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Metabolic characteristics of the lobate ctenophore *Bolinopsis mikado* (Moser)

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Abstract: Respiration, ammonia- and phosphate excretion rates were measured for various sizes of the lobate ctenophore *Bolinopsis mikado*. Elemental compositions (carbon and nitrogen) were also determined. Carbon and nitrogen contents of *B. mikado* of ≧15 mm in total length (TL) were 1.10 and 0.34% of dry weight (DW), respectively. The DW-specific respiration rate of *B. mikado* of 21–50 mm TL was in the range of 39.4 to 81.5 $\mu l\, O_2\, g\, DW^{-1}\, h^{-1}$ at temperatures ranging from 16 to 27°C. The DW-specific ammonia- and phosphate excretion rates were in the range of 4.1 to 13.0 $\mu g\text{-at}\, N\, g\, DW^{-1}\, d^{-1}$ and in the range of 0.6 to 1.8 $\mu g\text{-at}\, P\, g\, DW^{-1}\, d^{-1}$ at temperatures ranging from 16 to 24°C. The minimum food requirement of *B. mikado* was ca. 540 $\mu g\, C\, g\, DW^{-1}\, d^{-1}$ and was equal to 220 copepods (i.e. *Acartia*, assuming a body carbon of 2.5 μg) at 16°C. *B. mikado* requires >ca. 5 *Acartia* l^{-1} to supply its minimum food requirement. Total ammonia- and phosphate excretion rates of the *B. mikado* population that occurred with high abundance in August 1990 in Tokyo Bay were 46.5 $\mu g\text{-at}\, N\, m^{-3}\, d^{-1}$ and 5.9 $\mu g\text{-at}\, P\, m^{-3}\, d^{-1}$, respectively. The ammonia and phosphate excreted by this *B. mikado* population were equivalent to a maximum of 21% of the standing stock of nutrient in the seawater of Tokyo Bay, indicating that *B. mikado* may be a major nutrient source seasonally and locally.

Key words: ctenophore, *Bolinopsis mikado*, respiration, excretion, copepod

Introduction

Ctenophores are regarded as heavy predators on non-gelatinous zooplankton (Kremer 1979; Deason 1982; Purcell 1985) and a regulator on the oscillation of zooplankton standing stock (Deason & Smayda 1982; Suthers & Frank 1990; Båmstedt 1998). In addition, ctenophores play an important role as a nutrient source for phytoplankton (Kremer 1975; Deason & Smayda 1982). Many studies on the metabolism of ctenophores have been conducted on the lobate species *Mnemiopsis leidyi* (Kremer 1977), *M. mccradyi* (Reeve et al. 1978; Kremer 1982; Kremer et al. 1986b; Kremer & Reeve 1989; Reeve et al. 1989), *Bolinopsis infundibulum* (Hoeger 1983; Morris et al. 1983; Bailey et al. 1994) and *B. vitrea* (Kremer et al. 1986b). For the metabolic rates of cydippid species, *Pleurobrachia bachei* (Hirota 1972) and *P. pileus* (Ikeda 1976, 1977) have been measured. Youngbluth et al. (1988) reported on the metabolic rate of the midwater ctenophore *Bathocyroe fosteri*.

In Japanese coastal waters, *Bolinopsis mikado* (Moser) is the predominant ctenophore species (Komai 1915; Kanashiro & Senta 1985), and is most abundant from late summer to mid autumn in Tokyo Bay (Nomura & Ishimaru 1998; Kasuya et al. 2000). Because *B. mikado* is a fragile species, ecological studies on this species are rare (Kasuya et al. 1994), and little information on its metabolism is available. In the present paper, we describe the metabolic characteristics and potential impact of *B. mikado* on copepods and phytoplankton populations. The chemical composition, respiration, ammonia- and phosphate excretion rates of *B. mikado* were determined, and its minimum prey requirement was calculated.

Materials and Methods

Morphology

As lobate ctenophores develop, after hatching they pass through a cydippid larva stage with a pair of tentacles.

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Bolinopsis mikado loses its tentacles at a total length (TL) of ca. 15 mm, becoming similar to the adult morphology (Kasuya 1997). In this paper, those of <15 mm TL are defined as larvae, and those of ≧15 mm TL, as post-larvae. Larval *B. mikado* TL is measured from the aboral pole to the mouth. For larvae with developing oral lobes and post-larvae, TL is measured from the aboral pole to the end of the lobes (cf. Kasuya et al. 1994).

Sampling

A series of experiments was conducted from July to December 1992 and from October to November 1993 at the Banda Marine Laboratory of Tokyo University of Fisheries, Tateyama, Chiba Prefecture. Samples of *B. mikado* were collected using wide-mouthed plastic bottles by snorkeling in waters adjacent to the laboratory. Specimens were then maintained in a meshed bag immersed in running sand-filtered seawater for 4 h in the laboratory to clear food material from the pharynx. They were then used for the metabolic experiments and for determination of elemental composition. The sand-filtered seawater (salinity of 32–35 psu) had been pumped up from waters adjacent to the laboratory.

Metabolic experiments

A preliminary metabolic experiment was conducted on 10 indiv. of *B. mikado* ranging from 31 to 39-mm TL to determine the influence of the incubation time on their respiration. These ctenophores were incubated for 12 and 39 h at 27°C.

In the metabolic experiments, respiration and excretion (i.e. ammonia and phosphate) rates of *B. mikado* were measured. Fifty-two ctenophores ranging from 15 to 83-mm TL were used for determining respiration rate, and 20 ctenophores ranging from 18 to 67-mm TL for excretion. *Bolinopsis mikado* was incubated for 12 to 30 h at 16, 22, 27°C for respiration and 16, 22, 24°C for excretion, settings within ±4°C of the water temperature when samples were collected. When water temperature in the experiment and in the collected water differed by over 3 degrees, specimens were acclimated to the experimental temperature for 1 h. Because respiration and excretion of *B. mikado* were measured during different seasons, the experimental temperatures at the high end were set differently.

All incubations followed the same procedure. Cylindrical glass bottles of 450 and 950 ml capacity were used for the incubation. Prior to the experiments, the incubation bottles were soaked for 1 d in 0.1-N HCl and rinsed with distilled water. Well-aerated seawater that was first sand filtered, then further filtered using a Whatman GF/C filter, was siphoned from a single container into an incubation bottle. One or two *B. mikado*, after TL premeasurement, were transferred gently from the meshed bag into each incubation bottle. After adding more seawater, about half a liter, the bottles were tightly sealed and placed in a darkened incubator. One or two bottles without *B. mikado* were prepared simultaneously as controls. The size of the incubation bottles, the number of ctenophores per bottle and the incubation time were varied depending on ctenophore size and water temperature, to obtain a significant difference between control and experimental bottles, keeping dissolved-oxygen concentration in the bottles above 3 ml O_2 l^{-1}.

At the end of the incubation period, seawater in each bottle was carefully siphoned into three DO bottles and three test tubes for replicate measurements of dissolved oxygen, ammonia and phosphate concentrations. Dissolved oxygen and ammonia in seawater were determined by Winkler titration (Strickland & Parsons 1972) and by the salicylate-dichloroisocyanurate method (Krom 1980), respectively. Phosphate was determined by the method of Murphy & Riley (1962). The metabolic rates were calculated from the difference between the concentrations in the control and experimental bottles, assuming that the bacterial respiration is of the same magnitude in both.

Dry weight and elemental composition

Bolinopsis mikado used for the metabolic experiments was rinsed with 5% isotonic ammonium formate to remove seawater and dried upon preweighed Whatman GF/C filters in petri dishes at 90°C for 2 d. Then, dry weight (DW) was measured by a microbalance to the nearest 1 mg.

Carbon and nitrogen contents were determined on larval and post-larval *B. mikado* ranging from 5.5 to 75-mm TL. Eight to 30 larvae and 2 to 4 post-larvae of <30-mm TL of almost the same body size were pooled to form one sample. Ctenophores had the seawater removed using the same method as for the dry-weight measurement. Each sample was then dried on an evaporating dish of fluorocarbon polymers at 90°C for 24 h, homogenized using an onyx pestle and mortar, and redried for 24 h. A portion of the homogenate was then weighed using a microbalance, and determination of its carbon and nitrogen contents made with an elemental analyzer (Yanaco CHN corder Model MT-3).

Calculation of predation rate of Bolinopsis mikado

Kasuya et al. (1994) measured the predation rate of *B. mikado* in the laboratory using the calanoid copepod *Acartia* spp. as prey. The predation rate (P, number of *Acartia* ctenophore^{-1} h^{-1}) of *B. mikado* is calculated from the equation: $P=(1.8\times\ln F-2.2)WW^{0.67}e^{0.058(T-16)}$ (cf. Kasuya et al. 1994), where F is food concentration (*Acartia* l^{-1}), WW is wet weight (g) and T is temperature (°C).

Results

Morphometrics and elemental composition

The relationship between TL (mm) and DW (mg) of a post-larval *Bolinopsis mikado* was expressed by the equation, $DW=0.062TL^{2.34}$ (Fig. 1). In this paper, DW of post-larvae was estimated from TL using this equation.

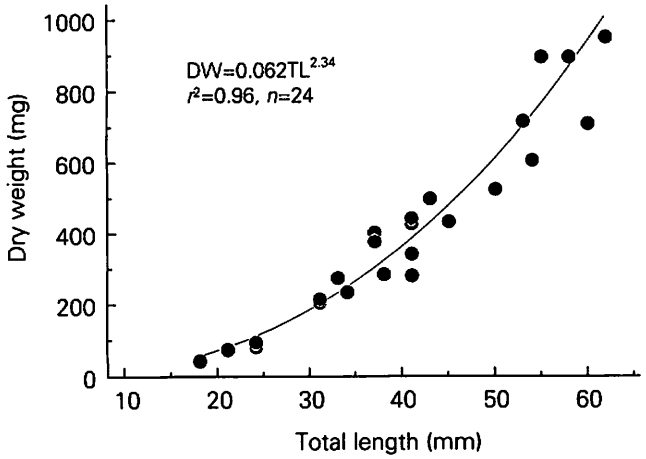

Fig. 1. Relationship between total length (TL) and dry weight (DW) of *Bolinopsis mikado*. The equation and line are derived from a linear least-square regression on log–log transformation of the data.

Amounts of carbon and nitrogen in *B. mikado* were expressed as percentages of DW (Fig. 2). Carbon and nitrogen contents of larval *B. mikado* were higher than those of post-larvae. The carbon content of larvae was 4.5–7% of DW at ca. 7-mm TL, and decreased with increasing TL. The nitrogen content of larvae varied, ranging from 0.5 to 2.5% DW. The body C : N ratio (by weight) ranged from 1.6 to 26. For post-larvae, the carbon and nitrogen contents were independent of body size, and the means were 1.10 (±0.28SD, n=21) and 0.34 (±0.21), respectively. The body C : N ratio ranged from 1.9 to 6.3 with an average of 4.0 (±1.4).

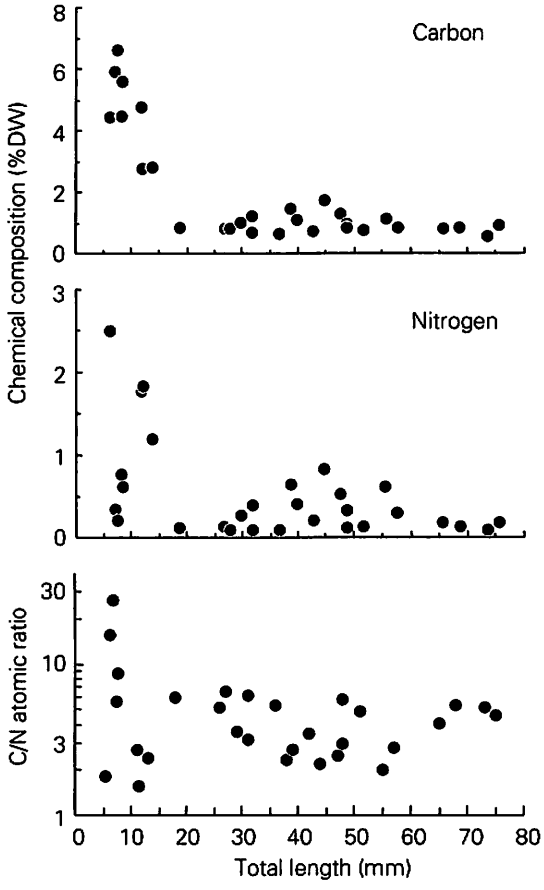

Fig. 2. Carbon (C) and nitrogen (N) contents as percentages of dry weight (DW) and the body C : N ratio of *Bolinopsis mikado*.

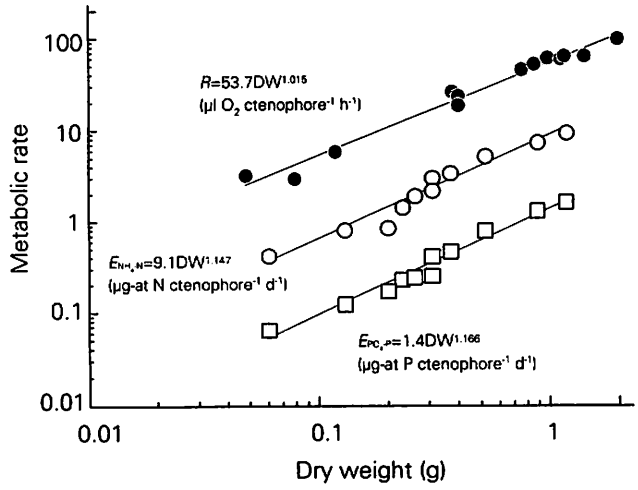

Fig. 3. Respiration (R, ●), ammonia- ($E_{NH_4\text{-}N}$, ○) and phosphate excretion ($E_{PO_4\text{-}P}$, □) rates of *Bolinopsis mikado* as a function of dry weight (DW) at 22°C. The equation and line are derived from GM regressions on log–log transformations of the data.

Metabolic rate

The mean DW-specific respiration rates for 12 and 39 h incubation times were 71.5 (±24.2SD, n=5) and 69.8 (±15.9, n=5) μl O_2 g DW^{-1} h^{-1}, respectively, and no significant differences were observed (t-test, $P>0.05$).

The metabolic rate of *B. mikado* at 22°C as a function of ctenophore size is shown in Fig. 3. When the relationships of respiration (R, μl O_2 ctenophore^{-1} h^{-1}) and excretion (E, μg-at ctenophore^{-1} d^{-1}) rates to DW (g) were expressed by the allometric equation: R (or E)$=aDW^b$, where a and b were constants, the respiration and excretion rates increased almost linearly with DW. GM regression (functional regression; Ricker 1973), a method generally superior to ordinary regression for predictive purposes, was used on log–log transformations of the data for finding the coefficients a and b. The coefficient b for R at 16, 22 and 27°C was 0.822, 1.016 and 1.122, respectively (Table 1). The b of E was 1.160, 1.147 and 1.110 for ammonia, and 1.133, 1.166 and 1.038 for phosphate at 16, 22 and 24°C, respectively.

The effect of water temperature on metabolic rate was evaluated using DW-specific respiration (R*) and excretion (E*) rates of *B. mikado* ranging from 21 to 50-mm TL (Fig. 4). R* and E* increased with increasing water temperature. Mean R* was 39.4 (±18.8SD, n=5), 51.3 (±10.7, n=6) and 81.5 (±22.3, n=22) μl O_2 g DW^{-1} h^{-1} at 16, 22 and 27°C, respectively. Mean E* was 4.1 (±0.7, n=3), 7.7 (±2.0, n=8) and 13.0 (±1.7, n=5) μg-at N g DW^{-1} d^{-1} for

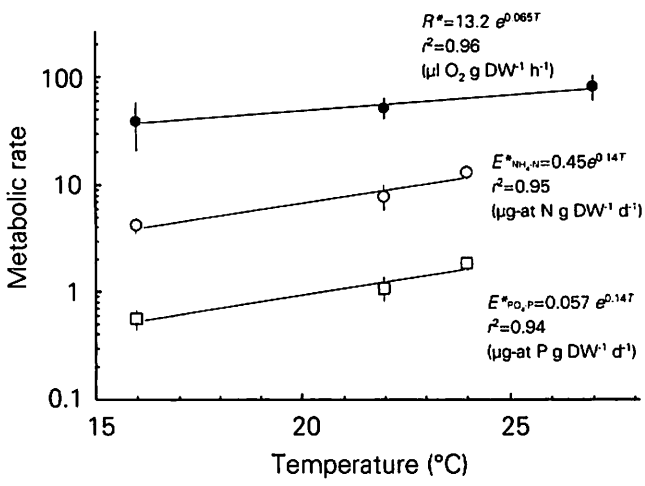

Fig. 4. Effect of water temperature on dry weight (DW)-specific respiration (R^*, ●), ammonia- ($E^*_{NH_4\text{-}N}$, ○) and phosphate excretion ($E^*_{PO_4\text{-}P}$, □) rates of *Bolinopsis mikado* ranging from 21 to 50 mm of total length. The equation and line are derived from linear least-square regressions on log–log transformations of the data.

ammonia and 0.6 (±0.1), 1.1 (±0.3) and 1.8 (±0.2) µg-at P g DW^{-1} d^{-1} for phosphate at 16, 22 and 24°C, respectively. The relationship between the specific metabolic rate and water temperature expressed as R^* (or E^*)=ae^{kT}, where a and k were constants and T, water temperature, gave coefficients k for R^*, and ammonia and phosphate E^* of 0.065, 0.14 and 0.14, respectively. These values of k were equivalent to Q_{10} values of 1.9 for R^* and 4.1 for ammonia and phosphate E^*.

The ratios of respiration to ammonia excretion (O : N atomic ratio) calculated using the mean R^* and E^* were 20.6 at 16°C and 14.4 at 22°C.

R^* of *B. mikado* was converted to the metabolic carbon loss using a respiratory quotient value (RQ) of 0.8 that was verified by direct measurements on ctenophores (Kremer 1977). The metabolic carbon losses at 16, 22 and 27°C were ca. 400, 530 and 840 µg C g DW^{-1} d^{-1}, respectively. Daily metabolic losses as percentages of body carbon and nitrogen at 16, 22 and 27°C for carbon and at 16, 22 and 24°C for nitrogen were 3.7, 4.8 and 7.6%, and 1.7, 3.2 and 5.4%, respectively.

By combining the metabolic carbon loss and the predation rate of *B. mikado*, the food concentration needed to supply its minimum prey demand could be estimated. Assuming the digestive efficiency of a ctenophore to be 75% (for *M. mccradyi*, Reeve et al. 1978), and the carbon content of a copepod (*Acartia*) to be 2.5 µg C copepod^{-1} (Kremer et al. 1986b), the minimum food requirement of *B. mikado* was estimated to be 540 µg C g DW^{-1} which equals about 220 *Acartia* at 16°C. The minimum food requirement at 22 and 27°C was determined to be about 280 and 450 *Acartia*, respectively. The daily carbon uptake (i.e. predation rate×digestive efficiency) of *B. mikado* at 16, 22 and 27°C exceeded the minimum food requirement at food concentrations of 5.3, 5.1 and 5.5 *Acartia* l^{-1}, respectively.

Discussion

Elemental composition

Larval *Bolinopsis mikado* had, at maximum, a 7-fold higher carbon content per unit DW than post-larvae. The larvae became fully lobate without tentacles at ca. 15-mm TL (Kasuya 1997), and this size coincides with the TL at which *B. mikado* reaches its average baseline carbon content. The high carbon content of larval *B. mikado* appears to be due to the presence of the tentacles. This agrees with the strong relationship between ctenophore size and carbon content previously reported for *Mnemiopsis mccradyi* (Reeve et al. 1989) and *Bolinopsis vitrea* (Kremer et al. 1986a, b), indicating that the presence of tentacles in the larval stage may contribute to carbon and nitrogen enrichment.

The body C : N ratio of larval *B. mikado* exceeded a value of 10 for larvae of 6-mm TL and 7-mm TL. Because a C : N ratio of about 3 indicates a high protein content in animal organic matter, and that of >10 has been reported for animals storing large amounts of lipid (cf. Omori & Ikeda 1984), solid parts of larval *B. mikado* may be mostly composed of lipid. Specimens larger than 7-mm TL generally had a low C:N ratio of <7, indicating organic matter of low lipid content. Although *B. mikado* generally developed oral lobes at ca. 6-mm TL and auricles at ca. 10-mm TL (cf. Kasuya 1997), it was unclear as to whether or not the rapid decline in the C:N ratios of the larval stages of *B. mikado* was due to a change in energy source with metamorphosis. Two exceptions were larvae of 6-mm TL and 11-mm TL which had a C:N ratio of <2, thus having little organic content.

For post-larval *B. mikado*, the body C:N ratio was similar to the values (3.7 to 4.8) reported for other ctenophores (Reeve & Baker 1975; Kremer et al. 1986a; Youngbluth et al. 1988; Bailey et al. 1994), indicating a high protein content in the organic matter.

Metabolism

Respiration and excretion rates are known to be high in freshly caught zooplankton due to stress such as from capture, and decrease with time under laboratory conditions (cf. Omori & Ikeda 1984). For *B. mikado*, however, R^* did not change until an incubation time of 39 h was reached. Therefore, the time averaged metabolic rates could be compared among experiments with different incubation times.

The relationship between metabolism and ctenophore size has been reported for other ctenophores as follows. A coefficient b of nearly 1.00 has been reported for the metabolism of *Mnemiopsis leidyi*, *M. mccradyi*, *Eurhamphaea vexilligera*, *Ocyropsis* spp., *Bathocyroe fosteri* and *Pleurobrachia bachei* (Hirota 1972; Kremer 1977, 1982; Kremer et al. 1986a; Youngbluth et al. 1988), indicating that DW-

Table 1. Regression coefficients a and b of the relationships between respiration (R) and dry weight (DW), and between excretion (E) rates and DW of *Bolinopsis mikado* as a function of water temperature. Regression model: R (or E)$=a\mathrm{DW}^b$. Coefficients a and b are derived from GM regression on log–log transformation of the data. r^2 represents the determination coefficient. CI is the 95% confidence interval for b. n, sample size; —, no data.

Temp (°C)	R (μl O_2 ctenophore^{-1} h^{-1})					E (μg-at ctenophore^{-1} d^{-1})							
								NH_4-N			PO_4-P		
	n	Size range (g DW)	a	b (95% CI)	r^2	n	Size range (g DW)	a	b (95% CI)	r^2	a	b (95% CI)	r^2
16	8	0.035–0.614	24.7	0.822 (0.509–1.135)	0.855	4	0.069–0.898	5.5	1.160 (0.865–1.455)	0.993	0.7	1.133 (0.725–1.541)	0.986
22	14	0.047–1.919	53.7	1.016 (0.923–1.109)	0.979	11	0.054–1.163	9.1	1.147 (0.946–1.348)	0.946	1.4	1.166 (0.992–1.340)	0.961
24	—	—	—	—	—	5	0.139–0.533	14.9	1.110 (0.659–1.561)	0.951	2.1	1.038 (0.692–1.384)	0.967
27	30	0.061–1.083	88.5	1.122 (0.999–1.245)	0.920	—	—	—	—	—	—	—	

Table 2. Dry weight (DW)-specific respiration (R^*) and ammonia excretion ($E^*_{NH_4\text{-}N}$) rates, and daily metabolic losses of *Bolinopsis mikado* ranging from 21 to 50 mm of total length and five other lobate ctenophores. The metabolic rate of *B. mikado* at 25°C was calculated from the regression equation in Fig. 4.

Species	DW specific metabolic rate		Metabolic loss (% d^{-1})		Temp. (°C)	Source
	R^* (μl O_2 g DW^{-1} h^{-1})	$E^*_{NH_4\text{-}N}$ (μg-at N g DW^{-1} h^{-1})	Carbon	Nitrogen		
Bolinopsis mikado	51.3	0.32	4.8	3.2	22	This study
	67.5	0.62	6.3	6.1	25	This study
B. vitrea	47.6	0.17	8.2	4.4	25	Kremer et al. (1986a)
Eurhamphaea vexilligera	63.0	0.46	7.7	6.4	25	Kremer et al. (1986a)
Ocyropsis spp.	126.0	0.71	11.8	8.0	25	Kremer et al. (1986a)
Mnemiopsis leidyi	228.2	1.48	18.8	18.4	25	Kremer (1977)
M. mccradyi	97.4	0.70	6	5	22	Kremer (1982)

specific metabolic rates were independent of size. For *Bolinopsis infundibulum* (Bailey et al. 1994) and *B. vitrea* (Kremer et al. 1986a), however, values of b were 0.67 and 0.64, respectively, indicating that DW-specific metabolic rates were size dependent. For *B. mikado* in the present study, 95% confidence intervals (CI) of b for the all data set indicated that b values were not significantly different from 1.00 (Table 1). Uye (personal communication) measured the metabolism of *B. mikado* captured from the Inland Sea of Japan, and the b-values obtained were statistically not different from 1.00. These results indicate that the DW-specific metabolic rate of *B. mikado* was independent of size.

The daily metabolic losses of body carbon and nitrogen in *B. mikado* were lower than those of *Ocyropsis* spp. and *M. leidyi* and similar to those of *B. vitrea*, *E. vexilligera* and *M. mccradyi* (Table 2). Species of *Ocyropsis* have been shown to be relatively active and forage prey at a swimming speed of 1.4–2.0 cm s^{-1} (Harbison et al. 1978; Matsumoto & Harbison 1993). The foraging speed of *B. mikado* has been determined to be 0.7 cm s^{-1} (Kasuya 1997), and that of *M. leidyi* and *M. mccradyi*, 0.6 cm s^{-1} (Kreps et al. 1997) and 0.2–1.2 cm s^{-1} (Larson 1988), respectively. Although metabolic loss in *M. leidyi* was relatively high, energy consumed during swimming may lead to differences in metabolic loss rates between lobate ctenophores.

The O : N ratio of *B. mikado* was similar to values (8.6–18) reported for other ctenophores (Kremer 1977, 1982; Kremer et al. 1986a; Youngbluth et al. 1988; Bailey et al. 1994). Generally, an O : N ratio ranging from 8 to 24 indicates protein-dominated metabolism (cf. Omori & Ikeda 1984). It can therefore be suggested that the substrate on which *B. mikado* feeds is mainly protein-based, indicating that this animal can be considered a strict carnivore.

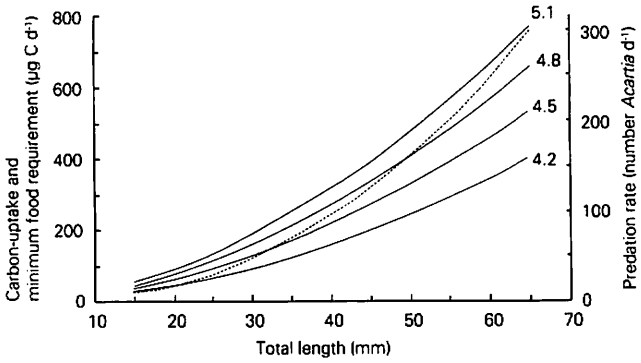

Fig. 5. Minimum food requirement (dashed line) of a post-larval *Bolinopsis mikado* at 22°C. Solid lines represent the daily carbon-uptake of *B. mikado* calculated from its predation rate at food concentrations of 4.2, 4.5, 4.8 and 5.1 *Acartia* l^{-1} at 22°C assuming a carbon content for *Acartia* of 2.5 μg C per animal. Numbers next to the lines are the number of *Acartia* l^{-1}.

Prey requirements

As the DW-specific metabolic rate of *B. mikado* was independent of size, the specific metabolic carbon loss and minimum food requirement values could be applied to *B. mikado* of all sizes (Fig. 5). The food concentration needed to supply the minimum food requirement ranged from 4.2 to 5.1 *Acartia* l^{-1} for *B. mikado* of 15–65-mm TL size class. *Mnemiopsis mccradyi* has been reported to require ca. 10 *Acartia* l^{-1} as the prey density needed to supply its minimum food requirement, and was found to occur in turbid, relatively eutrophic waters such as those in Biscayne Bay, Florida (Kremer et al. 1986b). For *B. vitrea* and *E. vexilligera*, the prey density needed to meet the minimum food requirement was 2 and 3 *Acartia* l^{-1}, respectively (Kremer et al. 1986a), and in Biscayne Bay, *B. vitrea* occurred in clearer, open waters (Kremer et al. 1986b), while *E. vexilligera* was found in the open ocean (Harbison et al. 1978). *Bolinopsis mikado*, however, has been found to not usually be an open-ocean species, but rather to occur in coastal waters influenced by the oligotrophic Kuroshio current (personal observation). *Bolinopsis mikado* can sometimes occur in clearer open waters where prey density has been recorded to be low because the prey density needed to meet its minimum food requirement is less than ctenophores with higher demands such as *M. mccradyi*.

Effect of *Bolinopsis mikado* population on zooplankton and phytoplankton populations

Trophic cascades are often initiated by ctenophores, suggesting that ctenophores can act as a keystone predator (Verity & Smetacek 1996). In Narragansett Bay, Rhode Island, mass occurrence of *M. leidyi* was accompanied by a rapid decline in zooplankton abundance and a summer phytoplankton (the diatom *Skeletonema costatum*) bloom, suggesting that ctenophores controlled phytoplankton abundance indirectly through predation on herbivorous zooplankton and directly by the nutrient excretion accompanying such grazing (Deason & Smayda 1982). In the Inland Sea of Japan, a sharp decline in abundance of the cyclopoid copepod *Oithona davisae* and the appendicularian *Oikopleura dioica* was observed and suggested to be attributable to predation by *B. mikado* (Uye & Ichino 1995; Uye & Sano 1995). In Tokyo Bay, a sharp decline in the copepod population (e.g. *Acartia omorii* and *O. davisae*) was also observed during the period of mass occurrence of *B. mikado* (45 indiv. m^{-3}) in August 1990 (Kasuya et al. 2000). Thus, the effect of the *B. mikado* population on copepod and phytoplankton populations was evaluated from its minimum food requirement and excretion rates of ammonia and phosphate using the data from August 1990 in Tokyo Bay. The biomass of the *B. mikado* population was estimated to be 2.05 g DW m^{-3} (Kasuya, unpublished data). As the DW-specific metabolic rate of *B. mikado* was independent of size, at a water temperature of 28°C, the metabolic rate of the *B. mikado* population was estimated to be 1729 μg C m^{-3} d^{-1} for respiration, 46.5 μg-at m^{-3} d^{-1} for ammonia and 5.9 μg-at m^{-3} d^{-1} for phosphate excretion.

The metabolic carbon demand of the *B. mikado* population was converted to the minimum food requirement assuming a digestive efficiency of 75%. The minimum food requirement of the *B. mikado* population was ca. 2300 μg C m^{-3} d^{-1}, equal to 920 indiv. of *Acartia* or 11500 indiv. of *Oithona* (0.2 μg C *Oithona* $^{-1}$; Uye & Sano 1995). In Tokyo Bay, *O. davisae* is a dominant species throughout most of the year, occupying 36–99% of the total zooplankton quantity sampled (Anakubo & Murano 1991), and *A. omorii* seasonally predominates the net zooplankton (Nomura 1993). The densities of *A. omorii* and *O. davisae* were 4 indiv. m^{-3} and 110000 indiv. m^{-3} in August 1990 in Tokyo Bay, respectively (cf. Nomura 1993). Therefore, the minimum food requirement of the *B. mikado* population could not be supplied by only the standing stock of *Acartia*, and appeared to feed mainly on *O. davisae* during the period of its mass occurrence.

The minimum food requirement of the *B. mikado* population comprised ca. 10% of the standing stock of *O. davisae*. The predatory impact of the *B. mikado* population on copepods, calculated from the predation rate, was estimated to be ca. 24% d^{-1} (Kasuya et al. 2000), indicating that *B. mikado* consumed much more carbon than its minimum food requirement. During summer in Tokyo Bay, *B. mikado* increases rapidly in numbers within a month or two (Kasuya et al. 2000). The investment of a high proportion of energy into egg production and growth may lead to the observed high population growth of *B. mikado*.

The standing stock of nutrients in Tokyo Bay ranged from 0.22 to 25.1 μM for ammonia and from 0.04 to 2.53 μM for phosphate in August 1990 (Yu 1994). Ammonia and phosphate excreted by the *B. mikado* population were 0.2–21% and 0.2–15% of those standing components in the seawater, respectively. In comparison, the ammonia excretion rate during the mass occurrence of *M. leidyi* in

Narragansett Bay ranged from 10 to 60 μg-at N $m^{-3} d^{-1}$, equal to 0.25–25% of the standing ammonia in the seawater (Kremer 1975). *Bolinopsis mikado* has been reported to occur in not only the inner part but also the outer and outside of Tokyo Bay, with strongly seasonal pulses and with patches of high abundance (Kasuya et al. 2000, personal observation). In the inner part of Tokyo Bay, because of its eutrophic waters, nutrients may not limit the growth of phytoplankton (Yu 1994). However, in the outer part and outside of Tokyo Bay with clearer water influenced by the Kuroshio, *B. mikado* may be a major nutrient source seasonally and locally.

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