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AGE, GROWTH, AND MORTALITY OF THE MYCTOPHID FISH, *BENTHOSEMA GLACIALE* (REINHARDT), FROM WESTERN NORWAY

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ABSTRACT

Age and growth of *Benthosema glaciale* collected by midwater trawl in western Norway have been studied. Otoliths were used for age determination. The mean annual mortality in age groups I to IV was 52 %. Older specimens were sparse.

Growth was fastest in winter. Back calculation of growth based on otoliths was tried, but the results deviated from those obtained by direct observations of length and age. *B. glaciale* is shown to grow faster and to have a higher maximum length in Norway than off Nova Scotia.

CONTENTS

INTRODUCTION

Benthosema glaciale (REINHARDT, 1837) is the most common member of the Myctophidae in the North Atlantic north of about 35°N, and is distributed from Davis Strait and southern Baffin Bay to Cape Hatteras in the west, and from about 80°N off Svalbard to Cape Verde Islands in the east. There are also isolated records from Point Barrow in Alaska (BOLIN 1959; HALLIDAY 1970; BACKUS et al. 1970). A subspecies, *B. glaciale thori* (TÅNING), is common in the Mediterranean (TÅNING 1918).

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In Norway *B. glaciale* is most common in the deep fjords from the Stavanger area and northwards (JOHNSEN 1923; BERNHOFT-OSA 1935), but it is also found in Oslofjorden (LID 1967) and Skagerrak (HAMRE & NAKKEN 1970).

The species is mesopelagic and is most often found offshore over depths of at least 400 m or in deep fjords. In Canadian waters the main daytime distribution is from 150 to at least 530 m with highest concentrations below 450 m. At night the highest concentrations were found between 45 and 90 m with more scattered specimens from approximately 0–300 m (HALLIDAY 1970). These data are from open waters, but also in the fjords a distinct vertical migration seems to occur.

While comparatively much work has been done on the taxonomy and distribution of the myctophids, little is known about their ecology and biology.

HALLIDAY (1970) treated age, growth, reproduction, and vertical distribution of *B. glaciale* in Canadian waters. Some aspects of the biology of this species and the mediterranean subspecies were also investigated by TÅNING (1918) and JOHNSEN (1923, 1945). *Myctophum affine* (LÜTKEN) was investigated by OGAWA (1961), ODATE & OGAWA (1961), and ODATE (1966) and *Stenobrachius leucopsarus* (EIGENMANN & EIGENMANN) by BOLIN (1956) and SMOKER & PEARCY (1970). Data on the biology of *Notolychnus valdiviae* (BRAUER) have been given by LEGAND (1967). Some notes on the biology of several Pacific myctophids are given by BEEBE & VANDER PYL (1944). Myctophids are very abundant in all oceans of the world, and several authors have pointed out their importance in the marine food web (e.g. ANON. 1970).

The need for further investigations on the myctophids has been stressed (BLACKER 1968).

The present investigation was carried out in order to obtain more knowledge about the biology of *B. glaciale* from the West-Norwegian fjords. Age, growth, and mortality are dealt with in this paper, while food and reproduction will be described in separate papers.

INVESTIGATED AREA

Byfjorden and Herdlefjorden (Fig. 1) are parts of a fjord system in the Bergen area of the west coast of Norway. In the southwest there is a sill depth of 190 m towards Hjeltefjorden, and in the north there is a sill at less than 10 m deep. In the east the two fjords are connected to Salhusfjorden.

The maximum depth in the fjord system is about 600 m, while most of the depths vary between 300 and 400 m.

According to LINDE (1970) the temperature below 100 m usually ranges between 7.0 and 8.2 °C. It is lowest in July–August. Salinity below 100 m varies between 33.4 and 34.8 ‰. At 10 m the mean temperature is approximately 9 °C (range 5.8°–13 °C) and salinity ranges between 30.5 and 33.2 ‰. Water below 200 m is renewed each year, usually in spring and summer.

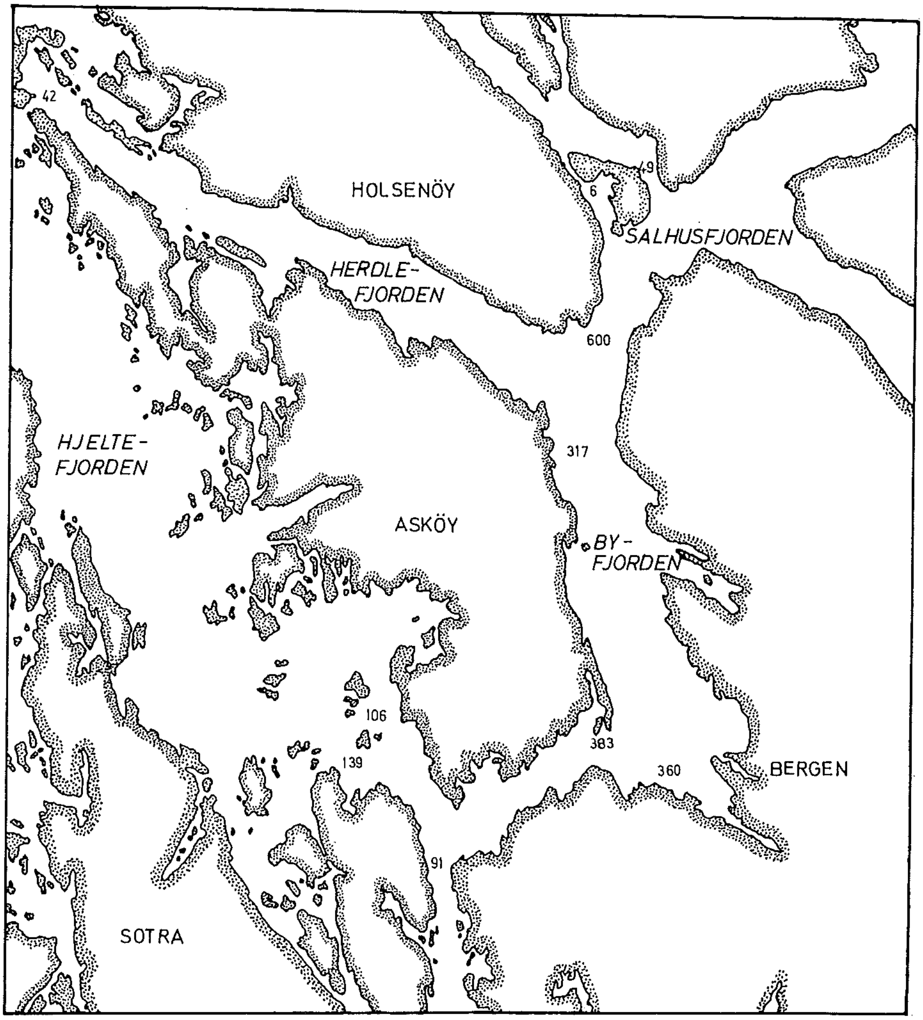

Fig. 1. The investigated area.

MATERIAL AND METHODS

Most fish were collected in 1969 when monthly samples were taken by R/V *Fritjof Nansen* of the Biological Station, University of Bergen. A number of samples was also taken by R/V *Peder Rönnestad* of the Institute of Marine Research, Bergen. In May 1970 two samples were taken. This material was supplemented with samples from Byfjorden collected by Dr. Kr. Fr. Wiborg during 1967 and 1968. All material is listed in Table 1.

The sampling was carried out with an Isaacs-Kidd three-foot midwater trawl (IKMT) with mesh size 2.6 mm (Isaacs & Kidd 1953) and a Beyer low speed midwater trawl (BLSMT) with mesh size 4.5 mm (Beyer unpubl.). Towing speed was 4 and 2 knots respectively. Towing time was approx. 20 min. for both. The depth at fishing was estimated from wire angle and wire out. Occasionally a Benthos depth recorder was used as a check. No closing device was used. A comparison of the catches from the two gears is given on page 10.

Table 1. Catch, number of tows, and catch pr. tow of *B. glaciale* in Byfjorden and Herdlefjorden 1967–1970.

Depth	Day			Night		
	Catch	tows	C/T	Catch	tows	C/T
			1967			
0– 30	0	2	—	15	4	3.8
30–100	0	6	—	30	13	2.3
100–200	27	7	3.9	54	8	6.8
>200	92	8	11.5	34	5	6.8
			1968			
0– 30	0	2	—	3	10	0.3
30–100	0	2	—	7	4	1.8
100–200	9	4	2.3	24	5	4.8
>200	19	3	6.3	6	3	2.0
			1969			
0– 30	0	1	—	0	2	—
30–100	0	2	—	91	4	22.3
100–200	93	17	5.5	34	3	11.3
>200	217	24	9.0	39	4	9.8
			1970			
>200	195	2	97.5	—	—	—

The material was preserved in 5 % formalin as soon as possible after being caught, but fish from 1969 and 1970 were first measured. The fish from 1967 and 1968 were measured after preservation. To make these measurements comparable, 35 fish between 15 and 77 mm were measured both fresh and preserved and the regression line $l_{fresh} = 1.050\, l_{preserved} - 0.574$ was calculated.

In the following all measurements are given as length of fresh specimens.

All measurements refer to standard length. Those from 1970 are to the nearest mm, those from earlier years to the nearest 0.5 mm.

Otoliths from 1967 and 1968 were partly dissolved by the formalin, and could not be used for age determination. Otoliths from 1969 and 1970 were removed and transferred to 70 % alcohol within three or four hours after the catch. Before reading the age, the otoliths were placed in absolute alcohol, transferred to creosote, and mounted in Canadabalsam or Eukitt (cf. JOHNSTON 1938). They were read under a binocular microscope, using reflected light and dark background.

Bones from the operculum were also tried for age determination (cf. MENON 1950). Concentric rings were found, but they could not be correlated with the age.

RESULTS

Otoliths and age determination

The saccular otoliths of *B. glaciale* (Fig. 2) are thin and almost elliptical with the longer axis parallel to the body axis. On the upper edge, slightly in front of the middle, there is an elevation, and in the lower edge a depression. The posterior edge is smooth, while the anterior edge has one or two spikes which seem to vary

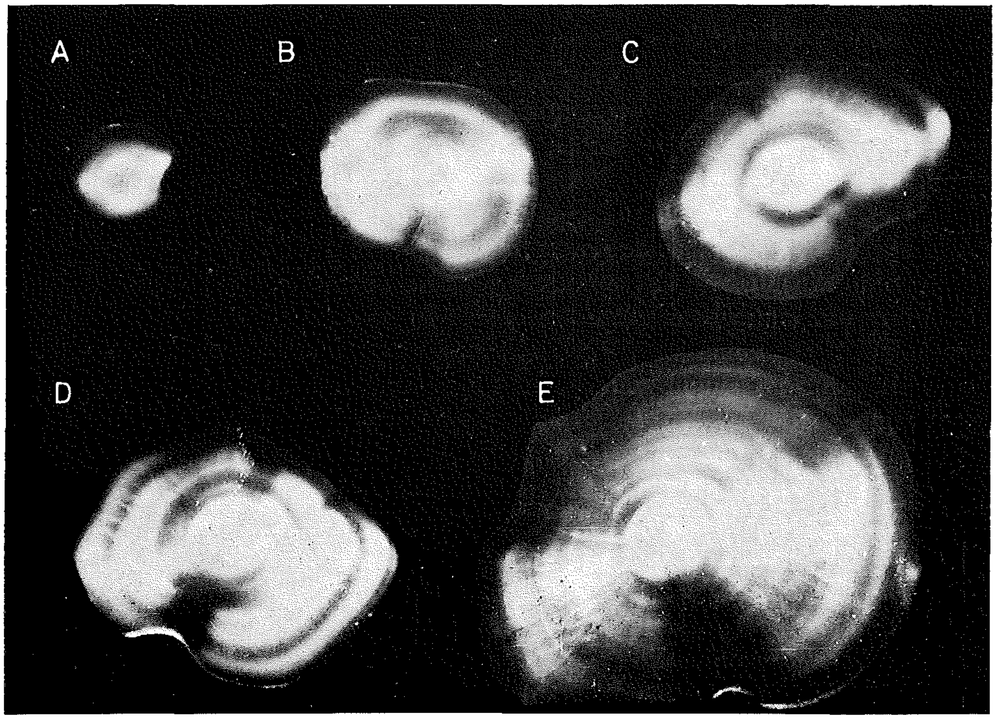

Fig. 2. Otoliths of *B. glaciale*. A. 0-group, hyaline edge, October. B. I-group, hyaline edge, September. C. II-group, opaque edge, February. D. II-group, hyaline edge, March. E. III-group, opaque edge, December.

in size and form. The nucleus is opaque in adult fish, while it frequently appears as a small opaque ring with a hyaline centre in the juveniles. Outside the nucleus, hyaline and opaque rings alternate. In the inner hyaline zone, one or two somewhat opaque rings with indistinct outlines are often found, but they may easily be distinguished from the annuli. To ascertain when the opaque and hyaline zones were laid down, the marginal character of 164 otoliths were studied. The opaque zones were not always formed along the whole margin simultaneously. All otoliths with distinct opaque zones along most of the margin were designated as opaque, and those with distinct hyaline zones along most of the margin as hyaline. In some otoliths a gradual transition from opaque to hyaline zone and vice versa was observed, and the marginal character was difficult to classify. These otoliths were noted as "undetermined".

Most fish taken from October to January had opaque margins (Fig. 3). In October the opaque zone often covered only parts of the margin, while in January it was usually broad. In March 44 % had undetermined margins, while the same percentage had a narrow but distinct hyaline margin. From May to September most otoliths had distinct hyaline margins.

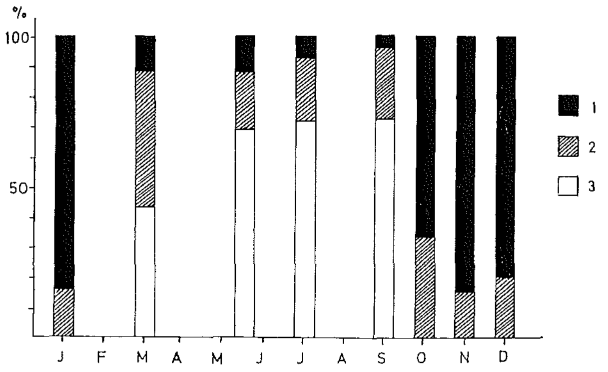

Fig. 3. Distribution of 1) opaque, 2) undetermined, and 3) hyaline otolith edges during the year.

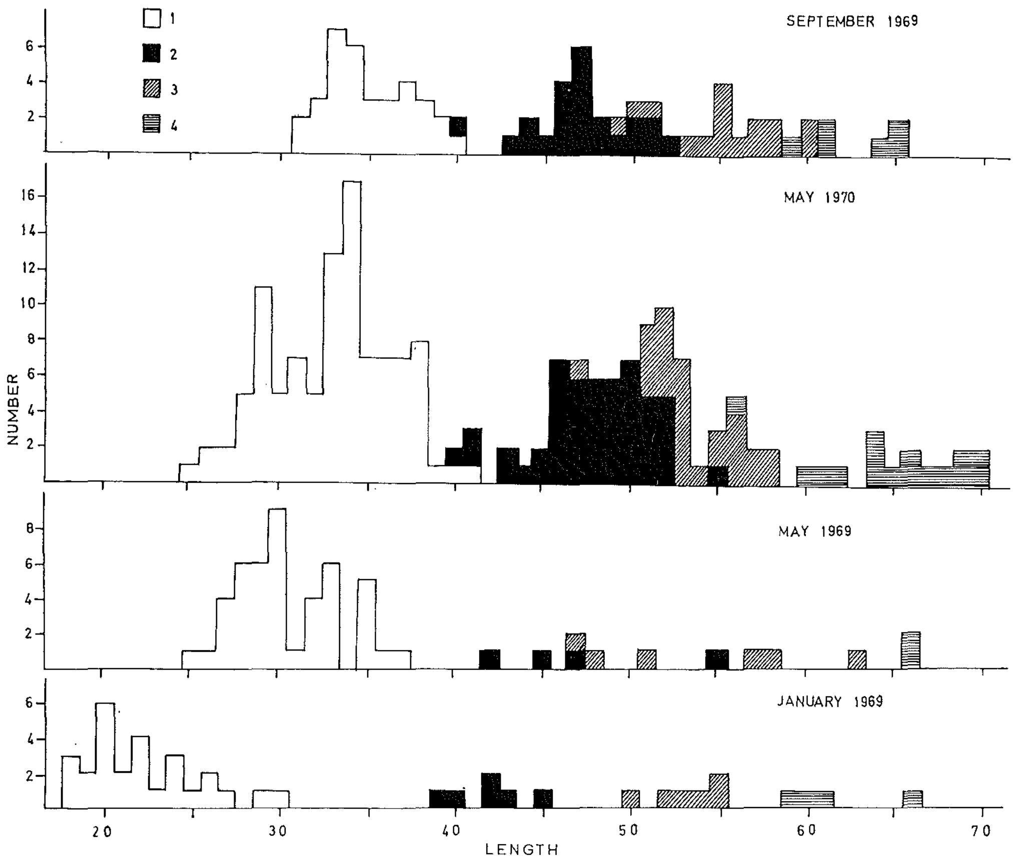

Fig. 4. Age distribution of *B. glaciale*. Numbers indicate age groups.

This indicates that the opaque zone is mainly laid down in the winter and the hyaline in summer. The few opaque margins observed in summer were probably due to formation of false zones. These could, however, in most cases, easily be distinguished from the annuli when they were completed.

The length of 0- and I-group fish showed little overlap with each other or with older fish, and their age could therefore be determined by their length. Among older fish a grouping in the length frequencies could still be traced. The correspondence between these groups and the groups found by reading the otoliths was good (Fig. 4). This evidence indicates that otoliths may be used for determining age. The age was calculated from 1 January.

Age and mortality

The age distribution of the material is shown in Table 2. The age of fish from 1967 and 1968 was only determined from the length-frequency distribution, and the data are therefore somewhat uncertain for the oldest.

To minimise effects of difference in year-class strength, material from all the years was combined for computation of mortality.

An instantaneous mortality rate, $Z = 0.74$, was obtained by plotting the natural logarithms of the total number caught of each age group against age (Fig. 5) and fitting a regression line (cf. GULLAND 1969). This equals an average mortality of approximately 52 % a year.

As a second approach the formula

$$M = 1 - \frac{N_2 + N_3 + \ \ N_r}{N_1 + N_2 + \, . \, . N_{r-1}}$$

(cf. JACKSON 1939), where N_1, $N_2 \dots N_r$ are the number of fish in successive year-classes and M is the average yearly mortality, was used. This method gave an approximate yearly mortality of 58 %.

In the preceding calculations age groups I–IV only are included.

Inclusion of age group V will result in approximate average mortalities of 66 % and 75 % respectively when the graphical method and Jackon's formula are used. This is the result of a sudden drop in the number of fish caught after age group IV.

Table 2. Age distribution of the material (age group 0 excluded).

Age group	I		II		III		IV		Older		Total
Year	N	%	N	%	N	%	N	%	N	%	
1967	133	60.2	42	19.0	32	14.5	13	5.9	1	0.5	221
1968	18	27.7	25	38.5	16	24.6	5	7.7	1	1.5	65
1969	271	69.5	56	14.4	44	11.3	17	4.4	2	0.5	390
1970	100	51.3	51	26.2	28	14.4	16	8.2	0		195
Total	522	59.9	174	20.0	120	13.8	51	5.9	4	0.5	871

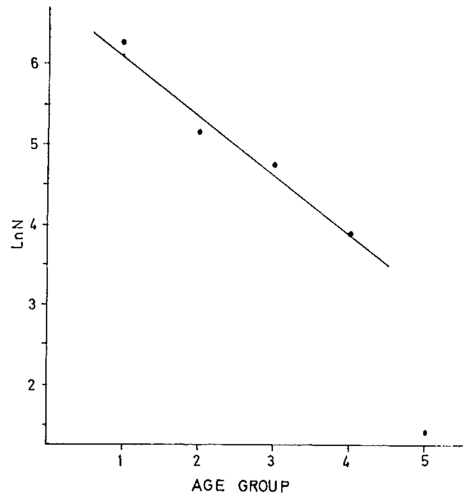

Fig. 5. Logarithms of total catch in each age group plotted against age.

Growth

Mean lengths with 95 % confidence limits for the months and age groups where data were available, are shown in Fig. 6. Lengths, confidence limits, ranges, and number of fishes for each month are given in Table 3.

The data for the 0- and I-groups are based on all the material from 1967 to 1970. For older fish, the age of which could only be determined with certainty from otoliths, only data from 1969 to 1970 could be used. Data from the different years were combined to obtain a mean growth rate.

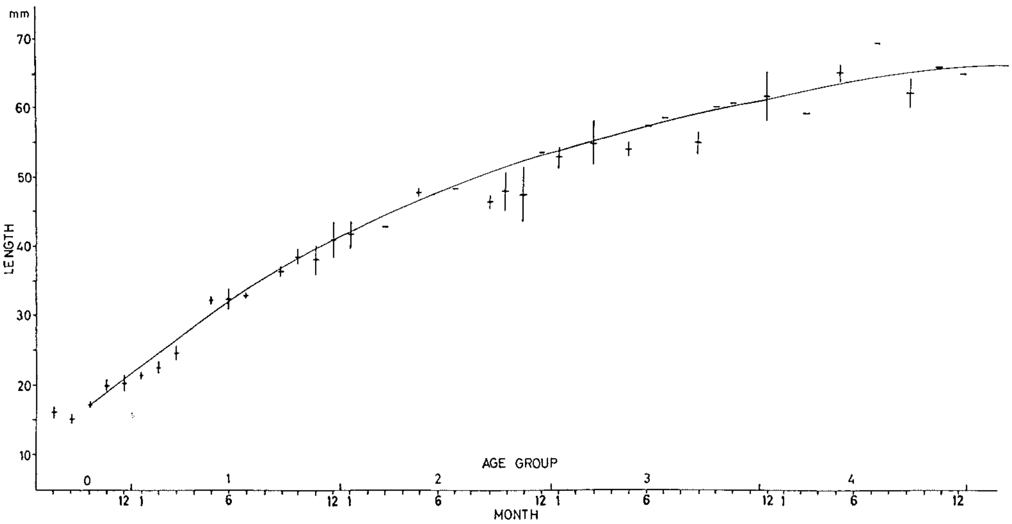

Fig. 6. The Bertalanffy growth curve of *B. glaciale* and monthly mean length with 95 % confidence limits.

Table 3. Number and mean length with range and 95 % confidence limits for *B. glaciale*. Measurements in mm.

Month	N	$\bar{l}$	Conf. lim.	Range
		Age group 0		
Aug.	6	16.08	0.900	15.0–17.0
Sept.	7	15.29	0.832	13.5–17.0
Oct.	51	17.25	0.363	14.0–20.5
Nov.	24	20.04	0.952	16.0–26.0
Dec.	24	20.38	1.216	15.0–26.0
		Age group I		
Jan.	73	21.31	0.468	14.5–29.5
Feb.	56	22.50	0.862	16.0–31.5
March	22	24.66	1.113	19.0–30.5
May	153	32.12	0.462	24.5–42.0
June	27	32.22	1.282	22.0–38.0
July	103	32.72	0.388	27.0–41.0
Sept.	35	36.09	0.718	31.0–40.0
Oct.	17	38.26	1.035	35.0–42.0
Nov.	8	38.06	2.390	31.0–42.0
Dec.	7	40.79	2.636	36.5–46.0
		Age group II		
Jan.	6	41.50	1.898	38.5–44.5
March	3	42.67	–	38.0–48.0
May	55	48.07	0.743	39.0–55.0
July	1	45.0	–	–
Sept.	22	46.36	0.856	43.0–52.0
Oct.	12	47.92	2.715	42.5–58.0
(cont.: Age group II)				
Nov.	4	47.38	4.383	43.0–52.0
Dec.	2	53.25	–	51.5–55.0
		Age group III		
Jan.	6	52.92	1.628	50.0–55.0
March	10	54.80	3.377	45.5–60.5
May	34	53.96	0.889	46.5–62.5
June	1	57.5	–	–
July	3	57.60	–	53.0–62.5
Sept.	16	54.94	1.383	49.0–59.5
Oct.	2	60.0	–	59.0–61.0
Nov.	1	60.5	–	–
		Age group IV		
Jan.	4	61.5	3.654	59.0–66.0
March	1	59.0	–	–
May	18	65.0	1.362	54.5–70.0
July	2	69.2	–	65.0–73.5
Sept.	6	62.17	2.119	58.5–65.0
Oct.	1	65.5	–	–
Dec.	1	65.0	–	–
		Age group V		
March	1	77.0	–	–
May	1	72.0	–	–

HALLIDAY (1970) has shown that in Canadian waters there was no sexual dimorphism in growth, and this is assumed to be generally valid. The sexes are therefore treated together.

The von Bertalanffy growth equation:

$$l_t = L_\infty (1 - \exp [- K (t - t_0)])$$

was fitted to the data by a method described by RICKER (1958).

The resulting equation was:

$$l_t = 75.0 (1 - \exp [- 0.45 (t - 0.25)]) \quad \text{(Fig. 6).}$$

The growth seems to vary throughout the year. This is most clearly seen when mean lengths for spring, summer, autumn, and winter are plotted together with the growth equation (Fig. 7). The growth was rapid in the period autumn-winter-spring and poor between spring and summer. The mean lengths decreased between summer and autumn except in the 0-group, which also showed

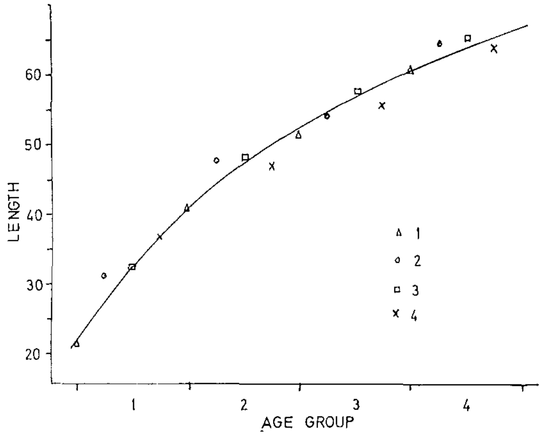

Fig. 7.
The Bertalanffy growth curve and mean lengths for 1) winter, 2) spring, 3) summer, and 4) autumn.

rapid growth that period. The growth cycle may be correlated with the spawning period which falls in May–July (GJÖSÆTER 1970). It should be noted that in the depths where *B. glaciale* is mainly found the temperature is highest in winter and lowest in summer-autumn.

Back calculations from the otoliths

When diameters of the otoliths were plotted against the length of the fish on logarithmic paper, a straight line was found. The equation lg l = 0.8259 lg d + 1.4587 was fitted (l: length of the fish, d: diameter of the otolith, both in mm). The correlation coefficient was 0.95 and the standard error of estimate 0.028. This indicates a very close correlation between the two sets of measurements.

For each age group the mean diameter of the hyaline zones was computed, and the length of the fish when these were laid down was found from the formula above (Fig. 8).

The length found from zone 1 in fish from age group II was similar to the observed length, while the length computed from zone 1 in age group III was smaller and that from age group IV smaller still. Length computed from zone 2 showed greater deviation from the observed length than that computed from zone 1. The value computed from age group III was slightly smaller than that computed from age group IV. Back calculations from zone 3 gave still greater deviations from the growth curve than those from zone 1 and 2.

If the constants from the von Bertalanffy's growth equation are computed from the back calculated lengths, K = c. 0.22 and L_∞ = c. 87 mm are found.

Comparison between catches in IKMT and BLSMT

To compare the catches from the two gears, five pairs of daytime tows to 200—300 m depth were made, each pair at the same place and with less than one hour's difference in time between the tows.

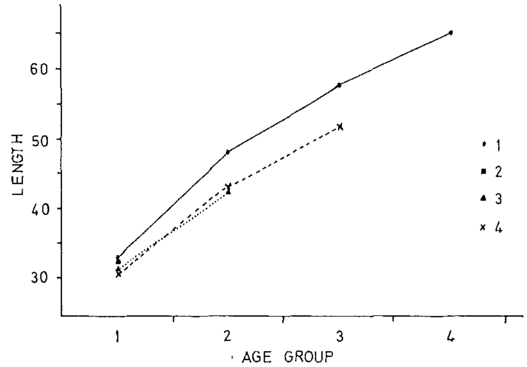

Fig. 8.
Growth calculated from otoliths. 1 mean lengths for summer from the Bertalanffy growth curve, 2, 3, 4 lengths obtained by back calculation from fish in age group II, III, and IV respectively.

A chi-square test showed that there were no differences ($p > 0.05$) from the values expected if the gears caught exactly alike, in regard to total number and numbers within each age group (Table 4).

Only one pair of tows (May 1970) gave so much material that a closer analysis was possible (Table 5). The greatest deviation in length was found in age group IV, but this would be reduced to 0.7 mm if one exceptionally small fish of group IV taken in IKMT is disregarded. "Students" t-test showed that none of the other length deviations were significant ($p > 0.05$).

The difference between catches taken with the gears is very small, and the bias introduced by treating them together seems negligible.

Table 4. Age distribution of fish taken in five parallel tows with IKMT and BLSMT. Numbers in brackets give the expected values if the gears caught alike.

Gear	Age group					Total
	0	I	II	III	IV	
BLSMT	9	61	38	18	12	138
	(7.1)	(70.1)	(32.3)	(17.5)	(11.0)	
IKMT	4	67	21	14	8	114
	(5.9)	(57.9)	(26.7)	(14.5)	(9.0)	

Table 5. Number and lengths of fish taken in parallel tows with IKMT and BLSMT in May 1970. Measurements in mm.

Age group	BLSMT		IKMT		Deviation	Age group	BLSMT		IKMT		Deviation
	N	l	N	l			N	l	N	l	
I	43	33.91	57	32.71	+ 1.20	III	17	53.76	11	54.34	− 0.56
II	34	48.28	17	47.92	+ 0.35	IV	10	65.84	6	63.51	+ 2.23

DISCUSSION

The mortality found is the natural mortality since there is no fishing for *B. glaciale*. The values found would be biased if there were an immigration or emigration which is selective for the age groups. The apparent sudden rise in the mortality coefficient between age groups IV and V may be due to the selectivity of the small gears used.

The mortality of myctophids has not been studied earlier, but data from Canadian waters (HALLIDAY 1970, table 2) may be used for such estimates. These data give a mean instantaneous mortality rate of approximately 1.75, i.e. a mean yearly mortality of approximately 83 %. *B. glaciale* from Canadian waters therefore seem to have a much higher mortality than in the area of the present investigation, and it seems to rise with age, while in my material it is fairly constant in the age groups I to IV. One reason for this may be that *B. glaciale* from Canadian waters has more predators than those in the Norwegian fjords where the mesopelagic fauna is much more sparse.

The age distribution from 1968 is clearly different from the other years, with a very low number in age group I. In 1969 the percentage in age group II was low. Catch per tow, in 1968 was lower in all depths and during both day and night, than in other years. This evidence seems to indicate that the 1967 year-class was very weak compared with the other year-classes caught during this study.

The growth data obtained by back calculation deviated from those found by direct observations of length at different ages, and this discrepancy grew more pronounced as the fish grew older. Within age group I a Rosa Lee's phenomenon was found. The parameters K and L_∞ from von Bertalanffy's growth equation computed from data obtained by back calculation were too low and too high respectively.

SMOKER & PEARCY (1970) used otoliths for back calculation in *Stenobrachius leucopsurus*. They found a correlation between the length of the fish and the diameter of the otoliths of the form $\lg l = a + b \lg d$ (l = fish length, d = diameter of otoliths). They also found a discrepancy between back calculated lengths and lengths derived by other methods. In *Myctophum affine* ODATE (1966) found a direct proportionality between fish length and radii of the otoliths.

The growth of *B. glaciale* from Norwegian waters has been studied by JOHNSEN (1923, 1945). His results do not agree with those found in this study. His material which was collected over many years, with different gears and from many parts of the Norwegian waters, was very small, and age was only established by grouping in the length frequency.

Both in the material treated by JOHNSEN (1945) and in the present material there were some fishes which were longer than $L_\infty = 75.0$ mm. But as pointed out by KNIGHT (1968) L_∞ is only a mathematical parameter, and often shows great deviation from the real maximum length.

October 1969 a *B. glaciale*, which after preservation measured 98.5 mm, was taken by IKMT in Korsfjorden, western Norway (Reidar R. Rasmussen personal commn). In the fjords in the Stavanger area a specimen measuring 96 mm has been taken (JOHNSEN 1945). The largest specimen known outside Norwegian waters is probably one measuring 84 mm from Greenland (JENSEN 1948). The specimen from Korsfjorden therefore appears to be the longest known. Calculated from the length of the preserved fish, length in fresh condition has been c. 103 mm. The otolith was difficult to interpret, but probably the age was 7 or 8 years.

In Canadian waters the growth of *B. glaciale* has been studied by HALLIDAY (1970). He found the growth equation

$$l_t = 68.28\ (1 - \exp\,[-0.36\ (t + 0.49)\ ]).$$

This was based on fish preserved in formalin and age was calculated from 1 April. For comparison with my data L_∞ may be transformed to fresh length, and the base for age determination shifted to 1 January. K is not altered by these transformations, and the resulting equation is

$$l_t = 71.1\ (1 - \exp\,[-0.36\ (t + 0.23)\ ]).$$

This indicates that the growth is faster and the maximum length somewhat greater in western Norway than in Canada.

SMOKER & PEARCY (1970) found the parameters K and L_∞ from von Bertalanffy's equation to be 0.34 and 85 mm respectively for the cold water species, *Stenobrachius leucopsurus*. Maximum age seemed to be 8 years. *Myctophum affine*, a mainly tropical species, grows to approx. 78 mm in 3 years (ODATE 1966). *S. leucopsurus* grows therefore more slowly than *B. glaciale* from Norway, while *M. affine* grows faster. The maximum age of *B. glaciale* also falls between the two others.

Notolychnus valdiviae taken in the eastern part of the Indian Ocean, probably has an annual life cycle, and reaches a length between 20 and 30 mm.

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