Filter-feeding behavior of three Asian Hediste species (Polychaeta: Nereididae)

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Abstract: The three Hediste species H. japonica, H. diadroma and H. atoka (Polychaeta: Nereididae) live in burrows in estuarine intertidal flats in eastern Asia and have been regarded as surface deposit feeders. Their filter-feeding behavior was investigated in laboratory experiments where the worms were placed in a U-shaped glass tube. The behavior is basically the same among the three species and the same as that previously observed in H. diversicolor inhabiting Atlantic coasts and consists of the following four steps: (1) Moving up to the end of the tube; (2) retreating slowly down, with the anterior body expanded laterally and moving from side to side in semicircles, making a transparent, funnel-shaped mucous net; (3) orientation of the head at 2.5–6.0 cm below the end of the glass tube, and pumping water through the net by means of active undulating movements of the body for 1–5 min; (4) moving forward and swallowing the mucous net together with the trapped particles. This behavior is accelerated by adding organic particles to the seawater. Such facultative filter feeding is judged as a unique generic characteristic of Hediste among the Nereididae and its ecological significance is discussed in relation to their estuarine habitats.

Key words: burrow, estuarine polychaete, facultative filter-feeder, mucous net, undulating movement

Introduction

Five species of the genus Hediste (Nereididae) have been described from shallow brackish or fresh waters in the North Temperate Zone: one Atlantic species, H. diversicolor (O. F. Müller) from Europe and eastern North America (Smith 1977); one east-Pacific species, H. limnicola (Johnson) from the North American western coast (Smith 1958); and three west-Pacific species from East Asia. The latter are H. japonica (Izuka), and H. diadroma and H. atoka, both described by Sato & Nakashima (2003). These species are the predominant burrowing macrobenthic fauna in estuarine ecosystems (Scaps 2002, Sato & Nakashima 2003).

Hediste diversicolor is a facultative filter-feeder, able to feed as an omnivore or predator (feeding on detritus or microorganisms deposited on the sediment surface), or as a filter-feeder (suspension-feeder). The latter habit involves consuming a mucous filter which it secretes to trap fine particles brought into the burrow by water circulation. This species shifts from predatory/surface deposit feeding to filter-feeding when the phytoplankton concentration is sufficiently high (Harley 1950, Rönn et al. 1988, Riisgård 1991, 1994, Riisgård & Larsen 1995, Nielsen et al. 1995, Scaps 2002). There is no record of filter-feeding in any other nereidid species, although obligatory filter-feeding is common in other polychaete families such as the Chaetopteridae, where the filter and pump system is quite similar to that of H. diversicolor (Riisgård 1989, Riisgård & Larsen 1995).

It is of interest to discern whether or not the other four species of Hediste, as well as H. diversicolor, show such facultative filter-feeding since only deposit feeding on the sediment surface is known for Asian Hediste species (Tsuchiya & Kurihara 1979, 1980, Sato & Nakashima 2003, Sato 2006). To investigate the presence of filter-feeding ability, the feeding behavior of three Asian Hediste species was observed in transparent glass tubes in aquaria.

Materials and Methods

Animals were collected as detailed in Table 1. The three Hediste species were identified according to the key of Sato (2004). Hediste diadroma and H. atoka are morpho-
logically very similar in sexually immature specimens, but at least in populations from Kagoshima Prefecture, they are distinguishable by the difference in the total paragnath number of group II (both right and left sides on the dorsum of maxillary ring of proboscis), i.e., more than 40 in *H. atoka*, less than 40 in *H. diadroma*, except for a few individuals with close to 40 paragnaths (Sato & Nakashima 2003). In the present study, the paragnath numbers were 47–63 in worms identified as *H. atoka*, and 23–29 in worms identified as *H. diadroma*. *Hediste japonica* is easily distinguished by the unique morphology of its parapodia (the neuropodial postchaetal ligule digitate throughout) (Sato & Nakashima 2003, Sato & Sattmann 2009).

The worms were maintained in aquaria containing sand and diluted seawater (natural seawater collected from Kagoshima Bay was diluted with distilled water to a salinity of about 27 or 17) with aeration at room temperature and fed on commercial dry fish food (Tetramin) until the period of the experiments. After a fasting period of 2 or 3 days, a worm was transferred to a U-shaped glass tube (inner diameter: 5 mm, height: 6–7 cm), which was immersed in aerated seawater (salinity as stated in Table 1) in a glass bottle (inner diameter 45 mm, height 10 cm, volume 150 mL; Fig. 1A). The behavior of the worm was observed for 90 min divided into three 30 min periods: (1) an initial period in the original condition; (2) a second period after 30 mL of seawater was replaced with the same amount of white turbid seawater used to wash 10 g of rice

Table 1. Summary of materials examined.

<table>
<thead>
<tr>
<th><em>Hediste</em> Species</th>
<th>Collection date</th>
<th>Locality</th>
<th>Salinity in aquaria</th>
<th>Date of experiments</th>
<th>No. of individuals examined (Wet-weight range)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. japonica</em></td>
<td>27 May 2007</td>
<td>Mudflats in Nanaura, Kashima, Saga Prefecture</td>
<td>27</td>
<td>10–26 December 2007</td>
<td>3 (0.2–0.6 g)</td>
</tr>
<tr>
<td><em>H. diadroma</em></td>
<td>9 November 2007</td>
<td>Sandflats about 2 km upstream from the mouth of Kotsuki-gawa River, Kagoshima City</td>
<td>17</td>
<td>12–22 November 2007</td>
<td>3 (5.2–5.9 g)</td>
</tr>
<tr>
<td><em>H. atoka</em></td>
<td>9 January 2008</td>
<td>Sandflats about 3 km upstream from the mouth of Kotsuki-gawa River, Kagoshima City</td>
<td>17</td>
<td>11–23 January 2008</td>
<td>3 (0.1–0.3 g)</td>
</tr>
</tbody>
</table>

Fig. 1. Experimental setup to observe the filter-feeding behavior of *Hediste* species. (A) Condition of the first and third periods, with a U-shaped glass tube immersed in clear seawater. (B) Condition of the second period, with white turbid seawater containing organic particles. Scale bar: 1 cm.

Fig. 2. Schematic diagram of the undulating movement of a *Hediste* worm in a glass tube. One stroke is defined as the series of movements from A to C.
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Fig. 1B; and (3) a third period following replacement of the turbid seawater with fresh clear seawater as in the initial condition. The white turbid seawater contained organic particles 1–5 μm in diameter and their aggregates, as observed and measured under a microscope. At every 5 min throughout, the pumping activity of the worm (the frequency of its undulating body movements for respiratory exchange) was determined by counting the strokes of undulation per 10 sec (Fig. 2). The series of experiments was repeated three times with an interval of at least one day for each individual at room temperature (around 20°C).

**Results**

A common pattern of filter-feeding behavior, consisting of the following four steps, was observed in all three *Hediste* species. (1) The worm moved up to one end of the glass tube, often extending its anterior end beyond the tube, and moved its anterior end from side to side in semicircles (Figs. 3A; 4A). (2) It then expanded its anterior body laterally (about 15 chaetigers) and retreated slowly down the glass tube with its anterior end moving from side to side in semicircles, making a transparent funnel-shaped mucous net (Figs. 3B, C; 4B). (3) The anterior tip of the worm was oriented 2.5–6 cm below the end of the glass tube, and it pumped water into the burrow through the mucous net by means of active undulating movements of its body for 1–5 min (Figs. 2; 4C). (4) It then moved forward, swallowing the mucous net in which particles suspended in the inhalant water had been retained (Figs. 3D; 4D–F).

For all three species, filter-feeding cycles were more frequent in the second period, when organic particles were added, than in the first and third periods without additional organic particles. Because there was no significant differ-

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**Fig. 3.** Schematic diagram of the main components of the filter-feeding behavior of *Hediste* observed in the present study. (A) Ascending and emerging from the end of the glass tube, with the anterior body performing semicircular movements. (B) Retreating slowly down, with the anterior body expanded laterally, performing semicircular movements while making a transparent funnel-shaped mucous net. (C) Orientation of the head at 2.5–6 cm below the end of the glass tube, with active undulating movements of the body. (D) Ascending while swallowing the mucous net together with trapped particles.

**Fig. 4.** Photographs showing the components of filter-feeding behavior of an individual of *Hediste japonica*. (A) Ascending beyond the end of the glass tube. (B) Retreating slowly down, with the anterior body expanded laterally. (C) Orientation of the head at the bottom of the glass tube, with active undulating movements of the body. (D–F) Ascending while swallowing the mucous net together with trapped particles. Scale bars: 1 cm.
ence in the frequencies of the filter-feeding cycles between the first and third periods in all individuals (ANOVA and Tukey HSD post-hoc tests, \( p > 0.2 \)), these data were pooled and compared with the data for the second period (Fig. 5). The mean values of the frequencies of the filter-feeding cycles in the second period (5.0–9.0 per 30 min) were 2–14 times higher than those in the first and third periods (0.5–4.3), with the differences being significant in most individuals (Wilcoxon–Mann–Whitney test, \( p = 0.02–0.03 \)). Exceptionally, in the smallest individual of \( H. atoka \) (0.1 g in wet weight, about 3 cm in body length), the filter-feeding cycle occurred only once in the second period in three separate runs of the experiment.

The time spent on each filter-feeding cycle in the second period and the length of the mucous nets were examined for 3 individuals of each of the three species (Figs. 6, 7). The time spent on a filter-feeding cycle (61–159 sec) in \( H. diadroma \) individuals with a large body size (5.2–5.9 g in wet weight, 8–9 cm in body length) was significantly shorter than that (80–274 sec) in \( H. japonica \) and \( H. atoka \) individuals with a small (0.1–0.6 g, less than 6 cm) body size (ANOVA and Tukey HSD post-hoc tests, \( p < 0.0005 \)). There was no significant difference in the time spent on the filter-feeding cycle (\( p = 0.82 \)) between \( H. japonica \) (0.2–0.6 g) and \( H. atoka \) (0.1–0.3 g). The mucous nets were 2.5–6.0 mm long with no significant difference among the three species (ANOVA, \( p = 0.16 \)) in spite of their marked difference in body size. In all three species, the time spent on each filter-feeding cycle (T sec) was positively correlated with the lengths of the mucous nets (L mm) according to the following regression formulae: \( T = 44.5 L − 13.1 \) (\( r = 0.97 \), \( p < 0.0001 \), \( n = 27 \)) for \( H. japonica \); \( T = 50.8 L − 31.7 \) (\( r = 0.97 \), \( p < 0.0001 \), \( n = 18 \)) for \( H. atoka \); and \( T = 26.2 L − 3.3 \) (\( r = 0.80 \), \( p < 0.0001 \), \( n = 26 \)) for \( H. diadroma \).

To compare the frequency of the undulating body movements (number of strokes) among the three periods, the mean number of strokes per 10 sec was calculated for each period in each individual. Because there was no significant difference in the mean frequency between the first and third periods in all individuals (ANOVA and Tukey HSD post-hoc test, \( p > 0.2 \)), these data were pooled and compared with those in the second period for each individual (Fig. 8). The mean frequency in the second period (6.3–15.1) was always higher than that in the first and third periods (3.7–10.5).
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Discussion

The present study revealed that three Asian Hediste species show the same filter-feeding behavior as the Atlantic species H. diversicolor, with an increase in both feeding frequency and pumping activity of undulating body movements in the presence of a high concentration of suspended organic particles in the ambient seawater. The behavior was basically the same among the three species, and the same as that previously observed in H. diversicolor (Harley 1950, Riisgård 1991). The lengths of the mucous nets (0.5–6.5 cm), time spent on the filter-feeding cycle (1–7 min), and undulation frequency during filter feeding (60–80 strokes min⁻¹ at 15–19°C) reported in H. diversicolor (Harley 1950, Riisgård 1991) were comparable to those in the present study (2.5–6.0 cm, 1–5 min, and 40–90 strokes min⁻¹, respectively). The shorter times of the filter-feeding cycle in large individuals of H. diadroma may be attributed to the higher efficiency with which their larger bodies pump water during filter feeding. It is unknown whether the exceptionally low activity of filter feeding in the smallest individual of H. atoka indicates a lack of the filter-feeding ability in juveniles or an experimental artifact, as the glass tube (5 mm in inner diameter) may have been too large for such a small individual to perform filter feeding.

Like H. diversicolor (Scaps 2002), the three Asian Hediste species live in a U-shaped burrow in the sediment (Sato 2004, 2006) and also feed as surface deposit omnvores. In the experimental aquaria, Hediste worms fed on commercial fish food (Sato & Nakashima 2003, present study), macro-algae (Sato 2006), and the deposits collected from the sediment surface of tidal flats and their isolated components (bacteria and protozoa, diatoms, cyanobacteria, Hediste faeces; see Tsuchiya & Kurihara 1979, 1980). Therefore, the filter feeding of the three Asian Hediste species is not obligatory but facultative, as for H. diversicolor (Nielsen et al. 1995) and is probably a generic feature of Hediste unique among nereidid polychaetes, although it has yet to be confirmed in the American species, H. limnicola.

The versatility in feeding methods of Hediste species is probably an adaptation to their habitat in temperate estuaries, where various organic particles (e.g., detritus, microalgae) exist in both sedimented and suspended forms, with the amount of each component changing both temporally and spatially (De Jong & De Jonge 1995, Little 2000, McLusky & Elliott 2004), varying between deposit- and filter-feeding according to the availability of, and ease of ingesting sedimented and suspended food resources. Variability of the feeding methods between the deposit and filter feedings is also known in other estuarine macrobenthos such as spionid polychaetes (Taghon et al. 1980, Taghon & Greene 1992), bivalves (Hughes 1969, Olafsson 1986), and such as spionid polychaetes (Taghon et al. 1980, Taghon & Greene 1992), bivalves (Hughes 1969, Olafsson 1986), and gastropods (Kamimura & Tsuchiya 2004). Stable isotope analyses of Hediste species in southern Korea (Kang et al. 2007) and northern Japan (Kikuchi & Wada 1996, Doi et al. 2005, Kanaya et al. 2008) have revealed that benthic diatoms and sediment organic matter derived mainly from terrestrial plant material constitute the major food sources, with their relative contributions varying among different estuaries and among different sites within an estuary. Kikuchi & Wada (1996) and Kanaya et al. (2008) showed that phytoplankton-derived organic matter is also a major carbon source for Hediste species (H. diadroma or H. atoka) in some areas, although only surface deposit feeding was considered in those studies. Retrospectively, their data seem to indicate the possibility that Hediste species shifted from surface deposit feeding to filter feeding where blooms of phytoplankton occurred.

Microphytobenthos (mainly benthic diatoms) is the major source of primary production in estuarine tidal flats, especially mudflats (De Jong & De Jonge 1995), constituting the most important food source for surface deposit feeders (Little 2000) and obligatory suspension feeders.

Fig. 8. Relationship between body weight (logarithmic scale) and frequency of strokes of undulating body movements in nine individuals of three Hediste species. Means and SD bars are shown for each individual of Hediste atoka (A), H. japonica (J), and H. diadroma (D). Filled circles represent data for the second period in the presence of additional organic particles; open circles are pooled data for the first and third periods in the presence of clean seawater. Differences between the second period and the pooled data for the first and third periods are significant for 7 individuals (*, Wilcoxon–Mann–Whitney test, p<0.05).
such as the bivalves *Ruditapes philippinarum* and *Macra venefirma* (Koike et al. 1989, Yamaguchi et al. 2004). Suspension of part of the microphytobenthos within the water column is maintained by the high hydrodynamic energy of estuaries (including tidal currents and wind-generated waves; Baillie & Welsh 1980, De Jonge & Van Beusekom 1992, 1995, Lucas 2003). It is therefore probable that *Hediste* species can ingest the microphytobenthos both by filter feeding during flooding and ebbing tides, and by surface deposit feeding around the turning of low and high tide.

**References**


Tsuchiya M, Kurihara Y (1980) Effect of the feeding behaviour...