

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

By

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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 radii 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

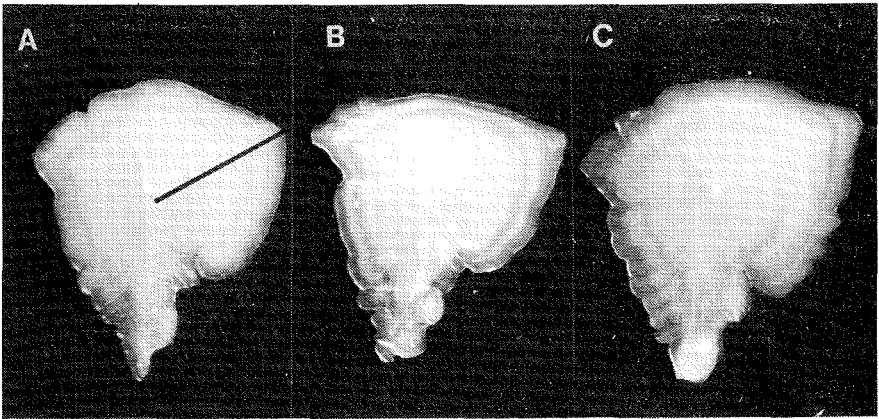


Fig. 1. Otoliths of *Maurolicus muelleri*. A: 2-year-old, B: 3-year-old, C: 4-year-old. The line in A shows the radius measured.

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

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

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

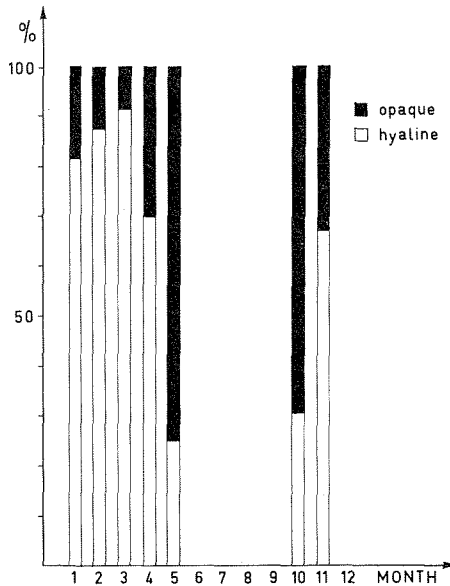


Fig. 2. Distribution of otolith edges during the year.

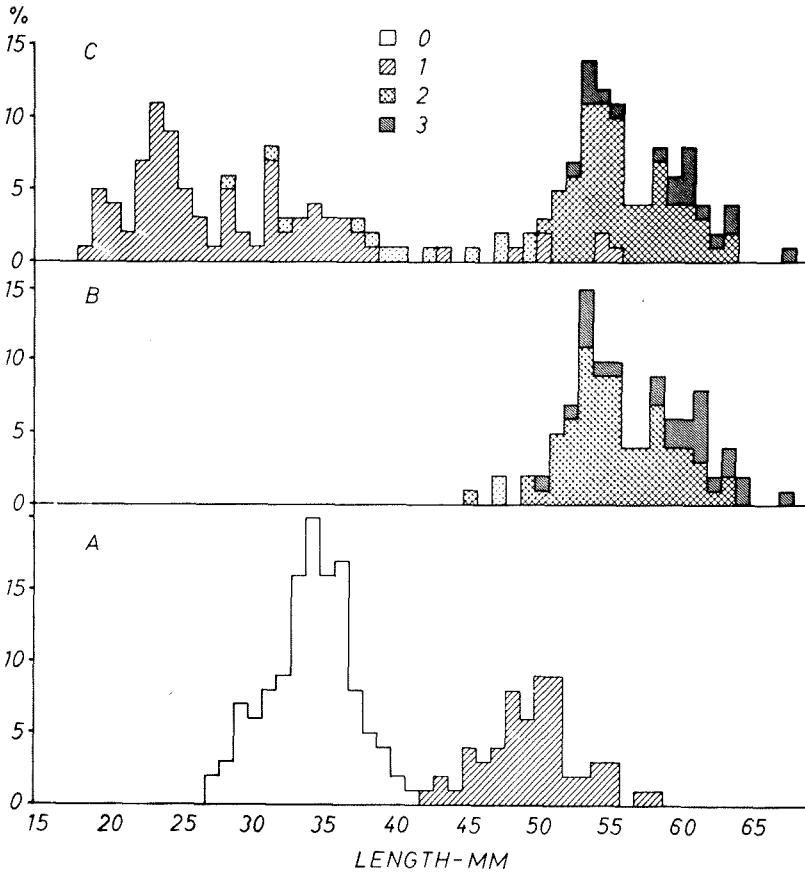


Fig. 3. Length distribution of *Maurolicus muelleri* designed as age groups 0 through III based on otolith reading. Fish caught during A: November–December, B: January and C: February.

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

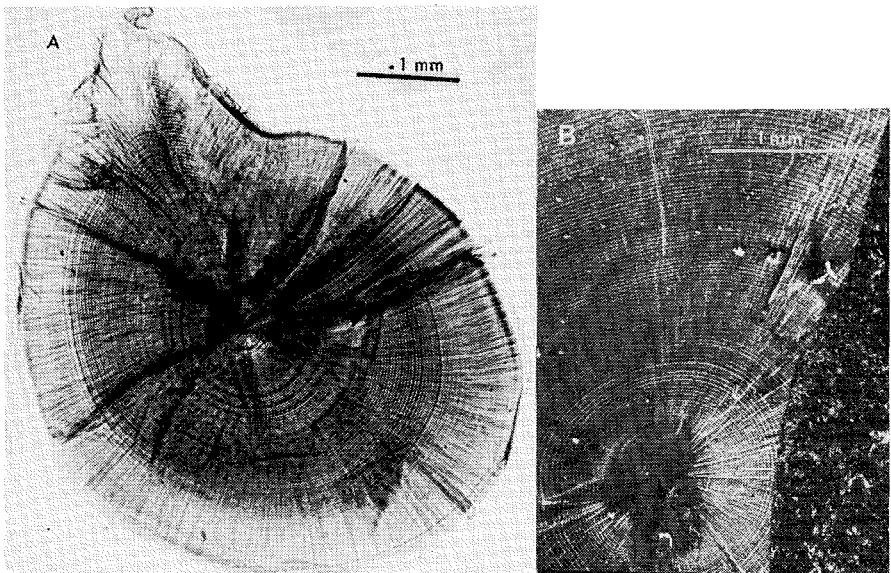


Fig. 4. Otoliths of *Maurolicus muelleri* showing primary growth rings. A: Light microscopy, 0-group fish caught in October. 200 x. B: Scanning electron microscopy, central part of otolith of adult fish. 300 x.

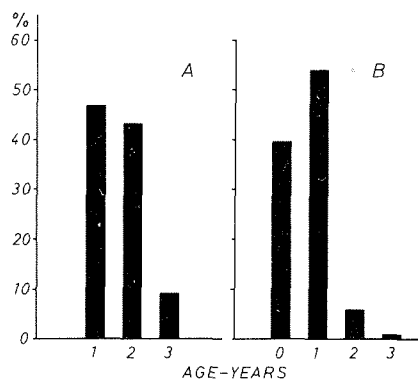


Fig. 5. Age composition of *Maurolicus muelleri* caught in the ocean. A: Fish caught during February–May (N=445). B: Fish caught during October–November (N=351).

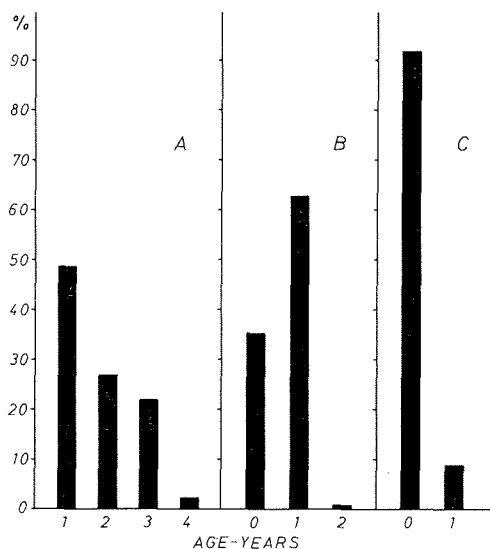


Fig. 6. Age composition of *Maurolicus muelleri* caught in the fjords. Fish caught with A: IKMT, April 1974 (N=122), B: Pelagic trawl, October 1974 (N=82) and C: Krill trawl, November 1975 (N=338).

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

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

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_0 and the estimates of their variances.

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

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

$$\hat{V}(L_\infty) = 3.35$$

$$\hat{V}(K) = 0.02$$

$$\hat{V}(t_0) = 0.005$$

For 771 fish from the oceanic areas the result was:

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

$$\hat{V}(L_\infty) = 3.16$$

$$\hat{V}(K) = 0.01$$

$$\hat{V}(t_0) = 0.008$$

Table 2. Length - weight relationship in *M. muelleri*. Parameters 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

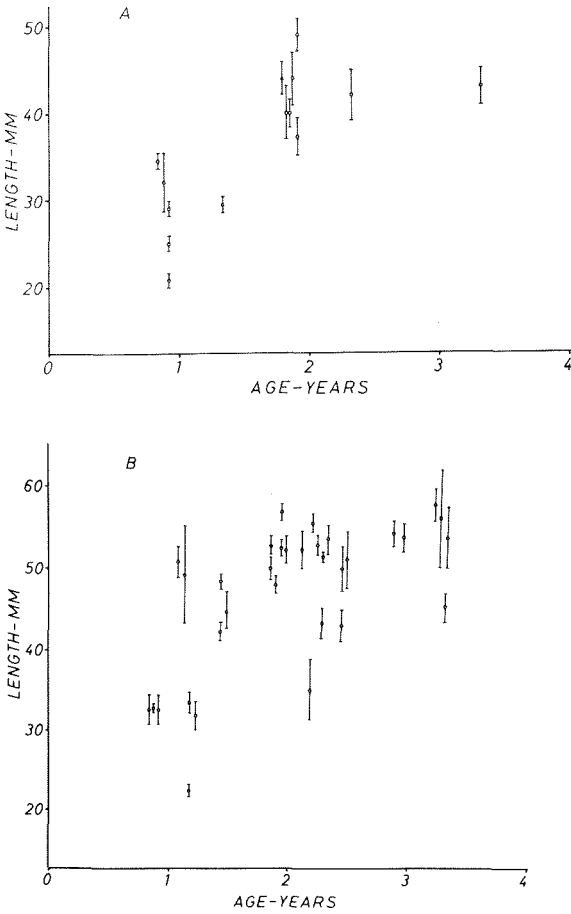


Fig. 7. Mean length (circles) with 95% confidence limits (vertical bars) of *Maurolicus muelleri*. All samples taken within one month and one geographical area are combined. A: Samples from the fjords and B: Samples from the ocean.

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 $W_{\infty} = 2.24 \text{ g}$.

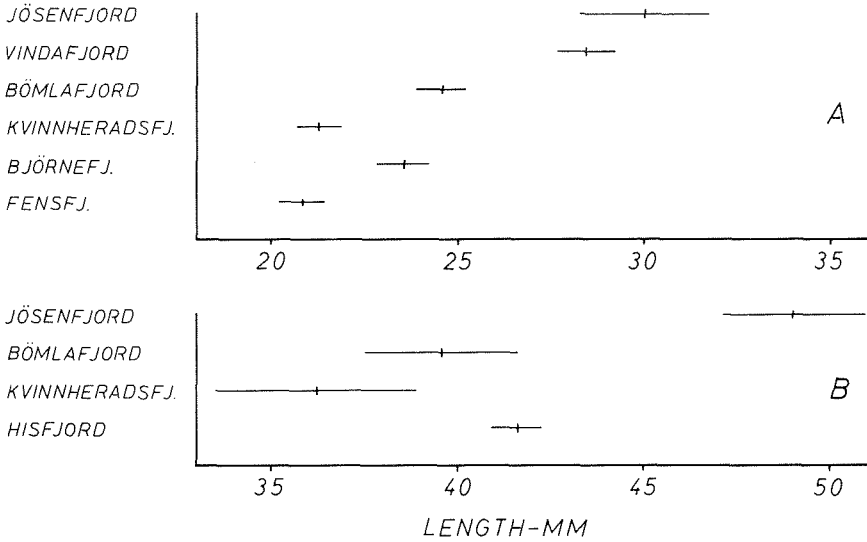


Fig. 8. Mean length (vertical bars) with 95% confidence limits (horizontal bars) in *Maurolicus muelleri* samples taken by krill trawl during November 1975. A: 0-group, B: 1-group.

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, radii of the hyaline zones and of the whole otoliths were measured as indicated in Fig. 1. A trial plotting of fish length against otolith radii 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

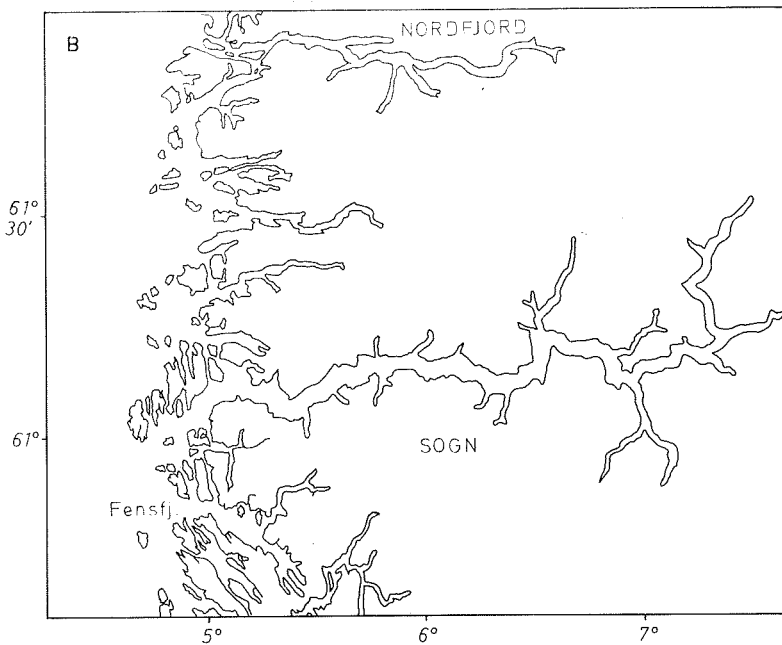
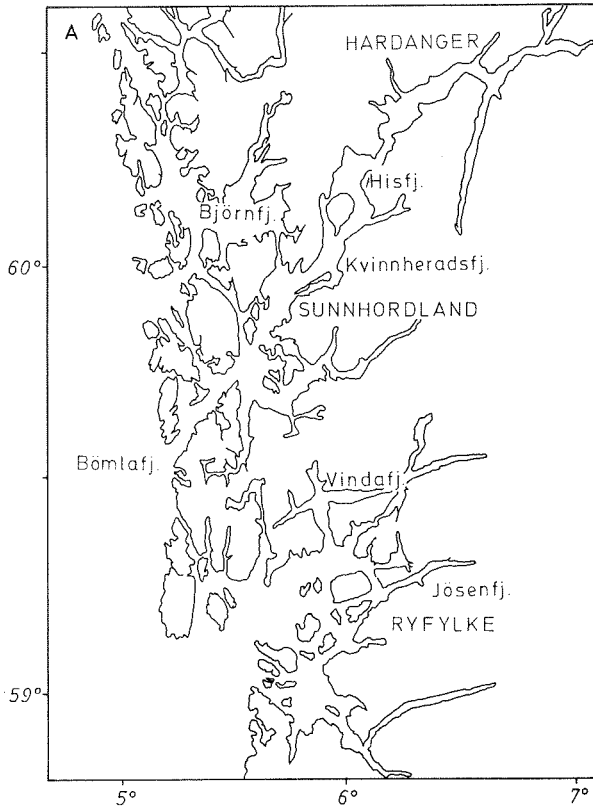


Fig. 9 A and B. Maps showing geographical names used.

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	Kvinnheradsfjord	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 radii 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

$$P = N_0 \cdot 3 \cdot KW_\infty \left[\frac{1}{M + K} + \frac{2}{M + 2K} + \frac{1}{M + 3K} \right]$$

where N_0 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_0 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

$$P = 0.23 N_0$$

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	Jøsenfjord	Bømlafjord
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 \pm	
OCEAN	1	361	0.604	0.014	
		227	0.600	0.017	
		75	0.536	0.028	
		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	100	0.580	0.028
			30	0.630	0.046
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,

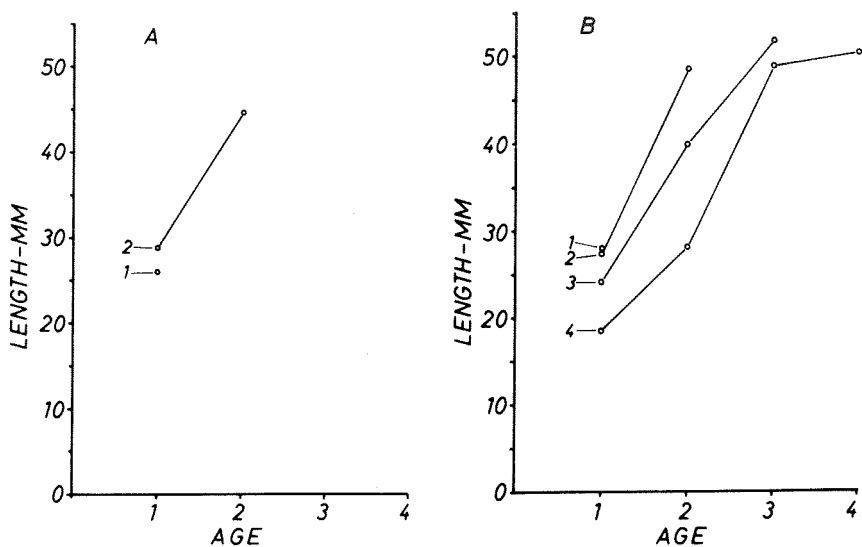


Fig. 10. Back-calculated lengths of *Maurolicus muelleri*. 1-4 indicate age of fish from which otoliths were taken. A: Fjord samples, B: Oceanic samples.

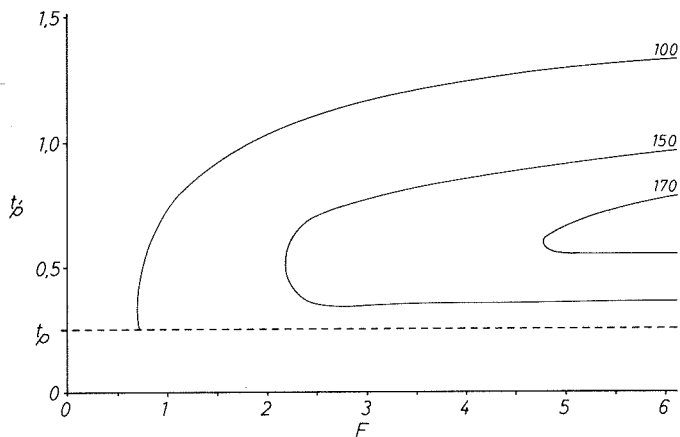


Fig. 11. Yield per recruit isopleth diagram for *Maurolicus muelleri*. The yield is given in mg. F is fishing mortality, t_0' age at first capture, t_p age of recruitment.

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 ($d > 500 \mu\text{m}$) 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

FOOD AND FEEDING

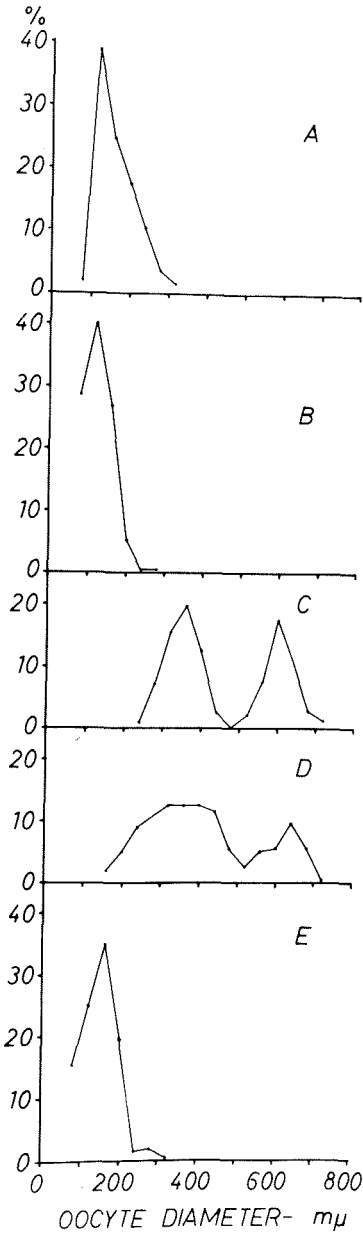


Fig. 12. Size distribution of oocytes from *Maurolicus muelleri*. A-B: immature fish caught during spring, C-D: mature fish caught during summer and E: female caught during autumn.

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 MAUCLINE (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	<i>l</i>	SD	N	<i>l</i>	SD	N	<i>l</i>	SD	N	<i>l</i>	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	<i>l</i>	SD	N	<i>l</i>	SD	N	<i>l</i>	SD	N	<i>l</i>	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						

