

Particle selection and feeding behaviour in two cirratulid polychaetes

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*Cirratulid polychaetes are abundant and diverse members of the benthic macrofauna and their particle collection mechanisms may strongly affect particle mixing and sediment grain size distribution in sediments. The feeding morphology differs in having a pair or many feeding tentacles and the ecological importance of both methods of food collection needs to be better investigated to understand their costs and benefits. Particle selection and feeding behaviour of a bitentaculate (*Aphelochaeta honouliuli*) and a multitentaculate species (*Timarete hawaiiensis*) were comparatively observed. Feeding behaviour observations were done with individuals with or without feeding tentacles and exposed to three different size ranges of glass beads (0–20, 40–70 and 70–110 µm in diameter). Particle selection was tested for coated and uncoated glass beads of three different size ranges in 20 specimens of each species. Feeding behaviour was similar in both species and the methods of particle collection and ingestion are described. Individuals of *T. hawaiiensis*, in which the feeding tentacles were removed, were observed collecting particles with the aid of branchiae. The multitentaculate species studied was more successful in collecting particles from greater foraging radii and at a faster rate than the bitentaculate species but the experimental design may have disfavoured the latter. Two-way ANOVA results showed that both bitentaculate and multitentaculate species significantly selected in favour of smaller particle sizes. Further studies about particle encounter, selection and ingestion are needed and may aid understanding of the phylogenetic relationships between the bitentaculate and multitentaculate cirratulids.*

Keywords: Deposit-feeding, Cirratulidae, selectivity, particle size

Submitted 2 November 2016; accepted 17 March 2017

INTRODUCTION

Deposit-feeding polychaetes collect food particles either with mucus-laden, ciliated tentacles (e.g. spionids and cirratulids) or by direct ingestion of particles with eversible pharynges (e.g. capitellids and nereidids). These two main deposit-feeding groups are often related to the ability to discriminate particles according to their size and composition. Thus, tentaculate deposit-feeders usually do not ingest sediment haphazardly as do those non-selective deposit-feeders using eversible pharynges (Rouse & Pleijel, 2011). The feeding morphology in tentaculate deposit-feeders is very diverse and Fauchald & Jumars (1979) characterized three groups of particle collection with a pair of palps, numerous tentacles or tentacular crowns. This characterization does not reflect phylogenetic relatedness but shows that similar methods of feeding mechanisms have evolved independently.

Many studies have shown that tentaculate deposit-feeders select positively for smaller particles (e.g. Jumars *et al.*, 1982; Taghon, 1982), but some species may either select for larger particles (Whitlatch, 1974; Dobbs & Scholly, 1986) or show no clear preference for particle size (e.g. George, 1964). The selection of smaller particles may actually be a result of selective loss of larger particles from the tentacles during the transport to the mouth (Jumars *et al.*, 1982), therefore, particle

selection has been better explained as the net result of particle contact, collection, and post-collection rejection (Hentschel, 1996). Self & Jumars (1978) also showed that particles might be selected on the basis of specific gravity and surface texture.

Food particles down to the range of 0–10 µm are preferred in most studied tentaculate species (e.g. Whitlatch, 1980; Shull & Yasuda, 2001). This has been explained because deposit-feeding organisms presumably digest organic matter from the sediment and there is a known inverse correlation between deposit feeder abundance and grain size resulting from the correlation of increasing grain size with decreasing organic content (Sanders, 1958). Conversely, some deposit feeder polychaetes are capable of ingesting nearly the whole range of particle sizes available that are below the morphological limit of mouth size (Jumars, 1993).

Cirratulid polychaetes may either have a pair (bitentaculate) or numerous (multitentaculate) feeding tentacles attached to the anterior region of the body. The tentacles on these two groups are morphologically identical and believed to be homologous but shifted backwards in multitentaculate species (Binard & Jeener, 1929; Brauer, 2014). Feeding tentacles in cirratulids are grooved and equipped with cilia and may either be placed ventro-laterally (as in *Dodecaceria*) or dorsally (all other genera). The method of food collection is similar to what is described for other tentaculate deposit-feeders. Particle collection is via mucous adhesives that are coupled with ciliary transport of the layer of mucus through a ventral groove down the length of the tentacle toward the mouth (Jumars *et al.*, 1982; Jumars, 1993; Dauer, 1994). Subsurface deposit feeding may be common among cirratulids

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but most species seem to be motile deposit feeders feeding from the burrow walls and also the sediment-water interface (Jumars *et al.*, 2015).

The bitentaculate and multitentaculate clades are well represented in number of genera and species although the number of described bitentaculate species has increased rapidly in the last decades (e.g. Blake, 1996; Magalhães & Bailey-Brock, 2013). The ecological importance of having a pair or multiple tentacles has never been comparatively investigated. The family Cirratulidae gives an opportunity to investigate closely related groups that possess two different feeding morphologies. The aim of this paper is to comparatively analyse particle collection and feeding behaviour in a bitentaculate and a multitentaculate cirratulid.

MATERIALS AND METHODS

Samples of a green alga containing specimens of *Timarete hawaiiensis* (Hartman, 1956) were collected from the Duke Kahanamoku Lagoon in February 2014. Muddy sediments containing the species *Aphelochaeta honouliuli* Magalhães & Bailey-Brock (2013) were collected from Waiupe Beach Park in March 2014 and processed over a 500 µm sieve. Both locations are intertidal regions on the south shore of Oahu, Hawaii. The specimens of *T. hawaiiensis* were sorted from the algae and kept alive in a 1 l glass beaker filled with filtered seawater (32 psu) and aerated. Individuals of *A. honouliuli* were kept in Petri dishes with filtered seawater (32 psu). Twenty-nine individuals of both species were selected, anaesthetized in 8% MgCl₂, cleaned of debris using a synthetic brush (round 4050R, Princeton Artist Brush Co.) and forceps and the body length, number of segments, and number of tentacles (for *T. hawaiiensis*) were measured. Tentacles were kept intact during manipulation of live worms. Each individual of *T. hawaiiensis* was then manipulated into a plastic capillary tube with dimensions 0.85 × 1.55 × 50 mm in length using forceps and a syringe. The capillary tubes used for *A. honouliuli* were cut in length to 15 mm due to the short length of the species. All specimens were kept for at least a day inside the capillary tubes before the beginning of the experiments.

Feeding behaviour observation

Nine individuals of each species (*T. hawaiiensis* and *A. honouliuli*) were cleaned from debris, manipulated into plastic capillary tubes and kept in Petri dishes with filtered seawater. The three solid Dragonite® (Jaygo, Inc.) glass bead size ranges (i.e. 20, 40–70 and 70–110 µm in diameter) were offered to three individuals each for both species and observed under a dissecting microscope at 20× magnification for *T. hawaiiensis* and at 40× magnification for *A. honouliuli*. Three individuals of each species had their feeding tentacles cut off at the base, the worms manipulated into plastic capillary tubes and observations were made using only 20 µm glass beads. Each individual was observed in five sessions of 2 min each with 10 min intervals. The first observational session was done immediately after the glass beads were offered. The number of feeding tentacles and branchial filaments protruded from the tube's aperture was noted as well as how often the anterior end was exposed outside the tube's entry. The first five individuals that were offered glass beads collected a small amount and

plugged up the entrance of the tubes. Right after that, the worms moved to the opposite entry. For this reason, before each observation, the worms were offered a small amount of the smallest sized glass beads (20 µm) and left overnight before observations began. The results are presented as mean observations and standard deviation (SD) is provided.

Bead selection experiments

To test for size-selection, three size ranges of glass beads were used: 20, 40–70 and 70–110 µm in diameter. Twenty specimens of *T. hawaiiensis* were selected according to the number of feeding tentacles rather than to its size. Immature individuals with total feeding tentacle number of 8–12 were selected. The size of these individuals ranged from 1.5–2.5 cm in length and possessed 85–115 chaetigers. Each specimen of *Timarete hawaiiensis* was placed in labelled Petri dishes (80 mm in diameter) with 20 ml of filtered seawater (32 psu). After 1 h of acclimation, it was offered a known amount of glass beads separately (dry weights: 0.05 g of 20 µm and 0.1 g of 40–70 µm and 70–110 µm) near the opening of the capillary tube. Glass bead weights were obtained by an A&D GR Series semi-micro analytical balance with minimum weighing value of 0.01 mg. A control dish was added to each round of each experiment and was given the same size and amount of glass beads but without a worm in the dish. The worms were left in a dark room with no overhead artificial light for 1 h. After the hour was up the worms were removed from the Petri dish and placed in separate holding containers. The amount of beads collected by the worms was obtained by subtracting the initial weight of the beads from the mass after the feeding bouts. This was obtained by removing the excess seawater from each dish. After removing most of the seawater, a wet weight was measured. The dishes were then placed in an Isotemp oven at 60°C for 1 h or until the remaining water had evaporated and a dry weight was obtained. The weight of remaining seawater was calculated by the difference between the wet and dry weight. The final weight of glass beads was corrected by the weight of salt from the remaining seawater in the dishes. The amount of beads collected by the worms includes the beads incorporated into the tube or to plug the tube entry and the beads ingested by the worms.

The same process using each size range of glass beads was applied using glass beads coated with TetraMin® fish food. Preparation of the coated beads involved 1 g of TetraMin ground by hand and mixed with 50 ml of filtered seawater. Five drops of the mixture was added to each amount of glass beads offered to the worms and allowed to dry overnight before use in the experiment. During the experiment, it was observed that the fish food remained adhered to the surface of the beads and not in suspension but it is unclear if the worms were sorting the food content from the glass beads or not. The same procedure was repeated for 20 specimens of *Aphelochaeta honouliuli* differing only in the amount of glass beads offered for each experiment (dry weights: 0.02 g of 20 µm and 0.05 g of 40–70 µm and 70–110 µm). The size of these individuals ranged from 0.5–0.8 cm in length and they possessed 35–58 chaetigers. The worms were placed in smaller Petri dishes (3.5 mm) with 5 ml of filtered seawater. Therefore, the feeding bouts consisted of six separate experiments (i.e. three different glass bead size ranges coated

and three uncoated) for each species containing 10 replicate worms each from a pool of 20 live worms.

The amount of beads collected by the worms by weight was transformed to percentage of collected beads, so the two species could be compared. A two-way ANOVA was performed to verify if there were significant differences within the two species in terms of bead size or coating collected by the worms.

RESULTS

Feeding behaviour in the multitentaculate *Timarete hawaiiensis*

The morphology of *Timarete hawaiiensis* described in Magalhães & Bailey-Brock (2010) showed that individuals possessed two groups of 7–9 feeding tentacles. The individuals included in these experiments had two groups of up to 3–6 feeding tentacles each since smaller individuals were chosen to fit inside the capillary tubes. Larger individuals frequently vacated the capillary tubes. Cilia are distributed along the entire length of the feeding tentacles and had an extended length of 25–29.4 μm .

Individuals of both species used all size ranges of beads to plug up the tube's entry. Feeding tentacles in *Timarete hawaiiensis* were very active and exhibited serpentine movements. Most feeding tentacles were extended anteriorly and at least two tentacles extended posteriorly (e.g. Figure 1A). Glass beads were captured by mucociliary action in the grooved region of the tentacles or interlaced by the tentacles before they were withdrawn. Food particles were not seen being transferred from the feeding tentacles to the mouth, but accumulated at the tube's entry and then they were engulfed by the eversible proboscis. Feeding tentacles were exposed immediately after being cleared of attached particles.

It was observed in nine individuals of *T. hawaiiensis* that 1–8 feeding tentacles may be used during feeding (3.53 ± 1.93 , $N = 45$), 1–5 branchial filaments were exposed during feeding activities (2.4 ± 1.34 , $N = 45$) and the anterior end was exposed outside the tube and the pharynx everted to directly collect particles up to two times during the 2 min of observation. In the three individuals without feeding tentacles, collection of particles was observed with the use of the branchial filaments. In this case, the branchial filaments waved across the bottom of the dish slightly touching the surface and particles were trapped in its mucous coating. Particles were transferred down the length of the filaments by mucociliary action or by retraction of the filaments and retention at the aperture of the tube. Larger particles (70–110 μm in diameter) were too heavy for the mucous coating and fell before being transferred to the inside of the tube. All three specimens in 15 observations collected glass beads with the aid of branchiae. Feeding tentacles were visibly regenerating from the third day after ablation and fully regenerated in 2 weeks.

Feeding behaviour in the bitentaculate *Aphelochaeta honouliuli*

Aphelochaeta honouliuli was recently described in Magalhães & Bailey-Brock (2013) but additional information on live specimens was not included. Feeding tentacles had an average of 75 μm width while branchial filaments had an average uniform width of 24.5 μm . Cilia are distributed along the entire length of the feeding tentacles and had an average length of 30 μm .

Individuals of *A. honouliuli* behave very similarly to *T. hawaiiensis* in respect to the collection of glass beads by the tentacles and accumulation of items at the tube before ingestion. The shorter length of this species inhibited feeding activities from the inside of the capillary tubes as most individuals

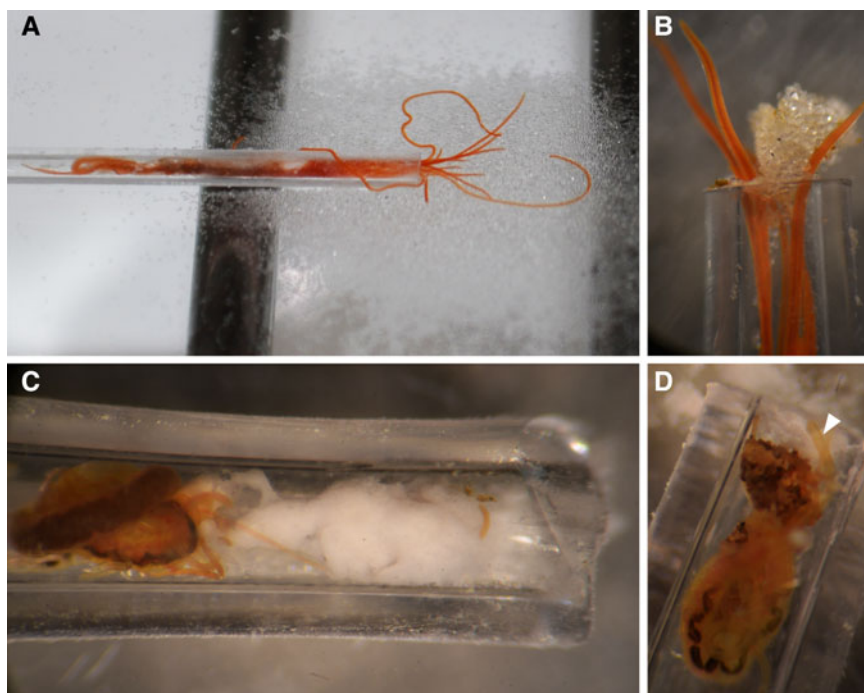


Fig. 1. (A) *Timarete hawaiiensis* during bead selection experiments showing exposed branchiae and feeding tentacles; (B) *T. hawaiiensis* with only branchiae exposed showing no feeding activity; (C) *Aphelochaeta honouliuli* immediately after bead selection experiments, showing large amount of glass beads collected; (D) *A. honouliuli* inside the tube showing one exposed feeding tentacle. Scale: Outer width of capillary tubes is 0.85 mm.

had locked the entrance of the tube and were not actively feeding. The feeding tentacles were not exposed beyond the entrance of the tubes (e.g. Figure 1D). In the nine individuals we observed, both feeding tentacles were used, 0–2 branchial filaments were exposed during feeding activities (0.64 ± 0.57 , $N = 45$) and the anterior end was exposed outside the tube and directly collected particles with the mouth only once during the 2 min observations. Feeding activities were not observed in the three individuals that had the feeding tentacles removed because all individuals remained inside the tubes. Branchiae were exposed three times (only one filament) in 15 observations and collection of particles was not observed. Short feeding tentacles were seen a week after ablation.

Bead selection experiments

ANOVA results of both species show that there are significant differences in terms of particle-size selection (Table 1). Also in both species, ANOVA did not result in significant differences in terms of selection for coated vs uncoated glass beads (Table 1). The interaction of coating vs particle size was the only significant difference for the multitentaculate *T. hawaiiensis* ($P = 0.024$).

In an average percentage of collected glass beads, both species seemed to prefer coated glass beads of sizes 20 μm (*T. hawaiiensis* with an average percentage of 37.08%, $N = 20$ and *A. honouliuli* with 5.31%, $N = 20$). Alternatively, large coated particles (70–110 μm) were the least collected by the feeding tentacles (*T. hawaiiensis* with an average percentage of 6.62%, $N = 20$ and *A. honouliuli* with 1.01%). In summary, both species favourably collected the smaller particles (Figure 2A, B).

The highest particle collection rate was observed in uncoated glass beads of sizes 40–70 μm for *T. hawaiiensis* with the lowest for coated particles of sizes 70–110 μm in *A. honouliuli* (Table 2). In general, particle collection rate was 1-fold greater in the multitentaculate species in comparison with the bitentaculate species but the amount of particles collected by the bitentaculate species may have been affected by experimental bias (see Discussion). This collection rate reflects the original amount of glass beads offered to these polychaetes and the density of the beads. Glass beads of small sizes were preferred by both species but are less heavy than larger ones, which resulted in a greater collected mass of larger beads.

Table 1. Effect of bead size and coating on bead consumption by cirratulids. Size range of glass beads and coating were used as factors and percentage of consumed glass beads per worm as variable.

Source of variation	d.f.	Mean square	F	P
<i>Timarete hawaiiensis</i> (multitentaculate) Coating	1	166.366	1.29	0.258
Size	2	5693.74	44.165	<0.001
Coating \times size	2	494.695	3.837	0.024
<i>Aphelochaeta honouliuli</i> (bitentaculate) Coating	1	0.548	0.048	0.827
Size	2	306.119	26.821	<0.001
Coating \times size	2	18.869	1.653	0.196

Differences are significant at $P < 0.05$.

DISCUSSION

Bitentaculate and multitentaculate cirratulids have a similar selective approach to food collection. The main difference between them is the number of tentacles available for particle selection and procurement. Both examined species presented similar feeding behaviours. The multitentaculate species collected a greater amount of particles with tentacles that were spread out in a complete hemisphere on the bottom of the dishes while tentacles of the bitentaculate species browsed for particles only at and around the aperture of the tube. Both species were very flexible in the number of feeding tentacles used during the observational sessions. The multitentaculate species used up to eight feeding tentacles at the same time while the bitentaculate species could use one or both. Feeding behaviour of *Timarete filigera* (as *Cirriiformia filigera*) was observed by Pardo & Amaral (2004). This species constructs temporary J-shaped tubes and feeds with up to four exposed feeding tentacles. Collection of particles is similar to what was observed in *T. hawaiiensis* and *A. honouliuli*; after a period of browsing, tentacles are withdrawn into the tubes and cleared of attached particles.

Cirratulids seem to be capable of behavioural adjustments in the case of losing the dorsal tentacles. Feeding with the aid of branchial filaments was observed a day after the tentacles were removed in *T. hawaiiensis*. Individuals of *A. honouliuli* remained inside the tube until feeding tentacles were fully regenerated. It was clear that particle adhesion to branchiae was not efficient because large particles were observed to fall off before they were withdrawn. Experimental ablation of the tentacles was done using the spionid species *Pygospio elegans* and feeding was observed by using the everted pharynxes to collect particles and retracting them coated with sediments (Jumars *et al.*, 1982). It was suggested that the value of the tentacles is to decrease the variability in selection, increase the effective feeding radius and decrease the risk of predation.

Cirratulids are considered either selective or non-selective deposit feeders (e.g. George, 1964; Wolff, 1973; Fauchald & Jumars, 1979). Whitlatch (1980) found that the digestive tracts of the bitentaculate species *Tharyx* sp. and *Chaetozone* sp. had a predominance of particles of 10 μm and 30 μm , respectively. A similar size range (16–32 μm) was also observed in the guts of the multitentaculate species *Cirriiformia grandis* (Shull & Yasuda, 2001). Pardo & Amaral (2004) report selective ingestion of fine sand grains in *Timarete filigera*. Both *T. hawaiiensis* and *A. honouliuli* presented a clear and significant preference for particles of 20 μm . These findings support the fact that cirratulids preferably collect and ingest particles of the size range 0–30 μm independently of the size of the worms and number of feeding tentacles available for particle encounter and collection.

The bitentaculate and multitentaculate worms did not significantly select particles coated with fish food. The ingestion of coated particles of 20 μm was greater than of uncoated particles but there was a very low ingestion of coated large particles. However, there were several limitations with the use of ground fish food on the coating of the glass beads. The fish food was ground by hand and the size of the particles was not accounted for and were most likely not uniform. The amount of energy content per weight of fish food offered was also not measured. It was also not observed if the

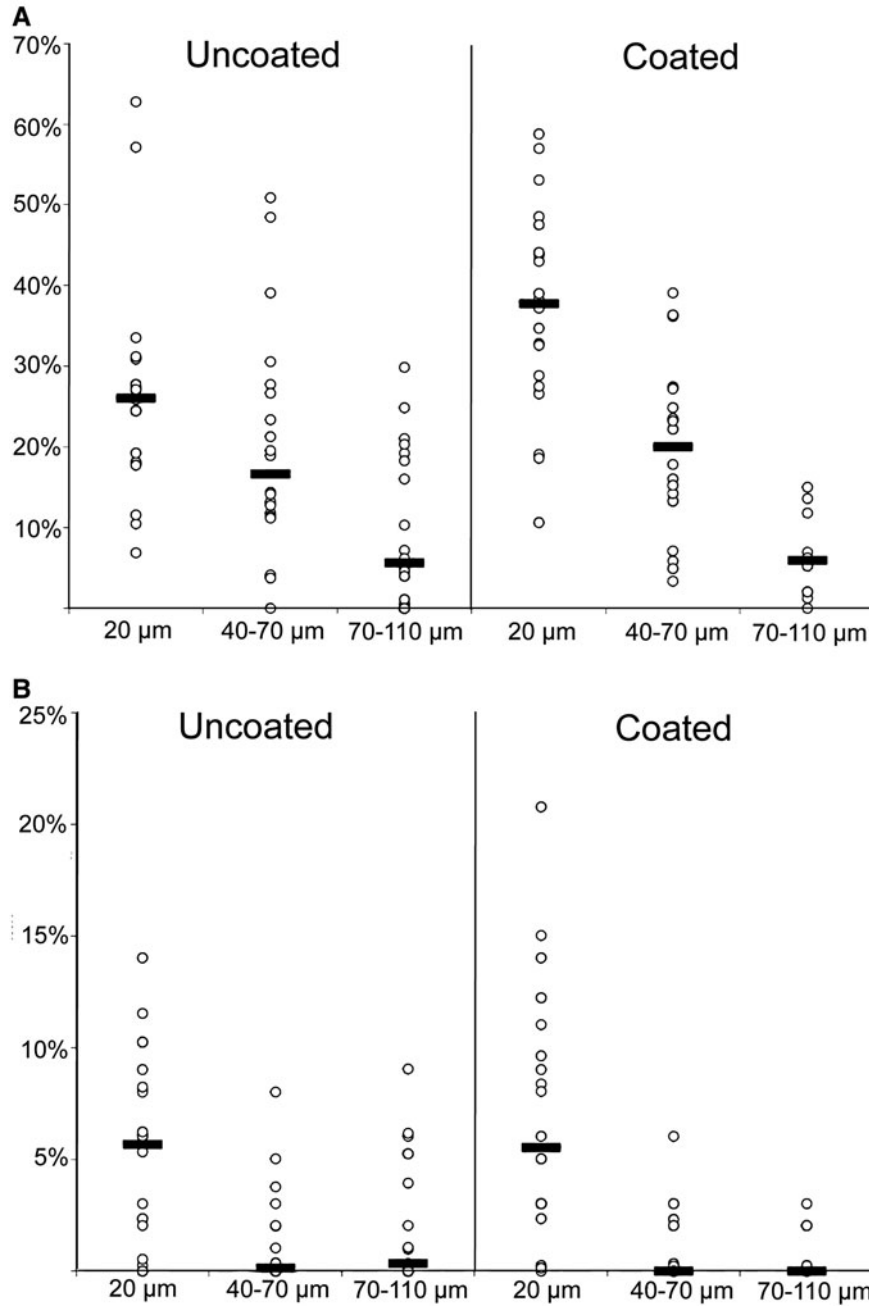


Fig. 2. Scatterplot showing percentage of collected glass beads at each size range (20, 40–70 and 70–110 μm) and coating type (coated and uncoated) (N = 20 for each species) in (A) *Timarete hawaiiensis* and (B) *Aphelochaeta honouliuli*.

worms were simply collecting the ground fish food and leaving the glass beads behind. Williams & McDermott (1997) observed for the spionid *Dipolydora commensalis* an active feeding response in regards to coated beads. Selection of high-quality items was discussed by Tagnon (1988) as not relevant in deposit feeding organisms because it may be

time consuming, therefore ingesting a greater mass of food of lesser quality is probably advantageous.

The mechanisms of deposit-feeding in tentaculate polychaetes are considered as dependent of the palp size (length and width) to model for particle contact (Whitlatch, 1989; Hentschel, 1996). Multitentaculate species would present a

Table 2. Particle collection rate in milligrams per hour for *A. honouliuli* and *T. hawaiiensis*.

Species/type particle	Uncoated 0–20 μm (mg h^{-1})	Uncoated 40–70 μm (mg h^{-1})	Uncoated 70–110 μm (mg h^{-1})	Coated 0–20 μm (mg h^{-1})	Coated 40–70 μm (mg h^{-1})	Coated 70–110 μm (mg h^{-1})
<i>Timarete hawaiiensis</i>	0.03 \pm 0.08	0.20 \pm 0.14	0.10 \pm 0.10	0.14 \pm 0.18	0.20 \pm 0.11	0.05 \pm 0.05
<i>Aphelochaeta honouliuli</i>	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.02 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01

The values are means and SD based on 20 replicates and expressed in milligrams of glass beads collected per hour.

clear advantage towards bitentaculate ones simply by the increased number of feeding tentacles. Our results showed that both bitentaculate and multitentaculate species significantly selected in favour of smaller particle sizes.

The multitentaculate species studied was advantageous in collecting particles at greater feeding radii and rate (Table 2) than the bitentaculate species. However, due to the small size of the bitentaculate species in relation to the thickness of the capillary tube used, the feeding activities of this species may have been obscured as they only collected less than 7% of the glass bead weight offered. Although a phylogenetic understanding of the cirratulids is lacking, there is a proposition that the bitentaculate clade is basal to the multitentaculate clade. The increase in number of feeding tentacles could have led to a greater feeding rate but selection of particles was observed in both clades.

Future studies regarding particle selection, ingestion rates and digestion by bitentaculate and multitentaculate species should be done to better understand the evolutionary implications of increasing or decreasing the number of feeding tentacles. Modelling deposit feeding activities can help in the understanding of the cost and benefits of both feeding morphologies.

ACKNOWLEDGEMENTS

We thank Taylor Shimabukuro and Dr Vasily Radashevsky for help with sample collection. Taylor Shimabukuro helped setting up some of the bead selection experiments. Dr P. Jumars provided valuable suggestions to a previous version of this manuscript. Two anonymous reviewers considerably improved an earlier version of this manuscript.

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