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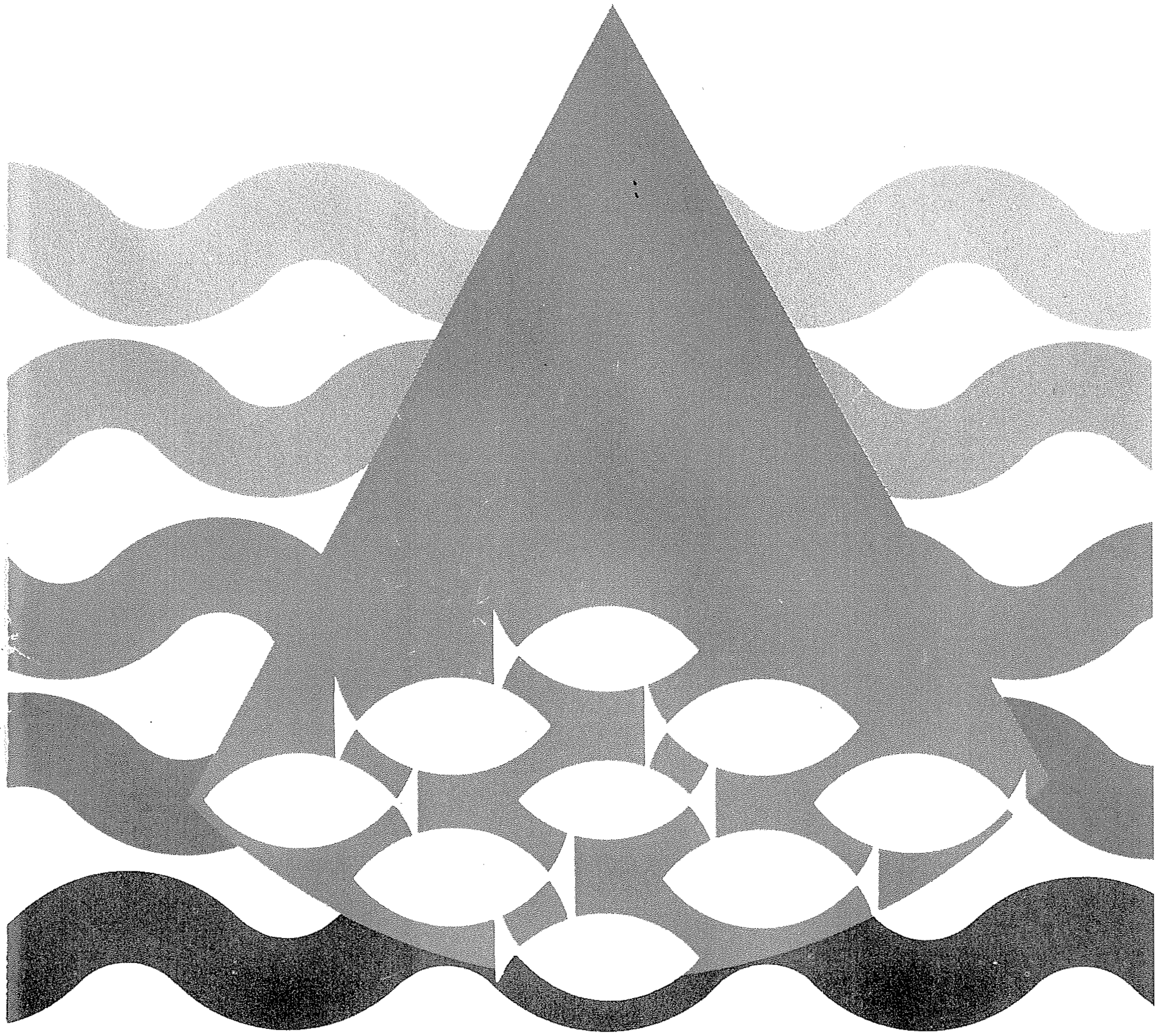

DIRECTORATE OF FISHERIES, BERGEN, NORWAY
1981

FiskDir. Skr. Ser. HavUnders., 17: 71–78.

VARIATION IN GROWTH RATE AND AGE AT FIRST MATURATION IN RAINBOW TROUT

By
GUNNAR NÆVDAL, RITA LERØY and DAG MØLLER
Institute of Marine Research, Directorate of Fisheries, Bergen, Norway

ABSTRACT

NÆVDAL, G., LERØY, R. and MØLLER, D. 1981. Variation in growth rate and age at first maturation in rainbow trout. *FiskDir. Skr. Ser. HavUnders., 17*: 71—78.

The present report is an account of the main results of a series of experiments on selective breeding of rainbow trout. The experiments started in 1972, but were discontinued in 1979 because IPN virus was detected in the material.

Growth rate and age at first sexual maturity were the main factors studied. Full sib and half sib correlations as well as parent/offspring correlations were applied. The results were not always conclusive because the different year classes gave somewhat different results. However, sib correlations indicated control by additive genetic factors for at least part of the variation in growth rate. This was also confirmed by the parent/offspring results.

Both additive and non-additive genetic factors were indicated as controlling the variation in age at first maturation. No effect of the age of first maturation of the individual parent fish could be found among the offspring, but there was a clear effect of the mean maturation age of the parent sib group on the maturation age of the offspring group.

INTRODUCTION

Farming of rainbow trout, *Salmo gairdneri,* has had growing interest in Norway during the last 25 years. Contrary to the West European fish farmers producing «pansize» rainbow trout, the Norwegians produce «salmon-like» rainbow trout, i.e. fish of individual weights of more than 1.5, often up to 3 or 4 kg.

The Norwegian-farmed rainbow trout originally came from Denmark. For several generations now, mass selection for high growth rate and high age at first maturation has been carried out by the fish farmers, but due to lack of unselected material for control, the effect of this selection is unknown.

Sexual maturity at early age or at small size is a serious drawback for production of large rainbow trout because maturation retards the growth rate of the fish and often causes increased mortality. For farming of rainbow trout, significant improvements would be higher mean growth rate and higher mean age at first maturation. The present investigations were planned to study the genetic part of the variations in the mentioned traits and use the results to produce an improved brood stock for fish farming.

The experiments started with collection of eggs in winter 1972 parallel to similar experiments on Atlantic salmon (NÆVDAL *et al.* 1978 a, b). Most emphasis was laid on salmon, and consequently the number of experiments each year concerned with rainbow trout was limited to about 20 sib groups.

In autumn 1977 virus of *Infectous pancreatic necrocis* (IPN) was discovered among the material. IPN is not common in Norway, and to prevent spreading of the virus, the experiments were discountinued. However, the adolescent fish at that moment (second generation experimental fish) were allowed to be raised to food fish size at selected fish farms to study the effect of selection, but they were not allowed to be further used as brood stock because IPN virus is easily transferred by the eggs.

This report gives an account of observed variations and evidence for genetic control of growth rate and age of maturation. Part of the results are presented in earlier reports (MØLLER *et al.* 1976, NÆVDAL *et al.* 1975, 1979).

MATERIALS AND METHODS

Egg and milt material was for the experiments mainly obtained from a Norwegian fish farm, Eros Laks, Bjordal, each winter from 1973 to 1975. In 1973 milt from three males from another fish farm, Bolstad Fiskeanlegg, Holdhus, was included, and in 1974 twelve groups of eyed eggs were obtained from the research station Forsøksstasjon for laksefisk, Sunndalsøra, where selective breeding of salmonids is carried out under the auspices of the Agricultural University of Norway. The year classes reared in 1975, 1976 and 1977 were based on selected parent fish from the year classes hatched in 1972 and 1973.

The present experiments are based on sib groups. In the four first year classes both paternal and maternal half sib groups were formed, usually by dividing the egg portion of each female into two equal parts and fertilizing them with milt from two different males. The last two year classes consisted of only paternal half sib groups, formed by using one male for three females.

The eggs were hatched at the hatchery at the research station Akvakulturstasjonen Matre. Except for the first year class, the fish were transferred to floating cages in brackish water when they were about eight months old. When they were 12–14 months old, the fish were transferred to full strength sea water in net pens or sea enclosures at a commercial fish farm. The 1972 year class was not transferred to brackish water until the fish were about 14 months old and to full strength sea water when they were about 20 months old.

At the egg stage and during their first months of life, each group was kept in separate trays or tanks. When the fish were 5–6 months old; they were marked by fin clipping, and several groups were kept together in the same tank. Part of the fish of the 1972 and all of the 1973 year class were individually tagged with Floy Tags (FT4 Spagetti Tag, FT4 Lock-on, FT6 Dart tag or FD67 C Anchor Tags, all from Floy Tag and Mfg., Inc., 4616 Union Bay Pl. N.E., Seattle, Washington 98105, U.S.A.). The technical results of the tagging experiments are dealt with in a separate report (NÆVDAL, HOLM and KNUTSSON 1977). The 1975 and later year classes were marked by cold branding (REFSTIE and AULSTAD 1975).

Some of the sib groups died out during the egg and fry stage. The main causes were partly accidental, i.e. problems with the water supply, and partly an outbreak of vibriosis. Unfortunately, these accidents extinguished groups from several 2 × 2 sets, thus making the material unfit for calculation of male × female interaction.

The total length of 100 or 200 fish was recorded every six months for the first two year classes, later at 12, 24 and about 30 months of age. Weights were recorded at slaughtering for all year classes and at 24 months of age for the 1973 year class. Sexual maturity was recorded during the second and third years of life.

At about 30 months of age, the main part of each group was slaughtered. Of the first three year classes 20–30 fish of each group were selected for brood stock, and the three last year classes were based on these selected fish from the first two year classes. When it was known that the fish could be carriers of IPN virus, the veterinary authorities forbade any further use of them for stock, but adolescent fish were allowed to be raised to normal food fish size at selected fish farms, and data could be collected as before.

RESULTS

VARIATION IN GROWTH RATE

Observations from sib correlations

Marked differences in mean growth rate were observed between sib groups in all year classes. This variation is illustrated in Fig. 1 where mean lengths at each half year of the 1973 year class are shown separately for each sib group. The other year classes showed similar variations. Correlations between length of the individual fish as well as of group means measured at different times are dealt with in an earlier report (NÆVDAL *et al.* 1979). Close connection between growth rate at different age both for individuals and for group means were found except when correlating growth rate during the first months to subsequent growth rate in the sea.

Evidently a significant correlation existed between growth rate and age at maturation as the mean length of fish maturing during their third year were on an average significantly larger than the fish still immature, and on the individually tagged fish this lower mean length could be found even one year before maturation (NÆVDAL *et al.* 1979). Effect of sex on growth rate was insignificant in most groups and in the total material, but in some groups the males were on average bigger than the females.

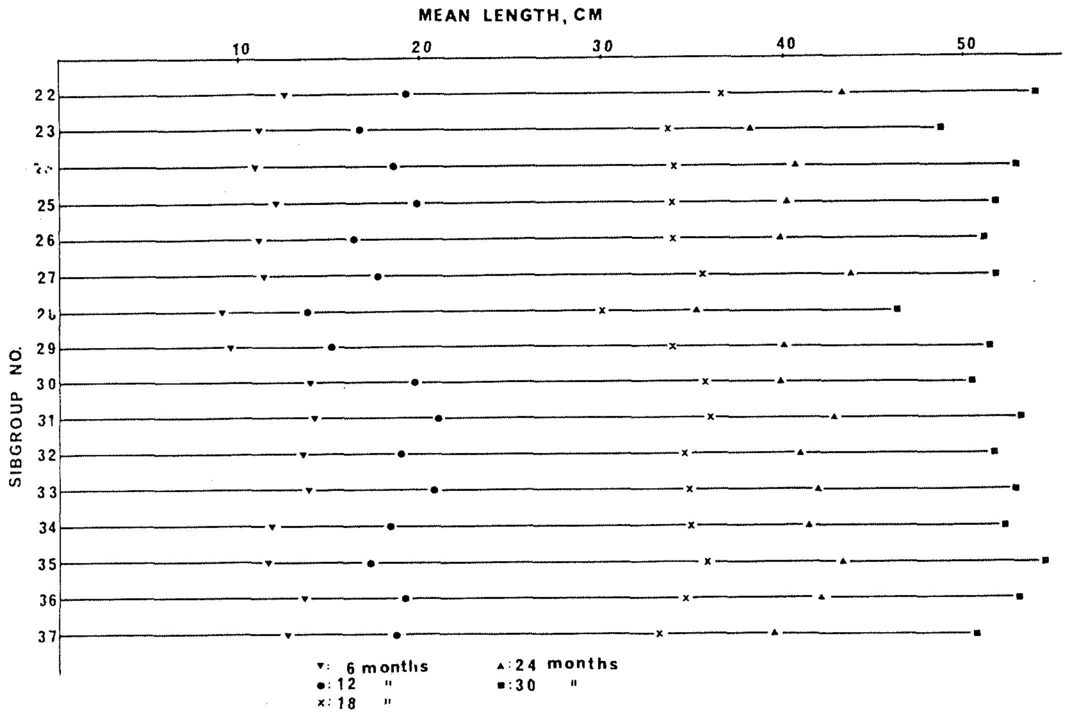

Fig. 1 Mean lengths of sib groups of rainbow trout hatched in 1973.

Calculations on heritability factors were based on half sib and full sib correlations. The results, however, were not very conclusive. The estimated factors varied from zero to about 0.5 and were occasionally even higher, depending on year class and age. On average, estimated factors from 0.2–0.3 were obtained. There was no indication of higher factors based on full sib correlations than on half sib correlations. Non-additive genetic factors contribute more to full sib correlations than to half sib correlations, and thus the present results give no indications of non-additive genetic factors controlling growth rate variations in rainbow trout. In the present study relatively few sib groups were represented in each year class, and thus the confidence limits of the calculated heritability factors were rather wide. Thus sample variations could account for part of the rather inconclusive results.

The estimates of the heritability factors and range of the group of the same year class based on weight and on length were not identical. Also, estimates of heritability factors based on individual condition factors,

$$k = \frac{100\ w\ (g),}{l^3\ (cm)}$$

gave values which were significantly greater than zero. Thus, body shape, which may represent both varying fat content and real height/length differences, seems to be affected by additive genetic factors.

Observation of parent/offspring correlation

The last three year classes were formed from selected parent fish from the first two year classes. Based on evidence from parent/offspring correlations, heritability factors in the same range as when based on sib correlations were obtained, with one exception, because in the 1975 year class no correlations between the size of father and offspring were found. Thus there seems to be favourable indication of control by additive genetic factors on growth rate variations in rainbow trout, and the effect of the selection was clear. Fish of inbred groups showed nearly the same mean growth rate as their non-inbred half sibs, while there was indication of somewhat reduced survival of inbred groups during their first year of life.

VARIATION IN AGE AT FIRST MATURITY

Observations from sib correlations

Preliminary results concerning age at first maturation of rainbow trout have been presented in earlier reports (Nævdal *et al.* 1975, 1979).

In all year classes considerable variation between sib groups was found in the proportion of fish maturing during their second and third years. This is exemplified in Fig. 2 where the results of the 1973 year class are shown. The

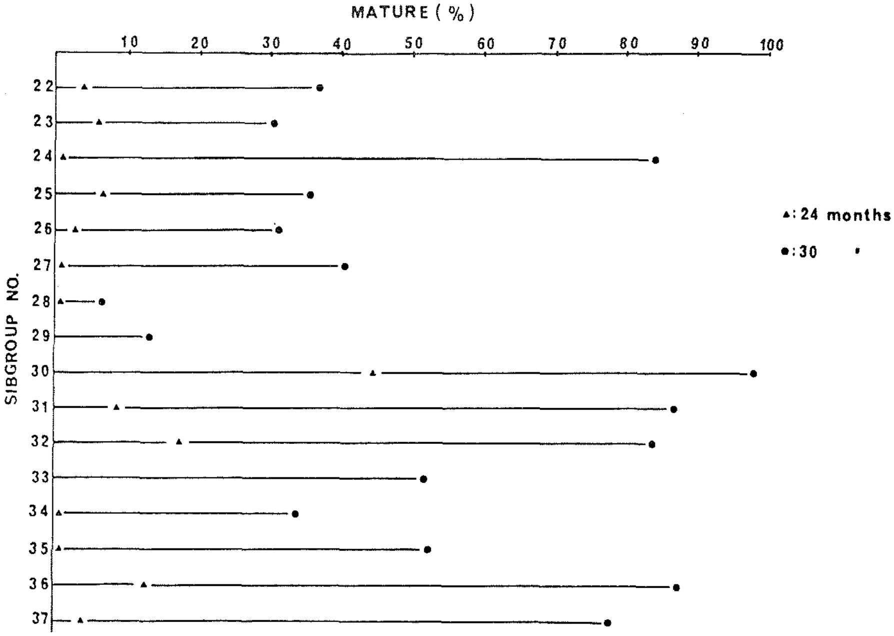

Fig. 2. Proportions of mature rainbow trout during second and third years of life of sib groups hatched in 1973.

other year classes showed similar variations, but usually with lower proportions of fish maturing during their second year. Fish maturing during their second year were, with few exceptions, males.

Heritability factors for proportions of mature fish were calculated from half sib and full sib correlations, (proportions were converted to $\sin^{-1}\sqrt{\text{proportion}}$). Concerning maturation during their second year, most estimates based on half sibs were low (0–0.15) while estimates based on full sibs varied considerably, but were usually high, (0.4–0.5 or even higher). This indicate, that non-additive genetic factors are more important than additive factors for early maturation of rainbow trout, although additive factors may also have some influence.

However, corresponding estimates for proportions of fish maturing during their third year gave higher estimates of heritability factors (mostly in the range 0.2–0.4) based on half sib coorrelations, while based on full sib correlations the estimates were also in the same range, giving no indication of control by non-additive genetic factors.

Part of the parent fish of the last three year classes matured for the first time during their third year and part of them during their fourth year. These two parent categories gave no clear difference in age of maturation of the offspring. However, significant positive correlations were found between proportions of mature fish in the sib groups of the parents and the offspring groups. This concerns both maturation during their second and their third years. These results correspond to the results of the sib correlations as far as maturation during their third year is concerned, but indicate higher values of heritability concerning maturation during their second year.

DISCUSSION

Genetics of rainbow trout have been dealt with by several authors. LEWIS (1944) altered both age of maturation, egg numbers and growth rate of fingerlings during two generations of mass selection of female rainbow trout. SAVOST'YANOVA (1972) and DONALDSON (1959) also reported on alteration of mean age of first maturity by selective breeding. KINCAID *et al.* (1977) reported on high gain in fingerling weight after three generation of selection. AULSTAD *et al.* (1972) reported heritability estimates from 0.01 to 0.29, and likewise CHEVASSUS (1976) found heritability estimates of from 0.045 to 0.375 in growth rate (weight and length) of rainbow trout and a very clear interstrain component of variation.

These examples, together with the results of the present study, show clearly that considerable genetic variations exist in rainbow trout, and although the estimates of heritability factors vary considerably, genetic improvement by selection seems possible, at least concerning growth rate. This is also confirmed by the results of the selection experiments of the present study, where clear effect of growth (size) of the parent fish at 2½ years of age was found in mean size of the offspring groups.

Concerning age at maturation, family selection gave clear results because positive correlations were found between mean maturity age of the parent sib group and the offspring. The effect of the maturity age (2½ or 3½ years) of the individual parent fish and the offspring was not clear in the present material.

Late maturing fish (3½ years or more) showed lower mean growth rate than earlier maturing fish of the same sib group. However, late maturing fish were also found among the fastest growing individuals of the sib groups, and thus the negative correlation between growth rate and age of maturity may be of minor importance for selective breeding.

The estimates of heritability factors are not very conclusive, but in most of the year classes and at most ages rather high factors were indicated in the present study, as well as in other studies reported. However, the high numbers of offspring in fish make it possible to have genetic gain even if the heritability is rather low.

As a conclusion it seems reasonably possible to produce a fast growing, late maturing «salmon-like» rainbow trout for fish farming. Unfortunately, the material of the present study could not be used for further selection experiments because it was infected by IPN virus, and thus could not give any practical results for fish farming. However, similar studies have been started again with new material for the purpose of obtained a rainbow trout better adapted to Norwegian fish farming than the brood stock used today.

The present study gives only little indication of unwanted effects of inbreeding, and no clear indication of such effects is found in the litterature. However, until it is proven that there are no bad effects, inbreeding should be paid attention to and probably avoided in schemes for selective breeding of rainbow trout and in practical fish farming as well.

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

By
JAKOB GJØSÆTER
Department of Fisheries Biology, University of Bergen, Norway

ABSTRACT

GJØSÆTER, J. 1981. Growth, production and reproduction of the myctophid fish *Benthosema 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 *Benthosema 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 *Benthosema 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 euphausids.

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

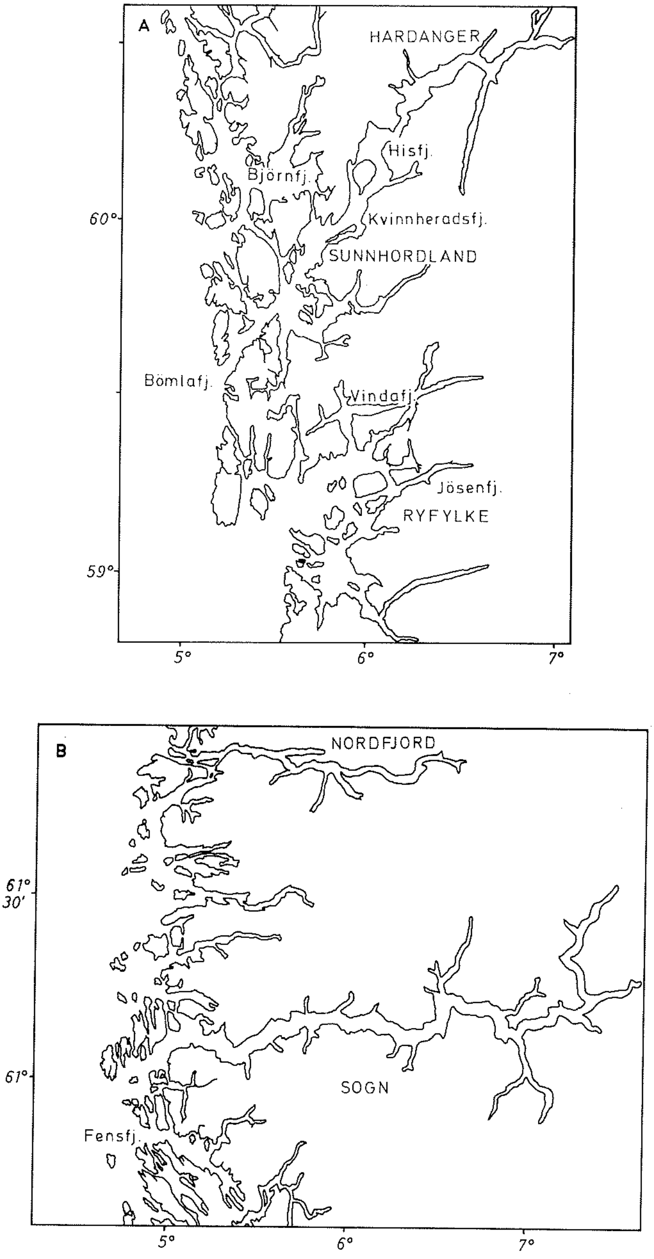

Fig. 1A and B. Geographical names referred to in the text.

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

$$l_{\text{frozen}} = 0.99 l_{\text{fresh}} + 0.16$$
$$l_{\text{fresh}} = 1.01 l_{\text{frozen}} - 0.16$$

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

$l_{\text{fresh}} = 1.05 l_{\text{formalin}} + 0.57$ (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

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

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

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		
		%	*l*	SD	%	*l*	SD	%	*l*	SD	%	*l*	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		

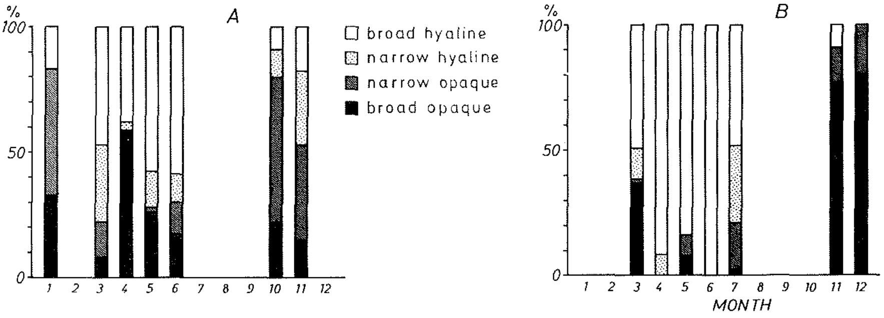

Fig. 2. Distribution of opaque and hyaline otolith edges in *B. glaciale* from the fjords (A) and from the ocean (B).

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:

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

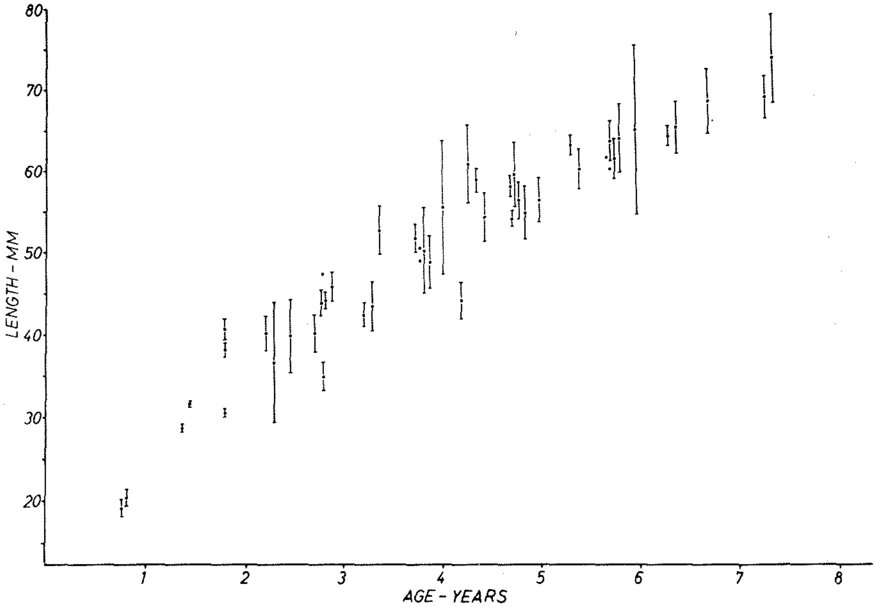

Fig. 3. Growth of *B. glaciale* from the fjords. The points represent mean length of a sample and the vertical bars 95% confidence limits.

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
$L\infty$	83.063	86.954	79.243	70.221	73.149
$\hat{V}$ ($L\infty$)	7.397	56.618	13.459	13.462	10.369
t_o	–0.640	–0.647	–0.632	–0.103	0.252
$\hat{V}$ (t_o)	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_∞ = 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 vurve

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

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,

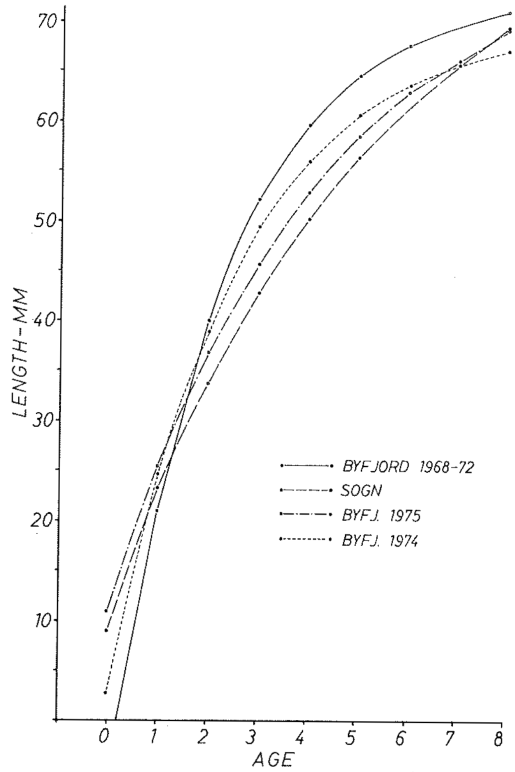

Fig. 4. Von Butalanffy's growth curves for *B. glaciale* from various areas and years.

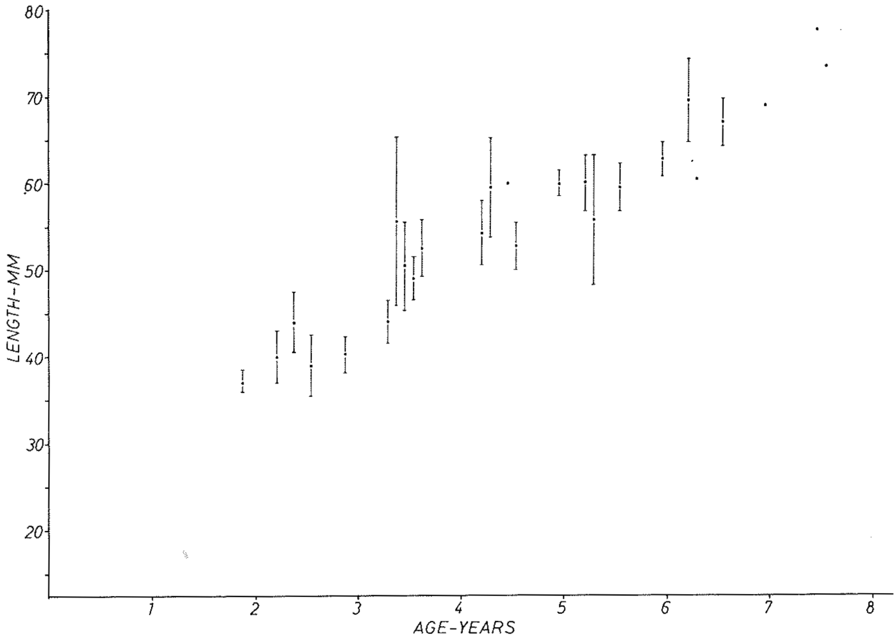

Fig. 5. Growth of *B. glaciale* from the oceanic population. The points represent mean lengths in a sample and the vertical bars 95% confidence limits.

the method used for the fjord samples proved unsuitable for fitting the von Bertalanffy's curve to the oceanic samples as t_o and K were determined with very low precision. An arbitrarily fixed $t_o = 0$ 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 $W_\infty = 5.49$ 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 heteroscedasicity. 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. ±	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

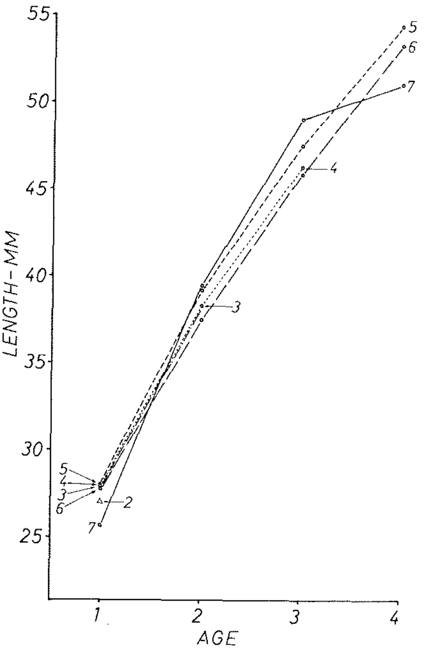

Fig. 6. Back calculated lengths of *B. glaciale* from the fjords. 2–7 indicate the age of the fish from which otoliths were taken.

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. ±	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	37.10
	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

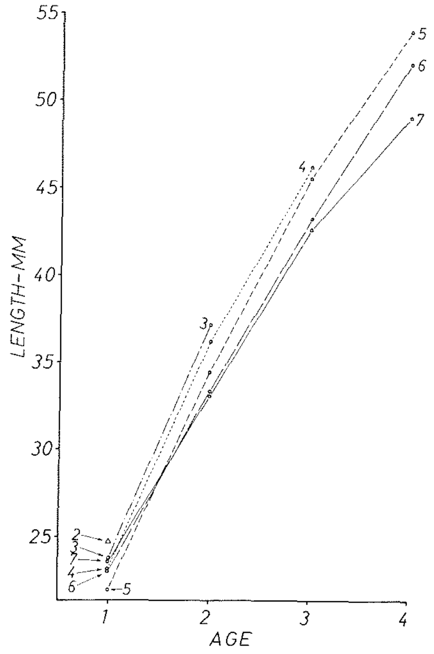

Fig. 7. Back calculated lengths of *B. glaciale* from the oceanic populations. 2–7 indicate the age of the fish from which otoliths were taken.

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 radia 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:

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

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), *Stenobrachius 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

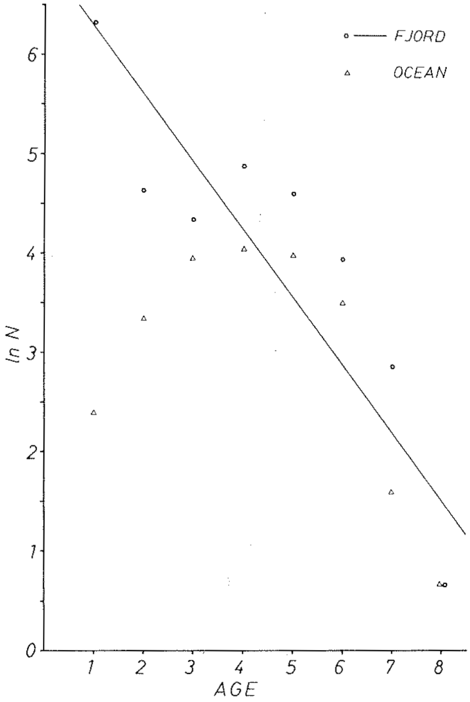

Fig. 8. Catch curve used to estimate the mortality of *B. glaciale*. The curve is fitted to the fjord material.

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

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

where N_o is the initial number, M is the instantaneous natural mortality rate, K and W_∞ are parameters from the growth equation, and t_o 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

$$P = 0.32\ N_o g$$

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

$$P = 0.45\ N_o g$$

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 $t_{\rho'}$. Fig. 9 shows an isopleth diagram for the fjord populations, where the parameters used are similar to those above except $t_o = -0.64$. Age at recruitment t_ρ 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 $t_o = 0$, $t_\rho = 0.5$ 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.

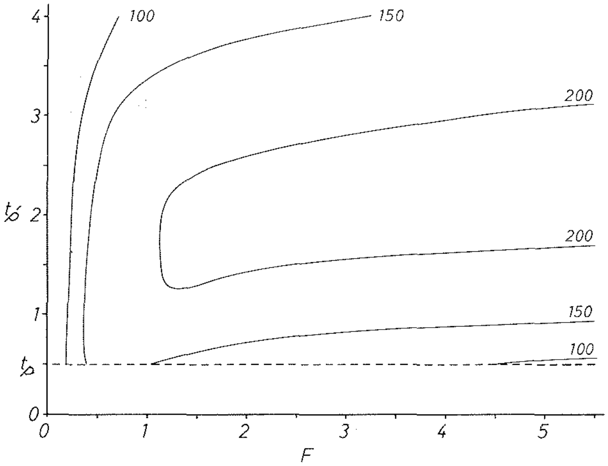

Fig. 9. Yield isopleth diagram for the fjord population of *B. glaciale*. The figures show yield in mg. F is fishing mortality, t_ρ' age at first capture and t_ρ age at recruitment.

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 TÅNING (1918) on *B. glaciale thori* (TÅNING) 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 NAFPAKTITIS (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.

	Standard length in mm				
	Males		Females		Unsexed
Month	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. gemellarei* 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% (±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

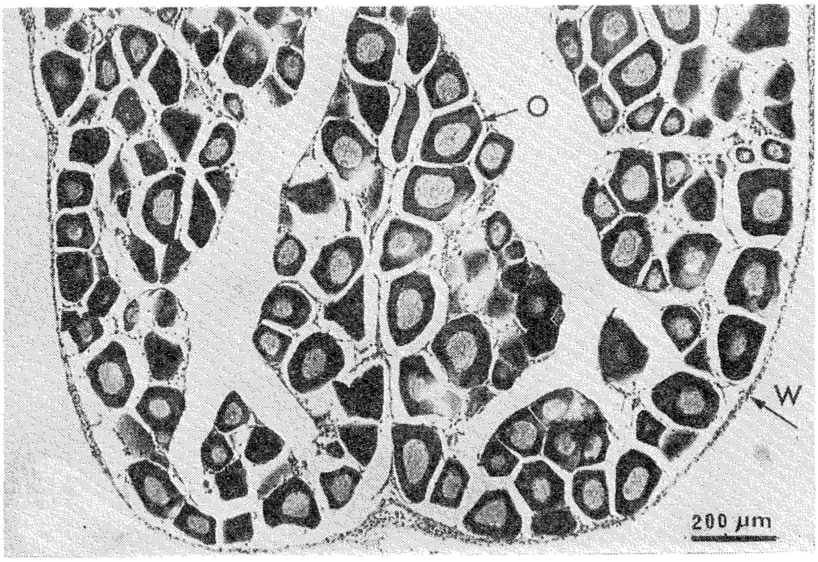

Fig. 10. Ovarium of *B. glaciale* in stage 2. O = oocytes in protoplasmatic growth period, W = ovary wall.

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

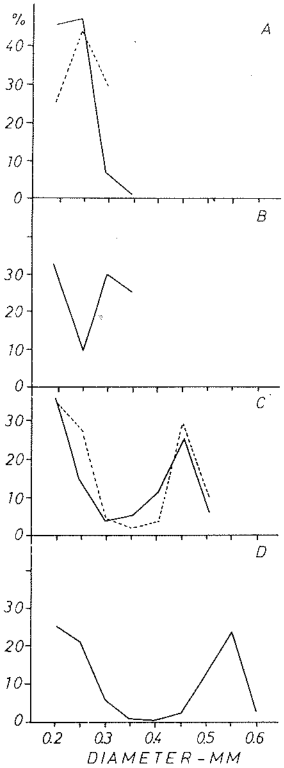

Fig. 12. Size distribution of oocytes in overies from *B. glaciale* in stage 1(A), 2(B), 3(C) and 4(D). Each line represents ovaries of one fish.

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 μm, the yolk grains measure 4–8 μ m in diameter. Later, the larger vacuoles of the central part of the protoplasm fuse. When the oocyte has reached a size of 500–600 μm, 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 μm. 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 μm and contained a pale yellow oil globule with diameter 200 μm. This may be derived from the central vacuole.

In the juvenile fish primary germ cells, oogonia and oocytes with size up to approximately 50 μm predominate. These stages are also found in older fish, but here resting oocytes (size 100–200 μm) 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 (<40µm), 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 ⅔ 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 *Stenobrachius 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
Myctophum punctatum	3	54.7 (51–61)	852 (794– 929)	TÅNING (1918)
M. affine	5	73 (72–78)	– (8000–9000)	ODATE (1967)
Hygophum benoiti	4	43.8 (42–45)	882 (849–1273)	TÅNING (1918)
Benthosema glaciale thori	6	36.0 (32–40)	323 (191– 467)	TÅNING (1918)
Diaphus garmani	20	46.3 (41–55)	1085 (350–1900)	NAKAMURA (1970)*
Lobianchia dofleini	4	34.0 (31–40)	388 (330–484)	TÅNING (1918)
Notolychnus valdivie	1	22	100	JOHNSEN (1916)
» »	1	22	120	TÅNING (1918)
Ceratoscopelus townsendi	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 *Ceratoscopelus 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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Table I. Samples of *B. glaciale* from the fjords used for growth calculations.

				Age group																										
				0			1			2			3			4			5			6			7			8		
Month	Year	Gear	Area	N	l	SD	N	l	SD	N	l	SD	N	l	SD	N	l	SD	N	l	SD	N	l	SD	N	l	SD	N	l	SD
10	71	PT	Sunnmøre										2	50.0		11	57.4	1.27	6	60.5	2.48									
10	72	PT	Sogn							2	47.0		5	49.8	5.27	11	53.6	1.27	2	57.0										
1	73	PT	Sogn													3	55.0	8.22	4	55.8	2.76	4	61.8	12.86						
3	74	KT	N. hordl.							11	39.8	2.11	14	41.9	1.38	9	43.4	2.28												
5	73	PT	N. hordl.				108	28.4	0.55																					
10	73	PT	Sogn				34	37.9	0.82	20	43.6	1.54	18	51.3	2.61	6	55.8	2.41												
4	74	PT	Hard.							5	36.2	7.36	10	42.9	2.94	7	60.3	4.80												
5	74	BT	Byfj.										18	52.3	3.07	55	58.3	1.52	56	62.5	1.24	31	63.5	1.27	14	68.1	2.64	2	67.0	
6	75	IKMT	Byfj.				296	31.4	0.36	10	39.4	3.32				19	53.8	3.02	17	59.5	2.39	12	64.5	3.18	4	73.0	5.33			
10	75	IKMT	Byfj.	10	19.0	1.13	23	40.4	1.33	24	43.7	1.12	3	49.7		7	58.9	4.10	6	60.8	2.64	5	67.8	3.89						
10	74	PT	Sogn	43	20.0	1.0	100	30.3	0.50	21	33.2	1.50	2	48.5					3	61.0										
11	75	KT	Rog.							11	45.4	1.76	12	48.2	3.32	9	54.2	3.34	6	63.2	4.37									

Table II. Samples of *Benthosema glaciale from the ocean used for growth calculations.*

				Age group																							
				1			2			3			4			5			6			7			8		
Month	Year	Gear	Area	N	L	SD	N	L	SD	N	L	SD	N	L	SD	N	L	SD	N	L	SD	N	L	SD	N	L	SD
12	70	PT	East of Iceland										9	59.8	1.63	9	62.8	1.96	2	69.0							
05	71	PT	N.W.Faroe Iceland				9	44.0	3.42	5	50.4	5.14															
06	71	PT	N. Finnmark							4	49.0	2.57	2	60.0													
11	73	PT	Norwegian Sea	11	37.1	1.41	8	40.3	2.15																		
03	74	PT	N. E. Hebrides				4	40.0	2.94	22	44.0	2.45	16	54.19	3.80	13	60.1	3.27	16	69.6	4.68	3	77.7				
04	74	PT	W. Ireland							7	55.6	9.69	4	59.5	5.70	11	55.7	7.54	2	60.5							
07	74	PT/BT	Norwegian Sea				7	39.0	3.60	15	52.5	3.27	26	52.8	2.60	22	59.6	2.59	13	67.1	2.77	2	73.5		2	77.5	

FiskDir. Skr. Ser. HavUnders., 17: 109–131.

LIFE HISTORY AND ECOLOGY OF *MAUROLICUS MUELLERI* (GONOSTOMATIDAE) IN NORWEGIAN WATERS

By
JAKOB GJØSÆTER
Department of Fisheries Biology, University of Bergen, Norway

ABSTRACT

GJØSÆTER, J. 1981. Life history and ecology of *Maurolicus muelleri* (Gonostomatidae) in Norwegian waters. *FiskDir. Skr. Ser. HavUnders., 17*: 109–131.

Samples of *Maurolicus muelleri* were collected by pelagic trawls from various fjords in western Norway and off the Norwegian coast. Otoliths were extracted for age determination. The growth of fish taken from the fjords can be described by the equation

$$l_t = 48.8 \text{ mm } (1 - e^{-1.05\ (t\ -\ 0.21)})$$

and those from the ocean areas by

$$l_t = 59.4 \text{ mm } (1 - e^{-0.88\ (t\ +\ 0.06)})$$

The instantaneous mortality rate was about 1.8 and maximum potential yield is tentatively estimated to 0.17 g/recruit.

Studies of the gonads showed that the first spawning may take place when the fish are one year old. The spawning period extends at least from March to September. The number of ripening oocytes per female ranged from 200 to 500.

The stomach contents in the youngest fish consisted mainly of copepods while copepods and krill were about equally abundant in adult fish. Other food items were rarely observed. No diurnal trend in the degree of stomach filling was observed.

INTRODUCTION

Maurolicus muelleri (GMELIN 1789) is widely distributed, and is an important component of the mesopelagic fauna in many areas. In the eastern and central Atlantic Ocean it ranges between northern Norway and Iceland to about 5°S off Africa and in the western Atlantic between Newfoundland and the Gulf of Mexico and the Caribbean Sea. It is also found in the South Atlantic and off South Africa and Argentina, in the western Pacific Ocean off Japan, off southeast Australia and off New Zealand (GREY 1964, WITZELL 1973, ROBERTSON 1976, ANON. 1977).

Taxonomically *M. muelleri* is usually placed in the family Gonostomatidae. WEITSMAN (1974) found, however, in a study of the osteology of the stomiatoid fishes that *Maurolicus* should rather be placed among the *Sternoptychidae*. Studies of larval development (AHLSTROM 1974) also demonstrated a close affinity to the sternoptychid fishes.

The ecology of the young stages of *M. muelleri* is fairly well known from studies in the Mediterranean Sea (JESPERSEN and TÅNING 1926), in the northeast Atlantic (KOEFOED 1958, WILLIAMS and HART 1974), from Japan (OKIYAMA 1971), Argentina (DE CIECHOMSKI 1971) and from New Zealand (ROBERTSON 1976). Other aspects of its ecology and life history are almost unknown.

M. muelleri appears to be the most abundant mesopelagic fish in some of the fjords of western Norway and in the Norwegian Deep. Occasionally it is found in very dense concentrations, and it may be a resource for future fisheries. A basic understanding of its life history is therefore needed.

This paper presents studies on aspects of the life history and some parameters needed to assess the population dynamics of *M. muelleri* from the Norwegian fjords and the seas around southern Norway. An attempt to estimate its abundance in these waters is presented in separate papers (GJØSÆTER 1978, GJØSÆTER and MYRSETH in prep.).

MATERIALS AND METHODS

Most of the materials used in this work was collected on cruises with the vessels of the Institute of Marine Research, Bergen. Samples were taken with 3-foot Isaacs-Kidd midwater trawls, small pelagic young fish or sprat trawls and with a larger 1600-mesh pelagic trawl. Occasionally a krill trawl designed by the Institute of Fisheries Technology Research was used. Trawling was usually carried out to identify acoustic scattering layers or to obtain samples of krill or commercial fish species and not primarily to catch *M. muelleri.* The depth of the trawl was usually monitored using a net sonde or a Benthos depth recorder.

Most samples of *M. muelleri* were frozen onboard and brought to the laboratory for examination. Standard length was measured to the nearest mm in all samples. Weight was recorded in some samples to the nearest 0.01 g. Frozen specimens were used for this purpose. Before weighing the fish were thawed, and water on their surfaces was removed with filter paper.

Otoliths were removed from most samples, cleaned and stored in 80% ethanol. For age reading they were transferred to creosote and viewed with a binocular microscope using reflected light and black background. The radia of the otoliths and of the hyaline zones were measured with an ocular micrometer as indicated on Fig. 1. All the otoliths were read independently by two people. When there was disagreement, the otoliths were reread and then discussed. If agreement was still not reached, the otoliths were not used.

Some otoliths were studied at higher magnification by a scanning electron microscope (SEM) or light microscope to find primary growth increments supposed to be laid down daily. The otoliths viewed by SEM were ground from

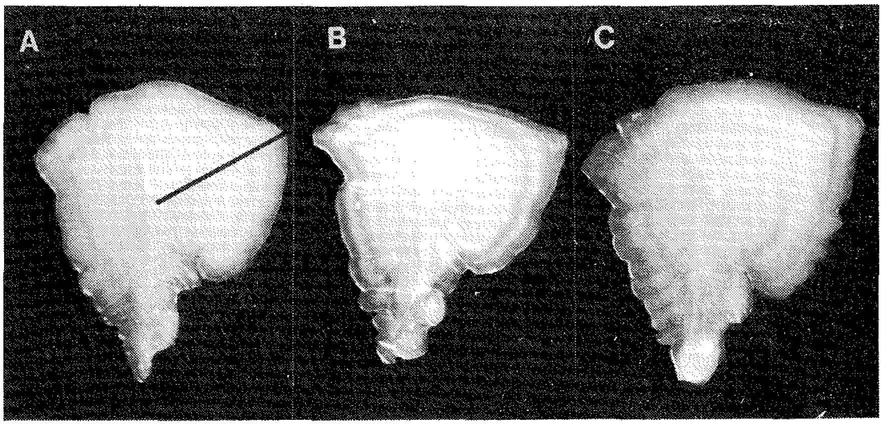

Fig. 1. Otoliths of *Maurolicus muelleri*. A: 2-year-old, B: 3-year-old, C: 4-year-old. The line in A shows the radius measured.

the lateral side till a plane through the nucleus was reached. This surface was etched with 1% HCl for approximately 5 minutes and was coated with gold in a vacuum evaporator. Only small otoliths were used for light microscopy. These were cleared in creosote and mounted between microscope slides (BROTHERS *et al.* 1976).

In frozen fish the gonads were usually in poor condition; therefore a classification mainly based on size was used to assess the stage of maturation. Some gonads preserved in formalin were sectioned and stained with haematoxylin and eosin for histological examination. Number and size distribution of eggs were studied using a binocular microscope with an ocular micrometer.

Stomach contents were examined from some samples. The degree of filling was assigned according to an arbitrary scale from 0 to 4. The stomach contents were sorted into groups, but the species composition was usually not identified.

Regression analysis was used to calculate fish length from otolith diameters, to describe the weight/length relationship and to estimate the mortality from a catch curve. In these types of situations, when both variates are subject to measurements error and the sample range truncates the real range of the variates, RICKER (1973) recommended use of a functional regression instead of the predictive type commonly employed. Although the mathematical implications are doubtful (see JOLICOEUR 1975, RICKER 1975), the geometric mean regression was used in the present work. The confidence limits of the regression coefficient b were calculated as

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

where $B = F\,(1 - r^2)/(N - 2)$, r is the correlation coefficient, N the number of pairs of variates and F the variance ratio at the 95% confidence level for $n_1 = 1$ and $n_2 = N - 2$ degrees of freedom (see RICKER 1975).

RESULTS

OTOLITHS AND AGE DETERMINATION

The sagitta of *M. muelleri* is laterally compressed and has a long rostrum (Fig. 1). The nucleus may appear hyaline or opaque with narrow hyaline and broader opaque zones alternating around it. In the rostral part of the otolith the zones are usually obscure.

Hyaline otolith edges were dominant in the November–April period (Fig. 2). During May and October opaque edges were most usual. In April and May the opaque zones were usually narrow while the opaque zones found during October and November were generally broad. Although samples from June through September are lacking, Fig. 2 indicates that hyaline zones are usually formed during winter and opaque zones during summer. The otoliths with opaque zones taken during winter may indicate formation of false zones. The otoliths used were taken from several different areas where the zones may be formed at different times. This may explain the mixture of opaque and hyaline edges found during most of the year. There may also be a difference in time of zone formation between mature and immature fish although the present material was found unsuitable for a detailed analysis of this.

The Petersen method (see TESCH 1968) was applied to some of the materials to verify the age determination based on otoliths. Age groups 0 and I are usually clearly separated (Fig. 3A) as are age groups I and II, at least during winter and early spring. Fig. 3B shows, however, that a few fish have lengths that make the assigned age doubtful. The age groups II and III cannot usually

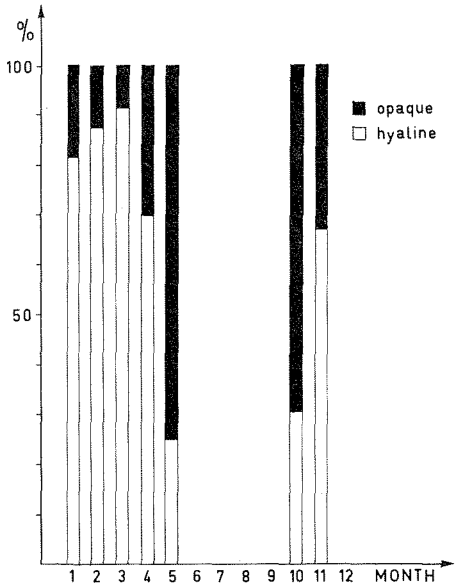

Fig. 2. Distribution of otolith edges during the year.

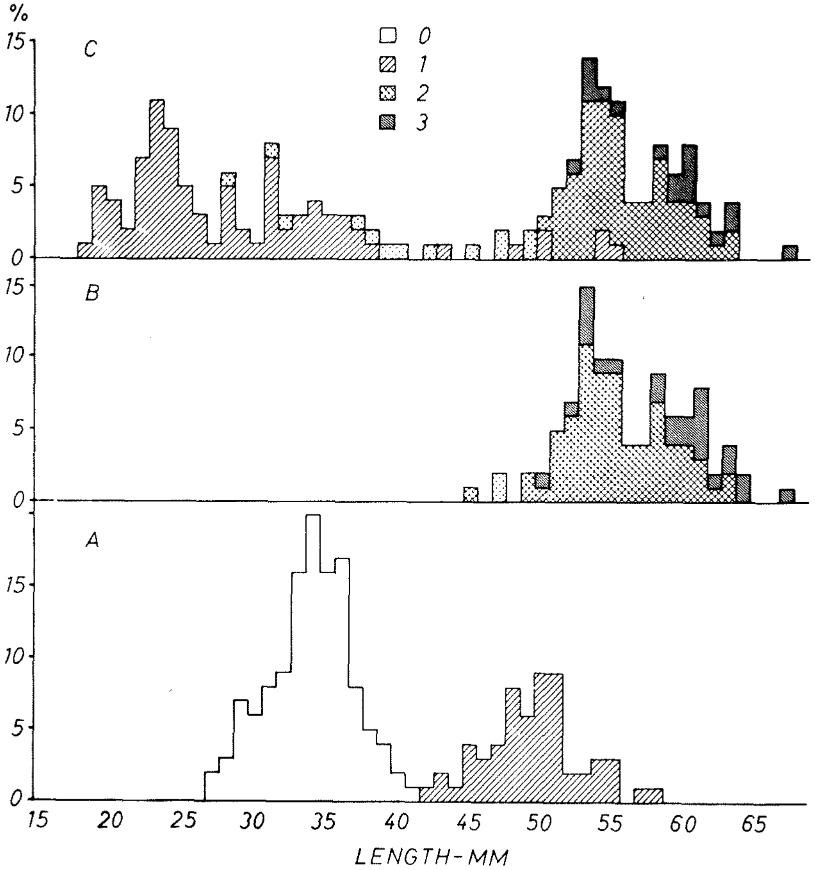

Fig. 3. Length distribution of *Maurolicus muelleri* designed as age groups 0 through III based on otolith reading. Fish caught during A: November–December, B: January and C: February.

be separated using the Petersen method (Fig. 3B, C). Although some otoliths may give a wrong age, it can be concluded that in general they can be used for age determination of *M. muelleri.*

In late autumn, the length of fish classified as 0-group, based on traditional otolith reading, varied between 16 mm and 48 mm. Otoliths from the two largest fish, the smallest and some of mean size were studied to find daily growth increments (see PANNELLA 1974, BROTHERS *et al.* 1976, TAUBERT and COBLE 1977). Provided that the primary growth rings are laid down daily, the results show that all the fish were 0-group and that they hatched within the April–June period (Table 1). Typical otoliths are shown in Fig. 4.

AGE AND MORTALITY

The age composition of *M. muelleri* is shown in Fig. 5 and 6. The oceanic samples were taken with pelagic trawls that probably do not catch the youngest ages representatively. The fjord samples taken by Isaacs-Kidd midwater trawl and krill trawl are supposed to be more reliable. Based on all the available data for the age groups I–IV, a catch curve was constructed and mortality estimated using geometric mean regression (see RICKER 1973). The result was Z = 1.8, but due to the selection of older age groups by some of the gears used, this is likely to be an underestimate. Due to the differences in gear used, it is not possible to assess the difference in mortality between the fjords and the ocean area. In both areas there seems to be a very high mortality in the two and three year old fish during the summer, possibly in connection with spawning.

Table 1. Primary growth rings in otoliths of juvenile *M. muelleri*. SEM: scanning electron microscope, LM: light microscope.

Otolith No.	Fish length mm	No. of rings	Radius of otolith mm	No. of rings per mm	Time of capture	Method
1	47	115	0.66	174	Aug. 74	SEM
2	48	130	0.70	186	Aug. 74	SEM
3	16	63	0.28	225	Aug. 76	LM
4	25	90	0.40	225	Aug. 73	LM
5	29	130	0.44	295	Aug. 73	LM
6	25	100	0.40	250	Aug. 73	LM
7	25	100	0.40	250	Aug. 73	LM
8	25	118	0.40	295	Aug. 73	LM

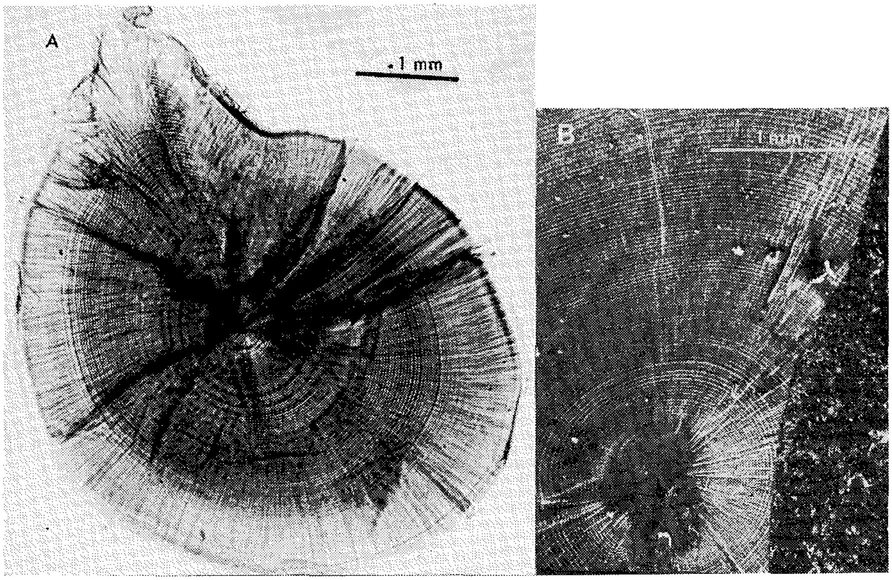

Fig. 4. Otoliths of *Maurolicus muelleri* showing primary growth rings. A: Light microscopy, 0-group fish caught in October. 200 x. B: Scanning electron microscopy, central part of otolith of adult fish. 300 x.

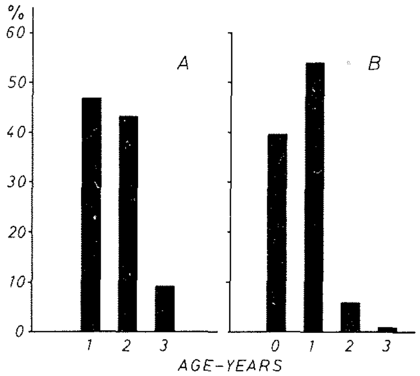

Fig. 5. Age composition of *Maurolicus muelleri* caught in the ocean. A: Fish cuaght during February–May (N=445). B: Fish caught during October–November (N=351).

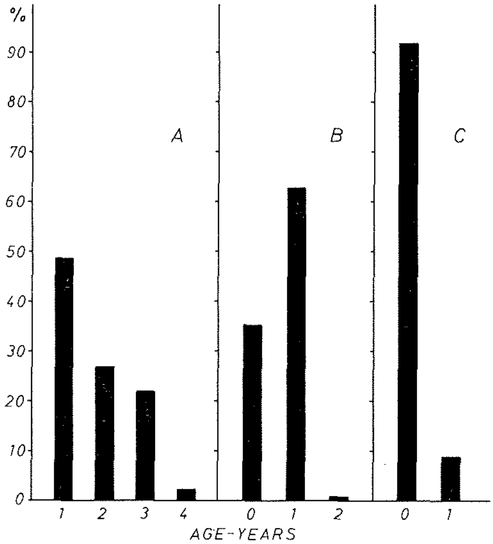

Fig. 6. Age composition of *Maurolicus muelleri* caught in the fjords. Fish caught with A: IKMT, April 1974 (N=122), B: Pelagic trawl, October 1974 (N=82) and C: Krill trawl, November 1975 (N=338).

LENGTH - WEIGHT RELATIONSHIP

Weight was recorded for 97 specimens taken in the fjords in autumn, 36 taken in the fjords in spring, and 95 taken during the spring from oceanic areas.

Lines of the type

$$\lg W = a + b \lg l$$

were fitted to the data using geometric mean regression, as recommended by RICKER (1973). The results are given in Table 2. The length – weight equations are:

Fjords, autumn $W = 1.41 \times 10^{-5}\ l^{2.97}$
Fjords, spring $W = 6.46 \times 10^{-5}\ l^{2.42}$
Ocean, spring $W = 3.63 \times 10^{-6}\ l^{3.33}$
Pooled $W = 2.04 \times 10^{-5}\ l^{2.87}$

where W is weight in grams and l is length in millimeters. Further analyses of the differences between areas and periods are probably not justified by the material.

GROWTH

The data based on the fjord samples and those based on the oceanic samples were treated separately for the growth calculations. Mean lengths of the age groups were calculated for each sample (Fig. 7A and B, Tables I and II) and the von Bertalanffy's growth curve

$$l_t = L_\infty\ (1 - e^{-K(t\ -\ t_o)})$$

was fitted to the data using the method described by ALLEN (1976). This method gives the best least-squares estimates of the parameters L_∞, K and t_o and the estimates of their variances.

For the fish taken in the fjords the following equation was found, based on 651 specimens:

$$l_t = 48.8\ \text{mm}\ (1 - e^{-1.05(t-0.21)})$$

$$\hat{V}(L_\infty) = 3.35$$
$$\hat{V}(K) = 0.02$$
$$\hat{V}(t_o) = 0.005$$

For 771 fish from the oceanic areas the result was:

$$l_t = 59.4\ \text{mm}\ (1 - e^{-0.88(t+0.06)})$$

$$\hat{V}(L_\infty) = 3.16$$
$$\hat{V}(K) = 0.01$$
$$\hat{V}(t_o) = 0.008$$

Table 2. Length – weight relationship in *M. muelleri*. Paramenters to the regression line lg W = a + b lg$l$.

Area	Season	b	95% conf.lim.	a	N	r^2
Fjords	Autumn	2.97	2.75 – 3.21	–4.85	97	0.888
Fjords	Spring	2.42	2.17 – 2.70	–4.19	36	0.927
Ocean	Spring	3.33	3.01 – 3.67	–5.44	95	0.826
Pooled		2.87	2.75 – 3.00	–4.69	228	0.917

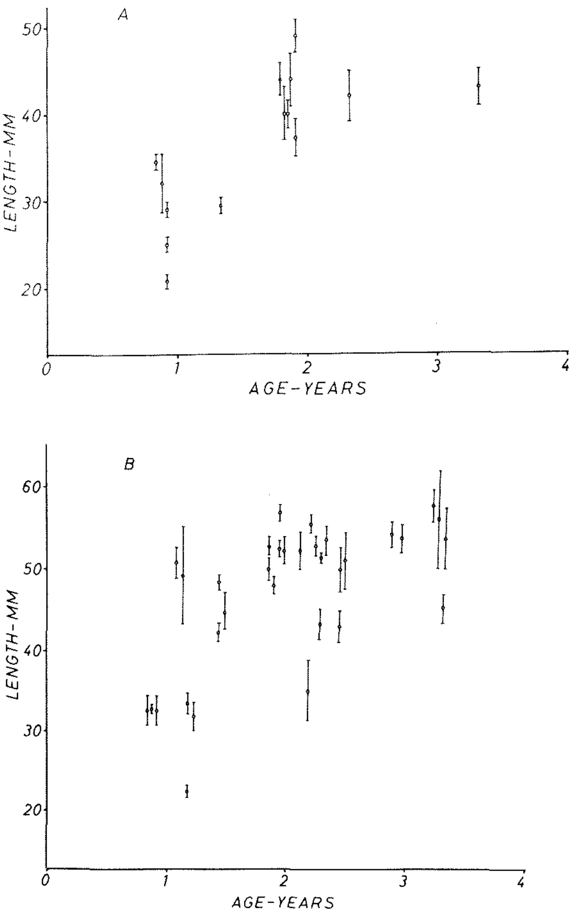

Fig. 7. Mean length (circles) with 95% confidence limits (vertical bars) of *Maurolicus muelleri*. All samples taken within one month and one geographical area are combined. A: Samples from the fjords and B: Samples from the ocean.

Table 3. Analysis of variance of geographical variation in length of 0-group *M.muelleri* (see Fig. 8). ***; significant at 99% level.

Source of variance	SS	df	MS	F
Total........................	5918.00	329		
Samples	3275.32	5	665.06	80.28***
Error........................	2642.70	324	8.16	

Provided the samples give an unbiased picture of the populations, there is significantly faster growth and lower maximum size (L_∞) in the fish from the fjords compared to those from the ocean. The differences may also reflect selectively of sampling gears and other sources of error. The conclusion is therefore tentative.

If all the material is combined, the following equation results:

$$l_t = 57.09 \text{ mm } (1 - e^{-0.94(t-0.14)})$$

The corresponding W_∞ = 2.24 g.

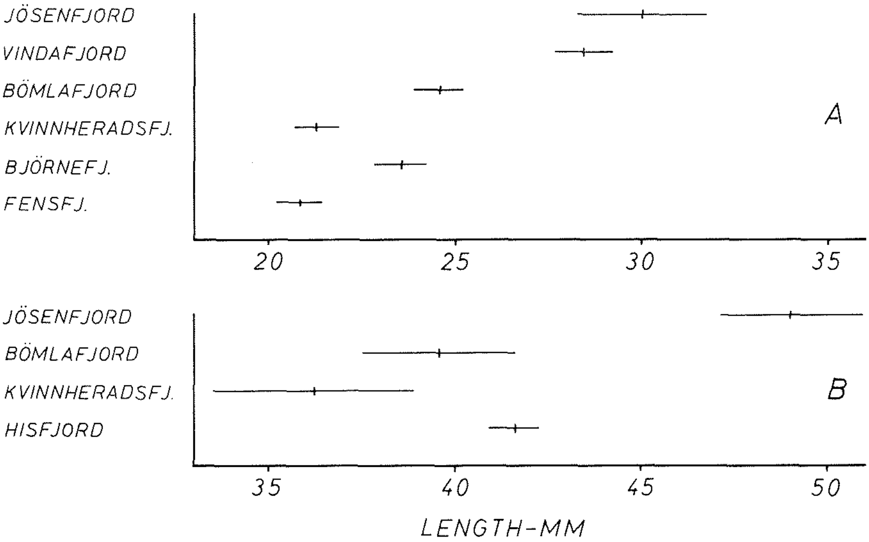

Fig. 8. Mean length (vertical bars) with 95% confidence limits (horizontal bars) in *Maurolicus muelleri* samples taken by krill trawl during November 1975. A: 0-group, B: 1-group.

Samples from seven fjords between Ryfylke and Nordhordland were taken with a krill trawl during November 1975. These samples contained 0- and I-group fish only. Mean length and 95% confidence limits of means are shown in Fig. 8. The geographical names used are shown in Fig. 9. An analysis of variance showed that among 0-group fish all the sample means did not belong to the same statistical population (Table 3), and a Newman-Keuls test (see ZAR 1974) was performed to further analyse the differences. With two exceptions, the hypotheses that sample means were equal could be rejected (Table 4).

Fig. 8, where the samples are arranged from south to north, suggests a decrease in mean size in the same direction. It is not clear whether the differences are due to differences in hatching time or in growth rates.

The mean length of the I-group was tested using similar procedures (Fig. 8, Tables 5 and 6). The samples from Jøsenfjorden (Rogaland) were highly different from the other samples taken in the Hardangerfjord area. Within the Hardangerfjord area the outermost sample and the innermost one had similar means while both differed significantly from that taken in the middle of the fjord. No geographical trend in size was observed among the oceanic samples although the variation in mean length between samples was extensive.

To carry out back calculation of growth from otolith zones, radia of the hyaline zones and of the whole otoliths were measured as indicated in Fig. 1. A trial plotting of fish length against otolith radia suggested that the variance increased with fish length. To minimize the effect of this, data were transformed to logarithms. Geometric mean regression was used to describe the

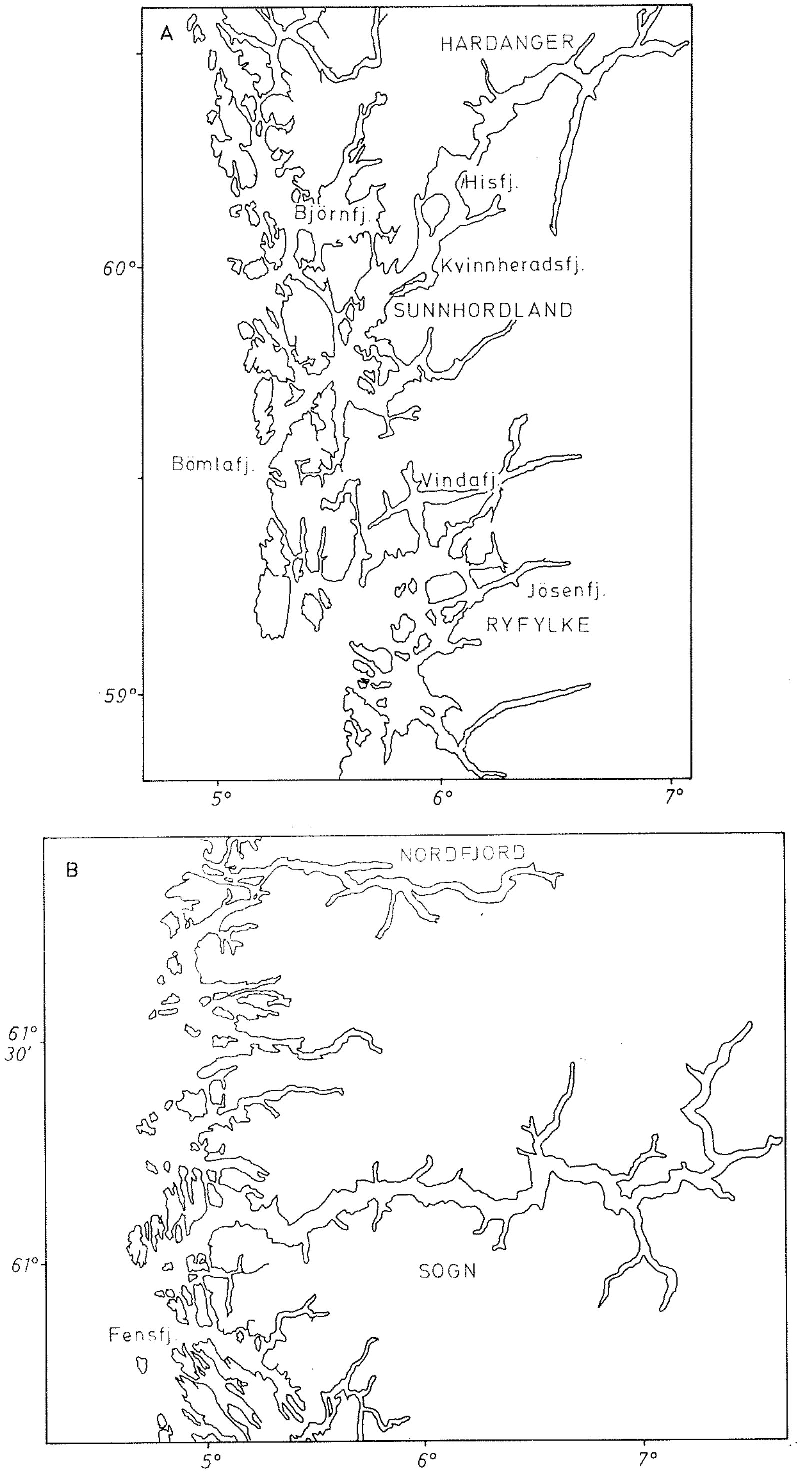

Fig. 9 A and B. Maps showing geographical names used.

Table 4. Newman-Keuls test of geographical variation in length of 0-group *M. muelleri*. + ; significant at 95% level, ns ; not significant.

Area	Mean length	Rank	Jøsenfjord	Vindafjord	Bømlafjord	Kvinnherads-fjord	Bjørnefjord
Jøsenfjord	30.00	1					
Vindafjord	28.41	2	+				
Bømlafjord	24.56	3	+	+			
Kvinnheradsfjord	21.27	5	+	+	+		
Bjørnefjord	23.58	4	+	+	ns	+	
Fensfjord	20.82	6	+	+	+	ns	+

relationship between the variables and to estimate fish length from otolith radius as recommended by RICKER (1973).

The equation

$$\lg l = 1.089 \lg r + 1.682$$

where l is fish length (mm) and r radius of the otolith (mm) was then derived. Confidence limits for the regression coefficient were 1.054 and 1.125, and the coefficient of determination $r^2 = 0.858$. The computation was based on 689 pairs of measurements.

Means with confidence limits for radia of the hyaline zones are given in Table 7. Only otoliths where the zones were clearly defined were used for these calculations. Lengths corresponding to the diameters are shown in Fig. 10. There was a pronounced Lee's phenomenon in fish from oceanic samples. This could be expected if there is a greater selectivity for the largest fish in the younger than in the older age groups. There are, however, also additional possible explanations (see RICKER 1969).

PRODUCTION

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

$$P = N_o \, 3 \, KW_\infty \left[\frac{1}{M + K} + \frac{2}{M + 2K} + \frac{1}{M + 3K} \right]$$

where N_o is the initial number of fish, M is the instantaneous natural mortality coefficient and K and W_∞ are parameters from the von Bertalanffy's growth equation; t_o is supposed to be zero. Using $W_\infty = 2.24$ and $K = 1.03$ from the pooled growth equation and tentatively letting $M = 2.0$, one arrives at

$$P = 0.23 \, N_o$$

Table 5. Analysis of variance of geographical variation in length of 1-group *M. muelleri* (see Fig. 8). ***; significant at 99% level.

Source of variance	SS	df	MS	F
Total	1886.90	88		
Samples	1217.00	3	405.66	51.48***
Error	669.90	85	7.88	

Table 6. Newman-Keuls test of geographical variation in length of 1-group *M. muelleri*. + ; significant at 95% level, ns ; not significant.

Area	Mean length	Rank	Hisfjord	Jøsen-fjord	Bømla-fjord
Hisfjord	39.56	2			
Jøsenfjord	49.00	1	+		
Bømlafjord	39.55	3	ns	+	
Kvinnherradsfjord . .	36.20	4	+	+	+

Table 7. Diameters of growth zones of *M. muelleri*.

	Zone No.	Age of fish (years)	Number of otoliths measured	Mean radius (mm)	95% confidence limit ±
OCEAN	1	1	361	0.604	0.014
		2	227	0.600	0.017
		3	75	0.536	0.028
		4	5	0.423	0.176
	2	2	255	1.016	0.016
		3	80	0.852	0.032
		4	5	0.615	0.244
	3	3	75	1.083	0.029
		4	4	1.029	0.092
	4	4	6	1.064	0.129
FJORDS	1	1	100	0.580	0.028
		2	30	0.630	0.046
	2	2	30	0.941	0.035

Using the formula provided by BEVERTON and HOLT (1957, equation 4.4), the yield per recruit can be calculated for various combinations of fishing mortality $\bar{F}$ and age at first capture, $t_{p'}$ (Fig. 11). The parameters are as above, except for $t_0 = 0.14$. Age at recruitment is arbitrarily set like 0.25 and maximum age like 3.5 years.

Maximum sustainable yield will, according to Fig. 11, be about 0.17 g/recruit, and this will be obtained with a fishing mortality between 5 and 6 and at an age of 0.6 year at first capture. The natural mortality can, however,

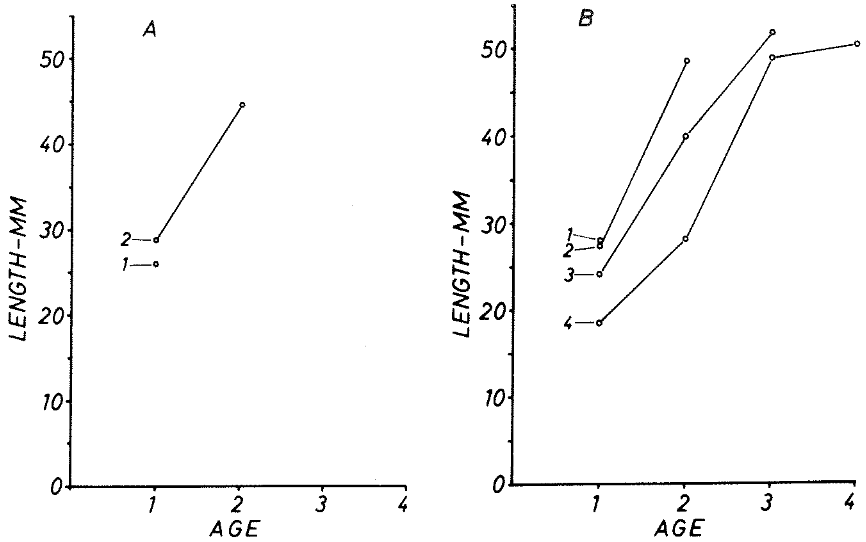

Fig. 10. Back-calculated lengths of *Maurolicus muelleri*. 1–4 indicate age of fish from which otoliths were taken. A: Fjord samples, B: Oceanic samples.

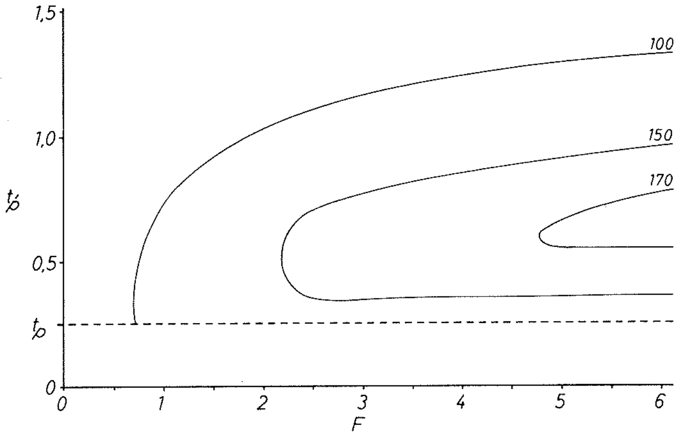

Fig. 11. Yield per recruit isopleth diagram for *Maurolicus muelleri*. The yield is given in mg. F is fishing mortality, $t_{\rho'}$ age at first capture, t_ρ age of recruitment.

decrease if a fishery removes a considerable part of the population. This will change the calculated values, and Fig. 11 must therefore be regarded as a first approximation only.

REPRODUCTION

Most of the *Maurolicus* samples were frozen and therefore unsuited for detailed examination of gonads. However, gonads from some of the samples were classified as small (immature), medium (ripening) and large (ripe), irrespective of sex. Fish smaller than 39 mm SL were always immature. Ripening and ripe fish appeared in the samples from March to May (Table 8). Fish classified as ripening were also observed in October and November, though they would probably not have spawned until the following year.

Diameters of oocytes were measured in some ovaries preserved in formalin. Females caught in the spawning season had two size groups of oocytes (Fig. 12). The smaller oocytes measured between 100 and 500 µm. They had large nuclei, and little or no yolk was deposited. The larger oocytes measured between 500 and 750 µm. The mean size was 580, 590 and 610 µm respectively in three gonads. In these oocytes the nuclei were disintegrating, and yolk was forming (Fig. 12). After the spawning season (October–November) and in early spring (March) only resting oocytes, measuring less than 300 µm and with a modal diameter between 100 and 200 µm were found. It is not clear what happens to the smaller oocytes observed in the ovaries before spawning. They may be partly resorbed and developed the next year, or they may develop and be spawned in a later batch in the same year.

The developing oocytes larger than 500 µm were counted in 15 fish. The mean standard deviation and range of their lengths were 50.8 mm, 2.78 mm and 47–55 mm respectively, and mean standard deviation and range of oocyte numbers were 312, 103 and 200–500. Within the size group studied, there was no correlation between number of oocytes and fish size. The ratio between number of the small oocytes (diameter about 160–500 µm) and the large oocytes (d > 500 µm) was studied in three fish, and the results were 2.6, 1.4 and 0.5 respectively. This indicates that there is no constant proportion between the number of oocytes in the various size groups.

Table 8. Development of gonads of *M. muelleri.*

Stage	Month					
	1	2	3	5	10	11
Immature	12	22		13	34	14
Ripening		1	22	58	6	11
Ripe			27	49		
N......................	12	23	49	120	40	25

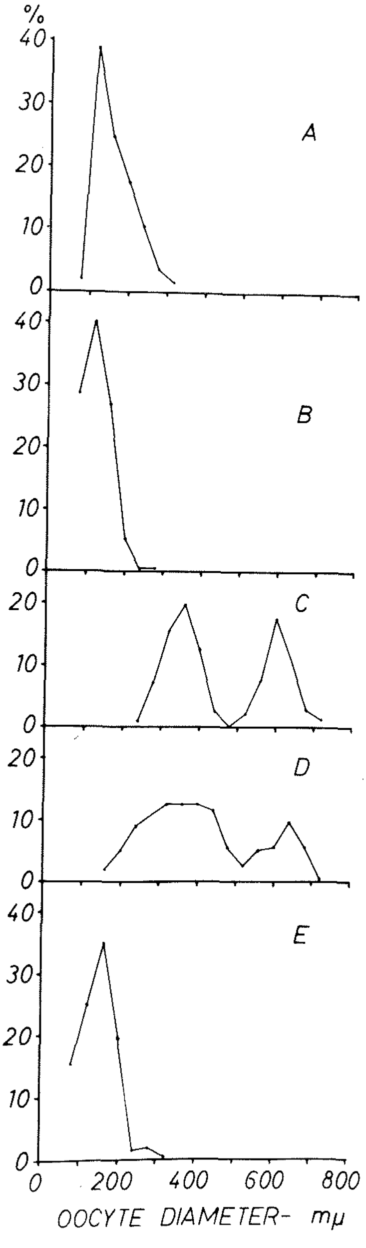

Fig. 12. Size distribution of oocytes from *Maurolicus muelleri*. A–B: immature fish caught during spring, C–D: mature fish caught during summer and E: female caught during autumn.

FOOD AND FEEDING

The types of stomach contents were studied in 308 specimens, of these only 224 had contents which could be identified (Table 9). In fish smaller than 20 mm, copepods were the most important food item while copepods and krill were about equally important in larger fish. Other food items (mainly pteropods) were found in only 2% of the stomachs studied. During spring (March–May) 60% of the stomachs contained copepods and 46% krill (Table 10). During autumn (September–November) 40% and 24% had eaten krill and copepods respectively, and for the winter the corresponding numbers were 90% and 2%. Both the material from the fjords and from the ocean showed the same trends. The degree of filling was classified according to the scale: 0) empty, 1) little contents, 2) half filled, 3) full, and 4) extended stomach.

From 406 specimens studied the following distribution was found:

Degree of filling	0	1	2	3	4
Percentage	18	18	25	35	4

No differences between season or area could be demonstrated from the scarce material at hand. No diurnal trend in degree of filling was observed. This agrees with the observations made by SAMYSHEV and SCHETINKIN (1971).

Table 9. Composition of stomach contents of *M. muelleri* in different size groups.

Stomach contents	Size of fish (mm)		
	< 20	21 - 30	> 30
Copepods	6	8	61
Krill	1	11	74
Copepods and krill			57
Others			6
Unidentified			84
N	7	19	282

Table 10. Seasonal variation in stomach contents of adult *M. muelleri* (*l*> 30 mm).

Stomach contents	Season		
	Spring	Autumn	Winter
Copepods	36	25	0
Krill	19	9	46
Copepods and krill	39	17	1
Others	0	2	4
Unidentified	31	52	1
N	125	105	52

DISCUSSION

M. muelleri is a small, short-lived and fast-growing fish. Its maximum size is about 7 cm, but fish longer than 5 cm are scarce. Growth and otolith zone formation seem highly variable within the time and area studied. The material available was not suited for a further analysis of this variation, but the variation must be taken into consideration in future studies of the species.

The growth of other Gonostomatidae is little known, although Mauchline (1977) gives some data. Neither is the growth pattern of *M. muelleri* from other areas known, even if the maximum size attained in the Mediterranean is about 65 mm (Grey 1964).

Production per year is estimated to be 0.23 g/fish. The method used presumes that the mortality is constant. In reality, the natural mortality seems to be low during the first part of life when production is high, and higher during older ages when growth, and therefore production, is very slow. These effects will tend to make P = 0.23 g an underestimate. Fig. 5 may indicate that the high mortality is connected with the spawning. Due to sampling problems, all mortality data are, however, uncertain.

M. muelleri spawn in the deep fjords of western Norway, at least from Ryfylke to Nordfjord (Gundersen 1953; Bakken, unpublished data; Foss-

HAGEN, unpublished data) and along the coast from Skagerak and as far north as Lofoten (LINQUIST 1968, WIBORG 1954). They also spawn in the open ocean (WILLIAMS and HART 1974; BJØRKE, unpublished data). There is no indication of spawning migration. The fish seem to spawn where they live, and in the fjords this behaviour may cause formation of small local stocks. The variation in growth and formation of otolith zones also implies that several small stocks exist. In case of a fishery, it may therefore be necessary to manage these stocks separately. The stock structure in the open ocean is not known, but separation into small stocks is less likely there.

The studies of the gonads suggest that the spawning season starts in March and ends in October. WIBORG (1954) studied plankton samples from four localities between Sogn and Lofoten and found eggs of *M. muelleri* at all the localities from May and June to October. Off western Norway, BJØRKE (unpublished data) found eggs from March to November, with peaks in late May, and at 59°N and 19°W spawning is observed from April to October, with peaks in June and July (WILLIAMS and HART 1974).

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Table I. Samples of *M. muelleri* from the fjords used for growth calculations.

Sample	Year	Month	Area	Gear	Age group											
					0			1			2			3		
					N	*l*	SD	N	*l*	SD	N	*l*	SD	N	*l*	SD
1	69	10	Sunnh.	IKMT				37	44.51	5.9						
2	74	4	Hard.	IKMT				44	29.54	3.4	32	42.9	7.86	24	43.5	5.1
3	74	10	Ryfylke	PT	17	34.53	1.9									
4	74	10	Sunnh.	PT	20	32.10	7.40	17	40.1	5.9						
5	74	10	Nordfj.	PT				23	40.2	3.8						
6	75	10	Ryfylke	PT				14	44.8	5.6						
7	75	11	Ryfylke	KT	76	29.00	3.51	15	49.0	3.40						
8	75	11	Hard.	KT	178	25.03	5.27	78	37.32	9.14						
9	75	11	Nordh.	KT	76	20.82	2.59									
					367			228			32			24		

Table II. Samples of *M. muelleri* from the ocean used for growth calculations.

Sample	Year	Month	Position	Gear	Age groups											
					0			1			2			3		
					N	*l*	SD	N	*l*	SD	N	*l*	SD	N	*l*	SD
1	71	01	62°00’N10°00’E	PT				6	51.17	1.83	6	52.70	2.30			
2	73	01	63°40’N05°10’E	PT				4	49.50	4.35						
3	70	02	61°04’N03°00’E	PT				32	33.81	3.50	7	35.28	4.40			
4	72	02	59°10’N02°02’E	PT				49	22.82	2.40						
5	72	02	57°47’N06°02’E	BT							40	56.08	3.50	18	58.44	4.25
6	72	02	57°21’N06°41’E	BT				6	32.16	1.94	35	53.71	3.68	5	56.60	4.97
7	73	03	52°00’N14°40’W	PT							42	51.85	1.97	7	54.42	4.23
8	74	03	57°26’N09°46’W	PT							14	43.79	3.40	14	45.71	3.41
9	75	03	60°29’N03°19’E	PT							18	54.33	4.01			
10	72	05	47°38’N36°55’W	PT				38	48.86	3.20	10	50.40	3.74			
11	72	05	52°46’N24°15’W	PT				55	42.70	5.16	15	43.53	3.52			
12	75	05	58°00’N08°00’E	PT				8	45.38	2.97	4	51.66	2.51			
13	70	10	55°14’N10°00’W	PT	24	32.95	4.25	22	50.45	3.30						
14	71	10	58°57’N07°57’W	PT	100	34.09	2.49	38	48.74	3.38						
15	73	10	59°21’N03°35’E	PT	10	32.80	2.78									
16	73	10	58°29’N04°31’E	PT				30	53.50	3.21	5	54.80	1.30			
17	71	11	60°51’N06°13’W	BT				48	52.94	2.77	13	54.31	2.98			
18	71	11	60°11’N05°59’W	PT				13	52.69	2.66						
19	71	11	61°00’N02°38’E	BT				35	57.29	3.11						

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LIFE HISTORY AND ECOLOGY OF THE MYCTOPHID FISH *NOTOSCOPELUS ELONGATUS KROEYERI* FROM THE NORTHEAST ATLANTIC

By
JAKOB GJØSÆTER
Department of Fisheries Biology, University of Bergen, Norway

ABSTRACT

GJØSÆTER, J. 1981. Life history of the myctophid fish *Notoscopelus elongatus kroeyeri* from the northeast Atlantic. *FiskDir. Skr. Ser. HavUnders., 17*: 133–152.

Samples of *Notoscopelus elongatus kroeyeri* were collected by large commercial pelagic trawls north and west of the British Isles and off the coast of Norway. Otoliths were used for age determination. Primary rings in the otoliths, assumed to be laid down daily, were counted to determine the time of formation of the first hyaline zone.

The growth of the fish followed the equation

$$l_t = 11.91 \text{ cm } (1 - e^{-0.89 (t + 0.17)})$$

Back calculation of growth revealed a pronounced Lee's phenomenon. The instantaneous mortality rate of the age groups 3 to 6 was 0.8. For fish recruited to the area at age 2, the production was about 3 grams per recruit per year.

None of the fish studied had ripening gonads which, in addition to the total lack of young fish and larvae in the area, suggests that the observed population was expatriated.

The main food of *N. e. kroeyeri* was euphausids, but during the spring copepods were also found in some stomachs. Feeding took place at all times, but most intensively at night-time.

INTRODUCTION

Notoscopelus elongatus kroeyeri (MALM 1861) is a widely distributed lantern fish in the temperate North Atlantic. In the western part of the ocean its northern limit is approximately 60°N and in the eastern part 65°N. Occasionally, it is also found further north. Its southern limit of distribution is approximately 37°N (BOLIN 1959, KARRER 1973, KASHKIN 1974, NAFPAKTITIS *et al.* 1978). *N.e. kroeyeri* is also found in the Mediterranean Sea (KREFFT and BEKKER 1973, NAFPAKTITIS 1975).

The taxonomy of the genus *Notoscopelus* was in a state of confusion until the work by BOLIN (1959) created a clearer scheme. This was further developed by NAFPAKTITIS (1975) who gave *N. kroeyeri* subspecific status. According to this, the population treated in the present paper should be named *N. elongatus kroeyeri*.

Few data have been published about ecology and life history of *N. e. kroeyeri*. As lantern fishes are supposed to play important parts in the marine ecosystem, and also seem to be a potential resource for the future fisheries, data on their abundance, production and life history are needed.

The subject for this work is aspects of the life history and some of the parameters needed to assess the population dynamics of an apparently expatriated population of *N. e. kroeyeri* found west of the British Isles and in the waters adjacent to Norway. Estimates of the abundance of this species and other mesopelagic fishes in the same area are treated in a separate paper (GJØSÆTER 1978).

The material used was collected from cruises conducted for other purposes and was therefore not optimal to the study of *N. e. kroeyeri*. However, in spite of its many limitations, the study was considered useful as a first step towards a better understanding of the biology of this species.

MATERIALS AND METHODS

The specimens and data used in this work were collected by the vessels of the Institute of Marine Research, Bergen, mainly during blue whiting surveys. Most samples were taken by a commercial 1600-meshes pelagic trawl. The sampling localities are shown in Fig. 1. On the whole, trawling was not carried out to catch mesopelagic fish, and these were taken only as a bycatch. The depth of the trawl was monitored by a net sonde.

Most samples from both day and night were taken at a depth between 200 and 500 m. Therefore it is not known whether fish taken at night-time are from the surface waters or from the maximum trawl depth. The samples of *N. e. kroeyeri* were frozen onboard and carried to the laboratory for examination. Standard length was measured on all specimens. Weight was recorded in some samples using an electronic balance. Before weighing, the fish were thawed and water on their surface removed with filter paper.

In most of the samples 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 percent of the cases) the otoliths were reread and discussed. If agreement was still not reached, the otoliths were disregarded.

Some otoliths were studied to find the primary growth increments supposed to be laid down daily. The otoliths were broken through the nucleus normal to the longest axis (the XZ-plane in Fig. 6) for studying under the scanning electron microscope (SEM). They were mounted to the specimen stubs and the broken surfaces were ground and etched with 1% HCl for approximately 5 minutes. The otoliths were then coated with gold in a vacuum evaporator

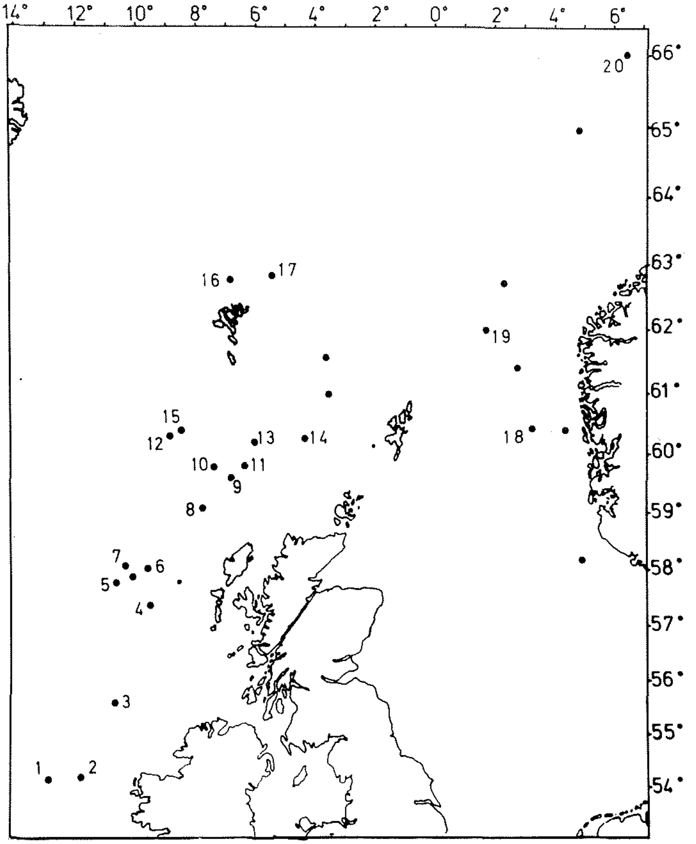

Fig. 1. Sampling localities for *Notoscopelus e. kroeyeri* 1971–1976. The numbers refer to Table I.

(Brothers, Mathews and Lasker 1976). Those used for light microscopy were ground from the medial and the lateral sides until a thin section through the nucleus (in the XY-plane in Fig. 6) was left. Before examination, they were cleared with creosote and mounted between glass slides.

In most of the specimens collected, the gonads were examined in order to determine their stage of sexual development. Some of them were sectioned and stained with haematoxylin and eosin for histological examination.

Stomach contents were examined in most samples. The degree of filling was assigned according to an arbitrary scale 0 to 4. The stage of digestion was also noted, but as the time between catch and conservation varied, it was not considered to be a useful parameter for the state at capture. The stomach contents were sorted into groups and in some cases into species. Dimensions of the stomach in a filled condition were measured in a few fish, and the volume was calculated.

Regression analysis has been used to calculate fish length from otolith diameters, to estimate the weight/length relation and the mortality from a catch curve. For these purposes Ricker (1973) recommended the use of a functional regression instead of the predictive type commonly applied. Although the mathematical implications are doubtful (see JOLICOEUR 1975, RICKER 1975), the geometric mean regression is used in the present work. The confidence limits of the regression coefficient b were calculated as

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

where $B = F\ (1 - r^2)/(N - 2)$, r is the correlation coefficient, N the number of pairs of variates and F the variance ratio at the 95% confidence level for $n_1 = 1$ and $n_2 = N - 2$ degrees of freedom (see RICKER 1975).

RESULTS

OTOLITHS AND AGE DETERMINATION

Viewed by reflected light against a dark background, a typical otolith (sagitta) of *N. e. kroeyeri* has a large, opaque central area (Fig. 2A). Infrequently there is a small hyaline zone near the nucleus (Fig. 2B). This was regarded as a larval zone and not counted (see ZURBRIGG and SCOTT 1972). Outside this central area hyaline and opaque zones alternate. In many otoliths the opaque zones contain narrow hyaline lines.

The edge of the otoliths was usually opaque during January and November, while hyaline edges dominated in samples taken in February, March, April, May and July. Samples from other months are lacking (Fig. 3). Usually the

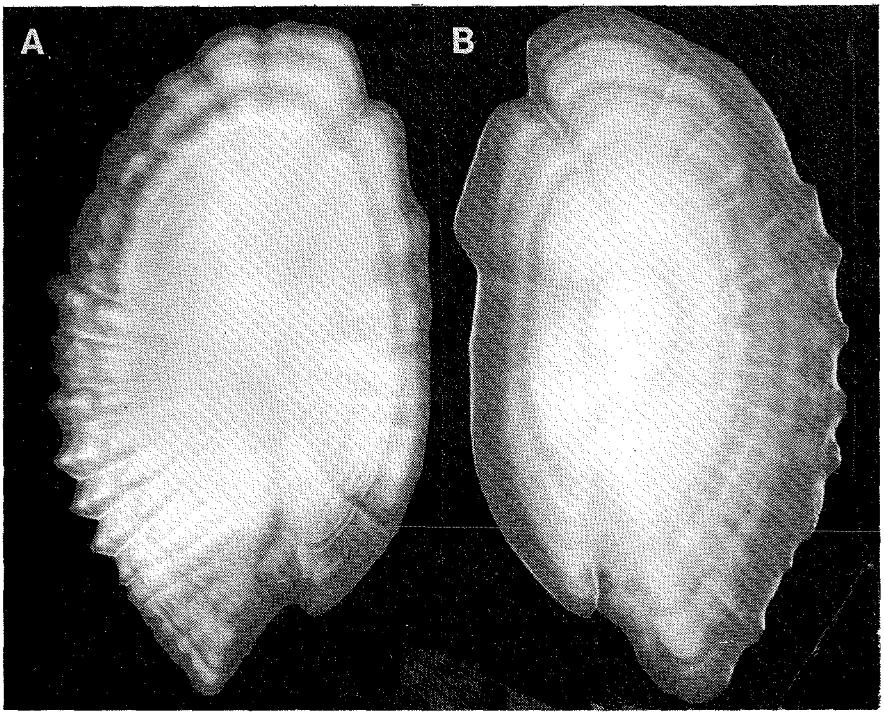

Fig. 2. Otoliths of *Notoscopelus e. kroeyeri*. A: Three years old, broad hyaline edge. B: Five years old, broad hyaline edge. The sentral zone is probably formed at the larval stage.

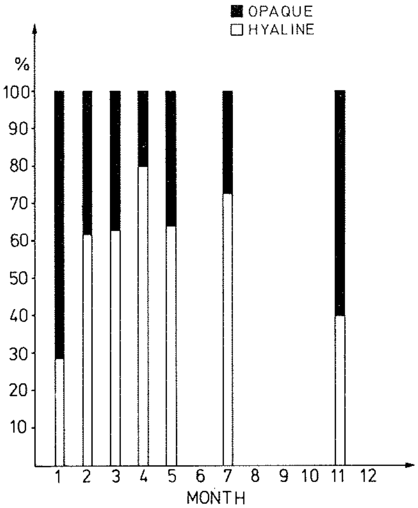

Fig. 3. Distribution of otolith edge characters during the year.

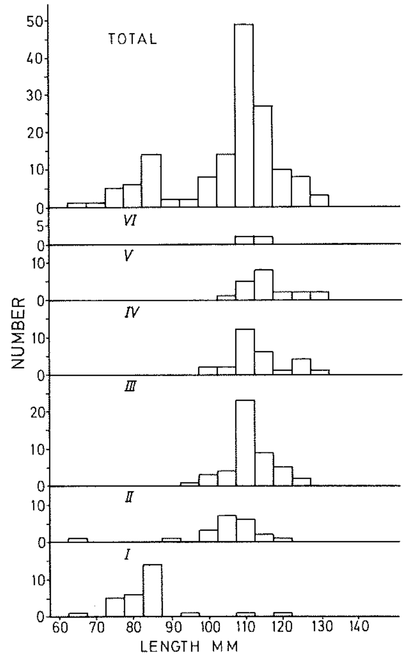

Fig. 4. Length distribution of *Notoscopelus e. kroeyeri* designed as age group I through VI based on otolith reading.

opaque edges found in the spring were broad, while opaque edges found in July were narrow. The hyaline edges found in wintertime were always narrow and may correspond to the hyaline lines often observed in the opaque zones. Exlusively hyaline or opaque zones were not found in samples from one particular month. The reason for this may be that the zones were not laid down simultaneously in the whole population, but it may also indicate formation of false zones or failure of zone formation.

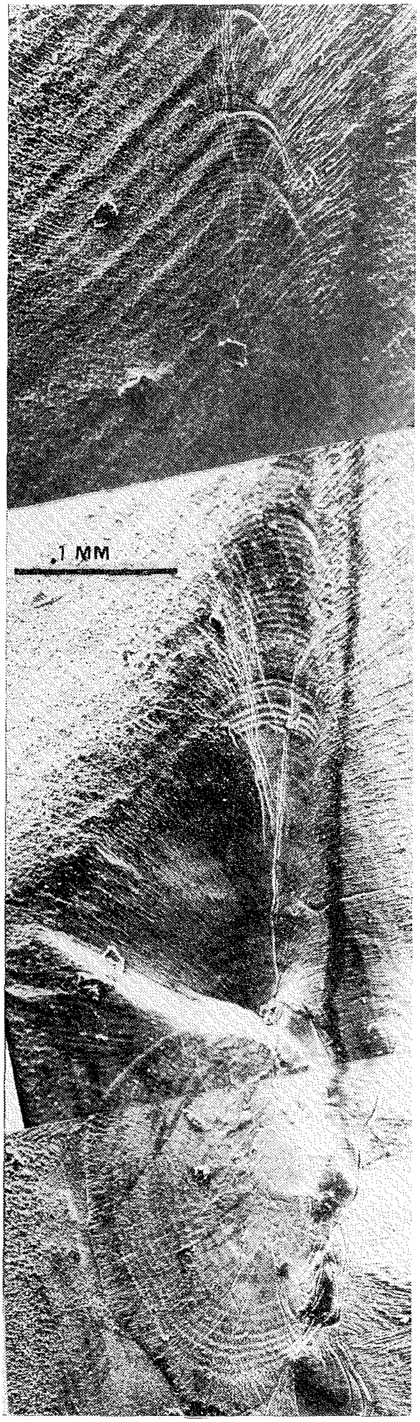

Fig. 5. Scanning electron microscope picture of sentral area of *Notodcopelus e. kroeyeri* otoloth.

Although the evidence from study of edge formation is not conclusive, zones are tentatively considered to be formed annually and used for ageing. To acquire further evidence for the validity of the ageing procedure, the Petersen method (see TESCH 1968) was tried on all aged samples from the months February and March (Fig. 4). The first age group corresponds well with the maximum in the length frequency distribution, but the older ages fall into one group. A Cassie curve (TANAKA 1962, MATHEWS 1974) was also tried. This made it possible to identify the second age group, but the older groups could still not be separated.

Three otoliths were studied by SEM. Two of these had a nucleus surrounded by 12 rings of the type described by PANNELLA (1971, 1974). Radia of the outermost of these 12 rings; measured along the X-axis (Fig. 5 and 6), were 0.12 and 0.15 mm respectively. A narrow area (0.15 mm) without visible rings followed before the rings continued (Fig. 5). In the third otolith there was no interuption in the rings. The mean number of rings per millimeter along the X-axis, indicated in Fig. 6, are given in Table 1.

Rings of three otoliths viewed by light microscope (Nos 4–6 in Table 1) were also counted. It was not possible to count rings near the nucleus in these otoliths. The number of rings per millimeter was much higher in the area adjacent to the hyaline zone than in the central and inner part of the opaque zone. It was not possible to count rings in the hyaline zones, although some irregularly spaced rings were observed.

There is no evidence from this study that the observed rings represent daily

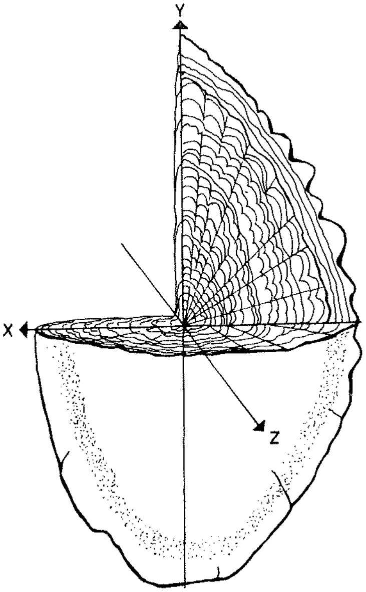

Fig. 6. Section of *Notoscopelus e. kroeyeri* otolith showing axis referred to in the text.

Table 1. Growth rings in otoliths of *N. e. kroeyeri*. Number of rings per mm indicating growth rate, and total number, indicating age in days when the first hyaline zone was formed.

Otolith no	Number of rings per millimeter along x-axis			Number of rings within first hyaline zone	Size of fish when first hyaline zone was formed (back calculated), mm.	Method
	near nucleus	central area	near hyaline zone			
1	120	230		ca 250	74	SEM
2	80	160		ca 260	79	SEM
3	98	210				SEM
4		225	415	ca 300	75	LM
5		225		ca 260	73	LM
6		160				

SEM: scanning electron microscope
LM: light microscope

growth layers. There are, however, many indications that rings like those observed are laid down daily in other fishes (PANNELLA 1971, 1974, BROTHERS, MATHEWS and LASKER 1976, TAUBERT and COBLE 1977). If the rings are formed daily, the rings observed inside the first hyaline zone indicate that the fish studied were spawned in autumn, approximately 200 to 300 days before they start forming the first hyaline zone (Table 1).

AGE AND MORTALITY

The age composition of fish caught during winter and spring is shown in Fig. 7. Usually the three-year-old fish were most abundant, while in 1972 and 1974, when the stock size in the area was very large (GJØSÆTER 1978), younger

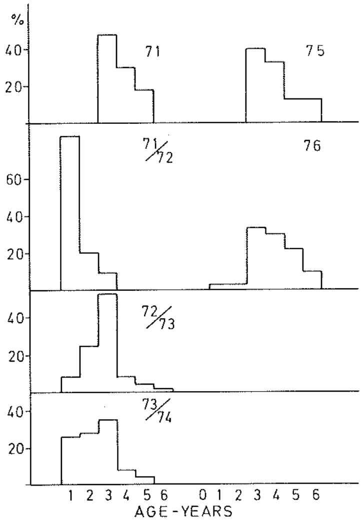

Fig. 7. Age composition of *Notoscopelus e. kroeyeri* caught during November–March. Those taken during November–December are given the age they would reach 1st January. The numbers refer to year of capture.

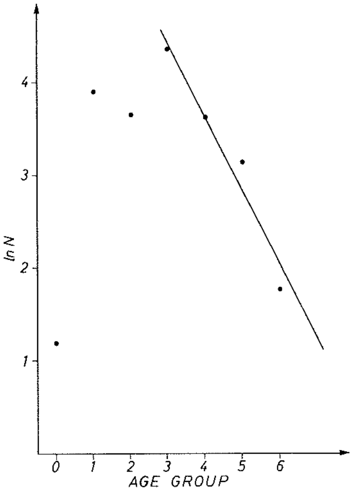

Fig. 8. Catch curve used to estimate the mortality of *Notoscopelus e. kroeyeri*. Only age groups 3 to 6 are used for estimating the regression line.

fish predominated. It appears that recruitment takes place between age one and three. As other mesopelagic species (*Benthosema glaciale, Maurolicus muelleri*) were taken at a much smaller size, the age composition evidently reflects the availability more than gear selection.

A catch curve (Fig. 8) was constructed using the data presented in Fig. 7. The mortality $Z = 0.8$ was found using a geometric mean (standard major axis) regression (see RICKER 1973) for the age groups 3 to 6 which seemed to be fully recruited. By taking the mean of the years concerned, the differences in recruitment and in effort between the years are levelled out and an average mortality is found. Constructing catch curves for the years separately gave mortalities ranging from 0.4 (1975 and 1976) to 1.1 (1974) with a mean $Z = 0.7$. These values are, however, sensitive to differences in the year class strength. The mortality, as here computed, represents both mortality *sensu stricto,* the difference between immigration (recruitment) and emigration, and it may also include gear selectivity. It is not possible to assess the relative importance of these components.

LENGTH - WEIGHT RELATIONSHIP

Weight was recorded for 60 fishes caught in the months January to April. The length-weights of the samples were plotted separately, but no difference between years or sampling areas was evident. All the samples were therefore combined without further tests.

Following RICKER (1973), the regression line $l_g = W = a + b \lg l$ was fitted to the data using a geometric mean regression (standard major axis). The results were:

$$b = 2.95$$

with 95% confidence limits 2.77 and 3.14

$$a = -1.926$$
$$r^2 = 0.94$$

Therefore

$$W = 0.01186 \, l^{2.95}$$

where W is weight in gram and l standard length in cm.

GROWTH

For each month mean length of the age groups was calculated (Fig. 9, Table I) and a Bertalanffy growth curve

$$l_t = L_\infty \left(1 - e^{-K \, (t - t_0)}\right)$$

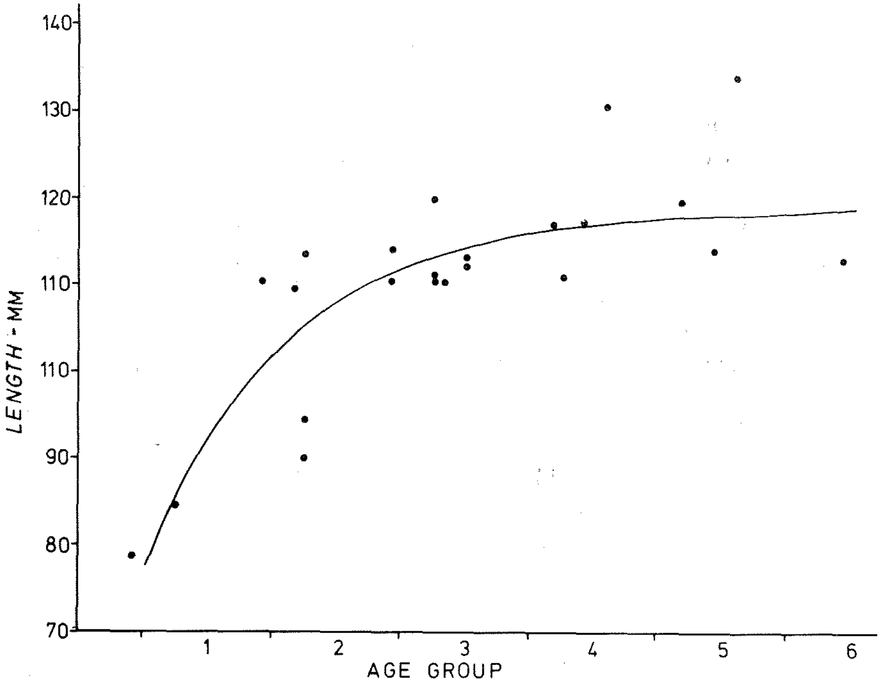

Fig. 9. Growth of *Notoscopelus e. kroeyeri*. The von Bertalanffy growth curve l_t = 11.9 (l-exp [–0,89 (t+ 0.17)]) is indicated. Each point represents a sample mean.

was fitted to the data using a method described by Allen (1966). This method gives the best least-square estimates of the parameters L_∞, K and t_0 and estimates of the variances of these parameters.

Based on 200 specimens, the following equation was obtained:

$$l_t = 11.91 \text{ cm } (1 - e^{-0.89\ (t\ +\ 0.17)})$$

$$\hat{V}\ (L_\infty) = 3.92$$
$$\hat{V}\ (K) = 0.03$$
$$\hat{V}\ (t_o) = 0.05$$

using the length/weight relation $W_\infty = 17.70$ g.

Fish taken in Norwegian waters were generelly older than those taken north or west of the British Isles, but the material at hand was not suited to demonstrate any differences in growth rate between the areas.

In order to carry out back calculation of growth, the diameters of the otoliths and of the hyaline zones were measured along their longest axis in Fig. 6) in 176 fishes. A trial plot of fish length against otolith length suggested that the variance increased with increasing fish length. All data were transformed to

Table 2. Diameters of zones in the otoliths of *N. e. kroeyeri.*

Zone no.	Age of fish, years	Number measured	Mean diameter, mm	95% conf. lim. ±
1	2	49	4.019	0.163
	3	78	3.778	0.066
	4	34	3.640	0.119
	5	21	3.607	0.146
2	3	78	4.739	0.071
	4	34	4.461	0.133
	5	21	4.310	0.223
3	4	34	5.000	0.126
	5	21	4.790	0.226
4	5	21	5.187	0.213

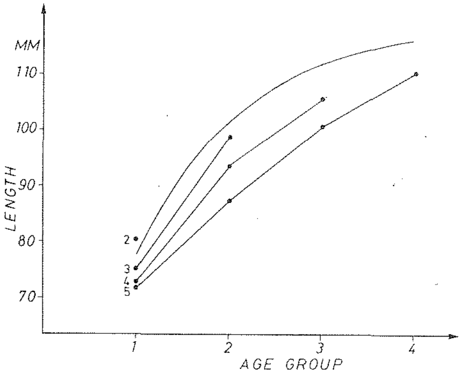

Fig. 10. Back calculated lengths of *Notoscopelus e. kroeyeri*: 2–5 indicates age of fish from which otoliths were taken. The curved line shows the von Bertalanffy's equation, $l_t = 11.9\ (1 - \exp[-0.89\ (t + 0.17)])$.

logarithmes to minimize the effect of this. Geometric mean estimate of the regression line for the data gave:

$$\lg l = 1.183 \lg d + 1.196$$

were l length of fish in cm and d diameter of otoliths in mm. The 95% confidence limits for the regression cofficient was 1.139 to 1.227 and the coefficient of determination $r^2 = 0.94$.

Means with confidence limits for diameters of the hyaline otolith zones are shown in Table 2. All fish were the zones were not clearly defined were omitted from this study. Lengths corresponding to the diameters were computed according to the equation above and are presented in Fig. 10. A Lee's phenomenon was very pronounced. Several explanation are possible (see

RICKER 1969), but the data were considered unsuitable for further analysis of this.

PRODUCTION

When the growth of a fish can be described by the von Bertalanffy's growth curve and the mortality is exponential, BEVERTON and HOLT (1957, equation 9.20) have shown that the annual production P of the recruited part of the stock is:

$$P = RW\infty \sum_{n=o}^{3} -n\ K\Omega_n\ e^{-n\ K\ (t_\rho - t_o)} \left(\frac{1-e^{-(M+nK)\ \rho}}{M+nK} + \frac{e^{-(M+nK)\ \rho}\ (1-e^{-(Z+nK)\ \lambda})}{Z+nK} \right)$$

when R is number of recruits, t_ρ is age at recruitment, W_∞, K and t_o are the constants from the Bertalanffy's growth equation, M and Z are natural and total mortality respectively, ρ is time between recruitment and start of exploitation, λ is fishable life-span and Ω_n is the summation constant ($\Omega_o = 1$, $\Omega_1 = -3$, $\Omega_2 = 3$, $\Omega_3 = -1$). When there is no exploitation, the equation is reduced to:

$$P = RKW_\infty \sum_{n=o}^{3} \frac{-n\Omega_n}{M+nk}\ e^{-nK\ (t_\rho - t_o)} \left(1-e^{-(M+nK)\ \lambda} \right)$$

In this case λ represents the whole life-span considered.

In the population studied, recruitment to the area west of the British Isles and northwards seemed to take place between age 1 and 3, and λ can be set like 5. Using parameters $W_\infty = 17.70$, $K = 0.89$, $t_o = -0.17$ and $M = 0.8$, fish recruited at age 1, 2 and 3 will produce 5.9, 5.3 and 1.5 g per recruit per year respectively.

REPRODUCTION

Gonads were studied in 185 specimens and 179 fish from 16 samples could be sexed. In 11 of the samples there were more females than males. In 4 samples there were most males, whereas in the remaining samples the sexes were equally abundant. Totally there were 75% females and 25% males. The difference in size between males and females was studied in 5 samples and in 4 of these the females were larger than the males (Table 3). Mann-Whitney tests (e.g. ZAR 1974) showed, however, that the difference was only significant ($p < 0.05$) in sample No. 6.

The samples were taken from January, February, March, April, May and December, but no gonads showed any sign of ripening. Histological sections of ovaries showed that they contained oogonia and resting oocytes containing no yolk (Fig. 11). The size of the largest oocytes was about 80–100 µm, and their nuclei measured about 40–50 µm. There was no sign of previous spawning (residual eggs, thick ovary wall etc.) in any of the gonads studied. This

Table 3. Mean length for males and females in 5 samples of *N. e. kroeyeri,* and results of Mann-Whitney U test. The sample numbers refer to Fig. 1.

Sample No.	Males N	Males *l*	Males SD	Females N	Females *l*	Females SD	U	Significance
6	9	115.0	7.5	8	127.3	11.6	12	$p < 0.05$
7	6	84.7	8.7	5	95.6	20.5	8	ns
8	3	107.0	3.0	3	115.0	2.7	0	$p = 0.05$
12	3	118.7	4.0	5	118.2	11.0	7	ns
18	4	112.5	8.9	36	115.7	6.0	44.5	ns

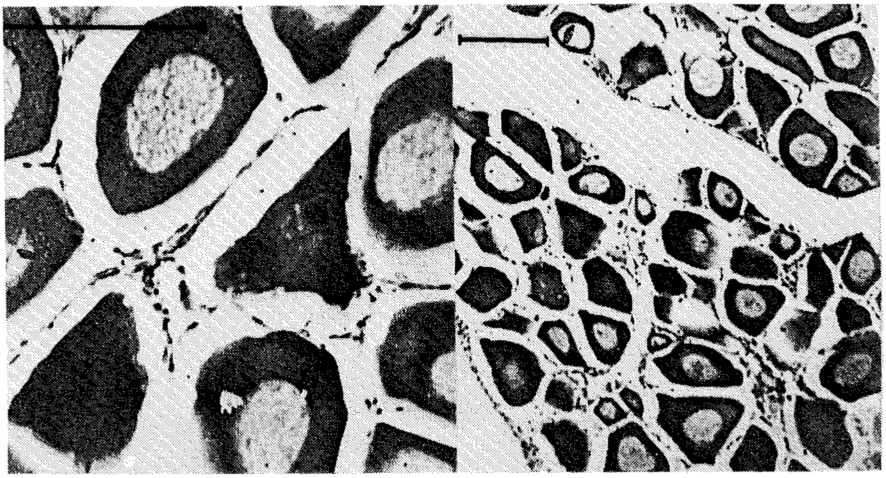

Fig. 11. Ovarian sections from *Notoscopelus e. kroeyeri* caught west of the British Isles. The scales (black lines) are 100 μm.

situation is similar to that described for expatriated myctophids by O'Day and Nafpaktitis (1967) and Zurbrigg and Scott (1972). The supracaudal lumineous organs of the males were poorly developed. The smallest specimen found in any sample was 68 mm, and no juveniles or larva were caught. It seems therefore that the population studied is not reproducing, but is maintained by fish drifting from another spawning population.

FOOD AND FEEDING

The composition of the stomach contents was studied in 128 specimens. Of these, 102 specimens had contents which could be identified to groups (Table 4). Euphausiids was the only food organism identified in fish taken during the winter season (December–February). During spring (March–May) the diversity was slightly higher, but euphausiids was still the most important food item found in 69% of the stomachs. The degree of filling was graded according to the

Table 4. Stomach contents of *Notoscopelus e. kroeyeri.*

	Winter		Spring	
	n	%	n	%
Copepoda only			1	1
Krill only	50	88	36	51
Copepoda and krill			13	18
Other			2	3
Unidentifiable	7	12	19	27
N	57		71	

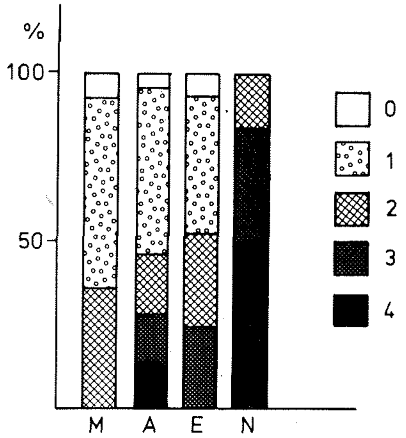

Fig. 12. Diurnal variation in degree of filling of stomachs of *Notoscopelus e. kroeyeri* caught during M, morning; A, afternoon; E, evening and N, night. The numbers indicate the degree of filling.

scale 0: empty, 1: little contents, 2: half filled, 3: full, and 4: extended stomach. The following distribution was found in 185 specimens studied:

Degree of filling	0	1	2	3	4
Percentage	5	42	22	23	8

There was no difference between fishes caught during winter and spring; material from other seasons is lacking.

The diurnal variation in degree of filling is shown in Fig. 12. In samples taken during night-time (0300–0500 hrs.) nearly 85% of the fish had full or extended stomachs, during the afternoon (1200–1600 hrs.) and in the evening (2000–2200 hrs.) about 25%, and in the morning (0900 hrs.) none of the fish examined had full or extended stomachs.

The semiaxes of the stomachs were measured in 17 of the specimens with degree of filling classified as full or extended. The volume was calculated according to the formula $\frac{4}{3}$ ab^2, where a and b are the major and minor semiaxes. The mean volume was 593 mm^3 (SD = 145) and the range

303–865 mm^3. The lengths of the fish studied were 105–142 mm. The volume of the fish was not recorded, but assuming that the volume of the fish equals weight × 1.05, stomachs represented 2–5% (mean 3.2%) of the volume of the fishes.

DISCUSSION

There is some evidence that the investigated population of *N. e. kroeyeri* is expatriated. The fish failed to show any sign of ripening or of previous spawning, and the supracaudal luminous glands of the males, which are secondary sexual characters, were weakly developed. The age distribution shown in Fig. 7 may also suggest a population drifting through the sampling area, as in a stable population it should be possible to follow strong year classes from one year to the next. The lack of juveniles in the area is probably not an effect of the gears used. FRASER (1961) lists larvae from several species of Myctophidae from extensive sampling in the northeast Atlantic by Scottish research vessels, but he did not observe any *N. e. kroeyeri*. Sampling depth can, however, not be ruled out as an explanation for the lack of juveniles.

According to KASHKIN (1974), *N. e. kroeyeri* reproduce east of the Azores, where juveniles from a length af about 10 mm were found in June. Sampling in the Golf Stream and adjacent waters west of 50°W indicated that *N. e. kroeyeri* were rare or absent (JAHN and BACKUS 1976). Sampling has also been carried out in the area influenced by the North Atlantic Drift east of 50°E (e.g. BOLIN 1959, BEKKER 1967, GEISTDOERFER, HUREAU and RANNOU 1971), but only few *N. e. kroeyeri* were caught. Larvae spawned east of the Azores will, if they follow the current in the upper 100 m, drift southwards (e.g. FRASER 1958), but extensive investigations in the Canary Islands area have not revealed any larval or adult *N. e. kroeyeri* (BADCOCK 1970, BADCOCK and MERRETT 1976). The hydrographical conditions east of the Azores, where KASHKIN (1974) found a reproductive population of *N. e. kroeyeri,* is similar to those slightly further northeast, where larvae would be expected to drift towards British waters (see e.g. FUGLISTER 1960, FRASER 1958). If the young stages live in deeper water masses, they can follow Lusitanean waters from Gibraltar and northwards (FRASER 1958, TULLOCH and TAIT 1959, HILL 1976). It is therefore an open question from which area the *N. e. kroeyeri* population here studied is recuited. Also, the time of spawning is unknown.

Age determination by means of otoliths is well established for boreal myctophids (ODATE 1966, HALLIDAY 1970, SMOKER and PEARCY 1970, GJØSÆTER 1973a). In an expatriated population of *Myctophum punctatum*, zones supposed to be laid down annually were also found, but as the formation time of the first zone was not known, they were not used for age determination (ZURBRIGG and SCOTT 1972).

Growth has been estimated in several myctophid species and parameters K and L_∞ from the Bertalanffy's growth equation are shown in Table 5. *N. e.*

Table 5. Growth parameters of the von Bertalanffy's equation for various myctophid species.

Species	K	L∞ mm	Author
Myctophum affine	0.45	83	ODATE (1966)
Stenobrachius leucopsarus	0.34	85	SMOKER & PEARCY (1970)
Benthosema glaciale	0.36	68	HALLIDAY (1970)
Benthosema glaciale	0.45	75	GJØSÆTER (1973 a)
Lampanyctodes hectoris	0.31	100	ANON. (1974)
Notoscopelus e. kroeyeri	0.89	114	this study

kroeyeri has a much higher growth rate and maximum length (L_∞) than the other species studied.

Measurements of stomach volumes indicated that a *N. e. kroeyeri* can eat about 5% of its body weight in one meal. HOLTON (1969) weighed *Lampanyctus mexicanus* and discovered that their stomach contents could weigh up to 14% of the total fish weight. The mean values from different samples range from about 4 to 7%. LEGAND and RIVATON (1969), who studied several myctophids from the tropical Indian Ocean, and SAMYSHEV and SCHETINKIN (1971) working with myctophids from northwest Africa, found mean values from about 0.3 to about 2% in various samples. BAIRD, HOPKINS and WILSON (1975), who studied *Diaphus taaningi,* used dry weights of both stomach contents and fish body and got 0.8% as a maximum value.

Krill was the most important food item of the fish studied and among the krill *Meganyctiphanes norvegica* was most commonly found. Both this species and the *Thysanoessa* species, which range next in abundance in the area, are omnivores (MAUCHLINE and FISHER 1969). *N. e. kroeyeri* are therefore partly on the third and fourth trophic level.

N. e. kroeyeri probably feed at any time of the day and at any depth, but most intensively at night-time. This feeding pattern of myctophids was suggested by MARSHALL (1960) and for several species confirmed by e.g. PAXTON (1967), HOLTON (1969), GJØSÆTER (1973b) and MERRETT and ROE (1974). Other species seem to feed during the night only (BAIRD *et al.* 1975) or equally well both day and night (SAMYSHEV and SCHETINKIN 1971).

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Table I. Length distribution of *N. kroeyeri*. The sample nos refer to Fig. 1.

Sample no.	Month	Year	Age group	N	$\bar{l}$ mm	Konf. lim.
1	11	72	0	3	78,3	74,50
2, 3	3	72	1	29	84,7	2,74
4	3	74	1	5	85,0	6,69
5	11	71	1	5	111,0	7,56
6	2	73	2	5	109,4	5,99
2	3	72	2	3	90,0	39,72
7	3	73	2	4	113,0	10,70
4, 8, 9,	3	74	2	7	94,6	12,71
5	11	71	2	4	111,5	16,95
1	11	72	2	5	114,4	14,91
10	1	73	3	12	112,6	2,86
11	1	73	3	6	109,5	4,90
12, 13	2	71	3	21	112,8	1,70
7	3	73	3	3	120,3	6,23
4, 8, 9, 14, 15	3	74	3	11	112,6	6,68
16	3	76	3	13	112,7	4,41
17	4	74	3	5	111,6	8,08
18	7	72	3	5	131,6	11,95
12, 13	2	71	4	13	117,3	5,17
16	3	76	4	12	112,3	2,54
19	5	75	4	5	117,4	12,47
18	7	72	4	3	135,7	5,71
12, 13	2	71	5	8	119,6	4,96
19	5	75	5	9	114,7	2,72
19	5	75	6	4	113,5	6,42