

## Resource-partitioning and predation impact of a low-latitude myctophid community

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**Abstract.** This study, based on data collected during summer 1985 in the eastern Gulf of Mexico, examined the degree of overlap in two prime niche parameters, space and food, in 17 of the most abundant myctophid species which inhabit the epipelagic zone at night. Cluster-analyses of vertical distribution information and diet characteristics revealed that while large groups of species overlapped (>60%) in either vertical distributions or diet, when both niche parameters were considered together, little interspecific or intraspecific (size class) overlap occurred. Our data suggest that for myctophids, trophic competition is reduced through resource-partitioning, although with considerable overlap at niche boundaries. Niche separation presumably is the result of competition during the evolution of the ecosystem and is maintained presently as “diffuse competition”: the effect on a species of the combined competition from all other species at that trophic level. We suggest that the large degree of niche overlap enables the “packing” of over 50 myctophid species in the epipelagic zone at night. Our calculations indicate that myctophid predation nightly removes 2% of the zooplankton biomass. Myctophid predation is selective in that greatest pressure is on certain size classes and types of prey (copepods, ostracods and euphausiids). In the case of copepods, impact is greatest on the larger, more mature stages and hence on the breeding population. It is estimated that myctophids account for at least one-third of the daily production of zooplankton removed from the epipelagic zone by micronekton in the eastern Gulf.

### Introduction

Low-latitude oceanic ecosystems are among the most ancient on earth, and are characterized by their stability and high species diversity (Hayward and McGowan 1979, McGowan and Walker 1979, Lehman 1988). A frequently revisited topic is the mechanism for coexistence among so many species which share the “structureless” upper

layer, the epi-mesopelagic zone, of these oceans. This is the fundamental “Santa Rosalia” problem considered in Hutchinson’s (1959, 1961) papers on species coexistence in biologically diverse environments. In the upper 600 m of the North Central Pacific, for example, over 200 species of copepods and 250 species of midwater fishes occur (Hayward and McGowan 1979, Barnett 1983). In contrast, in freshwater habitats, which are geologically more ephemeral, pelagic diversity is an order of magnitude less, even in tropical lakes (MacArthur 1972, Lehman 1988). Given the environmental stability of low-latitude oceanic ecosystems, the principal factors determining niche parameters would be predicted to be biological (McGowan and Walker 1979). This is in contrast to freshwater, estuarine, and high-latitude oceanic systems, which are regulated more by variability in physical factors (Koslow 1983, Lehman 1988).

An expected feature of spatially-packed species-complexes in ecosystems which are regulated by biological pressures would be resource-partitioning, especially of space and food resources (e.g. Domanski 1984). This should be particularly apparent in geologically old, stable ecosystems, where relationships could be fine-tuned over millenia to minimize competition and maximize overall ecosystem stability. Evidence for resource-partitioning and competition in the marine pelagial, however, is equivocal. McGowan and Walker (1979), in their study of the north Central Pacific copepod assemblage, found recurrent groups which, although broadly subdividing the water column, demonstrated a high degree of intra-group spatial and dietary concurrence. They observed that the closer the taxonomic relationship, the greater the niche overlap. In the absence of strong evidence for resource-partitioning they suggested that ecosystem structure may be regulated more by predation than by food limitation (see also Donaldson 1975, Domanski 1984). They proposed that heavy predation exacts such a toll that surviving prey have adequate food, and trophic competition is consequently minimized. Hayward and McGowan (1979) were aware of the paradoxes generated by the predation-control hypothesis and recognized the

conceptual difficulty of having the trophic levels immediately above and below copepods simultaneously regulated by predation. They stated that these trophic levels would be resource-limited, which implies competition. They cautioned that lack of evidence for resource-partitioning does not necessarily support the idea that predation is the only factor regulating community structure. In contrast to Hayward and McGowan, Domanski (1984) and Clarke (1978) both suggested that resource-partitioning does occur in midwater fishes, which implies that competition also has an important role in regulating community structure in the ocean.

Midwater fishes occupy the next trophic level above copepods in pelagic ecosystems and have certain advantages over copepods as subjects for the study of resource-partitioning, particularly of food resources. Their food is larger and is swallowed whole; it is therefore more readily identified and quantified. In the present paper, we examine the spatial distribution and aspects of the trophic ecology of the myctophid community in a low-latitude oceanic ecosystem. Over 50 species of this family occur at night in the epipelagic zone of the eastern Gulf of Mexico (Gartner et al. 1987, Gartner unpublished data) which, if not a direct analog, is quite similar in species composition to the tropical-subtropical Atlantic (Backus et al. 1977, Hulley and Krefft 1985). Our approach is to reveal, through hierarchical clustering procedures, the degree of vertical spatial and dietary overlap in 17 of the most abundant of these species and thus the degree to which resource-partitioning occurs in two principal niche parameters, space and food.

We also present estimates of predation impact of the post-larval myctophid populations on their zooplankton food resource. Myctophids constitute the dominant group of vertically migrating oceanic fishes, and account for the largest share of fish biomass in the epipelagic zone at night (Maynard et al. 1975, Hopkins and Lancraft 1984), the period of most active feeding. If predation is indeed a major factor in regulating population dynamics, patterns of relative abundance, and community composition of zooplankton, as suggested by McGowan and Walker (1979), then a substantial prey-removal rate should be apparent.

## Materials and methods

All collections were from within a circle of 18 km radius centered at 27°N, 86°W ("Standard Station"; Gartner et al. 1987) in the eastern Gulf of Mexico. The nets used were 1.8 × 1.8 m and 1.8 × 3.6 m opening-closing Tucker trawls and a 2 m<sup>2</sup> neuston net. The 1.8 × 3.6 m Tucker trawl had a 4 mm bar-mesh body, the 1.8 × 1.8 m trawl nets were either of 1.67 or 4 mm bar-mesh and the neuston net was of 0.5 mm-mesh. The cod ends of the Tucker trawls were 0.5 mm-mesh plankton nets. To minimize bias from net feeding, a "fish catcher" sleeve was used in all trawls which caught fish for diet analysis. This 4 mm bar-mesh sleeve was inserted ahead of the cod-end plankton net to retain fish while allowing zooplankton to pass through to the cod end (see Hopkins and Baird 1975). Fishes examined for diets came from collections made on a cruise in July 1985, one of a series of seven cruises made to Standard Station from September 1984 to March 1987. Several additional collections with the neuston net (September 1988) were also used for diet analysis of near-surface species, but no fish catcher was installed. Trawling

depth for the Tucker trawls was monitored on deck through conducting cable and a depth transducer, and a time-depth recorder was attached to each trawl to obtain a depth trace.

Three types of hauls were made: surface tows, discrete-zone trawls and oblique trawls. The surface was sampled with neuston nets in 30 min tows; discrete zones, which consisted of eight 25 m strata in the upper 200 m, were sampled with the Tucker trawls in 60 min tows; oblique hauls were made with open Tucker trawls which traversed the upper 200 m in 60 min tows. All Tucker trawl tows occurred at night during the new-moon phase between 21.00 and 05.00 hrs. Physical data from the water column were obtained during the cruise at regular time intervals with expendable bathythermograph and conductivity-temperature-depth casts.

Catches were preserved in 10% v/v buffered formalin and subsequently transferred to 50% isopropanol. Myctophids were identified to species and measured to the nearest millimeter standard length (SL), with all species counts being prorated to volume of water filtered (nos./km<sup>2</sup> in upper 200 m). The 17 species used in the analysis are listed in Table 1. Fish species were divided into 10 mm-interval size classes, with Size Classes 1, 2, 3, 4, and 5 representing 11 to 20 mm, 21 to 30 mm, 31 to 40 mm, 41 to 50 mm and >51 mm fishes, respectively. From the discrete-haul data, the portion of each size class of each species which occurred in each 25 m depth zone was expressed as a percent of the total population of that size class. The sum of these percentages for each of the eight discrete tow zones therefore totaled 100% of the population of that size class of that species in the upper 200 m. The vertical distribution data were subjected to hierarchical cluster analysis to discern spatial associations among species and size classes. Each size class was treated as a separate unit because of observed vertical separation of myctophid size classes related to ontogeny (Badcock 1970, Gibbs et al. 1971, Clarke 1973, Willis and Percy 1980, Hulley 1981, Gartner et al. 1987). Vertical distributions of all size classes of all species were first compared in pairs using the Bray-Curtis similarity test (Bray and Curtis 1957). The similarity indices were then clustered using Ward's estimate of cluster distance (Field et al. 1982, Sarle 1982). In the clustering procedure, dissimilarity (= 1 - Bray-Curtis-similarity index) rather than similarity was used, with 40% dissimilarity (= 60% similarity) being accepted as the level of significant vertical niche separation (see "Discussion - Resource partitioning").

For diet analysis, the entire gut was removed and data from both stomach and intestines were recorded. Food items were identified to the lowest taxonomic level possible, counted, and measured to the

**Table 1.** Species and size classes of the myctophid assemblage in the eastern Gulf of Mexico (July 1985) included in this study. Size classes were: 1, 11 to 20 mm; 2, 21 to 30 mm; 3, 31 to 40 mm; 4, 41 to 50 mm; 5, ≥ 50 mm

Species	Code	Size classes
<i>Bolinichthys photothorax</i>	Bp	2, 3
<i>Benthosema suborbitale</i>	Bs	1, 2
<i>Centrobranchus nigroocellatus</i>	Cn	1
<i>Ceratoscopelus cf. warmingii</i>	Cw	1-4
<i>Diaphus dumerilii</i>	Dd	1-3
<i>Diaphus lucidus</i>	Dl	3-5
<i>Diaphus mollis</i>	Dm	2, 3
<i>Diaphus perspicillatus</i>	Dp	4
<i>Diaphus splendidus</i>	Ds	2, 3
<i>Diaphus taaningi</i>	Dt	5
<i>Hygophuan hygomii</i>	Hh	5
<i>Lampanyctus alatus</i>	La	1-4
<i>Lepidophanes guentheri</i>	Lg	1-5
<i>Lobianchia gemellarii</i>	Lm	2
<i>Myctophum affine</i>	Ma	1-3
<i>Notoscopelus resplendens</i>	Nr	2-5
<i>Notolychnus valdiviae</i>	Nv	1, 2

nearest 0.1 mm. In cases of fragmented prey, key morphological characteristics were measured ( $\pm 0.01$  mm), and these measurements were converted to total prey length using regressions (Hopkins unpublished data). The most frequent measurements were of copepod mandible width, metasomal organ width (in the copepod genus *Pleuromamma*), euphausiid eye diameter, ostracod 2nd basipod antenna length, and chaetognath seizing-hook length. Biomass of food items was estimated from regressions of dry weight on prey length for each type of food (Hopkins unpublished data). Dry weight biomass was used because this measure approximates caloric content of ration and was considered a much more useful niche parameter than prey numbers (e.g. *Oncaea* spp. copepods were often a numerical dominant in myctophid diets yet contributed little to total food biomass).

Diet information was ordered into both taxonomic and prey-size categories. Fourteen general taxonomic categories were defined: copepods, ostracods, amphipods, euphausiids, decapods, larvaceans, salps, siphonophores, unidentified gelatinous tunic, polychaetes, molluscs, chaetognaths, fishes and other food. To obtain greater detail in comparisons of spatially co-occurring species with similar diets, copepod-biomass data were further divided into 37 taxa. Diet-size categories were divided into 1 mm intervals up to 10 mm, with three additional larger categories of 10 to 14.9 mm, 15 to 19.9 mm and  $\geq 20$  mm.

Diet composition was analyzed by fish species and size class using the same myctophid size-intervals as in the fish vertical-distribution analysis. The biomass of food in each taxonomic category was calculated as percent of the total diet. This was also done for the biomass of food items in each of the 13 prey-size categories. Diet similarity indices were then obtained for the taxonomic and size-distribution data for all myctophid category pair-combinations using the Bray-Curtis index. The similarity indices were subjected to cluster analysis as was done for myctophid vertical distribution, and 40% dissimilarity (=60% similarity) was again used as the criterion for niche separation of diets between and within (different size classes) species.

A summary pairs-matrix was prepared to determine which (if any) myctophid taxa shared the same vertical distribution and diet characteristics, i.e., were concordant in these primary niche parameters at the level of 60% overlap (=40% dissimilarity). The matrix consisted of all pair combination of the 41 species and size classes of myctophids analyzed, where each pair (820 pair-combinations) was evaluated for similarity in vertical distribution and taxonomic and size composition of diet. The resulting table was too large for inclusion in this paper.

Diet diversity indices were calculated for both taxonomic and size distribution of diets. This was done by substituting percentages of each kind or size class of food into the modification of the information index,  $D$  (Travers 1971):

$$D = \log_2 N - 1/N \sum n_i \log_2 n_i,$$

where:  $D$  = the diversity index for diet taxonomic composition or food size distribution, the range of  $D$  for the former is 0 to 3.8 and for the latter, 0 to 3.7;  $N$  = the total percentage (=100%) of all kinds or size classes of food in terms of biomass; and  $n_i$  the percentage of biomass of a single kind or size class of food.

Predation impact of the post-larval myctophid population on zooplankton was calculated for the epipelagic zone at night, with this estimate being based on the July 1985 collections in the upper 200 m. The zooplankton groups considered were total copepods, the copepod genus *Pleuromamma*, ostracods and euphausiids. Three kinds of information were used in the predation calculations: data on myctophid abundance, estimates of myctophid nightly food ration and data on zooplankton abundance in the upper 200 m.

Nightly ration of selected prey types was determined from the diet-analysis results. Numbers of prey ingested (stomach plus intestine contents) was calculated at two levels, average and maximum nightly ration. Average nightly ration was the mean value for the fish sample, while maximum ration was based on the average value of the five fullest guts. The supposition here is that the actual mean ration for the population falls within this range. The fish samples

analyzed for nightly ration were all collected between 02.00 and 05.00 hrs; hence, after a considerable period of foraging. Average nightly ration of a fish sample potentially underestimates true nightly ration because fish taken near 02.00 hrs would not have had the opportunity of obtaining their full nightly ration. The average for the five fullest stomachs, on the other hand, may overestimate actual mean nightly ration because these individuals may have had above-average feeding success. Food item counts for the 16 large (>25 fish) samples used in this analysis show that the maximum number of items ( $\bar{x}$  of 5 highest counts) was approximately double ( $\bar{x} = 1.9$ ;  $SD = 0.4$ ) that of the sample average. The midpoint, i.e.,  $1.5 \times$  average sample ration, was consequently used as an estimate of true nightly ration in the predation-impact model. There is some evidence to support our selection of this midpoint value. Data for *Lampanyctus alatus* (Hopkins and Baird 1985) show that an intermediate value between the two nightly ration levels was nearly identical to the total daily ration as determined with the Elliot and Persson (1978) gut-evacuation method, and was similar to Clarke's (1978) estimates of daily rations for myctophids off Hawaii. Nightly rations for all species were summed for the 200 m zone to estimate total predation impact in the epipelagic zone by the post-larval myctophid population.

Information on zooplankton abundance and vertical distribution in the upper 200 m was obtained from collections made with 162  $\mu\text{m}$ -mesh, 44  $\times$  44 cm collapsible plankton nets. These nets, fitted with flowmeters, were suspended in the mouth of Tucker trawls and opened and closed in synchrony with the trawls. The data used here were from ten nighttime discrete-zone hauls in eight 25 m strata of the upper 200 m during July 1985. Zooplankton were identified, counted, and measured ( $\pm 0.1$  mm) in two 1/64th aliquots of each sample, and the results averaged. Supplementary information on the abundance of zooplankton <1 mm was obtained with 30-liter bottle collections made at 25 m intervals in the upper 200 m in July 1985. Water was filtered through 30  $\mu\text{m}$ -gauze, and counts and measurements were made on the sievings in 10  $\times$  10 cm transparent plastic trays with gridded bottoms. The vertically integrated data for net and bottle catches yielded information on each major prey group which could be expressed in the same quantitative (nos./km<sup>2</sup>) units as myctophid abundance.

## Results

### Eastern Gulf hydrography

The physical characteristics of the eastern Gulf of Mexico in the vicinity of 27°N, 86°W are similar to those of other non-upwelling oceanic areas at low latitudes (McGowan 1974, Longhurst 1976), and have been detailed in previous papers (Hopkins 1982, Gartner et al. 1987). The eastern Gulf has two kinds of oceanic water in the epimesopelagic zone, the Loop Current of tropical Caribbean origin which intermittently penetrates into the eastern Gulf as an anticyclonic gyre, and residual Gulf water. All sampling reported here was in residual Gulf water, and temperature profiles encompassing the seasonal range at 27°N, 86°W are given in Hopkins et al. (1989).

Residual water is typified by low primary production (El-Sayed 1972, Hopkins unpublished data), and has zooplankton standing stocks comparable to that of other oligotrophic areas (Hopkins 1982). Faunal diversity is high; the major components of the zooplankton and micronekton communities have been quantified in papers by Hopkins (1982) and Hopkins and Lancraft (1984). Community structure and faunal components of the pelagic community which persist at 27°N, 86°W are essen-

**Table 2.** Nighttime vertical distribution of 17 myctophid species in epipelagic zone of eastern Gulf of Mexico (July 1985). Species and size-class codes as in Table 1. —=0%

Myctophid species and size class	(Nos./km <sup>2</sup> ; 0–200 m)	% of population at:							
		0–25 m	26–50 m	51–75 m	76–100 m	101–125 m	126–150 m	151–175 m	>176 m
<i>Bp</i> 2	(750)	—	—	67.0	33.0	—	—	—	—
3	(250)	—	—	—	—	100	—	—	—
<i>Bs</i> 1	(52 250)	18.2	38.8	24.9	7.7	2.9	3.4	2.9	1.4
2	(53 750)	8.4	43.7	22.3	2.8	19.5	—	2.8	0.5
<i>Cn</i> 1	ND	100	—	—	—	—	—	—	—
<i>Cw</i> 1	(10 750)	2.3	27.9	18.6	30.2	20.9	—	—	—
2	(16 750)	3.0	9.0	17.9	28.4	29.8	—	—	11.9
3	(18 500)	—	—	21.6	24.3	17.6	20.3	16.2	—
4	(11 750)	—	—	17.0	40.4	21.3	8.5	—	12.8
<i>Dd</i> 1	(117 000)	20.5	44.9	15.0	9.6	3.0	4.7	1.3	1.1
2	(67 500)	5.6	33.3	15.9	23.3	7.0	4.1	7.0	3.7
3	(41 000)	1.8	13.4	36.6	28.7	7.9	4.3	7.3	—
<i>Dl</i> 3	ND	ND	—	—	—	—	—	—	—
4	(2 000)	—	—	—	25.0	12.5	50.0	—	12.5
5	(4 750)	—	—	—	5.3	21.0	36.8	31.6	5.3
<i>Dm</i> 2	(5 250)	—	14.3	33.3	38.1	14.3	—	—	—
3	(6 750)	—	—	25.9	25.9	11.1	14.8	22.2	—
<i>Dp</i> 4	(500)	—	—	—	—	100	—	—	—
<i>Ds</i> 2	(3 500)	—	28.6	—	14.3	14.3	—	42.9	—
3	(2 000)	—	—	37.5	25.0	37.5	—	—	—
<i>Dt</i> 5	(500)	—	—	—	100	—	—	—	—
<i>Hh</i> 5	ND	ND	—	—	—	—	—	—	—
<i>La</i> 1	(15 000)	3.3	35.0	25.0	25.0	5.0	6.7	—	—
2	(31 000)	4.0	24.2	33.1	14.5	6.4	15.3	—	2.4
3	(22 500)	—	14.4	46.7	10.0	10.0	7.8	6.7	4.4
4	(14 250)	—	7.0	33.3	14.0	5.3	12.3	21.0	7.0
<i>Lg</i> 1	(39 250)	31.2	36.3	19.1	4.5	1.9	2.5	3.8	0.6
2	(50 000)	19.5	38.0	16.0	3.0	0.5	11.0	9.5	2.5
3	(35 000)	15.7	37.1	26.4	5.7	3.6	—	8.6	2.9
4	(27 000)	2.8	7.4	27.8	22.2	19.4	6.5	11.1	2.8
5	(19 500)	1.3	7.7	14.1	29.5	17.9	9.0	15.4	5.1
<i>Lm</i> 2	(5 000)	—	—	35.0	30.0	15.0	20.0	—	—
<i>Ma</i> 1	ND	100	—	—	—	—	—	—	—
2	ND	100	—	—	—	—	—	—	—
3	ND	100	—	—	—	—	—	—	—
<i>Nr</i> 2	(500)	—	—	50.0	—	50.0	—	—	—
3	(2 250)	11.1	—	11.1	22.2	—	44.4	—	11.1
4	(7 250)	—	6.9	6.9	58.6	10.3	13.8	—	3.4
5	(3 000)	—	—	8.3	33.3	25.0	33.3	—	—
<i>Nv</i> 1	(304 250)	1.4	36.3	30.4	13.5	10.4	3.9	3.1	1.0
2	(5 750)	—	—	52.2	8.7	13.0	—	26.1	—

tially the same as in the Caribbean Sea and tropical-subtropical Atlantic Ocean (Young and Roper 1969, Donaldson 1975, Michel and Foyo 1976, Backus et al. 1977, Heffernan and Hopkins 1981, Gartner et al. 1989, Hopkins et al. 1989, Passarella and Hopkins 1991, Flock and Hopkins 1992).

#### Cluster analysis

A total of 17 myctophid species and 41 size categories (Table 2) were examined for this study. Thirty-nine of these size categories from all species were used for the myctophid vertical distribution data. These formed 12 clusters at the 40% dissimilarity level (Fig. 1), with half of the myctophid categories (51%), and most of the myc-

tophid population numbers (97%) occurring in Clusters 2 and 3. These were centered at 25 to 75 m and 50 to 125 m, respectively. Clusters 4, 5, and 7 were all similar in that they grouped species which had polymodal vertical distributions. They included several size classes each of *Diaphus splendidus* (Size Classes 2, 3), *Lampanyctus alatus* (Size Classes 3, 4) and one size class each of *Notoscopelus resplendens* (2) and *Notolychnus valdiviae* (2). Cluster 12 was readily separable from the others in having species which centered in the upper 25 m. This cluster included *Centrobranchus nigroocellatus* (1) and *Myctophum affine* (1–3), species which primarily inhabit surface waters (Gartner et al. 1987) at night. The remaining five clusters, 6, 7 and 9 to 11, all consisted of single myctophid size-class and/or species categories. Where multiple size-class data were available, the general pattern was

CLUSTER CHARACTERISTICS

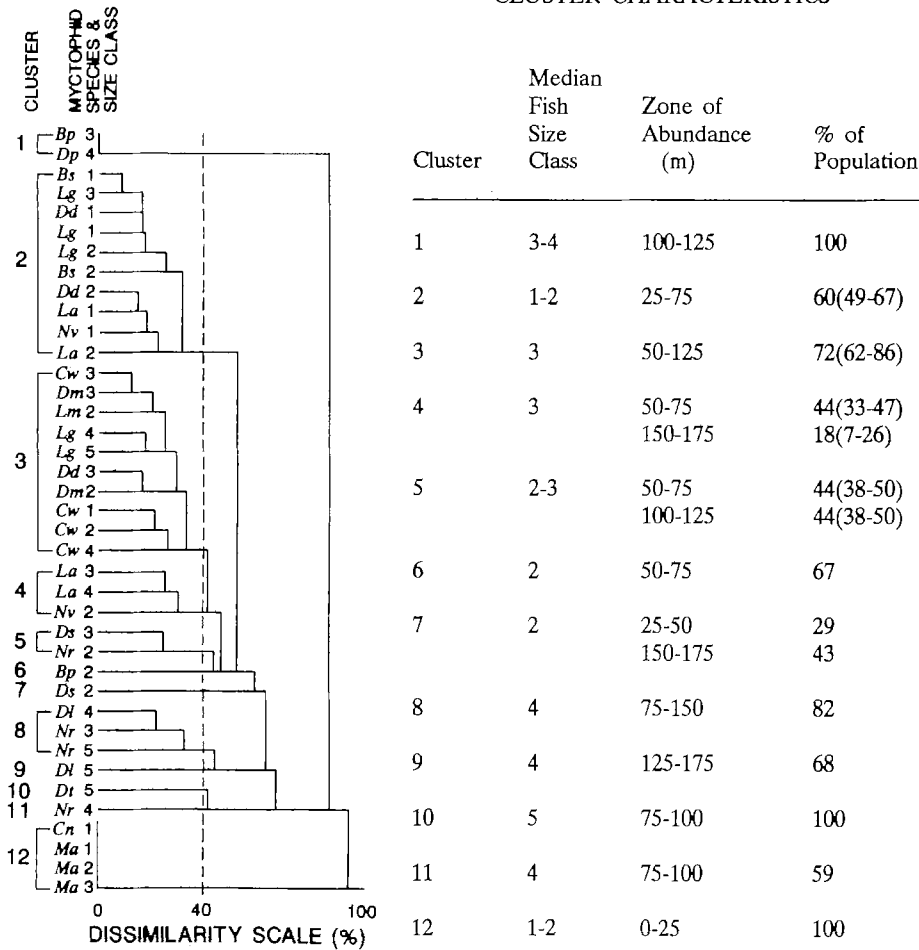


Fig. 1. Cluster analysis of myctophid vertical distribution in 0 to 200 m zone at night (July 1985), using data from Table 2. Species and size-class codes as in Table 1

for the larger individuals of a species to occur deeper. This was apparent, for example, in the distributions of *Diaphus dumerilii*, *Lampanyctus alatus* and *Lepidophanes guentheri* (see also Gartner et al. 1987).

Clustering of the data on diet composition in Table 3 divided the 41 myctophid categories into seven groups (Fig. 2) at the 40% dissimilarity level. Clusters 1 and 2 were the largest, containing 30 categories and 97% of the myctophid population occurring in the upper 200 m. Cluster 1 grouped relatively large myctophids (median size class = 4), which fed heavily on copepods as well as on larger prey such as euphausiids. Mean diet diversity was moderate ( $D=1.9$ ). Cluster 2, the largest group, was primarily composed of smaller individuals (median size class = 2) which had copepods as their principal food, with this prey averaging 71% of diet biomass. Diet diversity was correspondingly low ( $D=1.4$ ). The myctophids in Cluster 3, *Diaphus dumerilii* (Size Class 3) and *Diaphus splendidus* (2, 3), exhibited a balanced distribution of food types and consequently higher diet-diversity indices ( $D=2.6$ ).

Cluster 4 included only two size groups of *Ceratoscopelus cf. warmingii* (2, 3), with this species having a high diet diversity ( $D=3.2$ ) and also the largest component of non-crustacean food (see also Robison 1984).

Cluster 5 myctophids, *Diaphus lucidus* (3, 5) and *Hygophum hygomii* (5), were large, and fed heavily on large prey, decapods in particular. *Ceratoscopelus cf. warmingii* (4) alone constituted Cluster 6, with its diet resembling that of smaller size classes (2, 3) of this species in Cluster 4. Cluster 7 had only *Centrobranchus nigroocellatus* (1) which preyed exclusively on pteropods (mostly *Limacina* spp.), hence the null diet-diversity value.

Copepods accounted for much of the diet biomass in Clusters 1 and 2, where they averaged 42 and 71%, respectively, of diet biomass. Consequently, differences in proportions of individual copepod taxa (in this case, genera) potentially could yield >40% dissimilarity in overall diet composition and thus enable further resolution of feeding niches within these two large clusters. Diet-composition data for the myctophid categories in Clusters 1 and 2 were subjected to additional cluster analysis (Fig. 3) after substituting contributions of individual copepod genera in place of the single lumped value for total copepod biomass. The results show that Cluster 1 in Fig. 3A can be partitioned into four smaller units, but with most of the myctophid categories (9 of 13) occurring in Cluster A1. The genus *Pleuromamma* was the predominant copepod, averaging nearly a third (28 to 32%) of food biomass in all but Cluster A2. No other copepod

**Table 3.** Diet composition of 17 myctophid species from eastern Gulf of Mexico. Species and size-class codes as in Table 1. Diversity index (*D*) range=0 to 3.8

Myctophid species, size class	(n)	Diet component (% biomass)														(D)	
			[No. prey items]	Copepods	Ostracods	Amphipods	Euphausiids	Decapods	Larvaceans	Salps	Siphonophores	Unidentified gelatinous tunic	Polychaetes	Molluscs	Chaetognaths		Fish
<i>Bp</i> 2	(10)	[113]	64	7	12	<1	-	3	<1	4	4	-	-	6	-	-	(1.9)
3	(4)	[82]	56	12	1	-	-	1	-	-	-	-	<1	30	-	-	(1.5)
<i>Bs</i> 1	(30)	[61]	72	6	-	13	-	<1	-	-	-	-	<1	9	-	-	(1.3)
2	(99)	[361]	72	7	1	17	1	-	-	-	<1	-	<1	2	-	-	(1.3)
<i>Cn</i> 1	(22)	[170]	-	-	-	-	-	-	-	-	-	-	100	-	-	-	(0)
<i>Cw</i> 1	(20)	[117]	39	10	10	23	-	7	-	6	-	4	2	-	-	-	(2.5)
2	(28)	[285]	22	14	10	2	4	5	<1	29	4	1	2	7	-	-	(2.9)
3	(33)	[302]	15	9	17	6	2	2	2	22	11	1	5	3	5	-	(3.5)
4	(33)	[271]	11	10	2	2	29	1	21	16	4	<1	1	1	2	-	(2.8)
<i>Dd</i> 1	(34)	[328]	48	19	3	1	-	5	-	3	-	2	2	17	-	-	(2.2)
2	(34)	[739]	51	17	3	9	1	5	-	6	-	<1	3	4	1	-	(2.3)
3	(29)	[597]	29	9	13	14	4	1	1	10	-	1	1	17	-	-	(2.9)
<i>Di</i> 3	(9)	[90]	12	5	1	11	67	<1	-	-	-	-	<1	3	-	-	(1.6)
4	(9)	[88]	20	12	10	20	33	-	-	1	<1	1	1	2	-	-	(2.5)
5	(14)	[119]	8	10	5	29	43	-	-	<1	-	<1	-	4	-	-	(2.1)
<i>Dm</i> 2	(15)	[105]	54	5	6	1	-	<1	-	12	-	-	1	20	-	-	(2.0)
3	(26)	[197]	41	6	4	12	1	<1	-	10	1	-	<1	25	-	-	(2.3)
<i>Dp</i> 4	(3)	[160]	36	5	9	33	5	<1	-	-	-	4	-	8	-	-	(2.4)
<i>Ds</i> 2	(4)	[72]	29	22	15	-	-	7	-	-	-	2	10	15	-	-	(2.6)
3	(7)	[69]	20	11	21	20	-	-	-	-	-	-	4	24	-	-	(2.4)
<i>Dt</i> 5	(13)	[203]	41	2	3	45	1	<1	-	6	<1	<1	<1	2	-	-	(1.8)
<i>Hh</i> 5	(5)	[53]	25	4	4	15	51	-	-	-	1	-	-	-	-	-	(1.9)
<i>La</i> 1	(13)	[52]	92	6	-	-	-	2	-	-	-	-	-	-	-	-	(0.5)
2	(45)	[281]	71	2	5	22	<1	<1	-	-	-	-	-	-	-	-	(1.2)
3	(72)	[457]	51	2	4	37	1	-	-	-	-	-	-	-	5	-	(1.6)
4	(118)	[619]	42	2	8	37	7	-	-	-	-	<1	-	-	3	-	(1.9)
<i>Lg</i> 1	(24)	[123]	80	4	<1	11	2	<1	-	-	-	-	-	2	-	-	(1.1)
2	(18)	[85]	57	5	-	37	-	<1	1	-	-	-	<1	-	-	-	(1.3)
3	(23)	[155]	44	8	1	43	<1	<1	-	-	-	-	-	2	-	2	(1.7)
4	(30)	[249]	29	4	2	53	<1	<1	-	1	-	<1	11	-	-	-	(1.8)
5	(41)	[343]	40	2	4	31	1	<1	1	<1	-	-	-	<1	21	-	(1.5)
<i>Lm</i> 2	(12)	[79]	36	5	-	54	-	<1	-	-	-	-	<1	5	-	-	(1.5)
<i>Ma</i> 1	(17)	[222]	75	1	8	-	-	3	-	-	-	-	4	9	-	-	(1.3)
2	(16)	[437]	88	<1	2	4	-	<1	-	-	-	-	5	<1	-	-	(0.7)
3	(11)	[459]	81	-	3	5	2	<1	-	1	-	-	5	3	-	-	(1.2)
<i>Nr</i> 2	(16)	[161]	84	3	1	8	-	-	-	-	-	2	<1	2	-	-	(1.0)
3	(21)	[223]	39	1	1	15	28	<1	-	1	-	-	-	14	-	-	(2.1)
4	(34)	[587]	45	1	1	25	21	<1	-	1	<1	<1	-	5	<1	-	(2.0)
5	(24)	[429]	50	1	2	37	3	-	-	<1	<1	<1	-	1	5	-	(1.7)
<i>Nv</i> 1	(77)	[261]	94	3	<1	2	-	-	-	-	-	-	-	1	-	-	(0.4)
2	(17)	[58]	79	5	3	13	-	-	-	-	-	-	-	-	-	-	(1.0)

genera exceeded 10% of the diet biomass in the series of clusters in Fig. 3 A. Euphausiids and decapods were important non-copepod prey in the clusters in Fig. 3 A, but these crustacean groups could not be used in further partitioning of these clusters because their remains could not be consistently identified to genus.

Cluster 2 myctophids (Fig. 3 B) were divisible into eight smaller groups, Cluster B1 being the largest (7 myc-

tophid categories). *Pleuromamma* spp. was the principal copepod food in Clusters B1 to B5 ( $\bar{x}$ =18 to 74%), *Candacia* spp. in B6 myctophids, *Undinula* sp. in B7 and B8 fishes, and *Nannocalanus* sp. in B8 fishes.

Fig. 4 presents the results of cluster analysis of myctophid diets in terms of prey size. Eleven clusters were discernible at the 40% dissimilarity level. Fishes in Clusters 1 to 4, 6 and 11 fed mostly on prey <5 mm, but with

CLUSTER CHARACTERISTICS

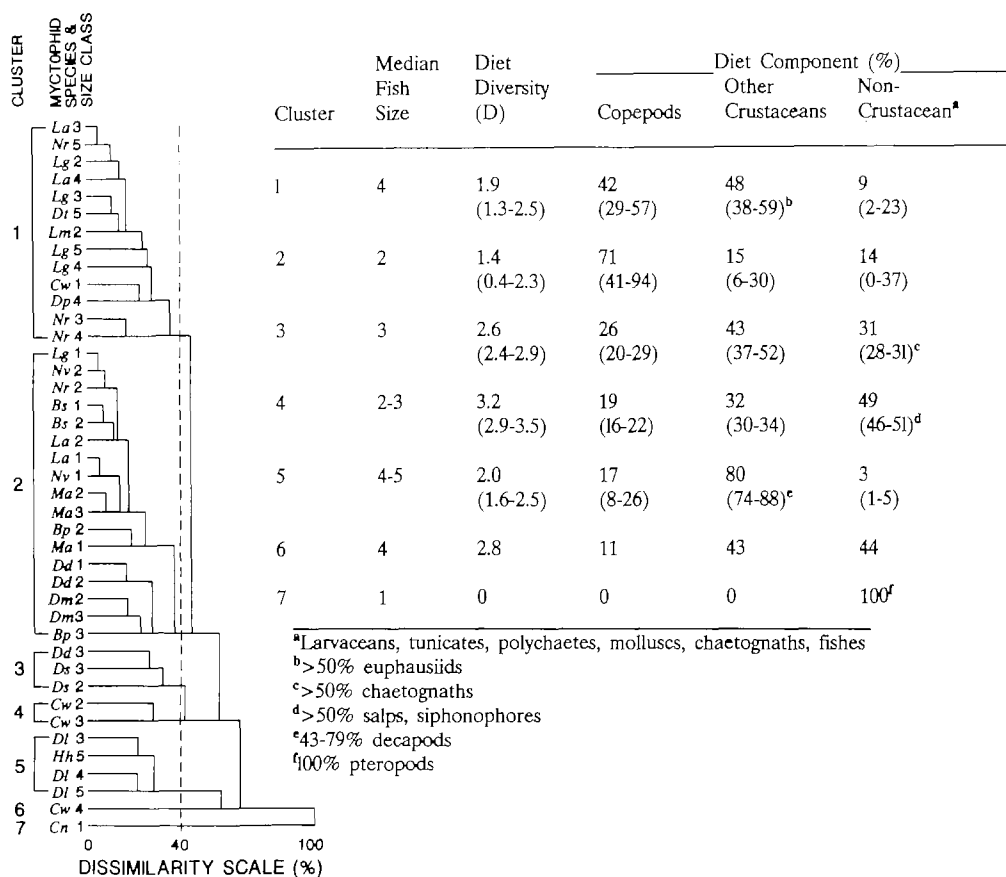


Fig. 2. Cluster analysis of data on myctophid diet in Table 3. Species and size-class codes as in Table 1

the size array of food varying considerably among the clusters. The mean *D* values for this group of clusters ranged from 1.4 (Cluster 4) to 2.7 (Cluster 6). Fishes in these six clusters were comparatively small, predominantly of Size Classes 1 and 2. The food of myctophids in Clusters 2, 5 and 8 had a bimodal size distribution, which is reflected in the moderate to high food-size distribution indices, 2.1 to 3.1. Relatively large fishes (Size Classes 3 to 5) were grouped in the remaining clusters, 7, 9 and 10, and fed heavily on prey > 8 mm.

The summary species-by-size-class pairs-matrix which combines information for all cluster analyses shown in Figs. 1-4 (see "Materials and methods", Paragraph 7) reveals that in only nine (Table 4) of 820 pair-combinations in the matrix is there 60% or more (≤ 40% dissimilarity) overlap. Overlap mostly occurs among the smaller fish-size classes, i.e. ≤ Size Class 3. Four pairings involving a total of three species, *Benthosema suborbitale*, *Lampantus alatus* and *Notolychnus valdiviae*, match different species, while the other five are intraspecific pairs of two size classes.

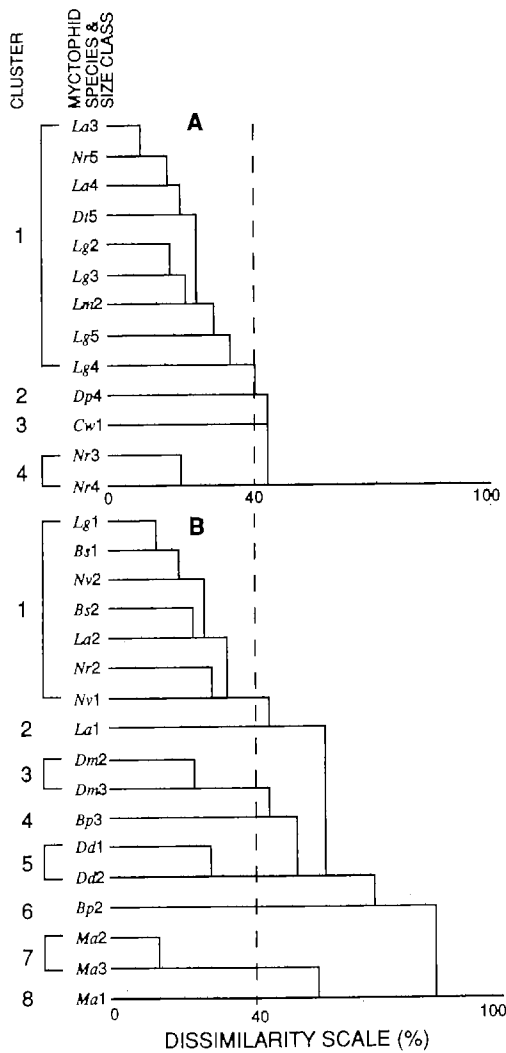
Predation impact

The principal myctophid food taxa were copepods (especially the genus *Pleuromamma*), ostracods and euphausi-

Table 4. List of myctophid species-by-size class category pairs which could not be differentiated by any of the vertical distribution and food characteristics using a 40% dissimilarity criterion (For cluster analyses see Figs. 1-4). Species and size-class codes as in Table 1

<i>Bs1</i> × <i>La2</i>	<i>Bs1</i> × <i>Bs2</i>
<i>Bs1</i> × <i>Nv1</i>	<i>Cw2</i> × <i>Cw3</i>
<i>Bs2</i> × <i>Nv1</i>	<i>Dd1</i> × <i>Dd2</i>
<i>La2</i> × <i>Nv1</i>	<i>Dl3</i> × <i>Dl5</i>
	<i>La3</i> × <i>La4</i>

ids. These three taxa combined accounted for 88 and 67% of zooplankton numbers and biomass, respectively, in the 0 to 200 m zone at night, as determined from July 1985 162 μm-mesh net-tows. While larval decapods were also important biomass items in the diets of some myctophids (e.g. *Notoscopelus resplendens*), they were relatively uncommon in the plankton and therefore were not considered in predation-impact estimates. We calculated predation rate on the above zooplankton groups using myctophid and zooplankton abundance data for the upper 200 m and estimates of myctophid nightly rations (see "Materials and methods", Paragraph 10). This enabled us to calculate the number of each type of prey eaten per km<sup>2</sup> per night in the 0 to 200 m layer, the months of standing stock available at this consumption rate assum-



CLUSTER CHARACTERISTICS

Cluster	<i>Pleuromamma</i> spp. biomass in diet % (Rn)	Other Prey >15% diet biomass % (Rn)
1	29(13-37)	Euphausiids: 42(31-54)
A 2	12	Euphausiids: 33
3	28	Euphausiids: 23
4	32(30-33)	Decapods: 25(21-28) Euphausiids: 20(15-25)
1	51(40-65)	0
2	74	0
3	40(33-47)	Chaetognaths: 23(20-25)
B 4	23	Chaetognaths: 31
5	(18(15-21))	Ostracods: 18(18-19)
6	7	<i>Candacia</i> spp.: 27
7	0	<i>Undinula</i> sp.: 64(58-70)
8	0	<i>Nannocalanus</i> sp.: 22 <i>Undinula</i> sp.: 19

Fig. 3. Additional cluster analysis of diet information from myctophids included in Clusters 1 (A) and 2 (B) of Fig. 2. Analysis was rerun with substitution of biomass data on individual copepod

genera for the previously undifferentiated category of total copepod biomass used in cluster analysis in Fig. 2. Rn: range of percentages

ing no stock replacement, and the fraction of zooplankton daily production (based on literature estimates of generation times) removed. A number of correction factors were applied to strengthen the validity of our estimates. Plankton abundance ( $\text{km}^{-2}$ ) was adjusted where possible using 30-liter bottle (30  $\mu\text{m}$  gauze) data to generate more accurate information on the number of <2 mm zooplankton in the epipelagic zone. Myctophid abundances were also corrected for escapement losses of smaller fish-size classes by using data from fine-mesh (1.6 mm) Tucker trawl catches. On the basis of the comparative tow information (1.6 vs 4.0 mm-mesh trawl catches) in Gartner et al. (1989, their Fig. 1), abundance estimates for the 0 to 200 m zone of Myctophid Size Classes 1 and 2 were multiplied by 4.7 and 1.7, respectively. All myctophid abundances were then multiplied by a factor of 1.1, since the component of the population reported on here (17 species) represented 90% of the total abundance of the assemblage in the upper 200 m at night in July 1985. No correction factor is available for the

fraction of the population that avoided our trawls, but we believe this to be a low number (see Clarke 1973, Gartner et al. 1989).

The results in Table 5 indicate that, with the exception of >4 mm *Pleuromamma* spp. (1.58%), <1% of the numbers of dominant types of prey was removed by myctophid nightly predation from the upper 200 m. In the food categories of total copepods and the genus *Pleuromamma*, predation impact increased with size of prey, although this was not apparent for ostracods and euphausiids. Predation rate in terms of months of prey stock available indicates that at least 5 mo and as many as 417 mo of prey stocks were available, at least during the July 1985 sampling period, for all categories except *Pleuromamma* spp. >4 mm (*P. xiphias*), of which there was only a 2 mo supply. Assuming a 15 to 30 d generation time for copepods and ostracods, and 90 to 180 d for euphausiids (see references in Footnote "b" of Table 5), the percentage of daily production consumed was estimated at a maximum of only 8.0 to 16.0% of total cope-



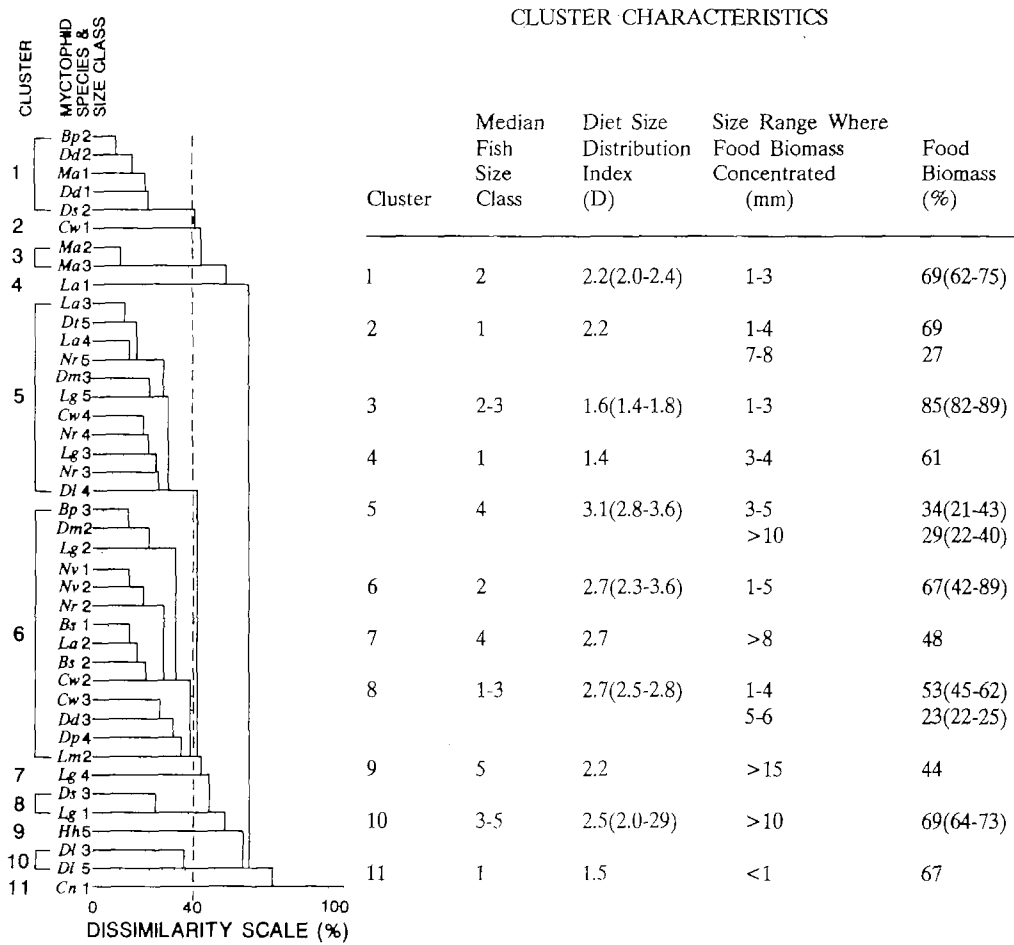


Fig. 4. Cluster analysis of size distribution of prey biomass in myctophid diets. Species and size-class codes as in Table 1

Table 5. Abundance of dominant zooplankton prey groups in upper 200 m of eastern Gulf of Mexico and estimates of nocturnal predation impact of the postlarval myctophid population

Zooplankton prey group	Nos./m <sup>2</sup>	No. consumed/m <sup>2</sup>	% standing stock consumed	Months prey stock available <sup>a</sup>	% daily production consumed <sup>b</sup>
<b>Total copepods</b>					
<2 mm	309 533 <sup>c</sup>	25.06	0.008	417	0.1-0.2
2-4 mm	1 555	7.06	0.454	7	6.8-13.6
>4 mm	139	0.74	0.532	6	8.0-16.00
<b>Pleuromamma spp.</b>					
<2 mm	>1 566	4.02	0.258	>13	<(3.9-7.8)
2-4 mm	508	3.39	0.667	5	10.0-20.0
>4 mm	36	0.57	1.583	2	23.8-47.5
<b>Ostracods</b>					
<2 mm	2 933 <sup>c</sup>	5.40	0.184	18	2.8-5.5
>2 mm	62	0.10	0.161	21	2.4-4.8
<b>Euphausiids<sup>d</sup></b>					
<5 mm	>182	0.74	0.407	>8	<(36.6-73.2)
5-10 mm	191	0.78	0.408	8	36.8-73.5
>10 mm	57	0.06	0.105	32	9.5-18.9

<sup>a</sup> Assumes no replenishment

<sup>b</sup> 15 to 30 d generation time assumed for copepods and ostracods, 90 to 180 d for euphausiids (Wickstead 1962, Roger 1974, Binet and Suisse De Sainte Claire 1975, Raymond 1983, Klein Breteler and Gonzalez 1986)

<sup>c</sup> Based on 30-liter bottle (30 μm gauze) data; all other estimates from 162 μm-mesh nets

<sup>d</sup> Postlarval euphausiids

Pods, but as high as nearly half (47.5%) of the daily production of the large *Pleuromamma* spp. appearing in the epipelagic zone at night. The rate of consumption of ostracods was <6%, which is intermediate between nightly predation rates on <2 mm and >2 mm copepods. Heaviest impact on euphausiids was on the 5 to 10 mm size fraction, where between one-third to three-fourths of the daily production was removed. Predation impact was apparently less on euphausiids >10 mm, but was still estimated at up to 19%.

## Discussion

### Resource-partitioning

Cluster analysis of vertical-distribution data and diet characteristics strongly suggests resource-partitioning among the myctophid community in the eastern Gulf of Mexico. Interspecific overlap is uncommon and, despite some overlap, intraspecific separation of size classes through vertical distribution and/or diet characteristics is more the rule (36 pairings in the summary matrix) than the exception (the five pairings in second column of Table 4). This points to intraspecific as well as interspecific resource-partitioning being prevalent in the myctophid community.

Obviously, the degree of species congruence is a function of the selected level of niche definition, which in the present case is 40% dissimilarity, as chosen in a number of investigations (e.g. Zaret and Rand 1971, Berkes 1976). If, for example, a 50% dissimilarity level had been chosen, the number of pairings exhibiting overlap in all parameters tested would increase to 57, with this group including 49 interspecific combinations involving 12 different species. Conversely, at the 30% dissimilarity level (i.e., 70% overlap) only two of the 820 pairings are congruent, with each of these involving neighboring size classes of the same species (*Bs1* × *Bs2*, *La3* × *La4*). Forty percent dissimilarity was therefore used because a dissimilarity of 50% in space and food characteristics intuitively seems too large a difference to be encompassed within a low-latitude pelagic niche, whereas the assumption of a dissimilarity level <40% has little effect on the present results.

These conclusions on resource-partitioning are based on a summer collection, which is our most complete data set. Seasonal abundance data on eastern Gulf myctophids (Gartner unpublished data) and zooplankton (Hopkins unpublished data) indicate that, while the summer dominants remain the most abundant year-around, relative abundance and rankings can change. Some preliminary data on *Diaphus dumerilii* and *Notoscopelus resplendens* suggest that at least some myctophid diets can also vary significantly with season (see also Cailliet 1972). In the absence of data sets comparable to that for summer, we can only speculate on how these changes affect niche dimensions in other seasons. In any event, resource-partitioning during summer may be of sufficient duration to ensure overall ecological separation of species and size-classes in this low-latitude system.

### Predation impact

Our calculations indicate that the eastern Gulf myctophid community can ingest ~16 kg dry wt km<sup>-2</sup> (~6.4 kg C) and 400 × 10<sup>6</sup> individuals km<sup>-2</sup> of zooplankton nightly in the epipelagic zone (0 to 200 m). As a reference point, zooplankton standing stock in this zone at night as determined from 162 µm-mesh net-hauls is 900 kg dry wt km<sup>-2</sup> (~360 kg C) and 10<sup>10</sup> individuals km<sup>-2</sup> (Hopkins 1982 and unpublished data). Nightly predation in the epipelagic zone, then, is estimated at ~2% of the zooplankton biomass. At this predation rate, the myctophid population could remove the equivalent of the entire biomass of zooplankton in the epipelagic zone in less than 2 mo. Nightly predation removes a much smaller fraction of zooplankton numbers, 0.3%. Since the percentage of zooplankton biomass eaten exceeds the numerical percent by a factor of >6, it is apparent that myctophid diets are skewed towards the larger prey. In the eastern Gulf, the myctophid species responsible for the greatest predation on zooplankton, *Notolychnus valdiviae*, is the smallest (max. = 22 mm standard length) and the most abundant (27% of the population). This species accounted for 27% of the total food biomass consumed by the assemblage in July 1985, a result of its abundance and the fact that *N. valdiviae* ingested copepods of large biomass (*Pleuromamma* spp.). The only other species accounting for >10% of the biomass eaten were *Lepidophanes guentheri* (17%) and *Diaphus dumerilii* (14%), which rank third and second, respectively, in abundance in the eastern Gulf (Gartner et al. 1989).

Gorelova (1984) calculated that nocturnal myctophid feeding accounts for 10% of the zooplankton biomass in the top 20 m of the water column in the equatorial Pacific. Sameoto (1988) determined that *Benthoosema glaciale* (41 to 100% of the midwater fish population at 0 to 1000 m) consumed 0.03 to 0.20% of the zooplankton biomass over the diel period in slope waters off Nova Scotia. These values, however, are not directly comparable to those from the present study because of variability in the depth zones considered.

Myctophid predation pressure is a function of prey abundance and size. This is especially the case with copepods, although it is less obvious for ostracods and euphausiids. Pressure is greatest on prey >4 mm in length, of which myctophids can consume from one-fifth to over one-half of daily production (e.g. *Pleuromamma* spp. and euphausiids). Thus, greatest pressure is on the intermediate to late growth stages of prey taxa, especially copepods. These larger prey-size classes are probably little utilized by the numerous smaller predator species in the zooplankton (see oceanic foodwebs described in Hopkins 1985, 1987, Hopkins and Torres 1989, Hopkins et al. 1992).

Myctophid predation impact is greatest on those zooplankton size classes closest to sexual maturity, that is, on the potential breeders among their prey populations. Some relief from myctophid predation in the epipelagic zone occurs when the myctophid community migrates into the mesopelagic zone during the day. However, certain prey, such as species of the genera *Pleuro-*

*mamma*, *Nematoscelis* and *Euphausia*, migrate with myctophids and co-occur with the myctophid populations over much of their depth range during the day (see Hopkins 1982, Gartner et al. 1987, Bennett and Hopkins 1989). Thus, further predation on migrating prey is possible during the daylight hours below the epipelagic zone. Some daytime feeding may occur (e.g. Legand et al. 1972, Hopkins and Torres 1989), but the literature on myctophid feeding chronology presents strong evidence that most feeding is at night in the epipelagic zone (Merrett and Roe 1974, Baird et al. 1975, Gorelova 1975, Clarke 1978, Hopkins and Baird 1985, Kinzer and Schulz 1985, Dalpadado and Gjøsaeter 1987).

In the eastern Gulf, myctophids account for approximately one third (32%) of the biomass in the epipelagic and upper mesopelagic zones (0 to 400 m) at night (Hopkins and Lancraft 1984). Most of the remaining micronekton biomass is constituted by various other fish groups (52%) and shrimps (18%). Myctophids therefore account for a major fraction of nightly predation by zooplanktivorous micronekton. If predation in other groups is approximately equivalent per unit biomass within the micronekton, then at least one-third of the total predation resulting from micronekton is attributable to the Myctophidae. This represents a substantial impact on the zooplankton community, because myctophid predation is heavily selective for particular size fractions and crucial life-history phases of important zooplankton biomass dominants, e.g. euphausiids > 5 mm and mature size classes of the copepod genus *Pleuromamma*.

#### Regulation of community structure

Resource-partitioning is not disjunct, as there is considerable overlap in both primary niche factors, space and food. For example, the average Bray-Curtis similarity indices for myctophid vertical distributions, food taxonomic composition and food size are 38, 51 and 51%, respectively. We hypothesize that this broad niche overlap enables the co-occurrence, i.e., the "packing" of over 50 myctophid species in the epipelagic zone at night, the diel period of maximum potential competition. In the present study, niche similarity > 60% was considered as more than one species occupying the same niche. In such cases (Table 4), the potential for intense competition would be high and, over time, could result in competitive exclusion and a change in community structure. We also postulate that what niche separation does occur is presumably the result of competition over the course of evolution of the ecosystem and may exist in present time as "diffuse competition". This has been defined (MacArthur 1972) as the cumulative impact of interspecific competition and, in the present case, would be interpreted as the total combined effect on one species, of competition from all other species in the myctophid community (it obviously can occur from other predators as well; e.g. other groups of midwater fishes, shrimps, cephalopods). As suggested by Pianka (1974), "diffuse competition" can be minimized by niche overlap such as that described for myctophids in the present study.

The present data for myctophids are similar to those for sergestid shrimps (18 species) in the eastern Gulf, where little interspecific congruence was demonstrated in comparisons of sergestid vertical distribution and diet characteristics (Flock and Hopkins 1992). Patterns from these Gulf of Mexico zooplanktivorous micronekton, i.e., the midwater fishes and shrimps, stand in contrast to what has been reported for copepods in low-latitude ecosystems (McGowan and Walker 1979), which occupy the next lower trophic level. Little difference was found in diets or vertical distributions among large clusters of copepod species. McGowan and Walker (1979, see also Hayward and McGowan 1979) suggested that this high degree of niche concordance among the copepod assemblage results from their occupying a trophic level where heavy predation enables the coexistence of reduced populations with little competition for food among the survivors. This is manifested in an apparent lack of specialization in space and food parameters. If this is the case, evidence for resource-partitioning among the zooplanktivorous micronekton occupying the trophic level above their copepod prey is not unexpected, because of the theoretical impossibility mentioned by Hayward and McGowan (1979) of successive trophic levels being predator-controlled. For at least the middle levels of the trophic web then, the available information suggests that both mechanisms are operating to reduce competition and to maximize trophic dynamic efficiency within low-latitude oceanic ecosystems. At the small-particle grazing level occupied by copepods, reduction in competition is achieved primarily through heavy predation (such as that occurring on *Pleuromamma* spp.), whereas at the next higher trophic level, competition among the zooplanktivorous micronekton is reduced largely through resource-partitioning. In the case of myctophids this is accomplished through partitioning of vertical space and zooplankton food resources.

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