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

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Abstract: The egg production rate (EPR) of the lobate ctenophore *Bolinopsis mikado* was measured in summer, fall, and winter using field-collected animals whose total lengths (TL) ranged from 17 mm to 73 mm. The TL of spawning *B. mikado* ranged from 22 mm to 73 mm, indicating that *B. mikado* matures at ca. 20 mm TL. Because the percentage of spawning individuals to the total ranged from 50% to 100%, *B. mikado* probably spawned intermittently or daily in Tokyo Bay. Spawning individuals were found even in December and January. *Bolinopsis mikado* seemed to reproduce continuously in Tokyo Bay throughout the year. A multiple regression analysis between the EPR and ctenophore body size and water temperature suggested that 21.5% of EPR can be explained by these variables. The EPR increased linearly with ctenophore size, i.e. the wet-weight specific EPR (EPR*) was independent of the body size. The relationship between the EPR* and water temperature was equivalent to a Q_{10} value of 4.7, and was considerably higher than that of the respiration, predation, and growth rates, which may lead to quick population growth and mass occurrence of *B. mikado* during summer and fall in coastal waters.

Key words: *Bolinopsis*, ctenophores, larvae, reproduction, Tokyo Bay

Introduction

Ctenophores are voracious predators that significantly affect mesozooplankton and fish egg/larva biomasses (Deason 1982, Purcell & Arai 2001). Recently, neritic and estuarine ctenophores were accidentally introduced into eutrophicated waters in various parts of the world, possibly through ship ballast water, and the outbreak has become a major problem in the Black Sea, the Sea of Azov, and elsewhere (Zaitsev 1992, Purcell et al. 2001). Drastic population growth and mass occurrences of ctenophores have been reported by many researchers (Deason & Smayda 1982, Kremer 1994, Mutlu et al. 1994, Kasuya et al. 2000a, Sullivan et al. 2001) and indicate that ctenophores have high growth and reproductive capabilities (Kremer & Reeve 1989). Since most ctenophores are too fragile to be preserved in formalin or in any preservative presently known, it is difficult to determine the egg production rate by count-

ing eggs in ovaries of preserved specimens collected from the field. Nevertheless, some quantitative information on the reproduction of ctenophores has been obtained from field and laboratory experiments. Such studies on ctenophore egg production have been conducted on the lobate species *Mnemiopsis leidyi* A. Agassiz (Kremer 1975), *Mnemiopsis mccradyi* Mayer (Baker & Reeve 1974, Reeve et al. 1989), and *Ocyropsis crystallina guttata* (Rang) (Harrison & Miller 1986), and the cydippids *Pleurobrachia pileus* Vanhöffen (Greve 1970) and *Pleurobrachia bachei* A. Agassiz (Hirota 1972, 1974). Greve (1970) reported on the reproduction of the beroid ctenophore *Beroë gracilis* Künne.

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-fall in Tokyo Bay (Kasuya et al. 2000a). Some ecological studies on the abundance, feeding, metabolism, and growth of *B. mikado* have been reported (Kasuya et al. 1994, 2000a, b, 2002), but its reproduction rate has not been determined. In the present paper, the egg produc-

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tion rate of *B. mikado* was determined from summer through winter using field-collected animals of various sizes. The elemental composition (carbon and nitrogen) of the eggs was also determined.

Materials and Methods

Preliminary experiment

A series of experiments was conducted from July to October 1994, from July to December 1995, and in January 1996 at the Banda Marine Laboratory of Tokyo University of Fisheries (present name: Tokyo University of Marine Science and Technology), Tateyama, Chiba Prefecture, which is located near the mouth of Tokyo Bay (34°58'30"N, 139°46'12"E).

A preliminary experiment was conducted on August and October in 1994 to examine the effect of the volume of seawater in a bottle on the egg production rate (EPR, eggs ctenophore⁻¹ d⁻¹) of *Bolinopsis mikado*. Four animals with total lengths (TL, Fig. 1) of 50, 51, 55, and 59 mm were incubated in 2-liter bottles containing 1 liter of seawater, and three animals of 54, 54, and 55 mm TL were incubated in 2-liter bottles containing 1.5 liters of seawater at water temperatures ranging from 23.1 to 26.9°C. The sampling method of *B. mikado* and procedure of the experiment were the same as those in "Measurement of egg production rate" as described below.

For measurement of the carbon and nitrogen contents of the eggs, the eggs of *B. mikado* remaining in the bottles were pipetted into a petri dish and rinsed with filtered seawater (Whatman GF/C filter). After replicating the above procedure, various numbers of eggs were rinsed with 5% isotonic ammonium formate to remove seawater and gently filtered through a precombusted Whatman GF/C filter (400°C for 3 h). A count of the eggs on the filter using a dissecting microscope provided four samples of eggs containing 15, 19, 39, and 52 eggs, respectively. The samples were dried at 90°C for 2 d, and the carbon and nitrogen contents of each were measured by a CHN Corder (MT-3, Yanaco Co. Ltd., Kyoto, Japan).

Measurement of egg production rate

Samples of *B. mikado* were collected using wide-mouthed plastic bottles by snorkeling in waters adjacent to the laboratory. In the experiment, 59 specimens, ranging from 17 to 73 mm TL, were used to determine the EPR. Immediately after collection, the TL of each *B. mikado* specimen was measured to the nearest 1 mm using calipers, after which the specimen was transferred into a cylindrical glass bottle containing seawater (0.5, 1.0, and 1.5 liters). The size of the bottle and the volume of seawater in it depended on the ctenophore body size. A 1-liter bottle containing 0.5 liters of filtered seawater was used to incubate individuals of <30 mm TL, and a 2-liter bottle containing 1.0 or 1.5 liters of filtered seawater was used for individuals ranging

Fig. 1. Photographs of an egg (upper) and a post-larva (lower) of *Bolinopsis mikado*. The double-arrowhead lines in the photographs represent measurements of the diameter of eggs and total length (TL) of the post-larva. The scale bar represents 0.1 mm for the egg and 5 mm for the post-larva.

from 30 to 60 mm TL or >60 mm TL. The seawater, pumped up from waters adjacent to the laboratory, was first sand filtered, then further filtered using a Whatman GF/C filter. The bottles were kept in a water bath of running sand-filtered seawater for 24 h under a 12 light : 12 dark light cycle. The water temperature of the sand-filtered seawater was determined every hour using a telemetry buoy (SEACOM, Sanyo Techno Marine Inc., Tokyo, Japan). The daily fluctuation of the water temperature during the experiments was at maximum 2.3°C (see Table 3). Therefore, in this paper, we employed the mean water temperature as the experimental temperature.

The released eggs sank and accumulated on the bottom of the bottle. Thus, at the end of the incubation period, *B. mikado* was removed, the seawater in the bottle was mixed well, the subsample was collected in a measuring cylinder in 200 mL of the seawater, and the number of eggs was counted under a dissecting microscope. The eggs of *B. mikado* are spherical and enclosed in a gelatin capsule (Fig.

1), approximately 0.7 mm in diameter including the capsule. Since many ctenophores are capable of self-fertilization (e.g. Baker & Reeve 1974), hatched larvae of *B. mikado* were also observed in the bottle. Thus, we counted the hatched larvae and eggs.

Results

Effect of container size on reproduction

The TL of *Bolinopsis mikado* was converted to the wet weight (WW, g) using an equation: $WW = 0.0005TL^{2.72}$ (Kasuya et al. 1994), and the WW-specific EPR (EPR*, eggs g WW⁻¹ d⁻¹) was obtained. Four specimens, with TLs ranging from 50–59 mm, incubated in 1.0 liter of seawater, spawned 6–100 eggs g WW⁻¹ d⁻¹ with a mean of 48 ± 38 . Three specimens with TLs ranging from 54–55 mm, incubated in 1.5 liters of seawater, spawned 34–52 eggs g WW⁻¹ d⁻¹ with a mean of 42 ± 9 . Assuming 1 mL of seawater equals 1 mg, the ratio of *B. mikado* WW to the volume of seawater was $\leq 1:30$, and no significant differences were observed between the reproduction rate in 1.0 liter and that in 1.5 liters of seawater (t -test, $p=0.38$).

Egg production rate

The relationships between the number of eggs and their carbon (C) and nitrogen (N) contents were fitted to a linear regression equation, and significant slopes of 0.57 ($r^2=0.98$, $p=0.0078$) for C and 0.15 ($r^2=0.97$, $p=0.016$) for N were obtained. Thus, the carbon and nitrogen weights in an individual egg were 0.57 μ g and 0.15 μ g, respectively.

The TL of the spawning *B. mikado* ranged from 22 mm to 73 mm. The minimum TL for a spawning individual was observed in August 1994, and its EPR was 10 eggs ctenophore⁻¹ d⁻¹. The maximum EPR was 2550 eggs ctenophore⁻¹ d⁻¹ obtained from an individual of

65 mm TL. Assuming the body carbon of *B. mikado* to be 1.10% of the dry weight (DW), the TL was converted to body carbon content using the equations: $DW = 0.062TL^{2.34}$ (Kasuya et al. 2000b). Thus, the EPR by 22 mm TL and 65 mm TL *B. mikado* mentioned above equals 6.0% and 13.5% of the individuals' body carbon, respectively.

The ratio of the number of spawning individuals to the total number of individuals was obtained using specimens exceeding a maturation size of 20 mm TL (see Discussion). The percentage of spawning individuals ranged from 50% to 100%, and no seasonal pattern was found (Table 1).

Multiple regression analysis of the egg production rate

Using the data of the spawning *B. mikado*, a multiple regression analysis was performed between the EPR and ctenophore body size and water temperature (T, °C). Since *B. mikado* seems to mature at ca. 20 mm TL, i.e., 1.7 g WW, the variable of body size was given by $WW - 1.7$, and a significant multiple regression equation,

$$EPR = 33.77(WW - 1.7) + 119.05T - 2734.21,$$

was obtained (Table 2). Coefficients of the variables $WW - 1.7$ ($p=0.0001$) and T ($p=0.0024$), and the y-inter-

Table 2. Multiple regression statistics of the relationship between the egg production rate (eggs ctenophore⁻¹ d⁻¹) of *Bolinopsis mikado* and body size ($WW - 1.7$, g) and water temperature (T, °C).

Item	Coefficient	Standard partial regression coefficient	<i>t</i>	<i>p</i>
Variable				
WW-1.7	33.77	0.616	4.169	0.0001
T	119.05	0.468	3.169	0.0024
y-intercept	-2734.21		-2.745	0.0081

$n=59$, adjusted $r^2=0.215$, $F=8.977$, $p=0.0004$

Table 1. Ratio of spawning individuals to the total number of *Bolinopsis mikado* individuals with a total length (TL) exceeding 20 mm.

Date	Range of TL (mm)	<i>n</i>	% of spawning individuals
1994			
9 Jul.	21–64	18	56
24–26 Aug.	20–65	26	85
4 Oct.	30–59	7	100
1995			
19 Jul.	44–62	5	100
12 Aug.	39–53	4	50
14 Oct.	52–58	4	75
13 Nov.	58–68	5	100
13, 17 Dec.	62–65	2	100
1996			
24, 28 Jan.	57–74	4	50

Fig. 2. Standardized residual plots of the egg production rate (EPR) of *Bolinopsis mikado* versus the experimental month.

cept ($p=0.0081$) were also significant. The standard partial regression coefficient was 0.616 for $WW-1.7$ and 0.468 for water temperature. An adjusted R^2 of 0.215 is the proportion of variance explained by the regression equation, i.e., 21.5% of EPR was able to be explained by ctenophore body size and water temperature.

To examine outliers, an analysis of residuals was performed using the standardized residual (SR) of EPR plotted versus the experimental month. The highest SR value of 3.265 was obtained from July 1995, and all the SRs for this month were positive (Fig. 2). Although the SR in 1994 was distributed almost uniformly around the axis of zero, the SRs after July 1995 were mainly negative.

Relationships of EPR to body size and water temperature

The relationship between the EPR and the ctenophore body size was expressed by an allometric equation $EPR = a(WW-1.7)^b$, where a and b are constants (Table 3). A significant regression equation was found for the data obtained from July ($r^2=0.71$, $p=0.001$) and August in 1994 ($r^2=0.71$, $p<0.000001$). The constant b of the significant regression equation was 2.54 for July 1994 and 1.20 for August 1994.

The effect of water temperature on the fecundity of *B. mikado* was evaluated by the EPR^* (Fig. 3). The relationship between the EPR^* and water temperature was expressed by an exponential equation, $EPR^* = ae^{kT}$, where a and k are constants and T is the water temperature ($^{\circ}\text{C}$). Be-

cause the EPR^* obtained from July and August in 1995 seemed to have been strongly affected by food supply (see Discussion), these data were excluded from the regression analysis. We obtained a significant regression equation: $EPR^* = 0.75e^{0.155T}$, $r^2=0.67$, $p=0.024$. A coefficient k of 0.155 was equivalent to a Q_{10} value of 4.7.

Fig. 3. Effect of water temperature on wet-weight-specific egg production rate (EPR^*) of *Bolinopsis mikado*. Closed circles indicate the mean EPR^* , and bars indicate the range of EPR^* in each data set. Because the data with crosses (EPR^* s obtained from July and August in 1995) appear to have been strongly affected by food supply, these data were excluded from the regression.

Table 3. Relationship between wet weight (WW, g) and egg production rate (EPR, eggs ctenophore $^{-1}$ d $^{-1}$) of *Bolinopsis mikado* at experimental water temperatures. Regression coefficients a and b were obtained from the regression equation, $EPR = a(WW-1.7)^b$. r^2 represents the determination coefficient, and n is the number of spawning individuals. CI is the 95% confidence interval for b . WW-specific EPR (EPR^*) at each experimental water temperature is also presented.

Date	Water temperature ($^{\circ}\text{C}$) Range	Mean	n	WW range (g)	a	b (95% CI)	r^2	p	EPR^* (eggs g WW $^{-1}$ d $^{-1}$) Range	Mean
1994										
9 Jul.	22.2–23.5	22.8	11	10.6–40.9	0.12	2.54 (1.33–3.75)	0.71	0.001	2–52	24
24–26 Aug.	24.6–26.9	25.7	22	2.2–42.7	26.5	1.20 (0.84–1.55)	0.71	<0.000001	5–111	47
4 Oct.	23.1–24.3	23.8	7	5.2–32.8	105.0	0.64 (–3.92–1.68)	0.34	0.17	8–75	44
1995										
19 Jul.	21.0–21.6	21.3	5	14.8–37.5	88.8	0.92 (–0.42–2.26)	0.61	0.11	50–106	66
12 Aug.	22.4–23.5	22.9	2	22.1–24.5	—	—	—	—	0.5–1.2	0.8
14 Oct.	20.5–21.1	20.8	3	24.5–31.3	1.15×10^8	–3.93 (–34.7–26.8)	0.72	0.35	7–27	14
13 Nov.	20.6–21.2	20.8	5	31.3–48.2	2.1	1.43 (–3.17–6.04)	0.24	0.39	4–14	10
13, 17 Dec.	16.7–18.1	17.4	2	37.5–42.7	—	—	—	—	12–27	19
1996										
24, 28 Jan.	14.7–15.6	15.1	2	29.9–58.5	—	—	—	—	4–11	8

Discussion

Effect of container size on reproduction

The fecundity of ctenophores may depend on experimental conditions such as container volume (e.g. Purcell et al. 2001). However, in the present study, no significant difference was found in the EPR* between the two water volumes when the ratio of ctenophore WW to the volume of seawater $\leq 1:30$. Except for the experiment performed in January 1996 ($\leq 1:17$), the ratio of WW to seawater volume was always $\leq 1:30$. In the experiment in January 1996, an individual of 73 mm TL spawned, and the mean EPR* of 11 eggs g WW⁻¹ d⁻¹ was almost the same as values found during November and December (cf. Table 3). Thus, we concluded that the volume of seawater did not influence the reproduction of *Bolinopsis mikado*.

Reproductive characteristics of *Bolinopsis mikado*

For *Mnemiopsis leidyi*, an EPR of 300–450 eggs g WW⁻¹ d⁻¹ was reported by Kremer (1975), which corresponds to 2.7- to 4-fold of the maximum EPR* of 111 eggs g WW⁻¹ d⁻¹ for *B. mikado* in August 1994 (Table 3). In contrast, the egg volume of *B. mikado* calculated from the egg diameter of ca. 0.7 mm (Fig. 1) is 2.4- to 6.2-fold of those of *M. leidyi* and *Mnemiopsis mccradyi* calculated using egg diameters of 0.42 ± 0.068 mm for the former (Kremer 1975) and 0.38–0.52 mm for the latter species (Baker & Reeve 1974). This is consistent with the fact that the individual egg carbon weight of 0.57 μ g for *B. mikado* is 5.7-fold of the 0.1 μ g for *M. mccradyi* estimated by Reeve et al. (1989). These results imply that there are different types of reproductive strategy among ctenophore species; small numbers of large eggs for *B. mikado* and vice versa for *M. leidyi*.

In the present study, the percentage of spawning individuals to the total ranged from 50% to 100%, suggesting that *B. mikado* spawns intermittently or daily in Tokyo Bay. A similar reproductive cycle has been shown for *M. mccradyi* reared in the laboratory (Baker & Reeve 1974). *Pleurobrachia bachei* has been also reported to spawn daily (Hirota 1972).

Spawning *B. mikado* were found even in December and January in the present study. Kasuya et al. (2000a) found small (5–15 mm TL) *B. mikado* in January and February in Tokyo Bay, a finding which supports the winter reproduction revealed in the present study. Since the minimum water temperature around 9°C in Tokyo Bay is generally recorded in January or February, *B. mikado* probably reproduces continuously throughout the year.

The TL of spawning *B. mikado* ranged from 22 mm to 73 mm, indicating that *B. mikado* matures at ca. 20 mm TL and that *B. mikado* spawns eggs over an extensive portion of its lifespan. Kasuya et al. (2002) reared *B. mikado* in a laboratory using calanoid copepods *Acartia* spp. consisting mostly of adults as prey, and created a growth curve under

a food concentration of 100 *Acartia* L⁻¹, i.e. $TL = 132.2/(1 + e^{5.80 - 0.134t})$ at 17°C and $TL = 55.3/(1 + e^{5.03 - 0.362t})$ at 24°C. These growth curves suggest that *B. mikado* reaches a maturation size of 20 mm TL within 30 d after hatching at 17°C, and reaches the same size within 13 d at 24°C. The instantaneous growth rate of *B. mikado* increases gradually from ca. 0.4 to 0.5 d⁻¹ with an increase in the food concentration from 10 to 100 *Acartia* L⁻¹ (Kasuya et al. 2002). In addition, in Tokyo Bay, where the standing stock of *Acartia*-sized copepods ranges from 10 to 60 copepods L⁻¹ (Anakubo & Murano 1991), and the water temperature typically ranges from 9 to 28°C annually, the maturation time of *B. mikado* appears to be around 13 d in summer and more than 30 d in winter.

Factors affecting reproduction of *Bolinopsis mikado*

Because an adjusted R^2 of 0.215 was obtained from the multiple regression analysis between the EPR and ctenophore body size and water temperature, 21.5% of the EPR can be explained by these variables. The standard partial regression coefficient of 0.616 for ctenophore body size was higher than that of 0.468 for water temperature (Table 2), indicating that the EPR is affected more by body size than by water temperature. Nevertheless, as the range of variables was from 2.2 to 58.5 g for body size and from 15.1 to 25.7°C for water temperature, the difference of range width might influence the contribution of variables to the EPR.

Although all SR values in July 1995, including the highest SR of 3.265, were positive, those values were negative in August 1995, and after that, they were mainly negative (Fig. 2). A positive SR means that the EPR exceeded the predicted EPR, and vice versa. We determined the EPR for August 1995 using specimens collected from an area of high abundance. During mass occurrences of ctenophores, drastic declines in the abundance of natural zooplankton have been observed in the field (e.g., Deason & Smayda 1982, Uye & Ichino 1995, Uye & Sano 1995). In the present study, no quantitative data were available on zooplankton abundance in the waters around the laboratory. Nevertheless, when we collected zooplankton as prey of *B. mikado* using a 0.33-mm meshed plankton net, we had difficulty in collecting enough prey during a mass occurrence of *B. mikado* in August 1995. Thus, in addition to the effect of body size and water temperature, the EPR below the predicted EPR in August 1995 seems to have been affected by low food supply, and vice versa in July 1995, before the mass occurrence of *B. mikado*.

The EPR of *B. mikado* varied with WW^{-1.7}; the significant coefficient b was 1.20 and 2.54 (Table 3), indicating that EPR depends on body size. For *M. leidyi*, fecundity increases linearly with ctenophore size but is variable *in situ* (Kremer 1975). For *B. mikado*, because b was highly significant at 1.20 ($p < 0.000001$), fecundity probably increases linearly with ctenophore size, i.e. EPR* is independent of

the body size.

The relationship between the EPR* of *B. mikado* and water temperature was equivalent to a Q_{10} value of 4.7. The relationships of the WW-specific predation and respiration rates of *B. mikado* to water temperature are equivalent to Q_{10} values of 1.8 (Kasuya et al. 1994) and 1.9 (Kasuya et al. 2000b), respectively. In addition, the relationship of the instantaneous growth rate to water temperature is equivalent to Q_{10} values of 5.9 and 1.4 at 17–21°C and at 21–27°C (Kasuya et al. 2002). The Q_{10} value for EPR* is much higher than that of others except for the instantaneous growth rate at 17–21°C, indicating that the investment into reproduction of the energy obtained from feeding is higher at water temperatures above 21°C.

In Tokyo Bay, drastic population growth of *B. mikado* has been observed in summer and fall (Kasuya et al. 2000a). Rising water temperatures in summer and fall shorten the maturation time and lead to enhanced investment of obtained energy into reproduction. These, in turn, may lead to quick population growth and the mass occurrence of *B. mikado* during the summer and fall in coastal waters, with the opposite occurring in the winter and spring.

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