カブトクラゲBolinopsis mikado Moserの摂餌特性

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Feeding Characteristics of the Lobate Ctenophore

*Bolinopsis mikado* MOSER$^{1, 2}$

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Abstract

Laboratory experiments were conducted to characterize the feeding behavior of *Bolinopsis mikado*, an indigenous ctenophore of Japanese coastal waters, using copepods (*Acartia*) as prey. The predation (*P*) and clearance rates (*CL*) were found to be power functions of the wet weight (*WW*) of ctenophores, i.e., power exponents are 0.67 for *P* and 0.74 for *CL*. As these values are close to 2/3, it is suggested that both *P* and *CL* are proportional to the surface area of the oral lobes. Effects of temperature and food concentration were examined using ctenophores of 34-50 mm in total length. *WW*-specific *P* increased with increasing water temperature, and calculated $Q_{10}$ is 1.8. *WW*-specific *CL* showed a maximum of about 170 ml g *WW* $^{-1}$ h $^{-1}$ observed at concentrations of 10 copepods l $^{-1}$. At food concentrations > 61 copepods l $^{-1}$, *CL* decreased, reaching a minimum rate of 5 ml g *WW* $^{-1}$ h $^{-1}$ at the highest food concentration of 1126 copepods l $^{-1}$. Predatory impact of *B. mikado* populations on copepods was estimated by using normalized ctenophore feeding rate on their size. At the station T-4 in Tokyo Bay, 6-13 % of the *Acartia* standing stock was estimated to be consumed per day in November 1990 when the ctenophore occurred abundantly.

Keywords: *Bolinopsis mikado*, ctenophore, feeding rate, predatory impact, copepods

*Bolinopsis* and *Mnemiopsis* are two well known genera of lobate ctenophores on which considerable information on their ecology has been accumulated (REEVE & WALTER 1978). Rearing and feeding experiments were conducted on *Bolinopsis infundibulum* from the North Sea (GREVE 1970) and on *Bolinopsis vitrea* from the Bahamas (KREMER et al. 1986). Predatory impacts and feeding behavior of *Mnemiopsis leidyi* and *M. mccradyi* were studied in the Patuxent River (BISHOP 1967, MILLER & WILLIAMS 1972), Narragansett Bay (KREMER 1979, DEASON 1982), Biscayne Bay (REEVE et al. 1978) and in the Indian River estuary (LARSON 1987, 1988). All of these studies indicate that lobate ctenophores are voracious predators and have a significant effect on the mesozooplankton biomass.

In Japanese coastal waters, *Bolinopsis mikado* MOSER (1908) is the predominant ctenophore species. In Tokyo Bay, *B. mikado* appears throughout the year and is most abundant from late summer to middle fall. Except for a few studies on classification (MOSER 1908, KOMAI 1918), no ecological studies have been made for this species. In this paper, we describe the feeding characteristics of *B.*
A relationship between ctenophore size and feeding rate at various food concentrations is determined in the laboratory and the predatory impact on copepods in natural waters is estimated.

**Materials and Methods**

A series of experiments was conducted from spring to summer of 1991 and 1992 at the Banda Marine Laboratory of Tokyo University of Fisheries (Figure 1). Ctenophores were individually collected by using wide mouthed plastic bottles by snorkelling in waters adjacent to the laboratory. Collected ctenophores were maintained in the laboratory, providing natural copepods (*Acartia*) as prey in clear plastic containers (10 l) for experimentation.
Figure 2. Schematic diagram of *Bolinopsis mikado* through the pharyngeal plane. Bars represent the measurements, *TL*: total length, *LL*: lobe length, *BW*: body width.

**Length and Wet Weight**

Total length (*TL*), lobe length (*LL*) and body width (*BW*) of *B. mikado* were defined (Figure 2) and measured using a measuring rule, which were accurate to 1 mm. After excess water was removed with tissue paper, ctenophores were placed on a pre-weighed petri dish and the wet weight was determined on an electronic balance with precision of 0.1 g.

**Feeding**

Depending on the size of ctenophores and food concentrations, different volumes of containers (1–11 l) were used for the experiment. Adult copepods of *Acartia omorii* or *A. erythraea* were used as prey. Copepods were collected daily by vertical hauls of a 330 µm mesh plankton net at Tateyama fishing port (Figure 1) and were maintained in a meshed bag (30 µm) immersed into running seawater in the laboratory. Only live copepods were fed at concentrations ranging from 3 to 1126 copepods l⁻¹ (Table 1). Copepods were counted individually to establish lower food concentrations (3 to 579 copepods l⁻¹), but aliquots of condensed copepod samples were used to prepare higher concentrations (≥829 copepods l⁻¹).
Table 1. Regression statistics of the relationships between predation ($P$) and wet weight ($WW$), and between clearance ($CL$) rate and $WW$ of Bolinopsis mikado as a function of prey concentration. Experiment was made at 16°C.

<table>
<thead>
<tr>
<th>Initial food concentration (inds/1)±SD</th>
<th>Ctenophore size</th>
<th>N</th>
<th>$a$</th>
<th>$b$</th>
<th>$r^2$</th>
<th>$a$</th>
<th>$b$</th>
<th>$r^2$</th>
</tr>
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<tbody>
<tr>
<td>3</td>
<td>34-64</td>
<td>10</td>
<td>0.70</td>
<td>0.471</td>
<td>0.250</td>
<td>121</td>
<td>0.727</td>
<td>0.286</td>
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<tr>
<td>5</td>
<td>26-65</td>
<td>7</td>
<td>4.5</td>
<td>0.081</td>
<td>0.069</td>
<td>1048</td>
<td>0.098</td>
<td>0.053</td>
</tr>
<tr>
<td>10</td>
<td>19-75</td>
<td>11</td>
<td>4.2</td>
<td>0.388</td>
<td>0.477</td>
<td>673</td>
<td>0.351</td>
<td>0.309</td>
</tr>
<tr>
<td>20</td>
<td>19-60</td>
<td>9</td>
<td>0.84</td>
<td>1.05</td>
<td>0.844</td>
<td>62</td>
<td>1.03</td>
<td>0.751</td>
</tr>
<tr>
<td>61±10</td>
<td>16-63</td>
<td>9</td>
<td>2.2</td>
<td>1.06</td>
<td>0.881</td>
<td>32</td>
<td>1.17</td>
<td>0.885</td>
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<tr>
<td>159±10</td>
<td>23-62</td>
<td>6</td>
<td>6.7</td>
<td>0.554</td>
<td>0.686</td>
<td>45</td>
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<td>0.614</td>
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<tr>
<td>349±22</td>
<td>22-63</td>
<td>9</td>
<td>5.0</td>
<td>0.754</td>
<td>0.724</td>
<td>15</td>
<td>0.792</td>
<td>0.672</td>
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<tr>
<td>468±23</td>
<td>19-70</td>
<td>9</td>
<td>9.3</td>
<td>0.659</td>
<td>0.864</td>
<td>19</td>
<td>0.760</td>
<td>0.846</td>
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<td>579±16</td>
<td>17-67</td>
<td>11</td>
<td>5.6</td>
<td>0.749</td>
<td>0.865</td>
<td>9</td>
<td>0.823</td>
<td>0.839</td>
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<tr>
<td>829±25</td>
<td>18-68</td>
<td>12</td>
<td>21</td>
<td>0.502</td>
<td>0.627</td>
<td>27</td>
<td>0.556</td>
<td>0.577</td>
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<tr>
<td>1126±20</td>
<td>19-63</td>
<td>9</td>
<td>15</td>
<td>0.529</td>
<td>0.962</td>
<td>13</td>
<td>0.567</td>
<td>0.965</td>
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Sand-filtered seawater was used throughout the experiment. Ctenophores were kept unfed for 4 hours before the experiments to clear food material from their pharynx. Then, ctenophores were placed individually in containers. Concurrently, one or two control containers were prepared without ctenophore. These containers were kept in the dark during the experiments. After 3 hours, ctenophores were removed from the containers and the remaining Acartia were collected on a 30 µm mesh netting, and counted under a microscope after being fixed with buffered formalin-seawater. Any Acartia which were ejected without being digested, and settled on the bottom of the container, were pipetted out in the course of the experiment and counted as part of the number consumed by ctenophore. There observed no mortality of Acartia in the control containers. The predation rate ($P$) and clearance rate ($CL$) of a ctenophore were calculated using the following equations (OMORI & IKEDA 1984).

\[
P = (N_0 - N_t)/t \quad \text{(copepods ctenophore}^{-1}\text{ h}^{-1})
\]
\[
CL = V(LnN_0 - LnN_t)/t \quad \text{(ml ctenophore}^{-1}\text{ h}^{-1})
\]

where $t$ is duration of experiment (i.e. 3 h). $N_0$ and $N_t$ are number of prey before and after the experiment. $V$ is volume of seawater in containers (ml). Experiments were conducted at 10, 16 and 22°C, which covered seasonal variations of water temperature in the field.

Preliminary feeding experiment was conducted by using 1, 2 and 10 l containers to determine the influence of container size on ctenophore feeding. Ctenophores of 42-54 mm TL were used in the experiment at two food concentrations (61 and 349 copepods l$^{-1}$) at 16°C.

Results and Discussion

Body Allometry

Figure 3 shows the relationship between wet weight ($WW$, g) and total length ($TL$, mm) of B. mikado. The relationship is expressed as,
Figure 3. Relationship between wet weight and total length of *Bolinopsis mikado* (N=21).

\[ WW = 0.0005 \cdot TL^{2.72} \]

\[ r^2 = 0.98 \]

In this study, *WW* of ctenophores were estimated from *TL* using this equation.

Relationships between *BW* and *TL* and between *LL* and *TL* are shown in Figure 4. *B. mikado* loses tentacles and becomes fully lobate at about 15 mm *TL*. With this change in body morphology, ctenophores smaller than this were excluded from the regression analysis. From the results that *BW* and *LL* were linearly proportional to *TL* and that *WW* of *B. mikado* is proportional nearly to the cube of *TL*, it is clear that the allometry of ctenophores greater than 15 mm *TL* is not affected by size.

*Effect of the Container Volume on Feeding Rate*

At the food concentration of 349 copepods l\(^{-1}\), mean specific clearance rates of *B. mikado* measured using 1 and 2 l containers were 7.0 (±1.8 SD, N=3) and 8.0 (±1.5, N=3) ml g *WW\(^{-1}\) h\(^{-1}\), respectively. At the food concentration of 61 copepods l\(^{-1}\), the mean specific clearance rates obtained from 2 and 10 l containers were 44 (±16, N=3) and 51 (±25, N=3) ml g *WW\(^{-1}\) h\(^{-1}\) respectively. In either experiments, differences between mean *WW* specific clearance rates from 2 container sizes were not different significantly (t-test, *P* > 0.05), i.e. the feeding rate of *B. mikado* is not influenced by the applied container size. However, it is likely that the rapid decrease in food concentration during experiment influences the ctenophore feeding more than the container volume. With this methodological reason, we used large containers (11 l) for experiments at the lower food concentrations.
Figure 4. Relationships of total length to body width and lobe length. Ctenophores sized <15 mm TL were excluded from the regression analysis.

Predation and Clearance Rates as a Function of Ctenophore Size
Figure 5 shows the relationship between $P$ and $WW$ at the food concentration of 468 copepods l$^{-1}$ at 16 °C. The relationship is expressed as,

$$P \ (or \ CL) = a \ WW^b,$$

(1)

where $a$ and $b$ are coefficients shown in Table 1. The mean and standard deviation of $b$ obtained from 10 different food concentrations (excluding the data at 5 copepods l$^{-1}$, which had excessively low determination coefficients) were 0.67 (±0.22 SD) for $P$-$WW$ relations and 0.74 (±0.23) for $CL$-$WW$ relations. Because the allometry of the ctenophore ($\geq$15 mm TL) is constant, the inner surface area of the oral lobe, by which $B. \ mikado$ captures prey, increases in proportion to $2/3$
power of the ctenophore wet weight. Accordingly, the predation and clearance rates are also in proportion to $2/3$ power of the ctenophore wet weight.

**Effects of Water Temperature and Food Concentration on Feeding Rate**

The effects of water temperature and food concentration on the feeding rate of *B. mikado* were evaluated using the WW specific $P$ and CL of the ctenophores ranging from 34 to 50 mm TL. The specific $P$ increased with increasing water temperature ($T$, °C) (Figure 6), and the relationship was expressed as $P=0.97e^{0.0617}$. Variations in predation rate (Figure 6) are equivalent to 1.8 of $Q_{10}$ value and is nearly equal to $Q_{10}$ of 1.4–1.8 for *M. leidyi* (KREMER 1979).

The WW specific $P$ increased rapidly with the increase of food concentration up to 61 copepods l$^{-1}$ and then slightly above it (Figure 7). The WW specific CL were high at food concentrations from 3 to 61 copepods l$^{-1}$ with a maximum rate of 170 ml g WW$^{-1}$ h$^{-1}$ at 10 copepods l$^{-1}$. At food concentrations >61 copepods l$^{-1}$, they decreased gradually to reach a minimum rate of 5 ml g WW$^{-1}$ h$^{-1}$ at 1126 copepods l$^{-1}$.

*B. mikado* has similar feeding behavior with an open water species, *B. vitrea* which also changes clearance rate depending on food concentrations (KREMER et al. 1986). The clearance rate of *B. vitrea* is highest at low food concentration of 2 copepods l$^{-1}$ and decreases with increasing food concentration. Different from *Bolinopsis*, the clearance rates of estuarine species, *M. mccradyi* (REEVE et al. 1978) and *M. leidyi* (KREMER 1979) are independent of food concentrations.

KREMER et al. (1986) reported that *B. vitrea* deteriorated rapidly and disintegrated at extremely high food concentrations of 200 copepods l$^{-1}$. We observed that some individuals of *B. mikado* damaged at oral lobes after the experiments in
Figure 6. Effect of water temperature on ctenophore feeding at food concentration of 150 copepods 1\(^{-1}\). The data are the mean wet weight specific predation rate of ctenophore ranging from 34 to 50 mm TL. Bars represent the standard deviations of the specific predation rate.

Figure 7. Effect of food concentration on predation (closed circle) and clearance (open circle) rates. The data are the mean wet weight specific predation and clearance rates of ctenophore ranging from 34 to 50 mm TL. Bars represent the standard deviations of the specific feeding rates. Lines drawn by eye.

high food concentrations (≥829 copepods l\(^{-1}\)). \textit{B. mikado} may not survive in such high food concentrations. On the contrary, \textit{Mnemiopsis} maintain themselves in very high food concentration of 3000 copepods l\(^{-1}\) (REEVE et al. 1978). These results indicate that \textit{Bolinopsis} are more sensitive to the contact with copepods than...
Figure 8. Effect of food concentration on ctenophore feeding evaluated by the coefficient $a(F, 16)$. The data are the mean coefficient $a(F, 16)$ given by the food concentration $(F)$.

Mnemiopsis.

The food concentration-dependent clearance rate seems advantageous for the ctenophore inhabiting coastal waters with large fluctuation in food concentration. A higher endurance of $B. \text{mikado}$ against the contact with copepods than $B. \text{vitrea}$ suggests that $B. \text{mikado}$ can live in the more eutrophic waters. These feeding characteristics of $B. \text{mikado}$ may explain the wide distribution from eutrophic waters in inner part of Tokyo Bay to coastal waters influenced by oligotrophic Kuroshio.

Normalization of Ctenophore Feeding

Feeding characteristics of ctenophores have been studied by several workers (KREMER 1979, REEVE et al. 1978, KREMER et al. 1986), all using similar sized animals. However, in order to calculate the predatory impact of $B. \text{mikado}$ in natural waters of various sized individuals, the application of the feeding rate to different sizes is necessary. Thus, we have tried to normalize the predation rate on ctenophore size.

Because the predation rate is nearly proportional to $2/3$ power of ctenophore wet weight, the relationship between the predation rate at a given food concentration $(F)$ and temperature $(T)$ is derived from Equation (1),

$$a_{(F, T)} = P/WW^{0.67}.$$  

Independent of the ctenophore size, the coefficient $a_{(F, T)}$ gives the feeding characteristics in a certain food concentration or water temperature.

The coefficient $a_{(F, 16)}$ on predation rate is recalculated from the data sets in Table 1. The relationship between $a_{(F, T)}$ and food concentration is plotted (Figure 8) and is fitted to the following regression equation,

$$a_{(F, 16)} = 1.8 \ln (F) - 2.2.$$  

(3)
Table 2. Size composition and a population of *Bolinopsis mikado* at Stn. T-4 in Tokyo Bay in November 1990, N=229.

<table>
<thead>
<tr>
<th>Total length (mm)</th>
<th>%</th>
</tr>
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<tr>
<td>10-14</td>
<td>25</td>
</tr>
<tr>
<td>15-24</td>
<td>31</td>
</tr>
<tr>
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<td>23</td>
</tr>
<tr>
<td>35-44</td>
<td>16</td>
</tr>
<tr>
<td>45-54</td>
<td>4</td>
</tr>
<tr>
<td>55-64</td>
<td>0.4</td>
</tr>
</tbody>
</table>

Figure 9. Predatory impact (% per day) of *Bolinopsis mikado* on the copepods. Bars are standard deviations. Note horizontal axis is logarithmic.

The effect of water temperature on the coefficient $a_{150,T}$ is also estimated from the same data sets used in Figure 6 and is fitted to the following regression equation,

$$a_{150,T} = 2.0 \times e^{0.058T}.$$  \hspace{1cm} (4)

$Q_{10}$ value for $a_{150,T}$ is 1.78 which is similar to that of the predation rate shown in Figure 6. From Equations (3) and (4), $a_{1,F,T}$ is rewritten as,

$$a_{1,F,T} = a_{1,F,16} \times e^{0.058(T-16)}.$$

Thus the predation rate at a given temperature and food concentration is shown as,

$$P = (1.8 \ln (F) - 2.2) \times WW^{0.67} \times e^{0.058(T-16)}.$$
Predatory Impact on Copepods

The predatory impact of *B. mikado* on copepods was estimated based on the examination in Tokyo Bay in November 1990. Ctenophores were quantitatively sampled by horizontal and vertical plankton net tows (diameter: 600 and 450 mm, mesh size: 1 and 0.33 mm) at Stn. T-4 in Tokyo Bay (Figure 1). The abundance of *B. mikado* (>10 mm TL) was 11 inds m⁻³ and they were composed of various sized ctenophore (Table 2). In the calculation of the predatory impact, ctenophores less than 15 mm TL were excluded since they had undeveloped oral lobes. Water temperature at Stn. T-4 was 18° C. Figure 9 shows the relationship between predatory impact of *B. mikado* and prey density. In Tokyo Bay, the standing stock of *Acartia omorii* ranges from 10 to 60 copepods l⁻¹ (ANAKUBO & MURANO 1991). Therefore, the predatory impact is estimated to be about 6-13 % of the *Acartia* standing stock per day. As to *M. leidyi*, the maximum predatory impact is calculated to be 5-10 % in Narragansett Bay (KREMER 1979) and 31 % in Patuxent River (BISHOP 1967). *M. leidyi* is thought to regulate zooplankton and phytoplankton dynamics and the nutrient cycle (DEASON & SMAYDA, 1982). Therefore, *B. mikado* seems to have a potential influence on the zooplankton-phytoplankton oscillation in Japanese coastal waters.

Acknowledgments

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