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Fine sediment effects on feeding and growth in the invertebrate grazers *Potamopyrgus antipodarum* (Gastropoda, Hydrobiidae) and *Deleatidium* sp. (Ephemeroptera, Leptophlebiidae)

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Abstract

The influence of fine sediment (<63 μm diameter) upon the assimilation rates of the snail *Potamopyrgus antipodarum*, and the mayfly *Deleatidium* sp. were determined by allowing individuals to feed upon ^{14}C radiolabelled periphyton which had been contaminated with varying quantities of sediment (sediment:food ratios of: 0:1, 1:1, 5:1, 10:1, 50:1, 100:1 [dry weight]). For both grazers, the assimilation rate falls in direct proportion to the sediment fraction in the (sediment+food) matrix. In a second experiment the growth of *P. antipodarum* was monitored over 3 months when fed organic matter that had been contaminated with fine sediment at ratios of 0:1, 1:1, 5:1, 10:1, 50:1, 100:1, 500:1. In contrast to the monotonic relation between sediment and short-term assimilation, growth rates (mm shell height d^{-1}) were highest at intermediate levels of sediment contamination (5:1 and 10:1 by dry weight) and lowest in the treatment with no sediment added. Growth rates were significantly lower, and mortality high, at sediment:food contamination ratios above 50:1. The reasons for the contrast between the results from the short-term and the long-term experiments are unknown at present, but the fact that snail growth was greatest at intermediate levels of sediment contamination might indicate that they derive trace nutrients from ingested sediment.

Introduction

Increased sediment loads in aquatic ecosystems often follow land-use changes and human activities such as agriculture, forestry-cutting, mining and urbanisation. For example, during a 3-year period of quarterly monitoring at the Whatawhata hillcountry Agricultural Research Station (west of Hamilton, North Island, New Zealand), epilithic DW:AFDW ratios have varied between 3:1 and 10:1 (exceeding 6:1 in only four of 27 samples) in intact or regenerating native forest reaches, whilst in otherwise similar pasture streams they have ranged between 3:1 and 82:1, exceeding 6:1 in 22 of 48 samples). Similarly, Davies-Colley et al. (1992) report that epilithic DW:AFDW ratios ranged between 3:1 and 10:1 above the points at which several gold mines discharged their sediment rich (non-toxic) waste-water, but between 10:1 and 20:1 below the discharges, and Quinn et al. (1992) report that macro-invertebrate (dominated by insecta) taxonomic diversity and abundance were both substantially lower at the downstream sites.

High sediment loads, particularly the deposition of fine sediments, have adverse effects on fish through clogging of gravel spawning grounds (Sear, 1993), and reducing feeding success in turbid streams (Rowe & Dean, 1998). Similarly, increased sediment loads may reduce the abundance and diversity of invertebrates by smothering interstitial habitat and reducing periphytic

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abundance or quality (Lloyd et al., 1987; Newcombe & MacDonald, 1991; Ryan, 1991; Wood & Armitage, 1997).

Fine substrates have been found to be unsuitable habitat for most New Zealand aquatic insects (Quinn & Hickey, 1990; Jowett et al., 1991; Death, 2000). Some New Zealand invertebrate species, notably *Deleatidium* spp. (Ephemeroptera, Leptophlebiidae) and *Pycnocentrodes* sp. (Tichoptera, Conoesucidae) show preferences for 'clean' rather than silted periphyton (Ryan, 1991) and, in colonisation trials, Ryder (1989) showed that the occurrence of fine sediment in the algal matrix reduced invertebrate densities by about 30%. Consequently, changes in the pattern of sediment deposition as a result of landuse change may modify the impact that invertebrate grazers have upon their periphytic prey. The Hydrobiid snail *Potamopyrgus antipodarum* is often dominant in the macroinvertebrate communities in low-order pasture streams throughout New Zealand, yet is it rare in otherwise similar afforested catchments in which the 'sensitive' Ephemeropteran, Plecopteran and Trichopteran taxa usually dominate (Quinn & Hickey, 1990). Of these latter taxa, the Leptophlebiid mayfly *Deleatidium* sp. is often the most abundant species, and this has been shown to be unable to separate food from silt prior to ingestion and to be less abundant on sediment-rich epilithic tiles than on sediment-poor ones (Ryder, 1989; Ryan, 1991). In contrast *P. antipodarum* was more abundant on the impacted tiles (Ryder, 1989) and has been shown to take (small) sediment particles into the buccal cavity, scrape the encrusting organic matter off and finally 'spit' the sediment particle out (Lopez & Kofoed, 1980).

These various lines of evidence suggest that *P. antipodarum* may be more tolerant of sediment contamination in its food than *Deleatidium* sp. are. We seek to determine whether this is so by: (a) determining the manner in which the assimilation rate is related to sediment contamination level in the two species, and (b) determining the long-term growth rate of *P. antipodarum* at a variety of sediment:food ratios.

Methods

Snails were collected from a stream draining pastoral land in the AgResearch Whatawhata Research Centre, west of Hamilton, New Zealand in December 1999, and the mayflies were collected from the same site in late January 2000. On each occasion, the invertebrates were brought back to the laboratory and held in aerated water in a 20 °C (near ambient for the local pasture streams at this time of year) controlled temperature room under permanent darkness until required. The invertebrates were provided with a combination of epilithon-encrusted stones together with fresh (largely watercress, *Nasturtium officinale*) and decaying vegetation (*N. officinale* and remains of allochthonous material such as bankside grasses) that were taken from the reach where the invertebrates were collected, as food sources.

A stock of sediment was obtained from a landslip site within the Whatawhata Research Centre prior to the experiment. This was washed through a series of sieves. Sediment which passed through a 63 μm sieve was retained and concentrated to a slurry by evaporation. The sediment content (measured as dry weight, DW) of this slurry was determined by drying a known volume at 100 °C overnight in a preweighed dish.

Assimilation experiment

Individual snails (*Potamopyrgus antipodarum*) and mayflies (*Deleatidium* sp.) were fed excess ^{14}C radiolabelled periphyton contaminated with varying quantities of fine sediment and the quantity of periphyton assimilated over a period of 12–14 h was measured. Periphyton was harvested from thick, senescent mats in December 1999. These had been growing under direct sunlight in artificial stream channels at the Whatawhata Research Centre for 2 months. The harvested periphyton were maintained as a slurry within gently stirred, ventilated aquaria until required. Sediment originally present within the harvested periphyton quickly settled to the bottom of the aquaria. Sub-samples of the slurry were drawn from mid-depth as required. The taxonomic composition of the periphyton was not examined but it was dominated by unicells. In an earlier, summertime experiment in these stream channels, Quinn et al. (1997) found that unicellular diatoms dominated the unshaded channels (77% by cell numbers), filamentous diatoms made up a further 15%, *Lyngbya* made up 4%, *Spirogyra* 2%, and other unicellular greens made up the remaining 2%. Filamentous algae were present in small quantities in our stock slurry, but would have been rare in the realised food preparations because they are not readily drawn into pipettes used during the various sub-sampling procedures described below.

The concentration of the periphyton slurry was determined by filtering two replicate 1 ml samples onto

pre-weighed glass fibre filters and drying these at 100 °C overnight. The ash free dry weight:dry weight (AFDW:DW) ratio of the periphyton was also established on one occasion by subsequent combustion at 400 °C overnight and reweighing of the filters.

Periphyton for each grazing trial was prepared as follows. A subsample was drawn from the periphyton slurry and incubated at 20 °C with ^{14}C bicarbonate (~0.1 μCi l^{-1}) under fluorescent light (~150 μE m^{-2}) and held in suspension using a magnetic stirrer for approximately 12 h. Excess free label was always present at the end of incubation. After incubation, the labelled suspension was drawn off and the periphyton centrifuged at 3000 rpm for 5 min and then resuspended in deionised water. This procedure was repeated three times in order to minimise the quantity of unincorporated radiolabel associated with the periphyton (preliminary trials indicated that this reduced the activity in the supernatent to <5% of that after the first spin (i.e. of the levels at the end of the incubation period), with little further reduction thereafter). Finally, four replicate samples of 2 ml were drawn from this 'clean' periphyton solution. Two were used to provide confirmatory measurements of the periphyton concentration (filtered and dried), and two were used to derive estimates of the radioactivity in the periphyton. These latter samples were placed in scintillation vials together with scintilant cocktail (Optiphase 'HiSafe') and counted in a Wallac 1409 liquid scintillation counter.

An appropriate quantity of the 'clean' suspension of labelled periphyton was then pipetted into 120 ml alkathene, screwtop containers in order to yield a food density of (approximately) 60 g DW m^{-2}. Appropriate quantities of the sediment slurry were also added in a similar manner in order to yield six different sediment:food ratios. These were 0:1, 1:1, 5:1, 10:1, 50:1 and 100:1 (by DW). Twelve replicates of each treatment were established. The containers were then topped up with filtered stream water and stirred. After the sediment/periphyton mix had settled out, a single grazer of known size (*P. antipodarum*: 5–9 mm shell height; *Deleatidium*: 4–7 mm body length) was added to each container. Two of these individuals were dead (killed with scalding water) and operated as controls. Each container was sealed using a fine plastic mesh and ventilated using a whisker bubbler (Hickey & Vickers, 1992) and the grazers incubated at 20 °C under lower intensity (~50 μE m^{-2}) fluorescent light for 12–14 h. At the end of this period each grazer was transferred into a clean container and left to empty its gut for 1–3 h. Grazers were subsequently removed and thoroughly cleaned of any adherent algae by rinsing with deionised water (*Deleatidium* sp) or scrubbing with a toothbrush and rinsing with deionised water (*P. antipodarum*). The individuals were subsequently killed by placing it in scalding water.

Each dead individual was placed in a scintillation vial with 0.5 ml of NCS-II tissue solubiliser and left for a minimum of 24 h. The small size of *P. antipodarum* makes it difficult to remove all of the soft tissue parts from the shell reliably, and so the snails were simply crushed in their shells before the solubiliser was added. After digestion, the radioactivity in each grazer was counted using the scintillation counter.

Passive uptake of bicarbonate-^{14}C by the snail shell was discounted by subtracting the mean ^{14}C-count of the two control (dead) snails in each treatment from the counts for each live snail in the treatment. Thus, (for both *P. antipodarum* and *Deleatidium* sp.) individual assimilation rates was calculated as

$$A_i = 24\frac{\mathrm{DPM_{grazer}} - \mathrm{DPM_{control}}}{H - \mathrm{DPM_{periphyton}}}, \qquad (1)$$

in which A_i denotes the grazer's assimilation rate (g periphyton AFDW d^{-1}), $\mathrm{DPM_{grazer}}$ denotes the decay counts in the grazer (decays per minute), and $\mathrm{DPM_{control}}$ denotes the average of the counts in the two dead (control) grazers from this food density treatment. $\mathrm{DPM_{periphyton}}$ denotes the decay counts per minute per g AFDW of periphyton, and H denotes the duration of the experiment (h).

Snail shell heights were measured with digital calipers (0.01 mm) prior to the beginning of an experiment. Mayfly body lengths were measured after death. Lengths were converted to weights using established weight–length relationships (Towers et al., 1994) and the individual assimilation rates were expressed as biomass-specific rates. In the case of *P. antipodarum*, this is based upon the $CaCO_3$-free weight (assuming this to represent 78% of the whole animal DW, Towers et al. (1994)) of the snail to allow comparison with *Deleatidium* sp.

Growth experiment

Individual *P. antipodarum* were raised on a diet consisting of excess organic matter contaminated to varying degrees with fine sediment and their growth was monitored over a period of almost 3 months. Commercial chicken feed (Harvey Farms Stock Feed

'Pro-Lay') was used as the food source in place of periphyton as its supply and quality could more easily be maintained throughout the experiment. The feed characteristics are as follows: minimum crude protein=14.5%, maximum crude fat=5.5%, maximum crude fibre=6.0% (by weight). It's principal ingredients are maize, barley wheat, legumes and milk products, but meat, blood, bone, vitamins, limestone, and minerals are also included.

Seven treatments (ratio of sediment DW to food DW) were established. These ratios were: 0:1, 1:1, 5:1, 10:1, 50;1, 100:1 and 500:1. Sediment was obtained as described above. The food was added to a fresh container with a small quantity of water and broken up. An appropriate quantity of sediment slurry was then added and the container filled. The suspension was then stirred and allowed to settle before the snail was added. Snails were provided with fresh food (0.1 g DW per snail) at fortnightly intervals. This quantity of food had previously been established to be in excess of requirements (unpublished data).

Twenty snails were randomly allocated to six of the treatments, but space limitations allowed only 10 individuals to be used in the seventh (500:1) treatment. Each snail was held in an individual 120 ml alkathene container, aerated by means of a whisker bubbler (Hickey & Vickers, 1992), and all were held within the 20 °C room under permanent darkness.

Snail shell heights were measured at fortnightly intervals for 12 weeks from 23 December 1999 to 3 March 2000. After being measured, each snail was transferred into a fresh container (prepared as described above). Proliferation of microbial growths within each container was limited by scraping the sides of the containers with a cloth in each of the intervening, alternate weeks. The mean initial length of those snails that survived until the end of the experiment in each treatment did not differ significantly (ANOVA, P=0.07, $F_{6,90}$=2.01, overall mean=2.03 mm, sd=0.35 mm) and growth continued in an approximately linear fashion throughout the experiment. Therefore, growth rates were calculated as the length increase per day and compared between treatments with ANOVA and Tukey's post hoc test for the difference between means. All statistical analyses were performed in Systat® 7.0 and DataDesk® 6.0.

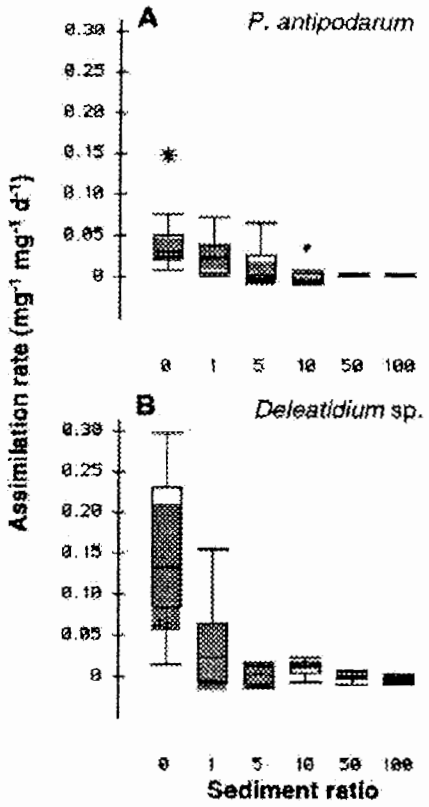

Figure 1. Box plots of the measured weight specific assimilation rates (mg algal DW mg^{-1} grazer DW d^{-1}) against the sediment ratio to one part food (DW:DW) for (A) *P. antipodarum* and (B) *Deleatidium* sp. In (1B), one outlying datum was not illustrated (assimilation rate=1.9 mg mg^{-1} d^{-1} at zero sediment) although included when generating the box-plot, as the *y*-axis has been restricted to facilitate comparison with (1A). In both plots, the box depicts data between the 25 and 75% quartiles. The line across the box displays the median value. The whiskers depict the extent of the main body of the data. Extreme values are plotted with a diamond. Very extreme data values are plotted with a starburst. The shaded area superimposed on each box is a 95% confidence interval around the median (Datadesk® 6.0).

Results

Assimilation experiment

Assimilation rates for *P. antipodarum* and *Deleatidium* sp. declined with increasing sediment content in the food mix (Fig. 1). One outlying point is not plotted in Figure 1B. This corresponds to an individual mayfly that had an assimilation rate almost 10 fold greater than all others (1.9 mg mg^{-1} d^{-1}). It seems likely that residual labelled algae remained adherent to this indi-

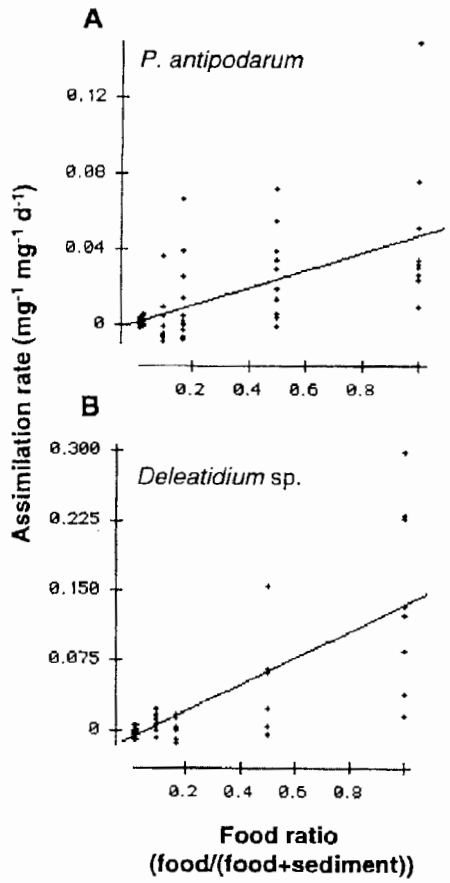

Figure 2. Assimilation rate vs. food-sediment content for (A) *P. antipodarum* and (B) *Deleatidium* sp. The solid lines are the least-squares linear regression curves.

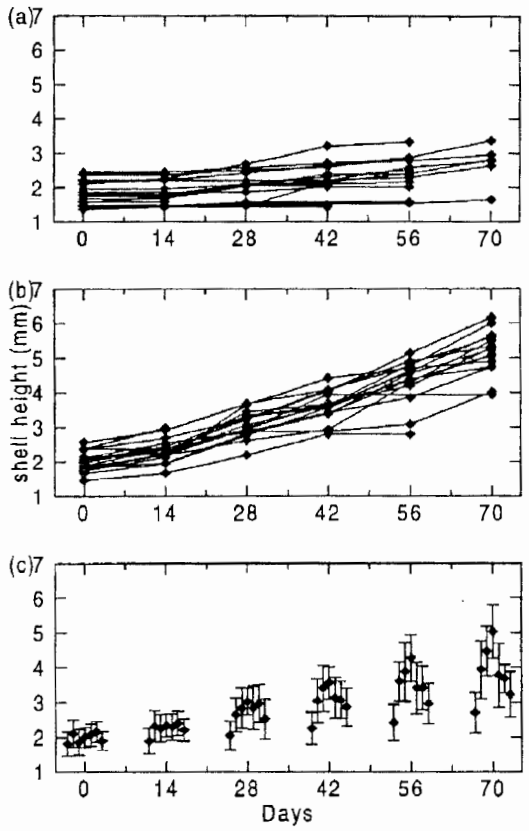

Figure 3. (a) Individual growth trajectories in the worst-performing (0:1 sediment:food) treatment, (b) Individual growth trajectories in the best performing (10:1 sediment:food) treatment, and (c) Mean growth trajectories (±1 sd) in each treatment. Treatment means for each sampling date are offset from one another to aid legibility. The treatments are arranged left-to-right in ascending order of sediment ratio (0:1, 1:1, 5:1, 10:1, 50:1, 100:1, 500:1) on each sampling date.

vidual after rinsing. This datum was included for the purposes of generating the box-plot in Figure 1B, but has been excluded from subsequent analyses. Plots of the assimilation rate against the ratio (Food DW/(Food DW+Sediment DW)=$F/(F+S)$) show little or no evidence of non-linearity (Fig. 2). Indeed, the slope of this line is almost exactly equal to the mean assimilation rate at zero sediment contamination. There is considerable scatter about this line, particularly at high food contents (low sediment content). We cannot account for this scatter. It could not be reduced by excluding grazers which showed low activity levels during the post-feeding (i.e. gut emptying) phase of the experiment, or on the basis of individual size.

Growth experiment

Contrary to expectation, within each treatment, growth was approximately linear with respect to time (Fig. 3) rather than being asymptotic. The largest snails reached a final size of approximately 7 mm, and even these showed no sign of slowing growth. Given the linear growth pattern, we determined the growth rate as: [(final size−initial size)/experimental duration] for those snails which survived to the end of the experiment. By this measure, sediment contamination had a significant impact upon the long-term growth of snails ($P<0.001$, $F_{6,90}=15.7$; Fig. 4). Surprisingly, mean growth rates (mm d^{-1}) were highest at intermediate

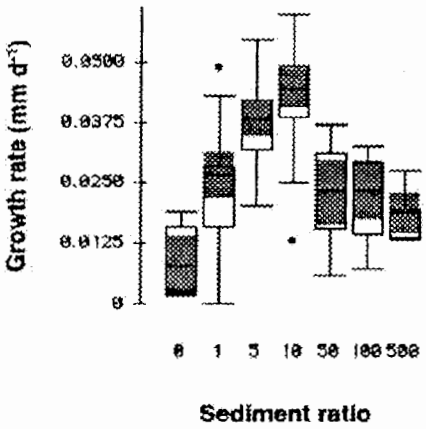

Figure 4. Box plots of the distribution of growth rates (length increase mm d^{-1}) for *P. antipodarum* in each sediment treatment. Refer to Figure 1 for explanation of symbols.

sediment contamination levels (0.04 mm d^{-1} in the 5:1 and 10:1 sediment treatments) and lowest in the treatment with no sediment added (0.01 mm d^{-1}) and the treatment with the highest sediment contamination (500:1, 0.02 mm d^{-1}). Growth at sediment:food ratios of 50, 100 and 500:1 were significantly lower than those at intermediate sediment contamination levels, suggesting a threshold level of sediment contamination above which growth is impaired. This unimodal pattern is also reflected in the mortality of snails: less than 60% of the snails in the 0:1 and 500:1 treatments survived, while 85% or more of those in the 1:1, 5:1 and 10:1 treatments survived.

Discussion

Our measurements of assimilation were made over a comparatively long period (12–14 h). It is possible that the ^{14}C content of the periphyton changed over this period (through respiration and photosynthetic fixation of unlabelled CO_2. Algal respiratory rates are usually in the range 1–5% d^{-1}, implying a rather small error over the term of our experiment, however, photosynthetic rates can be up to 2 d^{-1}. Fortunately, such high rates would not have occurred in our experiment. The light levels (~50 μE m^{-2}) at the water surface are unlikely to have been saturating and self-shading would have been very strong at the algal density (60 g DW m^{-2}) used in our assimilation experiments. Furthermore, in all but the zero sediment treatment, most algae would have received almost no light because they would have been further shaded by the sediments with which they were mixed. Thus, we believe that the biases associated with photosynthetic fixation of non-labelled CO_2 during the course of the experiment would also have been minimal.

The short term feeding experiments provide evidence that fine sediment has an adverse influence upon the rates at which *P. antipodarum* and *Deleatidium* sp. assimilate food. The assimilation rate declines in inverse proportion to the total dry weight of the food-sediment mix. Given that the same quantity of periphyton was added in all treatments, this implies that these two grazers are unable to selectively ingest periphyton when this is contaminated with fine sediments. Rather, they ingest the matrix of periphyton and sediment indiscriminantly, and their assimilation rate falls merely because the organic content of this matrix is increasingly 'diluted' by the sediment contamination. Ryder (1989) also found that the ratio of organic matter to sediment in the guts of *Deleatidium* sp. reflected the ratio in the substrates upon which they were feeding. Thus, there seems little doubt that this species cannot preferentially ingest organic material in favour of associated inorganic fines. Nor is it able to compensate for the 'dilution' of the ingested organic material by contaminants by increasing the ingestion rate or the assimilation efficiency.

Ryder (1989) also concluded that the caddisfly *Pycnocentrodes* sp. is unable to reject inorganic particulates associated with its periphytic food, and he also found that their growth rate was slowed. The chironomid *Stictochironomus annulicrus* has also been reported to feed non-selectively and suffer impaired growth when sediment contaminates their food (Mattingly et al., 1981). Thus, in the case of aquatic insects, the relationship between growth and sediment appears to be negative over the full range of sediment ratios.

In contrast, there is substantial evidence that snails benefit from the presence of low-moderate quantities of sediment in their diet. Storey (1970) found that *Lymnaea peregra* growth was maximal at intermediate levels of sand contamination, and James et al. (2000) came to a similar conclusion for *P. antipodarum* in Lake Coleridge (South Island, New Zealand). We also found growth to be maximal at intermediate sediment:food ratios in our own long-term growth experiment. It is surprising, therefore that our short-term assimilation experiment indicates that assimilation is inversely related to the sediment ratio of the food. It may be that over a period exceeding 12 h, *P. antipodarum* is able to increase its total ingestion in an

attempt to maintain the rate of ingestion of organic matter despite the presence of sediment contamination. This would at least explain why growth did not decline with rising sediment content from a maximum rate at zero sediment ratio in our long-term growth experiment, though it fails to explain why growth was maximal at intermediate sediment ratios. Such a compensatory response has been demonstrated in *Lymnaea auricularia*, though it was manifested within only a few hours rather than over many hours (Arakelova, 1993). A more likely explanation for this discrepancy is that *P. antipodarum* is capable of feeding upon the episammic biofilms which grow upon clays and sands (Lopez & Kofoed, 1980). Such biofilms would not have had time to develop in our short-term experiments, and therefore the sediment merely interfered with (diluted) the ingestion of the free periphyton in this study. In our long term growth experiment the sediment was replaced only at fortnightly intervals and episammic biofilms are likely to have developed during the intervening 14 days. Lopez & Kofoed (1980) have shown that *P. antipodarum* is able to browse such films (even those growing on $<63\ \mu$m sediment), and if these were more rapidly ingested or assimilated than the presumed primary food (chicken feed), or microbial films growing on the container walls, then ingestion of this episammic biofilm may explain our finding that snail growth was greater at intermediate sediment:(primary) food ratios than at the zero sediment ratio. It may also be that sediment provided a source of trace minerals or nutrients which were lacking in the primary food supply. Note, however that neither of these mechanisms explain why growth was suppressed at still higher sediment ratios.

Anoxic sediments (inferred from a change in colour from pale grey to near black) were occasionally noted in some of the 100:1 and 500:1 sediment treatments. In these latter treatments the layer of mixed sediment and food was in excess of 2 cm thick, and whilst the whisker bubblers should have prevented the overlying water from becoming anoxic, it seems that there was insufficient circulation to maintain oxic conditions in sediments. Thus, snails burrowing for food within the sediment would have been subject to oxygen stress. This stress would have been compounded by the associated release of sulphides from the matrix of sediment and organic matter. Thus, it may be that the growth of the surviving snails in the high sediment treatments was suppressed as a result of indirect consequences of the high sediment content rather than as a direct result of high sediment content in the diet.

The highest average growth rates in our study were around 0.04 mm d^{-1}. This is higher than rates reported elsewhere in the literature for this species. For example, Dahl & Winther (1993) report a maximum shell growth rate of 0.03 mm d^{-1} over a 250 d period at 21 °C for snails fed on periphyton growing on slides, and Dorgelo et al. (1995) also measured a rate of 0.03 mm d^{-1} for snails fed on a mixture of lettuce and lamb's heart over 10 weeks at 15 °C. Though confounded by the different food sources used and temperature differences, comparison of these results might be interpreted as providing further evidence that the presence of some inorganic sediment within the diet promotes the growth of this snail.

Although intermediate levels of sediment were beneficial to the growth of deposit feeding snails, this does not appear to be true of invertebrate grazers in general. Furthermore, high levels of sedimentation (>50:1 DW) substantially reduced snail growth rates. Though the mechanisms are unclear, our experiments demonstrate that the sediment contamination levels typical of pasture streams are more favourable to the growth of *P. antipodarum* than are the sediment contamination levels within streams draining afforested streams. It is probable that this higher sediment:organic food ratio in pasture streams contributes to the greater abundance of *P. antipodarum* in pasture streams though other differences such as the higher water temperatures (Scarsbrook unpubl. data; Rutherford et al., 2000) and perhaps also the higher absolute periphyton densities also benefit the snail. Similarly, although the long-term growth data are not available to prove this, our experiments have shown that, in the short-term, *Deleatidium* sp. is unable to compensate for the 'dilution' of its food with sediment by increasing the efficiency with which it assimilates organic material. Thus, our experiments provide some support for the hypothesis that increased sediment yield in pasture catchments has an adverse impact upon *Deleatidium* sp. and may play a role in reducing the abundance of this species in pasture streams relative to afforested streams.

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