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Feeding Habits of Mesopelagic Species of Fish and Estimation of Plankton Graze in the Northwest Atlantic

S. G. Podrazhanskaya
All-Union Research Institute of Marine Fisheries and Oceanography (VNIRO)
17, V. Krasnoselskaya, 107140, Moscow, Russia

Abstract

The feeding habits of lanternfishes of the family Myctophidae was investigated in one of the most productive regions in the Northwest Atlantic, where the oceanographic regime and character of bioproductive processes are formed under the influence of the Labrador, North Atlantic and Gulf Stream Currents. A total of 344 stomachs from 11 species of adult myctophids ranging from 30 to 135 mm in size were examined. The most representative data were on *Benthosema glaciale*, *Myctophum punctatum*, *Ceratoscopelus maderensis* and *Notoscopelus elongatus*. *Benthosema glaciale* is an arcto-boreal species endemic to the North Atlantic while the other three species are immigrants that are brought in with warm currents. The average volume of food in the stomachs examined was low and there were many empty stomachs (up to 82.5% in *B. glaciale*). The mean-value of the feeding index was also low, from 28.6°/₀₀₀ in *B. glaciale* to 173.3°/₀₀₀ in *Protomyctophum arcticum*. Copepods were the main food item found in the stomachs of *B. glaciale*, *Hygophum benoiti*, *Lobianchia dolfeni*, *Electrona risso* and *P. arcticum* whereas *M. punctatum*, *Diaphus rafinesque*, *N. elongatus* and *Notoscopelus bolini* fed mainly on euphausiids, and hyperiids dominated in the food of *C. maderensis*. The food spectra showed the spatial distribution and vertical structure of the main water masses, played an important role. The most favourable feeding conditions for myctophids were on the North Atlantic water mass with high values of the feeding index and narrow spectrum of food species. The investigation focusing on the summer–autumn season showed the diurnal diet was moderate ranging from 0.3 to 1.5%. The grazing rate of the known biomass of myctophids ranged widely and suggested that the availability of food in the area in the summer–autumn period may be a limiting factor. This and the hydrographic regime seemed responsible for the absence of fishable concentrations of myctophids in July–October, 1983.

Key words: Feeding habits, Myctophidae, Northwest Atlantic, plankton grazing

Introduction

The feeding habits, trophic webs, diurnal rhythms and diets of mesopelagic species of fish from the North Atlantic have not yet been adequately studied. No studies specifically investigating the feeding habits of lanternfishes of the family Myctophidae in the Northwest Atlantic is known to the author. The present investigation was undertaken to make a qualitative and quantitative estimation of the feeding habits of mesopelagic species of fish in the Northwest Atlantic. The area investigated is one of the most productive regions in the Northwest Atlantic, where the oceanographic regime and character of bioproductive processes are formed under the influence of the Labrador, North Atlantic and Gulf Stream Currents.

Most myctophids investigated and reported in literature belong to interzonal species (Bekker, 1967). The food spectra of these myctophids have been studied and are known to be wide, including practically all groups of zooplankton and consisting mainly of copepods, euphausiids and hyperiids while decapods and chaetognaths are of lesser importance. All zooplankton specimens found in the stomach contents of these myctophids usually fell in the group of interzonal species (Vinogradov, 1968).

Mesopelagic myctophids on the other hand are migrants, eating migrating zooplankton and forming a single mesopelagic trophical complex (Parin, 1971). In this study attempts were made to focus on the food spectra of the mesopelagic myctophids, particularly in relation to the water masses. An attempt was made to estimate, to a first approximation, the quantity of zooplankton grazed by the overall biomass of the mesopelagic species of fish in the Northwest Atlantic in the summer–autumn period.

Materials and Methods

The investigation was conducted on board R/V *Akademik Knipovich* (Cruise XXI) in the open waters of the Northwest Atlantic off the Canadian 200-mile

zone in Subarea 3 at the depths of 60–400 m in July–October 1983 (Fig. 1). A mid-water trawl was used. A total of 344 stomachs from 11 species of adult myctophids ranging from 30 to 135 mm in size were collected and examined (Table 1). Most of the myctophids were at maturity stages II and III. Stomachs were collected and examined according to the Russian manual on the study of feeding and food relations (Anon., 1961).

Results and Discussion

The most representative material was collected on four species of myctophids: *Benthosema glaciale*, *Myctophum punctatum*, *Ceratoscopelus maderensis* and *Notoscopelus elongatus*. *Benthosema glaciale* is an arcto-boreal species endemic to the North Atlantic. Among the other species, *Protomyctophum arcticum* is also endemic to the area. The other three species mentioned above are immigrants that

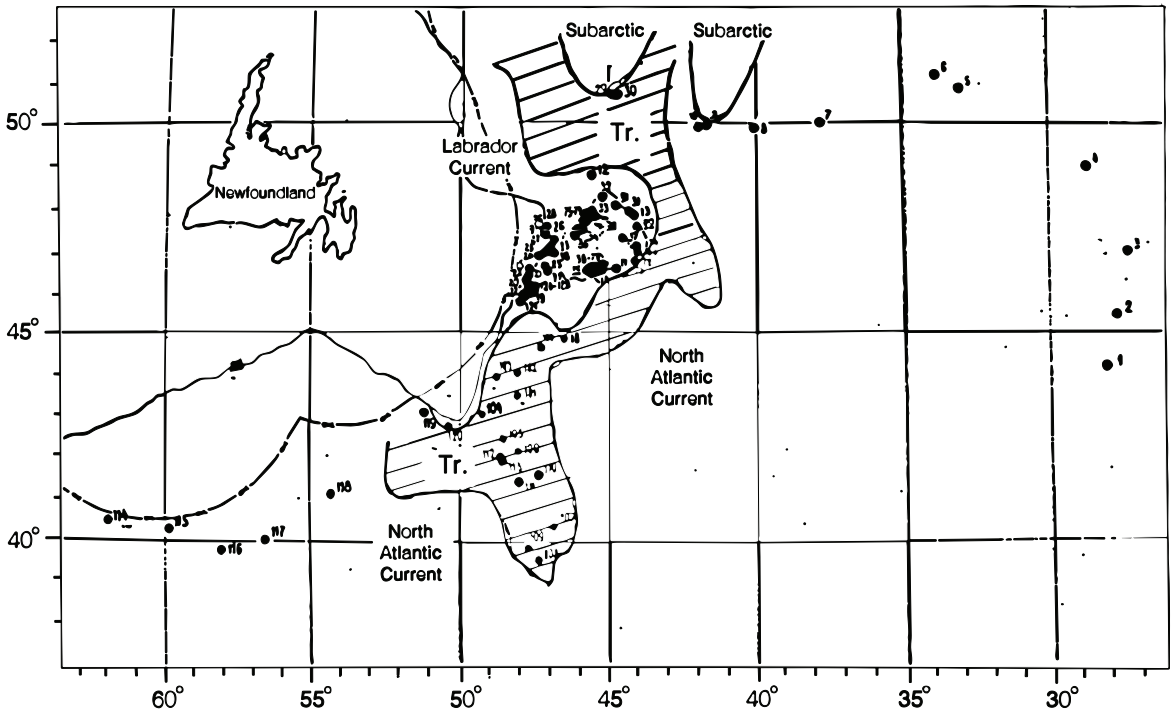

Fig. 1. Schematic map of hauls made on board R/V *Akademik Knipovich* and distribution of water masses in the Northwest Atlantic July–October 1983 (TR. = transformed).

TABLE 1. List of species of adult myctophids collected and examined for feeding study.

Species	No. of hauls	Size of specimens (mm)	No. of stomachs Total	No. of stomachs Including empty (%)	Mean extent of filling in stomachs (points)	Mean value of feeding index (‰)
Benthosema glaciale	7	35–65	86	82.5	0.2	28.6
Myctophum punctatum	4	55–90	44	38.6	0.9	66.9
Ceratoscopelus maderensis	6	45–80	65	50.7	0.5	86.3
Notoscopelus elongatus	4	75–135	41	31.7	1.4	88.0
Notoscopelus bolini	1	45–105	11	18.1	1.9	143.3
Lobianchia dolfeni	3	30–110	20	25.0	1.5	95.6
Diaphus rafinesque	2	30–70	24	16.6	0.3	131.0
Hygophum benoiti	2	40–60	28	25.0	0.8	97.8
Protomyctophum arcticum	1	35–40	7	57.1	0.4	173.2
Symbolophorus veranyi	1	85–120	3	0.0	–	422.3
Electrona risso	1	60–90	15	20.0	0.7	48.4

are brought in with warm currents and they do not spawn in the North Atlantic (*M. punctatum* and *C. maderensis* are species requiring warm waters and *N. elongatus* occupies an intermediate position requiring colder waters).

The average volume of food in the stomachs examined was not high, and ranged from 0.2 (*B. glaciale*) to 1.9 points (*Notoscopelus bolini*) in a 5-point scale. There were many empty stomachs (up to 82.5% in *B. glaciale*). The mean-value of the feeding index was also not so high, from 28.6°/₀₀₀ in *B. glaciale* to 173.3°/₀₀₀ in *Protomyctophum arcticum*. The one exception to all the species studied was *Symbolophorus veranyi*, which had a mean value of the feeding index equal to 422.3‰, and fish were predominant in the stomach contents.

The proportion of food species in the myctophids examined varied considerably. Copepods were the main food item found in the stomachs of *B. glaciale*, *Hygophum benoiti*, *Lobianchia dolfeni*, *Electrona risso* and *P. arcticum* (Table 2) whereas *M. punctatum*, *N. elongatus*, *Diaphus rafinesque* and *N. bolini* fed mainly on euphausiids. Hyperiids dominated in the food of *C. maderensis* and substituted euphausiids in *B. glaciale*.

Fish, mainly lanternfishes, occurred in the stomachs of several species of myctophids, but they dominated only in the food of *S. veranyi*. Representatives of other zooplankton groups were found in some species of myctophids, e.g. foraminiferans and algae occurred only in the stomachs of *B. glaciale*. Sagitta occurred only in *E. risso* and pelagic polychaetes (Tomopterus) were found in the stomachs of *N. elongatus*.

The area investigated is one of the most productive regions in the Northwest Atlantic. It was noted from the food spectra that it was not only the spatial distribution of the main water masses, but their vertical structure also played an important role (Table 3). The North Atlantic and Subarctic water masses and the vertical structures of the Labrador Current were encountered in the area investigated at the depths of up to 1 000 m (Fig. 1). There was a rather wide zone of transformed waters between the Labrador and North Atlantic Currents. It was evident that the southwesternmost part of the area investigated was influenced by the Gulf Stream waters, and that their hydrological characteristics did not differ from those of the North Atlantic Current in the summer of 1983 (Zozulya *et al.*, 1986).

The food composition of most species of myctophids from the Northwest Atlantic caught from different water masses is shown in Fig. 2. The most representative material was collected from the North Atlantic and Labrador water masses. The analysis of the material showed that the most favourable feeding conditions for myctophids were focused on the North Atlantic water mass. The evidence was supported not only by high values of the feeding index (from 78.8°/₀₀₀ in *N. elongatus* to 138.8°/₀₀₀ in *C. maderensis*), but also by a narrow spectrum of food species, e.g. *M. punctatum* and *N. elongatus* fed mainly on euphausiids, and C. *maderensis* on hyperiids.

Food species from the Labrador Current water mass were widely represented in the stomachs of myctophids and almost all groups of zooplankton known from that water mass were present in the contents. Values of the feeding index ranged from 40.1°/₀₀₀ in *B. glaciale* to 129.4°/₀₀₀ in *N. elongatus*. The zooplankton species composition found in the stomachs of myctophids inhabiting the Labrador water mass was represented by boreal fauna. The species with significant biomass were *Calanus finmarchicus*, *Parathemisto norvegica*, *Parathemisto compressa*, *Metridia lucens* and some species of the genera *Conchoecia* and *Pleuromamma.* The Arcto-boreal species *Calanus hyperboreus* and *Metridia longa* occurred fairly frequently.

TABLE 2. The composition of food in myctophids from the Northwest Atlantic (% by weight) July–September 1983.

Composition of food	*B. glaciale*	*M. punctatum*	*C. maderensis*	*N. elongatus*	*N. bolini*	*L. dolfeni*	*D. rafinesque*	*H. benoiti*	*P. arcticum*	*S. veranyi*	*E. risso*
Foraminifera	2.0	–	–	–	–	–	–	–	–	–	–
Polychaeta	–	–	–	0.4	–	–	–	–	–	–	–
Copepoda	38.6	24.2	19.4	23.1	35.2	45.4	24.6	44.7	61.9	1.2	67.6
Mysidacea	–	0.6	–	–	–	9.5	–	–	–	–	–
Parathemisto	28.9	17.4	30.6	0.2	–	13.2	–	20.2	–	19.7	–
Euphausiacea	11.3	36.0	27.1	70.6	57.7	17.7	48.0	14.8	–	3.3	8.6
Decapoda	–	–	–	–	–	–	14.5	12.8	–	10.1	1.3
Sagitta	–	–	–	–	–	–	–	–	–	–	7.0
Pisces	2.6	–	–	–	7.1	0.8	–	4.7	–	65.7	5.0
Algae	2.0	–	–	–	–	–	–	–	–	–	–
Digested food	14.6	21.9	22.9	5.7	–	13.4	12.9	9.2	38.1	–	11.1

TABLE 3. Food species of myctophids and their association with various water masses in the Northwest Atlantic.

Food species	Water masses			
	Subarctic	Labrador	North Atlantic	Transformed
Foraminifera		+		
Tomopterus		+		
Limacina sp.		+		
Microcalanus sp.		+		
Pleuromamma robusta			+	
Pleuromamma abdominalis		+		
Metridia lucens		+		
Metridia longa		+		
Euchaeta acuta		+	+	
Parauchaeta norvegica	+			
Undinula sp.			+	
Calanus hyperboreus		+		
Calanus finmarchicus	+	+		
Calanus sp.		+	+	
Gaidius tenispinus		+		
Neomysis		+		
Parathemisto abyssorum			+	
Parathemisto libellula	+	+		+
Parathemisto compressa				+
Vibilia sp.			+	
Nematoscelis megalops		+	+	+
Nematoscelis microps	+			
Thysanoessa longicaudata		+	+	
Thysanoessa raschii			+	
Meganyctiphanes norvegica		+		
Sergestidae	+			
Coechoecia borealis			+	
Sagitta	+	+	+	
Eukrohnia hamata		+		
Myctophidae	+			

The examination of the stomach contents of myctophids caught in the North Atlantic water mass showed that Arcto-boreal species were absent and the boreal fauna were substituted with subtropical *Eucalanus* sp. and *Pleuromamma* sp. This observation was supported by our data on food resources available in the area investigated (Podrazhanskaya, 1986).

The examination of the stomach contents of myctophids collected from the Gulf Stream water mass revealed a variety of zooplankton groups though neither groups nor species seemed to be predominant. Zooplankters were represented by boreal and subtropical forms: *Calanus* sp., *Undinula* sp., *Parathemisto abyssorum*, *Pleuromamma robusta*, *Vibilia* sp.

An attempt was made to obtain the lowest approximation of the quantity of zooplankton grazed by the large biomass species of mesopelagic myctophids in the study area, i.e. in the period when the feeding rate was not so intensive. This required a knowledge of the diurnal diets of fish, biomass of fish and biomass of food plankton. It is noted that the diurnal feeding rhythms of myctophids is still unknown. The North Atlantic myctophids are reported to belong to the so-called mesopelagic group of myctophids making diurnal vertical migrations, and at night they ascend to the surface layer.

The diurnal rhythm of feeding in Pacific myctophids is known to be characterized with a peak at night when they migrate to the surface layer. In the daytime they do not consume food in lower layers (Gorelova, 1978). This is specific, in part, to *Ceratoctopelus warmingi* and *Bolinichthys longipes*. So it may be arbitrarily assumed that food found in the stomachs of myctophids examined in this study will be the minimum diurnal diet that was necessary for the life activities of fish. The values of daily diets of the North Atlantic myctophids were not high (Table 4) or beyond the scope of diurnal diets of various myctophids from other areas of the ocean (Gorelova, 1985; Albikovskaya, 1989). The value ranged from 0.3 to 1.5% with the only exclusion in the diurnal diet of *S. veranyi* which equaled to 4.5%. The reason for the lower values of diets of myctophids

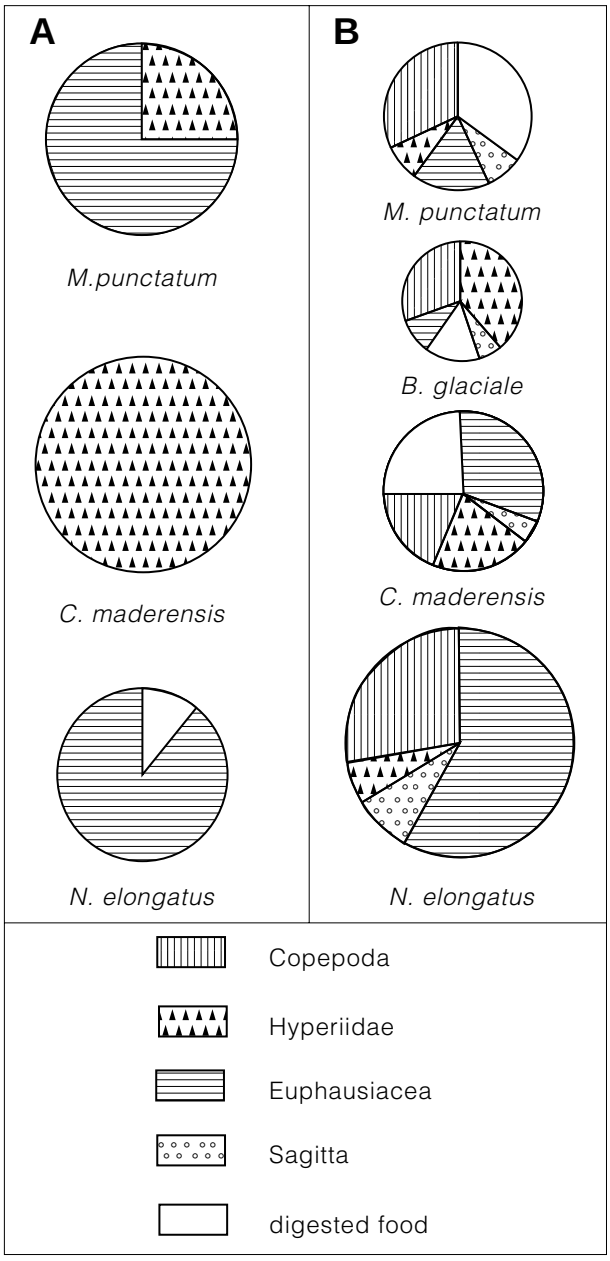

Fig. 2. Feeding habits of myctophids in (**A**) the North Atlantic Current and (**B**) the Labrador Current.

is likely to be related to the high percentage of the lipid content in tissues of the diets. This high energy diet along with the fact that in the daytime myctophids staying in lower layers "hover" almost without moving (Backus *et al.*, 1968), therefore apparently supports their metabolic rate which seems to be lower than that of more active species of fish.

The present investigation focusing on the summer–autumn season also showed other observable patterns. Concentrations were noted to form by the migrating myctophids in wave structures of the Labrador Current. This apparently was an economical method for their migrations, since it takes place in relation to the water dynamics. This mode of migration makes assessment of the myctophid resources very difficult. It is therefore suggested that two indices should be used for the assessment: the indices consisting of the instantaneous biomass of the myctophid assessed, and the biomass of the myctophid migrating through this particular fishing area. Both indices were employed in this study to assess the biomass. The first consisted of the echometric survey of these fish schools. This method yielded the instantaneous estimate of biomass of the stock north of 47˚N equal to 4 000–25 000 tons or 17.9–111.8 mg/m^3. This estimation related to the first 10 days of October in an area equal to 660 sq. miles at the 200–300 m layer of the water column. The next estimate was of the biomass of the fish migrating through the same area in the same period. This resulted in an estimate of 100 000–400 000 tons or 447.1–1 788.3 mg/m^3, depending upon the velocity of currents. The biomass of food plankton in the 200–500 m layer of the area investigated in the same period was equal to 75 mg/m^3 (Podrazhanskaya, 1986).

The amount of zooplankton grazed (ε) by the biomass of myctophids was calculated by the formula:

$$\varepsilon = \frac{A \cdot B}{100} (mg/m^3),$$

where A is a diurnal value of the fish diet (%) and B is the biomass of food plankton (mg/m^3).

The grazing rate was calculated as a ratio of the amount of plankton eaten (mg/m^3) and the zooplankton biomass (%) (Table 5). Thus, the assessed instantaneous biomass of myctophids was found to graze 0.1–22.6 mg/m^3 of zooplankton in the 660 sq. mile area. This represented a consumption of up to 0.1–30.1% of the zooplankton available (based on Podrazhanskaya (1986) estimation). Based on the estimated biomass of fish migrating through the same area, which ranged from 100 000 to 400 000 tons, the amount grazed was 1.3–80.4 mg/m^3 of zooplankton or 1.7–107.2% of the plankton biomass available. In comparison Gorelova (1983) made an attempt to obtain a first approximation the biomass of zooplankton grazed by myctophids in the subsurface layer of tropical waters. The grazing rate was estimated to range from 1 to 9 mg/m^3 a day or, on the average roughly 10% of the zooplankton biomass available.

The life cycle of mesopelagic species of fish from the Northwest Atlantic is closely associated

TABLE 4. Diurnal diets of myctophids from the Northwest Atlantic July–October 1983.

Species	No. of specimens	Mean weight of fish (g)	Diurnal diet (mg)	Diurnal diet (%)
Benthosema glaciale	86	1.4	4.2	0.3
Myctophum punctatum	44	3.8	30.4	0.8
Ceratoscopelus maderensis	65	3.6	32.4	0.9
Notoscopelus elongatus	41	11.0	66.0	0.6
Notoscopelus bolini	11	5.3	54.0	1.0
Lobianchia dolfeni	20	3.8	34.2	0.9
Diaphus rafinesque	24	1.8	27.0	1.5
Hygophum benoiti	28	1.9	13.3	0.7
Protomyctophum arcticum	7	3.7	11.1	0.3
Symbolophorus veranyi	3	10.6	514.6	4.5
Electrona risso	15	5.2	20.8	0.4

TABLE 5. Feeding habits of mesopelagic myctophids and utilization of their food resources in the Northwest Atlantic.

Diurnal diet of fish % (A)	Biomass of fish mg/m³ (B)		Biomass of food zooplankton (mg/m³) (C)	Amount of grazed zooplankton, mg/m³ $\varepsilon = \frac{A \cdot B}{100}$		Rate of grazing zooplankton, % $(\frac{\varepsilon}{C} \cdot 100)$	
	Estimated once	Migrating		Biomass estimated once	Migrating biomass	Biomass estimated once	Migrating biomass
0.3–4.5	17.9–111.8	447.1–1 788.3	75.0	0.1–0.3 0.8–22.6	1.3–5.4 20.1–80.4	0.1–0.4 1.1–30.1	1.7–7.2 26.8–107.2

with and depends on the current systems of the water in the area. Concentrations of myctophids in the North Atlantic are regularly associated with frontal zones and with the systems of the Gulf Stream flows and the North Atlantic Current. The heaviest concentrations of fish are known to be related to convergent and divergent zones of some flows of the currents, where meanderings and eddy outcrops are very intensive (Zozulya *et al.*, 1986).

The summer–autumn period in the area investigated was characterized with the highest intensity of both the Labrador and North Atlantic Currents, their velocities reaching 30–50 cm/sec. These conditions promote the formation of stable dense concentrations of both fish and food zooplankton. It is likely that feeding concentrations of myctophids were formed in the open ocean north of 50°N in summer where there are dynamic structures favourable for concentration of mesopelagic fish.

Under these circumstances the myctophids seem to move southward and eastward to spawn over deeper depths. Thus, in the summer–autumn period the area investigated can be considered a transit region for mesopelagic myctophids. Heavier localization of concentrations is impeded both by hydrographic characteristics of the area and by availability of food for myctophids. Feeding concentrations of myctophids are not unlikely to be formed in late–autumn and winter when fish may feed on the wintering stock of zooplankton.

Conclusions

1. The food spectra of myctophids examined were very wide, including representatives of all groups of zooplankton such as copepods, hyperiids, euphausiids, decapods and chaetognaths. All plankton species found in the stomachs of myctophids belonged to the group of interzonal species.

2. The most favourable conditions for feeding were focused in the North Atlantic water mass; the evidence of that was supported by high values of the feeding index and a narrow spectrum of food organisms in the stomachs of myctophids.

3. The diurnal diet of North Atlantic myctophids was rather moderate ranging from 0.3 to 1.5%.

4. The grazing rate of the known biomass of myctophids ranged widely. This suggested the availability of food in the area in the summer–autumn period may be a limiting factor. This reason together with some characteristics of the hydrographic regime seemed to be responsible for the absence of fishable concentrations of myctophids in July–October, 1983.

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