日本海におけるキュウリエソMaurolicus muelleriの餌料組成とそのサイズ

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Diet Composition and Prey Size of the Mesopelagic Fish *Maurolicus muelleri* (Sternoptychidae) in the Japan Sea[1), 2)]

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Abstract

Stomach content analysis was made on larvae, juveniles and adults of *Maurolicus muelleri* collected from the Japan Sea. Stomach fullness (SF: stomach content weight x 100/fish weight) was independent of fish size, but varied with season. SF was greater in spring (2.1 to 2.4%) than in other seasons (0.5 to 1.5%). Copepods (>40 species) were numerically the most important dietary component, with euphausiids (only *Euphausia pacifica*) second, indicating a largely tertiary trophic position of this fish. Cladocerans, amphipods, pteropods and other groups were minor diet components. Prey width increased with size of *M. muelleri*, and its overall range was 0.1 to 2.0 mm. Within this size constraint, prey organisms taken were in part determined by seasonal succession of species in the zooplankton community. Feeding niche width increased steadily as the fish grew. The present results are compared with those from other localities.

Keywords: *Maurolicus muelleri,* diet composition, stomach fullness, prey size, niche width

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 & MAUCHLINE 1987). GJØSAETER (1981) and KAWAGUCHI & MAUCHLINE (1987) reviewed its biology and ecology, and pointed out the geographical variability in the life mode of this fish. As a habitat for *M. muelleri* the Japan Sea is characterized by poor fauna (VINOGRADOV 1968). *M. muelleri* is the only micronektonic fish in the Japan Sea, yet its stock size has been estimated as 3.3×10^6 metric tons (OKIYAMA 1981). YUUKI (1982, 1984) and IKEDA (1994) found that *M. muelleri* matured at 1-year-old in the Japan Sea, and grew to 60 mm SL. Estimated life span of the fish is 20–22 months.

As mesopelagic fishes are an active agent of energy flow/matter cycling in the pelagic ecosystem, information about their prey organisms is important primarily to evaluate their trophic position, and their likely impact on the organisms at the preceding trophic level. Diet composition of *Maurolicus muelleri* has been investigated at various locations (OKIYAMA 1971, SAMYSHEV & SCHETINKIN 1973, GJØSAETER 1981, YOUNG & BLABER 1986, DALPADADO & GJØSAETER 1987) , but

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2) 日本海におけるキュウリエソ *Maurolicus muelleri* の餌料組成とそのサイズ

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most of these previous data do not cover the entire life cycle of the fish, and prey organisms are classified into large systematic groups.

We report here diet composition and stomach fullness of all developmental stages of *Maurolicus muelleri* collected at various seasons of the year, extending the analysis to the size relations between prey taken and *M. muelleri*.

Materials and Methods

Samples

Fishes were collected aboard the R.V. "Mizuho-Maru" from Toyama Bay (southern Japan Sea) in December 1991, and in March, April, July and September 1992. Supplemental collections were made in the waters around Yamato Rise (central Japan Sea) in September 1988. Collections were made using 6-feet Isaacs-Kidd midwater trawls (1.5mm mesh) and fish-larval nets (0.5 mm mesh), both of which were towed obliquely from 100 to 250 m depths to the surface, only at night (local time: 2100 – 0300). Specimens caught from several tows were pooled, and 20 to 35 specimens were selected arbitrarily for this study. Also specimens caught during April-May 1989 in a stationary-net (8 mm mesh at the cod-end) deployed at nearshore water in Toyama Bay were included in the present analysis. Collection of specimens from the stationary net was made before or at around sunrise. Specimens were measured, then frozen or preserved in 10% buffered formalin-seawater for later stomach content analyses.

Body Length and Weight

Total length (TL, mm) and/or standard length (SL, mm) were read under a Wild dissecting microscope to the nearest 0.2 mm for the smaller specimens, or directly using a ruler to the nearest 0.5 mm for larger specimens. TL was converted to SL using a formula, SL = 0.822 TL + 0.161 (IKEDA 1994), and SL was used as body length throughout this study.

Body wet weight (WW, mg) was determined on frozen specimens and the following relationship between WW and SL was established for them: $WW = 0.0037SL^{3.367}$ ($r = 0.997$, $N = 311$). WW of formalin preserved specimens was estimated from SL using this equation.

Diet Analysis

Stomachs were removed and contents were placed in small petri-dishes and dispersed in a small amount of 10% buffered formalin-seawater. Under the Wild dissecting microscope, organisms were counted and classified into broad taxonomic groups, then to genus and species levels whenever possible.

Prey width is known to be superior to prey length to define the size relation in trophic dynamics analysis (PEARRE 1986) since it determines whether or not prey can be swallowed. Maximum width of identified prey was measured under the microscope to the nearest 0.02 mm. For many copepods which were found to be compressed and flattened, body width was estimated from flattened body width by reconstituting a cylindrical body shape. The same procedure was applied to compressed bodies of other prey organisms. Prey width defined in the present study includes body depth. For example, copepods belonging to genera *Oncaea* and *Corycaeus*, the most numerous prey categories found in this study,

Table 1. Regression analysis of stomach fullness (SF: % of fish weight on wet weight basis) on body length of fish (SL: mm) in *Maurolicus muelleri*. Numbers in parentheses are those with empty stomachs which were omitted from the calculation

Sampling date		N	SL Range	Mean±1SD	SF Range	Mean±1SD	Regression model: SF = aSL + b		
							a	b	*r*
September	1988	35 (3)	7.6−46.2	23.5±13.0	0.01−2.10	0.50±0.51	0.002	0.456	0.043*NS*
April-May	1989	44 (26)	37.2−48.7	43.6± 2.8	0.03−5.28	2.05±1.52	0.208	−7.034	0.385*NS*
December	1991	20 (1)	9.3−15.2	12.0± 1.6	0.01−2.76	0.69±0.94	0.273	−2.587	0.470*
March	1992	20 (0)	19.0−34.5	26.3± 5.1	0.06−9.77	1.13±2.18	−0.192	6.182	−0.447*
April	1992	20 (1)	16.0−34.7	24.1± 5.0	0.01−5.48	2.35±1.50	−0.064	3.896	−0.214*NS*
July	1992	20 (0)	27.0−38.0	32.5± 2.9	0.01−3.42	1.09±0.94	−0.098	4.273	−0.299*NS*
September	1992	20 (1)	30.5−37.2	33.5± 2.1	0.56−2.81	1.54±0.80	−0.103	4.985	−0.267*NS*
Total		179 (32)	7.6−48.7	27.3±11.1	0.01−9.77	1.23±1.38	0.020	0.700	0.157*NS*

＊$p<0.05$

had greater body depth than body width, a feature different from dorso-ventral compression of most of other copepod genera.

Then, the entire stomach content of each fish was collected on a piece of netting (20 μm mesh) , rinsed briefly with a small amount of distilled water, and weighed on a Mettler microbalance to the precision of 1 μg. Stomach fullness (SF) is defined as percentage wet weight of stomach contents to WW of the fish.

Trophic Niche Width

Based on the concept that "half as big" and "twice as big" differ by the same amount from "just fine", PEARRE (1986) proposed a ratio-based statistical model for analysing the relationship between prey size and predator size in fishes. In this ratio-based model, either coefficient of variation (CV: standard deviation divided by mean) of prey size, or standard deviation (SD) of log-transformed prey size are used as measures of trophic niche width, though the latter appears more amenable statistically than the former. The increase or decrease of trophic niche width with the growth of fish is detected from positive or negative slope, respectively, in the regressions of above defined CV and SD of prey size on fish size.

Developmental Stage

Definition of "larvae" and "juveniles" of *Maurolicus muelleri* is from morphological features given by OKIYAMA (1971) and KAWAGUCHI & MAUCHLINE (1987) , respectively, and "adults" by the development of mature gonads (IKEDA 1994). Corresponding sizes for each developmental stage were <20 mm for larvae; 20 to 30 mm for juveniles; and >30 mm for adults.

Results

Stomach Fullness

Among 44 specimens collected in April-May 1989, 26 (12 females and 14 males) were found to have empty stomachs. Excepting this sample, the occurrence of specimens with empty stomachs was low in the rest of the samples (Table 1).

Mean stomach fullness (SF) varied from 0.50 to 2.35% among seasonal samples, with a grand mean of 1.23%. Correlation analysis between SF and fish size

Table 2. Diet composition of *Mauloricus muelleri* in the Japan Sea. In "Composition" blanked column indicates the absence of that organism. juv.=juveniles

Sampling date	Sept. 1988	Apr./May 1989	Dec. 1991	Mar. 1992	Apr. 1992	July 1992	Sept. 1992
Total prey number	853	16	132	1063	1560	1647	581
Composition, %							
COPEPODA							
01 *Calanus sinicus*	0.7		0.8	0.1	0.3	1.6	0.2
02 *Calanus minor*	1.6						6.4
03 *Mesocalanus tenuicornis*	17.1			3.2	0.8		
04 *Canthocalanus pauper*				0.4	0.3		
05 *Eucalanus subcrassus*							0.2
06 *Paracalanus aculeatus*			6.8			1.0	
07 *Paracalanus parvus* s.l.			4.5	35.1	16.0	1.3	
08 *Acrocalanus gracilis*							11.2
09 *Ischnocalanus plumulosus*						0.1	
10 *Calocalanus pavo*						0.1	
11 *Clausocalanus* spp.	9.3		1.5	27.6	16.5	2.9	1.7
12 *Pseudocalanus newmani*				5.4	3.7		
13 *Aetideus armatus*			2.3				
14 *Euchaeta plana*							0.2
15 *Euchaeta* sp.							0.2
16 *Scolecithrix danae*							0.2
17 *Temora discaudata*	0.1					2.4	6.4
18 *Centropages abdominalis*				0.3			
19 *Centropages bradyi*	2.6		2.3	0.1		18.3	
20 *Centropages furcatus*							2.4
21 *Pleuromamma gracilis*				0.1			
22 *Candacia bipinnata*	3.4					0.5	1.9
23 *Candacia catula*							1.5
24 *Candacia* spp.			4.5	0.2			0.5
25 *Acartia danae*							0.2
26 *Acartia omorii*				0.4	0.6		
27 Small calanoids, unidentified	7.3		3.0	14.2	22.6	1.2	1.9
28 Large calanoids, unidentified	0.3		18.9	0.1	1.4	0.7	14.6
29 *Oithona atlantica*					9.9	0.1	
30 *Oithona plumifera*						0.1	
31 *Oithona similis*				0.4			
32 *Oithona* sp.				0.1			
33 *Oncaea conifera*	0.1			0.1			0.2
34 *Oncaea media*	44.9		9.8	4.4	9.9	35.9	18.5
35 *Oncaea mediterranea*	2.2		16.7	0.9	0.2	1.0	14.3
36 *Oncaea venusta*	3.2		21.3	0.1	0.1	4.4	8.6
37 *Sapphirina* sp.						0.1	
38 *Corycaeus affinis*				2.4	3.9		
39 *Corycaeus speciosus*	0.5		3.0			0.1	0.2
40 *Corycaeus pacificus*							1.4
41 *Corycaeus* spp.	0.1		3.0		1.0	0.1	1.0
42 *Microsetella rosea*	0.4		0.8	0.4	0.1	0.1	
43 *Euterpina acutifrons*							0.3
44 Copepod nauplii						0.1	
CLADOCERA							
45 *Evadne* spp.				0.2	1.2	4.1	0.2
46 *Podon polyphemoides*					0.6	0.3	
47 *Penilia* spp.						8.1	

Table 2 (continued)

Sampling date	Sept. 1988	Apr./May 1989	Dec. 1991	Mar. 1992	Apr. 1992	July 1992	Sept. 1992
Total prey number	853	16	132	1063	1560	1647	581
DECAPODA							
48 Zoea, Megalopa larvae						0.5	3.1
EUPHAUSIACEA							
49 *Euphausia pacifica*,larvae & juv.	0.9	100.0	0.8	1.1	7.9	0.1	0.2
AMPHIPODA							
50 *Themisto japonica*, juv.	1.9			0.3	1.0	0.5	0.9
51 *Primno abyssalis*, juv.	0.1						
OSTRACODA							
52 *Conchoecia pseudodiscophora*				0.9		0.4	0.3
53 Ostracods, unidentified						0.5	0.2
CIRRIPEDIA							
54 *Balanus* cypris larvae						0.4	0.2
PTEROPODA							
55 *Limacina helicina helicina*					0.1	9.7	0.3
BIVALVIA							
56 Bivalve larvae				0.3		1.5	0.2
CHAETOGNATHA							
57 *Sagitta* spp.	3.3					0.7	0.2
APPENDICULARIA							
59 *Oikopleura* spp.						0.1	
PISCES							
60 *Maurolicus muelleri*, larvae						0.9	
BACILLARIOPHYCEAE							
60 *Coscinodiscus wailesii*				0.5	0.1	0.1	
OTHERS							
61 Eggs, unidentified				0.7	1.8		

(SL) revealed that the correlation was not significant in 5 out of 7 samples (Table 1). There was a positive correlation in December 1991, and a negative one in March 1992. Considering these inconsistent results the effect of SL on SF is considered to be negligible. Analysis based on pooled samples indicated also no significant correlation between these two parameters. There were highly significant differences between means of seasonal SF samples ($F = 6.71$, df = 6, 144, $p < 0.005$). A LSD-test (SNEDECOR & COCHRAN 1967) between means indicated admixture of three distinct mean groups at the $p = 0.05$ level; i.e. high group (April-May 1989, April 1992), intermediate group (September 1992) and low group (September 1988, December 1991, March 1992 and July 1992).

Prey Organisms

Sixty one prey categories were established in this study (Table 2). The greatest category number was recorded in the specimens caught in July 1992 (36 categories), and the number decreased in the order of September 1992 (34), March 1992 (28), April 1992 (23), September 1988 (20), December 1991 (15) and April-May 1989 (1).

A euphausiid *Euphausia pacifica* (larvae and juveniles) was the only prey category which was found commonly over all 7 seasonal samples. Copepods including *Calanus sinicus*, *Clausocalanus* spp., small and large unidentified

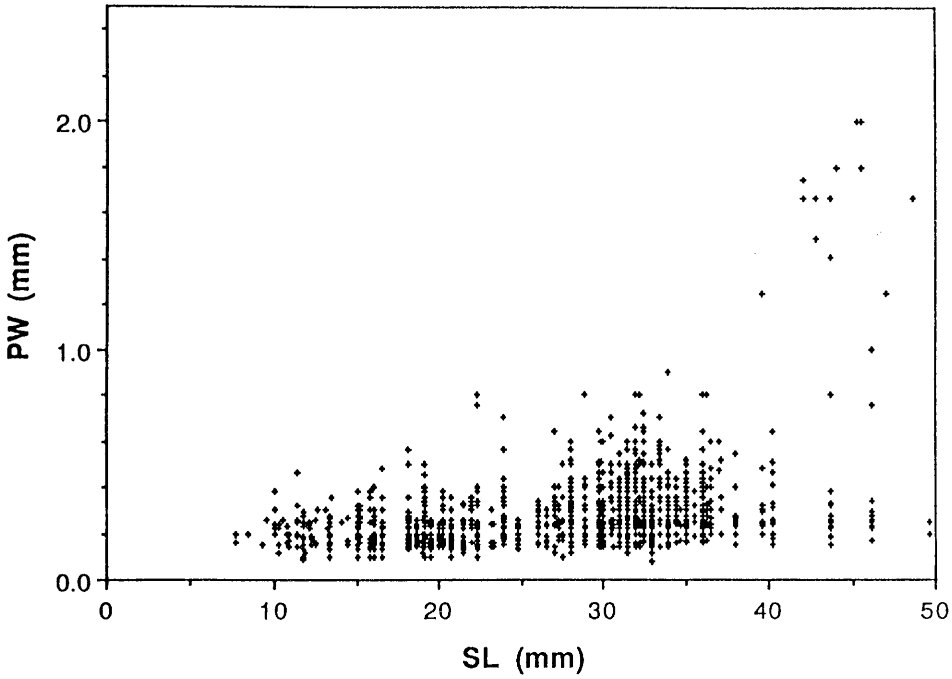

Fig. 1. The relationship between prey width (PW, mm) and the body length (SL, mm) of *Maurolicus muelleri* in the Japan Sea (N = 1730) .

calanoids, *Oncaea media*, *O. mediterranea* and *O. venusta* were recorded in 6 out of 7 seasonal samples. Of these preys, *E. pacifica* is a cold-water species and the rest warm-water ones. While most of the prey organisms recorded in this study are epipelagic forms, *Primno abyssalis*, *Conchoecia pseudodiscophora* and *Maurolicus muelleri* (cannibalism) are mesopelagic species.

Prey Size vs. Predator Size

All prey width (PW) data were plotted against SL of *Maurolicus muelleri* in Figure 1. It is seen that the lower limits of PW remained at almost the same level across SL, but the upper limits increased with increasing SL, with an overall PW range of 0.1 to 2.0 mm.

Following to the procedure of PEARRE (1986), mean and SD were computed first for $\log_{10}$-transformed or untransformed PW data of each fish. In this computation, fishes containing less than three prey organisms were omitted. Figure 2 (top) shows thus obtained mean and SD of $\log_{10}$-transformed PW of individual fishes plotted against its SL. Then, $\log_{10}$-transformed or untransformed PW data were normalized to mean = 0, SD = 1 in each fish, and summed over the range of SL. The summed normalized PW distribution was shown to be symmetrical and fit to the normal distribution curve for $\log_{10}$-transformed PW data, but was skewed and did not fit to the normal distribution curve for untransformed PW data (Chi-square test at the $p = 0.05$ level, SNEDECOR & COCHRAN 1967).

Residuals of regressions were tested for normality, resulting that this criterion of normality was satisfied in the regression of SD of $\log_{10}$-transformed PW

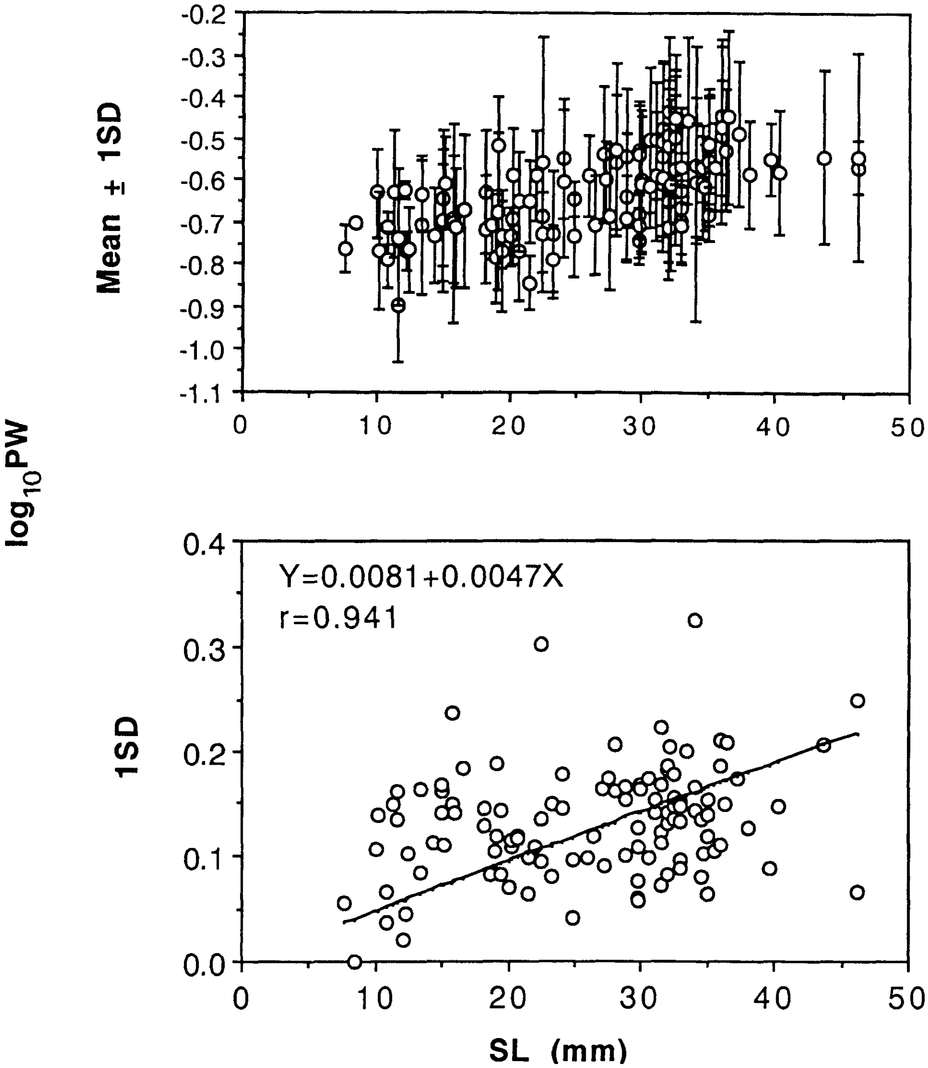

Fig. 2. The relationships between mean ± 1SD of $\log_{10}$-transformed prey width (PW) and the body length (SL, mm) (top figure) , and between standard deviation (1SD) of $\log_{10}$-transformed PW and SL of *Maurolicus muelleri* (bottom figure), the latter as the measure of feeding niche width. For the calculation of regression line of 1SD on SL, 1SD of each fish was weighted by the number of prey observed. See text for details.

on SL of the fish, but not in the regression of CV of untransformed PW data on SL of the fish (Chi-square test at the $p = 0.05$ level). SD from $\log_{10}$-transformed PW data and CV from untransformed PW data were weighted by the number of prey observed in each fish. Calculated regression equation of thus weighted SD (Y) on SL of the fish (X) was $Y = 0.0047$ (±0.0001, 95% confidence interval) $X + 0.0081$ (Figure 2, bottom), and of weighted CV (Y) on SL (X) was $Y = 1.1419$ (±0.0212) $X + 1.5594$. The slope of both regressions was "positive", suggesting

Table 3. Major diet composition across developmental stages and body length (SL) classes of *Maurolicus muelleri* in the Japan Sea

Developmental stage	Larva		Juvenile	Adult	
SL (mm)	<10	10 – <20	20 – <30	30 – <40	≥40
N	10	798	2495	2382	167
Diet composition, %					
Copepoda (mean PW=0.25mm)	100.0	95.2	87.9	82.7	62.9
Euphausiacea (1.00mm)	0.0	1.6	5.0	0.7	22.2
Cladocera (0.39mm)	0.0	2.1	1.9	6.7	0.0
Amphipoda (0.43mm)	0.0	0.6	0.8	0.6	1.8
Pteropoda (0.42mm)	0.0	0.1	1.8	2.8	0.0
Others	0.0	0.4	2.6	6.5	13.1

progressive increases of trophic niche width as this fish grows. However, this conclusion is valid statistically for the regression from $\log_{10}$-transformed PW data, and not for untransformed PW data because of violation from the criteria required for the model.

While the prey numbers of the <10 mm and ≥40 mm SL classes were small, copepods were of greatest importance throughout development (Table 3). Copepods occupied 100% of prey taken by <10 mm SL class, but their proportion decreased gradually as the fish grew, reaching 63% at ≥40 mm SL class. Preys ranked second in importance were euphausiids for 20 – <30 mm and ≥40 mm SL classes, and cladocerans for 10 – <20 mm and 30 – <40 mm SL classes. The third-ranked prey was varied; euphausiids for 10 – <20 mm, cladocerans for 20 – <30 mm, pteropods for 30 – <40 mm, and amphipods for ≥40 mm SL classes. The proportion of prey grouped as "Others" increased in the course of the development of the fish.

Discussion

Since the present collections were made mostly at night, diel feeding pattern, if it existed, was a potential source of error in estimating stomach fullness (SF) and possibly diet composition of *Maurolicus muelleri*. Published reports for the diel feeding rhythm of this fish are inconsistent; largely nocturnal feeding rhythm (Young & Blaber 1986), or absence of diel feeding rhythm (Samyshyv & Schetinkin 1973, Gjøsaeter 1981). Young & Blaber (1986) suggested that these differences might reflect local productivities of the habitats. In either case, the present samplings limited to mostly at night cover all or part of feeding time of *M. muelleri*, hence the effect of this source of error is considered to be not serious in the present analysis.

SF of *Maurolicus muelleri* was independent of fish size, but varied with season in this study. SF was greatest (2.1–2.4%) in spring (April–May), corresponding with the annual peak of zooplankton abundance in Toyama Bay (Hirakawa et al. 1992). Moderate or low SF (0.5–1.5%) was observed in summer to winter, when zooplankton abundance was low (Hirakawa et al. 1992). Similar close-coupling of SF of *M. muelleri* to seasonal zooplankton abundance has been noted in the continental slope water of eastern Tasmania (Young & Blaber 1986). The overall range of SF obtained by Young & Blaber (1986) was 1.0–2.2%, which overlaps 0.5–2.4% recorded in this study. In other mesopelagic fishes, SF has been reported as 0.8% for *Diaphus taaningi* (BAIRD et al. 1975); 0.4–2.4% for *Diaphus danae*; and 0.3–1.6% for *Lampanyctodes hectoris* (YOUNG & BLABER 1986); and 2.2–3.6% for *Benthosema pterotum* (DALPADADO & GJØSAETER 1988).

As prey organisms of *Maurolicus muelleri* in the Japan Sea, copepods were the most important numerical component. This is particularly true for its larvae (Table 3). Euphausiids (only *Euphausia pacifica* in this study) were second in importance. Euphausiids may be more significant than copepods for larger specimens, in terms of mass or energy, because an individual *E. pacifica* is much greater in size than any other groups including copepods(cf. Table 3). Copepods and/or euphausiids are also major prey organism groups in most of the previous studies (SAMYSHEV & SCHETINKIN 1971, OKIYAMA 1971, GJØSAETER 1981, YOUNG & BLABER 1986, DALPADADO & GJØSAETER 1987). The proportion of copepods in total diet decreased with the increasing size of *M. muelleri*, whereas euphausiids increased (GJØSAETER 1981, YOUNG & BLABER 1986). Large *M. muelleri* collected in April-May 1989 were feeding exclusively on *E. pacifica* (Table 2). In Norwegian waters *M. muelleri* is reported to feed largely on euphausiids in winter (GJØSAETER 1981). Judging from the kinds of major prey organisms (mostly herbivores) *M. muelleri* considered chiefly as a tertiary producer in the pelagic ecosystem of the Japan Sea and possibly of other seas.

Amphipods, ostracods, decapods, chaetognaths, gastropods, pteropods and thaliaceans have been found more or less as minor components in the stomach of this fish from various localities (OKIYAMA 1971, GJØSAETER 1981, YOUNG & BLABER 1986), excepting the data from the Red Sea, where ostracods were ranked as the second in numerical dominance (DALPADADO & GJØSAETER 1987). Cladocerans, *Maurolicus muelleri* larvae (i.e. cannibalism) and large centric diatom *Coscinodiscus wailesii* were first recorded in this study, although the nutritional significance of the diatom to this fish is doubtful. While possible "net-feeding" cannot be ruled out in any diet analyses of net-collected fishes, this source of error is considered to be not extensive for the study of mesopelagic fishes (cf. HOPKINS & BAIRD 1977). Comparing the mesh sizes of the nets used in this study (0.5 to 8 mm) with the prey size (0.1 to 2.0 mm PW, Figure 1), the effect of net feeding is presumed to be minimal in the present results.

Previous workers noted that diet composition of *Maurolicus muelleri* in a given location varied with season and size of the fish (OKIYAMA 1971, GJØSAETER 1981, YOUNG & BLABER 1986). From this view, the major breeding season of *M. muelleri* in Toyama Bay is late summer (IKEDA 1984) so that the size of the fish collected in this study was influenced strongly by the seasonal growth pattern of this summer cohort. In other words, the effects of season and size on diet composition cannot be separated in this study. Nevertheless, the seasonal effect is detected by some prey organisms whose occurrence is known to be limited in particular seasons. For example, cladocerans occur only in spring to summer (ONBÉ, personal communication), and *Euphausia pacifica* larvae are most numerous in spring in Toyama Bay (IGUCHI et al. 1992). These seasonal occurrences of cladocerans and abundances of *E. pacifica* are well reflected to the diet composition of *M. muelleri* (cf. Table 2). Exclusive feeding of *M. muelleri* on *E. pacifica* observed in April-May 1989 were considered to be a result from combined effects of season, large size of the fish (Table 1) and characteristic swarming behavior of *E. pacifica* (cf. ENDO et al. 1985).

Mesopelagic fishes are largely opportunistic predators, but this does not imply that preys are eaten in direct proportions to their abundance at the time of feeding (HOPKINS & BAIRD 1977). With regard to zooplankton composition in Toyama Bay, copepods are numerically the most important group, followed by ostracods, euphausiids, chaetognaths, appendicularians, amphipods and cladocerans (HIRAKAWA et al. 1992). Among a total of 87 copepod species listed in Toyama Bay (HIRAKAWA et al. 1990), 41 species were found from the stomachs of *Maurolicus muelleri* in this study (cf. Table 2). Most of uneaten copepod species are too large to be taken, but size alone is insufficient to explain the results. For example, a copepod *Metridia pacifica* was never found in the present diet analysis. *M. pacifica* is the most dominant copepod in Toyama Bay (17–61 % of total copepod biomass collected with 0.3 mm mesh net from 500 m depth to the surface, HIRAKAWA & IMAMURA 1993), and all its copepodite sizes fall well within the PW range of 0.1–2.0 mm. It undertakes a diel migration, whose pattern parallels that of *M. muelleri*. Taxonomic selectivity may be a result from complex attributes of both prey and predator including escape capabilities of prey, differential abilities of various prey taxa to provide stimuli to elicit predator responses, and factors concerned with palatability and assimilable energy (HOPKINS & BAIRD 1977). However, possible active avoidance of *Metridia* from *M. muelleri* is not conclusive since *Metridia lucens,* a close relative of *M. pacifica*, has been recorded in small amounts from the stomach of *M. muelleri* in the continental slope water of east Tasmania (YOUNG & BLABER 1986).

In the ratio-based statistical model of PEARRE (1986) used for feeding niche analysis in the present study, PW data less than three prey organisms were not incorpolated due to the difficulty to calculate mean and SD (which are required to normalize the data). Fewer prey number less than three was often the case for smaller larvae and larger adults of *Maurolicus muelleri*, and this appears to be a common phenomenon in other fishes (cf. PEARRE 1986). Despite this methodological constraint, overall increase of trophic niche width in the course of development was indicated for *M. muelleri* in this study (Figure 2, bottom). PEARRE (1986) analysed literature data on prey size and predator size for fishes and concluded that there was no consistent trend of niche-width of predator fishes of different sizes. It is noted however that his conclusions were from between-species comparisons dealing with greater predator size ranges (4–500 mm). In narrower size-ranged analyses on individual fish species, a divergent pattern, including both increasing and decreasing feeding niche width as the fish grows, was seen in the results of PEARRE (1986). The increase of trophic niche width in parallel with development ensures the maximum share of available food resources, hence is an effective mechanism for outcompeting with other fishes. From a global point of view, this may be one of the key mechanisms which allows worldwide flourish and plasticity of life history strategy of *M. muelleri.*

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Literature Cited

Baird, R. C., T. L. Hopkins, & D.F. Wilson, 1975. Diet and feeding chronology of *Diaphus taaningi* (Myctophidae) in the Cariaco Trench. *Copeia*, **1975**: 356–365.

Dalpadado, P. & J. Gjøsaeter, 1987. Observations on mesopelagic fish from the Red Sea. *Mar. Biol.*, **96**: 173–183.

Dalpadado, P & J. Gjøsaeter, 1988. Feeding ecology of the lanternfish *Benthosema pterotum* from the Indian Ocean. *Mar. Biol.*, **99**: 555–567

Endo, Y., Y. Hanamura & A. Taniguchi, 1985. *In situ* observations on the surface swarm of *Euphausia pacifica* in Sendai Bay in early spring with special reference to their biological characteristics. *La Mer*, **23**: 135–140

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

Hirakawa, K., T. Ikeda & N. Kajihara, 1990. Vertical distribution of zooplankton in Toyama Bay, southern Japan Sea, with special reference to Copepoda. *Bull. Plankton Soc. Japan* **37**: 111–126.

Hirakawa, K., A. Imamura & T. Ikeda, 1992. Seasonal variabilities in the abundance and composition of zooplankton in Toyama Bay, southern Japan Sea. *Bull. Japan Sea Natl. Fish. Res. Inst.*, **42**: 1–15.

Hirakawa, K. & A. Imamura, 1993. Seasonal abundance and life history of *Metridia pacifica* (Copepoda; Calanoida) in Toyama Bay, southern Japan Sea. *Bull. Plankton Soc. Japan*, **40**: 41–54.

Hopkins, T. L. & R.C. Baird, 1977. Aspects of the feeding ecology of oceanic midwater fishes. pp.325–360. In *Oceanic Sound Scattering Prediction* (eds. Anderson, N.R. & Zahuranec, B. J.). Plenum Press, New York.

Iguchi, N., T. Ikeda & A. Imamura, 1992. Growth and life cycle of a euphausiid crustacean (*Euphausia pacifica* Hansen) in Toyama Bay, southern Japan Sea. *Bull. Japan Sea Natl. Fish. Res. Inst.*, **43**: 69–81 (in Japanese with English abstract).

Ikeda, T., 1994. Growth and life cycle of the mesopelagic fish *Maurolicus muelleri* (Sternoptychidae) in Toyama Bay, southern Japan Sea. *Bull. Plankton Soc. Japan*, **40**: 127–139.

Kawaguchi, K. & J. Mauchline, 1987. Biology of sternoptychid fishes Rockall Trough, Northeastern Atlantic Ocean. *Biol. Oceanogr.*, **4**: 99–120.

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 (in Japanese with English abstract).

Okiyama, M., 1981. Abundance and distribution of eggs and larvae of a Sternoptychid fish, *Maurolicus muelleri*, in the Japan Sea, with comments on the strategy for successful larval life. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer*, **178**: 246–247.

Pearre, S. Jr. (1986). Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and the size-efficiency hypothesis. *Mar. Ecol. Prog. Ser.*, **27**: 299–314.

Samyshev, E. Z. & S. V. Schetinkin, 1973. Feeding patterns of some species of

Myctophidae and *Maurolicus muelleri* caught in the sound-dispersing layers in the northwestern African area. *Ann. Biol. Copenh.*, **28**: 212–215.

SNEDECOR, G. W. & W. G. COCHRAN, 1967. *Statistical Methods.* Iowa State Univ. Press, Ames, Iowa.

VINOGRADOV, M.E., 1968. *Vertical Distribution of the Oceanic Zooplankton.* Acad. Nauk SSSR Inst. Okeanol., Moscow (English translation, I.P.S.T., Jerusalem 1970).

YOUNG, J.W. & S.J.M. BLABER, 1986. Feeding ecology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia. *Mar. Biol.*, **93**: 147–156.

YUUKI, Y., 1982. Spawning and maturity of a sternoptychid fish *Maurolicus muelleri* in the southwestern waters of the Sea of Japan. *Bull. Japan. Soc. Sci. Fish.*, **48**: 749–753 (in Japanese with English abstract).

YUUKI, Y., 1984. Age and growth of a sternoptychid fish *Maurolicus muelleri* in the southwestern waters of the Sea of Japan. *Bull. Japan. Soc. Sci. Fish.*, **50**: 1849–1854 (in Japanese with English abstract).