of Oman, Feb. 1983

*sema pterotum* fed on similar food items although the importance of some of the food items differed between areas (Table 1). Copepods were dominant in all areas. In the Bay of Bengal ostracods were also important, as were amphipods in the Red Sea. Larvaceans were found in high numbers in fishes from Mozambique, but due to the advanced state of digestion only their presence was noted.

## Diurnal variation in diet

*Benthosema pterotum*, which occur at depths around 200 to 400 m during the day and migrate to surface layers at night, may exhibit variable composition in the diet throughout the diel cycle, if they feed at both day and night depths.

**Table 1.** *Benthosema pterotum*. Diet composition from the Gulf of Oman, Bay of Bengal, Mozambique and the Red Sea. Diet composition of some other mesopelagic fishes from the Indian Ocean are also included for comparisons. (Percentages given are based upon total number of prey items)

| Species | No of fish | Size range in mm | Oceanic area year | Copepods | Ostracods | Amphipods | Euphausiids | Other crustacea | Molluscs | Polychaetes | Larvaceans | Chaetognaths | Fishes | Others | Total | Diversity index, (D) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Benthosema pterotum* | 237 | 23–46 | G. Oman 1979 | 74.80 | 4.11 | 1.80 | 4.11 | 9.00 | 3.08 | 1.28 | + | + | 0.77 | 1.03 | 389 | 1.47 |
| *Benthosema pterotum* | 189 | 17–45 | G. Oman Nov. 1983 | 87.07 | 1.15 | 0.84 | 1.15 | 3.57 | 3.26 | 0.42 | + | 0.52 | 0.11 | 1.89 | 952 | 0.90 |
| *Benthosema pterotum* | 628 | 19–47 | G. Oman Feb. 1983 | 96.70 | 0.06 | 0.12 | 0.26 | 0.87 | 0.56 | 0.30 | + | 0.66 | 0.12 | 0.36 | 8582 | 0.31 |
| *Benthosema pterotum* | 65 | 32–43 | B. Bengal 1979 | 63.12 | 18.79 | 2.13 | 4.78 | 3.90 | 4.26 | 1.95 | + | – | 0.35 | 0.71 | 564 | 1.77 |
| *Benthosema pterotum* | 74 | 23–37 | Mozambique 1978 | 79.17 | 1.22 | 4.41 | 0.24 | 6.37 | 7.84 | – | + | – | – | 0.74 | 408 | 1.16 |
| *Benthosema pterotum** | 31 | 41–53 | Red Sea Mar. 1981 | 57.89 | 2.25 | 22.05 | 1.00 | 8.02 | 1.00 | – | 2.25 | – | 3.00 | 2.94 | 399 | 1.91 |
| *Ceratoscopelos warmingii*** | 60 | ND | Indian Ocean Central | 66.00 | 1.00 | 7.00 | 14.00 | 2.00 | – | – | 3.00 | 4.00 | 1.00 | – | 147 | 1.80 |
| *Lampanyctus alatus*** | 59 | ND | Indian Ocean Central | 73.00 | – | 3.00 | 13.00 | 11.00 | – | – | – | – | – | – | 38 | 1.20 |
| *Notolychnus valdiviae*** | 90 | ND | Indian Ocean Central | 77.00 | – | 14.00 | – | 6.00 | – | – | – | 3.00 | – | – | 35 | 1.10 |
| *Sternoptyx obscura*** | 14 | 10–30 | Indian Ocean Equatorial | 70.00 | 8.00 | 6.00 | 4.00 | 1.00 | – | 4.00 | – | 8.00 | – | – | 253 | 1.60 |

* Dalpadado and Gjøsæter (1987); ** Hopkins and Baird (1977)

D = Modification of Shannon's index as defined by Travers (1971); $D = \Sigma\ ni/N \log_2 ni/N$, where ni = number in each prey category and N = total number of prey items

**Table 2.** *Benthosema pterotum*. Diurnal variation in prey types. Total number of prey items observed in each category given from the Gulf of Oman 1979, Feb. 1983, and Nov. 1983

| Year | Depth layer | No. of fish | Copepods | Other crustacea | Molluscs | Chaetognaths, fish and polychaetes | Others | Total |
|---|---|---|---|---|---|---|---|---|
| 1979 Jul./Aug. | D1 | 161 | 217 | 40 | 9 | 4 | 2 | 272 |
| | D11 | 36 | – | – | – | – | 1 | 1 |
| | N1 | 46 | 74 | 34 | 3 | 4 | 1 | 116 |
| 1983 Feb. | D1 | 258 | 2 292 | 11 | 12 | 1 | 16 | 2 332 |
| | D11 | 60 | 35 | – | – | – | – | 35 |
| | N1 | 250 | 5 630 | 97 | 34 | 92 | 15 | 5 868 |
| | N11 | 60 | 342 | 4 | 1 | – | – | 347 |
| 1983 Nov. | D1 | 20 | 9 | – | 2 | – | – | 11 |
| | D11 | 34 | 25 | 4 | 1 | 1 | 1 | 32 |
| | N1 | 135 | 795 | 61 | 27 | 9 | 17 | 909 |

During the day echo recordings were divided into three zones: (1) epipelagic – usually upper 100 m; (2) upper mesopelagic (DI) – usually 100 to 200 m; (3) deep mesopelagic (DII) – usually below 200 m. At night, two zones could be recognized: (1) upper mixed layer (NI) – upper 100 m and (2) deep mesopelagic (NII) – below 200 m (Gjøsæter 1984).

Differences between individual layers (DI, DII, NI, NII) could not be tested due to the small number of fish involved in the DII and NII layers (Table 2). The samples from DI, DII layers were combined; these samples were compared with the combined samples from NI and NII layers. A log-likelihood ratio test was performed to test the null-hypothesis that there is no difference in the prey types eaten during the day and at night. The test yielded a G value of 41.46, df = 4, which is significant at the 0.05 level (Table 3) (Crow 1982). The difference probably arises from prey cate-

**Table 3.** Log-likelihood tests for data given in Table 2 from the Gulf of Oman 1979/1983

| Dept layer | No. of fish | Copepods | Other crustaceans | Molluscs | Chaetognaths fish and polychaetes | Others | Total | G value |
|---|---|---|---|---|---|---|---|---|
| D1 & D11 | 569 | 2 578 | 55 | 24 | 6 | 19 | 2 682 | 33.26 |
| N1 & N11 | 491 | 6 841 | 196 | 65 | 105 | 33 | 7 240 | 8.20 |
| Total | | 9 419 | 251 | 89 | 111 | 52 | 9 922 | |
| G value | | 0.55 | 3.48 | 0.01 | 35.19 | 2.23 | | 41.46 |

**Table 4.** *Benthosema pterotum.* Summary of the log-likelihood ratio test performed to see the ontogenetical variation in selection of prey types. The table gives observed number in each food category. Expected values are given in parentheses

| Prey category | Fish length class in mm | | | | Total | G value |
|---|---|---|---|---|---|---|
| | ≤ 30 | 31 − 35 | 36 − 40 | 41 ≥ | | |
| Prey 1<br>Copepods | 1 314<br>(1 355) | 2 721<br>(2 629) | 4 151<br>(4 111) | 834<br>(855) | 9 020 | 2.45 |
| Prey 2<br>Other crustaceans | 51<br>(37) | 62<br>(73) | 82<br>(111) | 50<br>(23) | 245 | 38.47 |
| Prey 3<br>Molluscs | 25<br>(3) | 30<br>(25) | 18<br>(37) | 10<br>(8) | 83 | 24.17 |
| Prey 4<br>Chaetognaths/fish/polychaetes | 21<br>(16) | 16<br>(32) | 66<br>(49) | 5<br>(10) | 108 | 19.85 |
| Prey 5<br>Others | 18<br>(8) | 13<br>(15) | 17<br>(23) | 3<br>(5) | 51 | 13.07 |
| Total | 1 429 | 2 842 | 4 334 | 902 | 9 507 | |
| No. of fish | 203 | 227 | 319 | 134 | | |
| G value | 27.2 | 13.51 | 29.00 | 28.29 | | 98.01 |

gory chaetognaths/fish/polychaetes. These seem to have been found more commonly in the stomach contents of fishes caught during the night than during the day. Some of the polychaetes and chaetognaths could be overlooked in samples because of their soft-bodied nature (and therefore the tendency to be digested quickly beyond recognition). Therefore the diurnal pattern in feeding is not conclusive.

The number of items in each prey category were summed over all time periods to obtain the total number of prey in each size class of fish. Due to the small sample size it was necessary to pool the stomach contents of all fish of a certain size class, although this could bias the data on composition of the diet, if fishes of all size classes were not taken in equal proportions from all sampled times.

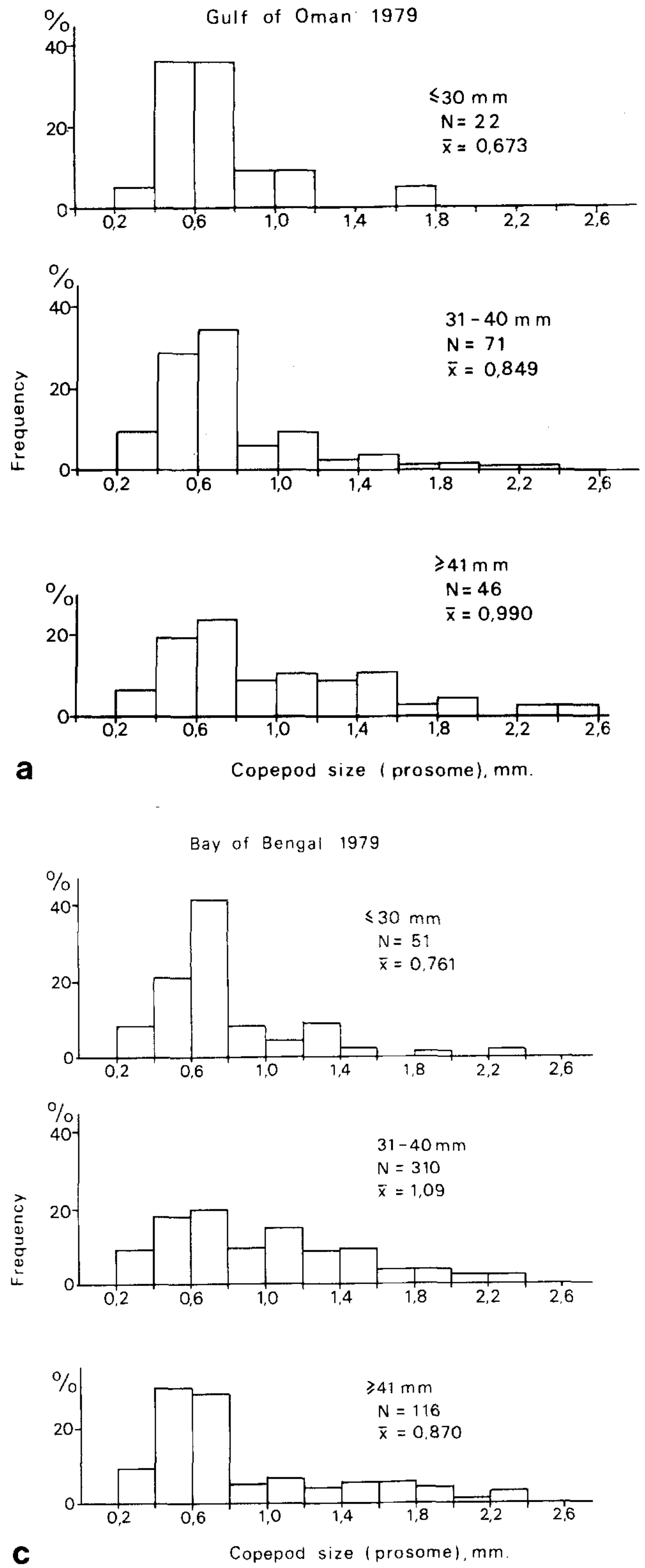
Table 4 summarizes the log-likelihood ratio test performed to see ontogenetical selection on five different types of prey categories. The different size groups have preyed upon different prey types with a significantly different frequency ($G = 98.01$, $df = 12$, $p < 0.05$). It is difficult, however, to find consistent trends, although "molluscs" and "others" seem to be over-represented in the smaller fishes and "chaetognaths etc." in the larger fishes.

## Ontogenetical variation in prey size

The size of the prey organisms eaten by different size classes of fish were analyzed to examine the ontogenetical variation in prey size selection (Figs. 4 and 5). Copepods which occurred in comparatively large numbers and were usually in a measurable state were analyzed separately.

Although in most cases the length frequency distributions were skewed toward small organisms, there was, nevertheless, a shift toward higher contributions of larger prey in larger fish. Smaller sized copepods (< 0.80 mm, prosome length) comprised an important part of the diet (40 to 80%) in the smallest size class of fish (Fig. 4). The importance of small organisms declined in the diet as the fish size increased. They contributed 40 to 70% in the diet of 31 to 40 mm fish and 18 to 65% in the diet of fish of 41 mm size and above.

In other prey organisms, the size of each prey category was summed over from all samples in all areas to obtain the mean size of prey per fish of each size class (≤ 30, 31 to 32, 33 to 34, 35 to 36, 37 to 38, ≥ 39 mm) (Fig. 6). Pooling was



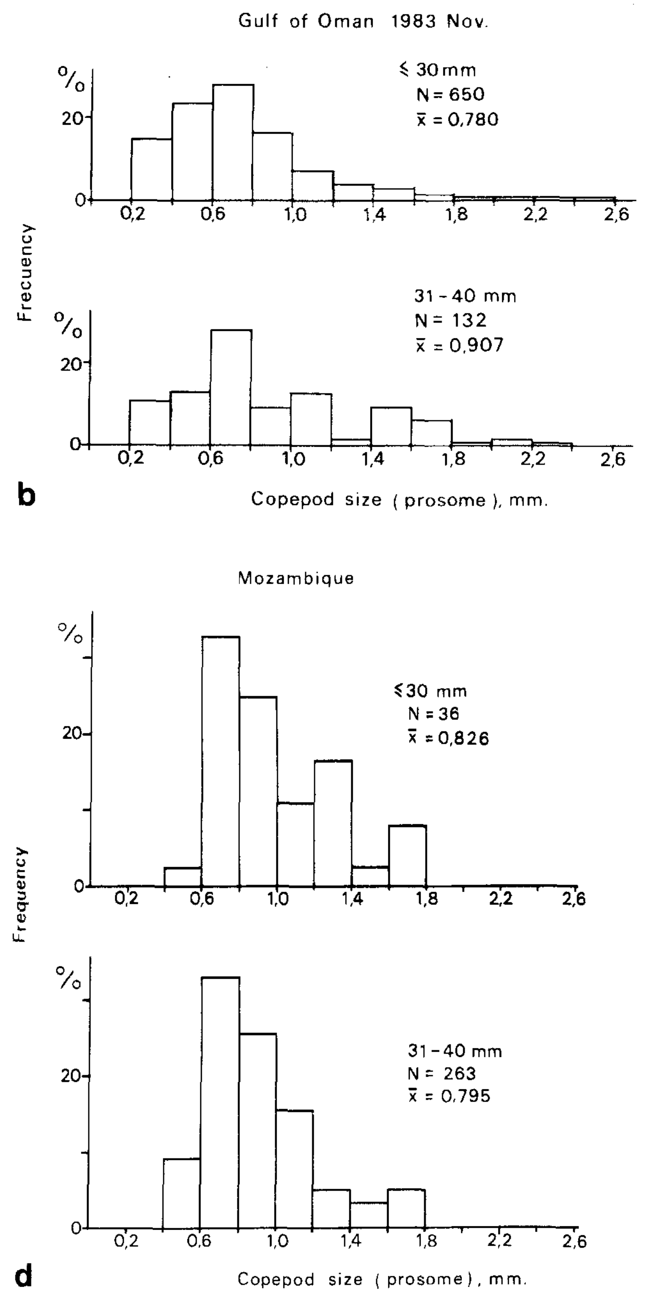




**Fig. 4.** *Benthosema pterotum*. Size distributions of copepods eaten vs different size classes (≤ 30, 31 to 40, ≥ 40 mm) of fish in (a) Gulf of Oman 1979, (b) Gulf of Oman Nov. 1983, (c) Bay of Bengal 1979, (d) Mozambique 1978, (e) Red Sea 1981 (Dalpadado 1985)

necessary as the data available were limited. Prey types were also consigned into four groups; molluscs, ostracods, other crustaceans (amphipods, crustacea larvae, euphausiids, and other groups) and the largest size group of prey which consisted of chaetognaths, polychaetes and fish.

The size range of prey ingested increased with increasing size of fish, but the minimum length did not change very much, which was also observed in the copepod size frequency distributions. The maximum length increased considerably with the fish size. In the smallest size class of fish the largest prey were about 12 mm, while the largest fish had ingested prey up to about 20 mm in length. The largest prey found in most size classes of fish were chaetognaths and fishes.

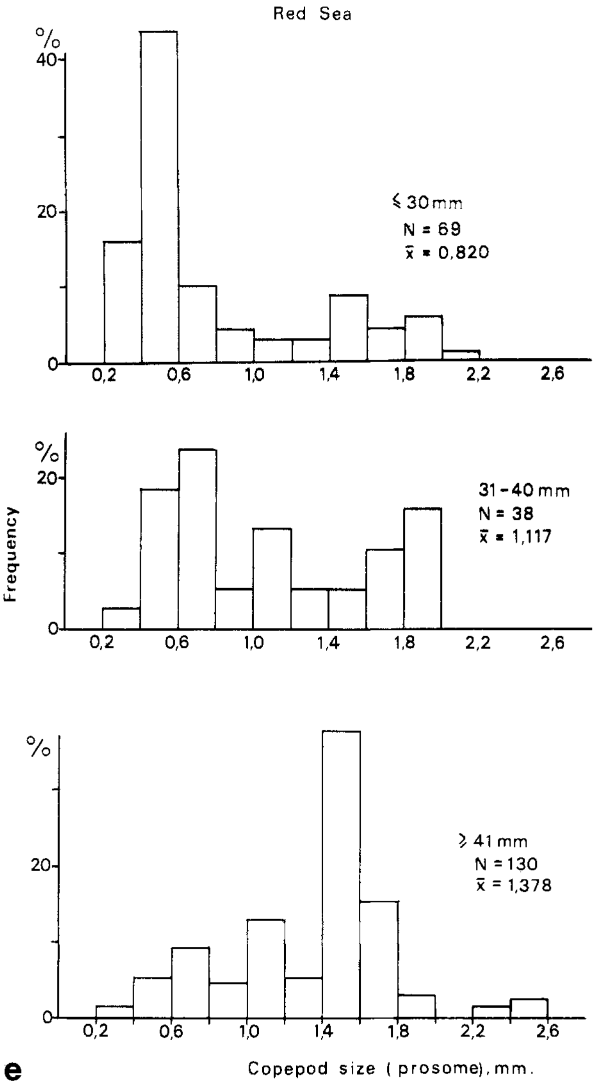



**Fig. 4e**

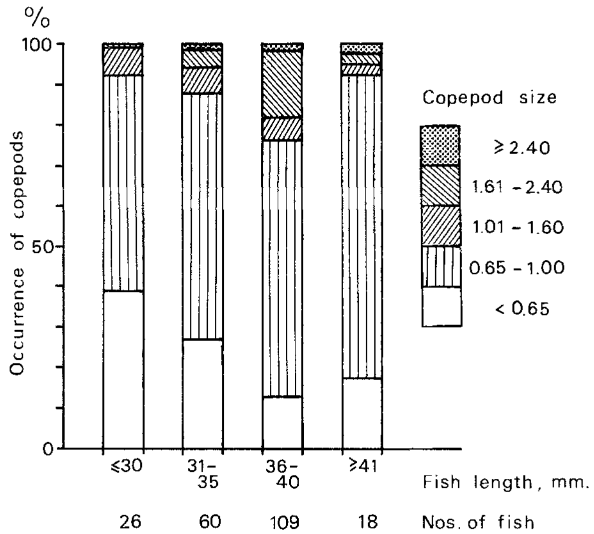



**Fig. 5.** *Benthosema pterotum.* Size distributions of copepods eaten vs different size classes of fish (≤ 30, 31 to 35, 36 to 40, ≥ 41 mm) from Gulf of Oman, Feb. 1983

## Feeding chronology

The feeding chronology was studied by analysing diurnal variation in amount of food and degree of digestion.

Fish captured during the day were characterized by a high proportion of empty stomachs (Fig. 7), increasing from about 7% in the morning (07:00–11:00 hrs) to ca. 80% in the evening (15:00–19:00 hrs). A sharp decrease in the number of empty stomachs was observed after sunset.

The highest percentages of full and distended stomachs (60%) were observed in samples taken late at night (03:00–07:00 hrs) just before decent from surface layers.

The variation in state of digestion is less clear (Fig. 8), but indicates that newly ingested and slightly digested food was common at night and much digested food was common during day.

The number of identifiable items in the stomachs is another indication of feeding cycles. Few identifiable items were found during the day (Fig. 9) in contrast to the night.

## Quantitative aspects of feeding

### Quantitative assessment of stomach filling

To see how the assessment of degree of filling of the stomachs fits with a quantitative measure of stomach content, regressions of the dry weight of stomach contents (WS) on dry weight of fish (WF) were fitted for the four subjectively assigned degrees of filling (Fig. 10).

The regressions are all significant ($p < 0.05$), although the coefficients of determination are rather low (Table 5). The mean ratio between fish weight and the weight of stomach contents increased by a factor of about 2 between the degrees of filling. The slope of the regression lines increased by a similar factor (Table 5).

The subjectively assigned degrees of filling seem to yield a reliable picture of the amount of stomach contents. It is likely that wet weight would have yielded a still closer correlation as it is more closely related to volume. A fish filled with appendicularians and one with copepods may have similar wet weights, but the copepods will have a much higher dry weight than the appendicularians because of their exoskeleton.

### Daily ration

The daily ration of a fish can be estimated using the formula

$$\frac{R}{W} = \frac{Ym}{Yf} \cdot \frac{Y}{T} \cdot 12$$

where $R$ = daily ration, $W$ = fish wet weight, $Ym$ = mean filling index for fishes where freshly swallowed prey were predominant (here taken as those with degrees of filling 4),

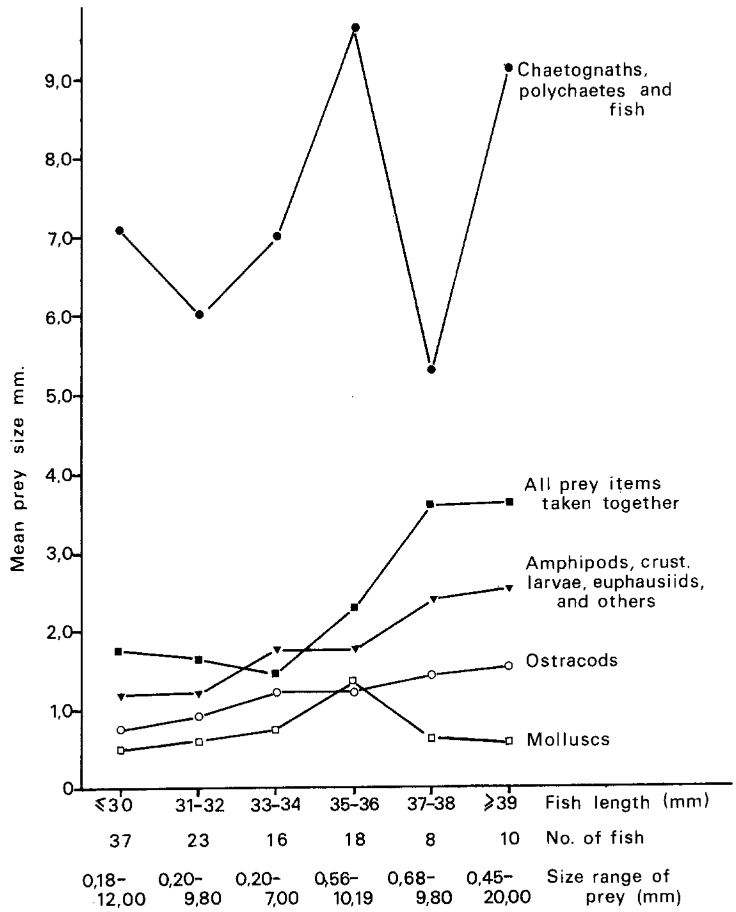



**Fig. 6.** *Benthosema pterotum.* Mean size of various food categories (except copepods) eaten

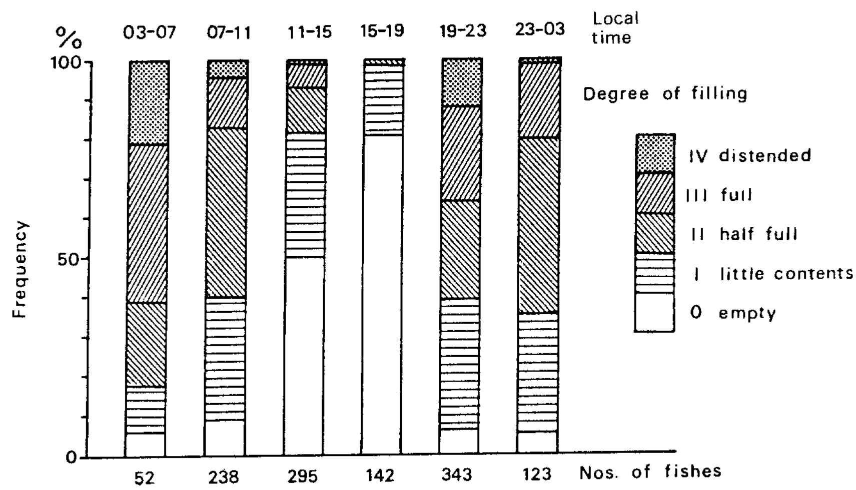



**Fig. 7.** *Benthosema pterotum.* Degree of stomach filling vs time of capture from Gulf of Oman 1979 and 1983

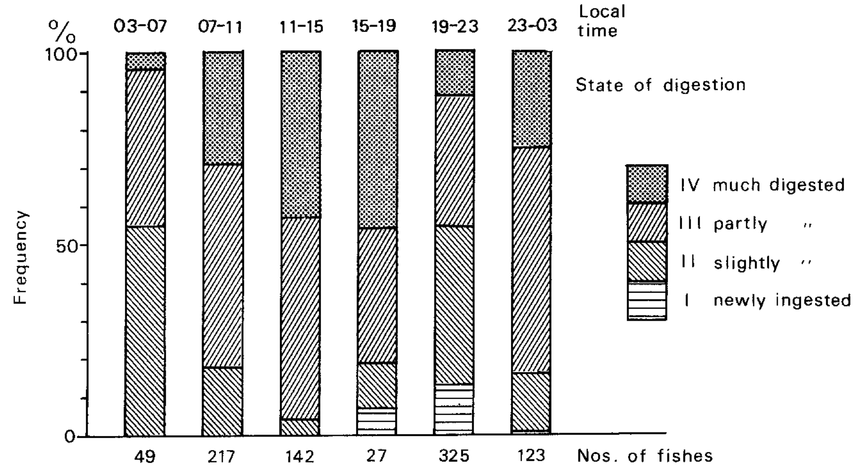



**Fig. 8.** *Benthosema pterotum.* State of food digestion of stomach contents vs time of capture from Gulf of Oman 1979 and 1983

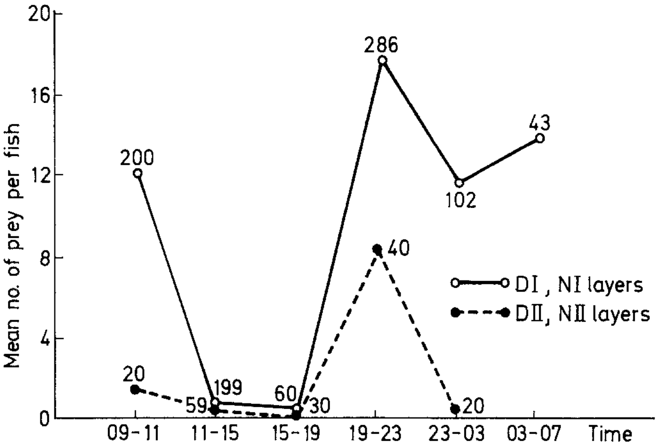



**Fig. 9.** *Benthosema pterotum.* Mean number of identifiable prey items in stomach contens vs time of capture. Numbers by data points indicate sample size of fish

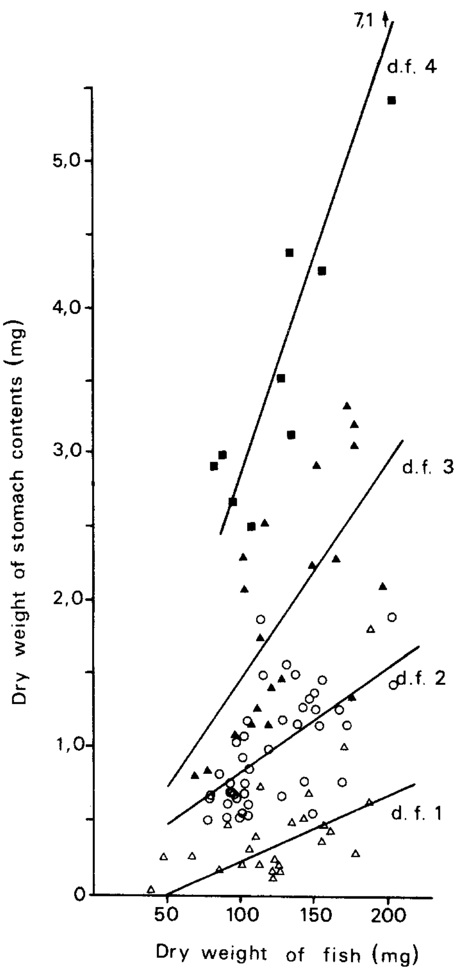



**Fig. 10.** *Benthosema pterotum.* Dry weights of stomach contents vs dry weight of fish from Gulf of Oman 1983. Regression lines for different degrees of filling (df 1–4) are shown. ▵: df 1; ○: df 2; ▴: df 3; ■: df 4)

*Yf* = mean index of filling of all fishes with stomach contents, *Y* = the mean index of filling of all fish caught (see Gorelova 1983 for further details). Filling index is taken as mean dry weight of stomach contents divided by mean dry weight of the fish.

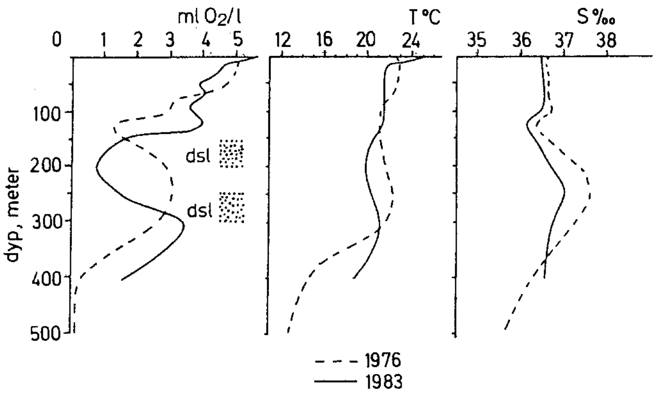



**Fig. 11.** Vertical distribution of oxygen, temperature and salinity in Gulf of Oman during cruises in 1976 and 1983. (Redrawn from Gjøsæter 1981 b and Gjøsæter and Tilseth 1983). dsl = deep scattering layer

**Table 5.** *Benthosema pterotum.* Relationship between dry weight of stomach contents and dry weight of fish for different degrees of filling from Gulf of Oman 1983. WS = dry weight of stomach contents in mg, WF = dry weight of fish in mg; a and b are regression coefficients from the regression WS = a + b WF

| Degree of filling | Regression $b \times 10^3$ | $a \times 10^3$ | $r^2$ | $N$ | WS/WF mean $\times 10^3$ | WS/WF range $\times 10^3$ | WF |
|---|---|---|---|---|---|---|---|
| 1 | 5.2 | −212 | 0.317 | 25 | 3.5 | 1.0– 6.7 | 125 |
| 2 | 7.1 | +107 | 0.359 | 41 | 8.0 | 4.4–16.6 | 122 |
| 3 | 15.0 | −0.6 | 0.409 | 20 | 14.7 | 9.8–24.1 | 132 |
| 4 | 30.0 | −184 | 0.783 | 10 | 28.6 | 21.6–35.5 | 139 |

The digestion time, *T*, can be estimated using the formula of Tseitlin (1980):

$$T = 84.1\ W^{0.31}\ Ym^{0.62}\ \{\exp(0.0806\ (20\text{-}t)\}$$

where W = wet weight of fish in grams and t = temperature in Celsius. The digestion time is given in hours till 90% of the stomach contents are digested.

Mean environmental temperature is taken as 21 °C (Fig. 11). *Ym* is taken as 0.03 (mean WS/WF for stomach filling 4). Assuming a mean fish length of 30 mm (weight 0.38 g) and a maximum index of filling of 0.03, this gives 6 h to digest 90% of the stomach contents, corresponding to a reduction from degree of Filling IV to I. Here it is assumed that the ratios between dry weights are equal to the ratios of wet weights.

*Yf* and *Y* are calculated using the distribution of stomach filling and the ratios of WS/WF in Table 5. Based on ca. 1 000 fishes, the values of *Yf* = 0.0089 and *Y* = 0.0066, were obtained.

This yields a daily ration R/W of ca. 4.5%. The mean filling will, however, be depend on the diurnal distribution of samples.

Alternatively, we can assume that a fish fills its stomach once a day. For an extended stomach this gives about 3% of the body weight (range 2.2 to 3.6%) and for a full stomach 1.5% (range 1.1 to 2.4%). The assumption of one filling a day would suggest a daily ration of 2 to 3% of the body weight a day (Fig. 10).

## Discussion

Regurgitation of food while captured in the net may influence the stomach content analyses. While fish with everted stomachs were not observed, very few with food items in the mouth were encountered. Also at the time of feeding most fishes had full or distended stomachs (see feeding chronology section). These observations indicate that regurgitation of food is not a major source of error in the present study.

Feeding in the net or cod-end could also bias the feeding analyses. Fish may encounter prey concentrations and compositions disproportionally to their natural habits while captured in the net. Studies by Hopkins and Baird (1975) and Clarke (1978) have indicated that feeding in the net is minimal for most midwater fishes. In the present study fish scales were observed in large numbers in *Benthosema pterotum*. These fishes had in general few stomach contents. All scales apparently belonged to myctophids, probably to *B. pterotum*, and these exhibited no signs of digestion. Though occurrence of fish scales in midwater fishes could be a result of net feeding, Hopkins and Baird (1975) and Kinzer (1982) have indicated that it could also be a result of active feeding of fish scales found in the water column, for nutritional purposes.

The zooplankton ingested by *Benthosema pterotum* are so small that only few are likely to be retained in the cod end. Net feeding is therefore assumed to be negligible in the present study.

### Types of prey organisms

Previous studies of fish of the family Myctophidae indicate that they are mainly zooplankton feeders. Only once has phytoplankton been found among the stomach contents of mesopelagic fishes. Investigations carried out on the diet of *Ceratoscopelus warmingii* from the tropical and sub-tropical gyre in the North Pacific revealed that this species feeds on diatoms (Robison 1984).

The most commonly reported food of myctophids is crustaceans, such as copepods, euphausiids, amphipods, ostracods and others. Other prey organisms are also important in the diet of myctophids. The most prevalent food item in the diet of the myctophid *Diaphus taaningi* was larvaceans (Baird et al. 1975), while molluscs are an important food item in the diet of *Centrobrachius nigroocellatus* (Hartmann and Weikert 1969). These findings are, however, based on a small number of observations and may not reflect the real preferences of these two myctophids. Micronektonic organisms, such as large euphausiids, fish larvae and squid larvae, are also preyed upon by myctophids, especially by the large fishes.

As in most other studies, crustaceans, in particular copepods, dominated the diet of *Benthosema pterotum*. Kinzer (1977), Gjøsæter (1981 b) and Kubota (1980) made similar observations on this species from tropical and sub-tropical waters. The importance of copepods in the diet of *B. pterotum* was clearly evident in the current study, as it constituted ca. 40 to 90% by number of the diet in most fishes, in all areas examined. Dry weight analyses on stomach content of specimens from the Gulf of Oman in February 1983 revealed that copepods constituted ca. 35 to 60% (average in samples) by biomass irrespective of the size class of fish (Fig. 2).

The variation in copepod species observed between the stomachs of *Benthosema pterotum* was rather small. Of the cyclopoid copepods observed in the diet of *B. pterotum*, *Corycaeus* sp., *Oncaea* sp. are regarded to be carnivorous (Dowidar and El-Maghraby 1970, Okera 1974). The calanoid copepods identified in the stomach contents of *B. pterotum* ranged from strictly herbivorous filter feeders to omnivorous and carnivorous species (Anraku 1963, Gaudy 1972, Arashkevich 1975, Moraitou-Apostolopoulou 1975, O'Connor et al. 1976). Among the calanoids the herbivorous group was dominated both in terms of numbers and of biomass, especially due to the relatively high abundance of *Eucalanus tenuis* and *Acartia danae*.

The copepods observed in the stomach content of *B. pterotum* are all epipelagic or near surface dwelling species (Dowidar and El-Maghraby 1970, Heinrikh 1971, Gaudy 1974, Okera 1974, Hulsemann and Fleminger 1975, Weikert 1975), though some, especially *Euchaeta marina*, is also frequently found in deeper waters (Roe 1972).

Diet preferences of *Benthosema pterotum* in relation to its environment could not be investigated since no plankton samples were available from similar time/depth series. Inter-regional differences in the diet were observed for *B. pterotum* (Table 1). Although copepods dominated the diet of this species in all areas examined, the relative importance of other prey types differed in various regions. This probably reflects the relative abundances of various prey species in different regions. Inter-regional differences in the diet reveal the ability of this species to ingest whatever prey is of suitable size and is available. Geographical differences in diet of midwater fishes were reported by Hopkins and Baird (1977). Examining the diet components of nine species of mesopelagic fishes, they revealed that the least inter-regional differences in the diet at higher taxonomic levels seem to occur in species which are relatively small as adults (15 to 30 mm).

### Seasonal variation in diet composition

It was not possible to examine the seasonal variation in diet in detail due to inadequate coverage of samples at different times. At higher taxonomic levels, *Benthosema pterotum* did not exhibit much variation in prey types taken at different times of the year. Pronounced shifts in relative abundances of various prey species in different seasons have been observed for other midwater fishes by Collard (1970), Gjøsæter (1973) and McCrone (1981).

## Diurnal variation in diet composition

Although the observations made on diurnal variation in diet may suggest that some feeding takes place both during the day and at night, and that the prey differs, they are not conclusive. To discuss this in further details, data on diurnal variation in plankton distribution is necessary.

## Ontogenetical variation in diet

The material available indicates that *Benthosema pterotum* of different size classes ingest similar types of prey, although the proportions of individual prey category sometimes varied considerably between the size class of fish. For example, the larger fishes (>36 mm) seem to eat more large prey such as chaetognaths, fish larvae, polychaetes (Table 4). Collard (1970), found no correlation between the size of lanternfish *Stenobrachius leucopsaurus* and the food category. Studies on ontogenetical variation in the diet of hatchetfish *Sternoptyx diaphana* also indicate that fish of four length categories had similar average prey diversity per stomach (Hopkins and Baird 1973).

Larger fishes tend to graze upon larger prey organisms within a given category (Figs. 4, 5 and 6). As the fish size increased, there was a prononced shift towards larger prey such as chaetognaths and fish larvae. However, the larger fish did not exclude the smaller prey organisms from the diet. In examining the ontogenetic selection on copepods, which were the most important food item in most fishes, it was clearly evident that the larger fishes ingested fairly small copepods (<0.80 mm) in addition to increasing proportions of larger copepods. *Benthosema pterotum* in general ingested prey of less than one third of its own body length, but on some occasions took prey over half its body size. Gorelova (1978) and McCrone (1981), report similar findings in other myctophids. Ontogenetic differences in the size of prey organisms have also been recorded for other midwater fishes (Tyler and Pearcy 1975, Hopkins and Baird 1977, Rowedder 1979, and Kawaguchi and Mauchline 1982).

## Feeding chronology

*Benthosema pterotum* is a vertically migrating species which undergoes diel changes in environmental parameters for numerous factors such as oxygen, salinity, temperature (Gjøsæter 1981 b, Gjøsæter and Tilseth 1983, present Fig. 11) and prey concentrations. Migration towards the surface at night seems to be associated with feeding as a large proportion of fish caught in the uppermost layers had full or distended stomachs and had food in a slightly digested condition. Feeding seems to occur to a lesser extent during the day.

This feeding pattern is also supported by the analysis of copepod species in the stomach contents, indicated by the fact that mostly epipelagic species were identified.

Analysis of number of intact prey items per fish through time provide further evidence of diel periodicity in the feeding of *Benthosema pterotum*. Although intact prey items were most frequently observed in samples taken at night, some were found at all times. This does not necessarily indicate that feeding had taken place throughout as some prey items may remain intact for long periods. Information on digestion rates of midwater fishes is sparse (Clarke 1978), therefore it is difficult to predict for how long different prey items could remain intact in the stomachs of these fishes. Combination of data from the Gulf of Oman region taken at different times/years may have affected the feeding periodicity observed as changes in temperature, prey availability and prey size in different localities and seasons could influence the results. Dalpadado (1983) analysed the areas and seasons separately and found no clear differences.

McCrone (1981) reviews some studies carried out on the feeding chronology of mesopelagic fishes and discusses shortcomings of most of the general methods used, and their implications on the interpretation of data. Nevertheless, the main feeding period suggested for *Benthosema pterotum* seems to agree with the general feeding pattern of some myctophids from tropical and subtropical waters (Holton 1969, Gorelova 1974, Baird et al. 1975, Kinzer 1977, Clarke 1978).

## Daily food ration

Gorelova (1983) calculated daily rations for some of the surface migrating myctophids in the equatorial Pacific Ocean and found values of 4 to 17%. Clarke (1978) estimated that *Myctophum proximum* (18 to 46 cm SL) consumed 5.7% of its dry body weight per day in Hawaiian waters. Hopkins and Baird (1985) studying *Lampanyctus alatus* from the Eastern Gulf of Mexico found a daily food consumption of 2.4 to 4.4% of the body weight for fish between 25 to 45 mm SL. The smallest fish had the highest percentage. All these studies were based on analyses of stomach filling.

Childress et al. (1980) used a different approach, calculating the energy requirements of some mesopelagic fishes off California. They estimated a daily energy requirement of 0.87% of the energy content of the fish per day as the average for the life cycle. Taking the first age group of fish (mean size 28 mm SL), compensating for different energy content in the fish and its food, and also compensating for temperature differences, they found that a small tropical myctophid should eat ca. 5% of its dry body weight per day.

An estimated food requirement of 4.5% of body weight per day for *Benthosema pterotum* fits well with other studies, though the methods used were crude, and based on many uncertain assumptions.

We can assume that *Benthosema pterotum* grow from 10 to 40 mm in 250 d (based on growth estimates of this species by Gjøsæter 1981). This corresponds to an increase of 0.93 g in wet weight or an average daily growth of 3.70 mg.

Assuming daily ration of 4.5%, the average daily food intake will be ca. 11 mg (an average fish is taken to be 25 mm in standard length and 250 mg wet body weight). This would correspond to a growth efficiency of ca 34%. Mesopelagic fishes are supposed to have high growth efficiencies (Childress et al. 1980). If in our calculations we had used the lowest values calculated for food consumption (2 to 3% per day) we would obtain even higher efficiencies.

## Food consumption compared to primary production

If we assume that the ratio between dry weight and wet weight for fish and their prey is similar, this means that a fish stock of $10 \times 10^6$ tons, which could be a reasonable average for the Gulf of Oman, would take 450 000 tons (wet weight) of food per day. From the figures of Cushing (1973) the mean primary production in the Gulf of Oman could be ca. 260 g C $m^{-2}$ 180 $d^{-1}$ during the South West monsoon. Although no data are available for the North East monsoon 100 g C $m^{-2}$ 180 $d^{-1}$ could be a reasonable figure. These volumes can be converted to wet weight using the factor 0.065 (Cushing 1971). Assuming that the area studied is about $9 \times 10^{10}$ $m^2$ the average daily primary production would be 1 400 000 tons (wet weight) a day.

Therefore the ratio primary production/fish consumption would be around 3. Even if the fishes feed exclusively on herbivorous plankton, this would indicate an unrealistic high efficiency.

From the data on stomach contents it seem reasonable to assume that *Benthosema pterotum* obtains between ½ and ⅔ of its food from herbivorous animals and the rest mainly from first level carnivores. This would make the ratio between primary production and fish consumption still more unrealistic.

It has also been shown in other areas that the production of mesopelagic fishes is higher than might be expected from estimates of primary production (Clarke 1973). No satisfactory explanation has been offered, although higher efficiency than expected in oceanic waters (Greze 1970) or bacterio-plankton production (Vinogradov 1973) have been suggested as possible reasons.

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