Laboratory study of growth of the lobate ctenophore *Bolinopsis mikado* (Moser)

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Abstract: The laboratory growth rate of the lobate ctenophore *Bolinopsis mikado* was measured under various water temperatures and food concentrations using calanoid copepods of *Acartia* spp. as prey. *Bolinopsis mikado* developed its oral lobes when its total length (TL) reached about 6 mm, and auricles at about 10 mm TL, becoming fully lobate without tentacles at about 15 mm TL. Larval *B. mikado* grew with 3 *Acartia* l^{-1}, indicating that the larvae were capable of growth under lower food concentrations than the post-larvae. The instantaneous growth rate rapidly increased with a rise in water temperature from 17° to 21°C, and moderately increased over 21°C, reaching a maximum of about 0.7 d^{-1} at 27°C. Net growth efficiency was about 90% at a TL of 15 mm and rapidly decreased with increases in TL at 24° and 27°C, suggesting that the investment of assimilated energy into egg production might be larger at higher temperatures. The growth curve obtained for *B. mikado* suggests that the life span of *B. mikado* in Tokyo Bay is less than one month during summer in contrast to more than 3 months during winter. The increase in growth rate and egg production rates of *B. mikado* with higher water temperatures appears to allow their quick population growth and mass occurrence during summer/fall, and vice versa during winter/spring in Tokyo Bay.

Key words: ctenophores, growth, culture, *Bolinopsis*, Tokyo Bay

Introduction

As ctenophores feed voraciously on mesozooplankton such as copepods (Kremer 1979; Deason 1982; Purcell 1985) and have high growth and reproductive capabilities (Reeve et al. 1989; Falkenhaug 1996), they are considered to be important regulators of these populations in marine coastal waters (Deason & Smayda 1982; Suthers & Frank 1990; Båmstedt 1998). As most ctenophores are too fragile to preserve in formalin or in any preservatives known at present, it is difficult to determine the growth rate from cohort analyses based on field data. Therefore, knowledge of the growth rate of ctenophores has been obtained mostly from laboratory culture. Laboratory cultures have been conducted on the lobate ctenophores *Mnemiopsis leidyi* (Kre-

mer 1975), *M. mccradyi* (Baker & Reeve 1974; Reeve & Baker 1975; Reeve et al. 1978, 1989) and *Bolinopsis infundibulum* (Greve 1970), and the cydippids *Pleurobrachia pileus* (Greve 1970) and *P. bachei* (Hirota 1972). Greve (1970) has also cultured the beroid ctenophores *Beroe cucumis* and *B. gracilis*.

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. 2000a). Some ecological studies regarding the abundance, feeding and metabolism of *B. mikado* have been reported (Kasuya et al. 1994, 2000a, b); however, little information regarding its growth is available. In the present paper, we describe the growth characteristics of *B. mikado*. The laboratory growth rate was determined under various water temperatures and food concentrations using calanoid copepods of *Acartia* spp. as prey.

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Materials and Methods

Morphology

As lobate ctenophores develop, after hatching they pass through a cydippid larval stage with a pair of tentacles. *Bolinopsis mikado* loses its tentacles at a total length (TL, mm) of about 15 mm and assumes a morphology similar to the adult (see Results). In this paper, organisms of <15 mm TL are defined as larvae and those of >15 mm TL are defined as post-larvae.

The TL of larval *Bolinopsis mikado* is considered the length from the aboral pole to the mouth. For larvae with developing oral lobes and for the post-larvae, TL is the length from the aboral pole to the end of the lobes (cf. Kasuya et al. 1994).

Sampling and culture technique

A series of experiments was conducted from June 1995 to January 1996 at the Banda Marine Laboratory of Tokyo University of Fisheries, Tateyama, Chiba Prefecture. Samples of *B. mikado* were collected using wide-mouthed plastic bottles during snorkeling in waters adjacent to the laboratory. The prey *Acartia* spp., consisting mostly of adults, were collected daily when possible, using a Norpac net (45-cm mouth diameter, 0.33-mm mesh) at Tateyama Fishing Port.

A "double kuvette", consisting of two chambers (cf. Greve 1970), was used for rearing *B. mikado*. Sand-filtered seawater (salinity of about 34 psu) pumped up from waters adjacent to the laboratory was used during the culture experiments. *Acartia* spp. were individually counted into a glass bottle containing 1 liter of sand-filtered seawater. A constant food concentration was obtained by diluting the water in the bottle, which contained a known number of prey, with culture water in the chamber of the double kuvette. Food and seawater in the double kuvette were changed every 12 h. After removing *B. mikado* to a beaker, the remaining food was removed by a hand net, and both food and a quarter of the volume of water was renewed.

Growth experiments

In a preliminary experiment, the effect of container size on the growth rate of *B. mikado* was examined with 9 larvae whose initial lengths ranged from 7 to 8 mm TL. One or two indiv. were cultured in a double kuvette with a 5-l chamber, and two or three indiv. in a 12-l chamber, at food concentrations of 10 and 20 *Acartia* l^{-1} at 21°C for 4 d.

In the growth experiment, 39 larvae ranging from 3 to 14 mm TL and 11 post-larvae ranging from 15 to 37 mm TL were used for determining growth rate. *Bolinopsis mikado* was cultured under various food concentrations ranging from 2 to 100 *Acartia* l^{-1} at 21°C. Assuming a carbon weight of 2.4 μg C *Acartia*$^{-1}$ (Kremer & Reeve 1989), these food concentrations were equal to carbon contents

ranging from 48 to 240 μg C l^{-1}. At a food concentration of 100 *Acartia* l^{-1}, *B. mikado* was cultured at various water temperatures ranging from 17 to 27°C. The number of *B. mikado* per chamber was two indiv. for larvae and one or two indiv. for post-larvae. A double kuvette of 12-l capacity was employed for culturing at food concentrations of 2–20 *Acartia* l^{-1}, and one of 5-l capacity was used at concentrations of 50 and 100 *Acartia* l^{-1}.

During the experiments, all ctenophores were maintained for 4–7 d under a 12 L : 12 D light cycle. The TL of *B. mikado* was measured to the nearest 1 mm every 24 h when seawater was changed. Water temperature in the double kuvette was adjusted by regulating the temperature of a water bath. When water temperature in the experiment and in the collected waters differed by over 3 degrees, specimens were acclimated to the experimental temperature for 24 h.

Wet weight of *Bolinopsis mikado*

After excess water around the body was removed with tissue paper, 13 larvae of *B. mikado* with their TL ranging from 5 to 13 mm were individually placed on a preweighed petridish, and wet weight (WW) was measured on an electric balance with a precision of 0.1 g. The WW of a post-larva was estimated from TL using the regression equation $WW = 0.0005 TL^{2.72}$ (Kasuya et al. 1994).

Calculation of instantaneous growth rate and net growth efficiency

The instantaneous growth rate (IG) was calculated using the following equation:

$$IG = (\ln WW_{t_2} - \ln WW_{t_1})/(t_2 - t_1)$$

where WW_{t_1} and WW_{t_2} are WW of the ctenophore at times (day) t_1 and t_2 in the experiment. Net growth efficiency (NGE) of *B. mikado*, which does not include egg production, was calculated using the following equation (cf. Omori & Ikeda 1984):

$$NGE = (C_{t+1} - C_t)/[C_{t+1} - C_t + (M_t + M_{t+1})/2],$$

where C_t and C_{t+1} are the body carbon content (μg) of the ctenophore, and M_t and M_{t+1} are the daily metabolic carbon-loss (μg) of the ctenophore at times (day) t and $t+1$ in the experiment. The body carbon content of post-larval *B. mikado* is calculated as 1.10% of dry weight (DW) from TL using the regression equation $DW = 0.062 TL^{2.34}$ (cf. Kasuya et al. 2000b). The relationship between DW specific respiration rate (R^*, μl O_2 $DW^{-1}h^{-1}$) of *B. mikado* and water temperature (T) was expressed by the regression equation $R^* = 13.2e^{0.065T}$ (Kasuya et al. 2000b), and R^* was converted to M using a respiratory quotient value (RQ) of 0.8. Considering an increase in respiration rate with an increase in body size, M was averaged by Ms at t and $t+1$.
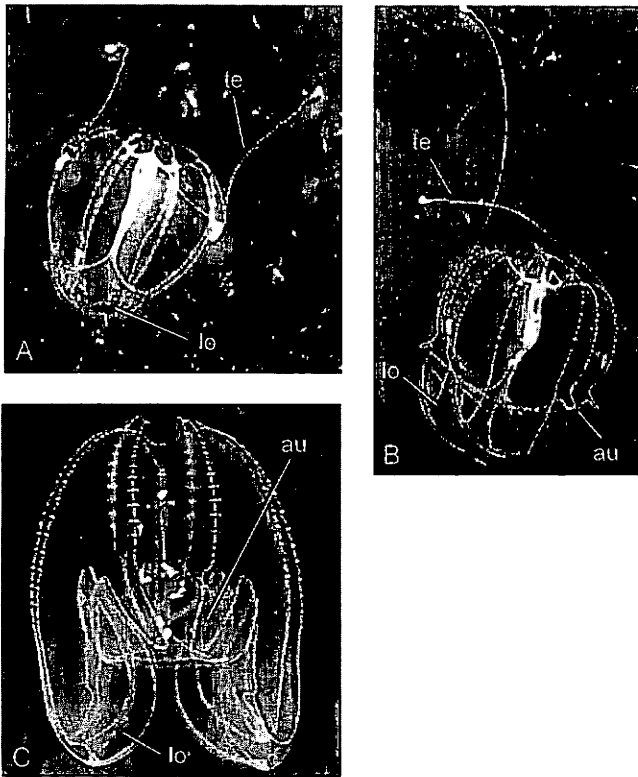
Fig. 1. Process of growth of *Bolinopsis mikado*. A–B. Larvae with TLs of 6 mm and 10 mm, respectively, and C. A post-larva of 15-mm TL (te tentacle, lo lobe, au auricle).

Results

Growth rate

Oral lobes and auricles of *B. mikado* generally began to appear in animals of about 6 mm TL (Fig. 1A) and 10 mm TL (Fig. 1B), respectively. We observed that larval *B. mikado* of about 13 mm TL captured prey both with their tentacles and oral lobes. Animals with TL reaching about 15 mm became fully lobate without tentacles and assumed a morphology similar to that of the adult (Fig. 1C).

The growth curve of *B. mikado* was obtained by combining growth rates of different sized individuals (Fig. 2). Assuming that the size of the animals is almost the same in a cohort, the mean TL was fitted with the growth formula $TL = TL_{max}/(1 + e^{a-bt})$, where TL_{max} is the theoretical maximum TL, t is time in days from hatching, and a and b are constants. At the food concentration of 100 *Acartia* l^{-1}, growth curves at 17 and 24°C, obtained over wide ranges of TL and days, were expressed by the following equations:

$$TL = 132.2/(1 + e^{5.80-0.134t}) \quad (17°C) \quad (1)$$

and

$$TL = 55.3/(1 + e^{5.03-0.362t}) \quad (24°C). \quad (2)$$

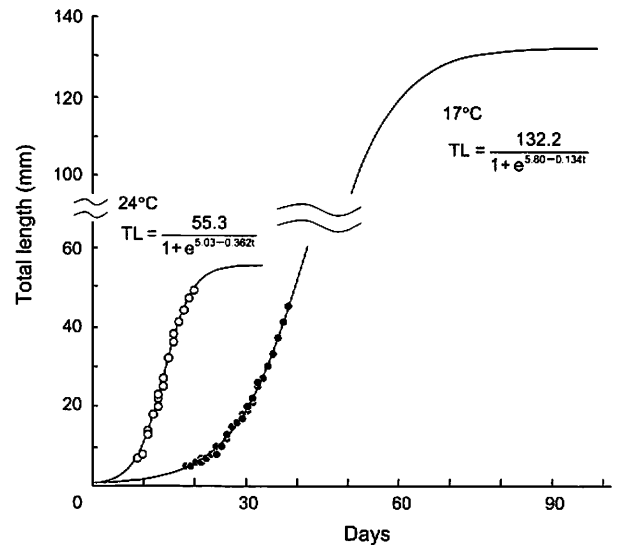The predicted maximum TL of *B. mikado* was about 132 mm at 17°C and 55 mm at 24°C.

Fig. 2. Growth curve of *Bolinopsis mikado* under water temperatures of 17°C (●) and 24°C (○) at a food concentration of 100 *Acartia* l^{-1}. The equation and line are derived from a logistic curve.
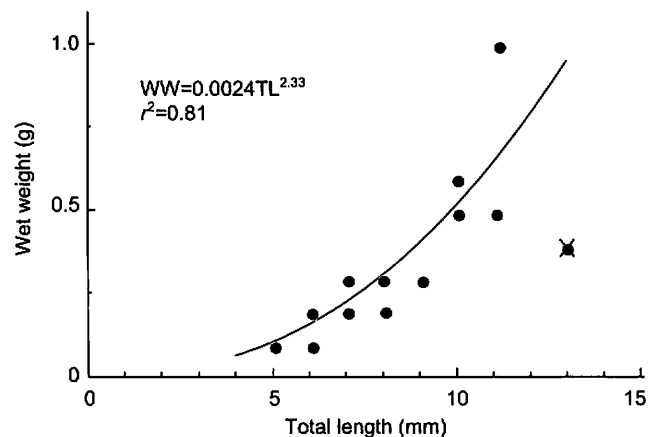

Fig. 3. Relationship between total length (TL) and wet weight (WW) of a larval *Bolinopsis mikado*. The equation and line are derived from a linear least-square regression on log-log transformation of the data. Datum with a cross was excluded from the regression because the lobes of the sample probably got injured in the process of removing water around the body.

Effects of container size, food concentration, and water temperature on growth

The relationship between TL (mm) and WW (g) of larval *Bolinopsis mikado* is expressed by the equation, $WW = 0.0024TL^{2.33}$ (Fig. 3). In this paper, the WW of a larva was estimated from TL using this equation.

The influence of container size on ctenophore growth was examined using IG. The mean IG was 0.44 (± 0.05SD, $n = 4$) for a double kuvette of 5-l capacity and 0.43 (± 0.05, $n = 5$) for one of 12-l capacity, and no significant differences were observed (t-test, $P > 0.05$).
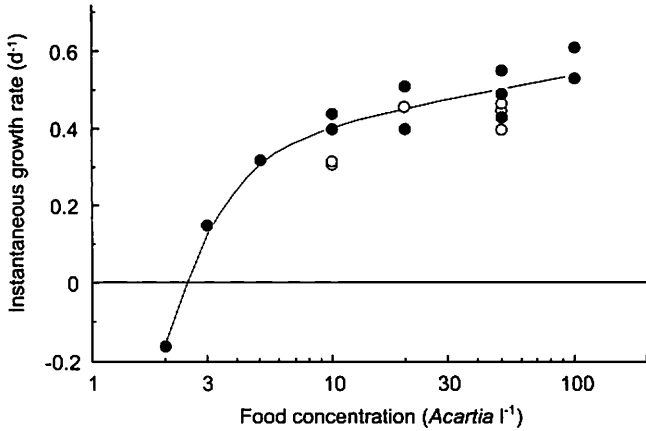
Fig. 4. Instantaneous growth rate (IG) of *Bolinopsis mikado* as a function of food concentration at 21°C. IG was obtained from WW increase for 2–4 d using specimens with TLs ranging 7–9 mm (●) or 15–18 mm (○).
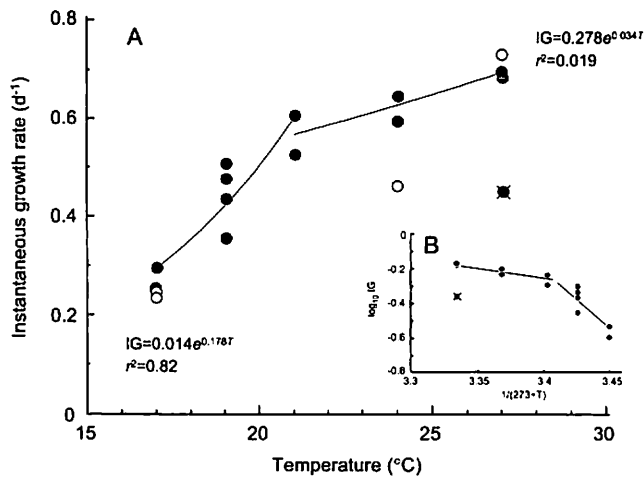

Fig. 5. A. Instantaneous growth rate (IG) of *Bolinopsis mikado* as a function of water temperature at a food concentration of 100 *Acartia* l^{-1}. IG was obtained from WW increase for 2–4 d using specimens with TLs ranging 7–9 mm (●) or 15–18 mm (○). The equation and line are derived from a linear least-square regression on log-log transformation of the data. Datum with a cross was excluded from the regression because the sample was obviously inactive in the experiment. B. The Arrhenius plot, $1/(273+T)$ vs. $\log_{10}$ IG, with lines drawn by eye.

To determine the effects of food concentration and water temperature on ctenophore growth, IG was obtained from changes in WW over a 2–4 day period using specimens with TLs ranging between 7–9 mm or 15–18 mm. Larval *B. mikado* could not maintain its initial WW at a food concentration of 2 *Acartia* l^{-1} (Fig. 4). The IG for a larva turned into a positive value at a food concentration of 3 *Acartia* l^{-1} and rapidly increased with an increase in food concentration up to 10 *Acartia* l^{-1}, thereafter increasing gradually to reach a maximum of 0.61 at a food concentration of 100 *Acartia* l^{-1} (Fig. 4). The IG for a post-larva ranged from 0.32 to 0.46 at food concentrations of 10–50 *Acartia* l^{-1}.
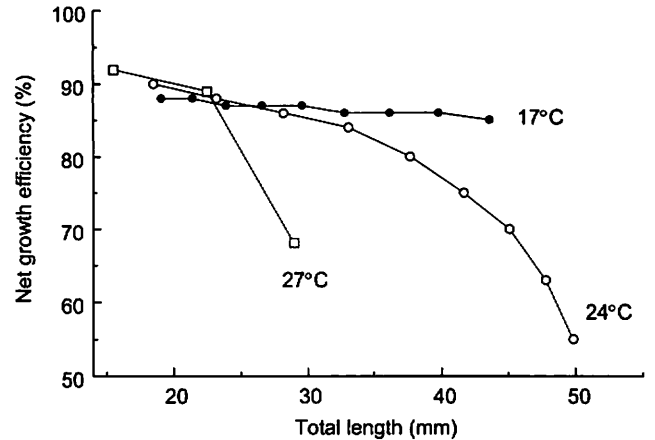

Fig. 6. Relationship between total length and net growth efficiency of *Bolinopsis mikado* at water temperatures of 17°C (●), 24°C (○) and 27°C (□).

IG increased with increases in water temperature, reaching a maximum of 0.71 at the highest water temperature, 27°C (Fig. 5A). The temperature effect on biological rate processes (Y) is usually described by the exponential equation $Y=ae^{bT}$, where a and b are constants and T is water temperature (cf. Kremer 1975; Reeve et al. 1978). This equation, however, does not fit for expressing IG over the entire temperature range, as shown in Fig. 5A. Furthermore, the Arrhenius plot, i.e., $1/(273+T)$ vs. $\log_{10}$ IG, was split into two slopes at a horizontal axis of 3.4×10^4 (i.e. 21°C) (Fig. 5B). Thus, using IG for larvae, the mean at each temperature in two temperature groups, i.e., 17–21°C and 21–27°C, was separately fitted with the above equation, and the following regression equations were obtained,

$$IG=0.014e^{0.178T} \qquad (T<21°C) \qquad (3)$$

and

$$IG=0.278e^{0.034T} \qquad (T\geqq21°C). \qquad (4)$$

Net growth efficiency

The relationship between the NGE and TL of *B. mikado* was obtained using the growth curve (Fig. 6). The NGE was about 90% for individuals of <20 mm TL, and then decreased rapidly with increasing TLs at 24° and 27°C in contrast to its stability at 17°C.

Discussion

Growth rate

Large copepods seem to inhibit the growth of the small larvae of ctenophores (Greve 1977; Stanlaw et al. 1981). For *Mnemiopsis mccradyi*, the mortality rate of larvae of <1.7 mm TL, cultured under prey concentrations of 100 copepods l^{-1} (200–500 μm size fraction), was much higher than that for those cultured under 50 copepods l^{-1}. For *B. mikado*, a larva of 3 mm TL, cultured under 20 *Acartia* l^{-1},

reached 12 mm TL in 4 d at 21°C. A larva of 4 mm TL, cultured under 100 *Acartia* l^{-1}, also reached 12 mm TL in 4 d at 19°C, indicating that larval *B. mikado* of $\geqq 3$ mm TL are able to feed on *Acartia*-sized copepods as prey.

Given 100 *Acartia* l^{-1}, the predicted maximum TL of *B. mikado* was 132.2 mm at 17°C and 55.3 mm at 24°C (Fig. 2). For carnivorous zooplankton, maintaining a continuous supply of food at mean environmental concentrations under small-scale experimental conditions would be as artificial as maintaining a continuously abundant supply, thus providing the maximum growth rate (Reeve & Baker 1975). In Tokyo Bay, large individuals of 85 mm TL and >100 mm TL were observed in winter/spring seasons, when water temperatures were under 20°C. During summer/fall seasons in which water temperatures exceeded 20°C, individuals of <25 mm TL occupied more than 65–95% of the *B. mikado* population and large individuals occurred with a maximum in the 55–65 mm TL size class (Kasuya et al. 2000a, Kasuya, personal observation). The growth characteristics obtained for *B. mikado* in the laboratory correspond with those in the field, suggesting that *B. mikado* usually consumes much more carbon than its minimum food requirement in Tokyo Bay.

B. mikado is estimated to reach 55 mm TL within 30 d after hatching at 24°C and reach 132 mm TL within 90 d at 17°C (Fig. 2). In Tokyo Bay, water temperatures typically range from 9 to 28°C annually, and the minimum and maximum values are recorded in January or February and in August or September, respectively. The life span of *B. mikado* in Tokyo Bay seems to be less than one month during summer in contrast to more than 3 months during winter.

Instantaneous growth rate

No significant difference was found between IG values obtained from the two container sizes, indicating that the growth rate of larval *Bolinopsis mikado* is not influenced by the size of the rearing container. Therefore, the growth rates can be compared among the experiments using different sized containers. During the culture, we observed that post-larvae, reaching a TL of over 40 mm, consumed a high amount of prey. It is possible that a rapid decrease in the food concentration in a container due to predation by large sized post-larvae may influence its growth rate, i.e. maximum TL.

We observed that the larvae of *B. mikado* grew under a food concentration of 3 *Acartia* l^{-1}, while the post-larvae have been reported to require at least 5 *Acartia* l^{-1} to survive (Kasuya et al. 2000b). This agrees with previous reports regarding the growth characteristics of *Mnemiopsis mccradyi* in which larvae grew at a food concentration of 2 *Acartia* l^{-1} (Reeve et al. 1978) while the post-larvae required about 8–10 *Acartia* l^{-1} (Kremer et al. 1986; Kremer & Reeve 1989). For lobate ctenophores, larvae and post-larvae capture prey with their tentacles and with their oral lobes, respectively (Fig. 1; cf. Reeve & Walter 1978). The

WW-specific clearance rates of larval *B. mikado* (Kasuya 1997) and *M. mccradyi* (Kremer & Reeve 1989) were much higher than those of post-larvae. This may lead to the difference in food concentration required to sustain their growth. Although a sharp decline in zooplankton abundance, accompanied with mass occurrences of ctenophores, has been observed (Deason & Smayda 1982; Uye & Ichino 1995; Uye & Sano 1995; Kasuya et al. 2000a), larvae would grow while maintaining their high predation capability under the lower food concentrations.

The relationship of IG to water temperature was equivalent to Q_{10} vales of 5.9 and 1.4 at 17–21°C and 21–27°C, respectively. The growth of *B. mikado* is very sensitive to temperature at <21°C. In Tokyo Bay, *B. mikado* is highly abundant mainly from August to November when the surface temperatures exceed 18°C (Kasuya et al. 2000a), suggesting that *B. mikado* metabolism is activated at a temperature of around 18°C. The low Q_{10} value of 1.4 indicates that the IG of *B. mikado* is almost independent of temperature at 21–27°C. In the experiment at water temperatures of 21–27°C, larvae of 7–9 mm TL reached 20–30 mm TL within 4 d (cf. Figs. 2, 6). *B. mikado* reaches maturity at a TL of ca. 20 mm (Kasuya unpublished data). Egg production rate was measured, with a high Q_{10} value of 4.3 at a temperature of 17–27°C (Kasuya unpublished data), indicating that its fecundity is very sensitive to temperature. *B. mikado* seems to invest more assimilated energy in egg production than in growth with a rise in water temperature, which might lead to a low Q_{10} value of IG at 21–27°C.

The IG of *B. mikado* is similar to those of *Pleurobrachia bachei* (0.47; Hirota 1974) and for *M. mccradyi* (0.69; Reeve et al. 1978). At a food concentration of 10 *Acartia* l^{-1}, which has been reported for the density of *Acartia*-sized copepods in Tokyo Bay (Anakubo & Murano 1991), the IG ranges from about 0.3 to 0.4 (Fig. 4), are equal to 35–50% growth as WW per day. In Tokyo Bay, the scyphomedusa *Aurelia aurita*, which is considered a competitor of ctenophores for food (Mutlu et al. 1994), also appears in high abundances during the summer season (Omori et al. 1995; Nomura & Ishimaru 1998). The daily growth rate of *A. aurita* was estimated as 7% of WW for a 0.3 cm bell-diameter medusa in Tokyo Bay (cf. Omori et al. 1995), which is relatively less than that of *B. mikado*. An inverse relationship between the distribution of abundance for *Mnemiopsis* sp. and *A. aurita* has been observed in the Black Sea (Mutlu et al. 1994). However, the different growth strategies between *B. mikado* and *A. aurita* may buffer their competition in Tokyo Bay.

Net growth efficiency

A strong relationship between NGE and ctenophore size was also reported for *M. mccradyi*, which decreases from about 80% to 40% with an increase in body size (Kremer & Reeve 1989). The predation and respiration rates of *B. mikado* have been measured, with Q_{10} values of 1.8 (Ka-

suya et al. 1994) and 1.9 (Kasuya et al. 2000b), respectively, indicating that the ratio of carbon-uptake by predation to metabolic carbon-loss is independent of water temperature. In the growth experiment of B. mikado at 24°C, we observed an animal, reaching 47 mm TL, spawning in the double kuvette. Thus, the decrease of NGE with increasing TL is probably due to investment of a high proportion of assimilated energy into egg production. This result assures the low Q_{10} value at 21–27°C in Fig. 5. The increase in growth and egg production rates of B. mikado with rising water temperatures appears to allow quick population growth and mass occurrences during summer/fall, and vice versa during winter/spring in Tokyo Bay.

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