DEPENDENCE OF THE SURF CLAM *PSEUDOCARDIUM SACHALINENSE* (BIVALVIA: MACTRIDAE) ON THE NEAR-BOTTOM LAYER FOR FOOD SUPPLY

KOICHI SASAKI¹, ATSUSHI SANEMATSU¹, YASUSHI KATO² AND KINUKO ITO¹

¹Graduate School of Agricultural Science, Tohoku University, Sendai, Miyagi 981-8555, Japan
²Soma Branch, Fukushima Prefectural Fisheries Experimental Station, Soma, Fukushima 976-0022, Japan

(Received 10 June 2003; accepted 10 October 2003)

ABSTRACT

We investigated the food sources of the surf clam *Pseudocardium sachalinense* by comparing the micro-algal composition in the stomach with that of the overlying water and in the bottom sediment. The microalgal composition in the stomach contents resembled that of the sediment, in which four microalgal species groups: Melosira, Coscinodiscus, solitary species of Nitzschiaeae and Naviculaceae constituted a large proportion of the total throughout the study. By contrast, the dominant microalgae in the water column changed through the year and was different from those in the stomach contents and the sediment. Since the surf clam is an obligate suspension feeder, these results indicate that it relies on the overlying water close to the bottom surface as a food source layer. Consequently, the surf clam may rarely ingest pelagic microalgae that are produced in the upper layers of the water column. Unlike bivalves on tidal flats or mussels in intertidal areas, few pelagic microalgae produced in the upper layers are supplied to infaunal suspension-feeding bivalves on open shallow sandy bottoms. So measurements of chlorophyll a in the water column do not indicate the food supply for such bivalves.

INTRODUCTION

The surf clam *Pseudocardium sachalinense* (Schrenck, 1862) is a large suspension-feeding bivalve inhabiting open sandy bottoms of the sublittoral zone, ranging from 5 to 15 m deep off northern and northeastern Japan, and forms commercially important fishery stocks. The stocks irregularly produce large year classes at intervals of several years (Sasaki, 1986, 1993). Such dense assemblages have been noted to exhibit reduced growth rates, attributable to a relative reduction of individual food supply due to the increase in population density (Ishikawa et al., 1989; Sasaki, 1993; Horii, Murakami & Sakurai, 2002). Various benthic suspension feeders compete for food (Wildish, 1977; Wildish & Kristmanson, 1979, 1984; Fréchette & Bourget, 1985; Peterson & Black, 1987; Fréchette, Butman & Geyer, 1989; Jensen, 1992, 1993). The reduction of growth attributed to competition for food at higher population densities has been reported for some bivalves such as Macoma balthica (Beukema & De Bruin 1977; Ølabø, 1986), Cerastoderma edule (Jensen, 1992, 1993), Mytilus edulis (Fréchette & Bourget, 1985; Kamermans, 1994) and Spisula solidissima (Ambrose, Jones & Thompson, 1980; Weinberg, 1998).

The food supply for each species is a dominant factor determining carrying capacity in an area. Suspension-feeding bivalves ingest various suspended organic particles, including planktonic and benthic microalgae, bacteria and resuspended detritus. In particular, infaunal species feed not only on particles suspended in the water column, but also on surface deposits on the bottom (Kamermans, 1994; Jorgensen, 1996). For infaunal bivalves living on tidal flats and mussels in intertidal areas, food supply is considered to depend on vertical and horizontal fluxes of phytoplankton to near-bottom layers caused by water movement (Wildish & Kristmanson, 1979; Muschenheim, 1987; Cahalan, Siddal & Luchenbach, 1989; Fréchette et al., 1989; Grizzle & Lutz, 1989). However, although the type and source of food for each species need to be identified so that the food supply can be quantified, few studies have compared the stomach contents of bivalves with ambient food particles (Hummel, 1985). The surf clam ingests particulate organic matter (POM) from the overlying water just above the bottom through siphons that are flush with the bottom, but little is known about its food regime.

This study aimed to assess the food sources and the environmental structure of food supply for the surf clam. Using the algal composition in the stomach as a tracer of food source, we compared the composition in the stomach with those in the overlying water and in the bottom sediment. Then, we examined the composition of organic matter ingested and its seasonal changes, the properties of the food supply layer, and their relationship to the primary production in the upper layers of the water column.

MATERIAL AND METHODS

Study areas

The study was conducted in two fishing grounds of the surf clam dredge fishery in Fukushima Prefecture: one off Isocket, Soma and the other off Yotsukura, Iwaki about 85 km south of the Isobe ground (Fig. 1). Both grounds lie on open sublittoral bottoms ranging from 5 to 15 m deep. Depth contours generally run parallel to the coastline. Three stations (Stations 1–3) were set in the Isobe ground, spaced about 1 km apart from inshore to offshore. Station 1 was in the shoreward fringe of the ground, about 7 m deep; Station 2 in the central part, about 10 m deep; and Station 3 near the offshore margin, about 14 m deep. The sediments were mostly composed of fine to very fine sand (Wentworth’s classification). The Yotsukura ground had one station (Station 4) on fine sand, about 10–12 m deep.
Field investigations were carried out at approximately monthly intervals from May 1999 to February 2000 in the Isobe ground and to January 2000 in the Yotsukura ground, by the research vessel Takusui of the Fukushima Prefectural Fisheries Experimental Station or a chartered fishing boat.

Water and sediment samples
Water samples were taken from three depths at each station by means of a Van Dorn water sampler: 0 m and 3 m deep, and 1 m above the bottom. The water samples were put in 14 polyethylene bottles, and formalin was immediately added to a concentration of about 10% in order to fix microalgae. The water samples were left for 3 days in the laboratory for the suspended particles to settle, and then were concentrated by decanting supernatant fluid for determination of the algal species composition in the water.

Bottom sediments were collected with a Smith–McIntyre grab sampler. An acrylic tube of 35 mm inner diameter was dropped to the sediment surface in the bucket of the grab sampler and took duplicate subsamples in the form of the top 2 cm of sediment together with 2–3 cm of overlying seawater. After refilling with filtered seawater, the sub-samples were stirred to suspend POM into the seawater and the POM was separated and fixed in 10% formalin. No procedure was used to separate attached POM into the seawater and the POM was separated and fixed in ethylene bottles, and formalin was immediately added to a concentration of about 10% in order to fix microalgae. The ethylene bottles were packed with ice bags to halt digestion and transported to the laboratory.

After the shell length was measured to the nearest 0.1 mm with a pair of vernier calipers, the soft parts were dissected out. The stomach contents were sucked up in a Pasteur pipette and were preserved in 10% formalin. Stomach contents of all individuals were combined together by date and station, owing to the small individual amounts. Stomach samples were not obtained at Stations 1 and 3 in June or July 1999.

Composition of microalgae
Microalgae in the water, sediment and stomach samples were identified to species group level (genus or family) according to the taxonomic nomenclature of Chihara & Murano (1997). For each sample, about 200–400 recognizable cells of microalgae were classified and counted by species group under a compound microscope, and then the proportion of the species groups was determined as a percentage of the total number of identifiable microalgal cells. Because stomach samples at Station 2 in September and at Station 4 in August and September 1999 contained fewer than 30 cells in total, they were regarded as empty.

RESULTS

Composition of microalgae in stomach contents
Stomach contents contained a large amount of amorphous material that consisted of detritus and digested matter, and a small number of cells of microalgae such as diatoms and dinoflagellates, fine fragments of zooplankton and sand grains.

Of the identifiable microalgae, four species groups dominated throughout the study period at Stations 1–3: centric diatoms of the genera Melosira and Coccosiidas and pinnate diatoms of solitary species of the families Nitzschiaaceae and Naviculaceae. Although the four species groups showed seasonal changes in percentage, together they comprised 50–97% of the total at each station (Fig. 2). Of the four species groups, Melosira constituted a relatively high proportion, followed by Coscinodiscus at Stations 1 and 2, and by solitary species of Nitzschiaaceae at Station 3. Some other species groups, which were always found in the water column, were occasionally found in the stomach contents: diatoms such as colonial species from the family Nitzschiaaceae of the genera Melosira and Coscinodiscus and pinnate diatoms of solitary species of the families Nitzschiaaceae and Naviculaceae. The genera Eucampia was found noticeably at each station in February 2000, when its numbers increased in all layers of the water column. Twelve clams collected at Station 2 in September 1999 had nearly empty stomachs that contained few microalgal cells or little amorphous material.

The microalgal composition of the stomach contents at Station 4 was very similar to those at Stations 1–3; i.e. the four species groups were present in high proportions (Table 1). The stomachs of clams collected in August and September 1999 were nearly empty or contained few recognizable cells of microalgae, similar to those at Station 2.

In July 1999 we could not obtain any sediment samples at Stations 1–3, and neither water nor sediment samples at Station 4, owing to bad weather.

Stomach content samples
Ten to fifteen surf clams were collected from the catch of fishing boats that had operated in the daytime in areas close to each station on the days of the field investigations or on the next day. Clams measuring about 90 mm in shell length, which were the dominant size in both grounds, were collected. They were immediately packed with ice bags to halt digestion and transported to the laboratory.

Figure 1. Maps showing the locations of the study areas.
Composition of microalgae in sediment

The sediment samples included microalgae distributed both in the top 2 cm of the sediment and in the 2–3-cm layer of water just above the sediment. The composition of identifiable microalgae in the sediment samples also showed a large proportion of the four species groups dominant in the stomach contents: 50–95% of the total (Fig. 3, Table 1). The total proportion of the four species groups showed no significant differences between the stomach and sediment samples throughout the study period (chi-squared test for independence, $P > 0.05$). The resemblance in algal composition between the stomach and sediment samples was common to both grounds. Diatoms such as the genera *Biddulphia*, *Chaetoceros*, *Skeletonema*, *Asterionella* and *Eucampia* occasionally constituted 10–20% at Stations 1–3, but no species groups other than the four main groups constituted more than 10% at Station 4.

Composition of microalgae in water column

Because Stations 1–3 showed nearly the same microalgal compositions at each investigation owing to the small distances between them, Figure 4 shows only data from Station 2. The microalgal compositions in the water column in both grounds differed from those in the stomach contents and in the sediment. Significant differences in the total proportion of the four species groups were detected even between the layer 1 m above the bottom and the stomach contents at both Stations 2 and 4 (chi-squared test for independence, $P < 0.01$). Dominant species groups changed seasonally, and a relatively small number of species groups constituted a large proportion. The dominant species groups were common among the three layers of the water column on the same day, although they differed a little in proportion. Notable species groups in the Isobe ground were *Ceratium* and *Leptocylindrus* in June, *Thalassionema* in July, colonial species of *Nitzschia* in July to September, *Asterionella* in September and October, *Chaetoceros* in August to December, and *Eucampia* in February. The compositions of dominant species groups in May 1999 differed among the three layers, but even that at 1 m above the bottom did not resemble those in the stomach or the sediment. Similarly, a small number of species groups dominated, changing seasonally in the Yotsukura ground (Fig. 5): *Ceratium* and *Leptocylindrus* in June, colonial species of *Nitzschia* and *Chaetoceros* in August to December, *Asterionella* and *Skeletonema* in October to February, and *Eucampia* in February.

The four species groups commonly dominant in the sediment and stomach contents increased their proportions even in the water column in December and January at Stations 1–3 (Table 1). They reached about 50% at 1 m above the bottom but...
constituted 30% or less at 0 and 3 m depth. The proportion remained smaller in other seasons. At Station 4, although the four species groups were found in the water column for a longer period, their proportions were smaller: 20–30% at 1 m above the bottom, and up to 14% at 0 and 3 m depth.

Of the four species groups, populations of *Melosira* and *Naviculaceae* were distributed mainly in the near-bottom layer from the water–sediment interface up to 1 m above the bottom and extended up to the sea surface only in winter. Although *Coscinodiscus* and solitary species of *Nitzschiaceae* were also distributed mainly near the bottom, they were present up to the sea surface all year. They were not necessarily benthic, although they were included in the category ‘others’ in the upper layers of the water column owing to their relatively low densities.

Colonial species of *Nitzschiaceae*, *Chaetoceros*, *Skeletonema*, *Eucampia* and *Thalassionema* were found in the stomach contents and the sediment when they seasonally increased. However, their proportions were noticeably smaller than those in the water column. This result shows that only some of them reached the water–sediment interface layer and the sediment. Furthermore, genera such as *Ceratium*, *Leptocylindrus* and *Asterionella* scarcely occurred in the stomach contents or in the sediment, even when they bloomed in the water column down to the layer 1 m above the bottom.

### Classification of vertical distribution patterns of microalgae

Vertical distribution patterns of major species groups of microalgae were classified into five categories depending on their manner of occurrence in the sediment and in the three layers in the water column. Of the categories shown below, the stomach contents of the surf clam contained mainly categories A1 and B, and occasionally some of category C1, which could not be summarized as benthic or attached species.

Category A species were distributed mainly in the near-bottom region, including the water–sediment interface. Subgroup A1 was found all year round despite its comparatively

---

**Table 1.** Total proportions in percentage of four dominant microalgal species groups: centric diatoms of the genera *Melosira* and *Coscinodiscus*, and pinnate diatoms of solitary species of the families *Nitzschiaceae* and *Naviculaceae*.

<table>
<thead>
<tr>
<th></th>
<th>1999</th>
<th>2000</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>May June</td>
<td>July Aug.</td>
</tr>
<tr>
<td>Stomach contents</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Station 1</td>
<td>73.3 –</td>
<td>50.5 – 97.0</td>
</tr>
<tr>
<td>Station 2</td>
<td>78.6 88.0</td>
<td>80.4 59.8</td>
</tr>
<tr>
<td>Station 3</td>
<td>84.9 –</td>
<td>53.8 72.1</td>
</tr>
<tr>
<td>Station 4</td>
<td>50.0 79.1</td>
<td>73.9 –</td>
</tr>
<tr>
<td>Sediment</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Station 1</td>
<td>80.2 86.3</td>
<td>80.0 60.9</td>
</tr>
<tr>
<td>Station 2</td>
<td>92.2 82.2</td>
<td>71.0 70.0</td>
</tr>
<tr>
<td>Station 3</td>
<td>86.9 94.7</td>
<td>60.9 82.0</td>
</tr>
<tr>
<td>Station 4</td>
<td>78.1 90.9</td>
<td>78.3 89.7</td>
</tr>
<tr>
<td>Water column</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Station 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 m deep</td>
<td>17.9 2.39</td>
<td>0.307 0</td>
</tr>
<tr>
<td>3 m deep</td>
<td>8.89 2.50</td>
<td>0.631 1.88</td>
</tr>
<tr>
<td>Bottom + 1 m</td>
<td>3.63 0.492</td>
<td>11.9 1.74</td>
</tr>
<tr>
<td>Station 4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 m deep</td>
<td>1.52 1.90</td>
<td>1.69 11.1</td>
</tr>
<tr>
<td>3 m deep</td>
<td>3.54 3.61</td>
<td>3.70 11.0</td>
</tr>
<tr>
<td>Bottom + 1 m</td>
<td>5.66 1.56</td>
<td>34.3 21.8</td>
</tr>
</tbody>
</table>

---

FOOD SUPPLY FOR THE SURF CLAM

The surf clam has united siphons like that of many other infaunal bivalves, e.g. *Spisula solidissima*, *Mya arenaria* and *Cerastoderma edule* (Zwartz & Wanink, 1989). The clam holds the inhalent siphon flush with the bottom surface and draws in suspended POM from the overlying water just above the bottom surface. It is a typical obligate suspension feeder that does not extend its siphon to graze the surrounding surface. The algal species composition of its stomach contents, however, closely resembled that of the sediment samples. The stomach contents also contained a relatively large amount of detritus. These results indicate that the surf clam relies for food on POM suspended in the layer next to the bottom surface, including stirred-up deposits. In contrast, the stomach contents differed distinctly from the algal composition in the water layers 1 m and more above the bottom. Thus, the near-bottom layer supplies the clam’s source of food. The food source layer (FSL) is less than 1 m thick. The FSL might overlap the lowermost part of the benthic boundary layer, where water movement is nearly zero (Fréchette, Lef landscape & Butman, 1993).

The regime of primary production is distinct between the FSL and the upper layers of the water column, owing to differences in the major constituents of microalgae between them. The four species groups dominant in the bottom layer characterized the primary production regime of the FSL in this study. However, the primary production regime consists of more than the microalgae inhabiting the sediments or being resuspended. Of the four species groups, the genus *Coscinodiscus* and the solitary species of Nitzschiaeae were found even in the middle and near-surface layers of the water column, though at relatively low densities there. On the other hand, the three layers from the sea surface down to 1 m above the bottom had a similar composition of dominant microalgae, showing that the water column had a relatively uniform microagal composition owing to vertical mixing. However, microalgal dominant even 1 m above the bottom rarely entered the FSL or the sediment. This may be because vertical mixing caused by turbulence decreases with decreasing height from the bottom.

The apparent distinction in microagal compositions between the FSL and the upper layers might be emphasized by the combined effects of relatively low densities of benthic microalgal groups in the upper layers of the water column and a minor transport of pelagic ones into the FSL. In winter, even when the four species groups extended upward and mixed with pelagic species groups, the pelagic species groups did not enter the FSL. Consequently, the surf clam may rarely ingest pelagic microalgae that are produced in the upper layers in any season, except for a few species groups that occasionally extend down to near the bottom when blooming, such as the genus *Eucampia* and the colonial species of Nitzschiaceae. So the algal composition in the stomach contents showed very little seasonal change, because the FSL is insensitive to the seasonal shifts in primary production in the upper part of the water column. This vertical separation in the primary production regime was found at both grounds, thus it might not be a local peculiarity.

Vertical and/or horizontal seston fluxes accompanying water flow in the water column are responsible for the supply of food particles to benthic suspension-feeding bivalves in rocky intertidal zones and tidal flats (Fréchette & Bourget, 1985; Muschenheim, 1987; Grizzle & Lutz, 1989; Grizzle & Morin, 1989; Wildish & Saulnier, 1992). For the mussel *Mytilus edulis*, phytotoxin flux caused by vertical turbulent mixing to near-bottom waters is important for sufficient food supply (Fréchette & Bouget, 1985; Fréchette et al., 1989; Butman, Fréchette, Geyer et al., 1994). This might be because mussels rely chiefly on pelagic microalgae in the water column on account of the elevation of mussel beds from the bottom. Also, in some bivalves inhabiting tidal flats, such as *Mercenaria mercenaria*, *Macoma balthica*, *Cerastoderma edule* and *Mya arenaria*, the algal group composition of the stomach contents was similar to that in the water column (Hummel, 1985; Emerson, 1990; Grizzle, Langan & Howell, 1992; Kamermans, 1994). These results imply that, because the tide replaces the whole of the overlying water on tidal flats, and layered structures do not develop there, bivalves ingest food from waters with relatively uniform POM distribution.

**DISCUSSION**

The surf clam has united siphons like that of many other infaunal bivalves, e.g. *Spisula solidissima*, *Mya arenaria* and *Cerastoderma edule* (Zwartz & Wanink, 1989). The clam holds the inhalent siphon flush with the bottom surface and draws in suspended POM from the overlying water just above the bottom surface. It is a typical obligate suspension feeder that does not

---

**Figure 5.** Microagal compositions in three layers of the water column at Station 4 (Yotsukura). Abbreviations: A, Asterionella; Be, Bacteriastrum; Ch, Chaetoceros; Co, Coscinodiscus; Cr, Ceratium; E, Eucampia; G, Guinardia; H, Hemiaulus; L, Leptocylindrus; M, Melosira; R, Rhizosolenia; S, Skeletonema; Tn, Thalassionema; Nc, colonial species of Nitzschiaceae; Ns, solitary species of Nitzschiaceae; Nv, Naviculaceae; O, others.

**FOOD SUPPLY FOR THE SURF CLAM**
However, our results indicate that the FSL for the surf clam is independent of the physical transport of POM by vertical mixing from the upper part of the water column. Unlike bivalves on tidal flats and mussels in rocky intertidal zones, infaunal suspension-feeding bivalves on open shallow sandy bottoms are supplied with few pelagic microalgae produced in the upper layers. The primary productivity assayed through measurements of chlorophyll a in the water column does not indicate the food supply for such bivalves. Thus, the analysis of food supply requires knowing the feeding mode of each species, their food and their distribution patterns.

Although detritus is generally considered to have low nutritive value, the stomach contents of the surf clam contained a large amount. Suspension-feeding bivalves consume a broad variety of suspended POM, including detritus (Langdon & Newell, 1990; Jorgensen, 1996; Charles, Amouroux & Grérame, 1999), and macrobenthos could depend heavily on algal detritus (De Jonge & Van Beusekom, 1992; Boon, 1999). Large mussel population could depend on the food supply for such bivalves. Thus, the analysis of food supply requires knowing the feeding mode of each species, their food and their distribution patterns.

REFERENCES


