Clearance rates and ingestion efficiency of the Japanese scallop *Patinopecten yessoensis*

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**Abstract:** In coastal ecosystems, variations in food quantity may have significant effects on the clearance and ingestion rates of suspension-feeding bivalves. In this study, clearance rates and ingestion efficiencies were determined for Japanese scallop (*Patinopecten yessoensis*) juveniles (60.6 ± 4.5 mm in shell height) under laboratory conditions. Scallops were kept individually in glass beakers at 15°C and fed with different cell numbers of *Pavlova* sp. (0.8 to 57.60 x 10⁶ cells) to provide a wide range of food quantity as particulate organic carbon (POC). Clearance rates (CR) and ingestion efficiencies (IE) were estimated by monitoring POC concentration over a two-day period, and from 2 to 14 days of feeding, respectively. Both CR and IE were significantly influenced by POC concentration. CR ranged from 15.8 to 38.5 mL ind⁻¹ h⁻¹ (or 8.9 to 49.6 mg C h⁻¹ g dry weight⁻¹) with maximum values at high POC concentrations. IE varied from 40 to 71% and differed significantly between the lowest (2,900 μg C L⁻¹) and highest (8,000 μg C L⁻¹) food rations. The feeding response of juvenile scallops to different POC concentrations was fitted to a power curve equation: IE (%)=0.9272 x POC⁻⁰·⁵¹⁰⁵, r=0.98. Extrapolated field-based estimates of IE ranged from 7.8 to 12.7% in response to seasonal changes in POC concentration (64.5 to 168.6 μg C L⁻¹). It is concluded that particle filtration rates by juvenile scallops are related to food quantity, as suggested by both field and laboratory-derived feeding rates.

**Key words:** clearance rate, ingestion efficiency, particulate organic carbon, *Patinopecten yessoensis*, *Pavlova* sp.

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**Introduction**

The Japanese scallop *Patinopecten yessoensis* (Jay, 1857) is a commercially important temperate scallop cultured extensively in the coastal areas of northern Japan. It is reared using the hanging method in shallow estuarine lagoons and by sowing or bottom culture in nearshore seabeds. Food and feeding studies of scallops have shown that they consume mainly phytoplankton (Shumway et al. 1981, Aya & Kudo 2007) or sinking particles in their natural habitats (Cranford & Grant, 1990, Aya & Kudo 2010). Elsewhere, cultured bivalves are known to ingest and assimilate phytoplankton with high efficiency depending on particle concentration, quality and size of food particles, and shell size (Cranford & Grant 1990, Alber & Valiela 1996, Shumway et al. 1997, Velasco 2006).

Increased filtration rates by mussels are also significantly affected by the physical parameters of the natural habitat such as water temperature, salinity and water flow (Lie et al. 1996, Eversole et al. 2008). The feeding rate of bivalves is an important factor influencing the growth of animals in suspension culture (Incze et al. 1981). Thus, knowledge of the ingestion or filtration rates of bivalve species should enable the prediction of the optimum food quantity required for their growth. However, studies on the ingestion rates of Japanese scallops have dealt mainly with juvenile and adult individuals in the limited environment of culture within their suspended cages (Kurata et al. 1991).

There are no published reports of the ingestion rates of juvenile scallops from sowing or nearshore bottom culture in northern Japan. Therefore, the present study investigated the feeding response of juvenile scallops in response to a wide range of particulate organic carbon (POC) concentrations under laboratory conditions. Using the
information derived from this study, the ingestion rates of juvenile scallops in their natural habitat were calculated based on measurements of suspended particulate organic matter (SPOM). The objectives of this study are to estimate the particle filtration rates of individual scallops, and to discuss the feeding behavior of this species.

**Materials and Methods**

**Study area and sampling**

Scallops were reared in Tokoro, Hokkaido, one of the main culture sites in northern Japan. Tokoro seabed (44°13′N, 143°55′E) is in the Sea of Okhotsk, which has a maximum depth of 40–65 m (Fig. 1). During summer, surface salinity was 32.3–34.1 and temperature 13–17°C. For the present experiments, juvenile scallops from Tokoro were packed on ice in a styrofoam box for transport to the laboratory.

**Culture of Pavlova sp.**

Culture starter of *Pavlova* sp. (a species of haptophyte microalga, 5 μm in diameter) was obtained from the Hokkaido Institute of Fisheries Research in Muroran, Japan. *Pavlova* sp. was cultured in Guillard f/2 media at 15°C, a light intensity of 150 μmol photons m⁻² s⁻¹ and 12:12 light/dark photoperiod. Cell densities during the exponential growth phase were counted using a haemacytometer (Burker-Turk) and 10 mL aliquot samples were filtered through pre-combusted (450°C, 5 h) Whatman GF/F glass fiber filters (25 mm diameter, nominal pore size 0.7 μm) for elemental carbon (C) content analyses. Elemental C content in each filter was analyzed with a CHN Elemental Analyzer (Yanaco MT-5 corder) at the Hokkaido Institute of Environmental Sciences in Sapporo. The total cell number was estimated by multiplying cell density (cells mL⁻¹) by diet volume (mL). To estimate the carbon cell quota (Qₚ), the elemental C content of samples was divided by the total cell number. Qₚ, estimated at 2.98×10⁻¹¹ g C cell⁻¹ was used to derive carbon-based values for *Pavlova* sp. Cell density was multiplied by Qₚ to estimate the amount of POC.

**Feeding experiments**

Each scallop (shell height 60.6±4.5 mm; mean±SD) was placed in a 1 L glass beaker and acclimatized at 15°C for four days before the experiment. Each beaker contained filtered seawater and was provided with mild aeration prior to introduction of the algal diet. Scallops were allocated randomly to one of four different treatment groups, fed with 10, 20, 40, or 80 mL of *Pavlova* sp. (hereafter denoted as the experimental groups P10, P20, P40, and P80). Feeding was once every 2 d to ensure a clear pattern of POC depletion between feeds. There were three replicates for
each treatment and three scallops were left unfed which served as the controls (P0). The food quantities were approximately 0.8 to 57.6 \times 10^6 cells of *Pavlova* sp. (carbon-based values as shown in Table 1). Prior to each feeding, the containment beakers were cleaned and the water replaced with fresh 0.7-μm filtered seawater. The duration of the experiment was 14 d.

Clearance rates (CR) were measured by monitoring the changes in POC concentration in triplicate 100-mL water samples collected 3, 6, 12, 24, 36 and 48 h after feeding for each treatment. To evaluate the feeding response (= ingestion efficiency (IE)) of juvenile scallops to different concentrations of POC, POC consumption was determined from the 1 L water removed at the end of each 2 d feeding period by filtering through pre-combusted and pre-weighted Whatmann GF/F glass fiber filters, which were stored at −30°C until analysis. Filters were freeze-dried, treated with 1 N HCl fumes for 24 h to remove inorganic carbon, and freeze-dried again before elemental C analyses. Filters were folded using forceps, placed in ceramic capsules and elemental C content was measured with a CHN elemental analyzer, quantified with arginine as standard.

**Field sampling**

The ingestion rate of juvenile scallops was estimated based on the concentration of SPOM obtained from samples collected in Tokoro from September to December 2008 and July to August 2009. Samples were taken from a depth of 40 m using a Van Dorn water sampler, dispensed into 2-L polyethylene bottles and transported on ice to the laboratory. SPOM was filtered through pre-combusted filters, freeze-dried, exposed to HCl fumes for 4 h to remove inorganic carbon and dried again before elemental C content analysis (CHN elemental analyzer).

**Calculations**

Clearance rate was calculated based on the equations of Jørgensen (1943) or Coughlan (1969), expressed as POC concentration filtered per unit time:

\[
CR = V \left( \ln \frac{C_0}{C_t} \right) / t
\]

where CR is the clearance rate in mL h\(^{-1}\); V is the volume of water in the experimental vessel in mL; \(C_0\) and \(C_t\) are the initial and final POC concentration (μg C L\(^{-1}\)); and \(t\) is incubation time in hours. CR was also expressed as mL h\(^{-1}\) per gram dry weight (g DW\(^{-1}\)) and mg C h\(^{-1}\) DW\(^{-1}\). Ingestion efficiency (IE) was computed as follows:

\[
IE(\%) = \left( \frac{C_{in}}{C_{add}} \right) \times 100
\]

where \(C_{in}\) and \(C_{add}\) are the ingested and the total POC concentration added into the beakers.

Field-based ingestion rates (IR) of juvenile individuals were estimated using the laboratory-derived regression model, where the *in situ* POC values were substituted for the food concentration and calculated using the following equation:

\[
IR (\text{mg C ind.}^{-1} \text{d}^{-1}) = IE(\%) \times \text{in situ POC (mg C ind.}^{-1} \text{d}^{-1})
\]

Food consumption (FC) was determined from the following equation:

\[
FC (\text{mg C m}^{-2} \text{d}^{-1}) = IR (\text{mg C ind.}^{-1} \text{d}^{-1}) \times \text{density of scallop (5 ind. m}^{-2}).
\]

**Data analysis**

Mean CR and IE were determined from the replicate values for each treatment. IE values were arc-sine transformed prior to statistical analysis. Differences between treatment means were analyzed using one-way analysis of variance (ANOVA) followed by Tukey’s post hoc test when significant differences were detected. Non-linear regression analysis was used to predict IE from POC concentration. All statistical analyses were performed using the Number Cruncher Statistical System (NCSS ver. 07.1.4; Hintze 2007).

**Results**

**Clearance rates**

The diurnal patterns of POC in relation to food quantity are shown in Figure 2. POC generally decreased 3 h after feeding in all treatments and leveled off from 12 to 48 h. After 48 h of feeding, POC was approximately 16 to 47% of initial concentrations. In Table 2, the percentage of POC cleared was lowest in the P10 and P20 treatment groups and highest in P40 and P80.

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Time of Feeding</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
</tr>
<tr>
<td>P10</td>
<td>5.33 (159)</td>
</tr>
<tr>
<td>P20</td>
<td>10.70 (318)</td>
</tr>
<tr>
<td>P40</td>
<td>21.30 (637)</td>
</tr>
<tr>
<td>P80</td>
<td>42.70 (1,274)</td>
</tr>
</tbody>
</table>
Feeding rates of Japanese scallop

Clearance rates of juvenile individuals were influenced by food quantity \((p<0.05)\) (Fig. 3). Scallops in the P10 group significantly cleared POC from the water, but the P20 group clearance rate was not significantly different from P10 performance. The P40 and P80 groups, too, showed no significant difference in their performance. Clearance rates relative to dry weight of scallop were lower for P10, P20 and P80 treatments than for P40. Clearance rates expressed as mg C were lower in P10 and P20 groups compared with P40 and P80.

**Ingestion efficiencies**

Consumption of POC revealed two contrasting patterns: the first pattern occurred during the period of days 2–4 of the experiment and the second pattern during the period of days 6–14 (Fig. 4). The second pattern, characterized by high POC consumption, coincided with elevated levels of POC presented at feeding. IE increased with POC above \(703 \mu g \text{ C L}^{-1}\), and continued to increase up to a maximum value of \(7,960 \mu g \text{ C L}^{-1}\) (Table 3, Fig. 5). Regardless of the period of the experiment (2–14 or 6–14 d), IEs were significantly higher \((p<0.05\), one-way ANOVA\) for P80 than for the P40 and P20 treatments, but did not significantly differ between P40 and P80 during days 2–6 (Table 3). Using non-linear regression analysis, IE can be predicted well from total POC concentration (Fig. 5). IE was positively correlated with POC concentration, which could be expressed as follows: \(\text{IE} (\%) = 0.9272 \times \text{POC}^{0.5105}; r^2=0.98\).

**Field-based feeding rates**

During the study period, bottom water temperature at Tokoro changed from 6.1 to 17.5°C. SPOM was relatively low and displayed seasonal variation, ranging from 64.5 \(\mu g \text{ C L}^{-1}\) in autumn to 168.6 in summer (Table 4). Ingestion rates decreased from September to December in 2008, and increased from July to August 2009, coinciding with fluctuations in POC (Table 4). IE decreased seasonally with lower values in autumn than in summer. Rates of food consumption varied similarly to that of food quantity and temperature: highest values in summer and lowest in autumn.
Discussion

In the present experiment with *P. yessoensis* juveniles, clearance rates varied with food quantity, as reflected by POC concentration (Table 2). Rajesh et al. (2001) also arrived at a similar conclusion for three Indian bivalves (*Perna veridis*, *Crassostrea madrasensis*, and *Paphia malabrica*). However, for the oyster, laboratory-based experiments have demonstrated that clearance rate decreases with POM (Barillé et al. 1997). The observed pattern of elevated clearance rates obtained in the present study reflects the rapid decrease in POC during the first 3 h after feeding, regardless of the initial quantity (Fig. 2), suggesting that scallops are efficient at particle clearance when there

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**Table 3.** Mean ingestion efficiency (IE, mean ± SD) calculated for *P. yessoensis* juveniles at different POC concentrations across arbitrary periods of the experiment.

<table>
<thead>
<tr>
<th>Period selected</th>
<th>Treatment</th>
<th>ΨC_initial (μg C L⁻¹)</th>
<th>IE (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2–6 d P10</td>
<td>594 ± 49</td>
<td>Below 0</td>
<td></td>
</tr>
<tr>
<td>2–6 d P20</td>
<td>660 ± 106</td>
<td>Below 0</td>
<td></td>
</tr>
<tr>
<td>2–6 d P40</td>
<td>703 ± 106</td>
<td>17.5 ± 7.0ᵃ</td>
<td></td>
</tr>
<tr>
<td>2–6 d P80</td>
<td>1,188 ± 90</td>
<td>23.4 ± 7.8ᵃ</td>
<td></td>
</tr>
<tr>
<td>6–14 d P10</td>
<td>1,943 ± 235</td>
<td>Below 0</td>
<td></td>
</tr>
<tr>
<td>6–14 d P20</td>
<td>2,293 ± 222</td>
<td>39.8 ± 10.7ᵃ</td>
<td></td>
</tr>
<tr>
<td>6–14 d P40</td>
<td>3,748 ± 227</td>
<td>62.1 ± 3.9ᵇ</td>
<td></td>
</tr>
<tr>
<td>6–14 d P80</td>
<td>6,774 ± 309</td>
<td>76.6 ± 8.7ᵇ</td>
<td></td>
</tr>
<tr>
<td>2–14 d P10</td>
<td>2,603 ± 264</td>
<td>Below 0</td>
<td></td>
</tr>
<tr>
<td>2–14 d P20</td>
<td>2,887 ± 180</td>
<td>39.8 ± 6.3ᵃ</td>
<td></td>
</tr>
<tr>
<td>2–14 d P40</td>
<td>4,451 ± 318</td>
<td>56.1 ± 5.6ᵇ</td>
<td></td>
</tr>
<tr>
<td>2–14 d P80</td>
<td>7,962 ± 229</td>
<td>71.1 ± 7.0ᶜ</td>
<td></td>
</tr>
</tbody>
</table>

Values in column with similar superscript letters in various feeding durations are not significantly different at *p*<0.05 (one-way ANOVA).

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Fig. 4. POC consumption of *P. yessoensis* fed with 10, 20, 40 or 80 mL *Pavlova* sp. of differing concentrations at two-day intervals. Lines connect the POC concentrations at the beginning and end of each feeding period.
is sporadic high abundance of food in the water, such as during a tide-induced resuspension event. Juveniles were fed only once every other day in the present experiments but the clearance rates obtained probably occurred within the first 3 h after feeding.

The ingestion rates of the scallops were significantly influenced by POC concentration since the lowest ingestion rates occurred during the period 2–6 days into the experiment and the highest during the 6–14-day period (Table 3), coincident with food quantity. This finding is also supported by the relationship between ingestion efficiency and POC concentration, which follows a non-linear equation (Fig. 5) with a plateau of ingestion efficiency at around 7,600 μg C L\(^{-1}\) suggesting saturation of the digestive tract (Iglesias et al. 1992, Pérez-Camacho et al. 1994, Hawkins et al. 1997). Likewise, the capacity of bivalve species to ingest organic matter is regulated by the production of pseudofaeces (Bayne et al. 1989, Pérez-Camacho et al. 1994, Strychar & MacDonald 1999). Rajesh et al. (2001) observed that three Indian bivalves produced pseudofaeces when fed 10^5 cells mL\(^{-1}\). Although the production of pseudofaeces was not quantified in the present study, juvenile scallops started producing biodeposits at algal cell concentrations of 10^5–10^7 (i.e. higher than that reported by Rajesh et al. 2001).

Measurements in Tokoro, Okhotsk Sea, enabled the estimation of ingestion rates in the field, which were compared with the clearance rates achieved in the laboratory. Laboratory-derived ingestion efficiencies varied within a wide range, between 17.5 and 76.6%, depending on initial POC concentration (Table 3). These values seem to indicate that the high ingestion efficiency of \(P. yessoensis\) juveniles would enable them to be grown at POC concentrations higher than those found in natural waters. This also means that the feeding processes of \(P. yessoensis\) appear well adapted to dealing with elevated particle concentrations. Extrapolated field-based estimates of ingestion efficiencies ranged from 7.8 to 12.7% in response to seasonal changes of POC concentration in the Tokoro area (Table 4). SPOM abundance, too, has a strong positive effect on ingestion rate and efficiency, particularly when the food supply is low (F. Aya, unpublished data).

The only previous information on the feeding rates of \(P. yessoensis\) juveniles is from those cultured in suspended net-cages. In the present study, feeding rates followed a seasonal pattern with the highest values observed in summer and the lowest in autumn (Table 4). Kurata et al. (1991) found that the feeding rates of juvenile scallops reared in a coastal lagoon varied from 106 mg C ind.\(^{-1}\) d\(^{-1}\) in summer to just 9 mg C ind.\(^{-1}\) d\(^{-1}\) in early spring. They also calculated that juvenile individuals can filter 268 L d\(^{-1}\) ind.\(^{-1}\). They also found that feeding rates are affected by water temperature.

In summary, the experiment reported here showed that food quantity (as POC) clearly influenced the clearance rates and ingestion efficiencies of \(P. yessoensis\) juveniles, suggesting that field and laboratory estimates of particle filtration rates are dependent on food density. An equation used to describe the relationship between POC concentration and ingestion efficiency is presented. This equation allows the estimation of ingestion rates of juvenile individuals and their food consumption in field conditions using in situ measurements of POC, which is of potential benefit to the scallop fishery in providing guidance in manipulating the size and quantity of scallops (i.e. carrying capacity) and eventually to improve the sustainability of the scallop fishery.

![Fig. 5. Relationship between ingestion efficiency (IE) and initial particulate organic matter (POC) concentration in \(P. yessoensis\) fed with different food rations.](image-url)

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Sampling period 2008</th>
<th></th>
<th>Sampling period 2009</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sept 2</td>
<td>Oct 21</td>
<td>Dec 3</td>
<td>Jul 22</td>
</tr>
<tr>
<td>Temperature (°C, 40 m)</td>
<td>16.5</td>
<td>13.0</td>
<td>6.1</td>
<td>13.1</td>
</tr>
<tr>
<td>POC (μg C L(^{-1}), 40 m)</td>
<td>168.6</td>
<td>125.6</td>
<td>64.5</td>
<td>117.8</td>
</tr>
<tr>
<td>Ingestion Efficiency (%)</td>
<td>12.7</td>
<td>10.9</td>
<td>7.8</td>
<td>10.6</td>
</tr>
<tr>
<td>Ingestion Rate (mg C ind.(^{-1}) d(^{-1}))</td>
<td>21.4</td>
<td>13.7</td>
<td>5.0</td>
<td>12.5</td>
</tr>
<tr>
<td>Food consumption (mg C m(^{-2}) d(^{-1}))</td>
<td>107.1</td>
<td>68.7</td>
<td>25.1</td>
<td>62.4</td>
</tr>
</tbody>
</table>

Table 4. Temperature, particulate organic carbon (POC) concentration, ingestion efficiency, ingestion rate and food consumption of \(P. yessoensis\) juveniles under field conditions.
fishery (Miyazono 2006). However, further studies of the feeding rates of this species are required to investigate the effects of different conditions of food quality in the scallop natural environment.

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