

GROWTH, PRODUCTION AND REPRODUCTION OF THE MYCTOPHID FISH *BENTHOSEMA GLACIALE* FROM WESTERN NORWAY AND ADJACENT SEAS

By

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ABSTRACT

GJØSÆTER, J. 1981. Growth, production and reproduction of the myctophid fish *Benthoosema glaciale* from western Norway and adjacent seas. *FiskDir. Skr. Ser. HavUnders., 17: 79–108.*

Age, growth, mortality, production and reproduction were studied on material of *Benthoosema glaciale* from some fjords of western Norway and from the adjacent ocean. Samples were collected using pelagic trawls and Icaacs-Kidd midwater trawls.

Age was studied by means of otoliths although the seasonal cycle of zone formation was variable. Growth was highly variable within the material, L_{∞} of the von Bertalanffy's growth equation ranging from 70 to 87 mm and K from 0.19 to 0.46.

The instantaneous natural mortality was about 0.7. The maximum sustainable yield per recruit can be obtained with a first age of capture of about 2 years and a fishing mortality of 1.5 or higher.

B. glaciale reaches maturity at an age of 2 or 3 years and spawn mainly during summer. The development of the ovaries is briefly described. Its mean fecundity is 700 eggs/female.

INTRODUCTION

The lanternfish *Benthoosema glaciale* (REINHARDT) is the most abundant mesopelagic fish in most of the North Atlantic north of about 35°N (BOLIN 1959, BACKUS *et al.* 1970, JAHN and BACKUS 1976). In this area it is an important part of the pelagic ecosystem and may also be a promising resource for future fisheries.

Compared to other lanternfish, *B. glaciale* has been much studied. TÅNING (1918) and JOHNSEN (1923, 1945) studied aspects of its life history and ecology. More recently HALLIDAY (1970) studied growth and vertical distribution of *B. glaciale* in the northwestern Atlantic, and GJØSÆTER (1973a) investigated growth and mortality in a population from a fjord system in western Norway. The reproduction was briefly dealt with by GJØSÆTER (1970) and the food and feeding habits by GJØSÆTER (1973b) and by KINZER (1977). These studies indicate that *B. glaciale* reaches a maximum size of about 7 cm in about 4 years. It has an annual natural mortality of more than 50% and spawns during spring and summer. In the Mediterranean it reaches a smaller size, lower age and probably spawns all the year round.

The aim of this paper is to further analyse the growth of *B. glaciale* from the fjords in western Norway and the adjacent ocean and to estimate the production of the species. The reproduction cycle and the fecundity are also discussed.

MATERIALS AND METHODS

The material, used for the age and growth studies, were mainly collected by the vessels of the Institute of Marine Research, Bergen. Some of the cruises were conducted mainly to collect mesopelagic fish in the fjords, but most samples are from cruises where the primary aim was to collect other fish or euphausiids.

Samples were collected with a pelagic fish trawl or a three foot Isaacs-Kidd midwater trawl (IKMT). Depth was usually monitored using a Benthos depth recorder or an acoustic net sonde. Lists of the samples used are given in Tables I and II. Geographical names used are shown in Fig. 1 A and B.

The studies of the reproduction are partly based on the above-mentioned material and partly on a material collected by IKMT in Byfjorden and Herdlefjorden on the west coast of Norway during the years 1967–1970 with a research vessel belonging to the Institute of Marine Biology, University of Bergen. Details about this sampling are given by GJØSÆTER (1973a).

The samples, used for age and growth studies, were, with few exceptions, frozen onboard and taken back to the laboratory for examination. Standard length was recorded on all specimens. Weight was recorded in some samples to the nearest 0.01 g. Before weighing, the fish were thawed and water on their surfaces removed with filter paper.

Otoliths were removed, cleaned and stored in 80% ethanol. For age reading they were transferred to creosote and viewed by binocular microscope using reflected light and black background. The diameter parallel to the longest axis of the otoliths and the corresponding diameters of the hyaline zones were measured using an ocular micrometer. All otoliths were read by two persons. In cases where disagreement arose (less than 10%), the otoliths were read again and discussed. In a few cases (less than 2%) agreement was still not reached, and these otoliths were not used. The samples intended for reproduction studies were preserved in formalin. The standard length was measured and the gonads removed for examination. Some gonads were sectioned and stained in Alun Haematoxylin and eosin.

A description of the stages of maturity of the females was based on histological and macroscopical characters. It was difficult to distinguish maturity stages in males by macroscopic examination, and therefore no scale was made. All maturing oocytes in both ovaries were counted for fecundity studies, and no subsampling had to be carried out.

The length measurements, used for growth studies, were made on frozen and thawed material while GJØSÆTER (1973a) used fresh fish. A sample of 32

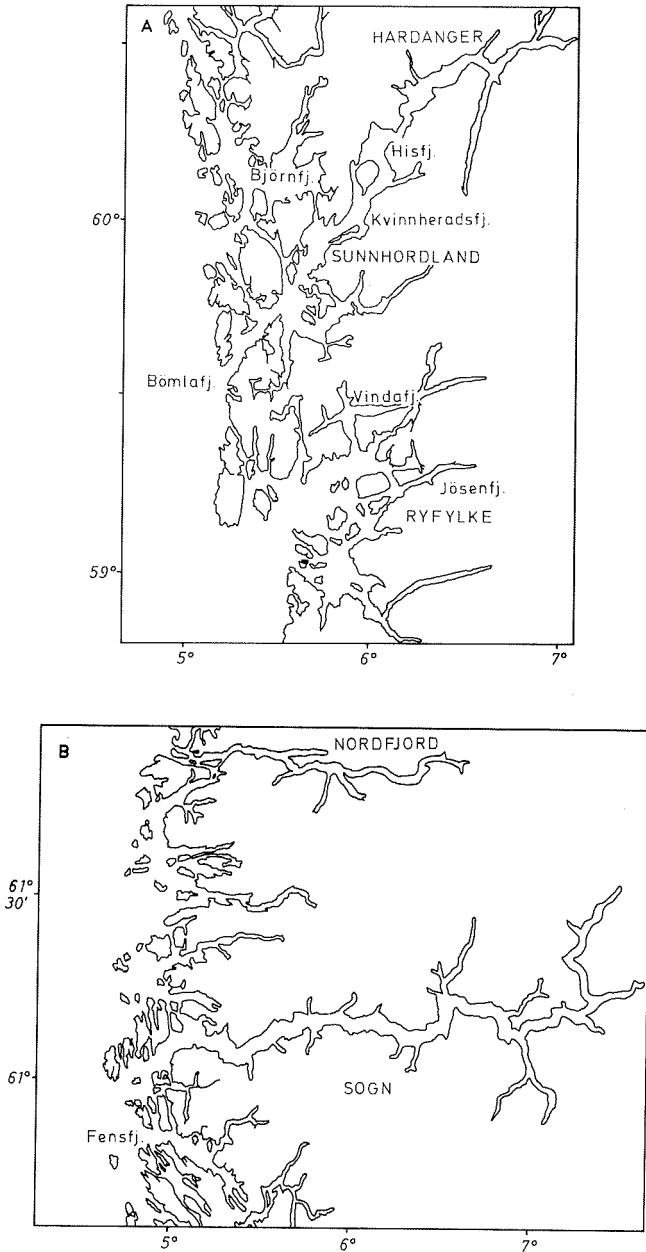


Fig. 1A and B. Geographical names referred to in the text.

specimens was measured before and after being frozen. Using geometric mean regression (see RICKER 1973), the lines

$$l_{\text{frozen}} = 0.99l_{\text{fresh}} + 0.16$$

$$l_{\text{fresh}} = 1.01l_{\text{frozen}} - 0.16$$

were fitted, where $r^2 = 0.949$. These regression coefficients are not significantly different from zero (confidence limits calculated as in RICKER 1975). The change in length due to freezing is probably within the error of measurement for all the size groups involved. Measurements based on fresh and frozen material were therefore used interchangeably without transformation. Lengths of fish preserved in formalin were transformed to fresh lengths using the equation

$$l_{\text{fresh}} = 1.05l_{\text{formalin}} + 0.57 \text{ (GJØSÆTER 1973a).}$$

Geometric mean regression has been used in several calculations when both variates are subject to measurement error, and the sample range truncates the range of the variates (see RICKER 1973, 1975). The confidence limits of the regression coefficient b were calculated as

$$b (\sqrt{B + 1} - B) \text{ and } b (\sqrt{B + 1} + B)$$

where $B = F (1 - r^2) \times (N - 2)^{-1}$, r^2 is the coefficient of determination, N the number of variates and F the variance ratio at the 95% confidence level for $N_1 = 1$ and $N_2 = N - 2$ degrees of freedom (RICKER 1975).

RESULTS AND DISCUSSION

GROWTH AND PRODUCTION

Otoliths and age determination

HALLIDAY (1970) and GJØSÆTER (1973a) used otoliths to age *B. glaciale*. HALLIDAY (1970) used the Petersen method (see TESCH 1968) to verify the age determination, GJØSÆTER (1973a) used both the Petersen method and a record of the seasonal variation in the edge characters of the otoliths.

In the oceanic areas (Fig. 2B) hyaline edges dominated in the samples from March to July while opaque dominated in November and December. Samples from the other months are lacking. In the fjords (Fig. 2A) hyaline zones dominated in samples from March to June while opaque dominated in January, October and November. There are, however, indications that different populations form zones at different times. Only the material from October was large enough for a more detailed analysis of this.

Table 1 shows distribution of edge characters in samples from Byfjorden, Sogn and Sunnmøre. A chi-square test on the frequencies of hyaline and opaque edges (with narrow and broad hyaline zones combined to get the highest possible expected frequencies) showed that the samples could not have been drawn from the same population ($\chi^2 = 39.06$, $P < 0.05$).

The data from Sogn appears to be different from the others (Table 2), and a separation of those data into single samples shows that this difference is mainly due to a sample from 1974 (sample No. 7). Although it will change the confidence level of the tests, sample No. 7 from Sogn was disregarded and the six other samples compared. For this analysis the narrow and broad zones were

combined both under hyaline and opaque. The expected frequencies were still low and a log-likelihood test, which is less sensitive to this than a chi-square test (ZAR 1974), was therefore applied. The results, $G = 1.08$, $P > 0.5$, indicates that the six samples compared could have been drawn from the same population although the level of significance is not reliable. These samples were combined and compared with the samples from Byfjorden and from Sunnmøre. In this case narrow and broad hyaline zones were combined while the opaque were kept separate. Although the differences were small, the result

$$\chi^2 = 17.4, 0.01 < P < 0.05$$

shows that the samples involved were probably still not drawn from the same population. However, in this case, too, the hypothesis was made a posteriori and the level of significance is therefore unreliable.

Different age groups may form edge zones at different times. This hypothesis was tested with the samples taken in Sogn in 1974 (Table 3). These samples were selected because they showed a wide variation in time of zone

Table 1. Distribution of edge characters of the otoliths of *B. glaciale* taken in October during the years 1971 – 1975.

Area	Year	No. of samples	N	Hyaline		Opaque	
				Narrow %	Broad %	Narrow %	Broad %
Byfjord	1975	5	70	0	0	58.6	41.4
Sogn	1972/74	7	264	12.5	14.0	57.6	15.9
Sunnmøre	1971	1	19	0	5.3	63.2	31.6
Total			353	9.4	10.8	58.1	21.8

Table 2. Distribution of edge characters of otoliths of *B. glaciale* taken in Sogn in October during the years 1972 – 1974.

Area	Year	Sample no.	N	Hyaline		Opaque	
				Narrow %	Broad %	Narrow %	Broad %
Sogn	1972	1	19	5.3	5.3	68.4	21.1
	1973	2	21	4.8	4.8	76.2	14.3
	1973	3	33	3.0	6.1	54.5	36.4
	1973	4	25	4.0	8.0	32.0	56.0
	1974	5	42	11.9	2.4	76.2	9.5
	1974	6	60	5.0	3.3	85.0	6.7
	1974	7	64	32.8	43.7	21.8	1.6
Total			264	12.5	14.0	57.6	15.9

formation. Again, narrow and wide edges had to be pooled. The difference turned out to be non-significant ($\chi^2 = 5.20$).

The same samples were used to test whether size of fish was related to zone formation. Table 3 shows that neither among the 0-group nor the I-group did the size of the fish with different otolith edge characters differ significantly at the 5% level. It is therefore concluded that fish from different geographical areas may have different patterns of zone formation (Table 1), and that even within an area there may be variation (Table 2). The age or size of the fish (Table 3) seems to have less influence on the pattern of zone formation. This geographical variation probably explains why the data used by GJØSÆTER (1973a) show a much more regular cycle in the zone formation than those given in Fig. 2.

Length-weight relationship

The length-weight relationship was studied in 13 samples, and one predictive regression line was fitted to each sample (Table 4). The slopes were compared using covariance analysis as described by e.g. ZAR (1974) and proved to be significantly different ($F = 3.0$, $P < 0.05$).

Table 3. Relation between edge characters of the otoliths, and length and age of *B. glaciale* taken in Sogn, October 1974.

Age	N	Hyaline						Opaque					
		Narrow			Broad			Narrow			Broad		
		%	<i>l</i>	SD	%	<i>l</i>	SD	%	<i>l</i>	SD	%	<i>l</i>	SD
0	44	18.2	19.50	4.56	25.0	18.90	0.94	50.0	21.13	3.75	6.8	20.33	1.15
1	97	10.3	31.25	1.04	15.5	30.25	4.24	68.0	30.06	2.46	6.2	28.83	4.45
≥2	16	12.5			31.3			56.3			0		
Total	157	12.7			19.7			61.8			5.7		

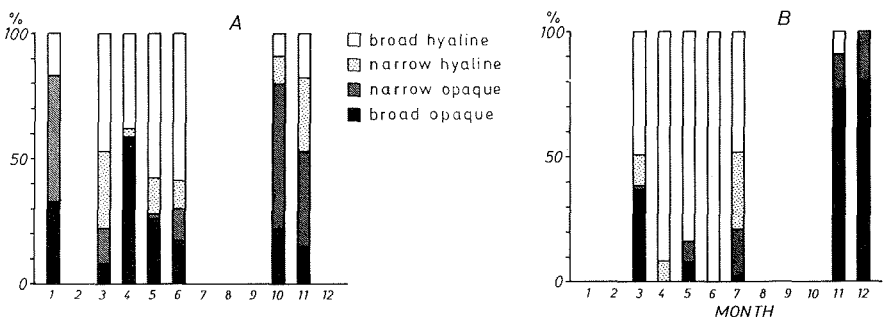


Fig. 2. Distribution of opaque and hyaline otolith edges in *B. glaciale* from the fjords (A) and from the ocean (B).

Table 4. Length/weight relation. Parameters of the predictive regression $\lg W = a + b \lg l$ and coefficients of determination in samples of *B. glaciale*.

Area	Month	N	b	a	r ²
Ocean	March	33	3.045	-4.998	0.894
»	July	91	3.445	-5.764	0.904
Fjords	March	30	2.833	-4.642	0.780
»	April	48	3.276	-5.374	0.986
»	May	39	2.748	-4.637	0.877
»	June	23	2.992	-4.833	0.996
»	»	53	2.959	-4.767	0.993
»	Sept.	62	2.866	-4.789	0.838
»	»	63	2.888	-4.617	0.981
»	»	64	3.076	-5.053	0.890
»	»	47	3.288	-5.356	0.940
»	»	30	3.315	-5.404	0.933
»	»	22	3.169	-5.226	0.922

Two samples were taken off the coast. These did not have significantly different slopes ($t = 1.25$), and they were therefore pooled. As recommended by RICKER (1973), a geometric mean regression was fitted to the pooled data, and the result based on 124 pairs of measurements was:

$$\lg W = 3.66 \lg l - 6.12 \text{ or}$$

$$W = 7.6 \cdot 10^{-7} l^{3.66}$$

where W is weight in gram and l length in millimeter. The coefficient of determination was $r^2 = 0.91$ and confidence limits of the regression coefficient 3.46 and 3.86.

Six samples taken from the fjords during autumn were compared. These had equal slopes ($F = 1.46$, $P > 0.05$), but unequal elevations ($F = 16.14$, $P < 0.05$). Five samples from the spring and summer had different slopes ($F = 4.26$, $P < 0.05$). In spite of these differences the material was pooled, and the following functional regressions were obtained:

Spring/summer:

$$\lg W = 3.10 \lg l - 5.07 \text{ or}$$

$$W = 8.4 \cdot 10^{-6} l^{3.10}$$

$N = 193$, $r^2 = 0.93$ and the confidence limits of regression coefficients were 2.99 and 3.22

Autumn:

$$\lg W = 3.41 \lg l - 5.54 \text{ or}$$

$$W = 2.8 \cdot 10^{-6} l^{3.41}$$

$N = 288$, $r^2 = 0.95$ and the confidence limits of regression coefficients were 3.32 and 3.50. These two equations are significantly different at the 95% level.

For the purpose of estimation of production, one equation was calculated on the total fjord material, and the material from the different seasons were weighed by a factor corresponding to the number of fish studied. The result was:

$$\lg W = 3.26 \lg l - 5.32 \text{ or}$$

$$W = 4.8 \cdot 10^{-6} l^{3.26}$$

where $N = 481$, $r^2 = 0.95$ and the confidence limits of the regression coefficient were 3.20 and 3.33.

The observed variation between the samples may be due to affects of area, season, sex composition in the samples and different selectivity of the gears used. With the scarce material available, it is not possible to separate these effects, and therefore no further attempts have been made to study seasonal variations in condition. The apparent difference between the oceanic samples and those from the fjords may also be caused by some of these factors.

Growth of the fjord populations

A list of the samples used for age studies and the mean lengths in the samples are shown in Table I and Fig. 3. A von Bertalanffy's growth curve $l_t = L_\infty(1 - e^{-K(t-t_0)})$ was fitted to the data using a method described by ALLEN (1966). This method gives the best least-squares estimates of the parameters L_∞ , K and t_0 and estimates of the variances of these parameters. The following equation was derived:

$$l_t = 83.06 (1 - e^{-0.20(t+0.64)})$$

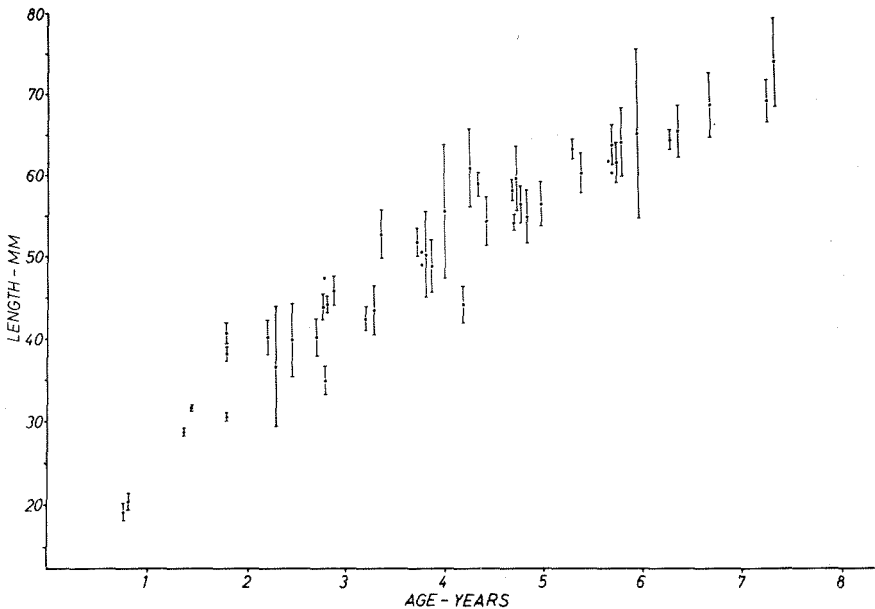


Fig. 3. Growth of *B. glaciale* from the fjords. The points represent mean length of a sample and the vertical bars 95% confidence limits.

Table 5. Parameters of the von Bertalaffy's growth equations for *B. glaciale* taken in the fjords.

Parameter	All samples 1973-75	Sogn/Møre	Byfjord		
			1975	1974	1968-72*
K	0.204	0.189	0.238	0.392	0.445
\hat{V} (K)	0.0002	0.001	0.001	0.023	0.002
L_∞	83.063	86.954	79.243	70.221	73.149
\hat{V} (L_∞)	7.397	56.618	13.459	13.462	10.369
t_0	-0.640	-0.647	-0.632	-0.103	0.252
\hat{V} (t_0)	0.007	0.001	0.021	1.230	0.003
N	1111	297	436	173	826

* material used by GJØSÆTER (1973 a)

The corresponding $W_\infty = 8.68$ g. Other data and variances are given in Table 5. For parts of the area the material was large enough to make separate growth curves.

For Byfjorden the material from 1974 and 1975 gave the equations:

$$l_t = 70.22 (1 - e^{-0.39(t+0.10)})$$

and

$$l_t = 79.24 (1 - e^{-0.24(t+0.63)})$$

respectively.

The curve

$$l_t = 86.95 (1 - e^{-0.19(t+0.65)})$$

was fitted to the data from Sogn.

GJØSÆTER (1973a), using graphic methods, fitted the equation

$$l_t = 75.0 (1 - e^{-0.45(t-0.25)})$$

to samples from Byfjorden and Herdlefjorden taken during 1968-1972 (BEVERTON and HOLT 1957). Using ALLEN's (1966) method on the same data, the equation

$$l_t = 73.15 (1 - e^{-0.46(t-0.25)})$$

was derived. Lengths at age calculated from the different curves are shown in Fig. 4.

Growth of the oceanic populations

The oceanic samples were taken along the Norwegian coast from Skagerrak to Finnmark and in the area west of the British Isles (Table II and Fig. 5), and several different populations were probably sampled. The 0-group was not found in any of the samples, and the I-group was taken only once. Therefore,

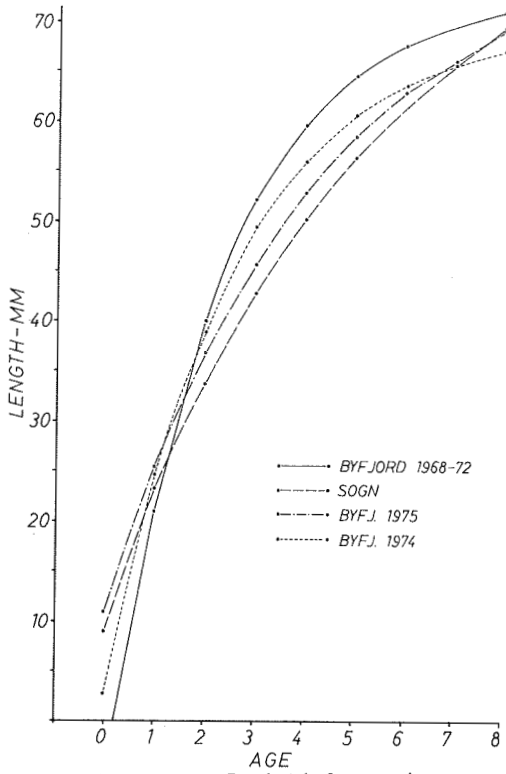


Fig. 4. Von Butalanffy's growth curves for *B. glaciale* from various areas and years.

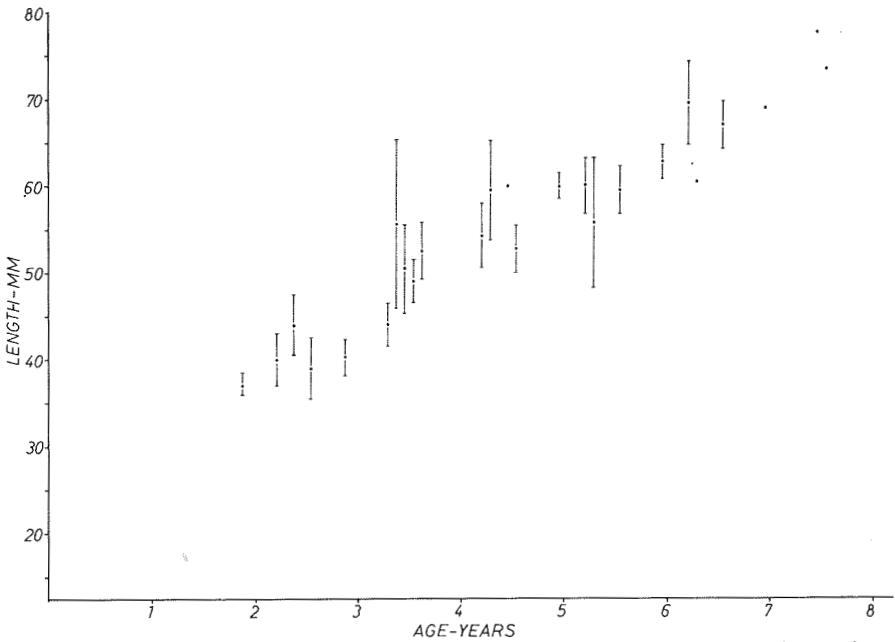


Fig. 5. Growth of *B. glaciale* from the oceanic population. The points represent mean lengths in a sample and the vertical bars 95% confidence limits.

the method used for the fjord samples proved unsuitable for fitting the von Bertalanffy's curve to the oceanic samples as t_0 and K were determined with very low precision. An arbitrarily fixed $t_0 = 0$ and a modification of the least-squares method for such cases (ALLEN 1966) was tried and gave a better fit. Based on 244 specimens, the resulting equation was:

$$l_t = 74.81 \text{ cm} (1 - e^{-0.31 t})$$

$$\hat{V}(K) = 0.001$$

$$\hat{V}(L_\infty) = 3.499$$

The corresponding $W_\infty = 5.49 \text{ g}$.

Back calculation of growth

To carry out back calculations of growth from otolith zones, diameters of the otoliths and of their hyaline zones were measured along their longest axis in 997 fish from the fjords and 253 fish from the ocean. All data were transformed to logarithms to avoid the effect of heteroscedasticity. As both variables were measured with error, a geometric mean regression was used, as recommended by RICKER (1973). For the fjord samples the result was:

$$\lg l = 0.880 \lg d + 1.495$$

where l and d are length of the fish and diameter of the otoliths respectively, both measured in mm. The confidence limits of the regression coefficient were 0.862–0.898, and the coefficient of determination r^2 was 0.918.

The equation

$$\lg l = 1.040 \lg d + 1.440$$

was derived from the oceanic samples. The confidence limits of the regression coefficient were 0.977–1.107, and the coefficient of determination r^2 was 0.804.

The two equations are significantly different. As only fish longer than 35 mm were found in the oceanic samples, the range both in length and otolith diameters was small, and this probably explains the low proportion of variance (80.4%) explained by the regression.

GJØSÆTER (1973a), using a predictive regression, obtained the equation:

$$\lg l = 0.8259 \lg d + 1.4587$$

for the population in Byfjorden and Herdlefjorden. Transformed to geometric mean regression the slope becomes 0.870 which is very close to the present result for the fjord populations. The observed diameters of the otolith zones and corresponding fish lengths computed from the regression given above are shown in Table 6. The lengths are also shown in Fig. 6.

Table 6. Diameters of zones in the otoliths and corresponding estimated fish length of *B. glaciale* from the fjords.

Zone no.	Age of fish	Number measured	Mean diameter mm	95% Conf. lim. \pm	Corresponding length mm
1	2	103	0.846	0.024	26.99
	3	78	0.873	0.030	27.74
	4	136	0.879	0.022	27.91
	5	115	0.882	0.022	27.99
	6	59	0.876	0.038	27.82
	7	13	0.799	0.126	25.66
2	3	79	1.257	0.042	38.23
	4	129	1.258	0.034	38.25
	5	113	1.292	0.021	39.16
	6	59	1.228	0.041	37.45
	7	15	1.297	0.098	39.30
3	4	127	1.562	0.036	46.28
	5	111	1.607	0.034	47.45
	6	52	1.546	0.053	45.85
	7	14	1.670	0.124	49.08
4	5	106	1.879	0.038	54.44
	6	48	1.834	0.055	53.30
	7	12	1.746	0.345	51.04

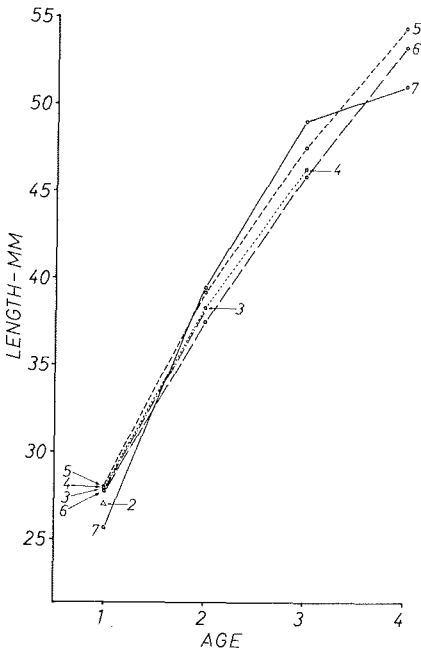
Fig. 6. Back calculated lengths of *B. glaciale* from the fjords. 2-7 indicate the age of the fish from which otoliths were taken.

Table 7. Analysis of variation of the diameters of otolith zones of *B. glaciale* from the fjords. The age groups are ranked with those having largest radia first.

Zone no.	Rank of age groups	F	df.	Probability
1	5 4 6 3 2 7	1.81	5/498	0.1 < p < 0.2
2	7 5 4 3 6	1.71	4/390	0.1 < p < 0.2
3	7 5 4 6	2.62	3/300	0.05 < p < 0.1
4	5 6 7	2.03	2/163	0.1 < p < 0.2

Table 8. Diameters of the zones in the otoliths and corresponding estimated fish length of *B. glaciale* from the ocean.

Zone no.	Age of fish	Number measured	Mean diameter mm	95% Conf. lim. \pm	Corresponding length mm
1	2	31	0.093	0.050	24.77
	3	53	0.868	0.031	23.79
	4	56	0.845	0.033	23.13
	5	53	0.811	0.026	22.16
	6	34	0.842	0.044	23.02
	7	7	0.862	0.092	23.61
	2	3	54	1.332	0.039
4		56	1.301	0.043	36.22
5		53	1.244	0.036	34.57
6		32	1.200	0.058	33.30
7		7	1.192	0.092	33.07
3	4	57	1.643	0.043	46.17
	5	53	1.625	0.040	45.62
	6	31	1.541	0.063	43.18
	7	7	1.522	0.113	42.63
	5	53	1.908	0.038	53.94
	6	32	1.845	0.064	52.07
	7	7	1.742	0.176	49.04

To test whether the different age groups had different diameters of the zones, a series of one-way analysis of variance was carried out. For the fjord populations, the hypothesis that the diameters of the hyaline zones were similar, irrespective of the age of the fish when they were measured, could not be rejected for any of the four zones considered (Table 7).

As the diameters showed no consistent variation with age of the fish, they were combined. The lengths, calculated from these mean diameters, were used

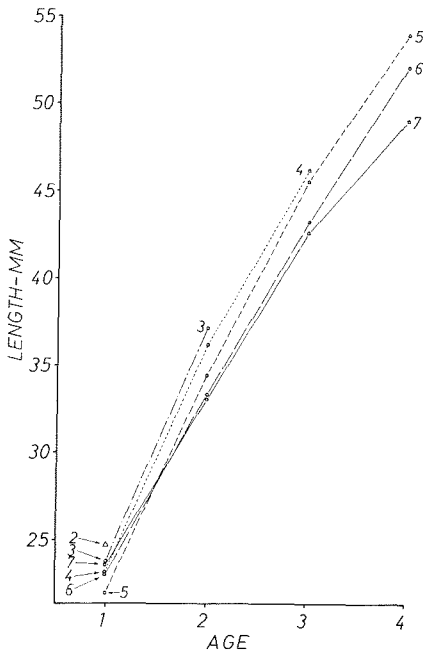


Fig. 7. Back calculated lengths of *B. glaciale* from the oceanic populations. 2-7 indicate the age of the fish from which otoliths were taken.

Table 9. Analysis of variation of the diameters of otolith zones of *B. glaciale* from the ocean. The age groups are ranked with those having the largest radii first.

Zone no.	Rank of age groups	F	df	Probability
1	2 3 7 4 6 5	2.76	5/228	0.01 < p < 0.05
2	3 4 5 6 7	5.58	4/197	p < 0.001
3	4 5 6 7	3.71	3/144	0.01 < p < 0.05
4	5 6 7	4.22	2/89	0.01 < p < 0.05

to calculate a von Bertalanffy's growth equation by ALLEN's (1966) method. The resulting equation was:

$$l_t = 66.13 (1 - e^{-0.36 (t-0.0)})$$

The parameters differ from those found by direct estimates of length at age, but l_t estimates from the two equations do not differ much for ages one to five which makes up the most important part of the populations.

The diameters of the otolith zones and corresponding fish lengths for the oceanic populations are shown in Table 8 and Fig. 7 respectively. Results of the test to find whether the diameters were significantly different in the different age groups in the oceanic populations are shown in Table 9. Generally the zones measured in young fish were larger than those measured in older fish. In order to test which of the diameters were different, a Newman-Keuls test (see ZAR 1974) was applied. For the first zone only those measured at ages 2 and 5

were different at the 5% level. For the second zone those measured at ages 3 and 7 were not different, and therefore all differences between these could be considered not significant. This result was, however, probably due to the low number of observations on 7-year-old fish. The test was continued although this may effect the significance level. Differences were found between age 4 versus 5 and 6. The diameters of the third zone measured at ages 4 and 7 were similar, but the test was continued. Measurements made at age 4 were found to be significantly different from those made at age 6 as were those made at age 5. For zone 4 the Newman-Keuls test failed to show significant differences. This reflects the low power of this test compared to the analysis of variance.

In spite of the Lee's phenomenon demonstrated in these tests, which made the result biased, average diameters were computed for each zone and converted to lengths. These lengths were weighed with number of observations and used to fit a von Bertalanffy's growth curve by ALLEN's (1966) method. The result was:

$$l_t = 87.93 (1 - e^{-0.21 (t-0.0)}) \quad (A)$$

Lengths calculated from equation A are smaller than those obtained from the equation based on the length at age data for fish younger than 6 years. For 6-year-old fish the lengths are similar, and for older fish lengths based on equation (A) are largest.

The present growth calculations give a wide range in K , L_∞ and t_0 . This may partly be caused by gear selectivity as many different gears were used for the sampling, but there were also probably real differences between areas and between years. Generally the growth rate was lower and L_∞ higher than estimated by GJØSÆTER (1973a) and more similar to the result obtained by HALLIDAY (1970) from the Canadian Atlantic.

Of other myctophids from temperate waters *Notoscopelus kroeyeri* seem to have a much faster growth ($K = 0.89$, $L = 114$) (GJØSÆTER 1980) while *Myctophum affine* (ODATE 1966), *Stenobranchius leucopsarus* (SMOKER and PEARCY 1970) and *Lampanyctodes hectoris* (ANON. 1974) have similar or slightly higher growth rates and larger asymptotic lengths.

Mortality

The fjord samples used for growth studies were also used for estimating the mortality. The catch curve method (see BEVERTON and HOLT 1957) was applied (Fig. 8). To minimize the effects of difference in year class strength and difference in selection of the gears used, all samples were combined. The mean instantaneous mortality rate between ages 1 to 8 was estimated to 0.7, using geometric mean regression. This is similar to the mortality for the ages 1 to 4 estimated by GJØSÆTER (1973a).

GJØSÆTER (1973a) showed that the year class strength may differ, and the present data show that the age composition in the catch taken by small pelagic gears and those taken near the bottom by shrimp trawl may be very different. Part of the differences in age group composition, as shown in Table 10, may be

Table 10. Age distribution (per cent) of *B. glaciale*.

Age	Fjord samples			Ocean samples
	Byfjord 1974 Shrimp tr.	Byfjord 1975 IKMT	Fjords total	
1	0	74.9	53.0	4.5
2	0	8.0	9.8	11.5
3	10.2	0.7	7.9	21.7
4	31.2	6.1	12.3	23.4
5	31.8	5.4	10.1	22.5
6	17.6	4.0	4.9	13.5
7	8.0	0.9	1.7	2.1
8	1.1	0	0.2	0.8
N	176	426	1058	224

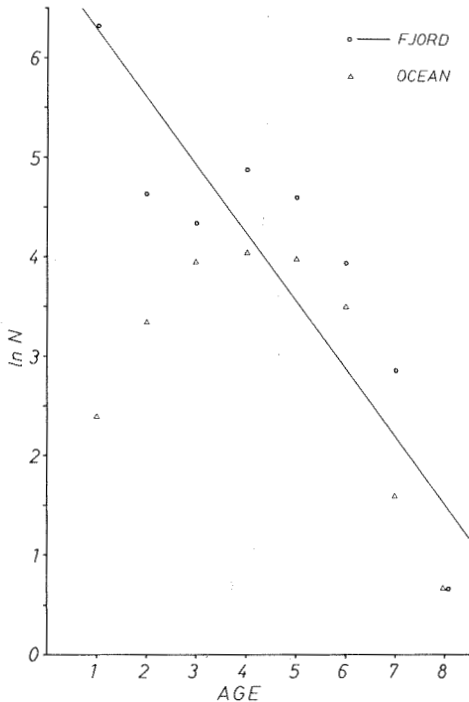


Fig. 8. Catch curve used to estimate the mortality of *B. glaciale*. The curve is fitted to the fjord material.

due to differences in year class strength, but probably the effect of the gear is more important. These factors make the mortality estimates unreliable, and they must be treated with caution. The oceanic samples were collected with trawls of mesh-width too large to catch the smaller groups of *B. glaciale* representatively. The catch curve (Fig. 8) is therefore not suited to make estimates of mortality of the oceanic populations.

Production

In an unexploited fish population, where growth can be described by the von Bertalanffy's growth equation and the mortality is constant exponential, ALLEN (1971) has shown that the annual production P is

$$P = 3 N_0 K W_{\infty} \left(\frac{1}{M + K} - \frac{2}{M + 2K} + \frac{1}{M + 3K} \right)$$

where N_0 is the initial number, M is the instantaneous natural mortality rate, K and W_{∞} are parameters from the growth equation, and t_0 is supposed to be zero. For the populations in the fjords $W_{\infty} = 8.68$ and $K = 0.20$ from the pooled growth equation and $M = 0.7$ are used, and the resulting annual production is

$$P = 0.32 N_0 g$$

For the oceanic populations $W_{\infty} = 5.49$ and $K = 0.31$. If M is set equal to that of the fjord populations, the annual production is

$$P = 0.45 N_0 g$$

Using an equation provided by BEVERTON and HOLT (1957 Eq. 4.4), the yield per recruit can be calculated for various combinations of fishing mortality F and age at first capture t_p . Fig. 9 shows an isopleth diagram for the fjord populations, where the parameters used are similar to those above except $t_0 = -0.64$. Age at recruitment t_p is arbitrarily set like 0.5 and the maximum age t_{λ} like 8 years. According to Fig. 9, a maximum sustainable yield of about 0.21 g/recruit will be obtained with a fishing mortality of about 1.5 or more and an age of 2 years at the first capture.

For the oceanic populations the maximum sustainable yield per recruit will be about 0.34 g and the best combination of fishing mortality and age at first capture as above (using $t_0 = 0$, $t_p = 0.5$ and $t_{\lambda} = 8$). The natural mortality can be expected to decrease if a fishery removes a considerable proportion of a population. This will change the form and the absolute values of the yield/recruit diagram. The assessment above must therefore be taken as a first approximation only.

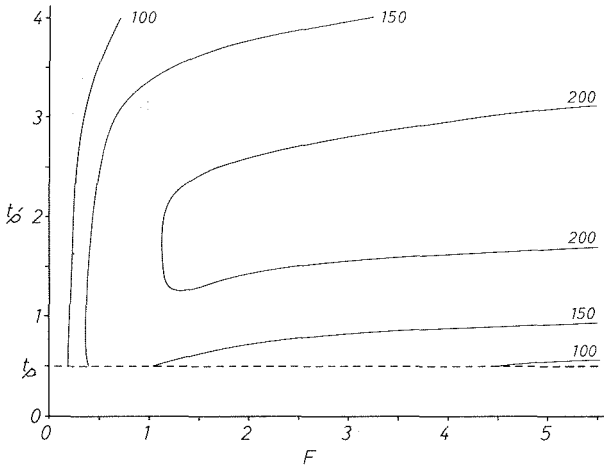


Fig. 9. Yield isopleth diagram for the fjord population of *B. glaciale*. The figures show yield in mg. F is fishing mortality, t_p' age at first capture and t_p age at recruitment.

REPRODUCTION

Development of external sex characters

The sexes of *B. glaciale* can be distinguished by the supracaudal light glands in the males and the infracaudal light glands in the females. The development of the glands is shown in Table 11, listing mean length and length range of 1-year-old fish with supra- or infracaudal glands and those without such glands. In July, fish with distinct and faintly developed glands were treated separately while they were combined in September. Very few 1-year-old fish taken during May had developed sex characters while nearly all those taken in November and December had such characters. This indicates that the external sex characters develop during summer and autumn when the fish are 1 year old and about 35 mm long. The characters seem to develop at a slightly shorter length in females than in males.

A few specimens had both supra- and infracaudal light glands, but one of them was always better developed than the other. In all these cases the gonads corresponded to the best developed gland. No sign of hermaphroditism was found although this has been observed in other families of Myctophiformes (MEAD 1960). Some cases of both supra- and infracaudal light glands on the same fish have also been observed by TÄNING (1918) on *B. glaciale thori* (TÄNING) from the Mediterranean.

In *B. glaciale*, infested by the copepod *Sarcotretes scopeli*, it was observed that the sexual dimorphism developed normally although the maturation of the gonads was hindered (GJØSÆTER 1971). O'DAY and NAFFAKTITIS (1967) have shown expatriation to have a comparable effect on *Lobianchia dofleini*, while

Table 11. Length (in mm) and development of external sexual characters of *B. glaciale*. Number of observations in brackets.

Month	Standard length in mm				
	Males		Females		Unsexed
	Well developed	Weakly developed	Well developed	Weakly developed	Not developed
July					
mean	33.0 (19)	32.4 (12)	32.7 (19)	31.4 (8)	30.5 (40)
range	30.5–39.5	28.5–37.5	29.0–37.0	27.5–34.0	26.5–35.5
September					
mean	35.1 (15)		34.9 (10)		33.8 (6)
range	32.5–39.5		31.0–38.5		21.0–39.0

expatriation of *L. gemellare* also lead to reduction or complete extinction of the sexual dimorphism.

Sex ratio

With few exceptions there were more females than males in the catches. In total, the females made up 54.8% ($\pm 4.0\%$) of the adult fish. No seasonal variation could be traced.

Development of the ovary

The primary germ cells of *B. glaciale* are rather similar in the testes and in the ovaries. They are often found in groups, together with oogonia 8–12 μm in diameter (Fig. 10). Oocytes in the protoplasmatic growth period are characterised by absence of vacuoles and yolk (Fig. 10). The smallest oocytes usually have an irregular shape, and the nucleus is larger than half the total diameter of the oocyte. The nucleoli are scattered in the nucleus. As the oocyte reaches a size of 100–150 μm , the nucleoli concentrate along the nuclear membrane. The diameter of the nucleus is usually about half that of the oocyte. The trophoplasmatic growth period, characterised by the formation of vacuoles and yolk, starts when the oocytes are 150–200 μm in size (Fig. 11). The first vacuoles are very small and scattered throughout the cytoplasm. As the oocytes grow, there is differentiation in the plasma. A narrow layer of homogeneous and densely staining cytoplasm then forms around the nucleus. Next there

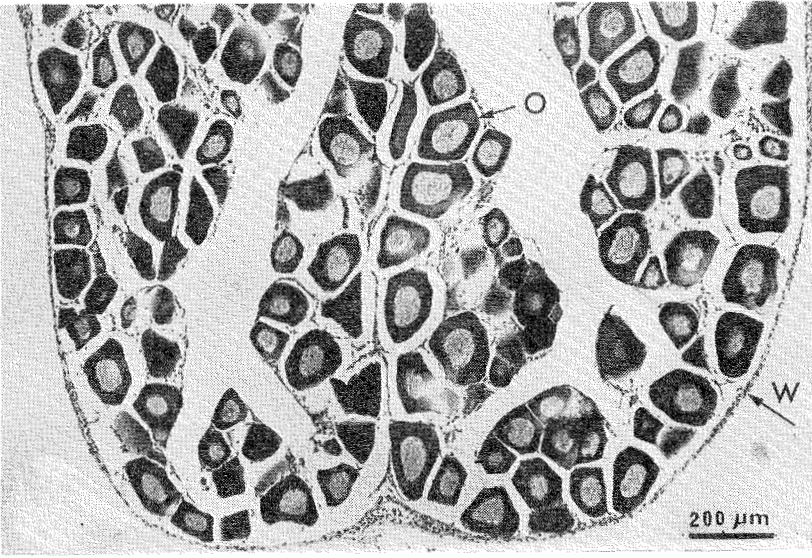


Fig. 10. Ovary of *B. glaciale* in stage 2. O = oocytes in protoplasmic growth period, W = ovary wall.



Fig. 11. Ovary of *B. glaciale* in stage 4. Y = yolk grains, V = vacuoles.

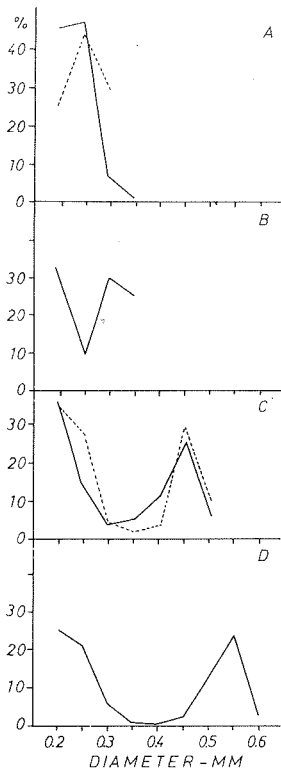


Fig. 12. Size distribution of oocytes in ovaries from *B. glaciale* in stage 1(A), 2(B), 3(C) and 4(D). Each line represents ovaries of one fish.

develops a layer with larger vacuoles and outermost a narrow zone with faintly staining cytoplasm and without vacuoles (Fig. 11). The small vacuoles are probably yolk vesicles, and as the growth proceeds, they fill with yolk grains. At an oocyte size of approximately $300\ \mu\text{m}$, the yolk grains measure $4\text{--}8\ \mu\text{m}$ in diameter. Later, the larger vacuoles of the central part of the protoplasm fuse. When the oocyte has reached a size of $500\text{--}600\ \mu\text{m}$, there is one large central vacuole, and the nuclear material is observed as a cone protruding into the protoplasm at the animal pole.

The rest of the oocytes becomes completely filled with yolk grains. The size of the central vacuole may reach $250\ \mu\text{m}$. In microscopic slides it appears empty though it probably contains oil or other alcohol soluble substances in live material. The largest oocyte observed in mature ovaries had a diameter of approximately $750\ \mu\text{m}$ and contained a pale yellow oil globule with diameter $200\ \mu\text{m}$. This may be derived from the central vacuole.

In the juvenile fish primary germ cells, oogonia and oocytes with size up to approximately $50\ \mu\text{m}$ predominate. These stages are also found in older fish, but here resting oocytes (size $100\text{--}200\ \mu\text{m}$) and developing oocytes make up the bulk of the egg stock. As maturation proceeds, the developing oocytes grow to their maximum size. After spawning, some eggs in various phases of trophoplasmatic growth are retained and seem to disintegrate during one or two months later. Oocytes in the resting stage and possibly some of those in early trophoplasmatic growth phase are retained and will probably be

Table 12. Description of developmental stages of the ovaries of *B. glaciale*.

Stage	Microscopical characters	Macroscopical characters
1. Juvenile	Primary germ cells and oogonia abundant. Most oocytes smaller than 50 μm and have an irregular shape.	Ovaries small, thread-like. Sex can not be distinguished by the naked eye.
2. Resting	Many oocytes in resting phase with diameter 100–200 μm . No oocytes larger than 300 μm . In first time spawners ovarium wall is thin (<40 μm), in repeated spawners it is thicker (40–80 μm).	Ovaries larger, typical 10 X 1 mm or less. The form is rounded. Eggs visible with the naked eye.
3. Developing	Oocytes in several stages of the trophoplasmatic growth phase. Diameters mostly 350–500 μm . Few eggs completely filled with yolk grains.	Ovaries fill about half of the body cavity and have a flat appearance. Typical size 10 X 2 X 0.7 mm. Eggs clearly visible.
4. Ripe-Spawning	Oocyte size larger than 500 μm . Most of the oocytes yolk filled. In addition to the oocytes in resting phase there are usually also some few in early trophoplasmatic growth phase.	Ovaries larger, hard and flattened, filling about $\frac{2}{3}$ of the body cavity. Eggs clearly visible and when pressed out, yolk globules can be seen.
5. Spent.	Many empty follicles and spaces filled with undifferentiated tissue. There is also disintergrating oocytes of various stages. The ovarium wall is thick.	Ovaries smaller and fill half of the body cavity or less. Less firm than stage 4. Blood vessels often visible.

spawned during the next season. Sometimes almost mature eggs are left in the ovaries after spawning. These are not resorbed, but encapsulated in connective tissue. They are retained and can be seen as dark grains in the ovaries. Some typical size distributions of oocytes are shown in Fig. 12.

Based on these histological and macroscopical characters, stages of ovary development have been described (Table 12). This scale is in general similar to that given by NIKOLSKY (1963) and used by SMOKER and PEARCY (1970) for *Stenobranchius leucopsarus*. The maturation of males was difficult to assess without histological methods although mature males could be distinguished by a bulbous anterior part of the testes. In fresh specimens the mature testes also looked more transparent than immature ones.

Time of spawning

Maturity stage 1, with one exception, was found in age groups 1 and 2 only (Table 13). Spent fish seem to go directly to stage 2, and after a short period to stage 3. Those maturing for the first time seem to reach stage 3 during the spring. In May and June, most fish were in stage 4. Stage 5 made up approximately 30% of the samples taken during the last part of June and was totally dominant in August and September. This indicates that the main spawning takes place in June and July. 0-group fish occurred in the catches from September onwards when they had reached a length of 15–16 mm.

JOHNSEN (1945) caught 9.5–14.0 mm fish in the Bergen area during September. BARANENKOVA (1971) reports larva of *B. glaciale* in the southwestern Barents Sea during April–May and larva and fry during June–July. Off Nova Scotia larvae were found in May–July, and according to HALLIDAY (1970) spawning occurs in the early spring. Off Iceland larvae were taken in May, June and August (MAGNUSSON, MAGNUSSON and HALLGRIMSSON 1965, MAGNUSSON 1966), and off Ireland mainly during May (HOLT and BYRNE 1911). According to TÅNING (1918) spawning in the Mediterranean mainly takes place during winter, but some spawning also seems to occur during other seasons. GOODYEAR *et al.* (1972) believe that spawning in the Mediterranean peaks in late spring and summer.

Table 13. Seasonal variation in development stages of ovaries of *B. glaciale*.

Stage	Month								
	½	3	4	5	6	7	8	9	10/11/12
1	9	3		2	9			1	5
2	10	5	2	11	10			5	29
3	15	16	5	20	34		2		16
4		5	2	36	41		2		
5				1	16	3	25	19	28
N	34	29	9	70	110	3	29	25	78

Table 14. Developmental stages of ovaries of two years old *B. glaciale* of various size caught 29 May 1970.

Stage	N	Length (mm)	
		mean	range
1	2	40.5	40 - 41
2	8	45.3	41 - 48
3	14	49.8	47 - 55
4	5	49.8	48 - 51
5	0		

Age and length at first maturity

In age group 1 no mature fish was found while all of group 3 and older seemed to spawn. Table 14 shows maturity stages of 2-year-old females taken 29 May 1970. Fish in stage 3 and higher would probably have spawned the same year. It is therefore indicated that at least 50% of the females spawn at an age of two years. This is also in accordance with data from Table 13. The data suggest that the length is decisive and that the lower limit for spawning lies between 45 and 50 mm standard length. Some males also spawn first when two years old.

The age at first spawning in Canadian waters (HALLIDAY 1970) seems to be the same as in Norway. In the Mediterranean *B. glaciale thori* first spawns at the age of one year and at a length of about 30 mm (TÅNING 1918). In other myctophids the age of first spawning seems to vary between four years for *Stenobrachius leucopsarus* (SMOKER and PEARCY 1970) to one year or less in e.g. *Notolychnus valdivia* (LEGAND 1967) and *Benthosema pterotum* (HUSSAIN in prep.). According to TÅNING (1918) *B. glaciale thori* from the Mediterranean spawn only once. JOHNSEN (1923) maintained that this was the case also for *B. glaciale* from Norwegian waters, but this conclusion is not supported by the present study.

Fecundity and egg size

The fecundity, defined as number of ripening eggs in the female prior to the next spawning period (BAGENAL and BRAUM 1968), was counted in 28 specimens. The fish selected were in stage 3 or early stage 4, and oocytes with diameter larger than 350 μm were considered maturing. All maturing eggs in both ovaries were counted.

The fecundity ranged between 162 and 1940 (mean 781), and the length of the fish studied was between 45 and 75 mm (mean 57.7 mm). Following the work of RICKER (1973), a geometric mean regression was fitted:

$$\lg F = 3.44 \lg l - 3.21 \text{ or } F = 6.16 \cdot 10^{-4} l^{3.44}$$

Table 15. Fecundity of some lanternfishes (F). Number of fish studied and their lengths l (mm) are also given.

Species	N	l (range)	F (range)	Author
<i>Myctophum punctatum</i>	3	54.7 (51–61)	852 (794– 929)	TÅNING (1918)
<i>M. affine</i>	5	73 (72–78)	– (8000–9000)	ODATE (1967)
<i>Hygophum benoiti</i>	4	43.8 (42–45)	882 (849–1273)	TÅNING (1918)
<i>Benthosema glaciale thori</i>	6	36.0 (32–40)	323 (191– 467)	TÅNING (1918)
<i>Diaphus garmani</i>	20	46.3 (41–55)	1085 (350–1900)	NAKAMURA (1970)*
<i>Lobianchia dofleini</i>	4	34.0 (31–40)	388 (330–484)	TÅNING (1918)
<i>Notolychnus valdiviae</i>	1	22	100	JOHNSEN (1916)
» »	1	22	120	TÅNING (1918)
<i>Ceratospelus townsendi</i>	2	72.3 (62.5– 82.0)	8000 (5150–10850)	BEKKER & BORDULINA (1968)

* Data taken from Fig. 2 of NAKAMURA (1970).

where F is fecundity and l fish length in millimeters. The coefficient of determination r^2 was 0.866, and 95% confidence limits of the regression coefficient were 2.90 and 4.08. As weight is proportional to $l^{3.3}$, the fecundity is approximately proportional to the weight.

The largest intra-ovarial eggs observed in *B. glaciale* measured about 0.75 mm. On several occasions eggs were pressed out from ripe females and fertilization was attempted, but this did not succeed. After about 12 hours in 4°C sea-water, the eggs were preserved in 5% formalin in sea-water. These eggs were round, with segmented yolks, narrow perivitelline spaces and pale yellowish oil droplets measuring about 0.20 mm. The diameters were about 0.75–0.80 mm.

ROBERTSON (1977) described planktonic eggs from *Lampanyctodes hectoris*. These were ovoid and measured from 0.73 to 0.83 mm (long axis) and 0.65 to 0.72 mm (short axis). As in *B. glaciale* they had segmented yolk and an oil droplet.

A few egg countings of lantern fish exist in the literature and some of these are referred to in Table 15. The fecundity ranges from about 100 in the small species, e.g. *Notolychnus valdiviae*, to about 11 000 in an 82 mm long *Ceratospelus townsendi*. The *C. townsendi* also had larger eggs than any other species studied. In addition to the largest yolk-filled eggs, they had a group of yolk containing oocytes with diameters of 0.7–0.8 mm. There were 4 300 and 9 400 of those in the two fish measured (BEKKER and BORODULINA 1968). ROBERTSON (1977) lists data showing that size of mature intra-ovarial eggs ranges between about 0.6 mm in *Triphoturus mexicanus* to about 0.8 mm in *Electrona rissoi*, but only a few species have been studied. BEEBE and VANDER PYL (1944) suggested a relationship between fecundity and egg size, but the sparse data available do not conform to this view.

MOSER and AHLSTROM (1970) suggested that the surprising lack of lantern fish eggs in planktonic samples may be due to the fragile nature of the chorion

which may cause the eggs to disintegrate on contact with the meshes of a plankton net. ROBERTSON (1977) reported that unfertilized eggs of *Lampanyctodes hectoris* were very fragile, but that those from plankton samples were stronger. The eggs of *B. glaciale* did not appear to be more fragile than other fish eggs.

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