Original Article

Interaction between handling cost and growth of the bivalve-feeder *Halla okudai* under rearing conditions, in relation to prey species

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**SUMMARY:** In order to evaluate the interaction between handling cost and growth of the bivalve-feeder *Halla okudai* (Polychaeta: Lysaretidae), the observation of foraging behavior and measurement of energy budget were conducted in laboratory feeding experiments by offering three different bivalves: the short-neck clam *Ruditapes philippinarum*, the blue mussel *Mytilus galloprovincialis*, and the Pacific oyster *Crassostrea gigas*. The total handling time was 1.6–2.7 times longer in the oyster-group (25.6±9.3 h) than in the clam and mussel-groups, while the total searching and feeding time hardly varied with prey species. No significant difference in the amount of ingestion (4.5–5.3 kcal/polychaete per 15 days) was shown among the three prey groups. However, the growth increment was 1.5–2.1 times higher in the clam-group (1.85±0.65 kcal/polychaete per 15 days) than in the other two prey groups. In contrast, the scope for active rate of respiration and jelly-like material secreted during handling was higher in the oyster-group (0.66±0.14 and 0.24±0.07 kcal/polychaete per 15 days, respectively) and mussel-group (0.62±0.07 and 0.16±0.05 kcal/polychaete per 15 days) than in the clam-group (0.48±0.09 and 0.06±0.01 kcal/polychaete per 15 days), although there were no significant differences in the standard rate of respiration, excretion, feces and jelly-like material secreted during feeding among the three groups. These results indicate that growth of *H. okudai* increases with a decreasing handling cost, when feeding on the optimal prey species.

**KEY WORDS:** energy budget, growth, *Halla okudai*, handling cost, optimal prey species, polychaete.

INTRODUCTION

In intertidal communities, predation by carnivorous invertebrates (e.g. crustaceans, asteroids and gastropods) is known to be an important factor influencing abundance, species, and size of prey organisms.1–3 In order to explain the predator–prey interaction, the optimal foraging model is introduced. The model predicts that the predator selects on prey maximizing net energy intake rate (energy gained—energy expended/time).4 However, the energy expended by predators has proven difficult to quantify; these costs are frequently estimated as the time required for predators to ingest prey.5,6

*Halla okudai* (Polychaeta: Lysaretidae) is a large carnivore (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 polychaete feeds on bivalves such as the short-neck clam *Ruditapes philippinarum*, the blue mussel *Mytilus galloprovincialis*, and the Pacific oyster *Crassostrea gigas*, and especially prefers the clam to the other two bivalves.10 The laboratory experiment showed that the growth efficiency of the polychaete was significantly higher in the clam-group (32.0%) than in the mussel-group (18.0%) and oyster-group (15.8%), and a correspondence of the selection of prey species with the growth efficiency was affected by the cost of foraging behavior.11 According to Imabayashi et al.,12 the foraging process of the polychaete is divided into four phases (i.e. responding, searching, handling and feeding) and they observed that the jelly-like material secreted during the handling and feeding phases differ in amount and transparency between these phases.
Recently, it has been suggested that the secretion of jelly-like material required a major energy drain in marine invertebrates, and 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; \( J \), jelly-like material.\(^{13,14} \) For \( H. \ okudai \), it was estimated that the jelly-like material secreted during handling was higher in the oyster-group (3.2%) than in the clam-group (1.6%).\(^ {11} \) However, difference of the above-mentioned growth efficiency between the clam-group and oyster-group (16.2%) can hardly be explained by that of the material (1.6%) alone. Therefore, it is necessary to clarify the energy expended during handling.

In this study, in order to evaluate an interaction between handling cost and growth of the polychaete, the observation of foraging behavior and measurements of energy budget were conducted in feeding experiments for 15 days under three different species of prey conditions.

**MATERIALS AND METHODS**

**Collection of animals and experimental apparatus**

Fifteen immature individuals of \( H. \ okudai \) without gonadal output (6.0–13.7 g in wet weight) were collected from intertidal sandy flats 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.

Three species of bivalves, the clam \( R. \ philippinarum \), the mussel \( M. \ galloprovincialis \), and the oyster \( C. \ gigas \) 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 \( 25^\circ \)C in temperature and at 32 p.p.t. in salinity, and was completely exchanged with fresh oxygen-saturated seawater at 7 mg/L every 8 h in order to keep the dissolved oxygen content higher than 3 mg/L. The photoperiod was kept usually in a dark condition except at the exchange of the water.

The polychaete was individually introduced to a respiration chamber, and fed separately with three different prey species. The prey size was restricted to 10–20% of its own bodyweight, which was the optimum size for the polychaete.\(^ {15} \) An ingested prey was replaced by a new intact one immediately after feeding. Each experiment consisted of 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 foraging processes, the foraging behavior was monitored by an infrared dark-field, video camera-video system (TK-S240; Victor, Co., Ltd., Tokyo, Japan).\(^ {12} \)

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 makes it possible to monitor the decline in the oxygen content in the chamber. The water was mixed in the chamber throughout the experiment with a magnetic stirrer at constant rpm. The oxygen content in the chamber was recorded by the camera-video system. The oxygen consumption rate of the polychaete was estimated by subtracting the rate of the bivalves measured in a preliminary experiment from the oxygen content in the chamber.

**Measurement of energy budget**

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 in the bodyweight between the initial and the final weights of the experiments. It was converted to the caloric value with the caloric equivalent of 857.4 cal/g wet weight.\(^ {11} \)

The respiration rate was measured as the oxygen consumption rate. It was converted into the caloric value by applying an oxy-caloric coefficient of 3.3 cal/mg O\(_2\).\(^ {16} \)

The excretion as the nitrogenous end products when protein is being respired could be estimated from the oxygen consumption for 15 days, multiplied by the oxycaloric coefficient of 0.51 cal/mg O\(_2\).\(^ {17} \)

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

The jelly-like material secreted during the handling and feeding was obtained from the feeding experiment offering different sizes of prey (10–50 mm in shell length). The caloric values of both the materials were determined by the method of Saito and Imabayashi.\(^ {15} \)

**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 all experiments, the oxygen consumption rate drastically
increased during the foraging period (i.e. 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 prey ingested and the total foraging time are shown in Table 1. The frequency of prey ingested showed no significant difference among the three prey groups (4.0–4.4/15 days). Consequently, the total searching and feeding time showed no significant difference among the three prey groups (17.4–23.5 and 6.0–6.2 h, respectively). However, the total handling time in the oyster-group (mean ± SD: 25.6 ± 9.3 h) was the highest among the three prey groups which differed significantly from the clam-group (9.6 ± 2.0 h).

Energy budget

All the components of energy budget are shown in Table 2. Since the number of prey ingested hardly varied among the three prey groups, the amount of ingestion showed no significant difference among them (4.45–5.28 kcal/polychaete per 15 days).

The growth increment and the percentage to the amount of ingestion were significantly higher in the clam-group (1.85 ± 0.65 kcal/polychaete per 15 days and 34.6 ± 7.0%, respectively) than in the oyster-group (0.87 ± 0.55 kcal/polychaete per 15 days and 19.3 ± 10.7%).

The total respiration rate was divided into the standard rate, defined as the stable level rate in the non-foraging period, and the scope for the active rate, calculated by subtracting the standard rate from the total rate. The former rate and the percentage showed no significant difference among the three prey groups (1.79–1.84 kcal/polychaete per 15 days and 35.4–40.6%). However, the latter rate and the percentage were significantly lower in the clam-group (0.48 ± 0.09 kcal/polychaete per 15 days and 9.3 ± 2.2%) than in the mussel-group (0.62 ± 0.07 kcal/polychaete per 15 days and 14.3 ± 4.9%) and oyster-group (0.66 ± 0.14 kcal/polychaete per 15 days and 15.1 ± 3.1%).

The amount of excretion and the percentage showed no significant difference among the three prey groups (0.36–0.38 kcal/polychaete per 15 days and 6.9–8.6%).

The amount of feces showed a significant positive relationship to that of ingestion for three prey species (Fig. 3). Since the amount of ingestion hardly varied among the three prey groups, there was no or little significant difference for the caloric value and the percentage among the three prey groups (0.43–0.58 kcal/polychaete per 15 days and 9.7–10.9%).

The amount of jelly-like material secreted during handling showed a significant positive relationship to prey size for three prey species (Fig. 4). The caloric value and the percentage were significantly lower in the clam-group (0.06 ± 0.01 kcal/polychaete per 15 days and 1.2 ± 0.1%) than in the mussel-group (0.16 ± 0.05 kcal/polychaete per 15 days and 2.3 ± 0.2%).
secreted during feeding showed a significant positive relationship to that of ingestion for three prey species (Fig. 6). Since the amount of ingestion hardly varied among the three prey groups, there was no significant difference for the caloric value and the percentage among them (0.07–0.09 kcal/polychaete per 15 days and 1.6–1.7%).

There was a significant positive relationship between the amount of the material secreted during handling and the scope for active rate of respiration (Fig. 5).

On the other hand, the amount of the material secreted during feeding showed a significant positive relationship to that of ingestion for three prey species (Fig. 6). Since the amount of ingestion hardly varied among the three prey groups, there was no significant difference for the caloric value and the percentage among them (0.07–0.09 kcal/polychaete per 15 days and 1.6–1.7%).

![Graph](image-url)

**Fig. 2** Examples of daily records of foraging behavior and oxygen consumption of the predator *Halla okudai*. The three processes of the foraging behavior are searching (△), handling (○) and feeding (●). Dotted lines indicate the standard rate of oxygen consumption. (a) Individual (initial body size, 12.4 g) in clam-group, (b) individual (initial body size, 11.1 g) in mussel-group, (c) individual (initial body size, 9.1 g) in oyster-group.

**Table 1** Number of prey ingested and total foraging time of the predator *Halla okudai* feeding on the three different prey species

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Initial body size (g wet weight)</th>
<th>No. of prey ingested (individual/15 days)</th>
<th>Searching (h)</th>
<th>Handling (h)</th>
<th>Feeding (h)</th>
<th>Total foraging time (h)</th>
</tr>
</thead>
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<tr>
<td>Short-neck clam</td>
<td>10.0 ± 3.2a</td>
<td>4.4 ± 1.1a</td>
<td>17.4 ± 7.5a</td>
<td>9.6 ± 2.0a</td>
<td>6.1 ± 1.1a</td>
<td>32.8 ± 7.0a</td>
</tr>
<tr>
<td>Blue mussel</td>
<td>9.4 ± 2.3a</td>
<td>4.2 ± 1.2a</td>
<td>20.4 ± 9.8a</td>
<td>16.2 ± 8.3ab</td>
<td>6.0 ± 1.6a</td>
<td>42.6 ± 16.9ab</td>
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<tr>
<td>Pacific oyster</td>
<td>8.6 ± 0.9a</td>
<td>4.0 ± 0.9a</td>
<td>23.5 ± 4.0a</td>
<td>25.6 ± 9.3b</td>
<td>6.2 ± 1.3a</td>
<td>58.8 ± 12.7b</td>
</tr>
</tbody>
</table>

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 Fisher’s PLSD test.
Table 2  Energy component of the predator *Halla okudai* feeding on the three different prey species

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Initial body size (g wet weight)</th>
<th>Ingestion (kcal²)</th>
<th>Growth increment (kcal²)</th>
<th>Respiration (kcal²)</th>
<th>Excretion (kcal²)</th>
<th>Feces (kcal²)</th>
<th>Jelly-like material</th>
<th>Total out (kcal²)</th>
<th>Handling (kcal²)</th>
<th>Feeding (kcal²)</th>
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<td>6.4</td>
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<td>1.79</td>
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<td>7.5</td>
<td>6.08</td>
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<td>1.90</td>
<td>0.46</td>
<td>2.36</td>
<td>0.36</td>
<td>0.67</td>
<td>0.08</td>
<td>0.11</td>
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<td></td>
<td>11.9</td>
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<td>0.61</td>
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<td>Mean ± SD</td>
<td>10.4 ± 3.2*</td>
<td>5.28 ± 1.11*</td>
<td>1.85 ± 0.65*</td>
<td>1.84 ± 0.25*</td>
<td>0.48 ± 0.09*</td>
<td>2.32 ± 0.31*</td>
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<tr>
<td>Mean ± SD</td>
<td>9.4 ± 2.3*</td>
<td>4.66 ± 1.42*</td>
<td>1.23 ± 0.62*</td>
<td>1.81 ± 0.37*</td>
<td>0.62 ± 0.07*</td>
<td>2.43 ± 0.36*</td>
<td>0.38 ± 0.08*</td>
<td>0.48 ± 0.15*</td>
<td>0.16 ± 0.05*</td>
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<td>7.2</td>
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<td>14.3 ± 4.9**</td>
<td>54.4 ± 10.4**</td>
<td>8.5 ± 1.6**</td>
<td>10.3 ± 0.1*</td>
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<td>103.3 ± 6.5**</td>
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<td>Pacific oyster</td>
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<tr>
<td>Mean ± SD</td>
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<td>4.45 ± 0.75*</td>
<td>0.87 ± 0.55*</td>
<td>1.79 ± 0.30*</td>
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<td>0.43 ± 0.08*</td>
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<td>Mean ratio¹ ± SD</td>
<td>19.3 ± 10.7*</td>
<td>40.6 ± 6.6**</td>
<td>15.1 ± 3.1**</td>
<td>55.7 ± 7.4**</td>
<td>8.6 ± 1.2**</td>
<td>9.7 ± 0.1*</td>
<td>5.3 ± 1.0*</td>
<td>1.6 ± 0.3*</td>
<td>100.2 ± 6.0**</td>
<td></td>
</tr>
</tbody>
</table>

¹Energy component as percentage of ingestion.
²kcal/polychaete, 15 days.
Values in the same column with different superscripts (a, b, c or *a, *b, *c) are significantly different (*P* < 0.05) when analyzed using an ANOVA coupled with a Fisher's PLSD test.
Fig. 3  Relationship between ingestion and feces of the predator *Halla okudai* under three different species of prey conditions. (a) Clam-group \( y = 0.11x + 1.81, n = 12, r = 0.901, P < 0.01 \), (b) mussel-group \( y = 0.10x + 1.08, n = 12, r = 0.815, P < 0.01 \), (c) oyster-group \( y = 0.10x + 0.99, n = 12, r = 0.859, P < 0.01 \).

Fig. 4  Relationship between shell length of the prey and energy content of jelly-like material secreted during handling by the predator *Halla okudai* under three different species of prey conditions. (a) Clam-group \( y = 0.88x^{1.58}, n = 147, r = 0.943, P < 0.01 \), (b) mussel-group \( y = 1.78x^{1.75}, n = 80, r = 0.828, P < 0.01 \), (c) oyster-group \( y = 1.66x^{2.50}, n = 86, r = 0.861, P < 0.01 \).
DISCUSSION

A previous study showed that *H. okudai* preferred *R. philippinarum* to *M. galloprovincialis* and *C. gigas*. This study showed that the growth increment was 1.5–2.1 times higher in the clam-group (1.85 ± 0.65 kcal/polychaete per 15 days) than in the mussel-group and oyster-group. This result suggests that growth is maximized when feeding on the optimal prey species. Such a correspondence of the growth with the prey preference can be explained by a quantification of the respiration rate and jelly-like materials, since there were no significant differences in the amount of ingestion, excretion and feces among the three prey groups.

The total respiration rate which was the largest energy loss of the budget, was divided into the standard rate and the scope for active rate. The former corresponded to standard metabolism and it showed no significant difference among the three prey groups (1.79–1.84 kcal/polychaete per 15 days). However, the latter was larger in the oyster-group (0.66 ± 0.14 kcal/polychaete per 15 days) than in the other two prey groups. It is considered that the scope for active rate corresponded to the heat increment during the pre-consumptive process (e.g. searching and handling), and the post-consumptive process (e.g. digestion and assimilation). In the pre-consumptive process, the heat increment is likely to occur during handling, since the handling time was 1.6–2.7 times longer in the oyster-group (25.6 ± 9.3 h) than in the other two prey groups, while the total searching time showed no sig-

![Fig. 5](image_url)  
**Fig. 5** Relationship between jelly-like material secreted during handling and scope for active rate of respiration by the predator *Halla okudai* under three different species of prey conditions ($y = 0.986x + 0.435$, $n = 15$, $r = 0.682$, $P < 0.01$). Prey species: Short-neck clam (●), Blue mussel (▲), and Pacific oyster (■).

![Fig. 6](image_url)  
**Fig. 6** Relationship between shell length of the prey and energy content of jelly-like material secreted during feeding by the predator *Halla okudai* under three different species of prey conditions. (a) Clam-group ($y = 0.08x^{0.79}$, $n = 147$, $r = 0.936$, $P < 0.01$), (b) mussel-group ($y = 0.27x^{0.60}$, $n = 80$, $r = 0.804$, $P < 0.01$), (c) oyster-group ($y = 0.23x^{0.61}$, $n = 60$, $r = 0.704$, $P < 0.01$).
significant difference among them. In the post-consumptive process, the heat increment for digestion and assimilation is unlikely to vary among the three prey groups, since no significant difference in the amount of ingestion and the feeding time was observed among them. Therefore, we consider the scope for active rate as a large handling cost, when feeding on the less preferred prey species. This is also supported by the result that the scope for active rate showed a significant relationship to the amount of jelly-like material secreted during handling.

Secretion of jelly-like material during the foraging process is a peculiar foraging style to polychaetes. Another carnivorous polychaete Arabella iricolor (Arabellidae) living in the rocky shore, has been observed to feed on mussels and barnacles while secreting material. For H. okudai, the material secreted during handling contains components with a paralytic activity which provided for efficient handling of prey, while that secreted during feeding contains digestive enzymes for quick ingestion of prey. Saito and Imabayashi clarified that the amount of material secreted during handling (1.4–4.4%) varied with relative prey size, defined as a ratio of bodyweight of the prey to the polychaete, and became a large handling cost in the case of relative prey size of more than 20%. In this study, the material secreted during handling also varied with prey species; it was 1.5–4.0 times higher in the oyster-group (0.24 kcal/polycheate per 15 days) than in the other two prey groups. Thus, it is clear that the material secreted during handling results in a large foraging cost when feeding on the less preferred prey species. On the other hand, the material secreted during feeding is unlikely to become a foraging cost, since no significant differences in the amount of the material was observed among the three prey groups (0.07–0.09 kcal/polycheate per 15 days).

The present study discussed an interaction between handling cost and growth of the polychaete using the calorific value. Likewise, the interaction can be evaluated by the percentage to the amount of ingestion: the difference in growth increment (15.3%) between the clam-group and the oyster-group is largely explained by the sum of the difference in the scope for active rate of respiration (5.8%), and the jelly-like material secreted during handling (4.1%). A similar explanation is possible for the difference between the clam-group and mussel-group. That is, the growth increased with decreasing the handling costs in feeding the preferred prey, the clam, while the growth decreased with increasing the handling costs in feeding the less preferred prey, the oyster.

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REFERENCES