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RESEARCH ARTICLE

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The trophic linkage between zooplankton and benthic suspension feeders: direct evidence from analyses of bivalve faecal pellets

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Abstract Using radiotracer (^{14}C) and microscopic observation, we demonstrated that mussels (*Mytilus edulis* and *Perna viridis*) could be predators of mesozooplankton (rotifer *Brachionus plicatilis*). At radio-labelled rotifer densities of 0.1, 0.2, 0.5, 1.0 individual ml^{-1}, faecal pellets of mussels showed different degrees of radio signals and most of the faecal pellets were expelled 4 h after pulse feeding on rotifers. The maximum gut retention time (GRT) of ^{14}C-labelled rotifers in the digestive diverticula did not o show any significant difference between the two mussel species or the different densities of rotifers, and the averaged GRT was 43.4 ± 3.06 h (mean ± SE). At a rotifer density of 4.5 individual ml^{-1}, rotifer lorica pieces and rotifer bodies without eggs were found in faeces of *M. edulis*, while in the pseudofaeces, only complete rotifer bodies were found.

Introduction

In the benthic–pelagic ecosystem, suspension feeding bivalve populations exert crucial effects on the plankton community by filtering large volumes of water, severely depleting the phytoplankton by selectively feeding, thus altering the species composition of the phytoplankton (Officer et al. 1982; Dame 1996). Recently, more and more studies have also addressed a potential benthos–zooplankton trophic loop. Species of micro- and mesozooplankton have been shown to be cleared from suspension by both marine (Kreeger and Newell 1996; Le Gall et al. 1997; Dupuy et al. 2000; Davenport et al. 2000; Lehane and Davenport 2002; Wong et al. 2003b) and freshwater bivalves (MacIsaac et al. 1991; Wong et al. 2003a). Large zooplankton have been found in the digestive tracts of bivalve molluscs, e.g. American oysters *Crassostrea virginica* in 1888 (Savage 1925, cited in Lehane and Davenport (2002) and references therein), stomach contents of scallops *Placopecten magellanicus* (Shumway et al. 1987), and mussels *Mytilus galloprovincialis* (Jasprica et al. 1997). In a 10-week culture experiment of blue mussel *Mytilus edulis* fed both phytoplankton and zooplankton (rotifers), we have found that individuals supplied with the mixture of phytoplankton and zooplankton demonstrated the best growth performance with the largest egestion rate and largest size of faecal pellets, and the zooplankton treatment produced larger faecal pellets with positive shell growth, while the control treatment (filtered water) had smaller faecal pellets with negative shell growth (Wong and Levinton 2004). Thus, the classic model of bivalve filtering of phytoplankton may be inadequate to describe the trophic effects of bivalves on planktonic ecosystems.

Apart from the feeding experiments on zooplankton as mentioned above, the current direct evidence for this benthos–zooplankton loop is mainly from analysis of stomach contents. Using cyanobacteria, *Synechococcus*, as an autofluorescent biomarker for ciliates *Uronema* (around 20 μm), Le Gall et al. (1997) showed that ciliates could be found in the stomach and intestine of oysters, *Crassostrea gigas*. By checking stomach contents, Davenport et al. (2000) and Lehane and Davenport (2002) have shown that bivalves can consume a wide range of zooplankton species both in the field and laboratory experiments. Radiotracers have been proven to be useful techniques to confirm the benthic predator–prey relationship and trophic dynamics in food web studies, such as to demonstrate the consumption of bivalve larvae by amphipod (Ejdung and Elmgren 1998; Ejdung et al. 2000), and the transfer of cadmium, mercury, methyl-

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mercury, and zinc in an intertidal rocky shore food chain (Blackmore and Wang 2004). The aim of the present study was to see if mussels are predators of mesozooplanktonic rotifers by analyses of their faecal pellets with radiotracer technique in conjunction with microscopic observation.

Materials and methods

The experiments were performed between March and August 2002. The temperate blue mussel, *M. edulis*, was collected from intertidal localities in Long Island Sound near Stony Brook, NY, USA, and the tropical and subtropical green mussel, *Perna viridis*, a recent invasive species into Florida (Ingrao et al. 2001), was sampled from a mid-intertidal area in Tampa Bay, FL, USA. The two species were both approximately 30 mm in length. Before the experiment, all mussels were acclimated to laboratory conditions for approximately 2 weeks in a recirculating seawater system (temperature, 20°C; salinity, 31 ppt), and they were fed on INSTANT ALGAE® *Isochrysis* (Reed Mariculture Inc., Campbell, CA, USA). Rotifers, *Brachionous plicatilis*, were hatched from their cysts produced by Florida Aqua Farms Inc. (Dade City, FL, USA) in the lab, and fed on the chlorophyte *Dunaliella tertiolecta* (culture CCMP 1312). Shell length of the rotifers without amictic eggs varied from 150.8 ± 8.6 μm (mean ± SE, $n = 10$) to 255.8 ± 17.9 μm (mean ± SE, $n = 14$) and those with eggs were 338.9 ± 4.7 μm (mean ± SE, $n = 17$) (see Fig. 4a).

Analysis of ^{14}C-labelled rotifers in faecal pellets of bivalves

In order to get radio-labelled rotifers, microalgae *D. tertiolecta* were labelled with ^{14}C and then fed to rotifers. On day 1, 370 kBq of ^{14}C ($NaH^{14}CO_3$ in filtered seawater) was added to 500 ml of *D. tertiolecta* suspension with an initial concentration of $2.0–5.0 \times 10^5$ cells ml^{-1}. On day 4, the cells were uniformly labelled and rotifers were added to the labelled cell suspension. Three hours later, radioactivity (DPM, disintegrations per minute) of rotifers was measured. Each rotifer had radioactivity (DPM) of 60.77 ± 16.08 ($N = 3$) used in pulse feeding experiments of *M. edulis* and the radioactivity (DPM) was 25.07 ± 2.32 ($N = 4$) per individual rotifer for experiment of *P. viridis*. Labelled rotifers were sieved out and in order to purge any undigested ^{14}C label from the rotifer digestive tract, resuspended in unlabelled microalgae for 25 min, which is longer than the gut passage time of rotifers (Starkweather and Gilbert 1977). Depurated rotifers were trapped on a 64-μm net. Faecal pellets of rotifers and microalgae were < 64 μm in size had thus passed through the net. The microscopic observation (25×) showed that only rotifers were found in the suspension. The filtered rotifers were washed twice with filtered seawater (GF/C filter) for 15–20 min and concentrated in a 50 ml beaker containing filtered seawater. In coastal waters, the density of rotifers is usually less than 1 individual ml^{-1} (Park and Marshall 2000), four different rotifer densities, 0.1, 0.2, 0.5, and 1.0 individual ml^{-1}, were used in the present experiment with the two mussel species, *M. edulis* and *P. viridis*. For each mussel species, two individuals were used in each rotifer density treatment with four replicates for each treatment. The two mussels were put into a 1,000-ml beaker filled with 500 ml of filtered seawater (GF/C filter). Different volumes of concentrated rotifers were added to the suspension at time zero to obtain the appropriate rotifer density. The rotifer densities were then readjusted to time-zero levels 15 min later to keep a constant suspension density (Roditi and Fisher 1999). To stimulate bivalve feeding, unlabelled *D. tertiolecta* at $1.0–2.0 \times 10^5$ cells ml^{-1} were also suspended into the 500 ml filtered seawater. Mussels were removed after 30 min feeding and moved to newly filtered seawater for a 72-h depuration, during which unlabelled rotifers and newly cultured microalgae *D. tertiolecta* were fed to mussels. To generate a similar food environment for mussels after their pulse feeding, *D. tertiolecta* and unlabelled rotifers were fed to mussels during their depuration. Faecal pellets were collected at different time intervals with a pipette, as long as they were found at the bottom of beakers. The ^{14}C activity in the faeces (no pseudofaeces were produced) was determined with a Packard Tri-Carb 2100TR liquid scintillation analyser after being dissolved in solvable (NEN Research Product) and scintillant (Ultima Gold XR, Packard) was added. A blank vial with the same volume of water suspension (usually between 0.5 and 2.0 ml) was also measured to correct the final radioactivity data by subtracting the label coming from mussels' respiration and excretion in the water column. The ^{14}C activity spectrum of the faecal pellets was thus monitored during the depuration time course to show the faecal pellets egestion process after feeding on rotifers. Since most of the faecal matter was expelled within the first 4 h of depuration (see Results), the total ^{14}C activity of the faecal pellets from the first 4 h were used to investigate the relationship between mussel egestion and rotifer density. Our hypothesis was if mussels did not ingest and consume rotifers, no radioactivity could be detected in the faecal pellets. If they did, radioactivity in the faeces should have been detected and the activity produced by each treatment different from each other because mussels' filtration rates varied with different rotifer densities (Wong et al. 2003b). Gut retention time (GRT) was also calculated. Different definitions of GRT have been adopted by various authors according to the experimental design; for example, minimum gut passage times (t_0), retention half-times (t_{50}) or the time when egestion reaches a maximum (t_{max}) as the criterion, but most of the time, the time at which 90% (t_{90}) or 95% (t_{95}) of the marker passes as the GRT was used for bivalves (see details in Brillant and MacDonald 2000). Therefore, t_{90}, the time at which 90% (t_{90}) of the

^{14}C passed through the gut was referred as the GRT in the present study.

Microscopic observation on rotifers in the faecal pellets of *M. edulis*

As shown in the above experiment, at rotifer densities of 0.1–1.0 individual ml^{-1}, no pseudofaeces were found. A higher density of rotifers (4.5 individual ml^{-1}) was therefore used in this part of the experiment for direct observations on mussels' faeces and pseudofaeces after feeding and digestion on rotifers. Two 1-l beakers were filled with 800 ml filtered (GF/C filter) freshly collected seawater with two mussels (*M. edulis*) about 40 mm in length in each beaker. One beaker was designated the experimental treatment in which rotifers (4.5 individual ml^{-1}) and *Isochrysis* (6,500 cells ml^{-1}) were added, while the other beaker acted as the control with only a density of 33,000 cell ml^{-1} *Isochrysis* (approximately equals to the mass of 4.5 rotifers plus 6,500 cells ml^{-1}). Faeces and pseudofaeces were then collected in a glass Petri dish. Five percent formalin with Rose Bengal stain (final concentration of 0.01% Rose Bengal) was added to the dish. The faecal pellets were observed under a microscope and photos were taken with a Nikon D1 digital camera. The lengths of those rotifers with eggs in the suspension and those bound with mucus in the pseudofaeces were measured under a binocular microscope at 25× power with an eyepiece reticule calibrated against a stage micrometer. There was a large variation between the smaller and larger individuals in length among rotifers without egg shells (see earlier text). No comparison was done on those rotifers without egg shells found in the pseudofaeces and those in the rotifer suspension.

Statistics

As all data in the present study were normally distributed (Kolmogorov–Smirnov test), no data transformation was required before doing other statistical analyses. Two-way analysis of variance was used to determine if there was a significant difference in GRT between species or among different rotifer densities. The length difference between rotifers in the suspension and the pseudofaeces was done with *t*-test. Linear regressions were used to investigate the relationship between radioactive labels in the faecal pellets and the rotifer density (Zar 1996); Software of SPSS 10.0 for Windows (SPSS Inc., Chicago, IL, USA) was used to do the analyses.

Results

^{14}C radio signals in the faeces of *M. edulis* and *P. viridis*

The spectra of ^{14}C activity in the faecal pellets of *M. edulis* and *P. viridis* are shown in Fig. 1. It is apparent that most of the faecal pellets with radio signal were egested within the first 4 h after the pulse feeding of *M. edulis* and the radioactivity was very weak 7–8 h later. For *P. viridis*, egestion of radioactive materials also sharply decreased 4 h after feeding. There was also a small pulse peak for both species around the 25th hour. With increasing rotifer density, the ^{14}C radioactivity in the faecal pellets expelled within the first 4 h increased linearly in the two species of mussels (Fig. 2). At high rotifer density, egested materials with more radio signals were expelled after ingestion and assimilation.

The GRT of ^{14}C-labelled rotifers is shown in Fig. 3. The time varied from 35 to 55 h for *M. edulis*, and 34 to 54 h for *P. viridis*. Two-way analysis of variance demonstrated no significant difference between species ($df = 1$, $F = 0.17$, $P = 0.69$) or among different densities of rotifers ($df = 3$, $F = 2.54$, $P = 0.08$). The averaged GRT was 43.4 ± 3.06 h (mean ± SE).

Rotifers in the faeces and pseudofaeces of *M. edulis*: direct evidence from microscopic observation

In the treatment beaker, rotifer lorica pieces (Fig. 4b) and dead bodies (Fig. 4c) were found in the faeces. The morphology of faecal pellets with rotifer body or lorica pieces was different from those produced by mussels in the control beaker (without rotifers but microalgae) with darker colour and faecal material was distributed more evenly (Fig. 4d). No pseudofaeces were found in the control beaker (without rotifers); while in the experimental beaker (with rotifers), pseudofaeces with or without rotifer bodies could be seen. Pseudofaeces were bound in mucus (Fig. 4e) and rotifers (without eggs or with egg shells) were also usually mucus-bound (Fig. 4f). It was impossible to determine whether those rotifers without eggs in the pseudofaeces originally had eggs or not, because rotifer bodies and eggs might have been broken into two parts by the feeding apparatus, such as gill filaments, before being rejected as pseudofaeces. The rotifers with egg shells in the pseudofaeces were around 297.3 ± 8.2 μm ($n = 4$) and their lengths were significantly shorter (*t*-test, $P < 0.001$) than those rotifers with eggs in the suspension (338.9 ± 4.7 μm; see Fig. 4a). Compared to those rotifers with eggs in the suspension (Fig. 4a), the rotifers in the pseudofaeces only showed egg shells (Fig. 4f). This was probably due to the fact that the thin shell of the rotifer amictic egg was not solid enough to sustain the physical processing force from mussel's feeding organs, such as gill and palp.

Discussion and conclusions

The radio signals found in the faecal pellets and the increase of radioactivity with radio-labelled rotifer density demonstrated that mussels did ingest and

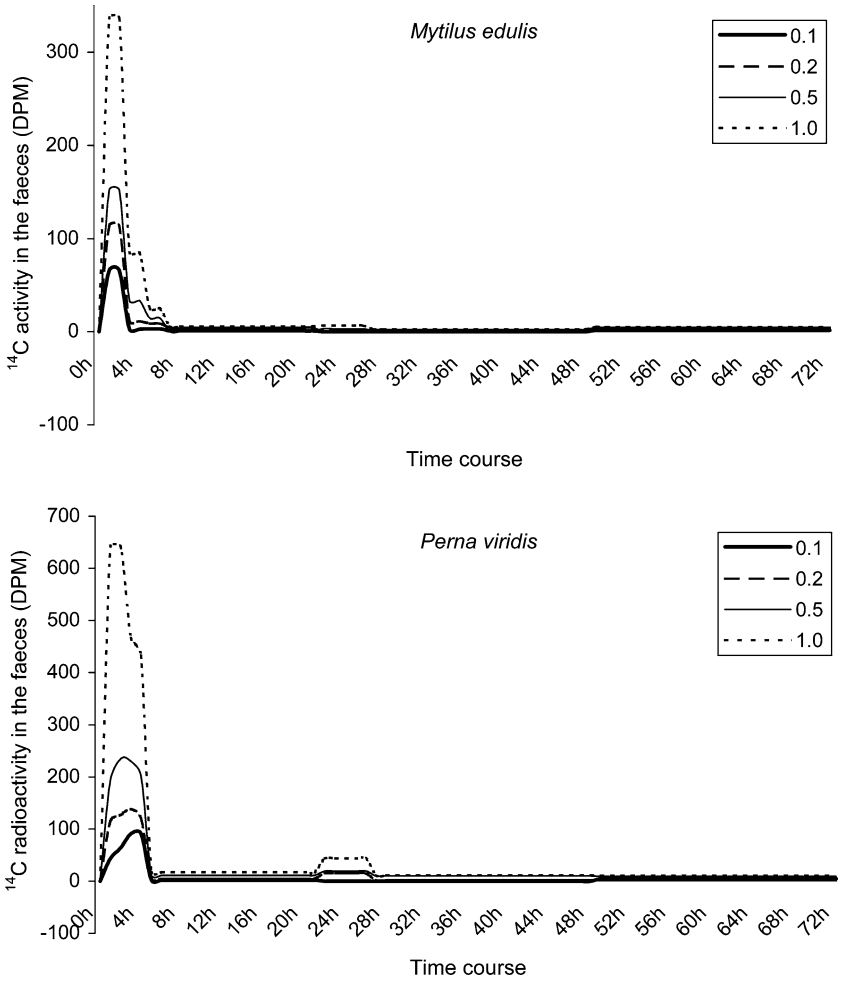

Fig. 1 ^{14}C radio spectra in the faecal pellets of *M. edulis* and *P. viridis* during the 72 h depuration

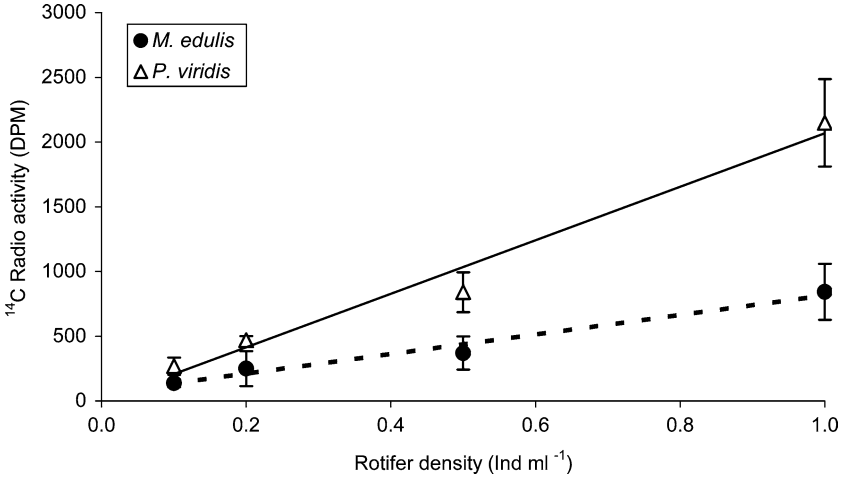

Fig. 2 ^{14}C radio activity of the faecal pellets in the first 4 h of depuration (*M. edulis*: $Y = 758.7x + 58.56$, $R^2 = 0.98$, $N = 4$, $P < 0.01$; *P. viridis*: $Y = 2065.9x + 1.96$, $R^2 = 0.98$, $N = 4$, $P < 0.01$)

consume rotifers, which provided direct evidence of a benthos–zooplankton loop in aquatic ecosystem (Wong et al. 2003a, b). Both mussels had higher ingestion and absorption rates on rotifers with increasing of rotifer density (Wong et al. 2003b), more radio signals from the faecal pellets in the present study showed that mussels also had higher egestion rates at a higher rotifer density. The GRTs found in the present study are among the longest reported on most bivalve species fed with other food items such as phytoplankton (Table 2 in Brillant and MacDonald 2000), which may be related to the digestive strategy of mussels. Rotifers are animals with solid rotifer loricae, which make them hard to be digested. Mussels have to spend more time to ingest and

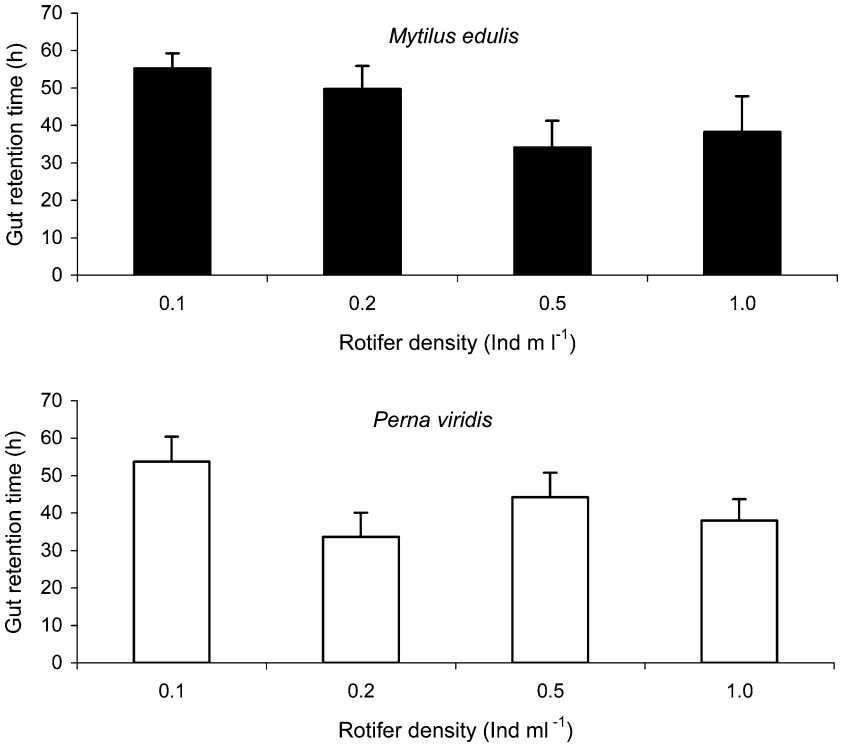

Fig. 3 Gut retention time (h) of *M. edulis* and *P. viridis* at different rotifer densities

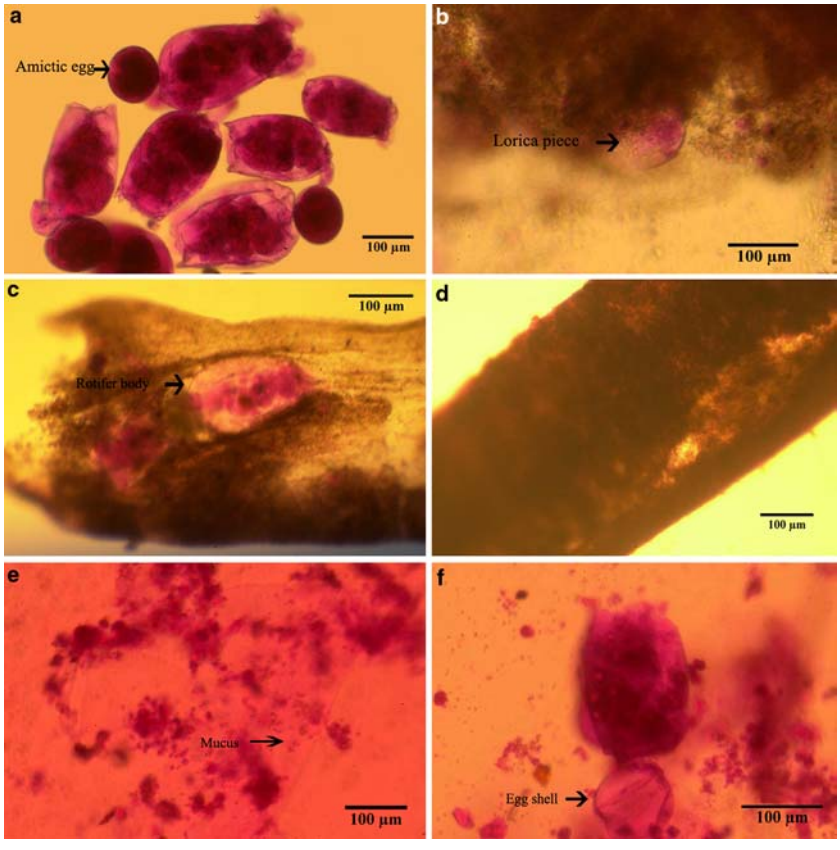

Fig. 4 Microscopic observation on the faeces and pseudofaeces produced by *M. edulis* (stained with Rose Bengal). **a** Normal living rotifers in the suspension. **b** Rotifer lorica piece in the faeces. **c** Rotifer in the faecal pellets. **d** Faecal pellets of *M. edulis* fed with microalge *Isochrysis*. **e** Pseudofaeces produced by *M. edulis*. **f** Rotifer with amictic egg in the pseudofaeces

assimilate nutrients from them. The rotifer lorica fragment and complete rotifer body found in the faecal pellets further confirm this point (Fig. 4b, c). It has been shown that larger organic particles are more likely to be retained, which would give more time for extracellular digestion to act, increasing the chances that the particles

will enter the digestive gland for intracellular digestion (Brillant and MacDonald 2000). The two mussel species we have studied show a similar egestion pattern characterized by a big pulse in the first 4 h and a small one around the 25th hour. It is therefore assumed that the big peak signifies the intestinal faecal pellets, while the small pulse should be the glandular faeces. A similar egestion pattern was also found in scallops fed on microalgae (Brillant and MacDonald 2000). It is obvious that most of the rotifers entering the digestive system were ingested after the first 4 h of filter feeding.

It is assumed that the loricae of rotifers are too hard to breakdown during extracellular and intracellular digestion since the lorica pieces and complete rotifer bodies were found in the faecal pellets. MacIsaac et al. (1991) also reported that loricae of rotifer *Keratella* had been observed in the digestive tracts of zebra mussel *Dreissena polymorpha*. Lehane and Davenport (2002) reported that the degree to which the zooplankton bodies were intact varied with species. There was no evidence of *Artemia* in the intestinal tract of mussels 40 min after their ingestion (Davenport et al. 2000), while in the stomach of bivalves *M. edulis, Cerastoderma edule, Aequipecten opercularis*, copepods with missing or broken antennae, uropods and the furcal rami, complete cladocerans with limbs intact, crustacean nauplii, metanauplii, and barnacle larvae with no damage, lamellibranch larvae completely undamaged by the ingestion/digestion process were found (Lehane and Davenport 2002). Sometimes, living undigested algae in the faeces of the bivalves were present under natural conditions (Haven and Morales-Alamo, 1966). In the present study, no living rotifer was found in the faeces or pseudofaeces. The opportunity for rotifers to survive after being rejected as pseudofaeces or after being egested as faeces is very small. In the former case, rotifers did not go through intestine, but may have been damaged due to the physical contact with the mussel filtration apparatus. The abnormal morphology of rotifers in the pseudofaeces of *M. edulis* shown in the present experiment confirms this point. More importantly, these rotifers are mucus-bounded. The mucus is the hydrated form of secretions produced by mucocytes within epithelia. Since the secretions consist of polysaccharides units with different degrees of viscosity, it would be difficult for those damaged rotifers to escape from the mucus. Rotifers in the pseudofaeces incorporated together with the mucus may not be completely dead, but must have been damaged severely to a point where they could not survive much longer. For example, no mucus-bound *Artemia nauplii* were seen to break free from the adhering mucus, even if left for 24 h (Davenport et al. 2000). In the later case, rotifers found in the faecal pellets were most likely primarily damaged by the gill and labial palp before entering the digestive system exposed to extracellular and intracellular digestion. They must have therefore died before being expelled in the faecal pellets, particularly during the longer ingestion/digestion processing in the digestive system (e.g., the longer GRT). Davenport et al. (2000) reported that inhaled mesozooplankton, particularly crustaceans, would be killed either by ingestion or by incorporation into pseudofaeces.

The active swimming behaviour of the ciliate *Uronema* allows some of the experimental animals to escape the strong inhalant current of the bivalves (Le Gall et al. 1997). Although a few rotifers could escape from inhalant current of bivalves far away from the valve through our routine microscope (lower-power) observation, we did observe directly that most of the rotifers could be removed from the water column by mussels, and those 'swallowed' could not escape from the inhalant stream once entrained. In most cases, we witnessed that there was a wider valve gape when the rotifer suspension was added compared to when there was only microalgae in the suspension. When studying the escape responses of copepod nauplii in the flow field of the blue mussel, *M. edulis*, Green et al. (2003) concluded that larger mussels are capable of capturing larger zooplankton and the maximum zooplankton size captured scales with the square root of the linear dimension of the mussel. Our preliminary videoscopy also showed that rotifers (10 individual ml^{-1}) could be transported along the gill filaments with the ventral flow, though some of them could escape capture by mussel latero-frontal cilia.

Current evidence suggests that mussels and other bivalve can discriminate between microalgae and non-nutritive particles (Ward et al. 1997, 1998; Brillant and MacDonald 2000) but new studies are needed to elucidate the degree of discrimination between phytoplankton particles and zooplankton of varying body size, mobility, and digestibility.

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