

Filtering impacts of larval and sessile zebra mussels (*Dreissena polymorpha*) in western Lake Erie

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Summary. We assessed the feeding biology of veliger larvae of the introduced zebra mussel (*Dreissena polymorpha* Pallas) in laboratory experiments using inert microspheres as food analogues. Mean clearance rate on 2.87- μm beads ranged between 247 and 420 μL veliger⁻¹ day⁻¹. Clearance rate was unrelated to bead concentration up to 100 beads μL^{-1} , but was positively correlated with veliger shell length. Clearance rates of *Dreissena* veligers are within the range of those reported for marine bivalve veligers of similar size and for herbivorous Great Lakes microzooplankton, but are orders of magnitude lower than those of settled, conspecific adults. The impact of settled zebra mussel grazing activities on phytoplankton stocks may be up to 1162 times greater than that exerted by veliger populations in western Lake Erie. Based on 1990 size-frequency distributions and associated literature-derived clearance rates, reef-associated *Dreissena* populations in western Lake Erie (mean depth ~ 7 m) possess a tremendous potential to filter the water column (up to 132 $\text{m}^3 \text{m}^{-2} \text{day}^{-1}$) and redirect energy from pelagic to benthic foodwebs. Preliminary analyses indicate that chlorophyll *a* concentration is strongly depleted ($< 1 \mu\text{g L}^{-1}$) above *Dreissena* beds in western Lake Erie.

Key words: *Dreissena* – Lake Erie – Ecological impact – Clearance rate – Biological invasion

Dreissena polymorpha, a bivalve mollusc native to the Caspian Sea region, was introduced to the St. Lawrence Great Lakes in 1986, apparently through the discharge of ballast water contaminated with planktonic, veliger larvae (Hebert et al. 1989). Since its initial discovery in Lake St. Clair in 1988 (Hebert et al. 1989), *Dreissena* has spread rapidly to all of the Great Lakes and to some of the inland rivers draining them (O'Neill and

MacNeill 1991). Mean population densities of settled mussels exceeded 6×10^3 and 3.4×10^5 individuals m^{-2} on solid substrates in Lake St. Clair (Hebert et al. 1991) and western Lake Erie (Leach 1992), respectively, during 1990. Zebra mussels are capable of prolific population growth and rapid dispersal because individual females produce up to 10^6 egg per year (Walz 1978a; Sprung 1990; Borcharding 1991) which, when fertilized in the water column, develop into planktonic veliger larvae $\sim 70 \mu\text{m}$ in length (Stańczykowska 1977). Veligers utilize a ciliated velum for propulsion and food collection and can remain in the water column for periods of 33 days or longer (Stańczykowska 1977). Individuals typically grow to between 200 and 250 μm shell length prior to settling from the plankton (Lewandowski 1982; Sprung 1989). Veligers were among the numerically-dominant herbivorous zooplankters (Table 1) in western Lake Erie throughout summer 1990, with June to September mean densities ranging between ~ 40 and 400 ind. L^{-1} (Leach 1992).

Despite the enormous literature devoted to the study of adult *Dreissena* (see Stańczykowska 1977; Mackie et al. 1989), very little is known about the nature or impact of veliger feeding. Sprung (1989) reported that *Dreissena* veliger diets were limited to particles between 1 and 4 μm , while Gliwicz (1969) suggested that veligers were 'microfiltrators' based on a positive correlation between veliger density and grazing intensity on 1.85–12.75 μm nanoplankton in Polish lakes. However, the rate at which *Dreissena* veligers filter water free of food (i.e. clearance rate) has not been determined. In order to understand the impact of larval and adult zebra mussels on phytoplankton stocks and energy flow patterns in western Lake Erie, the relative community clearance rate contributions of veligers, settled *Dreissena*, and other herbivorous zooplankton must be known. In this study we use polystyrene microspheres as a natural food analogue to determine the effects of 'food' concentration and veliger size on clearance rate, and to estimate veliger gut passage time. We then combine estimates of population density and clearance rate to compare poten-

Table 1. Mean population densities, maximum clearance rates and population filtering impacts of herbivorous zooplankton in western Lake Erie near Colchester, Ontario and settled *Dreissena* on Hen Island Reef, near Pelee Island, Ontario, during August and October 1990, respectively. Zooplankton population densities assume a 7 m water column. Clearance rate source key: 1 = Bogdan and Gilbert 1984; 2 = Starkweather 1980; 3 = Wu and Culver 1991; 4 = this study; 5 = Leach 1992; 6 = application of shell length – clearance rate equation in Kryger and Riisgård 1988 (see methods for addi-

tional information). *Daphnia* and *Diaphanosoma* densities are based on 41 μm -mesh Wisconsin net tows, but were checked against values obtained with a 110 μm -mesh Wisconsin net. Total settled

Dreissena filtering impact was calculated as: $(10^{-9} \sum_{i=1}^{29} \text{Density}_i \times \text{Clearance Rate}_i)$, where i = shell length size class in mm. * assuming clearance rate is equivalent to that of *K. crassa*. ** Values not specified; filtering impact based on Fig. 6, Wu and Culver (1991)

Taxon	Population Density (Thousands m^{-2})	Maximum Clearance Rate ($\mu\text{L individual}^{-1} \text{ day}^{-1}$)	Population Filtering Impact ($\text{m}^3 \text{m}^{-2} \text{ day}^{-1}$)	Source
<i>Polyarthra</i> spp.	4030	350	1.4	1
<i>Conochilus unicornis</i>	160	250	<0.1	1
<i>Keratella cochlearis</i>	<10	40	<0.1	1
<i>K. crassa</i>	<10	3730	<0.1	1
<i>K. earlinae</i>	30	3730	0.1	*
<i>Synchaeta</i> spp.	240	40	<0.1	2
<i>Diaphanosoma</i>	<10	8560	<0.1	1
<i>Daphnia</i>				
1990 survey	<10	11320	<0.1	3
Wu and Culver 1991	**	11320	4.6	3
<i>Bosmina longirostris</i>	90	2990	0.3	1
<i>Leptodiptomus minutus</i>				
adults	<10	9610	<0.1	1
copepodids	<10	7350	<0.1	1
nauplii	40	3660	0.1	1
<i>Dreissena polymorpha</i>				
veligers				
1990 survey	360	320	0.1	4
1990 midsummer mean	2800	320	0.9	5
Wu and Culver 1991	700	**	<0.1–0.4	3
settled individuals				
Hen Island Reef	270	9600– 12.40×10^6	132	6

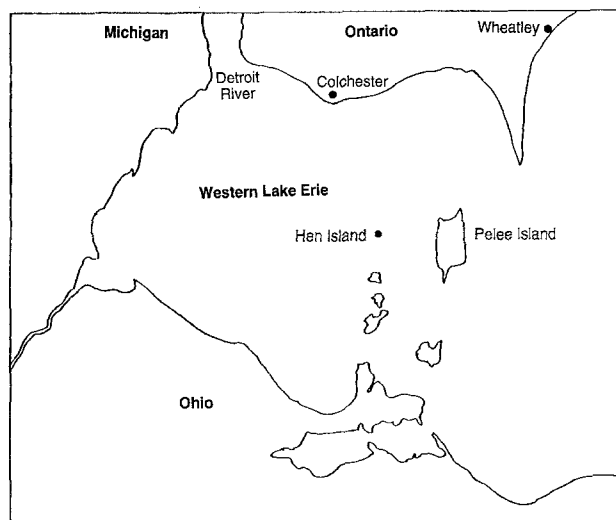


Fig. 1. Location of sampling sites near Hen Island Reef in western Lake Erie

tial filtering impacts of veligers, adult *Dreissena*, and other herbivorous zooplankton (*Daphnia*, rotifers) in western Lake Erie, and relate these impacts to vertical patterns of chlorophyll *a* concentration and water flow over Hen Island Reef (Fig. 1). Wu and Culver (1991) have proposed that filtering activities of *Daphnia* provide a more parsimonious explanation than do those of larval or settled *Dreissena* for recent changes in water column transparency and chlorophyll *a* concentration in western Lake Erie (Leach 1992).

Methods

Veliger samples were collected between 4–27 July 1991 from 1–2 m depth in Lake Erie near Wheatley, Ontario or Middle Sister Island, Ontario, with a 30 L Schindler-Patalas trap outfitted with a 41- μm Nitex mesh sock. Zooplankton was concentrated to $5 \times$ lake density and transported to the laboratory in chilled, 20-liter plastic carboys. Experiments were conducted at 19–21°C in 20 mL borosilicate test tubes using 15 mL of glass-fibre-filtered (Whatman 934-AH; retention to 1.5 μm) pond water collected on the campus of Erindale College, Mississauga, Ontario, and supplemented with fluorescent beads (\bar{x} diameter \pm SD = $2.87 \pm 0.14 \mu\text{m}$; Duke Scientific). Inert microspheres have been successfully employed in feed-

ing studies with many other zooplankton taxa (e.g. DeMott 1986). Veligers were added to bead suspensions rather than the converse because of the inherent difficulty with the latter procedure in obtaining homogeneous bead solutions while minimizing veliger disturbance during the feeding period. Veligers for each of the experiments described below were acclimated in filtered pond water lacking beads and food for 5 min before being transferred to test containers with a micropipet. Individuals that appeared quiescent with the velum retracted at the end of the acclimation period were discarded. Settling of beads from suspension was minimized by conducting experiments in 15 cm-high test-tubes and by everting test-tube suspensions 4 × prior to initiating the experiment. According to Stokes' Law, 2.87 µm beads (specific gravity = 1.05) would settle only 0.07 mm during the course of our experiments.

Veliger clearance rate (µL ind.⁻¹ day⁻¹) was measured indirectly based on the number of beads ingested during short-term experiments. In experiment 1, the effect of bead density on veliger clearance rate was determined by haphazardly placing 7 to 16 veligers (100–240 µm) in test-tube suspensions containing between 1 and 100 beads µL⁻¹. After 5 min, the suspension was poured into a plastic Petri plate and the individuals killed by addition of 10% buffered sugar-formalin. Individual veligers were serially transferred (i.e. washed) through two Petri dishes containing distilled water, placed on microscope slides and covered with cover slips. The number of ingested beads was counted at 150–400 × magnifications with a Leitz Wetzlar epifluorescent microscope outfitted with an ultraviolet light source. Three test-tube replicates were conducted at each bead concentration. Experimental animals were collected on the day of the experiment and were permitted to feed on lake water seston prior to the acclimation period. Differences in clearance rates among bead concentration treatments were analyzed using analysis of covariance, with veliger number per test tube entered as a covariate. The ANCOVA model employed mean veliger clearance rates per test-tube rather than individual values. Mean clearance rate values were log(x + 1)-transformed prior to analysis.

The relationship between clearance rate and veliger shell length (maximum dimension) was assessed in a similar manner. Veligers were collected and maintained for four days in a constant-environment chamber at 20° C with ambient lake food. On the day of the experiment, veligers were acclimated for 5 min prior to being placed, 9 individuals per test-tube, in filtered pond water lacking food but containing 8 beads µL⁻¹ (Exp. 2). After five minutes exposure to the bead suspension, individuals were killed, washed and measured to the nearest 9 µm with an ocular micrometer. Six test-tube replicates were run.

Gut passage time was estimated by placing 10 veligers collected on the day of the experiment in test-tube suspensions containing 25 beads µL⁻¹ for periods of between 1 and 30 minutes (Exp. 3). Animals were acclimated, fixed and washed as per the above experiments. Three test-tube replicates were run for each time treatment. Gut passage time is approximated by the time at which the initially high rate of bead accumulation begins to decline, presumably in conjunction with the onset of bead defecation by veligers (Peters 1984).

Clearance rate (CR; expressed as µL filtered ind.⁻¹ day⁻¹) was calculated for individuals that consumed beads as:

$$CR = 1440 B/C_0 t \quad (1)$$

where B is the number of beads ingested per individual, C₀ is the initial bead concentration (beads µL⁻¹), and t is the experimental period (min⁻¹). Bead depletion was minimal in all suspensions (<0.5%).

The impact of veliger grazing activities on phytoplankton in western Lake Erie was compared to that exerted by *Dreissena* adults and other herbivorous zooplankton in the basin. Settled *Dreissena* populations were censused on 22 October 1990 by divers at 9 locations on Hen Island Reef, west of Pelee Island, Ontario. Because *Dreissena* forms nearly continuous colonies on the reef (MacIsaac, pers. obs.), densities were estimated by collecting between 6 and 12 representative rock samples from each location.

Dreissena shell length (SL) was measured to the nearest mm and converted to mussel soft-part dry weight (DW, in g) and thence to clearance rate (CR, in µL ind.⁻¹ day⁻¹) using formulae adapted from Kryger and Riisgård (1988):

$$DW = 1.54 \times 10^{-5} SL^{2.42} \quad (2)$$

$$CR = 1.64 \times 10^8 DW^{0.88} \quad (3)$$

Filtering impact refers to the volume of water cleared of food per day by a suspension-feeding population. In order to facilitate comparisons between planktonic (zooplankton) and benthic (settled *Dreissena*) suspension-feeders, all species densities (individuals m⁻²) and filtering impacts (m³ filtered m⁻² day⁻¹) are expressed on an aerial basis. The combined filtering impact of settled *Dreissena* was calculated as:

$$10^{-9} \sum_{i=1}^{29} (\text{Density}_i \times \text{Clearance Rate}_i), \quad (4)$$

where i = shell length size class (1–29 mm). Because clearance rate measurements of settled mussels vary strongly between studies, filtering impact of benthic mussels was also calculated using clearance rate formulae derived from data originally presented in Kondratév (1963) and Micheev (1966) (see Kryger and Riisgård 1988). Kryger and Riisgård (1988) regressed clearance rate on dry weight for *Dreissena* with body masses between ~1.1 and 95 mg (i.e. ~6.6 to 31 mm shell length). We have assumed that these regression relationships extend to mussels with masses as low as 15.4 µm (1 mm) because clearance rate measurements are lacking for *Dreissena* of low body mass.

Three zooplankton samples were collected on 23 August 1990 with individual hauls (~1 m per second) of a metered 30-cm mouth diameter, 41-µm mesh Wisconsin net from 1 m above lake bottom to the surface. Samples were taken offshore on a 10 km transect adjacent to Colchester, Ontario, at depths of 8–9 m. Additional zooplankton samples were collected at four sites adjacent to Hen Island Reef on 5–6 September 1991. At each site, two samples were collected from each of 0.5 m, 2.5 m depth and from 1 m above bottom using a 30-L Schindler-Patalas trap outfitted with a 41-µm mesh sock and bucket. Zooplankton samples were preserved in 4% sugar-formalin and enumerated at 63 magnifications with a compound microscope. Estimates of zooplankton filtering impacts were obtained by utilizing maximum zooplankton clearance rates reported from the literature (Table 1).

Our estimates of settled *Dreissena* filtering impact assume that the water column is mixed sufficiently well as to destroy patterns of grazing-induced phytoplankton depletion in benthic waters, i.e. refiltration of water by settled bivalves is minimal. A preliminary study of vertical profiles of current velocity, water temperature and chlorophyll *a* concentration was conducted on 5–6 September 1991 at four locations above settled *Dreissena* beds on Hen Island Reef in conjunction with the zooplankton sampling described above. A Neil Brown current velocity and water temperature meter was suspended from an adjustable central shaft of a 3 m aluminum tripod (Fig. 2) that had been placed on the lake bed. A ten minute interval elapsed after the tripod was placed on the lake bed before sampling was initiated. Sampling was generally conducted in 20 cm increments between 25 and 145 cm above the lake bed. At its highest position, the meter was 50 cm from the tripod legs – a distance sufficient to avoid disturbance of the current flow by the tripod legs. Temperature and current velocity were averaged over sequential 60 s intervals for 10 min. A submersible pump capable of pumping 5 L min⁻¹ was attached to the tripod platform (Fig. 2). The intake hose was secured to a leg of the tripod with removable clips, permitting water to be collected from each of the depths contemporaneously sampled for current velocity and temperature. Hosing was attached to a down-current leg to prevent interference with water flow past the meter. Water was pumped to the lake's surface for 10 min, filtered through 209 µm mesh to retain zooplankton, and collected in a large plastic bucket. At the end of the 10 min period water in the pail was mixed, a subsample was withdrawn, and three replicate 1.5–2.0 L aliquots were filtered

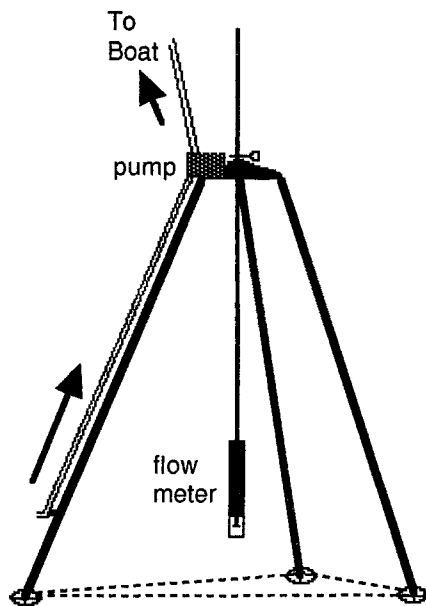


Fig. 2. Tripod used to measure vertical patterns of water temperature, current velocity, and chlorophyll *a* concentration in western Lake Erie. See methods for complete description

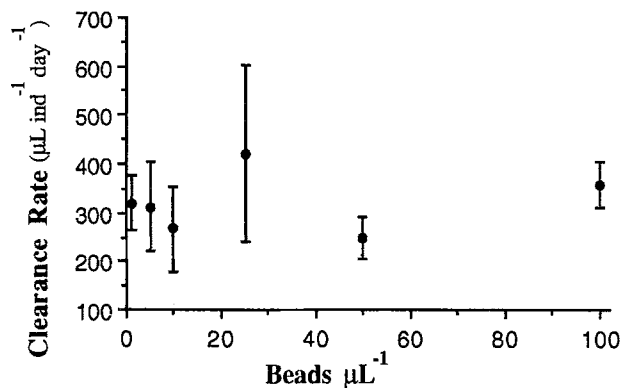


Fig. 3. Clearance rate ($\bar{x} \pm 1$ SD) of *Dreissena* veligers determined with suspensions of fluorescent 2.87 μm beads (Exp. 1). Three test-tube replicates were conducted at each bead density. Experimental veligers ranged in size from 100–240 μm

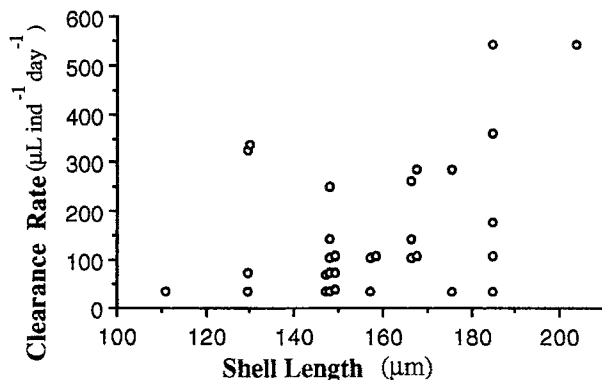


Fig. 4. Veliger clearance rate in relation to maximum shell length (Exp 2). Overlapped values have been slightly offset. Pearson's $r = 0.44$, $P < 0.05$, $n = 31$

through Whatman GF/C filters for chlorophyll *a* analysis. Additional water samples for chlorophyll *a* analysis were collected at 0.2 and 1.5 m depth and at 2.5 cm above the lake bed. Filters were frozen on dry ice and transported to the lab for analysis. Chlorophyll *a* was measured spectrophotometrically following extraction in 90% acetone, and corrected for phaeophytin (Strickland and Parsons 1972).

Results and discussion

Veliger clearance rates

Mean veliger clearance rate varied between 247 and 420 $\mu\text{L veliger}^{-1} \text{ day}^{-1}$, but was virtually invariant over bead densities ranging between 1 and 100 beads μL^{-1} ($F_{5,11} = 1.19$, $P = 0.38$; Fig. 3). Clearance rate was also unrelated to the number of veligers tested per test-tube ($F_{1,11} = 0.01$, $P = 0.92$). The maximum observed clearance rate of 922 $\mu\text{L veliger}^{-1} \text{ day}^{-1}$ was obtained with two veligers at an intermediate density of 25 beads μL^{-1} . Clearance rate variability was pronounced at most bead concentrations (Fig. 3), possibly as a result of handling-induced feeding rate reductions. Some veligers withdrew the velum and ceased filtering activities when transferred between acclimation dishes. Though these individuals were not used in feeding trials, a similar phenomenon may have occurred when test organisms were transferred to trial containers. Additional variation in clearance rate likely resulted from the broad size classes (100–240 μm) of veligers used in our experiment. Clearance rate was positively correlated (Pearson's $r = 0.44$, $P < 0.05$; $n = 31$) with veliger shell length (Fig. 4). A similar finding was reported by Sprung (1985) for veliger larvae of the marine mussel *Mytilus edulis*.

Our clearance rate measurements, estimated from the ingestion of beads (Fig. 3), are generally consistent with those of *M. edulis* veligers of similar size feeding on algae (Table 2). As with our study, however, variation in clearance rates of *Mytilus* veligers is extensive. This variation appears to result from the dependence of clearance rate on food concentration (Riisgård et al. 1981; Jespersen and Olsen 1982; Sprung 1984), body size (Jespersen and Olsen 1982; Sprung 1984) and temperature (Riisgård et al. 1981; Sprung 1984, 1985). The maximum clearance rate observed in our study, 922 $\mu\text{L veliger}^{-1} \text{ day}^{-1}$, is 50–67% lower than the maximum rates reported for *Mytilus* veligers (Riisgård et al. 1981). It is difficult to determine whether this difference represents methodological artifact or is real. We calculated clearance rate based on the ingestion and accumulation of inert particles over a 5 min period, whereas Riisgård et al. (1981) calculated it based on the grazing-induced reduction in cell density over a 3 h period. In addition, our experiment involved the use of unflavored 2.87 μm beads, whereas Riisgård et al. (1981) used natural 3.5 μm *Monochrysis* cells (Table 2). Some invertebrates consume 'algal-flavored' beads at higher rates than unflavored ones (Rassoulzadegan et al. 1984; DeMott 1986). Our clearance rate measurements are likely to be very similar to those of *Dreissena* veligers in nature despite the use of unflavored beads, because the beads also approximat-

Table 2. Comparison of clearance rates of *Dreissena polymorpha* and *Mytilus edulis* veligers in relation to temperature and food type and concentration. Modified from Sprung (1984)

Species	Food Type	Food Concentration (cells μL^{-1})	Experimental Temperature ($^{\circ}\text{C}$)	Clearance Rate ($\mu\text{L ind}^{-1} \text{ day}^{-1}$)	Source
<i>Dreissena polymorpha</i>					
	beads	1–100	19–21	245–418 (922 max)	this study
<i>Mytilus edulis</i>					
	<i>Isochrysis</i>	25–365	11–18	48–600	Bayne 1965
	<i>Isochrysis</i>	1.5–5.5	12	274	Riisgård et al. 1980
	<i>Isochrysis</i> + <i>Monochrysis</i>	3–6	15	216–2448	Riisgård et al. 1981
	<i>Isochrysis</i> + <i>Monochrysis</i>	3–~95	17–19	96–816	Jespersen and Olsen 1982
	<i>Isochrysis</i>	1–40	6–18	19–2040	Sprung 1984

ed very closely the diameter of maximum particle retention (Riisgård et al. 1981; Sprung 1989). Finally, the possibility that *Dreissena* veliger clearance rates may be lower than those of their marine counterparts must be considered in the light of Kryger and Riisgård's (1988) findings that water transport rates of freshwater bivalve adults are 50–88% lower than those of marine bivalves of similar size.

Our use of $2.87 \mu\text{m}$ beads was justified by the restricted food niche of *Dreissena* veligers. Particle retention efficiency of *Dreissena* veligers apparently peaks between 1.59 and $2.00 \mu\text{m}$ equivalent spherical diameter; other particles between 1 and $4 \mu\text{m}$ are consumed at lower rates (Sprung 1989). Sprung's results are supported by our unsuccessful attempts to feed *Dreissena* veligers a nutritious cryptomonad ($7 \times 14 \mu\text{m}$; dry weight $\sim 9 \times 10^{-5} \mu\text{g cell}^{-1}$) that is readily ingested by a broad array of rotifers, cladocerans, copepods, and by settled *Dreissena* (HJ MacIsaac, pers. obs.).

Our experiments, conducted between densities of 1 and $100 \text{ beads } \mu\text{L}^{-1}$ (Fig. 3), provide no evidence for the existence of an incipient limiting concentration i.e. the bead level above which clearance rate decreases. This finding is somewhat surprising considering that the incipient limiting concentration for *Mytilus* veligers feeding on 3 to $7 \mu\text{m}$ *Isochrysis galbana* cells lies between 5 and $10 \text{ cells } \mu\text{L}^{-1}$ (Sprung 1984). It seems quite likely that clearance rate would have been affected at high but not low bead densities had our experiments lasted longer than five minutes (Fig. 3). For example, doubling the experimental period to ten from five minutes would not affect clearance rates of veligers in solutions with low bead concentrations because these animals did not have full stomachs at the end of five minutes exposure, and any increase in the number of beads ingested and retained would be offset by a commensurate increase in experimental duration (see Eq. 1). By contrast, the ingestion of additional beads by veligers exposed to high bead concentrations would have required the excretion of an equivalent number of beads already in the digestive tract because these individuals appeared to have full stomachs at the end of five minutes exposure (see below).

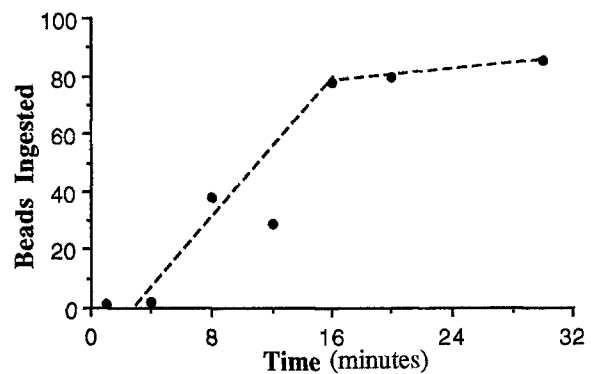


Fig. 5. Median number of beads ingested by veligers in a suspension containing $25 \text{ beads } \mu\text{L}^{-1}$ (Exp. 3). Lines were fitted by eye

This would result in a reduction in clearance rate because only the denominator of the clearance rate formula (Eq. 1) would increase. Our clearance rate values for higher bead densities (e.g. $100 \text{ beads } \mu\text{L}^{-1}$) may overestimate steady state clearance rates and should, therefore, be viewed as maximal.

Veliger gut passage time, estimated from the accumulation of beads in animals exposed to solutions containing $25 \text{ beads } \mu\text{L}^{-1}$, is between 14 and 18 minutes (Fig. 5). The number of beads ingested and retained appeared to level off at $\sim 80 \text{ beads veliger}^{-1}$. Assuming that a full stomach contains 80 beads and that water is cleared at $319 \mu\text{L veliger}^{-1} \text{ day}^{-1}$ (our overall mean; Fig. 3), it would take veligers 4 , 72 and 361 min to fill the stomach when exposed to suspensions containing 100 , 5 , and $1 \text{ bead } \mu\text{L}^{-1}$, respectively. These calculations support the hypothesis that veligers exposed to suspensions containing low bead concentrations (Fig. 3) were clearing water at a maximum, steady-state rate (cf. Riisgård et al. 1980). By contrast, animals exposed to high bead concentrations had reached, or were close to, gut saturation and a substantially longer incubation period would be necessary to achieve a lower, steady-state clearance rate. Clearance rates measured at low bead concentrations ($\leq 10 \text{ beads } \mu\text{L}^{-1}$; Fig. 3) are the most instructive

because they most closely approximate food levels encountered by veligers in nature (Riisgård et al. 1981).

Dreissena filtering impacts

The mean density of settled zebra mussels inhabiting Hen Island Reef during October 1990 (2.68×10^5 ind. m^{-2}) and October 1991 (2.53×10^5 ind. m^{-2}) are among the highest reported for *Dreissena* or any other mollusc in a freshwater ecosystem (see Stańczykowska 1977; Burky 1983; Mackie et al. 1989). The size-frequency distribution of the population during October 1990 was skewed toward small (≤ 5 mm) size-classes, but mussels as large as 29 mm were found (Fig. 6). Our calculations of settled *Dreissena* filtering impact assume a well-mixed water column of 7 m, approximating the mean depth of Lake Erie's western basin. The Hen Island Reef population had a potential filtering impact during October 1990 of $132 m^3 m^{-2} day^{-1}$ based on Kryger and Riisgård's (1988) formulae (Table 1), and $115 m^3 m^{-2} day^{-1}$ and $25 m^3 m^{-2} day^{-1}$ based on equations derived from Krondratév's (1963) and Michéev's (1966) data, respectively. Kryger and Riisgård's (1988) original equations may provide the most reliable estimates of *Dreissena* filtering impact because their experiments were conducted with natural food (*Chlorella*) and minimally-disturbed animals. Clearance rates of settled *Dreissena* are sensitive to the type of 'food' (e.g. clay, Kondratév 1963) used (Kryger and Riisgård 1988), and disturbed animals may require 24 h or longer to resume normal feeding activities (Reeders et al. 1989). Though filtering impact varies considerably between calculation methods, these formulae indicate that settled *Dreissena* populations on Hen Island Reef are theoretically capable of filtering a 7 m water column between 3.5 and 18.8 times per day.

Our results indicate that settled *Dreissena* in the western basin of Lake Erie possess an unprecedented capability to filter the water column. The tremendous filtering potential of this population results from the combined effects of high population density (Fig. 6) and high per capita clearance rates (Table 1). Because the western basin of Lake Erie is usually well mixed vertically during summer months, with differences between surface and bottom waters usually confined to $1^\circ C$ or less (Schertzer et al. 1987), settled *Dreissena* should have access to phytoplankton throughout the water column at most times. Our survey of 4 sites on Hen Island Reef (mean depth = 4.4 m) indicates that chlorophyll *a* concentration was low ($\leq 2 \mu g L^{-1}$) throughout most of the water column, and particularly so immediately above *Dreissena* beds (Fig. 7). Water temperature was almost invariant over the depths sampled, ranging from 23.0 to $23.3^\circ C$, and cannot account for the observed patterns. Localized phytoplankton depletion associated with suspension-feeding *Dreissena* is consistent with the observed patterns however. Moreover, studies conducted in western Lake Erie prior to the introduction of *Dreissena* failed to reveal significant differences in chlorophyll *a* concentration between surface and bottom waters at any six

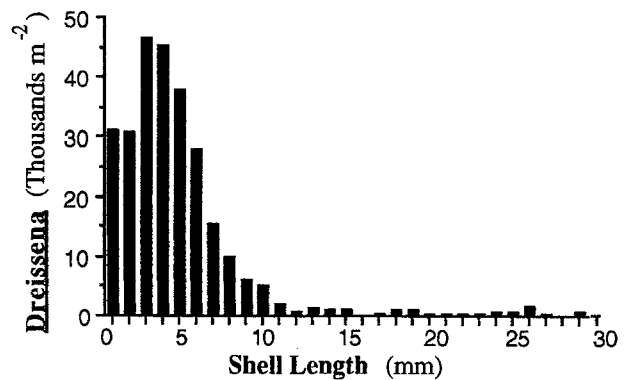


Fig. 6. Mean size distribution of settled *Dreissena* inhabiting Hen Island Reef west of Pelee Island in western Lake Erie ($n=9$ sites) in October 1990

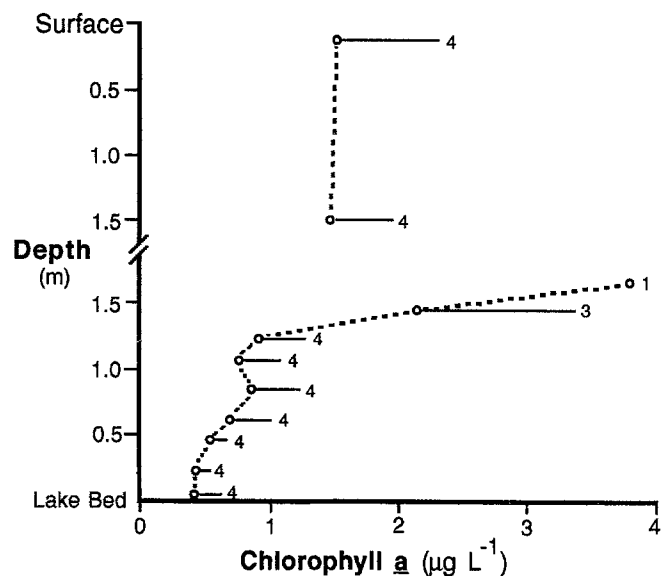


Fig. 7. Mean ($+1$ SE) corrected chlorophyll *a* concentration at different depths at four sites in western Lake Erie adjacent to Hen Island Reef. Depth at the sites varied between 3.9 and 4.8 m and averaged 4.4 m. collections were made every 20 cm off the lake bed, as well as at 0.2 and 1.5 m depth, on 5–6 September 1991 (see methods). Numbers beside SE bars indicate the number of sites sampled

sites (JH Leach, unpublished data). The localized chlorophyll *a* depletion pattern apparent in our study is not surprising because the survey was conducted on two windless days and was preceded by another. Water flow rates over *Dreissena* beds were quite low (0.9 to $3.4 cm s^{-1}$), doubtless in association with the calm weather, and served to maintain the vertical chlorophyll *a* concentration gradient. Our preliminary survey was not fully characteristic of the conditions experienced by settled *Dreissena*, nor of their influence on vertical patterns of chlorophyll *a* concentration, because Lake Erie experiences major storms approximately every ten days during summer and every five days during fall, early winter and spring (Bedford and Abdelrhman 1987). These storms would increase the turbulent transfer rate of ses-

ton to benthic *Dreissena* and destroy vertical gradients in chlorophyll *a* concentration.

Other workers have also reported impressive filtering impacts for bivalve molluscs in both freshwater and marine ecosystems. For example, Reeders et al. (1989) calculated that *Dreissena* populations at densities of 190 and 170 individuals m^{-2} filtered the entire water columns of Lakes IJsselmeer and Markermeer (the Netherlands) in 11 days and 18 days, respectively. A littoral population of *Dreissena* at a density of 300 individuals m^{-2} was capable of filtering the entire epilimnion of Mikolajskie Lake, Poland, twice during the six months of the productive season (Stańczykowska et al. 1976). Another freshwater bivalve introduced to North America, *Corbicula fluminea*, was potentially capable of clearing the overlying water column of Meyers Branch, Savannah River, Georgia, in twenty-one hours in regions where it was abundant (Leff et al. 1990). Peterson and Black (1991) observed that chlorophyll concentration in incoming tides at Shark Bay, Australia, was progressively depleted by suspension-feeding, intertidal bivalves. Similarly, intertidal mussels in the St. Lawrence River estuary depleted phytoplankton concentration close to the seabed at current velocities between ~ 4 and 15 cm s^{-1} (Fréchette et al. 1989). A mixed mollusc community in San Francisco Bay was capable of filtering the water column at least once per day, and may have regulated phytoplankton biomass during summer and fall in consequence (Cloern 1982). The closest analogue to the filtering impact exerted by *Dreissena* in western Lake Erie was reported for a *Mytilus* population inhabiting the Danish fjord Limfjorden, the daily filtering capability of which was equivalent to ten times the water column volume (Jørgensen 1980). However, the fjord was often stratified by temperature and salinity, rendering the effectiveness of mussel filtering activities to benthic waters only.

Based on Kryger and Riisgård's (1988) original clearance rate equations for settled mussels and a mean veliger clearance rate from our experiments of $319 \mu\text{L ind}^{-1} \text{ day}^{-1}$ (Fig. 3), settled *Dreissena* of 1–29 mm possess respective clearance rate capabilities 30–38871 times greater than those of veligers on an individual basis. However, a different pattern emerges if mass-specific clearance rates are considered. The mass-specific clearance rate of a $170 \mu\text{m}$ veliger, calculated using our average of $319 \mu\text{L ind}^{-1} \text{ day}^{-1}$ and Jespersen and Olsen's (1982) shell length – dry weight equation for *Mytilus* veligers, is 6 to 9 times higher than those of 6.6 and 31 mm *Dreissena*, respectively (Kryger and Riisgård 1988).

On a population basis, settled *Dreissena* clearance capacities are between 147 (2800×10^3 veligers m^{-2} ; 400 veligers L^{-1}) and 1162 (356×10^3 veligers m^{-2} ; 50.8 veligers L^{-1}) times greater than those of veligers (Table 1). These calculations suggest that the impact of benthic *Dreissena* should greatly exceed that of planktonic larvae at most times. It should be recognized, however, that direct comparisons between clearance rates and filtering impacts of larval and adult mussels are complicated by a number of factors. On the one hand,

our use of inert beads may overestimate clearance rate differences when compared to adult *Dreissena* fed natural foods (Kryger and Riisgård 1988). On the other hand, the narrow food niche of veligers (Sprung 1989) contrasts with the catholic diet of adults which are capable of ingesting foods between $0.7 \mu\text{m}$ (Sprung and Rose 1988) and $750 \mu\text{m}$ (Ten Winkel and Davids 1982). The suite of resources consumed by adult mussels is therefore much broader than that ingested by veligers. Finally, veliger densities in western Lake Erie are more variable temporally than those of adults (Leach 1992). This difference should result in a more ephemeral impact by veligers on water quality. Nevertheless, when present at peak density (628 ind. L^{-1} ; Leach 1992) veligers clearing water at $319 \mu\text{L ind.}^{-1} \text{ day}^{-1}$ could process $\sim 20\%$ of the water column per day. This value approximates that calculated for *Daphnia* in western Lake Erie (Wu and Culver 1991), but is considerably lower than the 40–50% of the water column filtered by *Mytilus* veligers in Isefjord, Denmark (Jørgensen 1981).

The filtering impact of settled *Dreissena* should also greatly exceed those of other herbivorous zooplankton in western Lake Erie at most times. The late August 1990 zooplankton community was dominated by *Polyarthra* spp. (*P. vulgaris*, *P. remata* and *P. major*) both numerically and by filtering impact ($1.4 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$) (Table 1). *Bosmina longirostris*, the most common cladoceran, had the second highest filtering impact ($0.3 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$) (Table 1). Most other herbivorous zooplankton species had negligible filtering effects during late August 1990. These results would vary by depth, season, and from year to year in relation to zooplankton species successions. For example, our 1991 survey revealed that while *Polyarthra* again dominated the plankton community numerically at each depth, copepod nauplii had the greatest potential impact on phytoplankton (Table 3). *Daphnia* appeared to be a relatively unimportant component of the plankton community during both of our surveys (Tables 1, 3). For example, *Daphnia*'s contribution to community grazing was only 9, 15 and 24% at 1, 2.5, and 3.5–4.5 m, respectively, during our 1991 survey (Table 3). These findings contrast sharply with the results and interpretations of Wu and Culver (1991), who also studied herbivory in western Lake Erie. *Daphnia retrocurva* and *D. galeata mendotae* were collectively capable of processing up to $5.1 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$ and $2.5 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$ in nearshore and offshore waters, respectively, between June and July 1989, assuming water column depth of 6 and 10 m (Wu and Culver 1991). Despite *Daphnia*'s greater contribution to community clearance rate during early summer, its impact on phytoplankton stocks was almost certainly overshadowed by that of settled *Dreissena*. May through November mean chlorophyll *a* concentration declined by 66% in western Lake Erie between 1988 and 1991 coincident with the expansion of mussel populations (Leach 1992; JH Leach, unpublished data); seasonal variability in chlorophyll *a* concentration also declined during this period (Leach 1992). These patterns are more consistent with those of a growing suspension-feeding population active throughout the year (i.e. settled *Dre-*

Table 3. Spatial variability in mean densities and filtering impacts of major herbivorous zooplankton taxa near Hen Island reef based on the 5–6 September 1991 survey. Values are based on two repli-

cate plankton samples from each of four sites at each depth. Filtering impact was calculated as per Table 1

Taxon	Depth (m)					
	1		2.5		3.5–4.5	
	Population Density (Thousands m^{-2})	Filtering Impact ($\text{m}^3 \text{m}^{-2} \text{d}^{-1}$)	Population Density (Thousands m^{-2})	Filtering Impact ($\text{m}^3 \text{m}^{-2} \text{d}^{-1}$)	Population Density (Thousands m^{-2})	Filtering Impact ($\text{m}^3 \text{m}^{-2} \text{d}^{-1}$)
<i>Keratella</i> spp.	300	0.01	710	0.03	470	0.02
<i>Polyarthra</i> spp.	900	0.31	1430	0.50	690	0.24
veligers	10	<0.01	40	0.01	50	0.02
<i>Bosmina</i>	40	0.13	130	0.38	70	0.22
<i>Eubosmina</i>	10	0.03	30	0.10	40	0.13
<i>Daphnia</i> spp.	10	0.13	40	0.51	60	0.63
<i>Diaphanosoma</i>	10	0.05	30	0.22	40	0.34
<i>Leptodiaptomus minutus</i>						
copepodids	10	0.06	20	0.14	20	0.16
copepods	10	0.05	10	0.06	10	0.04
nauplii	180	0.66	370	1.37	210	0.76
Total Volume Filtered		1.44		3.32		2.56
% Contribution by <i>Daphnia</i>		9		15		24

issena) than with those of seasonally abundant herbivores like *Daphnia* and *Dreissena* veligers. Two additional pieces of information support the hypothesis that the major suspension-feeders in western Lake Erie are sessile *Dreissena* and not *Daphnia* or *Dreissena* veligers. First, Wu and Culver (1991) reported large decreases in 'inedible' as well as 'edible' phytoplankton in western Lake Erie between 1988 and 1989. While all three herbivore groups apparently can consume small 'edible' phytoplankton and thus account for its decline, neither larval *Dreissena* (Sprung 1989) nor *Daphnia* (Lampert 1987) consume larger 'inedible' forms. By contrast, adult *Dreissena* can ingest and perhaps limit the abundance of large 'inedible' foods including *Ankistrodesmus* (Ten Winkel and Davids 1982) and *Pediatrum* (MacIsaac, pers. obs.), particularly when starved. Second, whereas May to November chlorophyll *a* concentration was consistently lower in western Lake Erie in 1989 than in 1988 (Leach 1992), a consistent converse pattern was not evident for *Daphnia* filtering impact (grazing rate *sensu* Wu and Culver 1991). These findings are inconsistent with Wu and Culver's hypothesis and indicate that daphnids were probably not the primary agents responsible for the decline in chlorophyll *a* concentration. A more likely scenario incorporates settled *Dreissena* as the primary suspension-feeder determining gross chlorophyll *a* level, upon which are added smaller, seasonal contributions by *Daphnia*, larval *Dreissena*, and other zooplankton.

It seems likely that large quantities of matter and energy are being redirected by sessile *Dreissena* from pelagic to benthic foodwebs. This redirection of energy provides cause for concern for commercial fisheries on Lake Erie. Many of the exploited fish species, including walleye (*Stizostedion vitreum vitreum*) and yellow perch

(*Perca flavescens*), are zooplanktivorous during some developmental stages and would be adversely affected by reductions in phytoplankton and zooplankton stocks. Small rotifers declined by 75% in abundance in western Lake Erie between 1988 and 1990, whereas abundances of larger-bodied cladocerans and copepods did not change appreciably or consistently (JH Leach, unpublished data). These patterns support the hypothesis that adult *Dreissena* suppress small- but not large-bodied zooplankton directly by preying on them (MacIsaac et al. 1991). It remains to be determined whether *Dreissena* and zooplankton also compete indirectly for algal resources.

The exceptionally large populations and filtering impacts of *Dreissena* in Lake Erie's western basin result from many interacting factors. Chief among them are the basin's high surface area to volume ratio, its warm, non-stratifying water column (Schertzer et al. 1987), and the relative abundance of rocky substrate. The absolute and relative filtering impact of settled *Dreissena* should decline commensurate with the degree of water refiltration (Fr  chette et al. 1989), which, in turn, is affected by the extent of water column mixing. In addition, our calculations of settled *Dreissena* filtering impact are based on densities observed on Hen Island Reef. Mussel densities on this reef during 1990 were intermediate to those observed on Chickenole Reef (1.4×10^5 ind. m^{-2}) and Sunken Chicken Reef (3.4×10^5 ind. m^{-2}) (Leach 1992), but because reefs and other hard surfaces constitute only 15% of benthic substrates in the western basin (Hartman 1973), the filtering impacts reported above would not apply universally. Filtering impact may also be affected by the duration of mussel activity per day (Walz 1978b), by food concentration, and by water tem-

perature (Reeders and Bij de Vaate 1990). Our calculations assume that mussels filter continuously at 20° C (Kryger and Riisgård 1988), 16–17° C (Kondratév 1963), or 20–22° C (Micheev 1966). Incorporating benthic surface area (15%; Hartman 1973) and daily filtering activity (18.6 hours day⁻¹; Walz 1978b) into our calculations yields a basin-wide, settled mussel filtration impact of 13.9 m³ m⁻² day⁻¹. Even when these additional factors are considered, the filtering impact of settled *Dreissena* is still very impressive and should exceed those of most species of herbivorous zooplankton at most times, even if our calculated values are an order of magnitude too high.

It appears highly unlikely that current population densities of settled mussels in western Lake Erie can be sustained. Densities of settled mussels and planktonic veligers increased 75-fold (Garton and Haag 1990) and 3-fold (Leach 1992), respectively, between 1989 and 1990, yet the number of newly settled postveligers declined by 44% (Garton and Haag 1990). This reduction in recruitment may have been caused by the pre-emption of settling substrates by adults or by cannibalism on settling larvae (MacIsaac et al. 1991). Suitable settling substrate appears to be severely limited in the vicinity of Hen Island Reef; most inhabitable surfaces support large, often layered, populations of *Dreissena*. Satellite colonies (druzes) now occur on some surrounding substrates (sand, mud) hitherto thought to be inhospitable, perhaps as a result of dislodgement from the main colony by natural disturbance (e.g. ice scour). Colonies may provide settled individuals on these substrates with greater structural resistance to subsequent disturbance, and 'new' habitat for settling postveligers.

The low chlorophyll *a* standing stock and extraordinary density of settled mussels in western Lake Erie suggest that intensive food limitation may be forthcoming. Food limitation has been documented in marine systems at mussel densities orders of magnitude lower than those extant in western Lake Erie (Peterson and Black 1987, and references contained therein).

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