INTRODUCTION
There have been many studies on the optimal foraging of bivalve-feeders to explain predator–prey interactions in the intertidal zone.1–3 Those studies suggested that predators select on prey maximizing net energy intake rate (energy gained—energy expended/time).4 However, the energy expended searching has proven difficult to quantify and it is frequently estimated as the time required for predators to ingest prey.5,6

Halla okudai (Polychaeta: Lysaretidae) is a large bivalve-feeder (90 cm in maximum body length) living in coarse sediments of the intertidal zone of the Seto Inland Sea and the Ariake Sea.7–9 The field survey showed that the condition factor of the polychaete increased with an increasing density of the short-neck clam Ruditapes philippinarum.10 The laboratory experiment showed that the polychaete selected larger prey with increasing body size, and the optimal size of prey was estimated to be 10–20% of its own bodyweight from the viewpoint of growth efficiency.11,12 Imabayashi et al.13 observed that the foraging process of the polychaete was divided into four phases (responding, searching, handling, feeding) and suggested that the prey preference was related to the energy cost of searching and handling. Saito and Imabayashi12 suggested that the growth efficiency decreased with increasing locomotion for searching when feeding on too small a size of prey (<10% of its own bodyweight), while it decreased with an increase of jelly-like material secreted during handling and feeding when feeding on too large a size of prey (>20% of its own bodyweight). Saito et al.14 regarded the scope for the active rate of respiration and jelly-like material secreted during handling as the handling cost, and clarified that growth of the polychaete decreased with increasing those handling costs. However, the searching cost of the polychaete was not evaluated.

In this study, to evaluate an interaction between searching cost and growth of H. okudai, observations of foraging behavior and measurement of energy budget...
were conducted in feeding experiments for 15 days under two different prey size conditions.

MATERIALS AND METHODS

Collection of animals and experimental apparatus

Nine immature individuals of *H. okudai* without gonadal output (body length, 22.2–32.5 cm; bodyweight, 6.4–13.7 g wet), were collected from an intertidal sandy flat of Hiroshima Bay in May 1996. The individuals were transferred to an aerated 120 L aquarium in the laboratory, and thereafter they were kept for a week without feeding before the experiment to exclude the influence of past feeding experience.

A large number of *R. philippinarum* (shell length, 14.0–43.0 mm; soft bodyweight, 0.2–3.0 g wet) were also collected from the same area as the polychaete. They were stored in another 120 L aquarium in the laboratory, and were used as prey for the polychaete in experiments.

All experiments were performed in a 5 L respiration chamber with a 5 cm layer of autoclaved sediment (gravel, 51%; sand, 47%; mud, 2%) and 4.5 L of oxygen-saturated artificial seawater. The water was maintained at 25°C and at 32 p.p.t. in salinity, and was completely exchanged with fresh oxygen-saturated seawater at 7 mg/L every 8 h to keep the dissolved oxygen concentration higher than 3 mg/L. The luminous condition was kept as dark throughout the experiment except on exchange of the water.

The polychaete was individually introduced to the respiration chamber and fed separately with two different prey groups: a small-prey group (shell length, 24.2 ± 1.5 mm; soft bodyweight, 6.0 ± 2.2% of predator weight) and a medium-prey group (shell length, 34.0 ± 4.1 mm; soft bodyweight, 16.7 ± 1.3% of predator weight). An ingested prey was replaced by a new intact prey after feeding. Each experiment consisted of four to five trials over a duration of 15 days.

Observation of foraging behavior and measurement of oxygen consumption

Since the polychaete is known to appear on the sediment surface during the foraging processes, the foraging behavior was monitored by an infrared dark-field video camera-video system (TK-S240; Victor, Co., Tokyo, Ltd). The oxygen consumption rate was measured in the respiration chamber with a membranous oxygen electrode (YSI model 58; YSI Japan Ltd, OH, USA) using a closed method which enables monitoring of the decline in the oxygen content in the chamber. The water was mixed in the chamber throughout the experiment with a magnetic stirrer that ran at constant rpm. The oxygen content in the chamber was recorded by the video camera-video system. The oxygen consumption rate of the polychaete was estimated by subtracting the rate of the bivalve measured in a preliminary experiment from the oxygen content in the chamber.

Measurement of energy budget

In this study, the energy budget equation has been expressed as:

\[ I = P + R + U + F + J \]

where *I* represents ingestion; *P*, growth; *R*, respiration; *U*, excretion; *F*, feces; and *J*, jelly-like material.

The amount of ingestion was measured as the total caloric content of prey tissue consumed by the polychaete. The caloric value of prey was estimated from the regression to shell length (Fig. 1).

The growth rate was measured as the difference between the initial and final bodyweights of the experiment. It was converted to the caloric value with the caloric equivalent of 857.4 cal/g wet weight.

The respiration rate was measured as the oxygen consumption rate. It was converted into the caloric value by applying the oxy-caloric coefficient of 3.3 cal/mg O₂.

Excretion, as the nitrogenous end products when protein is being respired, could be estimated from the oxygen consumption for 15 days multiplied by the oxy-caloric coefficient of 0.51 cal/mg O₂.

Feces were collected by pipetting up from the sediment surface at the end of feeding. The caloric value was determined by bomb calorimetry (OSK150; Ogawa sampling, Co., Tokyo, Ltd).

The jelly-like materials secreted during the handling and feeding were obtained through the feeding ex-

![Fig. 1](https://example.com/fig1.png) Relationship between shell length and energy content of the prey *Ruditapes philippinarum* (*y = 35.7x^2.77, n = 30, r = 0.967, P < 0.01*).
periment offering different sizes of prey (shell length, 14.0–43.0 mm). The caloric values of both the materials were determined by the method of Saito and Imabayashi.12

RESULTS

Foraging behavior and daily records of oxygen consumption

Examples of daily records of the foraging behavior and the oxygen consumption are shown in Fig. 2. In both prey groups the occurrence of foraging behavior was restricted to the nocturnal period, although the luminous condition was kept as dark throughout the experiment. The frequency of prey ingested was higher in the small-prey group (5.8 ± 0.4 per 15 days) than in the medium-prey group (4.2 ± 1.1 per 15 days). The oxygen consumption rate drastically increased during searching, handling, and feeding, and then reached a peak after feeding. Subsequently, it slowly declined to the pre-feeding level within a few days.

The frequency of foraging behavior and total foraging time are shown in Table 1. The frequency of searching was not less than twice of that of prey ingested. It was higher in the small-prey group (13.5 ± 1.5 per 15 days) than in the medium-prey group (9.2 ± 1.2 per 15 days). However, handling and feeding behavior did not always occur following searching. The total searching time

![Fig. 2 Examples of daily records of oxygen consumption of the predator Halla okudai. Arabic numerals above horizontal bars express the frequency of searching. The three processes of foraging behavior are searching (△), handling (□), and feeding (●). Dotted lines indicate the standard rate of oxygen consumption. (a) Individual (initial body size, 10.6 g) in small-prey group, (b) individual (initial body size, 12.4 g) in medium-prey group.](image)

<table>
<thead>
<tr>
<th>Prey size group</th>
<th>Frequency of searching (No. per 15 days)</th>
<th>Frequency of prey ingested (No. per 15 days)</th>
<th>Total foraging time (h)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Searching</td>
<td>Handling</td>
<td>Feeding</td>
</tr>
<tr>
<td>Small</td>
<td>13.5 ± 1.5&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.8 ± 0.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>28.9 ± 2.5&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Medium</td>
<td>9.2 ± 1.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>4.2 ± 1.1&lt;sup&gt;b&lt;/sup&gt;</td>
<td>16.4 ± 6.4&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>1</sup>Small, 24.2 ± 1.5 mm; medium, 34.0 ± 4.1 mm in shell length.
Values are shown as mean ± SD.
Values in the same column with different superscript (a,b) are significantly different (P < 0.05) when analyzed using an ANOVA coupled with a Scheffé’s test.
during the experimental period increased with the increasing frequency of searching. It was significantly longer in the small-prey group (28.9±2.5 h) than in the medium-prey group (16.4±6.4 h). In contrast, the total handling time and total feeding time hardly varied with prey size.

Energy budget

All the components of energy budget are shown in Table 2. Since prey size (soft bodyweight) was approximately three times larger in the medium-prey group than in the small-prey group, there was a large difference in the amount of ingestion between them (3.18–5.68 kcal/polychaete per 15 days). Hence, the components were evaluated by the percentage of each value to total output.

The growth rate was significantly higher than in the medium-prey group (36.3±5.7%) than in the small-prey group (17.0±9.7%).

The total respiration rate was divided into the standard rate and scope for active rate, calculated by subtracting the standard rate from the total rate. No significant difference in the former was observed between both prey groups (34.5–40.3%). However, the latter was significantly lower in the medium-prey group (8.5±1.6%) than in the small-prey group (20.3±5.5%).

The amount of excretion was significantly lower in the medium-prey group (6.6±0.8%) than in the small-prey group (9.4±1.5%).

The feces were excreted in 7–12 h intervals over a few days after feeding on a prey. The amount of feces showed a significant positive relationship to the amount of ingestion (Fig. 3). Hence, there was little difference in the feces output between both prey groups (10.0–11.0%).

The amount of jelly-like material secreted during handling showed a significant positive relationship to prey size (Fig. 4a). However, there was no significant difference in the material between both prey groups (1.3%), since the frequency of prey ingested in the small-prey group was high compared to that in the medium-prey group.

The amount of the material secreted during feeding, showed a significant positive relationship to that of ingestion (Fig. 4b). Hence, there was no significant difference in the material output between both prey groups (1.7–1.8%).

Fig. 3 Relationship between ingestion and feces of the predator *Halla okudai* (*y* = 0.11x + 1.81, *n* = 12, *r* = 0.901, *P* < 0.01).

Fig. 4 Relationship between (a) shell length of prey and energy content of jelly-like material secreted during handling (*y* = 0.88x^{2.58}, *n* = 147, *r* = 0.943, *P* < 0.01), and between (b) ingestion and energy content of jelly-like material secreted during feeding (*y* = 0.08x^{0.79}, *n* = 147, *r* = 0.936, *P* < 0.01) by the predator *Halla okudai*.
Table 2  Energy component of *Halla okudai* feeding on the two different sizes of prey

<table>
<thead>
<tr>
<th>Prey size group</th>
<th>Initial body size (g wet weight)</th>
<th>Ingestion (kcal)</th>
<th>Growth increment (kcal(^3))</th>
<th>Respiration</th>
<th>Excretion (kcal(^3))</th>
<th>Feces (kcal(^3))</th>
<th>Jelly-like material (kcal(^3))</th>
<th>Total output (kcal(^3))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Standard for active feeding</td>
<td>Scope for active feeding</td>
<td>Total</td>
<td>Handling</td>
<td>Feeding</td>
<td>output</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small</td>
<td>10.6</td>
<td>2.39</td>
<td>0.15</td>
<td>1.31</td>
<td>0.65</td>
<td>1.96</td>
<td>0.31</td>
<td>0.27</td>
</tr>
<tr>
<td></td>
<td>12.0</td>
<td>2.91</td>
<td>0.51</td>
<td>1.32</td>
<td>0.78</td>
<td>2.10</td>
<td>0.32</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td>10.6</td>
<td>2.78</td>
<td>0.59</td>
<td>1.18</td>
<td>0.71</td>
<td>1.89</td>
<td>0.29</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>11.9</td>
<td>4.65</td>
<td>1.36</td>
<td>1.79</td>
<td>0.57</td>
<td>2.36</td>
<td>0.36</td>
<td>0.51</td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>11.3 ± 0.7(^a)</td>
<td>3.18 ± 0.87(^a)</td>
<td>0.65 ± 0.51(^a)</td>
<td>1.40 ± 0.27(^a)</td>
<td>0.68 ± 0.09(^a)</td>
<td>2.08 ± 0.21(^a)</td>
<td>0.32 ± 0.03(^a)</td>
<td>0.36 ± 0.11(^a)</td>
</tr>
<tr>
<td>Mean ratio ± SD</td>
<td>17.0 ± 9.7(^**)</td>
<td>40.3 ± 4.6(^**)</td>
<td>20.3 ± 5.5(^**)</td>
<td>60.6 ± 8.5(^**)</td>
<td>9.4 ± 1.5(^**)</td>
<td>10.0 ± 0.5(^**)</td>
<td>1.3 ± 0.1(^**)</td>
<td>1.8 ± 0.1(^**)</td>
</tr>
<tr>
<td>Medium</td>
<td>7.5</td>
<td>6.08</td>
<td>2.40</td>
<td>1.90</td>
<td>0.46</td>
<td>2.36</td>
<td>0.36</td>
<td>0.67</td>
</tr>
<tr>
<td></td>
<td>12.4</td>
<td>6.35</td>
<td>2.70</td>
<td>2.03</td>
<td>0.42</td>
<td>2.45</td>
<td>0.38</td>
<td>0.70</td>
</tr>
<tr>
<td></td>
<td>13.7</td>
<td>5.63</td>
<td>1.45</td>
<td>2.03</td>
<td>0.57</td>
<td>2.60</td>
<td>0.40</td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>12.0</td>
<td>6.65</td>
<td>2.53</td>
<td>2.26</td>
<td>0.55</td>
<td>2.81</td>
<td>0.44</td>
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<tr>
<td></td>
<td>6.4</td>
<td>3.67</td>
<td>1.33</td>
<td>1.43</td>
<td>0.36</td>
<td>1.79</td>
<td>0.28</td>
<td>0.40</td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>10.4 ± 2.9(^b)</td>
<td>5.68 ± 1.06(^b)</td>
<td>2.08 ± 0.64(^b)</td>
<td>1.93 ± 0.31(^b)</td>
<td>0.47 ± 0.09(^b)</td>
<td>2.40 ± 0.38(^b)</td>
<td>0.37 ± 0.06(^b)</td>
<td>0.62 ± 0.13(^b)</td>
</tr>
<tr>
<td>Mean ratio ± SD</td>
<td>36.3 ± 5.7(^**)</td>
<td>34.5 ± 3.1(^**)</td>
<td>8.5 ± 1.6(^**)</td>
<td>43.0 ± 4.8(^**)</td>
<td>6.6 ± 0.8(^**)</td>
<td>11.0 ± 0.6(^**)</td>
<td>1.3 ± 0.1(^**)</td>
<td>1.7 ± 0.1(^**)</td>
</tr>
</tbody>
</table>

\(^1\) Small: 24.2 ± 1.5 mm; medium, 34.0 ± 4.1 mm in shell length.

\(^2\) Percentage of each component to total output.

\(^3\) kcal/polychaete per 15 days.

Values in the same column with different superscripts (a,b or *a,*b) are significantly different (*P* < 0.05) when analyzed using an *ANOVA* coupled with a Scheffé's test.
DISCUSSION

The frequency of prey ingested in *H. okudai* was higher in the small-prey group (5.8±0.4 per 15 days) than in the medium-prey group (4.2±1.1 per 15 days). In this study, foraging behavior was restricted to the nocturnal period, although the luminous condition was kept as dark throughout the experiment. Some handling and feeding behaviors were inhibited by such a circadian rhythm, with the frequency of searching not less than twice of that of prey ingested. Furthermore, the total searching time markedly increased with increasing the frequency of searching; it was 1.8 times longer in the small-prey group than in the medium-prey group. According to Imabayashi et al.,13 the distance for searching showed a significant positive relationship to searching time. In contrast, there was no significant difference in the total handling and feeding time as well as the jelly-like material secreted during handling and feeding between both prey groups. Thus, it was found that the foraging behavior of the polychaete was clearly different in the searching process between both prey groups.

Bayne and Newell19 suggest that energy expended on searching in carnivorous gastropods is an important factor affecting growth efficiency, and in natural populations growth efficiency decreases as time spent searching for prey increases. In this study, all the components of energy budget in the polychaete were evaluated by the percentage of each value to total output, since the amount of ingestion varied with prey size. As a result, it was found that the difference in the growth between both prey groups was caused by searching cost. The growth rate was 2.0 times higher in the medium-prey group (36.3±5.7%) than in the small-prey group (17.0±9.7%). Previous studies showed that *H. okudai* selected larger prey with increasing body size, and the optimal size of prey was estimated to be 10–20% of its own body weight from the growth efficiency.11,12 Hence, this result supports the hypothesis that a predator determines the relative costs and benefits of feeding on different prey types, and prey selection to maximize growth can be justified on an energetic basis.20,21 Such a correspondence of the growth with the prey preference can be explained by quantification in the respiration and excretion, since the feces and jelly-like material secreted during handling and feeding hardly varied with prey size.

The total respiration rate was divided into the standard rate and scope for active rate. The former can be regarded as standard metabolism, and showed no significant difference between the both prey groups. However, the latter was lower in the medium-prey group (8.5±1.6%) than in the small-prey group (20.3±5.5%). It is considered that the scope for active rate corresponded to the heat increment during the pre-consumptive process (i.e. searching and handling) and the post-consumptive process (i.e. digestion and assimilation). In the pre-consumptive process, the heat increment probably occurred during searching since, as noted above, the searching activity was markedly observed in the small-prey group. In contrast, in the post-consumptive process, although the heat increment was reported to increase with increasing the amount of ingestion, this was not observed in the present study.12 Therefore, it is likely that the heat increment is greatly affected by the pre-consumptive process, rather than the post-consumptive one. Consequently, we consider the scope for active rate of respiration as a large searching cost when feeding on too small a size of prey.

The amount of excretion was significantly lower in the medium-prey group (6.6±0.8%) than in the small-prey group (9.4±1.5%). Kalarani and Davies13 suggest that an increase of oxygen consumption by predation results in the formation of nitrogenous end products which are excreted (exogenous excretion), immediately resulting in additional energy losses. Thus, it is considered that the excretion of the polychaete also results in an additional searching cost, when feeding on too small a size of prey.

Saito et al.14 suggested that the difference in the handling cost among different prey species groups (i.e. the scope for active rate of respiration and jelly-like material secreted during handling) has great effects on the growth. In contrast, the present study emphasizes that the difference in searching costs between both prey groups [i.e. the scope for active rate of respiration (11.8%) and excretion (2.8%)] have great effects on the growth (19.3%).

ACKNOWLEDGMENTS

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REFERENCES