Metabolism, body composition, and energy budget of the mesopelagic fish *Maurolicus muelleri* in the Sea of Japan

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Abstract.—Metabolic activity (=oxygen consumption), chemical composition (water, ash, carbon [C], hydrogen [H], nitrogen [N]), and caloric content were determined for various developmental stages of the mesopelagic fish *Maurolicus muelleri* from the Sea of Japan. Oxygen consumption rates were estimated from enzyme activity involved in the respiratory electron transport system (ETS). Body composition varied with development of the fish, ranging from 68.3 to 78.3% of wet weight (WW) for water, 10.7 to 25.7% of dry weight (DW) for ash, 34.1 to 54.4% of DW for C, 5.1 to 8.4% of DW for H, 7.2 to 12.2% of DW for N, and 1.02 to 1.98 Kcal/g WW or 3.51 to 6.33 Kcal/g DW for caloric content. Condition factor index (CFI) ranged from 5.2 to 9.5 (mg WW$\times 10^3$/(mm TL)^3). Caloric content, C, H, and CFI increased with development, but the reverse was the case for water, ash, and N. Age-to-age and lifetime energy budgets were established, i.e. metabolic data from ETS assay and caloric data from body composition analyses, combined with natural growth data. The results indicated that higher age-specific net growth efficiency was associated with younger ages, decreasing toward the end of life, with a lifetime average of 17%. Estimated age-specific daily ration followed the same pattern, with a lifetime average of 2.9%/day. From the gonad index and caloric contents of gonads, energy invested in reproduction was calculated as 1.3% of the lifetime sum of assimilated energy for females and as 0.6% for males. Because the number of iterative spawnings during the lifetime of *M. muelleri* is unknown, this energy partition to reproduction is a conservative estimate. From the comparison of the present results with those for other mesopelagic fishes off southern California, it is suggested that *M. muelleri* is a more efficient mediator of energy flow and matter cycling in the pelagic ecosystem because of its smaller size and shorter life span.

Manuscript accepted 8 September 1995.
Fishery Bulletin 94:49–58 (1996).

Maurolicus muelleri (Gmelin) is a small, short-lived sternoptychid fish distributed in the mesopelagic zone of tropical, subtropical, subarctic, and subantarctic waters of the Pacific and Atlantic Oceans (Kawaguchi and Mauchline, 1987). Gjøsaeter (1981) and Kawaguchi and Mauchline (1987) have reviewed the biology and ecology of *M. muelleri* and have pointed out the geographical variability in the life mode of this fish.

Maurolicus muelleri is the only micronektonic fish in the Sea of Japan, yet its stock size has been estimated as 3.3×10^6 metric tons (Okiyama, 1981). It is reported to mature at age 1 yr in the Sea of Japan, and to grow to 60 mm SL (Yuuki, 1982, 1984; Ikeda, 1994). The estimated life span of the fish is 20–22 months. Spawning is aseasonal with two peaks in spring and autumn or only one peak in autumn (Yuuki, 1982; Ikeda, 1994). Possible iterative spawnings have been suggested (Okiyama, 1971; Yuuki, 1982), and migrations up to a 50-m depth at night and down to below a 150-m depth during the day have been reported (Hamano et al., 1992). Copepods are numerically the most important dietary component of this species, with euphausiids second (Ikeda et al., 1994).

In order to evaluate the quantitative roles of *M. muelleri* in the pelagic ecosystem of the Sea of Japan, information about partitioning of materials or energy for various processes is required. However, little information about material and energy budget is available for this fish because of the lack of appropriate physiological data. A major problem inherent in an experimental study of *M. muelleri* is the difficulty in maintaining them under laboratory conditions. This problem is not limited only to *M. muelleri* but is also seen in other mesopelagic fishes (cf. Robinson, 1973). Along with this difficulty, direct measurement of the respiratory oxygen consumption rate of mesopelagic fishes is currently limited to those living for a short period of time in the laboratory after capture (Torres et al., 1979; Donnelly and Torres, 1988). Since "metabolism," estimated from respiratory oxygen consumption, is of central importance in estimating the energy budget of fishes (Winberg, 1956), the lack of adequate techniques for maintaining mesopelagic fishes makes it difficult to calculate energy used for metabolism.

Because of this difficulty in measuring respiratory oxygen consumption directly, Ikeda (1989) used the enzyme activity of the respiratory electron transport system (ETS) as an indirect measure of routine metabolism of myctophid fishes in the field. The energy-producing process

through oxygen consumption in cells is mediated mostly by the formation of adenosine triphosphate (ATP), and this oxidative phosphorylation is driven by ETS that is embedded in the inner membrane of eukaryotic mitochondria and in the cell membrane of prokaryotes (cf. Packard, 1985). The ETS assay was first introduced for the study of plankton respiration (Packard et al., 1971, 1975), and additional data have been accumulated (Packard, 1985). Although application of this assay to fish respiration is currently limited to only a few studies (Ikeda, 1989; Yamashita and Bailey, 1990), this method is advantageous in that incubation of live specimens is not necessary, and it is almost free from the effect of physiological stress incurred during capture of fish in the field. The ETS activity represents a potential rather than an actual oxygen consumption rate. In this respect, the ratio of ETS activity to respiratory oxygen consumption is known to be quite constant across various systematic groups of animals (King and Packard, 1975). The biochemical basis of the ETS assay and the rationale for the estimation of respiratory oxygen consumption rates are detailed in Packard (1985).

In the present study, ETS activity was determined and used as a basis to estimate respiratory oxygen consumption rates of *M. muelleri* from the Sea of Japan. The chemical composition of fish and gonads at various developmental stages was determined. These metabolic and chemical composition data were combined with natural growth rate data to establish an energy budget pattern for *M. muelleri* over its lifetime.

Materials and methods

Fish

Fishes were collected from Toyama Bay and Sado Strait (both within the southern Sea of Japan) and from waters around Yamato Rise (central Sea of Japan) aboard the RV *Mizuho-Maru* from September 1988 through September 1992. Collections were made at night with a 2-m Isaacs-Kidd midwater trawl (1.5 mm mesh) which was towed obliquely from 100–250 m depths to the surface. Fish-larvae nets (0.5 mm mesh) were used to collect larvae and small juveniles. For the collection of specimens used for the ETS assay, the trawl and nets were towed slowly (1.5 knots) for a short time period (10 min) to avoid damage to the specimens. Immediately following net retrieval, fishes in the codend were transferred to a bucket filled with seawater. For body composition analyses and ETS assay, specimens were placed on filter paper to remove excess water on the body surface, measured for body length, and were frozen (<–20°C). Total length (TL: from tip of the snout to end of the tail), instead of standard length (SL), was used throughout this study to facilitate work on shipboard. For conversion of TL to SL the equation $SL = 0.822TL + 0.161$ may be used (Ikeda, 1994).

Metabolism

ETS activity was measured in individual fish within two weeks after collection by the modified tetrazolium reduction method (Owens and King, 1975). The general procedure of ETS assay for fish samples is described elsewhere (Ikeda, 1989). No significant loss of ETS activity during storage for 36 days at –20°C has been reported for two fish species (Ikeda, 1989). The homogenates were incubated at 12°C, the estimated daily mean temperature encountered by *M. muelleri* during their diel vertical migration. In a separate test, the effect of temperature on ETS activity was assessed at six temperatures (0.5°, 4°, 8°, 12°, 16°, and 20°C).

For the conversion of ETS activity to actual respiratory oxygen consumption (R), $ETS/R = 2$ was proposed on the assumption that Michaelis-Menten kinetics could be applied to respiratory chemistry and that the concentration of the respiratory regulator (i.e. ADP) was maintained near the Km (cf. Packard, 1985). The ETS:R ratios obtained directly from crustacean plankton and fishes are close to this theoretical value (Table 1). Hence, $ETS/R = 2$ was used to convert ETS to R in this study.

Oxygen consumption was converted to caloric units by using the equivalent of 4.80 cal/mL O_2 (Gnaiger, 1983).

Condition factor index and body composition

Condition factor index (CFI) was defined as wet weight $(WW) \times 10^3/(TL)^3$ for this study.

Frozen specimens were weighed (WW in mg) and then freeze-dried, dried further at 60°C for 5 hours to remove residual water, and then weighed (DW in mg). Dried specimens were pooled on the basis of TL into eight size groups (<10, 10 to <15, 15 to <20, 20 to <30, 30 to <40, 40 to <50, 50 to <60, and ≥60 mm TL) and were ground into a fine powder with a ceramic mortar and pestle. No separation by sex was made. However, adult males are known to be 35 to 55 mm TL in the Sea of Japan (Ikeda, 1994), therefore some males may have been included in the 30 to <40 mm, 40 to <50 mm, and 50 to <60 mm TL groups but none in the ≥60 mm TL group. Powdered samples were used for elemental analyses and ash determinations.

Table 1

The ETS:R ratio for zooplankton and fishes. Note that the ratio is dimensionless.

Animal	*n*	ETS:R Mean ±SD	Reference
Zooplankton			
Calanoides carinatus	13	1.74 ±0.62[1]	Packard et al. (1975)
Calanus pacificus	48	2.02 ±0.29	Owens and King (1975)
Acartia tonsa	13	1.91 ±0.21	Bamstedt (1980)
"Antarctic zooplankton"	12	1.86 ±0.74	Ikeda and Hing Fay (1981)
Fish			
Pomacentrus popeii	5	1.54 ±0.53	Ikeda (1989)
Gobiidae sp.	12	1.63 ±0.28	Ikeda (1989)
Theragra chalcogramma (feeding larvae)	27	2.13 ±0.72	Yamashita and Bailey (1990)

[1] Recalculated by Packard (1985).

Gonads (ovaries and testes) were removed from frozen specimens >36 mm TL and weighed (WW). Prior to freeze-drying and grinding, the diameter of oocytes was measured by using a microscope, and ovaries with oocytes >0.5 mm diameter were defined as "mature" (Ikeda, 1994). For some mature ovaries, the individual oocytes were dissected after freeze-drying. These gonads and isolated oocytes were used in subsequent analyses.

Carbon (C), hydrogen (H), and nitrogen (N) were analyzed with an elemental analyzer (Yanaco CHN Corder MT-5, Yanagimoto Co., Ltd., Kyoto) with antipyrine as a standard. A weighed fraction of each sample was incinerated at 480°C for 5 hours and reweighed for ash determination. All measurements were made in duplicate for each sample. From replicated determinations (n=10) on the same sample, the precision of these analyses, as expressed by the coefficient of variations (SD/mean, %), were 1% for C and H, 2% for N, and 7% for ash. The elemental composition data were expressed as the percentage of DW, or as the percentage of ash-free dry weight (AFDW). The caloric content was calculated by using a formula given by Gnaiger (1983), amended by Gnaiger and Shick (1985): $(4.436W_N + 66.265W_c - 11.2)/4.18$, where W_N and W_c are fractions of N and C, respectively, on an AFDW basis.

Energy budget

Calculation of the energy budget is based on the basic balanced equation of Winberg (1956), i.e.

$$0.8 \times F = M + G,$$

and

$$K_2 = 100 \times G/(G + M),$$

where 0.8 is the generalized assimilation efficiency, F is the daily food ingestion, M is the daily metabolism, G is the daily growth, and K_2 is the net growth efficiency (note that some symbols were changed from those used by Winberg [1956]). Energy associated with loss in scales, mucus secretion, excretion, etc. were considered to be negligible and were omitted. Energy use for reproduction was estimated from calorific data of isolated gonads. F is often expressed as the percentage of body energy (=daily ration, F').

The growth in length of *M. muelleri* has been shown to fit well to the von Bertalanffy curve (Gjøsaeter, 1981; Yuuki, 1984; Ikeda, 1994): $TL = TL_\infty (1 - e^{-K(t-t_0)})$, where TL_∞ is the theoretical maximum size, K is a growth factor, and t_0 is the time (yr) at which growth starts. In the calculation of the energy budget, the curve of *M. muelleri* in Toyama Bay, southern Sea of Japan, established by Ikeda (1994) was used: i.e. TL_∞= 59.5 mm, K = 1.19, and t_0 = 0.65 (yr). On the basis of the hatching size (ca. 3 mm) of *M. muelleri*, t=0.7 (TL=3.6 mm) was assumed as the start of growth for this fish, and the growth calculation was made in 0.1 yr (=36.5 d) increments. Total length at a given age of the fish was converted to wet weight (WW in mg) by using the allometric equation established in the present study (WW=0.00211$TL^{3.346}$ [r=0.997, n=312]), then to caloric units by multiplying with the appropriate conversion factor (Kcal/g WW) obtained from chemical composition analyses. For the calculation of between-age metabolic expenditure, a mean value, multiplied by 36.5 d, was used. Between-age values thus obtained were also used to compute age-specific net growth efficiency (K_2) and daily ration (F').

Results

Metabolism

A total of 49 fishes (57–1,327 mg WW) were used for the ETS assay. A scatter diagram showing the relationship between specific oxygen consumption rates (R/WW: μL O_2/(mg WW·h)) and WW is presented in Figure 1. The effect of WW on oxygen consumption rates (R: μL O_2/(fish·h)) was examined by using a GM regression model (Ricker, 1973), $\log_{10}R = v \log_{10}WW + \log_{10}u$, where v and u are constants. Estimates were v = 0.987 (95% CI: 0.917–1.053) and $\log_{10}u$ = –0.609 for the data derived from the ETS assay. The v did not differ significantly from unity (v=1). On this basis, a mean specific oxygen consumption rate (R/WW) was calculated as 0.225 (±0.038 SD).

The relationship between ETS activity (ETS: μL O_2/(mg WW·h)) and temperature (°C) was linear over the temperature tested (0.5 to 20°C) on a semilog graph (Fig. 2). The relationship was expressed as

$$\log_{10}ETS = 0.0541\ (95\%\ \text{CI: } 0.0472 - 0.0610)T - 1.0440, \text{ for fish 1}$$

and

$$\log_{10}ETS = 0.0554\ (95\%\ \text{CI: } 0.0490 - 0.0618)T - 1.0038, \text{ for fish 2.}$$

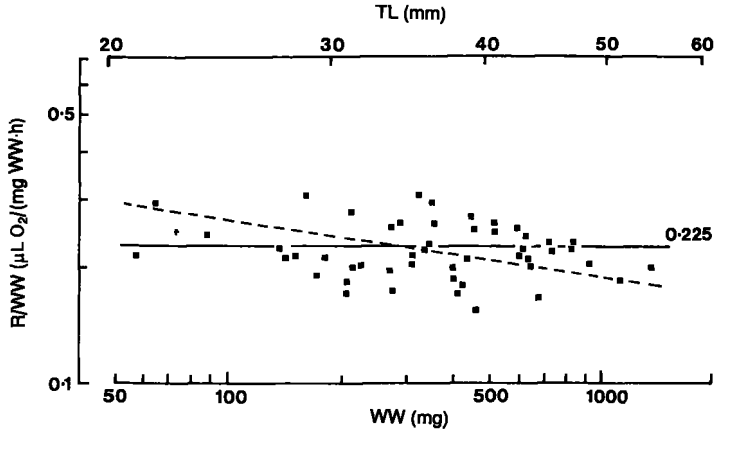

Figure 1

Relationship between specific oxygen consumption rates (R/WW, μL O_2/(mg WW·h) at 12°C) and wet weight (mg WW) obtained from ETS assay (ETS activity × 0.5) for *Maurolicus muelleri*. Because statistical analysis indicated no effect of WW, a mean was calculated and superimposed. The broken line is the relationship expected when size-dependent metabolism is assumed for ETS data (i.e. $R \propto WW^{0.85}$ or $R/WW \propto WW^{-0.15}$, see text for details). Top abscissa denotes body length (mm TL) equivalent to mg WW of bottom abscissa.

The slope of these two regression lines did not differ significantly. From a common slope (0.0547) that was computed, a Q_{10} = 3.52 was derived.

Condition factor index, body composition, and caloric content

Over all size groups (<10 to >60 mm TL), the ranges recorded were 5.23 to 9.53 for CFI, 68.8 to 78.8 (% WW) for water, 10.7 to 25.7 (% DW) for ash, 34.1 to 54.4 (% DW) for C, 7.2 to 12.2 (% DW) for N, 5.1 to 8.4 (% DW) for H, and 1.02 to 1.98 (Kcal/g WW) or 3.51 to 6.33 (Kcal/g DW) for caloric content (Table 2).

Changes in these variables with increasing TL were examined by using three regression models: linear ($Y = aX + b$), power ($Y = aX^b$) and exponential ($Y = ae^{bX}$). In these analyses, X was represented by the mid-range value for each size group except that 10 was used for the <10 mm TL group and 60 for the ≥60 mm TL group. Among these three regression models, the best was selected, as judged by the highest correlation coefficient. The analyses revealed two opposite patterns, i.e. an increase (CFI, C, H, and caloric contents) or a decrease (water, ash, and N) with the growth of *M. muelleri*. All regressions were significant (Table 2) except for N. The decrease of N with an increase in TL, however, was significant if data from the <10 mm TL group were removed (r=–0.947, P<0.01).

The results of analyses on gonads are summarized in Table 3. Among mature ovaries, oocytes, and testes, the oocytes exhibited the highest caloric content (5.61 Kcal/g DW), followed by mature ovaries (4.88 Kcal/g DW). The lowest caloric content (4.66 and 4.79 Kcal/g DW) was recorded on two testicular samples.

Energy budget

The patterns of energy utilization for cumulative growth (G) and cumulative metabolic expenditure (M), and changes in age-specific net growth efficiency (K_2) and age-specific daily ration (F') of 0-yr-old through 1.8-yr-old *M. muelleri* are shown in Figure 3. K_2 and F' were the highest at the beginning of life and decreased progressively toward the end of life at 1.8 years. Irregularities in the pattern, which are most pronounced for K_2, reflect the change of multiplier (Kcal/g WW) to convert WW to calories. The overall ranges of K_2 and F' were 7.6 to 61.6% (lifetime average: 16.7%) and 2.4 to 10.4% (2.9%), respectively.

Table 2

Condition factor index (CFI), water and ash contents, elemental composition (C, N, H), and calculated caloric content (per WW and per DW bases) of eight size groups of *Maurolicus muelleri*. Mean ± SD. *n* denotes the number of samples from different sampling dates (replicates for ash, elemental composition, and calorific content), and the total number of fishes is in parentheses (replicates for CFI and water). The changing pattern with the increase of size was examined by using three regression models (linear, power, exponential) and its significance was judged by the correlation coefficients. Models indicated had the highest correlation coefficient. ND = not determined.

					Elemental composition			Calorific content	
TL (mm)	*n*	CFI	Water (%WW)	Ash (%DW)	C (%DW)	N (%DW)	H (%DW)	(Kcal/g WW)	(Kcal/g DW)
<10	1(14)	ND	ND	25.7	34.1	8.5	5.1	ND	3.51
10 to <15	2(31)	5.23 ±0.52	77.0 ±0.9	16.0 ±0.5	42.3 ±0.5	11.9 ±0.1	6.4 ±0.1	1.05 ±0.03	4.83 ±0.29
15 to <20	2(34)	5.51 ±0.55	77.0 ±1.8	15.8 ±0.2	42.1 ±0.2	12.1 ±0.3	6.1 ±0.1	1.05 ±0.08	4.74 ± 0.31
20 to <30	3(40)	6.91 ±0.43	78.8 ±0.2	14.0 ±0.9	43.8 ±0.2	12.2 ±0.5	6.4 ±0.1	1.02 ±0.02	4.91 ±0.24
30 to <40	4(52)	7.35 ±0.46	77.7 ±2.2	13.7 ±1.9	45.3 ±2.8	11.1 ±1.3	6.8 ±0.7	1.13 ±0.20	4.95 ±0.34
40 to <50	6(59)	7.69 ±0.73	75.5 ±2.6	13.4 ± 4.0	48.0 ±3.4	9.5 ±1.1	7.1 ±0.5	1.33 ±0.24	5.51 ±0.61
50 to <60	5(46)	7.99 ±0.98	74.1 ±3.2	10.7 ±2.0	50.0 ±2.7	8.8 ±1.2	7.5 ±0.4	1.47 ±0.27	5.43 ±0.62
≥60	2(6)	9.53 ±0.78	68.8 ±1.1	11.4 ±5.4	54.4 ±2.3	7.2 ±0.1	8.4 ±0.4	1.98 ±0.13	6.33 ±0.22
Correlation to TL (*r*)		0.966**	–0.782*	–0.892**	0.926**	–0.620	0.925**	0.908**	0.864**
Regression model		Power	Linear	Power	Linear	Exponen	Linear	Exponen	Linear

*$P<0.05$, **$P<0.01$.

Energy invested in reproduction is partly included in *G* in the present calculation (e.g. *G* is derived from intact fishes including gonads, but neither eggs nor sperm already released were included). The greatest proportional weight of gonads for *M. muelleri* in Toyama Bay has been reported as 10% of WW for females and 6% of WW for males (recalculated from gonad index data in Ikeda, 1994). From the caloric content of adults given in Table 2 (1.47 Kcal/g WW) and those of ovaries (1.12 Kcal/g WW) and testes (0.93 Kcal/g WW) in Table 3, the proportions of energy in the form of ovaries and testes were computed as 7.6% (10 × 1.12/1.47) and 3.8% (8.6 × 0.93/1.47), respectively, of *G* (1,820 cal) in 1.8-yr-old fish (53 mm TL). When *M* is combined with *G* (i.e. assimilated energy: 1,820 + 9,075 cal), the fraction of energy stored in gonads becomes 1.3% for females and 0.6 % for males. Alternatively, energy invested in egg production in females may be estimated by knowing the number of mature oocytes. The DW of single mature oocytes is 34 μg (±1.76, n=5), and the maximum number counted for *M. muelleri* in Toyama Bay is 283 (Ikeda, 1994). These figures, combined with calorific content of the oocytes (5.61 Kcal/g WW, Table 4) yield 54.0 cal ($34 \times 10^{-6} \times 5.61 \times 10^{3} \times 283$), which corresponds to 0.5% of energy assimilated (1,820 + 9,075 cal) by 1.8-yr-old fish.

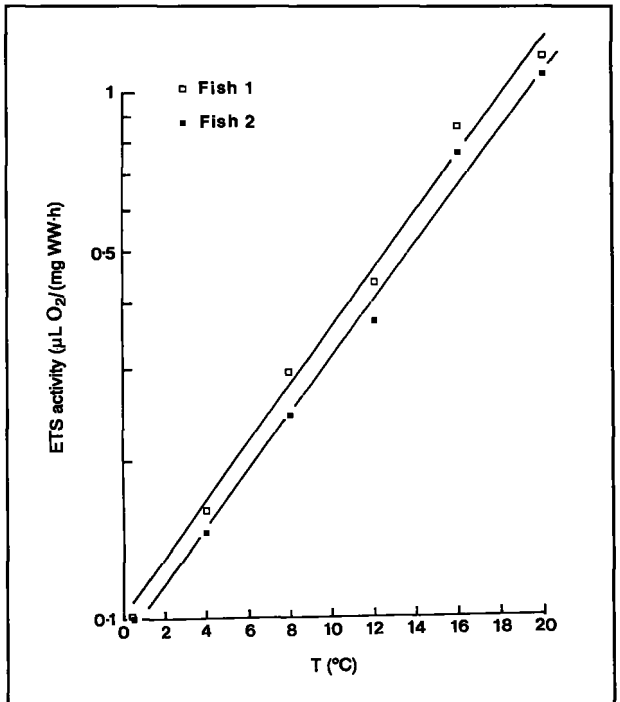

Figure 2

Relationship between ETS activity (ETS: μL O_2/(mg WW·h)) and temperature (°C)(fish 1: 442 mg WW, and fish 2: 472 mg WW) for *Maurolicus muelleri*. Slopes are not significantly different (*t*-test, $P>0.05$).

Table 3

Water and ash contents, elemental composition (C, N, H), and calculated caloric content (per WW and per DW bases) of gonads in *Maurolicus muelleri*. Mean ±SD. The number of ovaries and testes combined for the analysis is in parentheses. Ovaries with oocytes >0.5 mm in diameter are designated as mature ones. ND = not determined.

	Sampling date	Water (%WW)	Ash (%DW)	C (%DW)	N (%DW)	H (%DW)	Kcal/g WW	Kcal/g DW
♀ mature ovaries (9)	Apr 1989	77.0 ±2.3	9.0 ±0.2	45.5 ±0.1	10.7 ±0.4	6.6 ±0.0	1.12 ±0.00	4.89 ±0.01
♀ oocytes	Apr 1989	ND	5.6 ±0.1	50.7 ±0.8	10.0 ±0.1	7.6 ±0.1	ND	5.61 ±0.12
♂ testes (2)	Apr 1989	83.0 ±1.4	9.7 ±0.1	43.9 ±0.1	11.5 ±0.1	6.2 ±0.1	0.79 ±0.00	4.66 ±0.01
♂ testes (4)	Sep 1992	80.5 ±0.3	17.5 ±0.4	43.0 ±0.0	12.8 ±0.2	6.2 ±0.0	0.93 ±0.00	4.79 ±0.00

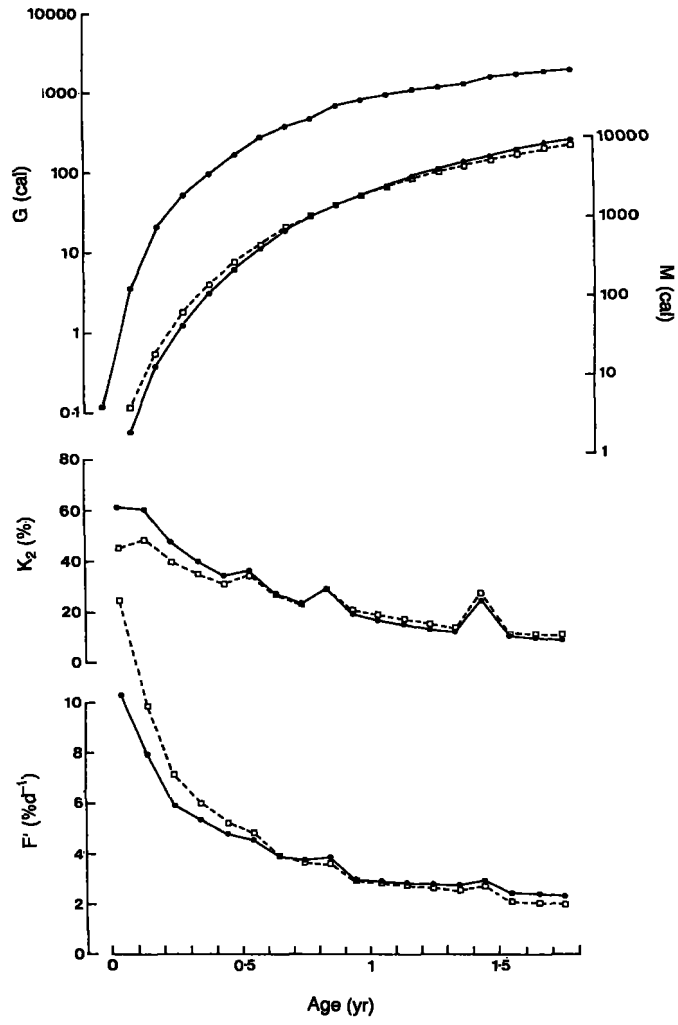

Figure 3

Changes with age of cumulative energy utilized for growth (*G*) and metabolism (*M*)(top), age-specific net growth efficiency (K_2)(middle); and daily ration (*F'*)(bottom) for *Maurolicus muelleri*. For *M*, K_2, and *F'*, solid line represents size-independent metabolism, and broken line size-dependent metabolism.

Discussion

The decrease of specific oxygen consumption rates (R/WW) with the increase of body size is a widespread phenomenon in animals (Zeuthen, 1953; Hemmingsen, 1960) but is often masked by narrow size coverage and the scatter of data (Hemmingsen, 1960). From this view, R/WW independent of size of specimens obtained in this study may be an artifact due to incomplete coverage of the entire body-size range of *M. muelleri* (specimens less than 57mg WW or 20 mm TL were not used in the ETS assay). If a general body weight exponent of $v = 0.85$ given for fishes (Winberg, 1956; modified by Ricker, 1973) is adopted, $R = 0.534WW^{0.85}$ is obtained from the same ETS assay data (cf. Fig. 1). In the present study, differences in the energy budget calculations due to the use of size-dependent *M*, instead of size-independent *M*, were also examined (Fig. 3; Table 4).

The differences due to the use of size-dependent *M*, instead of size-independent *M*, were most pronounced at younger stages, in which the size-dependent *M* yielded lower age-specific K_2 and higher age-specific *F'* (Fig. 3). However, choice of size-independent *M* or size-dependent *M* had little effect on the results of lifetime averages of K_2 (16.7% vs. 18.5%) and *F'* (2.9% vs. 2.6%)(Table 4). The choice of size-dependent *M*, instead of size-independent *M*, again had little effect on calculations of the fraction of energy stored in gonads (the former added only 0.1% to figures derived from size-independent *M*).

Information about metabolic rate of micronektonic fishes is currently limited. Whole-animal respirometry data of typical epipelagic fish were obtained by Lasker (1970), who successfully maintained Pacific sardine (*Sardinops caerulea*) in the laboratory and measured

Table 4

Energy budget parameters and calculated lifetime sums of energy expenditure for metabolism (M) and growth (G), and lifetime averages of net growth efficiency (K_2) and daily ration (F') for *Maurolicus muelleri*. Both size-independent (v=1) and size-dependent metabolism (v=0.85) were assumed for the calculation of M and parameters including M. Note that 0.9 yr is the mid-lifetime of this fish.

Life span (yr)	1.8	
Body size at 0 and 1.8 yr (0.9 yr)		
Length (TL in mm)	3.6, 53.0 (36.0)	
Wet weight (WW in mg)	0.15, 1,238 (537)	
Energy (cal)	0.12, 1,820 (722)	
Lifetime sum		
Metabolism (M, cal)	when v=1	9,075
	when v=0.85	7,998
Growth (G, cal)		1,820
Lifetime average		
Net growth efficiency (K_2, %)	when v=1	(1,820 × 100)/(1,820 + 9,075) = 16.7
	when v=0.85	(1,820 × 100)/(1,820 + 7,998) = 18.5
Daily ration (F', %)	when v=1	((1,820 + 9,075) × 100)/(0.8 × 1.8 × 365 × 722) = 2.9
	when v=0.85	((1,820 + 7,998) × 100)/(0.8 × 1.8 × 365 × 722) = 2.6

0.3 μL O_2/(mg WW·h) at 16.5–22°C (median 19°C) for specimens weighing 25–189 g WW (median 48.5 g WW). For mesopelagic fishes off southern California, Torres et al. (1979) reported 0.059–0.095 μL O_2/(mg WW·h) (mean 0.073 μL O_2/(mg WW·h)) at 10°C on four species weighing 2.1–9.3 g WW (mean 6.1 g WW). Because body size and temperature are two dominant factors affecting oxygen consumption, direct comparison with the present data on *M. muelleri* is not possible. To overcome this problem, the specific oxygen consumption data given by these previous workers were extrapolated to the mean size of *M. muelleri* (429 mg WW) used for ETS assay, assuming size-dependent metabolism as mentioned above ($R \propto WW^{0.85}$), and adjusted to the rates at 12°C by using a factor for temperature adjustment in Winberg (1956). As a result, we obtain 0.31 μL O_2/(mg WW·h) for the Pacific sardine, and 0.11 μL O_2/(mg WW·h) for four mesopelagic fishes off southern California. Specific oxygen consumption rates for *M. muelleri* (0.225 μL O_2/(mg WW·h)) estimated from ETS activity in this study fall near the center of the range of these high epipelagic and low mesopelagic rates. Lower specific oxygen consumption rates of deeper living fishes are attributed to their greatly reduced locomotion (Torres et al., 1979). From this view, the results of this comparison suggest differential activity levels for each fish. The activity of *M. muelleri* is relatively lower than that of the Pacific sardine but higher than those of its mesopelagic counterparts off southern California.

The Q_{10} = 3.52 derived from the relationship between the ETS activity and temperature for *M. muelleri* (Fig. 2) in the present study appears rather anomalous (i.e. Q_{10}=2 to 3 for various biological processes, cf. Prosser, 1961) but is close to Q_{10} = 3.90 and 3.24 for myctophid and nonmyctophid (*Anoplogaster cornuta*, *Gonostoma elongatum*) fishes, respectively, from the eastern Gulf of Mexico (Donnelly and Torres, 1988). Because *M. muelleri* and both myctophid and nonmyctophid fishes studied by Donnelly and Torres (1988) are diel vertical migrators, these greater Q_{10} values suggest that diel fluctuations in metabolic rates are associated with daily vertical movements in stratified water. Diel fluctuation in metabolic activity associated with diel vertical migration was ignored in this study on the premise that daily metabolism of *M. muelleri* was determined by integrated daily mean temperature (12°C), as has been demonstrated experimentally on the hyperiid amphipod *Themisto japonica*, which exhibits an extensive diel vertical migration (Ikeda, 1992).

With regard to the developmental changes in body condition and composition, there are no published data available for comparison with the present data on *M. muelleri*. However, studies on nonmesopelagic fishes, including red sea bream (*Chrysophrys major*) by Anraku and Azeta (1973) and walleye pollock (*Theragra chalcogramma*) by Harris et al. (1986), have demonstrated increases of CFI, C, and caloric contents and decreases in water, ash, and N in asso-

ciation with growth of these fishes. Although neither of these previous studies on nonmesopelagic fishes included adult individuals, the general patterns of change in body condition and composition over the course of growth are consistent with those observed in *M. muelleri*. Progressive accumulation of lipid in the body is thought to be the cause of these developmental changes in CFI, elemental composition, and caloric content (Anraku and Azeta, 1973; Harris et al., 1986). Accumulation of lipid around the digestive tract, gonads, and liver was confirmed for mature adults of *M. muelleri* in the present study, supporting the idea that accumulation of body lipid results in the other changes noted.

On the basis of analyses of 37 fish species of mixed ages and living at various depths off southern California, Childress and Nygaard (1973) concluded that deeper living fishes are characterized by higher water and lower caloric contents. Compared with the results of Childress and Nygaard (1973), the present data on water and caloric contents of *M. muelleri* fall somewhere between those living in epipelagic and mesopelagic zones off southern California. Thus, the general bathymetric level at which the population of *M. muelleri* lives, extrapolated from body composition data, is in general agreement with direct field observation (50 to >150 m depth, Hamano et al., 1992).

Childress et al. (1980) compared life history patterns among epipelagic, mesopelagic, and bathypelagic fishes off southern California and indicated that epipelagic species had the highest growth rates, mesopelagic species the lowest, and bathypelagic species were intermediate. In terms of energy budget, deeper living species are characterized by higher lifetime averages of K_2. In calculating energy budgets, Childress et al. (1980) assumed size-independent M, so that the present results of size-independent M for *M. muelleri* can be compared directly with their results. This comparison revealed that K_2 of *M. muelleri* (17%) is much higher than that of epipelagic fishes (3%) but falls within the range of mesopelagic fishes (15–26%) off southern California. The lifetime average of daily ration F' estimated by Childress et al. (1980) is 3.3 for epipelagic, 0.79 for mesopelagic, and 0.62% for bathypelagic fishes (recalculated by using the assimilation efficiency of 80%, instead of 73%). The present estimated lifetime average of F' (2.9%) for *M. muelleri* is higher than mesopelagic F', and closer to the epipelagic F' given by Childress et al. (1980). Greater F' in *M. muelleri* is a result expected from higher metabolic activities of this fish compared with mesopelagic fishes off southern California. As a mesopelagic fish in the Sea of Japan, *M. muelleri* is different from mesopelagic fishes off southern California in that the former is much smaller in size (53 mm TL or 44 mm SL vs. 72–118 mm SL) and shorter lived (1.8 yr vs. 5–7.5 yr) than the latter. Energy budget comparison indicates that *M. muelleri* is a more active swimmer (has a higher metabolic activity), thereby consuming more food than those off California, although net growth efficiency is identical between the two. A general implication gained from these comparisons is that *M. muelleri* in the Sea of Japan are more efficient mediators in energy flow and matter cycling in the pelagic ecosystem than are mesopelagic fishes off southern California.

Caloric contents of ovaries and testes of the Pacific sardine (*Sardinops caerulea*) have been reported as 5.43 and 4.85 Kcal/g DW (Lasker, 1970), both of which are greater than the respective values for *M. muelleri* (4.89 and 4.79 Kcal/g DW, cf. Table 3). Caloric content of mature oocytes, instead of intact ovaries, of *M. muelleri* is comparable to that of the Pacific sardine. Lasker (1970) estimated the energy investment in reproduction to be only 2% of assimilated energy. The energy partitioned for reproduction in *M. muelleri*, on the basis of the maximum gonad index, is 1.3% of the assimilated energy of 1.8-yr-old fish for females and 0.6% for males in this study. The presence of different size groups of yolked oocytes in the ovaries has been observed for *M. muelleri* from various geographical locations including the Sea of Japan, and is considered to be evidence of multiple or serial spawning (Okiyama, 1971; Gjøsaeter, 1981; Yuuki, 1982; Melo and Armstrong, 1991; Prosch, 1991). From this view, the present estimations of energy partition to reproduction in this fish are conservative ones, but the lack of information about spawning frequency prevents quantitative calculation at present. When the spawning frequency and the number of eggs released at each spawning become known for *M. muelleri* in future studies, the reproductive effort of the females will be better defined with the data for caloric content of oocytes given in this study.

Acknowledgments

I am grateful to C. B. Miller for critically reading the manuscript and for valuable comments. I thank two anonymous referees for comments that improved the text. Thanks are extended to T. Nagasawa for elemental analysis, T. Nagasawa and N. Nakao for providing some specimens used in this study, and K. Hirakawa and N. Iguchi for their help in field samplings. This research was supported by the fund "Encouragement of Basic Research at the National Re-

search Institute" from the Science and Technology of Japan.

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