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Aggregations of myctophid fishes with other pelagic fauna

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Synopsis

Direct underwater observations of myctophid fishes were conducted to 630 m in submarine canyons along the outer margin of the northeast United States continental shelf with the Johnson-Sea-Link II submersible. Data revealed that myctophids occurred in aggregations of other pelagic fauna (e.g., ctenophores, sergestids, amphipods) when densities of the former were low but the latter were high. We suggest that myctophids selectively occur with other pelagic fauna to reduce the probability of direct contact with predators and to take advantage of aggregate search abilities for common prey taxa.

Introduction

Worldwide, the family Myctophidae is represented by 32 genera and about 235 species (Nelson 1984). Myctophids are a major component of the mesopelagic ichthyofauna in the northwest Atlantic (e.g. Backus et al. 1970, Jahn & Backus 1976, Gjosaeter & Kawaguchi 1980). While much is known regarding aspects of the life history of myctophids such as geographical distribution, vertical migration patterns, population structure, and food habits (e.g. Backus et al. 1970, 1977, Badcock & Merrett 1976, Clarke 1973, Gartner et al. 1987, Gjosaeter 1973, Halliday 1970, Roe & Badcock 1984, Sameoto 1982, 1988, Willis & Percy 1980), data on the interactions of these fishes at the small-scale (i.e. cm-m) are lacking because direct observations are difficult to make.

Beebe (1935) was the first person to observe myctophid fishes in the mesopelagic zone of the

ocean. During his historic bathysphere dives off Bermuda, he saw myctophids either singly or in schools. No interactions with other taxa were reported. Underwater observations by Barham (1963, 1966) described occurrences of myctophids with other pelagic fauna associated with sound scattering layers off southern California (U.S.A.) but no small-scale spatial relationships were discerned. Milliman & Manheim (1968) described high densities of squids, myctophids and sergestids in relatively discrete layers in the water column on a submersible dive northeast of Cape Hatteras. Although myctophids were reported to be mixed with squids in the middle and bottom of the squid layer, no associations on the scale of cm to m were noted. Only recently has Robison (1983) reported on the small-scale associations of individual myctophids with other fishes and gelatinous zooplankton from a more recent series of dives off California.

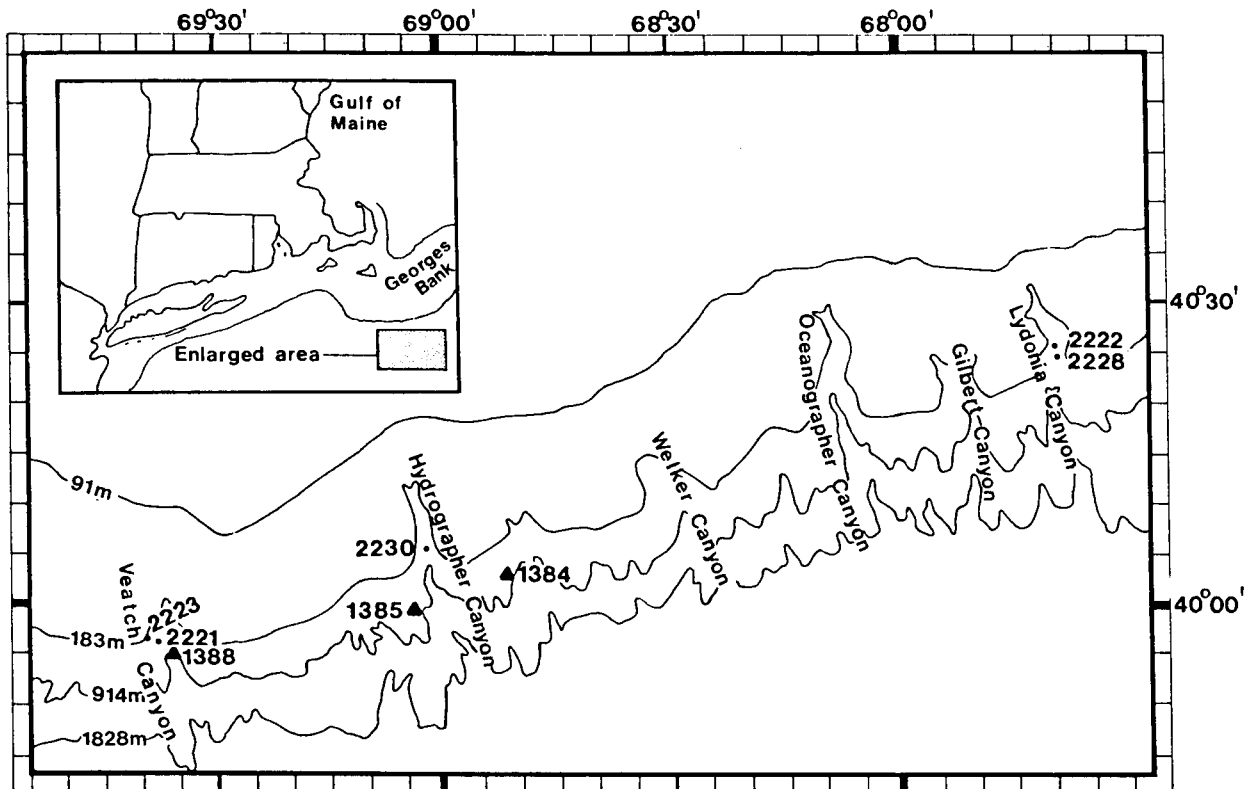


Fig. 1. Locations of submersible dives in 1983 (triangle) and 1987 (dot). The following are 1983 dive number, date, and time (Eastern Daylight Time): 1384–15 July (0257–0500 h EDT), 1385–15 July (2030–2230 h EDT), 1388–16 July (1930–2130 h EDT). Data for 1987 dives are included in the text.

In this paper, we present the results of submersible-based observations of myctophid fishes that aggregated with other pelagic fauna in the northwest Atlantic. The significance of these findings is discussed with regard to predator avoidance and prey location.

Methods

Two daytime and 3 night dives were made during September 1987 to observe epipelagic and mesopelagic fauna in submarine canyons along the southern flank of Georges Bank (Fig. 1). Observations of pelagic fishes were made from both forward and rear compartments of the Johnson-Sea-Link II submersible to depths of 630 m (see Youngbluth 1984 for a more complete description of the vehicle). Horizontal visibility from the submersible

was greater than a 6 m radius during all dives. Total dive time was approximately 15 h.

During this series of dives, qualitative and quantitative observations were made of the intra- and inter-specific associations and behavior of myctophid fishes and associated fauna. All estimates of individual size (i.e. total length for fishes, longest dimension for ctenophores, rostrum or eyespots to telson for crustaceans), abundance and nearest neighbor distance (n.n.d.) were obtained visually. Objects of known size on the outside of the submersible were used as references. Care was taken not to record observations of individuals which were obviously reacting to submersible lights. During 3 dives, a running tally was kept of the number of myctophids occurring with aggregations of other species.

After the 1987 dives, it was apparent some relationship existed between occurrence of myctophids

and other fauna in the water column. Presence-absence data of all visible fauna on surface-to-bottom vertical transects from 3 dives in 1983, in approximately the same location, were re-examined for associations with myctophid fishes. Frequency of occurrences of myctophids with other taxa were computed.

Taxa were identified only by common names (e.g. myctophid, euphausiid, hydromedusa) since it was not possible to identify all individuals from the submersible. However, identification to lower taxa was possible in many instances (visually or with voucher specimens collected with the submersible) and the following are the most common genera or species associated with each common name: myctophid, genera include *Diaphus*, *Ceratoscopus*, *Myctophum* and *Lobianchia*; euphausiid, primarily *Meganyctiphanes norvegica*; hyperiid amphipod, primarily *Themisto compressa*; sergestid shrimp, primarily *Sergestes* spp.; hatchetfish, *Argyropelecus* sp., hairtail fish, *Trichiurus* sp.; snipe eel, *Nemichthys scolopaceus*; physonect siphonophore, primarily *Nanomia cara*; and lobate ctenophore, primarily *Bolinopsis infundibulum*.

Results

Observation summary – 1987 dives

Myctophids were observed on every dive. Typically, diel differences in vertical distribution were apparent. For example, in vertical transects, the first occurrence of myctophids was deeper during the daytime than at night. Individuals generally were smaller at shallower depths, although this also could be due to changes in species composition with species of smaller maximum size occurring at shallower depths. The shallowest occurrence was a single individual at 60 m.

The distribution of myctophids was very patchy and they appeared either in groups with other taxa (e.g. other myctophid species, ctenophores, euphausiids, amphipods) or in single species aggregations. There was no apparent trend as to the type of aggregation of other taxa (i.e. species composition or size of aggregation) in which myctophids oc-

curred. In all aggregations, the sizes of all individuals were similar regardless of taxa. Nearest neighbor distances always were less than 2 m. No 'coherent' aggregations of any species were observed with distances between individuals greater than 2 m. Myctophids also occurred in homotypic aggregations that were not associated with other taxa. Figure 2 depicts a generalized summary of the types of distributions we describe.

1987 dive narratives

DIVE 2221 – 22 September (0630–1000 h EDT): Myctophids occurred in mixed groups of hatchetfishes, amphipods and euphausiids at 275, 326, and 344 m during descent. Over the bottom (6 m height) from 390 to 610 m, mixed groups of myctophids, hatchetfishes, snipe eels, and euphausiids appeared in dense aggregations (at 390 m, n.n.d. 0.25–1.0 m). Sergestids also occurred in these aggregations towards the deeper end of the transect (at 600 m, euphausiids, sergestids and an occasional myctophid, n.n.d. 30 cm–1.0 m). Myctophids, euphausiids and sergestids were 2.5–4.0 cm length.

During ascent small patchy aggregations of myctophids, hatchetfishes and lobate ctenophores were observed (5–30 individuals, n.n.d. 1.0–2.0 m, all 8–15 cm length). Numerically, myctophids were a minor component of the aggregations observed.

DIVE 2223 – 22 September (2318–0207 h EDT): The first myctophid was observed at 60 m (2 cm length). A homotypic aggregation of myctophids, probably *Diaphus* sp., was observed at 82 m (5–7 cm length). Mixed groups of myctophids and hydromedusa (numerically dominant) occurred between 107 and 122 m along with an occasional physonect siphonophore. A mixed group of hairtail fishes and myctophids were observed at 150 m. Heterotypic aggregations of myctophids occurred from 168 to 183 m (n.n.d. 30 cm), 213 m (n.n.d. 30 cm), 275 m (n.n.d. 15 cm), and 335 m (n.n.d. 60 cm). The size of fishes increased with depth.

DIVE 2227 – 27 September (1445–1700 h EDT): Myctophid distributions were very patchy from 305 to 550 m. Eighteen myctophids occurred in a dense patch of ctenophores, siphonophores, and amphi-

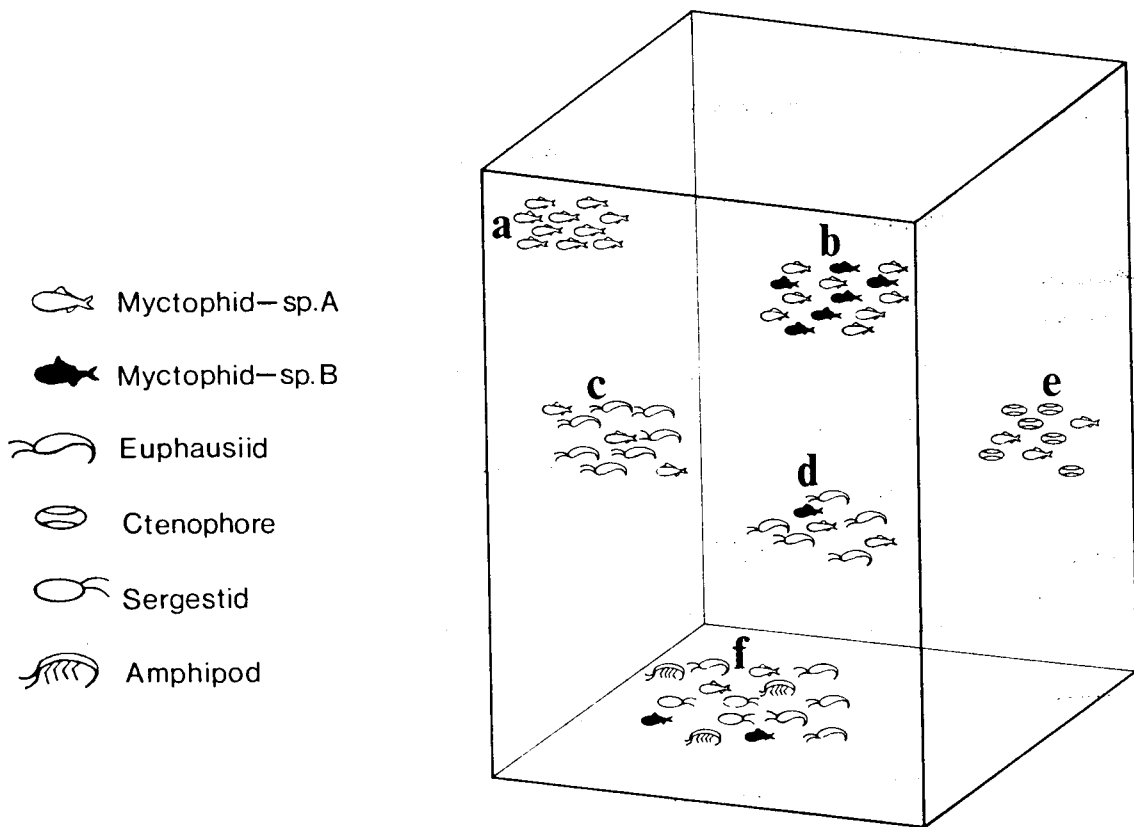


Fig. 2. Pictorial representation of aggregations observed during submersible dives: a – homotypic aggregation of myctophids, b – heterotypic aggregation of myctophids, c – a single myctophid species aggregated with a single numerically dominant taxon, in this case euphausiids, d – multiple myctophid species aggregated with a single numerically dominant taxon, in this case euphausiids, e – a single myctophid species with an aggregation of gelatinous zooplankton, although multiple myctophid species also occurred, we emphasize that crustacean and gelatinous zooplankton were ecologically equivalent in this context, f – multiple myctophid species in an aggregation of mixed taxa. The illustration represents a cross section of the midwater environment. Spatial relationships and orientation of individuals within and between aggregations are simply for the convenience of presentation.

Pods at 480 m (n.n.d. 0.5–2.0 m) while only 7 fishes were observed out of the patch (n.n.d. greater than 4 m).

DIVE 2228 – 28 September (0055–0420 h EDT): No large aggregations of any species were seen throughout the dive to 630 m. Euphausiids, amphipods, and ctenophores were observed individually, in homotypic pairs, or in groups of 3 individuals (n.n.d. 15–30 cm). Myctophids (1 or 2 individuals) were occasionally present in these groups. Twenty-eight fishes were associated with these groups and 31 were observed singly.

DIVE 2230 – 28 September (2310–0245 h EDT): Myctophids first were observed in a dense aggrega-

tion of lobate ctenophores at 100 m (n.n.d. 20–30 cm). Thirty-six myctophids occurred with the ctenophore aggregation with only 3 observed outside the aggregation. A dense homotypic aggregation of myctophids (n.n.d. 30 cm, 70–100 fishes) was observed at the bottom (510 m). On ascent, myctophids were concentrated near the thermocline with euphausiids (180–240 m, n.n.d. 1 m).

1983 vertical transect data

Forty-six separate observations of individuals or aggregations of myctophids were recorded on 3

dives. Myctophids occurred with other taxa in 95.7% ($n = 44$) of all observations. Table 1 summarizes the frequency of occurrence with various taxa. Amphipods, sergestids, and ctenophores were the most common taxa with which myctophids occurred. Myctophids were associated with sand lances, siphonophores, copepods, euphausiids and snipe eels in less than 10 of the observations. There was no trend in the abundance of individual taxa and associations with myctophid fishes.

Discussion

Our observations demonstrate that myctophids occurred in aggregations of other pelagic fauna (e.g., other myctophid species, sergestids, ctenophores, amphipods) or in homotypic aggregations when aggregate abundance was high. There appeared to be no affinity of myctophids for particular taxa. Size classes of taxa within an aggregation appeared to be more important than attractions to particular species, hence other fish species, crustaceans and gelatinous zooplankton may be ecologically equivalent in this context.

Observational data from this study indicated nearest neighbor distances in aggregations were always less than 2 m (range 0.15–2.0 m or 418–0.18 individuals m^{-3} based on a conversion in Mackie & Mills 1983). No 'aggregations' occurred with indi-

viduals at greater nearest neighbor distances. Robison (1983) described similar associations of mid-water fauna from a series of submersible dives in the Santa Barbara Basin. Approximately 75% of the midwater fishes he observed were associated with the siphonophore *Apoemia* sp. Deepsea smelt, *Leuroglossus stilbius*, oriented perpendicular to the long axis and within 50 cm of siphonophores. The myctophid *Stenobranchius leucopsarus* had no specific orientation to siphonophores and occurred within a range of 1 to 3 m. Density estimates of fishes noted in these aggregations were 2.5 fishes m^{-3} while those not in any association occurred at 0.03 fishes m^{-3} .

The explanation for our observation of increasing size of myctophids with increasing depth may be due to partitioning of the water column by species or size classes. The occurrence of larger myctophids with increasing depth has been documented for myctophid fishes caught in trawls (e.g. Badcock & Merrett 1976, Clarke 1973, Gartner et al. 1987, Willis & Percy 1980). This pattern has been shown for a large number of species at night as well as during the day. However, Halliday (1970) and Sameoto (1988) found no significant changes in the size class composition, with depth, of the myctophid *Benthosema glaciale* off Nova Scotia.

Formation of heterotypic schools and aggregations of fishes has been suggested to be an adaptive response to increase protection afforded to individuals when population abundance is low but aggre-

Table 1. Percent occurrence and number of occurrences of taxa observed with myctophids during 1983 submersible dives. Total number of observations of myctophids with other taxa = 44. Note that multiple taxa can occur during any single observation, hence the total 'Percent of observations with myctophids' exceeds 100 and the total 'Number of observations with myctophids' exceeds 44. 'Total fauna observed' is the total number of discrete aggregations or individuals (if not in an aggregation) observed during the descents of 3 dives.

Taxa	Percent of observations with myctophids	Number of observations with myctophids	Total fauna observed
Sergestid	63.0	29	82
Amphipod	56.5	26	103
Ctenophore	21.7	10	36
Sand lance	19.6	9	28
Siphonophore	19.6	9	38
Copepod	17.4	8	66
Euphausiid	15.2	7	69
Snipe eel	15.2	7	21

gate abundance is high (Ehrlich & Ehrlich 1973, Keenleyside 1979, Morse 1977, Nursall & Pinsent 1969, Ogden & Ehrlich 1977). Individual prey have a higher probability of being detected by a solitary predator if they are dispersed than if they are aggregated (Brock & Riffenburgh 1960, Pitcher 1986). If predation is solely a size-specific phenomenon, advantages accrue to individuals that aggregate regardless of their taxonomic affinities. Further, if individuals are within a narrow size frequency, they gain an additional advantage by being potential prey for a relatively narrow range of size specific predators. Frank & Leggett (1982) found that in co-occurring aggregations of fish larvae, the numerically dominant species swamped the predator field and reduced daily individual mortality rates by up to 5-fold.

Increases in the size of aggregations have been shown to reduce prey capture rates by causing predators to frequently switch targets causing a reverse to an earlier segment of the predation sequence. In addition, preying on individuals in aggregations elicits 'irrelevant' or 'avoidance' behaviors not related to prey capture but which also reduces capture success (Neill & Cullen 1974).

Pitcher et al. (1982) have demonstrated that foraging in a group decreases the search time for patches of prey. Myctophids, euphausiids, ctenophores, amphipods and sergestids all prey on copepods (e.g. Anderson 1974, Deason & Smayda 1982, Foxton & Roe 1974, Gjosaeter 1973, Omori 1974, Sameoto 1982, Shearer & Evans 1975). Myctophids also prey on euphausiids, amphipods, and sergestids (e.g. Gjosaeter 1973, Omori 1974, Sameoto 1982, Tyler & Percy 1975). Therefore, myctophids may join aggregations of other pelagic fauna when all are of similar size classes, in search of prey such as copepods.

Our observations suggest that myctophids often selectively occur with other pelagic fauna. The reason for such behavior may be to reduce the probability of direct contact with predators and to benefit from the aggregate search ability of other taxa for common prey resources.

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