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Life-history parameters and vertical distribution of *Maurolicus muelleri* in Masfjorden in summer

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Abstract Population characteristics, individual life-history variables, feeding and vertical distribution of the mesopelagic fish Müller's pearlside *Maurolicus muelleri* collected in 1990 in Masfjorden, western Norway, are reported as well as environmental variables from the fjord. Minimum size at maturity was far smaller than reported from previous investigations in the same region. Fecundity was size-dependent and total egg numbers were higher than reported from other investigations of *M. muelleri* world wide, while the number of maturing eggs was far lower than observed in the same region earlier. Food concentration in the fjord was an order of magnitude lower than previous early summer observations, and several factors indicated that feeding opportunities may have been low for a long period. Daily feeding rate (g prey g⁻¹ fish) decreased with increasing fish size. These observations fit well with a model of maximizing fitness by means of a flexible size at maturity. Minimum age at maturity seems to be achieved at the expense of fecundity. *M. muelleri* was concentrated in a 20 to 30 m deep sound scattering layer (SSL). The SSL stayed close to the surface during the night and at 100 to 180 m during the daytime. The vertical position of the SSL varied instantaneously with changes in surface light intensity, remaining at 10⁻³ to 10⁻⁴ μmol m⁻¹ s⁻¹ at the top of the SSL. Stomach fullness was highest during the night; feeding intensity seems to have been peaked at dusk. Cladocerans were the main prey ranked by number, copepods by biomass. Intake of large copepods increased with fish size.

Introduction

Mesopelagic fishes are important planktivores in Norwegian fjords and coastal areas (Gjøsæter 1973, 1981a, b, 1986; Kaartvedt et al. 1988; Bergstad 1990, 1991b; Giske et al. 1990) as well as in continental slope areas worldwide (Gjøsæter and Kawaguchi 1980; Clarke 1982; Gjøsæter 1984; Dalpadado and Gjøsæter 1987; Kawaguchi and Mauchline 1987) and they are important prey for several continental slope fishes (Clarke 1982; Bulman and Blaber 1986; Bergstad 1991a,b). In Masfjorden, western Norway, the mesopelagic fishes are both the most important planktivores and the most important food for larger fishes.

In the Norwegian and North Atlantic waters the two most numerous mesopelagic fish species are Müller's pearlside *Maurolicus muelleri* (Gmelin) and the northern lanternfish *Benthoosema glaciale* (Reinhardt) (Gjøsæter and Kawaguchi 1980; Skjoldal et al. 1993). The mesopelagic fishes form dense populations and Gjøsæter and Kawaguchi (1980) estimated their biomass in these waters to be 2.2 million tons. Although this estimate corresponds to the current stocks of Norwegian spring spawning herring *Clupea harengus* L. or western mackerel *Scomber scombrus* L. in the same area (Skjoldal et al. 1993), this is still probably an underestimate, being largely based on the slow and small Isaac Kidd Midwater Trawl (IKMT). The mesopelagic fishes feed mainly on copepods and euphausiids (Gjøsæter 1973, 1981b; Mauchline and Gordon 1983; Giske et al. 1990) and are thus potential competitors with other planktivores like mackerel, herring and blue whiting *Micromesistius poutassou* (Risso) (Skjoldal et al. 1993). On the other hand, they are also prey for saithe *Pollachius virens* L., salmon *Salmo salar* L. and blue whiting (Skjoldal et al. 1993).

Maurolicus muelleri is a short lived fish and only a small proportion of the population reaches the age of 3 yr (Gjøsæter 1981b), and in other areas as the Rockall Trough longevity may be close to 1 yr (Kawaguchi and Mauchline 1987). Gjøsæter (1981b) found *M. muelleri* in Norwegian waters to mature after 1 yr at a minimum female length of

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39 mm. Investigations performed other places give nearly the same lengths at maturity (Okiyama 1971; Yuuki 1982; Kawaguchi and Mauchline 1987; Young et al. 1987), but smaller sizes have also been reported (Dalpadado and Gjøsæter 1987; Prosch 1991). According to Giske et al. (1990) *M. muelleri* in Masfjorden (Western Norway) exerts a predation pressure on the zooplankton biomass in the upper 150 m. The main predators on *M. muelleri* in the fjord are blue whiting and saithe (Giske et al. 1990). *M. muelleri* is an important contributor to sound scattering layers (SSL) in Masfjorden (Giske et al. 1990; Balifio and Aksnes 1993), off southern Norway and west of the British Isles (Gjøsæter 1986), in the Norwegian trench (Bergstad 1990) and off continental shelf areas (Samyshev and Schetinkin 1971; Young and Blaber 1986; Dalpadado and Gjøsæter 1987; Armstrong and Prosch 1991).

Giske et al. (1990) found that *Maurolicus muelleri* during the winter period in Masfjorden was distributed in two SSL, the upper SSL contained juveniles and the lower layer adults. Both layers consisted almost entirely of *M. muelleri*. Giske and Aksnes (1992) found from stomach samples that adults in winter had a low ingestion rate and calculated that they had negative growth. The juveniles located in more shallow waters had at the same time feeding rates which resulted high somatic growth rates. This fits with observations by Gjøsæter (1981b) in western Norwegian fjords and by Kawaguchi and Mauchline (1987) in the Rockall area that winter is the major growth season for juveniles.

Giske and Aksnes (1992) explained the difference in spatial distribution and feeding rates with different ontogenetic stages: (1) The juveniles have to eat and have a positive somatic growth rate in order to reach a minimum adult mass the coming spring; their fitness premium in return for a high feeding rate and somatic growth is to become adults in 1 yr. (2) Adults are already mature and must try to reduce the mortality risk and increase fecundity. However, both Giske and Aksnes (1992) and Rosland and Giske (1994) concluded that due to deep distribution in winter adults did not feed enough to contribute to their fecundity, but rather maximized their overwintering survival probability (cf. McNamara 1990). Thus, adult vertical behaviour in winter does not fit completely with a life history (ontogenetic) model, and descriptions of the optimal habitat must also consider the season and the physiological state of the fish (Giske and Aksnes 1992; Rosland and Giske 1994).

Mesopelagic fishes have generally slower growth than both epipelagic and bathypelagic fishes (Childress et al. 1980; Mauchline 1991), but due to their short generation time they have higher birth rates than epipelagic fishes. The potential competition between epipelagic and mesopelagic fishes due to interannual variations in secondary production may be an important structural factor in large marine ecosystems (cf. Skjoldal et al. 1993). An increased knowledge of how *Maurolicus muelleri* is influenced by the environment and how such fishes respond to environmental changes may increase our understanding of their influence on their prey and predators as well as on competitors.

Early in summer the *Maurolicus muelleri* population in Masfjorden is expected to consist of adult (1 and 2+) individuals. Here we will study the vertical distribution, feeding patterns, fecundity and the length distribution of *M. muelleri* in early summer and relate the distribution and life history variables to the season and the environmental variables.

Materials and methods

Samples were collected during a cruise with R.V. "Håkon Mosby" 26 May to 2 June 1990. The study area was Masfjorden (West Norway, 60°50'N, 5°30'E) a 20 km long and 0.5 to 1.5 km wide fjord, with a sill depth of 75 m and a maximum depth of 494 m (Fig. 1). All samples were taken in the deep central part marked with a line in Fig. 1. Ecological features of the fjord are given by Kaartvedt et al. (1988), Aksnes et al. (1989), Giske et al. (1991) and Fosså et al. (1994).

Vertical distribution patterns of the SSL were continuously monitored using 120 Khz Simrad EK400 echo sounder. From the echopapers obtained the depth of the upper and lower part of the single SSL was measured every 15 min. This SSL was identified by Giske et al. (1990) to consist of *Maurolicus muelleri*, and samples of the SSL by a pelagic midwater trawl confirmed this. The words SSL and *M. muelleri* may, therefore, be used interchangeably in the text.

A Harstad trawl was used to catch *Maurolicus muelleri*. The opening of this pelagic trawl is 20×20 m² during trawling at 1.5 m s⁻¹ at 0 to 50 m depth, and the opening area decreases slightly with increasing depth. The maximum and minimum stretched mesh size of the trawl is 100 and 30 mm, respectively, while the stretched mesh size of the cod end is 8 mm. The cod end is 15 m long, and its opening during trawling varies between 1.5×1.5 m² and 3.1×3.1 m² (Nedreaas and Smedstad 1987). There is no opening or closing device on the Harstad trawl. Twelve pelagic midwater trawls were taken in or near the SSL during a 27-h period on 29 to 30 May (Table 1). Trawl 10, which was above the SSL, did not contain any *M. muelleri*, and is therefore omitted from further analyses. This sample above the SSL confirmed that the other samples were not contaminated during shooting and hauling. Subsamples were taken from each trawl and preserved in a 4% neutralised formaldehyde solution. All large fishes in the trawls were immediately counted, weighed and their stomach contents examined, but food items probably eaten in the trawl (i.e., fresh and totally undigested food items) were excluded.

In the lab, 200 *Maurolicus muelleri* were taken randomly from Trawls 1, 3, 5 and 9 for weight and length measurements. These trawls covered both day and night in time and were taken at differ-

Table 1 Trawl number, time of each trawl and sampling depth for the pelagic midwater trawls in Masfjorden 29 and 30 May 1990

Trawl no.	Time trawled (hrs)	Depth interval (m)
1	19:00 – 1930	128 – 111
2	21:18 – 2133	80 – 110
3	00:03 – 0018	0 – 24
4	04:08 – 0423	0 – 24
5	06:32 – 0647	70 – 100
6	09:16 – 0931	119 – 104
7	12:07 – 1222	138 – 127
8	13:54 – 1409	270 – 240
9	15:24 – 1539	150 – 138
10	16:45 – 1700	70 – 80 ^a
11	18:45 – 1900	152 – 139
12	21:09 – 2124	78 – 70

^a Trawl 10, which was above the sound scattering layer, did not contain any *Maurolicus muelleri*

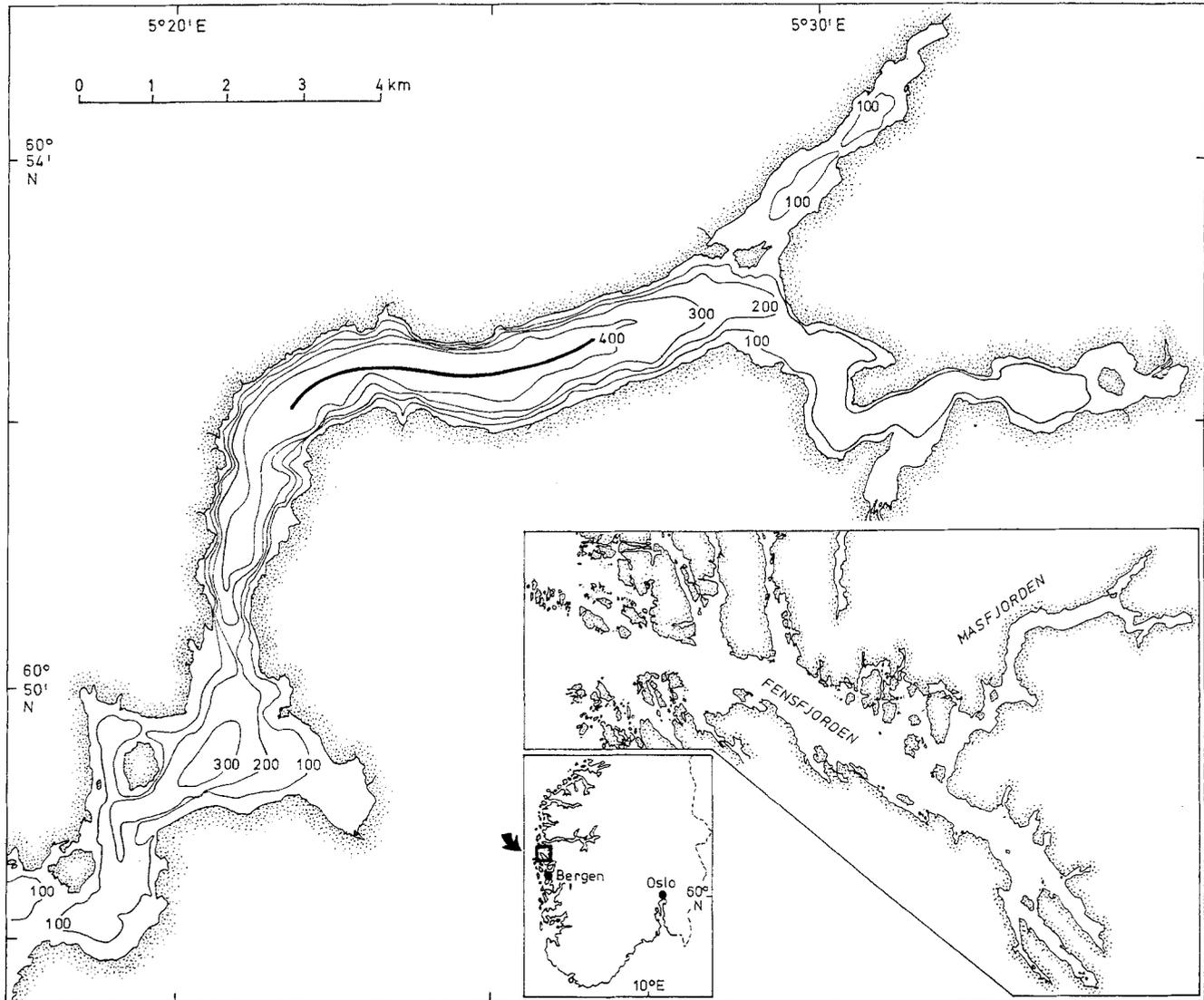


Fig. 1 Masfjorden (western Norway, 60°50'N, 5°30'E). Central deep basin where measurements were made is indicated with a line

ent depths (Table 1). Fish length (from snout tip to the distal end of the caudal peduncle) was recorded to the nearest mm and weight to the nearest mg wet weight. Before weighing excess moisture was absorbed by absorbent tissue. From each of the 11 trawls, 50 *M. muelleri* were randomly taken out for stomach analyses ($N=550$), and length, weight and sex were determined. Fishes without eggs or milt were defined as immature. The degree of fullness of the stomachs was judged in accordance with a 1 to 5 scale (empty=0, some contents=0.25, half full=0.5, more than half full=0.75, and full=1). The numerical values in parentheses above were used to estimate the average stomach filling of the population at each trawl. Individual food items were identified to the lowest possible taxon. The degree of digestion was divided into five main categories (fresh=1, digestion started=0.75, partly digested=0.5, unidentifiable=0.25 and empty/completely digested=0). The numerical values in parenthesis were used to estimate the average degree of decomposition of the stomach contents of the population at each trawl. A length-weight relationship was established by linear regression on \log_{10} transformed data. A correction on the regression line was made according to Rickert (1973, 1975) and Krebs (1989).

Annual mortality rate was calculated from the length frequency distribution of the combination of the length-weight sample of 4×200

ind and the stomach data of 11×50 ind, yielding a total $N=1350$ (Fig. 2). Annual instantaneous mortality rate from 1 to 2-yr-old fish was estimated by

$$Z = \ln(N_2/N_1), \quad (1)$$

(Gulland 1969; Gjøsæter 1973) where N_1 and N_2 are the number of individuals aged 1 and 2 yr, respectively. This measure should be used with caution, as it assumes that year class strength measured as 1-group was equal for the two year classes. From Fig. 2 it was assumed that all individuals shorter than 39 mm were 1-group and all larger than this were 2-group. From the length-frequency distribution of these 1350 fishes, it seems that some 3- and perhaps also some 4+ individuals are present. These are so few, however, that the error of lumping them into 2-group fish may be ignored, and it is impossible to give separate reliable estimates of mortality of 2 to 3 and 3 to 4-yr-old-fish.

From Trawl 5 (06:40 hrs) eight *Maurolicus muelleri* were taken out for a pre-examination of fecundity, later 75 *M. muelleri* were selected in order to obtain a length distribution similar to the pooled sample of Trawls 1, 3, 5 and 9 (Fig. 2). This was done to give comparable samples and to allow all fish lengths to be represented. Egg numbers were counted after cutting the yolk sac into small parts. Egg diameter was measured to the nearest 100 μm from random subsamples of 100 eggs in each female. Egg volume (cm^3) was calculated assuming spherical eggs. Individual egg mass (g) was then calculated from egg volume distribution, egg number and specific density of 1 g cm^{-3} . A relationship between length and fecundity and length

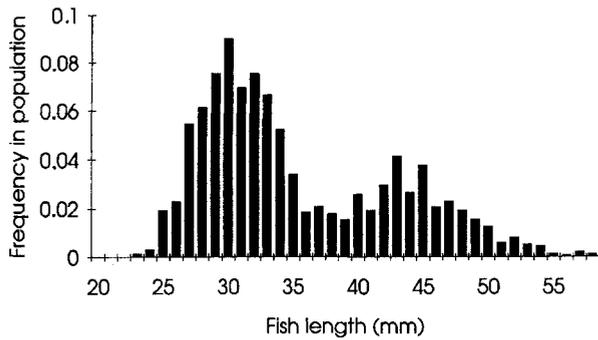


Fig. 2 *Maurolicus muelleri*. Length frequency distribution in Masfjorden 29–30 May 1990 ($N=1350$)

and ovary mass was established by linear regression on \log_{10} transformed data. A correction on the regression line was made according to Ricker (1973, 1975) and Krebs (1989). In the fish length group 28 to 40 mm a relationship between length and % ovary mass of body weight was established by linear regression on untransformed data.

Zooplankton sampling was performed by MOCNESS (Wiebe et al. 1985), a sampling gear with eight nets, 330 μm mesh size, 1.4 m^2 opening and all nets sampling at different depth strata. Two MOCNESS series were taken along the same line as the Harstad trawls (Fig. 1), one during the daytime (16:00 hrs on 29 May) and one at night (02:00 hrs on 30 May). Due to the very high replicability obtained by Giske et al. (1990) at the same position in January, replicate samples were not taken. Each sample was subdivided by a sieve into two size classes: A > 2 mm and B < 2 mm. The latter was split into two subsamples (B_1 and B_2) utilising a Folsom splitter, and B_1 was used for determining ash free dry weight (mg AFDW m^{-3}). B_2 was stored in 4% neutralised formaldehyde solution for later examination of species composition. The biomass (carbon contents) in the fjord were estimated by multiplying the AFDW m^{-3} estimates with the volumes of the different depth layers (Table 2). Each of the preserved subsamples (B_2 's) were split using a modified Wiborg splitter (Aksnes 1981) in the laboratory. Copepods and other known food items for *Maurolicus muelleri* were counted and grouped to the lowest possible taxon; 300 individuals were counted from each sample. The dry weight of all copepod length groups and cladocerans were estimated according to Blom et al. (1991). Zooplankton species not known as food for *M. muelleri* (e.g. Cnidaria, Ctenophora, Bryozoa and other) were omitted.

Surface light and vertical diffuse attenuation was measured in order to calculate the ambient light in the SSL. Surface light was continuously registered by a 2π LI 185 photometer during the cruise. Underwater light (UW) was measured on two occasions using a 4 π QSP 160 scalar irradiance quantum sensor. At each depth, UW light was corrected for instantaneous changes in surface light. Measurements are assumed to be reliable down to the depth where the value

Table 2 Estimated volume (million m^3), mg AFDW (ash-free dry weight) m^{-3} and carbon contents (biomass) of the different depth layers and total in Masfjorden. Mg AFDW m^{-3} estimates are from the MOCNESS night sample (day sample not available). Carbon con-

	Depth								Sum
	0–30	30–60	60–90	90–120	120–150	150–180	180–210	210–494	
Volume ($\times 10^6 \text{ m}^3$)	800	710	610	535	500	380	346	1482	5363
mg AFDW m^{-3}	3.347	0.825	0.864	0.754	0.467	0.697	0.305	0.703	1.089
Tons AFDW	2.678	0.586	0.527	0.403	0.234	0.265	0.106	1.042	5.840
Tons carbon	1.440	0.315	0.283	0.217	0.126	0.142	0.057	0.560	3.140

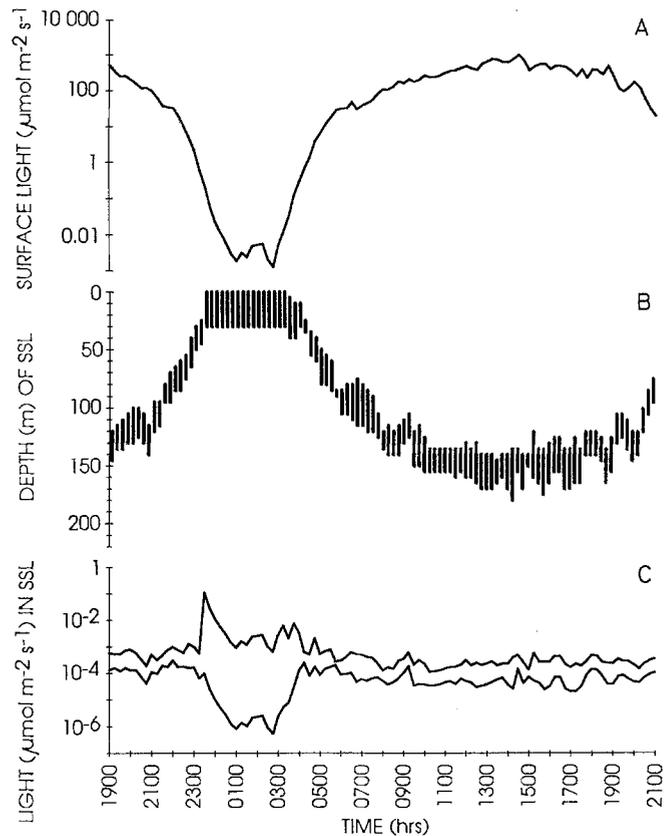


Fig. 3 a Surface light in Masfjorden 29–30 May 1990. Log scale on y-axis. b Vertical distribution of the sound scattering layer (SSL) consisting of *Maurolicus muelleri*. c Calculated light intensity in the SSL. Top and bottom of layer indicated. Log scale on y-axis

of the diffuse attenuation coefficient (K) for the measurement below was found to be $< 0.04 \text{ m}^{-1}$, which was at 40 m. Ambient light below 40 m was calculated from K in the layer 30 to 40 m, assuming water mass characteristics below 40 m as in 30 to 40 m.

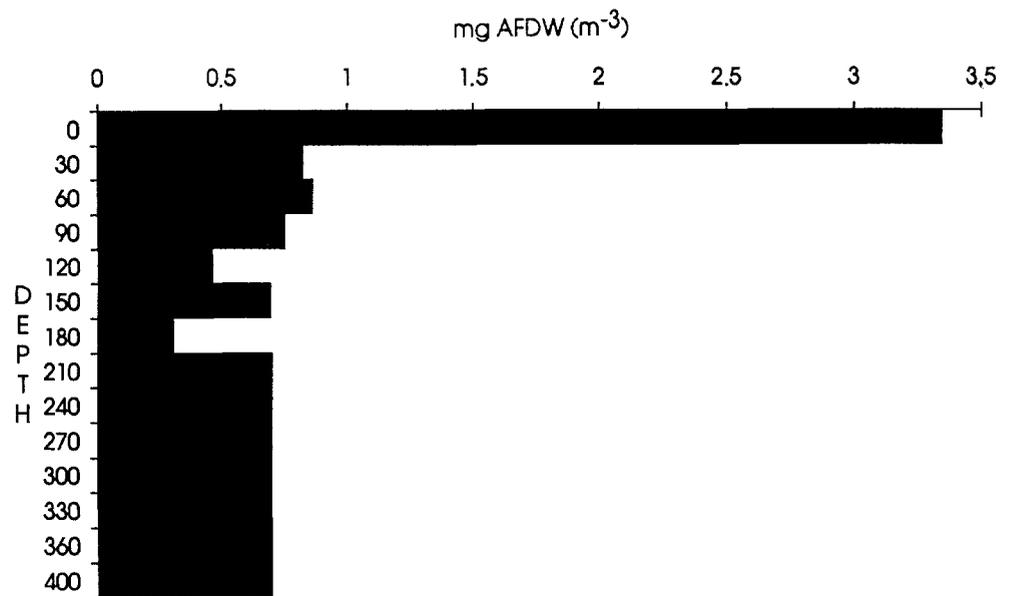
Results

Light and vertical distribution of *Maurolicus muelleri*

The surface radiation during 29 to 30 May is given in Fig. 3a. The extinction coefficient (K) between 30 and 40 m

tents = $\text{AFDW}/1.86$ (Parsons et al. 1984). The AFDW m^{-3} in the layer 210–494 m is estimated from the mg AFDW m^{-3} measurements of the layer 210–400 m and mg AFDW m^{-3} is assumed to be the same for the layer 400–494 m as for 210–400 m

Fig. 4 Night time vertical distribution of zooplankton (< 2 mm) biomass [mg ash-free dry weight (AFDW) m^{-3}]



was found to be 0.06 m^{-1} . The vertical distribution of the SSL is shown in Fig. 3b. The vertical extension of the SSL was approximately 20 m during the daytime and 30 m at night.

The ten trawl hauls in the SSL contained almost only *Maurolicus muelleri*. Two of the 12 pelagic midwater trawls were not taken in the SSL. Trawl 10 sampled water above the SSL and only contained remains of *M. muelleri* from previous trawls. Trawl 8 was taken below the SSL (270 to 240 m); it contained less than 200 *M. muelleri*, but the size distribution (bimodal) of these fishes was similar to the pooled sample (minimum length=25 mm, maximum length=51 mm, Fig. 2). The deep trawl contained 83 *Benthosema glaciale*, 18 *Sergestes arcticus* (Krøyer) and 6 *Meganyctiphanes norvegica* (M. Sars). We assume that the *M. muelleri* were captured in the SSL, either when the trawl descended or on the way up. Trawl 8 is, therefore, treated in the same manner as the other ten trawl samplings in the SSL.

The SSL (consisting of *Maurolicus muelleri*) reached the surface at 23:30 hrs and stayed in the upper water layer until 03:30 hrs, when it descended. After 06:00 hrs the SSL stayed below 100 m throughout the day. The lowest depth recorded for the SSL was 180 m at 14:15 hrs. The estimated light in the SSL 29 to 30 May is given in Fig. 3c. The continuous relocation of the SSL during the daytime kept the light intensity in the layer around 10^{-3} to $10^{-4} \mu\text{mol m}^{-2} \text{ s}^{-1}$. *M. muelleri* compensated for reduced surface light so that light in the SSL was as high as 10^{-2} to $10^{-1} \mu\text{mol m}^{-2} \text{ s}^{-1}$ at 23:30 hrs.

Zooplankton and piscivores

The biomass (mg AFDW m^{-3}) estimates obtained from the nighttime MOCNESS samples are shown in Fig. 4. The biomass was nearly four times higher in the upper 30 m than

below. The total carbon contents (of individuals < 2 mm) in the fjord were estimated to be 3.4 tons, of which the upper 30 m accounted for slightly less than half and 60% of the biomass was found in the advective layer above sill depth.

The zooplankton species composition from the two MOCNESS-samples are given in Table 3. *Maurolicus muelleri* eggs were found at all depths, but the dominating fraction was observed in the near surface samples. The most abundant zooplankton species in the upper layer from both samples was *Evadne nordmanni* (Lovén) with a density of 304 ind m^{-3} at night and 179 ind m^{-3} during the day. Both day and night there were more than 20 ind m^{-3} of *Calanus finmarchicus* (Gunnerus) in the upper 30 m of the water column, and 70% of the population was located above sill depth. *Metridia* sp. was also an abundant copepod, during the daytime in the lower water masses (400 to 210 m) and during the night in the upper 120 m.

Thirty four large fishes were caught during the 12 pelagic midwater trawl catches: 30 blue whiting *Micromesistius poutassou*, three spiny dogfish *Squalus acanthias* L., and one blue ling *Molva dipterygia* (Rafinesque). There were no large fishes in Trawl 10, which was above the SSL. Of these fishes the *S. acanthias* were not examined for stomach contents, and the *M. dipterygia* was empty. Of the 30 *M. poutassou*, 23 fishes had prey in their stomachs (Table 4), seven were empty. A total of 227 recognizable food items were found. *Maurolicus muelleri* was by far the dominant prey.

Life-history parameters of *Maurolicus muelleri*

The length frequency distribution of *Maurolicus muelleri* was bimodal with peaks around 29 and 42 mm (Fig. 2). This suggests that two year classes dominated. The weight at length distribution of pooled samples is shown in Fig.

Unident. copepods	> 1	0.1	0.2	+	+	0.2	0.3	+	0.054
Unident. copepods	< 1	0.1	0.1	+	+	0.1	0.1	0.025	
Unident. fish eggs		0.2	+	+	+	0.1	0.5	0.201	2.5
Veliger bivalvia		0.4		0.2	0.1	4.3		0.265	
Veliger gastropoda		0.1		0.1	0.2	1.7		0.123	0.8
<i>Aetideus armatus</i>		+	0.1	1.1	1.6	13.3	0.2	0.150	0.1
Zooplankters m ⁻³		13.8	3.2	14.5	13.3	234.4	234.4		0.1
			0.6	6.3	6.3	6.5	6.5		11.5
			0.9	1.4	1.4	3.2	4.4		8.5
			1.4	3.2	4.4	6.3	6.3		358.8

Table 4 *Micromesistius poutassou*. Stomach contents from 23 fish caught in Masfjorden 29–30 May 1990

Food items	No. of items	%	Mean no. of items fish ⁻¹
<i>Mauroliticus muelleri</i>	188	82.8	8.17
<i>Meganycitiphanes norvegica</i>	33	14.5	1.43
<i>Benthoosema glaciale</i>	2	0.9	0.09
<i>Pasiphaea multidentata</i>	1	0.4	0.04
Unidentified prawns	3	1.3	0.13

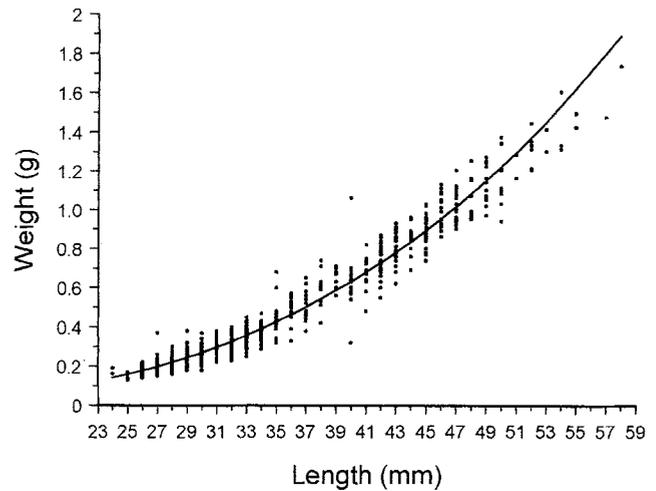


Fig. 5 *Mauroliticus muelleri*. Weight (W) as function of length (L). Regression line is: $W=9.0 \times 10^{-6} L^{3.03}$ ($N=800$, $r^2=0.95$, $24 \leq L \leq 58$)

5. No fishes had a weight below 0.12 g. There were only seven individuals heavier than 1.4 g. Wet weight (W , g) can be calculated from length (L , mm) by

$$W=9.0 \times 10^{-6} L^{3.03} \quad (N=800, r^2=0.95, 24 \leq L \leq 58). \quad (2)$$

The females accounted for 67% of all fishes investigated, males accounted for 19% and immature individuals for 14% (Fig. 6). The overall ratio of females to males in the population was 3.5 (Table 5). No males or immature individuals were found among fishes longer than 48 mm. Fishes shorter than 29 mm were dominated by males and immature individuals. Annual mortality from the 1-group to the 2-group was $Z=0.84 \text{ yr}^{-1}$ which corresponds to 45% yr^{-1} .

There was an increase in fecundity with size (Fig. 7), although large variation was observed especially among larger individuals. Size-dependent fecundity F (eggs per fecund female) can be described from length by

$$F=0.0072 L^{3.05} \quad (N=83, r^2=0.80, 28 \leq L \leq 59). \quad (3a)$$

The highest egg number (1930) was recorded for a 56-mm female. Eight females, having a length ranging from 47 mm to 59 mm, contained more than 1200 eggs. The lowest fecundity was found in a 29-mm *Mauroliticus muelleri*, which had 132 eggs. The smallest fecund female observed

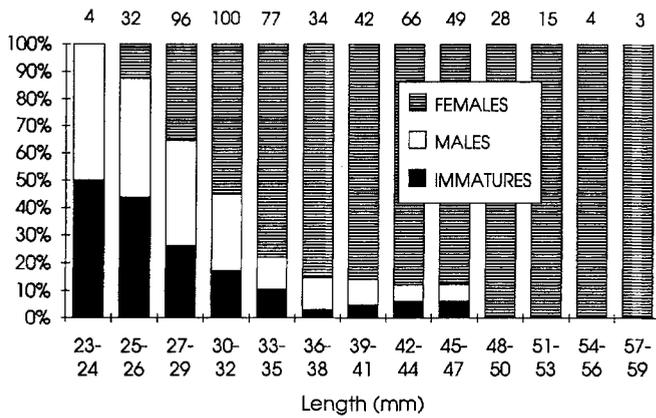


Fig. 6 *Maurolicus muelleri*. Distribution of mature and immature individuals ($N=550$). Note shorter intervals for first two and the last length group. Number on top of bar is no. of fish examined in length group

Table 5 *Maurolicus muelleri*. Sex ratio distribution ($N=550$)

Length (mm)	Males	Females	Sex ratio
23 – 26	15	4	0.27
27 – 29	38	34	0.89
30 – 32	28	55	1.96
33 – 35	9	60	6.67
36 – 38	4	29	7.25
39 – 41	4	36	9.00
42 – 44	4	58	14.50
45 – 58	3	93	31.00
Total	105	369	3.51

was 25 mm, and was found among the fishes ($N=550$) used in the stomach analyses (Fig. 6). Some investigations have only counted mature or maturing eggs and used the diameter of 500 μm as a minimum (Gjøsæter 1981b; Kawaguchi and Mauchline 1987). With this criterion, a linear relationship between the number of mature or maturing eggs and the length of the mother was found (Fig. 7b):

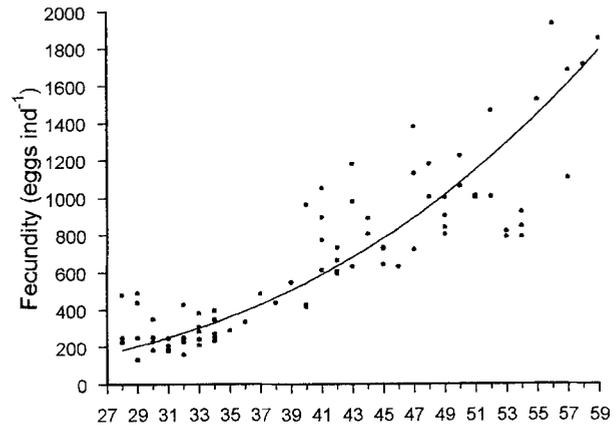
$$F_{>500}=10.0 L-281 \quad (N=66, r^2=0.63, 28 \leq L \leq 59). \quad (3b)$$

After counting all eggs, the minimum, maximum, and average number of oocytes and the standard deviation were found to be 132, 1930, 682 and 440 ($N=83$), respectively. For eggs >0.5 mm, these figures were 2, 483, 140 and 107 ($N=66$).

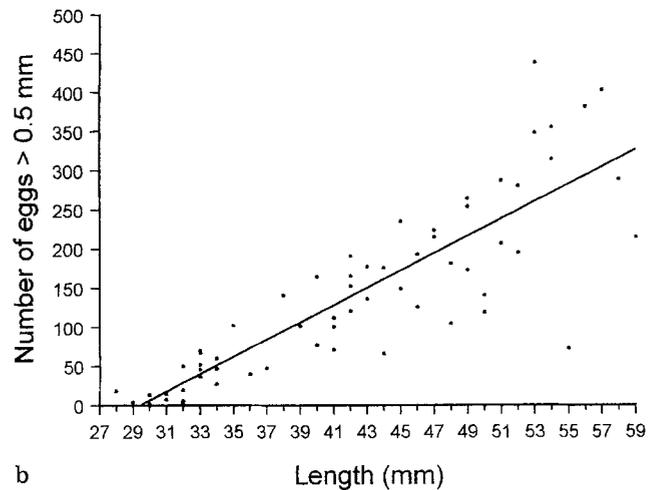
In all but the smallest fishes, egg size distribution was bimodal with peaks at 100 to 200 and 500 to 700 μm (Fig. 8). For females shorter than 35 mm more than 70% of their eggs were smaller than 0.4 mm. The largest egg measured 0.93 mm and was found in a 49-mm female. In fishes of all size classes ($N=75$) the different egg size groups were mixed in the ovaries.

Ovary mass increased with fish size, but individual variation was large among large fishes (Fig. 9). Ovary mass (OM, g) can be calculated from length (L , mm) by

$$OM=0.0019 L-0.058 \quad (N=75, r^2=0.70, 28 \leq L \leq 59). \quad (4)$$



a Length (mm)



b

Fig. 7 *Maurolicus muelleri*. Fecundity (F) as function of length (L). **a** All eggs in ova. Regression line is: $F=0.0072 L^{3.05}$ ($N=83, r^2=0.80, 28 \leq L \leq 59$). **b** Eggs larger than 500 μm . Regression line is $F_{>500}=10.0 L-281$ ($N=66, r^2=0.63, 28 \leq L \leq 59$)

Investment in gonad production as calculated here, is only partly an individual measure, as fish weight is based on the average length-weight relationship in Eq. (2). There was an increase in % gonadal investment (GI) of body weight in the length group 28 to 40 mm:

$$GI=0.29 L-7.7 \quad (N=36, r^2=0.65, 28 \leq L \leq 40). \quad (5)$$

There was no size dependent trend for fishes larger than 40 mm (Fig. 10). Maximum gonad investment (calculated) was found for intermediate sized fishes, with more than 4% gonadal tissue of body weight. All fishes below 30 mm had less than 2% ovary mass.

Feeding and stomach contents

The degree of stomach fullness for *Maurolicus muelleri* from 11 pelagic midwater trawls is shown in Table 6, and the diel variation in population average is given in Fig.

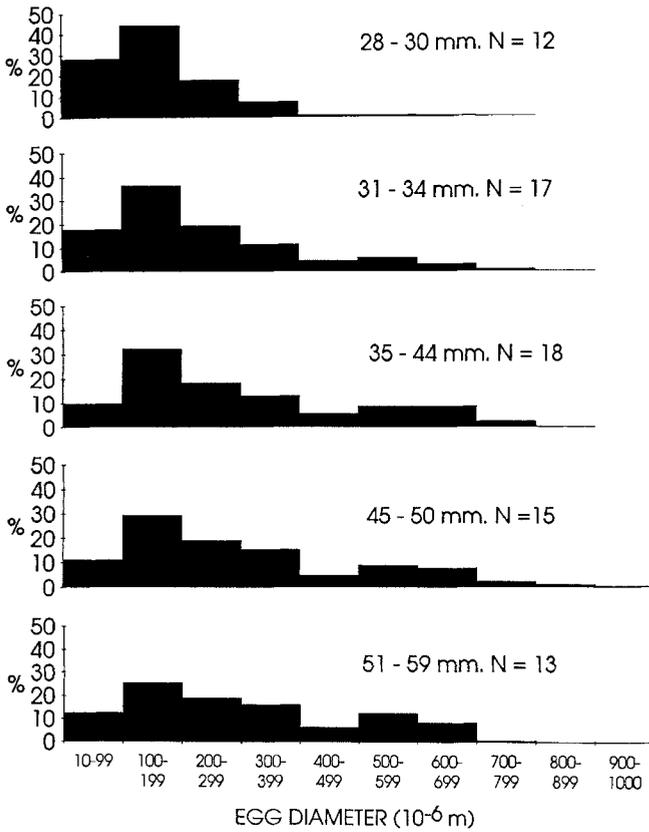


Fig. 8 *Maurolicus muelleri*. Egg diameter distribution in five length groups. 100 eggs measured from each of 75 females

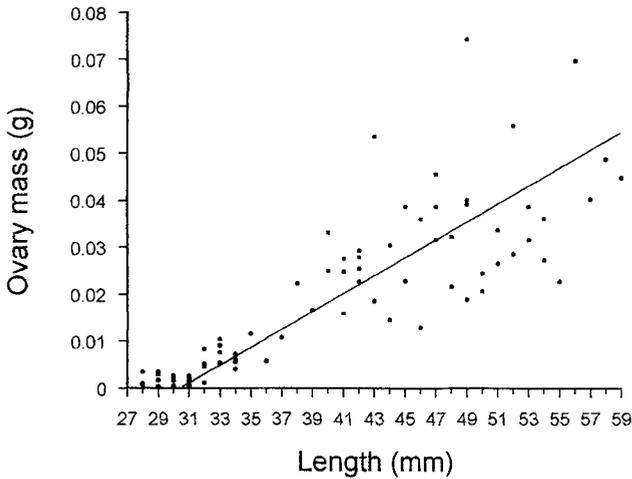


Fig. 9 *Maurolicus muelleri*. Calculated ovary mass (OM, g: L length). $OM=0.0019 L-0.058$ ($N=75$, $r^2=0.70$, $28 \leq L \leq 59$)

11a. Trawl 1 and 2 overlapped with Trawl 11 and 12 in time but not in date. The stomach fullness decreased beginning at 09:20 hrs during the day, reaching a minimum at 21:30 hrs when all the fishes had stomachs in the category "some contents" or "empty". In the three trawls taken during the night (when the SSL occurred nearest the sur-

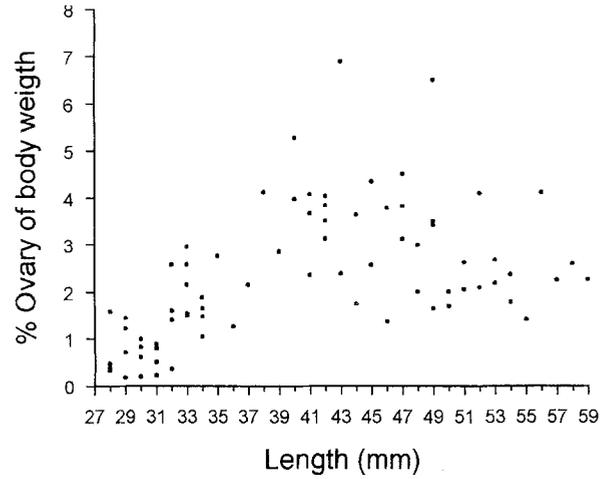


Fig. 10 *Maurolicus muelleri*. Individual investment in ovary, as % of total weight ($N=75$)

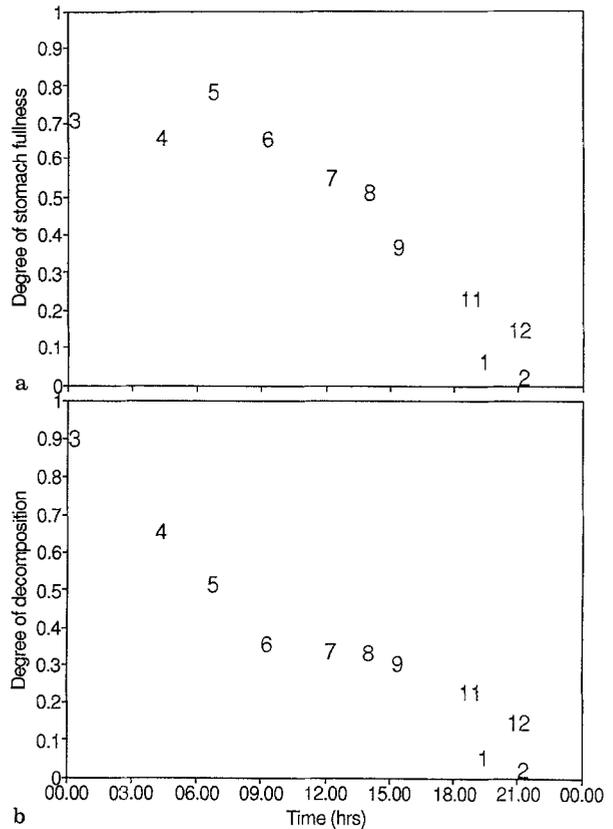


Fig. 11 *Maurolicus muelleri*. **a** Diel variation in average degree of stomach fullness. 50 fish examined from each trawl. Average obtained by assigning a value to each of the five categories in Table 6: empty=0; some contents=0.25; half full=0.5; more than half full=0.75; and full=1. **b** Diel variation in average degree of decomposition of stomach contents. Average obtained by assigning a value to each of the five categories in Table 8: empty=0; unidentifiable=0.25; partly digested=0.5; digestion started=0.75; and fresh=1. Numbers on graphs refers to trawl number. Trawls 1 and 2 were taken 29 May, the others on 30 May 1990

Table 6 *Maurolicus muelleri*. Stomach fullness of 50 fishes from each trawl haul ($N=550$)

Trawl no.:	1	2	3	4	5	6	7	8	9	11	12
Time trawled (hrs):	19:15	21:30	00:15	04:15	06:40	09:20	12:15	14:00	15:30	18:50	21:15
Empty stomachs	38	47	3	4	1	1	3	3	1	8	20
Some content	11	3	8	5	0	3	6	7	30	36	30
Half full	1	0	4	12	10	19	26	28	13	6	0
More than half full	0	0	16	11	19	16	6	6	4	0	0
Full	0	0	19	18	20	11	9	6	2	0	0

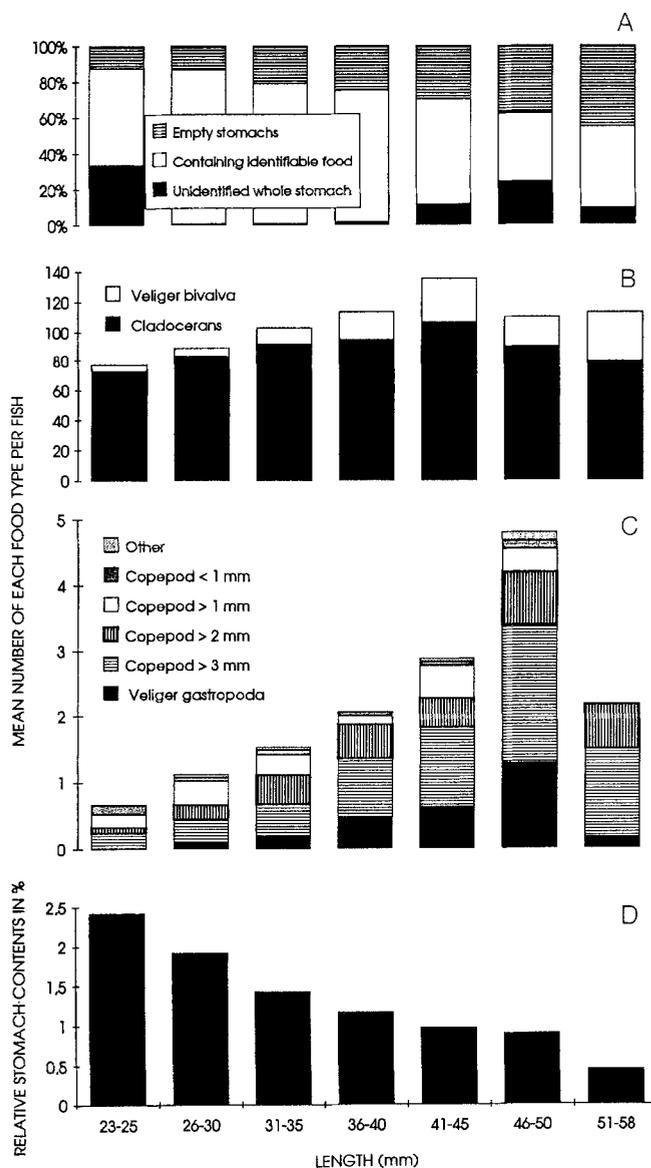


Fig. 12 *Maurolicus muelleri*. Composition of stomach contents in fish length groups. **A** Status of stomachs. **B** Occurrence of the two most numerous food types in diet. **C** Less common food types. The category "other" includes euphausiids, chaetognaths, fish eggs, ostracods and zoea larvae. **D** Relative stomach mass in % of fish body mass. Prey dry weight from Blom et al. (1991), fish weight from Eq. (2)

face), 60 to 80% of the individuals had more than half full or full stomachs.

There was a size-dependent trend in diet and food intake, as shown in the stomach analyses (Fig. 12). The fraction of empty stomachs increased with fish size (Fig. 12A; $p < 0.00001$). In all size classes cladocerans were the dominant food type, followed by veliger bivalvia (Fig. 12B). The number of copepods in each stomach increased almost by a factor of ten from the smallest fishes (23 to 25 mm) to the size group 46 to 50 mm (Fig. 12C). The maximum number of the three most numerous or large food types (cladocerans, veliger bivalvia and copepods > 3 mm) found in the stomach contents of *Maurolicus muelleri* were 300, 200 and 18, respectively. The cladocerans and the veliger bivalvia were found in two different 42 mm fishes, the copepods in a 47 mm *M. muelleri*. The mean number of the different food types (Table 7, Fig. 13) showed a decrease as the day progressed and the feeding stopped. The relative stomach contents in % of total weight (Fig. 12D) decreased with increasing fish size ($p < 0.001$); the smallest fishes had eaten more than five times more per body mass than the largest fishes.

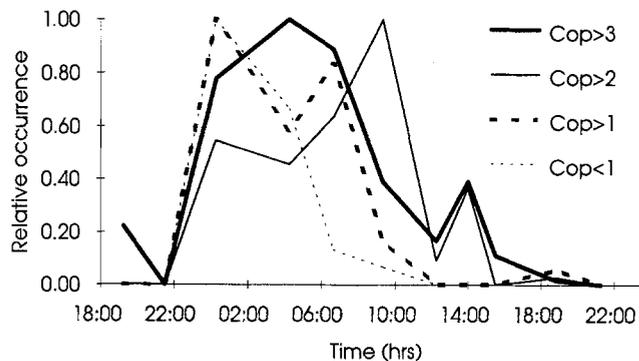
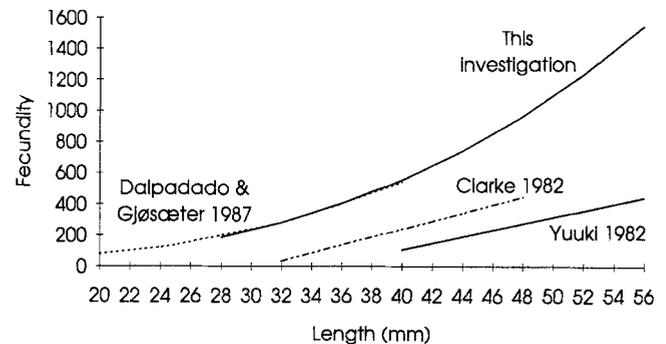
The degree of decomposition of stomach contents varied over the diel cycle (Table 8, Fig. 11b). Fresh contents were found in the three night trawls (00:15, 04:15 and 06:40 hrs) with a maximum at 00:15 hrs, at which time 84% of the fishes had fresh food in their stomachs. This percentage decreased during the night, indicating most active feeding at the beginning of the night. The decomposition degree increased throughout the night and day, reaching a maximum at 18:50 hrs, when 97% of the fishes who had prey in their stomachs had unidentifiable stomach contents. Considering the time it took the stomach contents to change from "fresh" to "digestion started" (Table 8), it seems plausible to assume a recent food intake (maximum 1 h) before Trawl 3 at 00:15 hrs. The relative occurrence of copepod size classes in the stomachs (Table 7, Fig. 13) indicates that 80% of the copepods were digested in 9 h. The mean number of copepods in the stomachs was low, maybe due to the large number of cladocerans. A digestion estimate of 12 h for digestion of copepods may, therefore, be too low.

Table 7 *Maurolicus muelleri*. Mean number (from stomachs containing food) of the most abundant food items per stomachs. 50 stomachs examined from each trawl. (– indicates not found)

Trawl no.:	1	2	3	4	5	6	7	8	9	11	12
Time trawled (hrs):	19:15	21:30	00:15	04:15	06:40	09:20	12:15	14:00	15:30	18:50	21:15
Empty stomachs:	38	47	3	4	1	1	3	3	1	8	20
Cladocerans	26.0	35.0	117.6	120.3	138.9	137.6	108.3	75.7	70.8	48.7	49.0
Copepod > 3 mm	0.4	–	1.4	1.8	1.6	0.7	0.3	0.7	0.2	0.0	–
Copepod > 2 mm	–	–	0.6	0.5	0.7	1.1	0.1	0.4	–	0.0	–
Copepod > 1 mm	–	–	1.2	0.7	1.0	0.2	–	–	–	0.1	–
Copepod < 1 mm	–	–	0.3	0.2	0.0	0.0	–	–	–	–	–
Veliger bivalvia	1.4	–	12.3	11.6	16.6	24.7	27.3	17.7	13.5	4.9	6.5
Veliger gastropoda	–	–	0.9	0.5	0.3	1.2	–	–	–	–	–
Other	–	–	0.1	0.2	0.1	–	0.0	–	–	–	–

Table 8 *Maurolicus muelleri*. Degree of digestion of stomach contents ($N=550$)

Trawl no.:	1	2	3	4	5	6	7	8	9	11	12
Time trawled (hrs):	19:15	21:30	00:15	04:15	06:40	09:20	12:15	14:00	15:30	18:50	21:15
Fresh	0	0	42	11	2	0	0	0	0	0	0
Digestion started	0	0	3	20	13	2	3	1	1	1	0
Partly digested	0	0	1	11	21	19	15	17	11	0	0
Unidentifiable	12	3	1	4	13	28	29	29	37	41	30
Empty stomachs	38	47	3	4	1	1	3	3	1	8	20

**Fig. 13** *Maurolicus muelleri*. Relative occurrences of copepod (Cop) size classes in stomachs during the 26 h trawling. Relative occurrence of each size class is scaled against its peak value (=1)**Fig. 14** *Maurolicus muelleri*. Reported size-dependent fecundities in different sea areas

Discussion

The results obtained here differ from many other studies of *Maurolicus muelleri*: minimum length at maturity was much smaller than observed earlier in western Norwegian fjords. Mortality rate for 1 to 2-yr-old fish seems to be lower than other northern European observations, and fecundity (as measured by large eggs, $F_{>500}$) seems to be much smaller than other reports from this region. [However, counting all eggs gives the same size-dependent fecundity as observed by Dalpadado and Gjøsæter (1987) for the Red Sea, and a maximum number of eggs which is far higher than observed elsewhere (Fig. 14)]. Food concentrations seem to have been an order of magnitude lower

than previous early summer registrations in Masfjorden, and the principal prey was cladocerans and not copepods. Age at maturity was, however, 1 yr, as found in all other investigations.

Life-history variables

The minimum length at maturity of *Maurolicus muelleri* in Masfjorden in the present investigation was shorter than Gjøsæter (1981b) found in other Norwegian fjords, where no female *M. muelleri* below 39 mm was mature. Okiyama (1971) found no ripe females in the Japan Sea shorter than 42 mm. Maturing lengths for males and females, respectively, have been reported to be 34 to 36 mm off Tasmania

Table 9 *Maurolicus muelleri*. Spawning locality and period, average or minimum/maximum fecundity, length range among sampled fish and fecund females

Locality	Main spawning period	Average fecundity and/or min-max egg no.	Length range sampled (mm)	Length range among mature females (mm)	Source
Japan Sea	Spring	109 – 331	42 – 47.8	–	Nishimura 1959
Norway	Spring/summer	312 (200 – 500)	16 – 55	47 – 55	Gjøsæter 1981b ^a
Japan Sea	Spring/autumn	120 – 490	Eggsize –56	40 – 56	Yuuki 1982
South East Australia	Winter/spring	30 – 456	14 – 51	33.5 – 48.5	Clarke 1982
Red Sea	Spring	50 – 820	14 – 40	20 – 40	Dalpadado and Gjøsæter 1987
Tasmania	Spring/summer	376 (104 – 942)	34 – 54	43 – 54	Young et al. 1987 ^b
South Africa	Spring	334 (161 – 738)	10 – 53	26 – 53	Prosch 1991
Norway	Spring/summer	675 (132 – 1930)	23 – 59	24 – 59	Present study

^a Only eggs >0.5 mm were counted

^b Only eggs >0.35 mm were counted

(Young et al. 1987) and in the Rockall Trough (Kawaguchi and Mauchline 1987), 24 to 26 mm in the southern Benguela (Prosch 1991) and 19 to 20 mm in the Red Sea (Dalpadado and Gjøsæter 1987). Off the southeastern coast of Australia, Clarke (1982) found females to have a length of 33.5 at maturity and a weight of 0.38 g. These matured in 1 yr, which is in agreement with the present study although the weight here is below 0.2 g for the smallest mature females. Weight at length are similar for Clarke (1982) and our investigation. A review of spawning locality and period, fecundity, sampling length and female length from different places including the present investigation is given in Table 9, and reports of length-specific fecundity are compared in Fig. 14.

Size-dependent fecundity was observed by Clarke (1982), Yuuki (1982), Dalpadado and Gjøsæter (1987) and Kawaguchi and Mauchline (1987), but not by Gjøsæter (1981b), Young et al. (1987) and Prosch (1991). Kawaguchi and Mauchline (1987) found higher fecundity ($F_{>500}$) in the Rockall Trough than Gjøsæter (1981b) found in Norwegian fjords, and related this to differences in life history strategies and adult survival: few individuals in Rockall Trough survived to a second breeding season. This population difference in the ratio between the current and future reproductive value of 1-group fish should lead to higher investment in offspring production for 1-group fish in the Rockall area. The average fecundity $F_{>500}$ found here is 45% of that observed by Gjøsæter (1981b) and only 31% of that observed by Kawaguchi and Mauchline (1987). The average mortality for 1- to 2-yr-old fish was also lower than reported by Gjøsæter (1981b). Kawaguchi and Mauchline (1987) did not estimate mortality, but the almost total absence of individuals >40 mm indicates a very high mortality between 1 and 2 yr. The ecological consequence of this will be discussed later.

The pronounced sex ratio differs from other investigations that have found weakly skewed (Clarke 1982; Dalpadado and Gjøsæter 1987; Prosch 1991) or even sex ratios (Lopes 1979; Gjøsæter 1981b). However, Young et al. (1987) found a sex ratio of 2.6, although there were great differences among the samples, and the largest sex ratio

(5.1) was found in the size range 36 to 40 mm. The progressively larger sex ratio with fish size in the present study may indicate a higher mortality rate for males, especially for individuals shorter than 32 mm (Fig. 6); eventually they may indicate sexual differences in growth patterns. The size of the largest females found may also indicate a relatively low mortality rate for large (older) females than found elsewhere.

The bimodal egg size distribution found in *Maurolicus muelleri* (longer than 31 mm) was also found by Dalpadado and Gjøsæter (1987) and Melo and Armstrong (1991). In Norwegian waters Gjøsæter (1981b) found no such trend in the size distributions of oocytes. Egg diameters have been examined in several investigations (Okiyama 1971; Gjøsæter 1981b; Clarke 1982; Yuuki 1982; Dalpadado and Gjøsæter 1987; Young et al. 1987; Melo and Armstrong 1991). Jespersen and Tåning (1926), Sanzo (1931) and Grey (1964) (cited in Okiyama 1971) found the diameter of fully matured eggs in the Atlantic and Mediterranean to be 0.84 to 0.97 mm. In our study the fishes in the size range 35 to 59 mm were those which had the largest proportion of fully developed eggs. By number these eggs were few, and only in the fish length group 45 to 50 mm were eggs larger than 0.9 mm found.

In other sea areas, multiple spawning seems to have occurred (Dalpadado and Gjøsæter 1987; Melo and Armstrong 1991). Dalpadado and Gjøsæter (1987) found two clearly separable modes of ova in all females examined and took this as an indicator of batch spawning. The presence of different size groups of yolkeoocytes in the ovaries of fish is considered to be evidence of multiple or serial spawning (Clark 1934; Hickling and Rutenberg 1936; Hunter and Goldberg 1980; and Hunter and Macewicz 1985 cited in Melo and Armstrong 1991). In this material egg sizes were mixed in the ovary, and it is difficult to imagine that only a certain egg size could be spawned. A bimodal egg size distribution in the ovaries combined with *Maurolicus muelleri* eggs in the MOCNESS plankton samples indicate multiple spawning of batches of eggs. If some females had spawned all their eggs, one would expect to find a few large females with empty ovaries, but no such

females were found. With batch spawning the spawned eggs would be of mixed size (as judged from the ovaries) and possibly with a varying survival probability.

Vertical distribution

During the summer in Masfjorden *Maurolicus muelleri* concentrates in one layer located at approximately 120 to 170 m during the daytime and 0 to 30 m from 23:30 to 03:30 hrs (Fig. 3). In other areas where *M. muelleri* is found this layer was located between 100 and 300 m during the daytime (Gjøsæter 1986; Young and Blaber 1986; Dalpadado and Gjøsæter 1987; Gorelova and Krasil'nikova 1990). The diel depth distribution of the SSL in the present investigation was closely related to changes in surface radiation. However, during the dusk migration to the surface, light intensity at the top of the SSL increased by a factor of 100 for a short time. This better light regime coincides with the timing of stomach filling.

During the winter in Masfjorden the situation was much different. The juveniles were located in an upper layer at 70 to 100 m (depending on the surface light). The adults also followed these oscillations in the surface light but were located in a layer about 50 m deeper than the juveniles (Giske et al. 1990; Baliño and Aksnes 1993). In summer both year classes are fecund, entering vertical migrations, and enter the surface around midnight (23:30 to 03:30 hrs), while only juveniles performed morning (08:00 to 09:00 hrs) surface migrations in winter (Giske et al. 1990). Giske and Aksnes (1992) and Rosland and Giske (1994) calculated the energy budget of adults in winter to be negative and ascribed their vertical distribution as a means of maximising overwintering survival. The situation for adults in summer is quite different as (batch) fecundity relies on a feeding surplus.

Feeding rhythm

Maurolicus muelleri was primarily a nighttime feeder during our investigation, although fresh copepods were found in a few stomachs from fishes taken during the daytime. Samyshev and Schetinkin (1971) and Gjøsæter (1981b) found no diel differences in feeding, but this may be ascribed to low sampling frequency. Okiyama (1971) detected that post larvae (4 to 20 mm) *M. muelleri* were most active feeding at night. Young and Blaber (1986) found a feeding pattern that indicated that most feeding took place in the evening (18:00 to 24:00 hrs) and Gorelova and Krasil'nikova (1990) also found most active feeding in the upper layers of water in the evening. Giske et al. (1990) and Giske and Aksnes (1992) found that *M. muelleri* during January in Masfjorden were daytime feeders.

This complex pattern probably relates to seasonal and latitudinal variation in day (or better, night) length and mid-night light intensity. During the winter in Masfjorden it is too dark at night for visually oriented feeding anywhere in the water column, so feeding has to take place during the

daytime. In the summer the situation is different, feeding is possible both day and night (cf Aksnes and Giske 1993). Since the risk of predation is light-dependent and food is concentrated in the near surface water, feeding takes place during the night. It seems that nighttime feeding is a means of keeping mortality risk low while keeping the feeding rate high.

Masfjorden in May to June 1990 and life-history patterns of *Maurolicus muelleri*

The estimated zooplankton biomass in May to June 1990 (3.4 tons C) is low compared to data from Masfjorden in May and June other years (17 to 40 tons C, Giske et al. 1991), and the zooplankters were also small. The pelagic zooplankton biomass in Masfjorden is heavily dependent on advection from the coastal waters (Aksnes et al. 1989; Giske et al. 1991; Salvanes et al. 1992). Aksnes et al. (1989) found the renewal rate of zooplankton biomass in June 1985 to be 13% d⁻¹ as a consequence of current profiles and zooplankton vertical distribution. Similar dependencies have been found in other fjords (Matthews and Heimdal 1980; Lie et al. 1983; Lindahl and Hernroth 1988; Kaartvedt 1991).

Due to its large size *Calanus finmarchicus* is a major component in the mesozooplankton in the fjord. However, it is uncertain to which extent, if at all, this Norwegian Sea copepod (cf Skjoldal et al. 1993) reproduces in this fjord, and its biomass is strongly dependent on advection. In winter, *C. finmarchicus* migrates below sill depth of Masfjorden (Giske et al. 1990) effectively stopping its advection. In spring and summer the population is more shallowly distributed; 70% of the population was above sill depth both during the day and at night in our investigation. Thus, very low densities of *C. finmarchicus* in May 1990 may indicate that a major zooplankton inflow had not occurred since autumn 1989.

Eventually, the low zooplankton biomass may indicate a recent major outflow of zooplankton, so that feeding conditions earlier in this particular spring may have been better than those judged from the zooplankton samples. However, there are indications that feeding conditions for littoral planktivores may have been unusual by bad during the winter and spring in question. According to Fosså et al. (1994) the sublittoral planktivorous gobiid fishes in Masfjorden had a weak 1989 year class, and pollack *Pollachius pollachius* L. had a low condition factor. The planktonic food for these sublittoral fishes is, to a large extent, transported to the near shore from the pelagic (Fosså 1991; Giske et al. 1991). A low condition factor for sublittoral planktivores may, therefore, indicate bad feeding conditions for pelagic planktivores as well. The dominating zooplankton taxa in May to June were the cladocerans *Evadne nordmanni* and *Podon* sp. These short-lived marine animals have a life-history of continual reproduction during the summer (Eriksson 1974; Poggensee and Lenz 1981), and their dominance may indicate that the zooplankton biomass observed had been built up over a short time period.

Stearns and Crandall (1984) showed that flexibility in age and size at maturity may be an optimal strategy to offset the fitness consequence of what they called "unavoidable stress" (for example bad feeding and growth conditions). This theory applied to *Maurolicus muelleri* may explain the short length at maturity and low fecundity ($F_{>500}$) in Masfjorden in May 1990 compared to the findings of Gjøsæter (1981b) and Kawaguchi and Mauchline (1987). *M. muelleri* is a short-lived fish, and a doubling of generation time (i.e., age-plasticity) would result in a large fitness cost in terms of reproductive rate (cf. Giske et al. 1993). As fecundity is size dependent, maturation at a lower size has a cost in fecundity as well as in somatic growth rate. It seems that the smaller fishes try to achieve both a minimum generation time and a reasonable somatic growth rate: the investment in gonads was low for the smaller adults and increased linearly for 25 to 40 mm fishes (Fig. 10). It is, therefore, reasonable to find smaller adult *M. muelleri* (1-group) after a poor year. The assumed bad feeding conditions seem to have affected growth more than survival. This is clearly a life-history trade-off, because if there had been a shallower distribution the fishes could probably have found ample food, due to their increased visual range (Giske and Aksnes 1992; Aksnes and Giske 1993; Rosland and Giske 1994).

Werner and Gilliam (1984), Aksnes and Giske (1990) and Giske and Aksnes (1992) have constructed life-history models based on reaching a minimum adult mass. This does not seem to apply to *Maurolicus muelleri* in years with low zooplankton biomass. Table 9 indicates that size plasticity is widespread among *M. muelleri* populations.

The size-dependent trend in increase in reproductive effort with size for small but not for large individuals reflects that small (i.e., 1-group) *Maurolicus muelleri* both grow and spawn, while the 2-group and older individuals seem to have been most concerned with spawning and, to a lesser degree, with growth. This is reflected in the number of empty stomachs which increased from 13 to 46% with larger fish size and also by the low mortality rate estimate from 1-group to 2-group. These results may indicate that feeding and growth have a cost (in mortality), since those individuals that gained most from growing had eaten most relative to body mass.

Trophic implications

As also observed in winter (Giske et al. 1990), *Maurolicus muelleri* seems to be the major prey for the large pelagic fishes. Other investigations of blue whiting in the North Sea area (Gordon 1977; Bailey 1982; Bergstad 1991b) indicate that this species seems elsewhere to feed on krills and shrimps, also where *M. muelleri* is present. However, our results fit well with the estimations of Gjøsæter (1981a, b), who found mortality rates of *M. muelleri* to be 2 to 3 times higher than of *Benthosema glaciale* in the same western Norwegian fjords.

The low zooplankton biomass found in Masfjorden in May to June is not reflected in increased generation time

or mortality rate for *Maurolicus muelleri*. Instead, the assumed poor feeding conditions have been compensated for by a smaller size at maturity and possibly by lower fecundity. Due to its behavioural flexibility *M. muelleri* may be assumed to dampen the effects of interannual variations in zooplankton biomass on the feeding conditions for piscivores. The present study indicates that an improved understanding of the dynamics between the trophic levels may be gained from studies of life history patterns and the corresponding optimal policies.

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