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Flow rate and vertical position influence ingestion rates of colonial zebra mussels (*Dreissena polymorpha*)

NANCY C. TUCHMAN, ROMI L. BURKS, CHRISTOPHER A. CALL AND JOHN SMARRELLI
Department of Biology, Loyola University Chicago, Chicago, IL, U.S.A.

SUMMARY

1. Zebra mussels aggregate to form dense colonies where, depending on the flow rate, individuals in different vertical locations within the colony may experience restricted food availability.
2. Using ^{32}P-labelled *Chlamydomonas angulosa*, we found ingestion rates of individual mussels located at the surface to exceed those in the bottom of a 6 cm thick colony by up to 75%.
3. Higher velocities (10 and 20 cm s^{-1}) increased algal delivery to the colony's middle layer (2–4 cm depth), subsequently increasing ingestion rates to equal those in the surface layer, while increasing ingestion only for the smallest mussels in the bottom (4–6 cm).
4. At all vertical locations within the colonies, smaller mussels showed higher ingestion rates per unit mass than larger mussels, particularly at higher flow rates.

Keywords: *Chlamydomonas*, colonial aggregates, flow rates, ingestion rates, ^{32}P, zebra mussels

Introduction

The vigorous filtering capacity of zebra mussels (*Dreissena polymorpha* Pallas) in lakes results in dramatic changes in food web structure and function (MacIsaac, 1996; Idrisi *et al*., 2001). In a highly productive lake, zebra mussels may easily reach densities of 200 000 m^{-2} (MacIsaac *et al*., 1992) and at these densities can remove large quantities of phytoplankton (Holland, 1993). A noticeable shift occurs from pelagic primary production to benthic production because of transfer of nutrients and seston to the sediments and increased light penetration (Reeders & Bij de Vaate, 1990; Lowe & Pillsbury, 1995; Thayer *et al*., 1997). The magnitude of this benthic-pelagic shift depends on lake productivity, zebra mussel density, average mussel size (Bunt, MacIsaac & Sprules, 1993) and filtering efficiency (Horgan & Mills, 1997).

Research conducted in the Western basin of Lake Erie has provided the most comprehensive effort to quantify the ecosystem-level impact of zebra mussel filtering (Madenjian, 1995; Klerks, Fraleigh & Lawniczak, 1996). MacIsaac *et al*. (1992) estimated that densely-populated zebra mussels in the Western basin of Lake Erie possessed the potential to filter 132 000 L of water per square metre of zebra mussels per day, which equates to filtering a 7 m water column between 3.5 and 18.8 times per day. In a bioenergetics model applied to this lake basin, Madenjian (1995) calculated that zebra mussels transferred the equivalent of 26% of the planktonic primary production to the benthos. Moreover, Bunt *et al*. (1993) suggested that even small zebra mussels (2–11 mm), which in 1990 comprised 90% of individuals in Western Lake Erie, could theoretically pump between 39 and 96% of the water column daily.

Most estimates of filtering capacity, however, are based on rates from individuals or from clusters of zebra mussels under controlled laboratory conditions that are extrapolated to field densities. Ackerman

Correspondence: Nancy C. Tuchman, Department of Biology, Loyola University Chicago, 6525 N. Sheridan Rd, Chicago, IL 60626, U.S.A.
E-mail: ntuchma@luc.edu
Present address: Romi L. Burks, Department of Biology, Southwestern University, Georgetown, TX 78626, U.S.A.
John Smarrelli, Le Moyne College, 1419 Salt Springs Road, Syracuse, NY 13214, U.S.A.

(1999) stressed the importance of examining zebra mussel clearance rates under flowing versus stagnant conditions. However, Yu & Culver (1999) argued that, even with flowing conditions, this method of extrapolation overlooks refiltration and thus overestimates the grazing impact of zebra mussels. Here we suggest that the colonial nature of zebra mussels can also have a significant impact on the overall filtration of individuals. For example, in south-western Lake Michigan, zebra mussels commonly occur as 4–6 cm thick colonies, and individuals at the bottom are at a physiological disadvantage compared with those at the surface of the aggregate for several reasons. Oxygen levels, for instance, are significantly reduced and ammonia levels are higher at the colony base (Burks *et al*., 2002) as a result of slower exchange rates of the interstitial water. In addition, larger mussels are less able to migrate out of the base of the aggregate to the surface where conditions are more favourable (Burks *et al*., 2002), probably because they are used as attachment surfaces for multiple smaller mussels, effectively increasing their size and decreasing their manoeuvrability. Besides poor interstitial water quality, food accessibility may pose an added stress to organisms living at the base of thick assemblages and possibly limit their ability to filter effectively.

This paper investigates whether zebra mussels positioned at the base of dense colonies have reduced access to food particles compared with those at the surface and how an increase in flow rate from 0 to 20 cm s^{-1} may enhance distribution of algae into the colony, subsequently increasing ingestion rates of individuals at the colony base. Three hypotheses were explored with laboratory experiments: (i) individuals at the base of a dense aggregate will exhibit lower ingestion rates than those at the surface, (ii) higher flow rates will deliver food particles deeper into the colony facilitating higher ingestion rates therein and (iii) smaller zebra mussels will filter greater quantities per unit mass per unit time than larger individuals at both surface and bottom depths in the colony, regardless of flow rate.

Methods

Laboratory filtration experiments were performed in small flumes (10 L; $50 \times 10 \times 30$ cm) to test how individual zebra mussel size and location within a dense colony influenced their ability to ingest algal food particles under different flow rates. Four recirculating flumes (modified from Vogel & LaBarbera, 1978) were constructed of 5 mm thick glass sealed with aquarium grade silicon caulk (Fig. 1). A rectangular glass baffle secured into the center of each flume acted as an island around which water flow was directed, producing a vertical circulation within the flume. A motorised 2 cm propeller was employed to produce unidirectional flow around the island baffle. In addition, the island baffle served to cradle a Plexiglas removable chamber ($9 \times 10 \times 6$ cm) where experimental zebra mussel colonies were contained (Fig. 1). The Plexiglas chamber containing the zebra mussel colony was countersunk into the island baffle so that the only portion of the colony exposed to the current was the colony surface, simulating conditions of a large, contiguous, densely populated zebra mussel colony in nature. Two collimators were constructed using stacks of 3 cm length plastic drinking straws arranged parallel to the current. These flow regulators were placed just upstream and downstream of the zebra mussel colony to produce near-laminar flow within the experimental section of the flumes. This flume design maximised control of flow rates, while minimising volume of water and therefore the amount of radioactive waste material produced with each trial.

Zebra mussels (*D. polymorpha*) used in the experiments were collected in early fall by SCUBA divers in Belmont Harbour in south-western Lake Michigan by cutting clusters of mussels from the iron piers with wide-blade (6 inch) paint scrapers. This technique cut the byssal threads of those mussels on the bottom of the clusters that were directly attached to the pier, while leaving the 3-dimensional stratigraphy of the clusters intact. Clusters ranged in size from approximately 15–50 mussels per druze. These zebra mussels were returned to the lab and stored for 24 h in a holding tank containing unfiltered Lake Michigan water maintained at 18 °C (Lake Michigan ambient temperature at collection site) with constant aeration. The size class composition of mussels in the holding tank reflected that commonly found in zebra mussel colonies collected from Lake Michigan; 50% size I (<5 mm shell length), 30% size II (5–15 mm) and 20% size III (>15 mm) (Burks *et al*., 2002). For each experimental trial, approximately 2000 live zebra mussels were collected from the holding tank and about 500 were placed into each of four Plexiglas chambers,

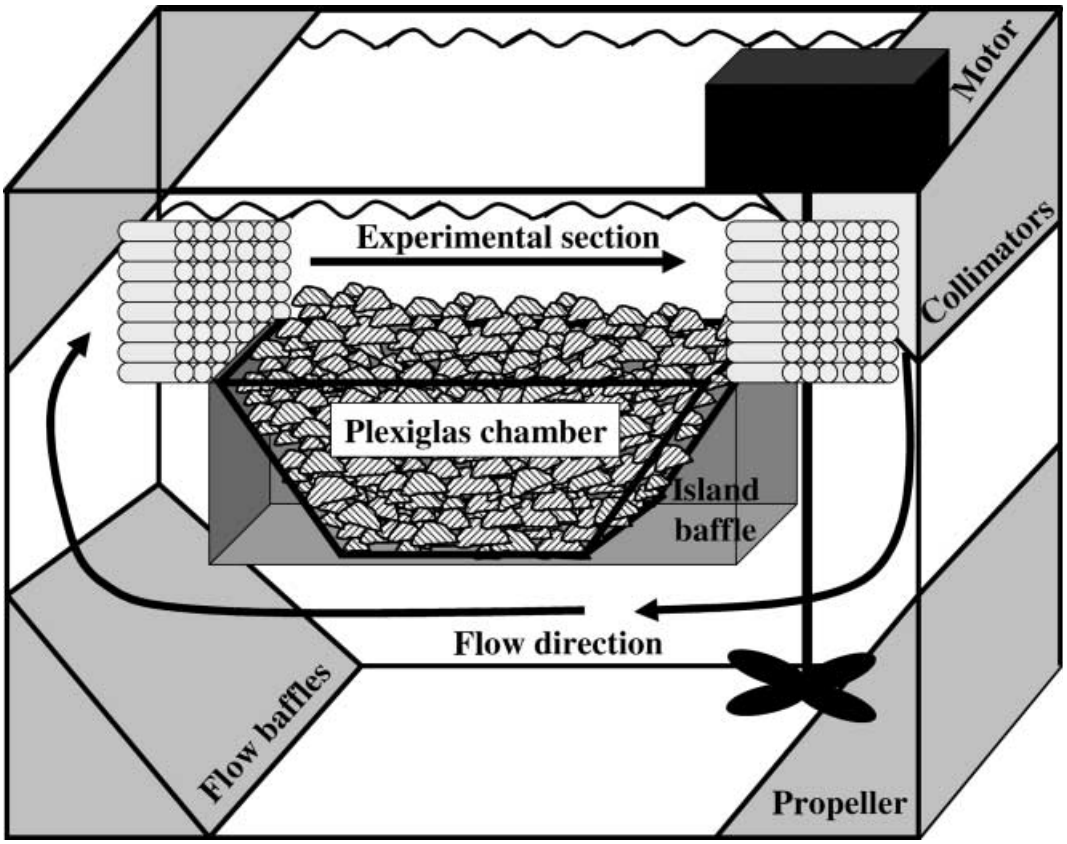

Fig. 1 Schematic diagram of experimental flumes. Each flume had a separate flow rate assigned and the experiment was repeated four times for replication.

creating a dense colony with dimensions of $9 \times 10 \times 6$ cm and an approximate density of 70 000 mussels m^{-2}. Initial druzes were left intact as much as possible when transferring mussels from the holding tank to the experimental Plexiglas chambers. These chambers were then lowered into the island baffle within the flumes. The four experimental flumes contained 18 °C Lake Michigan water, filtered (0.45 μm) to ensure removal of all food particles. Zebra mussels were allowed to acclimate until normal siphoning activity (i.e. opening of valve and protrusion of inhalant and exhalant siphons) was observed (at least 30 min) prior to each experiment.

Using motorised propellers, four flow rate treatments were established: 0 (control), 2.5, 10 and 20 cm s^{-1}. Flow rates were determined by timing the rate at which small, neutrally buoyant crystals of methylene blue travelled across a 20 cm path length within the experimental area of the flume. In the control treatment, airstones produced turbulent mixing with a net flow rate of 0 cm s^{-1} in order to keep the algae in suspension. Three replicate trials were conducted for each flow rate using a different group of zebra mussels for each trial. Proportions of size classes (determined by naturally occurring size distributions in Lake Michigan as indicated above) in the experimental chamber were kept consistent for all flow rates and replicate trials.

Chlamydomonas angulosa (Dill), cell size 15–18 μm diameter, was used as a representative food source for zebra mussels during the experiment (Berg, Fisher & Landrum, 1996). *Chlamydomonas angulosa* was cultured in a 7 L flask with a stir bar at room temperature with natural light and photoperiod in a phosphorus-free Guillard's medium (Stein, 1979). To quantify rates of ingestion of algae by zebra mussels, the *Chlamydomonas* culture was inoculated with 4 m Ci of ^{32}P as $K_2H^{32}PO_4^{3-}$ 6 days before the experiment to ensure at least two cell divisions and subsequent labelling of all cells. After 6 days the inoculated culture was filtered, spun down, washed and respun to remove unmetabolised and non-specifically bound ^{32}P, and then

resuspended in dilute Guillard's medium. The density of algal cells in the recirculating flumes was determined by averaging the number of cells within six, 10 mL replicate subsamples using Nomarski optics microscopy at 1000× in a haemocytometer counting chamber behind a Plexiglas shield. The radioactivity of the stock culture was measured with a Beckman LS 7000 scintillation counter (Beckman Coulter, Fullerton, CA, U.S.A.) and standardised to algal density for an estimate of radiation counts per minute per cell. Homogeneously radiolabelled algal culture (70 mL) was added to each 10 L flume in each experimental trial producing a density of 13 000 cells mL^{-1} (9.925×10^6 m^3 mL^{-1}) which is similar to the incipient limiting level (16 000 cells mL^{-1}) for *D. polymorpha* as determined by Sprung & Rose (1988). Therefore, in our experiments zebra mussels were filtering at the maximal rate. Zebra mussels were allowed to filter for 30 min at each of the different flow rates, an interval of time sufficient to maximise the ^{32}P signal in dreissenid guts, but too short for egestion of ^{32}P to occur, allowing for accurate quantification of ingestion rates. Ingestion rate estimates were unaffected by pseudofaecal production, as no pseudofaecal production was observed during the 30 min feeding trials, presumably because *Chlamydomonas* cells are an optimal food for dreissenids.

After 30 min of filtering, the Plexiglas colony chambers were removed from the flumes, drained, and rinsed. Zebra mussels in the colony were manually separated into three 2 cm horizontal layers: top, middle and bottom. We further separated zebra mussels from the top and bottom layers by size class. To determine the relative quantity of algae ingested by specific size classes of mussels in the top and bottom layers, all individuals within each size class were counted, weighed and then pulverised in a tissue grinder with 50 mL of distilled water for 2 min. The same procedure was conducted for mixed sizes of zebra mussels in the middle layer. The pulverised zebra mussel homogenate was then filtered through several layers of cheesecloth to remove large shell particles. Three 1 mL subsamples of filtrate were added to 4-mL of a 10% trichloroacetic acid (TCA) solution in a test tube and refrigerated for 24 h to precipitate any soluble radioactive material. Each sample was vacuum-filtered through a glass fibre filter and rinsed with a 10% TCA solution to concentrate the radioactive material. Because TCA residue can quench radioactive signal, the filters were rinsed with a 95% ethanol solution to remove any remaining TCA, and allowed to dry for at least 10 min. After drying, each filter was placed face up in a scintillation vial, to which 10 mL of Aquasol-2 (DuPont-NEN Research Products, Boston, MA, U.S.A.) scintillant was added. Radioactivity in each vial was measured in a Beckman LS 7000 scintillation counter.

Statistical analyses

The rate of *Chlamydomonas* particle ingestion by zebra mussels was statistically analysed using analysis of variance (ANOVA) tests. A 2-way ANOVA was used to examine the effect of flow (0, 2.5, 10 and 20 cm s^{-1}) on zebra mussel ingestion at different vertical positions (top, middle, bottom) in the colony, regardless of size class. Ingestion data were log-transformed to equalise variance and Tukey's Multiple Comparison Tests (MCT) were used to examine specific differences. To test the impact of flow rate on ingestion of algae by different sized zebra mussels, 2-way ANOVAs were conducted for two of the three vertical layers (top and bottom). When analysed as individual layers, only the top and middle vertical layers met the ANOVA assumptions of normality; therefore, a square-root transformation was performed on the data from the bottom layer to meet the assumptions of ANOVA. Following significant ANOVA results, Tukey's MCT was used to examine specific differences among different flow rates or size classes. All statistical analyses were performed with SAS V.8.2 (SAS Institute, 1999).

Results

Ingestion of algae at the surface layer was significantly higher than at the bottom layer at all flow rates and higher than at the middle at low flow rates (Fig. 2; layer, 2-way ANOVA, $F_{2,72} = 95.36$, $P < 0.0001$). Uptake rates in the middle and bottom layers were approximately 50 and 25% (respectively) of that measured for mussels in the top layer. Significant differences in uptake rates also occurred between the middle and bottom layers for all flow rates (Tukey's MCT, $P < 0.01$). No significant interaction between vertical layer and flow rates occurred (flow × layer, 2-way ANOVA, $F_{6,72} = 1.79$, $P = 0.1136$).

When radiation counts per minute are used to calculate the approximate density of *Chlamydomonas*

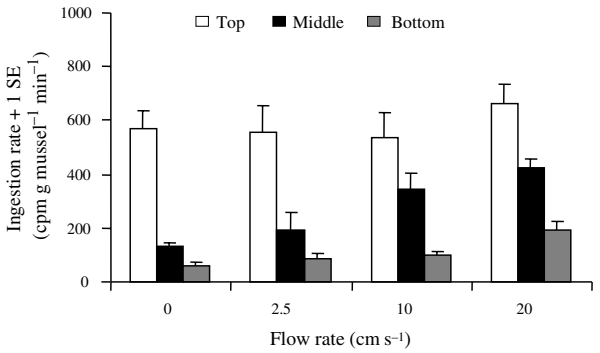

Fig. 2 Concentration of $^{32}PO_4^{3-}$ (radiation counts per minute) per unit mass (g wet weight) of zebra mussels located at the top 2 cm, the middle and the bottom 2 cm of a dense colony at four different flow rates (0, 2.5, 10.0 and 20.0 cm s^{-1}). All size classes were pooled within vertical layers for this analysis. Error = +1 SE (standard error). Statistical comparisons between flow rates can be found in Table 1.

cells ingested per mass wet weight mussel per minute, mussels in the surface layer filtered an average of 124 800 cells g wet weight (gww)$^{-1}$ min^{-1} across all flow rates. Mussels in the middle layer filtered an average of 34 036, 40 435, 79 005 and 88 585 cells gww^{-1} min^{-1} at flow rates of 0, 2.5, 10 and 20 cm s^{-1}, respectively. Mussels in the bottom layer filtered an average of 11 345, 19 605, 22 418 and 38 756 cells gww^{-1} min^{-1} at flow rates of 0, 2.5, 10 and 20 cm s^{-1}, respectively.

While increased flow did not affect uptake rates for mussels located at the surface, higher velocities significantly increased algal uptake by mussels in the middle layer, and to a lesser extent, in the bottom layer (Table 1; Fig. 2, flow, 2-way ANOVA, $F_{3,72} = 6.79$, $P = 0.0004$), although no significant interaction occurred. The bottom layer showed the most dramatic differences between the two higher flow rates (10 and 20 cm s^{-1}), although the difference did not meet statistical significance (Table 1; $P = 0.06$).

Table 1 Statistical analyses of algal uptake (after 30 min) by zebra mussels comparing different flow rates (cm s^{-1}) for each of the three vertical layers. Zebra mussel size classes were pooled for these comparisons

Flow rate comparisons	Top	Middle	Bottom
0 versus 2.5	n.s.	n.s.	n.s.
0 versus 10	n.s.	*	**
0 versus 20	n.s.	**	***
2.5 versus 10	n.s.	n.s.	n.s.
2.5 versus 20	n.s.	*	***
10 versus 20	n.s.	n.s.	+

n.s., $P > 0.05$; +, $0.05 < P < 0.10$; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

Standardised for mussel mass (blotted wet weight with shells), small mussels (<5 mm) showed higher rates of ingestion than medium (5–15 mm) and large sized mussels (>15 mm) at all flow rates in both the top and bottom layers (Fig. 3a; size, 2-way ANOVA, $F_{2,24} = 11.34$, $P = 0.0003$, Fig. 3b; $F_{2,24} = 5.76$, $P = 0.0090$, respectively). Ingestion rates of medium and large mussels did not differ within either layer. Within the surface layer, size class was unaffected by flow (Fig. 3a, flow, 2-way ANOVA, $F_{3,24} = 0.67$, $P = 0.5802$), whereas ingestion rates of smaller mussels were stimulated at higher flow conditions in the bottom layer (Fig. 3b; $F_{3,24} = 7.11$, $P = 0.0014$). However, as increased flow did not increase ingestion rate of larger mussels in the top or bottom layers, significant interactions between size classes and flow rate did not occur (2-way ANOVA, top layer, $F_{6,24} = 0.94$, $P = 0.4866$; bottom, $F_{6,24} = 1.09$, $P = 0.3966$).

Discussion

This study was designed to test how vertical position of individual mussels within a dense, 3-dimensional colony influenced their ability to ingest algae, and how increasing flow rates may alleviate the restricted food resources for those individuals located at the bottom. In accordance with our expectations, at low flows individuals at the base of dense aggregates exhibited significantly lower ingestion rates than those located at the surface. Higher flow significantly increased ingestion rates for all size classes only within the middle 2 cm of the 6 cm thick colony. Flow rates of up to 20 cm s^{-1} were not sufficient to stimulate ingestion rates of larger mussels located at the base of these colonies, but did increase ingestion rates for the smallest size class individuals at the base. In general, mussels at the bottom filtered only between 10 and 28% as much as mussels in the surface layer, even at the highest flow rate.

Increasing flow rates up to 20 cm s^{-1} in this experiment enhanced filtration for individuals positioned deeper within the colony. This could imply that lotic environments are potentially more conducive to zebra mussel success than lentic environments. However, living in lotic environments does not necessarily facilitate greater aggregate densities for three reasons: (i) filtration is inhibited by physical

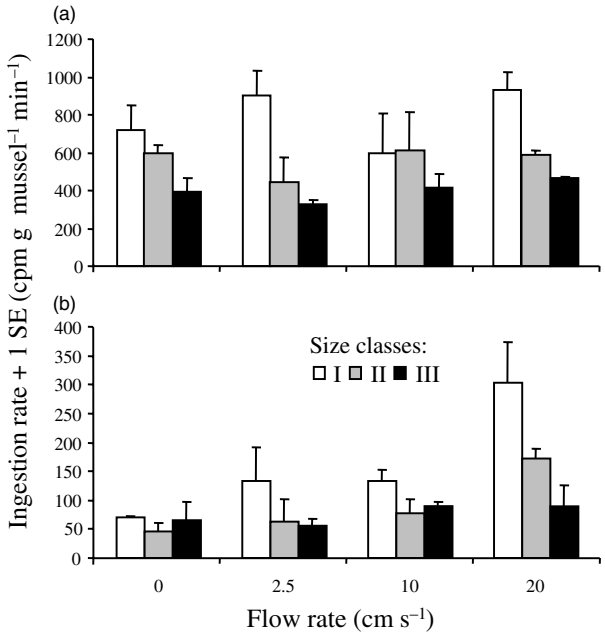

Fig. 3 Concentration of $^{32}PO_4^{3-}$ (radiation counts per minute) per unit mass (g wet weight) of three size classes of zebra mussels located at the top 2 cm (a) and the bottom 2 cm (b) of a dense colony at four different flow rates (0, 2.5, 10.0 and 20.0 cm s^{-1}). Error = +1 SE (standard error). Note the different scales on the *y*-axes.

abrasion at flow velocities at or above 30 cm s^{-1} (Newell, Wildish & MacDonald, 2001), (ii) oversaturation of food resources or production of pseudofaeces may occur (Lei, Payne & Wang, 1996; Ackerman, 1999) and (iii) veliger mortality is increased at high flow velocities (Horvath & Lamberti, 1999).

In addition to the effect of vertical position and flow rate within a dense colony on zebra mussel ingestion rates, the size of individual zebra mussels also impacts filtering rates (Bunt *et al.*, 1993). Vertical layers within our experimental zebra mussel colonies were comprised of homogeneously mixed size classes representing size class distributions in south-western Lake Michigan where smaller sizes were prevalent. We found that mussel size significantly affected ingestion rates at all positions within the colony. In contrast to previous studies (Horgan & Mills, 1997; Ackerman, 1999), smaller zebra mussels in our experiment exhibited higher ingestion rates per unit mass per unit time than larger individuals at both surface and bottom depths in the colony, regardless of flow rate. The differences in the delineation of size classes among these three studies makes direct comparison between them difficult; however, the variation in methods used to measure zebra mussel filtration probably offers the best explanation for the discrepancies among studies. While larger mussels may effectively ingest large quantities of food when tested individually (Ackerman, 1999), inclusion within a dense colony might impede their ingestion. Our results use an accurate measure of ingestion through radiolabelled food particles and consider the collective ingestion rates of each mussel size class in the context of their spatial distribution within a dense 3-dimensional colony. Previous experiments suggest that the abundant small mussels in our experiments may be able to position themselves better to maximise food intake through increased mobility and manoeuvrability (Burks *et al.*, 2002). Collectively, this better positioning could result in higher ingestion rates per unit mass. Lower feeding efficiencies by larger mussels might result from lack of manoeuvrability when they are positioned at the base of dense colonies and their shells are colonised by multiple smaller individuals (Burks *et al.*, 2002), which could also potentially impede their siphoning functions. Therefore, we suggest that the relationship between zebra mussel ingestion and size class is closely linked to individual spatial location within a dense colony.

When trying to estimate the large-scale potential of zebra mussels to filter water columns in lakes, ecologists often calculate this capacity by multiplying zebra mussel density (measured as numbers per square metre) by laboratory-derived filtering rates of individual, or perhaps small groups of mussels (Ackerman, 1999). This method ignores the 3-dimensional nature of zebra mussel colonies as well as the potential for refiltration (Yu & Culver, 1999). Results from the present study suggest that these extrapolations may overestimate the actual filtering capacity of colonial zebra mussels, especially those individuals located at the base of dense colonies. Our results suggest more conservative estimates should be applied to the filtering capability of natural zebra mussel colonies as not all mussels filter at maximal efficiency. The densities used in this study (70 000 m^{-2}) fall within the range of naturally occurring field densities and do not represent the higher densities reported in the literature. Even at this moderate density, mussels at the bottom layer suffered a distinct disadvantage, with reduced access to food resources.

Given the great capacity of zebra mussels to strip the water column of phytoplankton (MacIsaac *et al*., 1992), some research has examined the potential of zebra mussels to serve as 'biological filters' (Reeders & Bij de Vaate, 1990) in highly eutrophic lakes. Reed-Andersen *et al*. (2000) modelled the potential impacts of zebra mussel invasion on eutrophic Lake Mendota, which has been free of zebra mussels but plagued by periodic cyanobacterial blooms. In their model, Reed-Andersen *et al*. (2000) estimate that at relatively low densities of zebra mussels (>2000 m^{-2}), chlorophyll concentrations would rarely (<1% of the time) rise above 50 $\mu g\ L^{-1}$. The accuracy of modelling zebra mussel ingestion of seston as a potential management tool in eutrophic lakes (Fanslow, Nalepa & Lang, 1995; Klerks *et al*., 1996) may be improved by considering the differential ingestion rates of zebra mussels as a function of size class distribution, the thickness of the zebra mussel colonies and subsequent position of individuals within the vertical profile of the colony.

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