Marine Biology (1995) 124: 185–195

M. S. Goodson · J. Giske · R. Rosland

Growth and ovarian development of *Maurolicus muelleri* during spring

Received: 26 June 1995/Accepted: 20 July 1995

Abstract The size, fecundity and gonad development of *Maurolicus muelleri* (Gmelin) were studied in Herdlefjorden, western Norway, from January to June 1994. In January, the two age groups formed separate sound-scattering layers (SSL). Juvenile 1-group fish were found to form the upper SSL, while adult 2+ individuals inhabited the lower, these distributions reflecting the different feeding to fitness functions of these two age groups. In June there was only one SSL, and in March and May some 2+ were also found in the upper SSL. Growth of the younger fish to 2+ fish size was observed over the period, and it was found that *M. muelleri* mature after 1 yr, although size at maturity was lower than found in previous studies. Growth of the 2+ fish changed as the period progressed, to allow gonadal development after a winter of low feeding. Increased investment in development of the gonads was also observed in the 1-group fish over the study period, but substantial maturation only occurred from May to June. Absolute fecundity was size dependent, although high variability was found in the larger size ranges. Oocyte development occurred in discrete batches, although lack of gonadal synchrony between individuals means that spawning is continuous in the population as a whole, once the spawning period begins. Batch fecundity was found to be similar to previous studies, and 2+ fish were found to start spawning earlier, and with an increased intensity, than the 1-group fish.

Communicated by T.M. Fenchel, Helsingør

M.S. Goodson[1]
University College of Swansea, School of Biological Sciences, Singleton Park, Swansea SA2 8PP, Wales

J. Giske (✉) · R. Rosland
University of Bergen, Department of Fisheries and Marine Biology, Høyteknologisenteret, N-5020 Bergen, Norway

Present address:
[1]Oceanography MSc course, Department of Oceanography, University of Southampton, Southampton Oceanography Centre, European Way, Southampton SO14 3ZH, England

Introduction

Maurolicus muelleri (Gmelin) is an important planktivore in continental slope areas worldwide (Okiyama 1971; Robertson 1976; Clarke 1982; Yuuki 1982; Gamulin and Hure 1985; Kawaguchi and Mauchline 1987; Young et al. 1987; Melo and Armstrong 1991; Prosch 1991) and also in Norwegian fjords (Gjøsæter 1981; Kaartvedt et al. 1988; Giske et al. 1990; Baliño and Aksnes 1993; Rasmussen and Giske 1994). It is a small fish, with a maximum size of about 70 mm and a short life span. Only a small proportion of the population reach the age of 3 yr in Norwegian waters (Gjøsæter 1981).

Like many mesopelagic fish, *Maurolicus muelleri* have been observed to undergo extensive diel vertical migrations, ascending at dusk and descending at dawn (Giske et al. 1990; Baliño and Aksnes 1993; Rasmussen and Giske 1994). Relative to a permanent deep location, this serves to increase the length of the feeding period (Clark and Levy 1988) for a visual feeder, allowing fish to remain in illuminated conditions for a greater length of time. And relative to a shallow distribution, migrants reduce mortality risk from visual predators. In the nearby Masfjorden, Giske et al. (1990) observed two separate sound scattering layers (SSL) in January, consisting of adults (2+ fish) and juveniles (1-group fish) in the lower and upper layers, respectively. The distribution pattern shown was ascribed to differences in the trade-offs between mortality risk and food requirement in the two age groups (Werner and Gilliam 1984; Aksnes and Giske 1990; Utne and Aksnes 1994). The 1-group fish, being concerned with both growth to the adult size and gonadal development, stayed higher in the water column, where mortality risk from visually feeding predators was greater, but visual range, and hence prey encounter, was also increased (Clark and Levy 1988; Aksnes and Giske 1993; Rosland and Giske 1994). However, the 2+ fish were more

concerned with surviving to the next spawning season (Giske and Aksnes 1992), and by staying in the poorer light conditions, they decrease the risk of being seen, although feeding opportunities are also reduced. Giske and Aksnes (1992) and Rosland and Giske (1994) have hypothesized that the 2+ fish have a negative energy budget over the winter. As the spawning season approaches in early spring, 2+ fish have to retain feeding in order to provide energy for gonad production. Combined with maturation of 1-group fish, this results in the fusion of the two winter SSLs into one summer SSL, as observed by Rasmussen and Giske (1994).

The present study aims to investigate the growth of the 1-group and 2+ fish from January to June. Gonadal development will be assessed to ascertain spawning strategy and to elucidate the beginning of the spawning period in Herdlefjorden. The relationship between fecundity and fish size over the study period will also be investigated and will be compared to previous studies.

Methods

Samples were collected during four cruises of the RV "Håkon Mosby" in Herdlefjorden during spring 1994 (Table 1). Herdlefjorden (5°10'E; 60°32'N) is 17.5 km long and has a maximum width of 2.3 km. Its maximum depth of 476 m is at the southern entrance (Fig. 1). The fjord volume is 4.1×10^9 m^3, and the cross-sectional area at the sill is 512000 m^2.

Samples were taken by a Harstad trawl in sound scattering layers (SSLs), the opening of this pelagic trawl being 20×20 m^2 during trawling at a towing speed of 1.5 m s^{-1}, at a depth of 50 m, the opening area decreasing slightly with increasing depth. Maximum and minimum stretched mesh size of the trawl is 100 and 30 mm, respectively, the stretched mesh size of the 15 m long cod end being 8 mm (Nedreaas and Smedstad 1987). The depth of the trawl was controlled during sampling by a Simrad trawl eye, and the locations of SSLs were obtained from printouts from a 38 KHz Simrad EK 500 echo sounder. Subsamples were taken from each trawl and preserved in a 4% neutralised formaldehyde solution, for later inspection.

In the laboratory, 200 *Maurolicus muelleri* from each sample were randomly chosen, the standard length (from tip of snout to distal end of caudal peduncle, mm) and the total length (tip of snout to end of caudal fin, mm) being measured for each fish. A regression analysis was performed on this data to investigate the relationship between total length (TL), as used in the present study, and standard length (SL), as used in several other investigations.

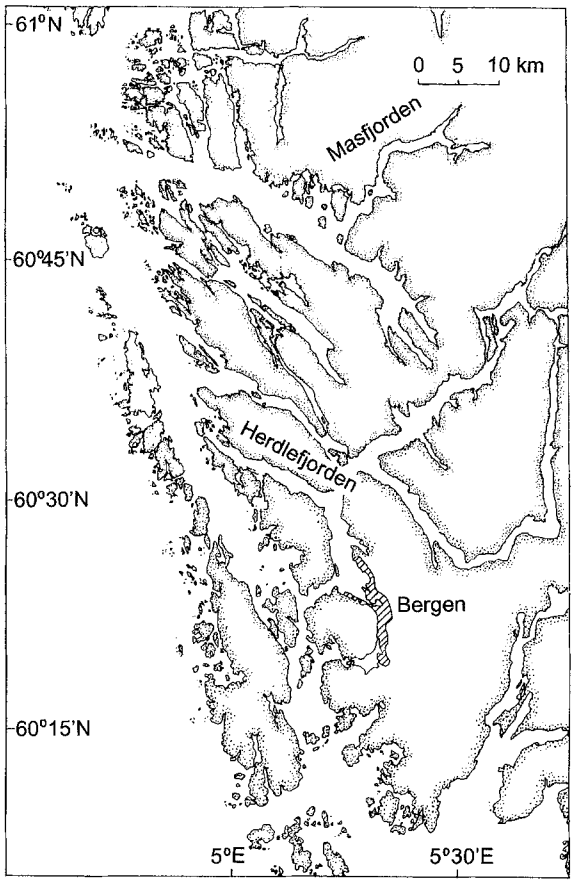

Fig. 1 Location of Herdlefjorden. Major inlet is to the south. Fjord is connected to coast through Byfjorden and Hjeltefjorden. Location of nearby Masfjorden also shown

A total of 150 *Maurolicus muelleri* were randomly chosen from each trawl subsample, and their TL, to the nearest mm, and weight, to the nearest mg wet wt, were measured. The relationship between TL and fish weight (FW) for each trawl was then determined by regression analysis of ln transformed data; differences between regression coefficients of trawls from similar SSLs were tested by use of a Chow-test (Koutsoyiannis 1977). The null hypothesis is that there is no difference in the regression coefficients in the regression of ln(FW) on TL for the pooled sample and the subsamples of trawls from similar SSLs for *M. muelleri*.

Table 1 *Maurolicus muelleri*. Trawl data for samples used in this investigation. Other species are *BG Benthosema glaciale*; *MN Meganyctiphanes norvegica*; *SA Sergestes arcticus*

Date	Layer	Trawl time (GMT)	Depth (m)	Catch (kg)	%*M. muelleri*	Other major species
13 Jan	Upper	13:15–13:55	70–95	5.5	100	–
	Lower	10:00–10:20	105–135	56.2	> 99	MN
29 Mar	Upper	09:15–09:35	93–121	16.8	> 99	MN
	Lower	13:05–13:25	165–185	6.9	46	BG (53%), MN
5 May	Upper	15:55–16:05	100–123	11.7	98	MN
	Lower	17:07–17:27	235–270	81.0	27	SA (47%), BG (26%)
17 Jun	Upper	20:55–21:10	74–96	17.3	88	BG (6%), MN (4%), SA (2%)
	Lower	11:38–11:58	210–230	74.8	40	BG (44%), SA (10%), MN (6%)

Sex-frequency distributions were obtained by determining the sex of fish until 25 females were found from each SSL each date. The TL and FW of each fish were measured as before, the body cavity then being opened to expose the gonads, whereupon the fish could be sexed. Sex of fish in which the gonads were underdeveloped was impossible to ascertain by the methods used here, and these fish were thus classified as immature. The paired ovaries were removed and opened; the total number of oocytes contained in the ovaries were then counted using a binocular microscope and a counting chamber. Oocyte diameters were measured to the nearest 10 µm to construct oocyte size–frequency distributions for each sample. Otolith readings (L.A. Hamre, Department of Fisheries and Marine Biology, personal communication) have shown that the upper SSL in March and May consists of a mixture of 1- and 2+ fish. In the present study, aging has been judged from size-dependent differences in egg numbers and gonadal mass (see Fig. 4). Both these measures indicate that individuals smaller than 0.4 g in March and 0.5 g in May are 1-group. Six fish in March and 9 in May of the 25 females investigated for reproductive status from the upper SSL were above this size and not used further in the analysis. None of the fish caught in the lower SSL were below minimum 2+ size. The remaining fish are assumed representative for their age groups.

Relationships between absolute fecundity (AF), and TL and FW for the pooled trawl samples were determined by regression analysis. This method was also employed to determine the relationship between AF and FW for each month sampled, whereupon differences in regression coefficients between months were tested by a Chow-test.

Oocyte volume was calculated assuming spherical oocytes, individual oocyte weight being calculated by assuming a specific density of 1 $g cm^{-3}$. Ovary weight was then calculated for each fish by the multiplication of individual oocyte weight and AF. These values were used to determine the mean gonadosomatic index (GSI) for each trawl sampled. The GSI is the average ovary weight as percentage of the mean fish weight in the SSL.

From the oocyte distribution results, the average diameter of the ten largest oocytes in the ovaries was determined and used as a measure of ovarian development (Mackay 1973; Dipper and Pullen 1979). Microscopic appearance of whole oocytes was assumed to be sufficient to determine the approximate minimum diameter of yolked and ripe oocytes (Hilge 1977), since West (1990) states that, on the basis of unyolked, yolked and ripe categories, comparison of histological and whole-oocyte staging showed that the accuracy of the latter method was 88, 99, and 93%, respectively. Hislop (1975) and Hislop and Bell (1987) have shown that shrinkage of oocytes preserved in 4% formaldehyde in sea water varied between 0.5 and 2.0% in the seven species studied, and thus, in the present study, shrinkage of oocytes due to preservation is assumed to be negligible.

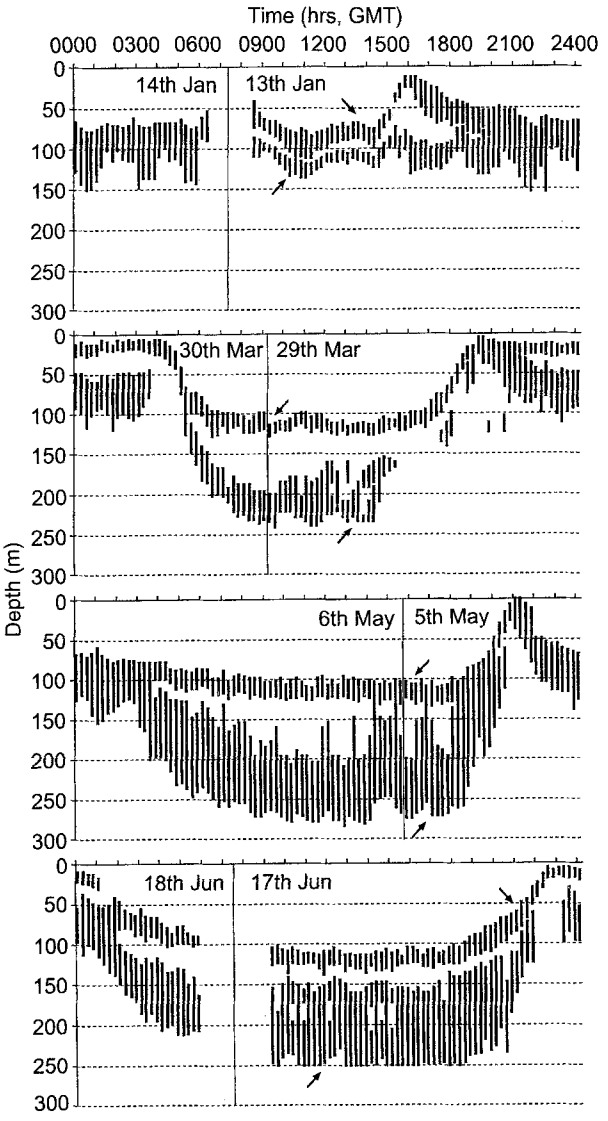

Fig. 2 *Maurolicus muelleri.* Redrawn echo registrations of the two sound scattering layers. Time is GMT and midnight is at 23:30 GMT. Time of trawl hauls marked with *arrows*. The lacking recordings in January and June are due to the short duration of these cruises

Results

The relationship between total length (mm) and standard length (mm) of *Maurolicus muelleri* is described by

$$SL = 0.169 + 0.853\ TL\ (N = 200,$$

$$r^2 = 0.99,\ 23 < TL < 63) \qquad (1)$$

Two SSLs (Fig. 2) were found on each cruise. Individuals caught in the two layers in June did not differ significantly with respect to total length and weight, absolute fecundity, relative ovary weight, GSI, average oocyte diameter and diameter of ten largest oocytes. Thus we assume that the few *M. muelleri* caught in the lower SSL originated from the upper layer, and therefore the data for *M. muelleri* caught in June are pooled. The daytime distribution of both layers was shallower in January than later. The SSLs were separable in terms of size distribution (Fig. 3). *M. muelleri* predominated the upper layer, while the lower layer contained an increasing percentage of other species as the study period progressed (Table 1). In January there was a clear size separation between the SSLs, with small (22 to 34 mm TL), "1-group" fish making up the upper SSL, while the lower SSL contained larger (36 to 57 mm TL), "2+" fish, the few *M. muelleri* of a smaller size range found in the lower SSL sample being assumed to have been taken from the upper SSL on descent and ascent of the trawl. In March and May there was a distinct size overlap between the layers,

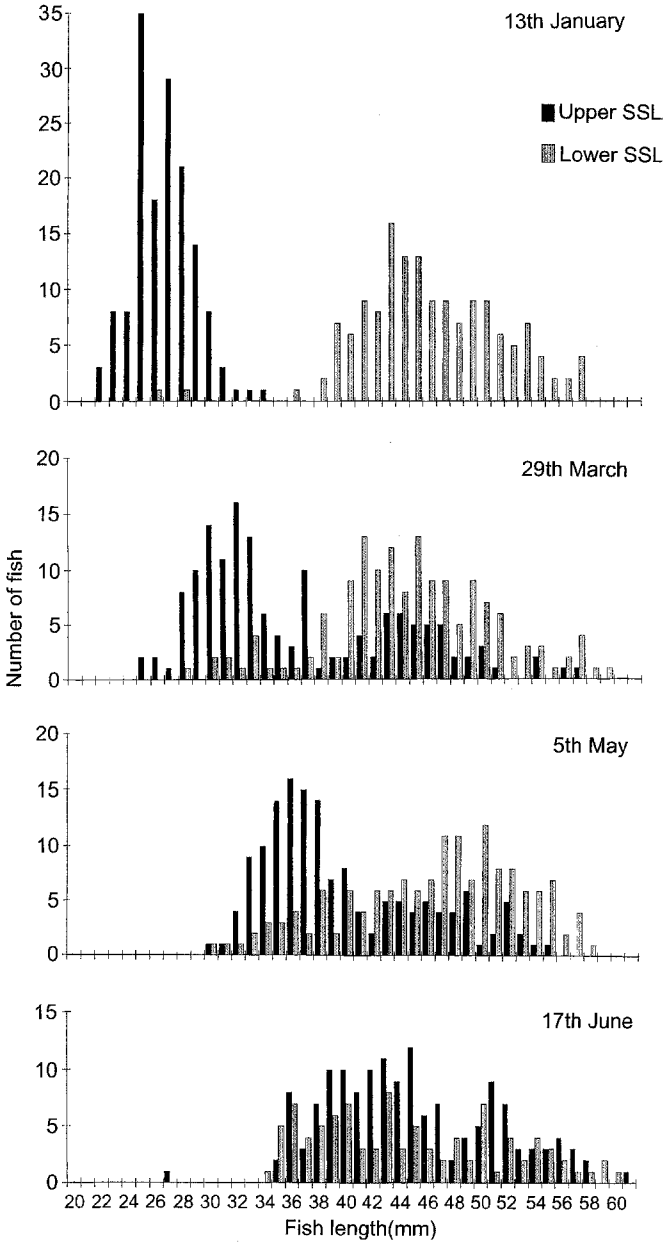

Fig. 3 *Maurolicus muelleri.* Length–frequency distributions in the two sound scattering layers (*SSL*)

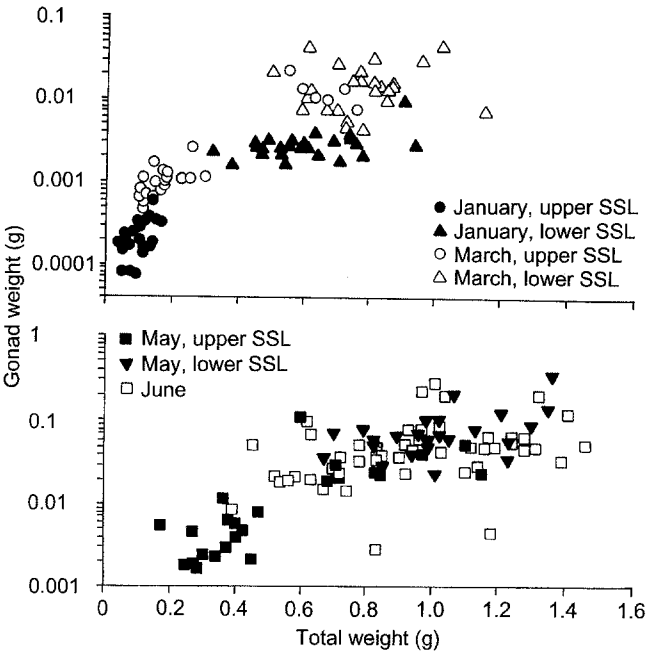

Fig. 4 *Maurolicus muelleri.* Gonad weight of fishes from upper and lower Sound Scattering Layers (*SSL*). On this basis, fish smaller than 0.4 g in March and 0.5 g in May were judged as 1-group. Note log-scale on *y*-axis

with a substantial proportion of larger fish in the upper SSL. Hamre (personal communication) aged larger fishes caught in the upper SSL in March as 2- and 3-group fish. The gonads seem to give reliable estimates of age in this period, as the large individuals caught in the upper layer are clearly distinguished from smaller individuals with respect to oocyte development (Fig. 4). By June, there was no bimodality in the length–frequency distribution (Fig. 3).

Total length (mm) and fish weight (g) were found to describe exponential relationships in all samples (Eqs. 2a–g), although Chow-tests (Zar 1984, p. 487) showed that these relationships differed significantly with season and between age goups:

$$\text{Jan U-SSL: } \ln(\text{FW}) = -5.25 + 0.11\ \text{TL}\ (N = 150,\ r^2 = 0.80,\ 22 < \text{TL} < 34) \quad (2a)$$

$$\text{March U-SSL: } \ln(\text{FW}) = -4.45 + 0.085\ \text{TL}\ (N = 150,\ r^2 = 0.95,\ 25 < \text{TL} < 57) \quad (2b)$$

$$\text{May U-SSL: } \ln(\text{FW}) = -4.10 + 0.080\ \text{TL}\ (N = 150,\ r^2 = 0.93,\ 30 < \text{TL} < 55) \quad (2c)$$

$$\text{Jan L-SSL: } \ln(\text{FW}) = -3.74 + 0.068\ \text{TL}\ (N = 150,\ r^2 = 0.90,\ 26 < \text{TL} < 57) \quad (2d)$$

$$\text{March L-SSL: } \ln(\text{FW}) = -3.73 + 0.069\ \text{TL}\ (N = 150,\ r^2 = 0.94,\ 28 < \text{TL} < 59) \quad (2e)$$

$$\text{May L-SSL: } \ln(\text{FW}) = -3.59 + 0.070\ \text{TL}\ (N = 150,\ r^2 = 0.92,\ 30 < \text{TL} < 58) \quad (2f)$$

$$\text{June SSL: } \ln(\text{FW}) = -3.59 + 0.068\ \text{TL}\ (N = 246,\ r^2 = 0.92,\ 27 < \text{TL} < 61) \quad (2g)$$

Females dominated the larger size ranges in all months sampled, but also the smaller size ranges in January and March (Fig. 5), with males being most abundant at intermediate sizes. With the exception of January, immatures were rare, consistently having a length of less than 40 mm TL.

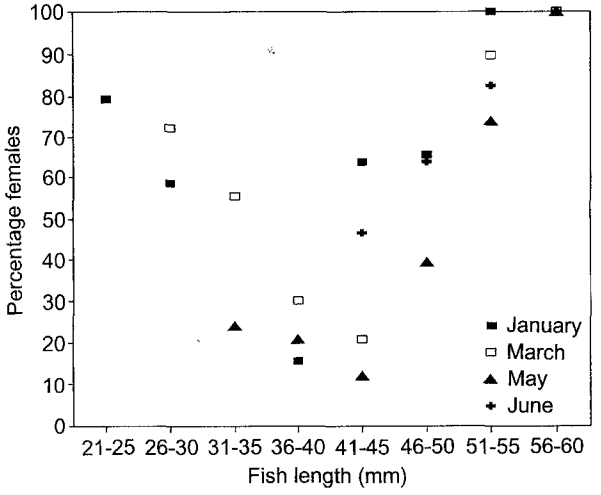

Fig. 5 *Maurolicus muelleri.* Size-dependent frequency distribution of females

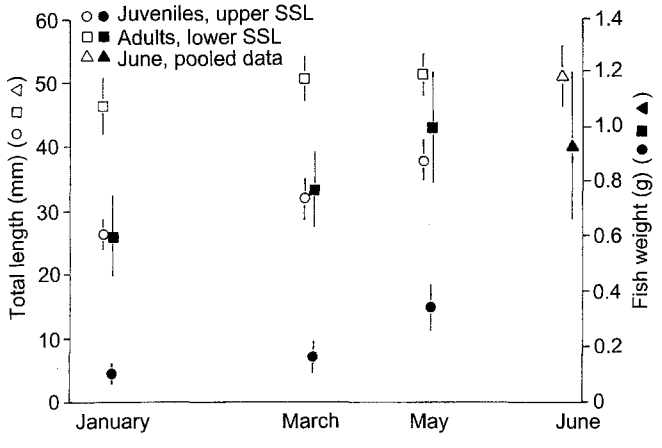

Fig. 6 *Maurolicus muelleri.* Mean and standard deviations of total length and weight of 1-group and 2+ fish

Growth patterns differed between 1-group and 2+ fish (Fig. 6 and Table 2). The growth rate of juveniles was higher than for the adults from January to May. In the same period, juveniles invested almost all growth in soma, while adults invested considerably in gonads (Table 2). The ratios between largest and smallest juveniles caught in the upper SSL were 4.0, 3.0, and 2.8 in January, March, and May, respectively. For adults caught in the lower SSL, the values were 2.9, 2.3, and 2.0, respectively. Thus the size differences within the age groups, as well as among them, decreased during the period. In June there was no clear division among the age groups with respect to fecundity and gonad size (Fig. 7), which shows that the juveniles invested much in gonadal growth during May and June, and by 17 June all female *Maurolicus muelleri* sampled had developing ovaries.

For both length and weight, there was a positive linear relationship with absolute fecundity, i.e. the total

Table 2 *Maurolicus muelleri.* Mean growth rates of 1-group in upper and 2+ group in lower Sound Scattering Levels (*SSL*)

Period	Upper SSL		Lower SSL	
	$g g^{-1} d^{-1}$	% gonadal	$g g^{-1} d^{-1}$	% gonadal
13 Jan–29 Mar	0.008	1.2	0.004	8.1
29 Mar–5 May	0.020	1.8	0.007	28.1

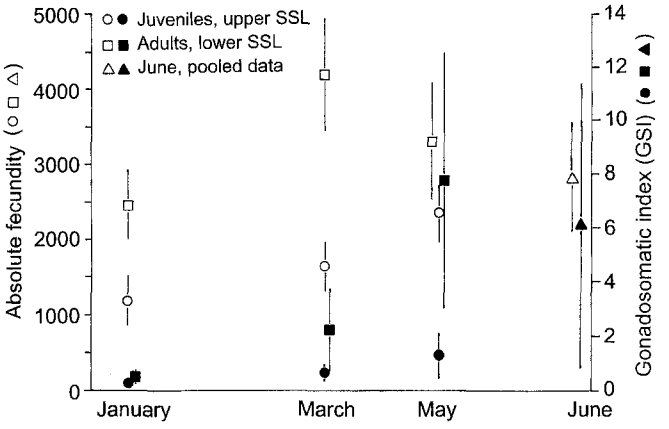

Fig. 7 *Maurolicus muelleri.* Mean and standard deviations of absolute fecundity and gonadosomatic index of 1-group and 2+ fish

number of oocytes in the ovaries (Fig. 7, Eqs. 3a–b).

$$AF = 1336 + 2107\ FW\ (N = 200,$$
$$r^2 = 0.54,\ 0.04 < FW < 1.46) \quad (3a)$$

$$AF = -1055 + 84.77\ TL\ (N = 200,$$
$$r^2 = 0.61,\ 21 < TL < 59) \quad (3b)$$

Much of the variation in AF among larger fish was an effect of season (Fig. 8, Eqs. 4a–d). Correlation coefficients for January and March (Eqs. 4a–b) are higher than when all months were combined, whilst the correlations from May and June (Eqs. 4c–d) are similar to the pooled sample (Eq. 3a).

$$\text{Jan: } AF = 1007 + 2292\ FW\ (N = 50,$$
$$r^2 = 0.70,\ 0.04 < FW < 0.94) \quad (4a)$$

$$\text{March: } AF = 1028 + 3935\ FW\ (N = 50,$$
$$r^2 = 0.83,\ 0.10 < FW < 1.15) \quad (4b)$$

$$\text{May: } AF = 1668 + 1796\ FW\ (N = 50,$$
$$r^2 = 0.56,\ 0.17 < FW < 1.36) \quad (4c)$$

$$\text{June: } AF = 1122 + 1814\ FW\ (N = 50,$$
$$r^2 = 0.46,\ 0.39 < FW < 1.46) \quad (4d)$$

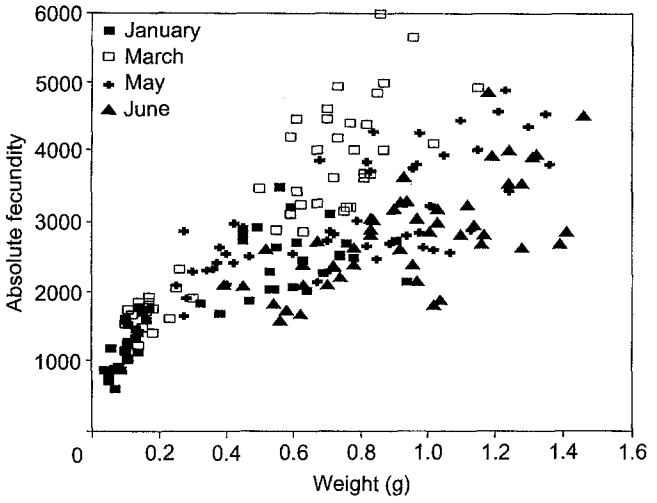

Fig. 8 *Maurolicus muelleri.* Relationship between fish weight and absolute fecundity for each period

The most pronounced size dependent trend in AF was found in March, and each month was found to be significantly different from the previous month. June was, however, not significantly different from January.

Other investigations have found a relationship between size and fecundity by only counting mature or maturing oocytes, using an oocyte diameter of 500 μm as a minimum (Gjøsæter 1981; Kawaguchi and Mauchline 1987). Calculating this fecundity by multiplying % oocytes larger than 500 μm diameter in the ovaries (as determined from 100 oocytes) with AF, no statistically significant relationship between AF and TL or FW were found in Herdlefjorden in spring 1994.

Variation in mean GSI over the study period (Fig. 7) indicates that the highest ovary weight in relation to fish weight occurs in the May sample for 2+ *Maurolicus muelleri* of the lower SSL, whilst the highest mean GSI of the 1-group fish from the upper SSL occurs later than this date (assuming GSI values to be similar for both groups of *M. muelleri* at time of spawning).

Ovarian oocytes less than 180 μm were nearly always transparent, while oocytes over this size were seen to range from clear to opaque, suggesting that vitelogenesis occurs in oocytes around this size range. Oocytes greater than 600 μm were almost always translucent, exhibiting a blue hew under the light microscope, oocytes over 800 μm seemed hydrated, often containing a single oil droplet, characteristic of the planktonic egg (Robertson 1976).

Oocyte size–frequency distribution in January (Figs. 9 and 10) had a modal diameter of about 70 and 140 μm in the upper and lower SSL, respectively. In both SSLs there were large populations of small primary oocytes, but a few oocytes over 200 μm were detected in fish from the lower SSL. By late March the primary oocytes were larger among 1-group fish, and in

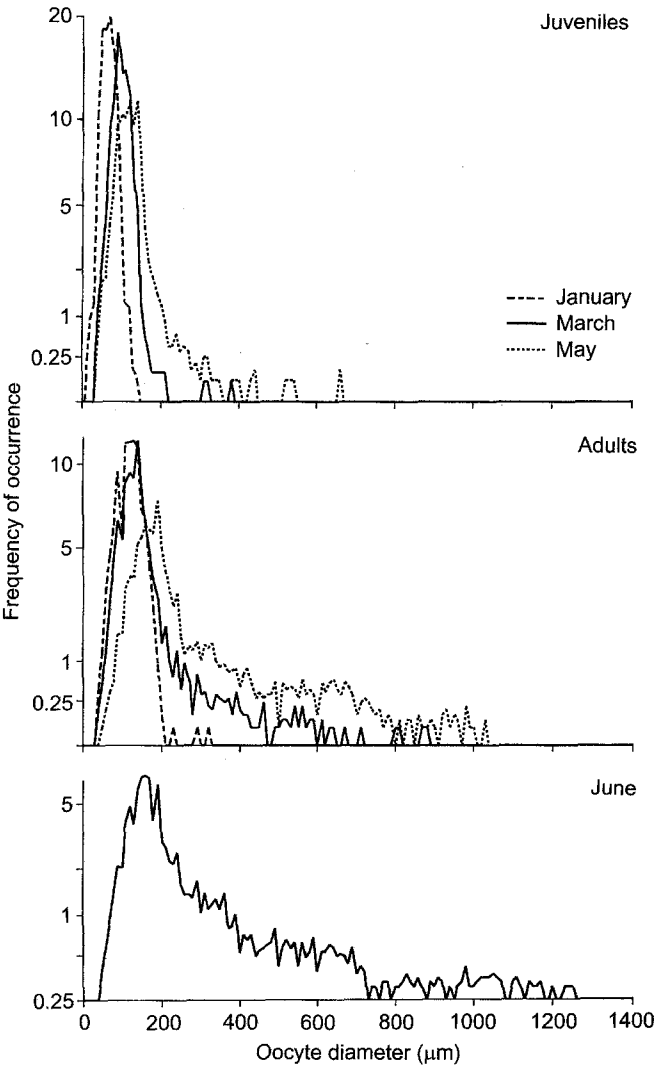

Fig. 9 *Maurolicus muelleri.* Population oocyte size–frequency distributions. Note that *y*-axis is square root transformed

both age groups there was a spread in oocyte size distribution. Among 2+ fish two distinct modes appeared. It seems that once oocytes in the most developed clutch have reached a diameter of about 600 μm, a new batch is recruited from the large population of primary oocytes (Fig. 10). Hence, successive batches are produced in this manner throughout the breeding season.

Oocyte diameters were even more diverse in May, and distinct groups of oocytes above 200 μm were evident. If these are taken as batches, the fecundity is about 200 to 500 oocytes per batch. The pooled June sample continues the trend of growing oocytes during spring and with a diminishing number of primary oocytes. The abrupt lowering in frequency of oocytes over 700 μm may indicate that oocytes over this size are spawned.

In late January, all fish had a mean diameter less than 200 μm of the largest 10% of oocytes in each

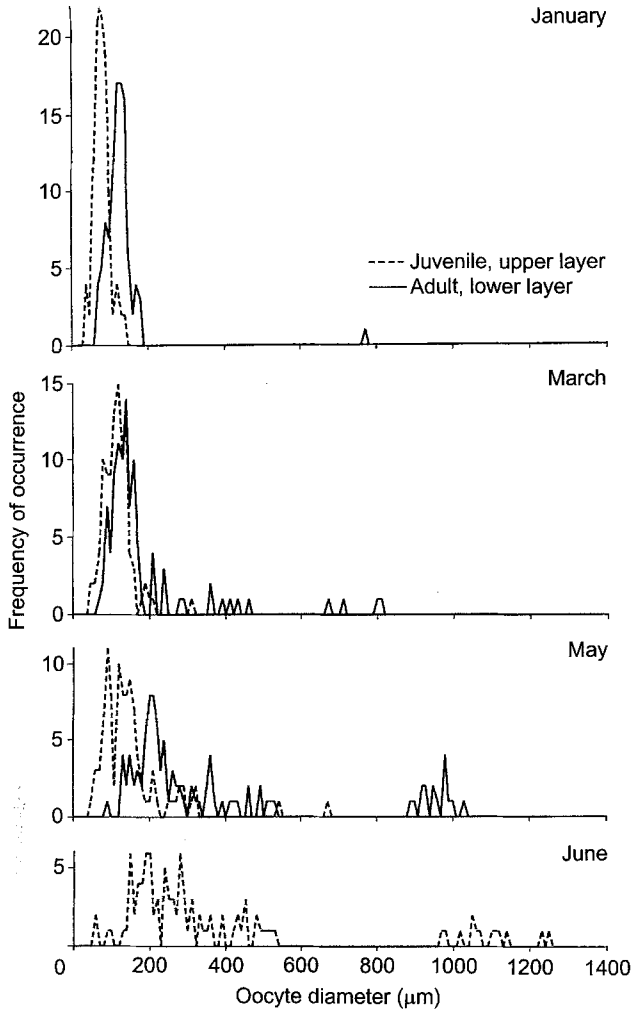

Fig. 10 *Maurolicus muelleri.* Individual oocyte size–frequency distribution of the fish with largest overall size of its ten largest oocytes. 100 oocytes counted for each fish

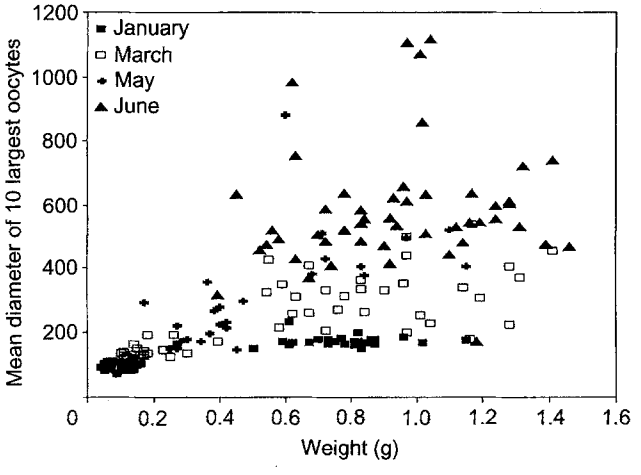

Fig. 11 *Maurolicus muelleri.* Mean diameter (μm) of the ten largest oocytes (among the 100 counted in each fish) in the ovaries as function of fish size

female (Fig. 11). By late March, mean maximum oocyte diameters were above 200 μm for elder fish, while still small for 1-group. The size difference among age groups was also clear in May, although oocytes had grown among all fish. In June these differences were not evident, and mean maximum oocyte diameter was high, but variable, regardless of fish size.

The large fish caught in the upper SSL in March and May fall within the range of adults from the lower SSL in most respects. However, in March the adults caught in the upper layer were significantly ($p < 0.01$, zM-test, Langley 1979) smaller and had lower absolute fecundity. They were also probably of lower weight ($p < 0.05$). In May, the adults from the upper layer seem to have been ($p < 0.05$) of lower total weight and ovary mass and with smaller average oocyte diameters. These results are also reflected in Fig. 4.

Discussion

Vertical distribution

Diel vertical migration (Fig. 2) with symmetrical dusk ascent and dawn descent was observed in March and June, and probably also took place in January (although the dawn descent was not covered by the sampling period), as also observed by Giske et al. (1990), Baliño and Aksnes (1993) and Rasmussen and Giske (1994). In May, the surface encounter in the morning was abandoned, perhaps because of the short time interval between dusk and dawn in late May. This is even more distinct in June, where, due to the high latitude, dusk and dawn overlap in time. Giske et al. (1990), Baliño and Aksnes (1993) and Giske and Aksnes (1992) observed that adults did not migrate in January in Masfjorden. Our findings were similar; the diel vertical migration of adults increased markedly between January and March, indicating a shift in motivation from the winter season of survival to the spring and summer seasons of gonadal growth and reproduction.

Growth

The distinction in size–frequency distribution between the two sound scattering layers (SSL), the 1-group fish inhabiting the upper SSL, older fish inhabiting the lower, decreases over the period of study [as also observed by Clarke (1982) off SE Australia and by Giske et al. (1990) in the nearby Masfjorden]. This is due to the growth of the 1-group fish over the period, while little growth is observed in the 2+ fish. By June, the 1-group fish are of a similar size to the 2+ fish, no clear distinction between SSLs in terms of size distribution or echograms being observed.

Giske et al. (1990) also observed shorter dusk ascents and dawn descents in the lower SSL than the upper

layer of 1-group *Maurolicus muelleri* in January in Masfjorden, vertical migrations increasing the length of the feeding period (Clark and Levy 1988) of these visually feeding fish. The difference in feeding motivation for the two age groups was explained by Giske and Aksnes (1992) as due to differences in growth allocation; the 1-group fish grow to become mature and keep generation time low, while the 2+ fish grow to increase fecundity. The more pronounced diel migrations of the 2 + fish in May and June are thus thought to be due to an increase in feeding rate of these fish after a winter of sub-maximal feeding (Giske and Aksnes 1992), with more energy being directed to gonad development than somatic growth in the 2+ fish than 1-group fish (Table 2).

The domination of females in the upper size ranges of *Maurolicus muelleri* appears to be a worldwide trend [as observed by Clarke (1982) off SE Australia, Young et al. (1987) off E. Tasmania, Prosch (1991) in the S. Benguela ecosystem, and Rasmussen and Giske (1994) in Masfjorden, W. Norway]. The domination of females in the smaller size ranges in January and March has not been reported in other studies.

With the exception of a single, smaller fish, no immatures were sampled in June. Along with the similar sizes of 1- and 2+ fish in this month, this indicates that most *Maurolicus muelleri* mature after 1 yr, as found in all previous investigations. No immatures were found over 40 mm TL, and it is thus thought that this is the maximum size before differentiation of sex can be seen. Maturity of *M. muelleri* has been defined differently by various authors (Gjøsæter 1981; Kawaguchi and Mauchline 1987; Young et al. 1987; Prosch 1991; Rasmussen and Giske 1994). In the present study, the smallest mature female, determined by the presence of oocytes in the ovaries, was found to be as short as 21 mm TL (from the upper SSL in January). However, even if oocytes over 300 µm are used as a minimum oocyte diameter indicating gonadal activity (Gjøsæter 1981), smallest size at maturity of *M. muelleri* in our study still only corresponds to a 31 mm TL (27 mm SL) fish (from the upper SSL in May). This is very small compared with other observations. Fjordic populations of *M. muelleri* may perhaps, due to the dependence on a variable advective food supply, exhibit more pronounced (inter-annual) variability in life history traits than oceanic populations. Besides, the spawning season in these northern waters is shorter than at lower latitudes (e.g. Kawaguchi and Mauchline 1987), and this would probably also act to reduce minimum size at maturity.

Fecundity

Some previous investigations of *Maurolicus muelleri* have concluded that there is no significant relationship between size and fecundity (Okiyama 1971; Gjøsæter and Kawaguchi 1980; Gjøsæter 1981; Young et al. 1987; Prosch 1991). The difference in results may be attributed to the fact that these studies only counted oocytes over a certain diameter, which from the relationships shown in Fig. 8 would put their data in the area of greatest scatter (since the largest fish have the largest oocytes in their ovaries). The high scatter among the larger fish may also be due to these fish having already begun to spawn (cf. June data in Fig. 11), thus reducing their fecundity and increasing the variance in the data. However, Clarke (1982), Kawaguchi and Mauchline (1987), Melo and Armstrong (1991), and Rasmussen and Giske (1994), all found a correlation between fecundity of eggs over 500 µm and fish size.

Seasonal differences in the regression of absolute fecundity against weight indicate that oocytes are being produced as the fish grows, a characteristic of most fish. This is also shown by the 2+ fish of the lower SSL having a greater absolute fecundity than the younger fish and by the clear separation between upper and lower SSLs in January (cf. Fig. 7). In March, the regression line has a steeper gradient than in January indicating that the larger fish are increasing in fecundity without a great increase in size. Oocyte production has thus continued, with separation between SSLs in terms of AF and FW being less than in January. By May, the regression line gradient is reduced, indicating that even the smaller fish are becoming more fecund. Also a fall in AF of the lower SSL fish is observed, indicating that some 2+ fish have lost oocytes, presumably through spawning. The June results reinforce this point for the 2+ fish. 1-group fish are seen to increase their absolute fecundity after March. This evidence thus suggests that the 2+ fish spawn earlier and with greater intensity than the 1-group fish. Mean GSI values (Fig. 7) agree with this hypothesis since mean GSI increases at a faster rate in the lower SSL than in the upper, with spawning period theoretically between the time of maximum GSI and the time when GSI attains a near minimum value (Mayer 1987), and with GSI for maturing and ovulating fish greater than that of vittelogenic fish (Clearwater and Pankhurst 1994). This trend is not uncommon in marine teleosts, since the same result has been shown by studies on bass (Mayer et al. 1989) and plaice (Simpson 1959). It may also explain the occurrence of the two modes in the 0-group population observed by Kawaguchi and Mauchline (1987) in the Rockall Trough in November, which they explained by the "presence of a period of increased spawning early on in the course of the spawning season", the most intense spawning being attributed to the older fish spawning first.

Gonad development

By microscopic observation, and categorising the oocytes by the system proposed by Hilge (1977),

vitelogenesis is thought to occur at oocyte diameters of about 180 μm, with oocytes over 600 μm being categorised as ripe and ready to be spawned. Similar observations were made by Clarke (1982) and Melo and Armstrong (1991), although no hydrated oocytes were found in the former study. These values for vitelogenesis and ripeness fit well with the oocyte size–frequency distributions since in the upper SSL in January, all oocytes are under 180 μm in diameter, indicating that the ovaries of these 1-group fish did not contain any vitelogenic oocytes. However, in the lower SSL in January, a small number of oocytes are over 180 μm, indicating that oocytes may start to be recruited from the large population of primary oocytes long before conditions are conducive for survival of the spawned young. The modal size of the large population of primary oocytes (as also observed by Melo and Armstrong 1991) in 1-group fish is seen to increase to that of the older fish by May, indicating that gonadal development in the younger fish occurs later than in the 2+ fish.

The increased spread in the oocyte size–frequency distribution in March, according to similar studies on bass (Mayer et al. 1987), indicates that these oocytes are being recruited from the large population of primary oocytes into vitelogenesis. This observation is supported by the fact that these oocytes are over 180 μm, which is thought to mark the onset of vitelogenesis. A greater number of larger oocytes are found in fish from the lower SSL, adding further evidence to the older fish spawning first, or at least with greater intensity, than the 1-group fish, although some oocytes were found over 800 μm in the upper SSL.

As the study period progressed, the frequency of the primary oocytes is reduced, while that of the larger oocytes is increased, indicating that oocytes are being recruited into vitelogenesis at a faster rate than primary oocytes are being produced. This is also shown by absolute fecundity falling, especially in the 2+ fish, as the period progresses, and by the reduction in the gradient of the regression lines after March.

Batches of oocytes can be distinguished by the March sample in both SSLs, especially in the 2+ fish. It appears, however, that the batches found in Fig. 9 are a result of the pooling of 25 females, since Fig. 10 shows that the batches in individual *Maurolicus muelleri* are in fact discrete from one another. This result differs from that of Melo and Armstrong (1991) who found that batches were not sharply differentiated from each other and thus classified the fish as an asynchronous oocyte developer. It appears that once the first clutch of oocytes is in the size range corresponding to ripe eggs (i.e. around 600 μm in diameter), a second clutch of oocytes is recruited into vitelogenesis, and hence, once spawning has started, successive batches of oocytes are produced until the end of the spawning period of the fish. The large batch of oocytes, around 1000 μm in the individual fish from June, may indicate that these oocytes were to be imminently spawned. The few oocytes found between 650 and 1000 μm may well be due to oocytes in this size range being spawned and/or undergoing hydration. The rapid increases in oocyte diameter (Mayer et al. 1987) would mean that accumulation of oocytes at any certain size is unlikely.

Thus it can be concluded that *Maurolicus muelleri* shows group synchronous oocyte development, at least two size groups of oocytes being present in the ovaries at the same time, the larger group being more homogeneous than the smaller (Wallace and Selman 1981). Up to three groups may be observed in May and June, one group always being the large population of primary oocytes that the subsequent batches are recruited from. Studies from the Japan Sea (Okiyama 1971), W. Norwegian fjords (Gjøsæter 1981; Rasmussen and Giske 1994), SE Australian waters (Clarke 1982), S. African waters (Melo and Armstrong 1991), and the Red Sea (Dalpadado and Gjøsæter 1987) have also shown batches of oocytes to occur in *M. muelleri*, indicative of a number of spawnings taking place, with batch size showing little geographical variation. Thus it can be concluded that *M. muelleri* spawn several, relatively small batches of oocytes in each breeding period, since no females are found in June without postvitelogenic oocytes in the ovaries. Taking into account their very high absolute fecundity, *M. muelleri* may have evolved group synchrony due to the ovary physically not being able to accommodate all the oocytes ripening at once. De Vlaming (1983) noted that some species showing group synchronous oocyte development have protracted spawning seasons due to lack of population synchrony in gonadal development, as observed here. This observation was used by Karasiova et al. (1987) to explain the length of the spawning season of *M. muelleri* in the N. Atlantic. The "lack of population synchrony in gonadal development" may be explained in *M. muelleri* by the 2+ fish spawning earlier and with greater intensity than the younger fish.

It appears that no postvitelogenic oocytes are held over until the next season, since very few oocytes were found over 180 μm in January in the 2+ fish, indicating that all postvitelogenic oocytes are either spawned or regress. Since 17 June was the last sample studied, no comment can be made as to which of these occurs. However, Melo and Armstrong (1991) did not find atretic oocytes in *Maurolicus muelleri* off S. Africa, while Clarke (1982) did observe what appeared to be regressing oocytes in *M. muelleri* off SE Australia in December. Thus, conclusive evidence awaits the outcome of further work.

The development of the ovary, as determined by the mean of the ten largest oocytes (Fig. 11), shows that in January, all *Maurolicus muelleri* have oocytes that have not yet undergone vitelogenesis. By March, vitelogenesis is seen to occur in the larger fish, with the largest fish having oocytes that are approaching "ripe" oocyte

size, this being achieved in May, especially in the 2+ fish. This further indicates the earlier spawning in older fish.

By June, all fish have oocytes over or approaching ripe size, regardless of fish weight. This would seem to indicate that environmental and/or genetic factors will induce spawning in all fish by June regardless of fish size, this time presumably being the most conducive to egg and larval survival.

Thus it seems that spawning of *Maurolicus muelleri* in Herdlefjorden starts in early spring, with 2+ fish spawning earlier in the year than the 1-group fish, and that, since the whole population of *M. muelleri* does not spawn in discrete pulses, once spawning has started it is more or less continuous until the end of the spawning period. Spring spawning is analogous with other studies on *M. muelleri*, such as Lopes (1979) in the nearby Masfjorden and Fensfjorden, Gjøsæter (1981) in W. Norwegian fjords, Williams and Hart (1974), and Kawaguchi and Mauchline (1987) in the N. Atlantic, and Robertson (1976) in New Zealand waters, although *M. muelleri* was found to spawn throughout the year in the Mediterranean (Steuer 1913; Jespersen and Tåning 1926; Sanzo 1933; all cited by Gamulin and Hure 1985) and in the S. Benguela ecosystem off S. Africa (Prosch 1991), with a spawning period between late winter and spring off SE Australia (Clarke 1982) and off E. Tasmania (Young et al. 1987).

Acknowledgements We thank O.I. Rasmussen, B. Baliño, O. Bjelland, L.A. Hamre, A.G.V. Salvanes and S. Shackley for technical assistance and stimulating discussions, the captains and crews of "*Håkon Mosby*" for kind assistance in Herdlefjorden and E. Holm for graphical assistance. MSG was supported by an ERASMUS stipend and RR was supported by the Norwegian Research Council.

References

Aksnes DL, Giske J (1990) Habitat profitability in pelagic environments. Mar Ecol Prog Ser 64: 209–215

Aksnes DL, Giske J (1993) A theoretical model of aquatic visual feeding. Ecol Modelling 67: 233–250

Baliño BM, Aksnes DL (1993) Winter distribution and migration of the sound scattering layers, zooplankton and micronekton in Masfjorden, western Norway. Mar Ecol Prog Ser 102: 35–50

Clark CW, Levy DA (1988) Diel vertical migration by juvenile sockeye salmon and the antipredation window. Am Nat 131: 271–290

Clarke TA (1982) Distribution, growth and reproduction of the lightfish *Maurolicus muelleri* (Sternoptychidae) off south-east Australia. Rep mar Lab CSIRO 145: 1–10

Clearwater SJ, Pankhurst NW (1994) Reproductive biology and endocrinology of female red gurnard, *Chelidonichthys kumu* (Lesson and Garnot) (Family Triglidae) from the Hauraki Gulf, New Zealand. Aust J mar Freshwat Res 45: 131–139

Dalpadado P, Gjøsæter J (1987) Observations on mesopelagic fish from the Red Sea. Mar Biol 96: 173–183

De Vlaming V (1983) Oocyte developmental patterns and hormonal involvements among teleosts. In: Rankin C, Pitcher TJ, Duggan RT (eds) Control processes in fish physiology. Croom Helm, London, pp 176–199

Dipper FA, Pullen RSV (1979) Gonochorism and sex-inversion in British Labridae (Pisces). Comp Biochem Physiol 187: 97–112

Gamulin T, Hure J (1985) The distribution of midwater fish *Maurolicus muelleri* (Gmelin) eggs in the Jabuka Pit region of the Adriatic Sea. Mar Ecol Naples 6: 321–328

Giske J, Aksnes DL (1992) Ontogeny, season and trade offs: vertical distribution of the mesopelagic fish *Maurolicus muelleri*. Sarsia 77: 253–261

Giske J, Aksnes DL, Baliño BM, Kaartvedt S, Lie U, Nordeide JT, Salvanes AGV, Wakili SM, Aadnesen A (1990) Vertical distribution and trophic interactions of zooplankton and fish in Masfjorden, Norway. Sarsia 75: 65–81

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

Gjøsæter J, Kawaguchi K (1980) A review of the world resources of mesopelagic fish. FAO Fish tech Pap No 193

Hilge V (1977) On the determination of the stage of gonad ripeness in female bony fishes. Meeresforsch 25: 149–155

Hislop JRG (1975) The breeding and growth of whiting, *Merlangus merlangus*, in captivity. J Cons int Explor Mer 36: 119–127

Hislop JRG, Bell MA (1987) Observations on the size, dry weight, and energy content of the eggs of some demersal fish species from British marine waters. J Fish Biol 31: 1–20

Jespersen P, Tåning Å V (1926) Mediterranean Sternoptychidae. Rep Dan oceanogr Exped Mediterr 1908–1910 2: 1–59

Kaartvedt S, Aksnes DL, Aadnesen A (1988) Winter distribution of macroplankton and micronecton in Masfjorden, western Norway. Mar Ecol Prog Ser 45: 45–55

Karasiova EM, Feldman VN, Malkov AS (1987) Seasonal and spatial spawning dynamics of *Maurolicus muelleri* in the North Atlantic. Int Counc Explor Sea Comm Meet (Pelagic Fish Comm) H: 28

Kawaguchi K, Mauchline J (1987) Biology of Sternoptychid fishes Rockall Trough, northeastern Atlantic Ocean. Biol Oceanogr (NY) 4: 99–120

Koutsoyiannis A (1977) Theory of econometrics: an introductory exposition of econometric methods. Macmillan Press Ltd, Hong Kong

Langley R (1979) Practical statistics simply explained. 2 edn. Pan Books, London

Lopes P do C (1979) Eggs and larvae of *Maurolicus muelleri* (Gonostomatidae) and other fish eggs and larvae from two fjords in western Norway. Sarsia 64: 199–210

Mackay NJ (1973) Histological changes in the ovaries of the golden perch, *Plectroplites ambiguus*, associated with the reproductive cycle. Aust J mar Freshwat Res 24: 95–101

Mayer I (1987) Reproductive biology of the bass, *Dicentrarchus labrax* L. Unpublished Ph.D. thesis, University of Wales, Swansea

Mayer I, Shackley SE, Witthames PR (1989) Aspects of the reproductive biology of the bass, *Dicentrarchus labrax* L. II. Fecundity and pattern of oocyte development. J Fish Biol 36: 141–148

Melo YC, Armstrong MJ (1991) Batch spawning behaviour in Lightfish *Maurolicus muelleri*. S Afr J mar Sci 10: 125–130

Nedreaas K, Smedstad OM (1987) Abundance and distribution of postlarvae in the 0-group saithe survey in the North Sea and the northeast Arctic in 1986 and 1987. Int Counc Explor Sea Comm Meet (Demersal Fish Comm) G: 31

Okiyama M (1971) Early life history of the gonostomatid fish, *Maurolicus muelleri* (Gmelin), in the Japan Sea. Bull Japan Sea reg Fish Res Lab 23: 21–53

Prosch RM (1991) Reproductive biology and spawning of the myctophid *Lampanyctodes hectoris* and the sternoptychid *Maurolicus muelleri* in the southern Benguela ecosystem. S Afr J mar Sci 10: 241–252

Rasmussen OI, Giske J (1994) Life-history parameters and vertical distribution of *Maurolicus muelleri* in Masfjorden in summer. Mar Biol 120: 649–664

Robertson DA (1976) Planktonic stages of *Maurolicus muelleri* (Teleostei: Sternoptychidae) in New Zealand waters. NZ J1 mar Freshwat Res 10: 311–328

Rosland R, Giske J (1994) A dynamic optimization model of the diel vertical distribution of a pelagic planktivorous fish. Prog Oceanogr 34: 1–43

Sanzo L (1933) Uova, larve e stadi giovanili di Teleosti. Famiglia Argentinidae, Microstomidae, Sternoptychidae, Stomiatidae. Fauna Flora Golfo Napoli 38: 21–92

Simpson AC (1959) The spawning of the plaice (*Pleuronectes platessa*) in the North Sea. Fishery investigations. Series II, marine fisheries. Great Britain Ministry of Agriculture, Fisheries, and Food, London No. 22 (7)

Steuer A (1912) Einige Ergebnisse der VII Terminfahrt S.M.S. "Najade" im Sommer 1912 in der Adria. Int Rev ges Hydrobiol Hydrogr 5: 551–570

Utne ACW, Aksnes DL (1994) An experimental study on the influence of feeding versus predation risk in the habitat choice of juvenile and adult two-spotted goby *Gobiusculus flavescens* (Fabricius). J exp mar Biol Ecol 179: 69–79

Wallace RA, Selman K (1981) Cellular and dynamic aspects of oocyte growth in teleosts. Am Zool 21: 325–343

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. A Rev Ecol Syst 15: 393–425

West G (1990) Methods of assessing ovarian development in fishes: a review. Aust J mar Freshwat Res 41: 199–222

Williams R, Hart PJB (1974) Vertical and seasonal variability of fish eggs and larvae of Ocean Weather Station "India". In: Blaxter JHS (ed) The early life history of fish. Springer-Verlag, Berlin

Young JW, Blaber SJM, Rose R (1987) Reproductive biology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia. Mar Biol 95: 323–332

Yuuki Y (1982) Spawning and maturity of a sternoptychid fish *Maurolicus muelleri* in the southwestern waters of the Sea of Japan. Bull Jap Soc scient Fish 48: 749–753

Zar JH (1984) Biostatistical Analysis. Prentice-Hall, New Jersey