

Pumping Rates and Projected Filtering Impacts of Juvenile Zebra Mussels (*Dreissena polymorpha*) in Western Lake Erie

Christopher M. Bunt, Hugh J. MacIsaac,¹ and W. Gary Sprules

Department of Zoology, University of Toronto, Erindale College, Mississauga, Ont., Canada L5L 1C6

Bunt, C.M., H.J. MacIsaac, and W.G. Sprules. 1993. Pumping rates and projected filtering impacts of juvenile zebra mussels (*Dreissena polymorpha*) in western Lake Erie. *Can. J. Fish. Aquat. Sci.* 50: 1017–1022.

Small-bodied (2–11 mm), settled zebra mussels (*Dreissena polymorpha* Pallas) comprise up to 90% of individuals inhabiting reefs in western Lake Erie. We assessed pumping rates of these size classes of *D. polymorpha* by injecting an inert dye into inhalant filtering currents and monitoring exhalant flows using high-resolution videography. Pumping rates ranged between 0.20 and 4.45 mL·ind⁻¹·h⁻¹ and increased in relation to mussel shell length. Based on 1990 size–frequency distributions for reefs in western Lake Erie and our pumping rate – shell length regression, small settled *D. polymorpha* were theoretically capable of pumping between 39 and 96% of the water column daily. Small-bodied mussels inhabiting Sunken Chicken Reef were collectively capable of processing between 110 and 400% of the values previously reported for *Daphnia*. Recent changes in water quality in western Lake Erie could be primarily related to zebra mussel filtering activities, including those of small-bodied individuals.

Les individus fixés de petite taille (2–11 mm) composent jusqu'à 90 % des populations de moules zébrées (*Dreissena polymorpha* Pallas) qui habitent les récifs de l'ouest du lac Érié. Nous avons calculé le rythme de pompage de ces classes de taille de *D. polymorpha* en injectant un colorant inerte dans les courants aspirés au filtrage et en contrôlant les courants rejetés par vidéographie à haute résolution. Le volume pompé se situait entre 0,20 et 4,45 mL·ind⁻¹·h⁻¹, et augmentait en fonction de la longueur des mollusques. À partir des distributions des fréquences par taille calculées en 1990 sur les récifs de l'ouest du lac Érié et de notre régression volume de pompage – longueur de la coquille, il apparaît que les petites moules zébrées fixées étaient théoriquement capables de pomper chaque jour entre 39 et 96 % de la colonne d'eau. Les moules de petite taille habitant le récif Sunken Chicken étaient collectivement capables de traiter entre 110 et 400 % du volume signalé antérieurement pour *Daphnia*. Les changements récemment observés dans la qualité de l'eau de l'ouest du lac Érié pourraient être avant tout liés aux activités de filtrage des moules zébrées, notamment celles des individus de petite taille.

Received May 21, 1992

Accepted December 2, 1992
(JB497)

Reçu le 21 mai 1992

Accepté le 2 décembre 1992

Zebra mussels (*Dreissena polymorpha* Pallas) are now a component of the benthos in all five of the North American Great Lakes (Griffiths et al. 1991). One of the primary influences zebra mussels are expected to have on Great Lakes ecosystems is a general grazing-induced reduction in phytoplankton abundance. *Dreissena polymorpha* adults are capable of filtering particles ranging in diameter from 0.7 µm (Sprung and Rose 1988) to 750 µm (Ten Winkel and Davids 1982). Considering the broad size classes of food ingested, and the extraordinary population densities of settled animals — up to 3.41×10^5 ind·m⁻² in western Lake Erie (MacIsaac et al. 1991) — *D. polymorpha* may well become the primary herbivore in some regions of the Great Lakes, particularly in western Lake Erie and Lake St. Clair.

The western basin of Lake Erie has undergone substantial change during the past 4 yr coincident with the establishment and growth of *D. polymorpha* populations. For example, Leach (1992) reported that mean Secchi disc transparency in the western basin increased by 85% between 1988 and 1989, while chlorophyll *a* concentrations during the same years decreased

by 43%. These changes were further accentuated during 1990 (Leach 1992). To assess the role of *D. polymorpha*, if any, in promoting these changes, the size–frequency distributions, length-specific clearance rates, and densities must be known for populations in western Lake Erie.

Clearance rate refers to the volume of water from which a suspension-feeding animal has removed all of the food per unit time. A number of studies have been undertaken to quantify clearance rates of *D. polymorpha* of different body sizes (Kryger and Riisgård 1988, and references cited therein). In these studies, clearance rate was measured indirectly by monitoring the depletion of suspended natural algal foods or food analogues, including clay and graphite particles. Clearance rate is equal to the rate at which water flows through the mantle cavity (i.e., pumping rate) only when particles are strained and retained with 100% efficiency (Coughlan 1969). Jørgensen et al. (1984) reported that *D. polymorpha* retained particles >4 µm with 100% efficiency. To date, however, no measurements of either clearance rate or pumping rate have been made for *D. polymorpha* of ≤6.5 mm shell length. Clearance rates have not been measured for juvenile *D. polymorpha*, presumably due to difficulties in handling small individuals and, more importantly, because each individual would be capable

¹Present address: Department of Biological Sciences, University of Windsor, Windsor, Ont., Canada N9B 3P4.

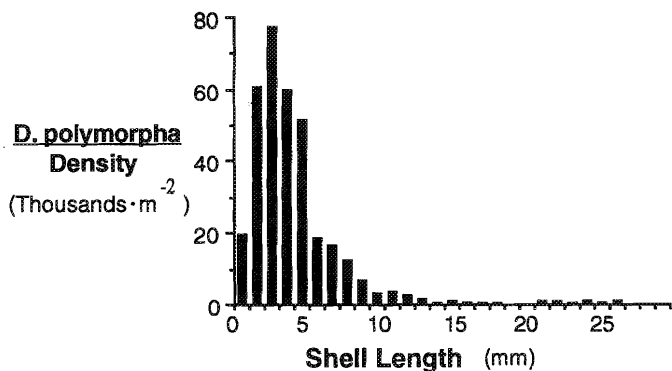


FIG. 1. Mean size–frequency distribution of *D. polymorpha* from eight sites on the Sunken Chicken Island reef in the western basin of Lake Erie during October 1990. Population densities and size distributions were estimated from the collection of representative rock samples from each site (modified from Leach 1992).

of depleting food resources only slightly. Knowledge of clearance and pumping rates is essential, however, to calculations of population filtering impact because a large percentage of some populations, including those in Lake St. Clair (Griffiths et al. 1991) and western Lake Erie (Fig. 1; Leach 1992), are composed of individuals of <10 mm shell length. The purpose of this study is to directly measure the pumping rates of these abundant size classes of *D. polymorpha* (2–12 mm shell length) using a nontoxic dye and high-resolution videography. In addition, we estimate the filtering potential of small (<12 mm) *D. polymorpha* inhabiting three reefs in western Lake Erie.

Methods and Materials

Dreissena polymorpha were gathered near Wheatley, Ontario, in the west-central basin of Lake Erie in mid-June 1991. Animals were maintained in controlled environment chambers at 20°C in aerated aquaria containing glass-fibre-filtered (Whatman 934-AH; retention to 1.5 µm) Erindale Pond water (Erindale College, University of Toronto, Mississauga, Ont.). Batch cultures of the unicellular, motile alga *Cryptomonas* sp. (7 × 14 µm), a preferred food for *D. polymorpha* (Ten Winkel and Davids 1982), were provided every 2 d at a concentration of approximately 9 × 10³ cells·mL⁻¹ (1.46 µg dry wt·mL⁻¹). Animals were exposed to a 15 h light : 9 h dark photoperiod, which approximated natural conditions at the time of collection. Animals were acclimated to these conditions for at least 10 d prior to experimentation.

Individual mussels, with shell lengths measuring 2–12.5 mm, that appeared to be healthy (i.e., siphons extended) were haphazardly selected during June and July 1991 for experimentation. Shell length was measured to the nearest 0.01 mm with a Fowler ultra-cal II digital caliper. A microcomputer-based caliper measurement system (Sprules et al. 1981) was used to measure the major and minor axes (to the nearest 0.001 cm) of the elliptical exhalant siphon aperture of a pumping individual in a small glass aquarium (5 × 5 × 5 cm). The means of four measurements per axis per individual were used in the determination of pumping rate. In order for the siphon dimensions to remain relatively constant between this measurement process and the dye-injection process, it was necessary to maintain the constancy of the microenvironment around the mussels at all times. The siphon measurement process and the dye-measurement process were conducted in filtered Erindale

Pond water at 20°C with a *Cryptomonas* sp. density of approximately 5 × 10³ cells·mL⁻¹ (0.81 µg·mL⁻¹) to simulate natural food conditions. This food density falls within the range found in western Lake Erie and is apparently below *D. polymorpha*'s incipient limiting concentration (i.e., the food level above which pumping rate declines (Walz 1978)). In addition, care was taken to ensure that shells were fully gaped and siphons fully extended before measurements were made. As such, all mussels were pumping at or near their maximum capacity (Jørgensen et al. 1988). The exhalant plume was made visible by injecting a small quantity of red, unflavoured food colouring (Club House Foods Inc.) near the aperture of the inhalant siphon of a pumping mussel using a borosilicate micropipette with a drawn out tip. On the rare occasion that a test animal responded to the dye, pumping ceased only for a few seconds and was most probably the result of hydromechanical disturbance associated with the micropipette tip. Coughlan and Ansell (1964) reported similarly insignificant responses to a nontoxic dye by their siphonate bivalves.

Exhalant flow velocity was determined by recording the field directly adjacent to the exhalant siphon of a pumping mussel with a high-resolution video system coupled with a time–date generator. This process was performed in a 7-L aquarium with the same food concentration (5 × 10³ cells·mL⁻¹) and temperature (20°C) as the siphon measurement process. Mussels were allowed to acclimate for at least 5 min before recording began. At this time, a stopwatch on the time–date generator was started and dye was carefully introduced close enough to the inhalant siphon that it was drawn within the mantle cavity (Fig. 2A). This was best achieved by guiding the micropipette from above rather than from the side of the aquarium. Each trial lasted approximately 5 min, during which it was assumed that the exhalant aperture area remained constant as previously measured (C.M. Bunt, personal observation). A valid plume was one with a clearly discernable leading edge and a linear and laminar flow path over the distance measured (Fig. 2B).

Following repeated dye injections, a reference scale was placed in the field of view of the camera at approximately the same angle as the exhalant plumes to correct for camera magnification and the angle of the exhalant plume travel. The velocity of the exhalant plume was measured over distances from 1.25 to 10 mm depending on animal size. Exhalant flow velocities were transcribed by marking a distance, *l*, on the video screen and determining the time, *t* (to the nearest 1/100 s from the time–date generator), for the plume to traverse the distance. From five to nine travel times were averaged per individual for use in the pumping rate formula for animals of each size class.

Pumping rate (PR, millilitres per individual per hour) was calculated as

$$PR = [(\pi \cdot a \cdot b) / 4] \times (3600 / l \cdot t)$$

where *a* and *b* are the mean minor and major axes, respectively, of the exhalant siphon (centimetres), *l* = length of exhalant plume travel (centimetres) and *t* = the time (seconds) required for the plume to travel distance *l*. Shell lengths, siphon areas, plume velocities, and computed pumping rates for individual mussels are available on request from the authors.

Results and Discussion

Shell length represents an easily measured variable that is correlated with less readily quantifiable aspects of *D. polymorpha* morphology and feeding biology. For example,

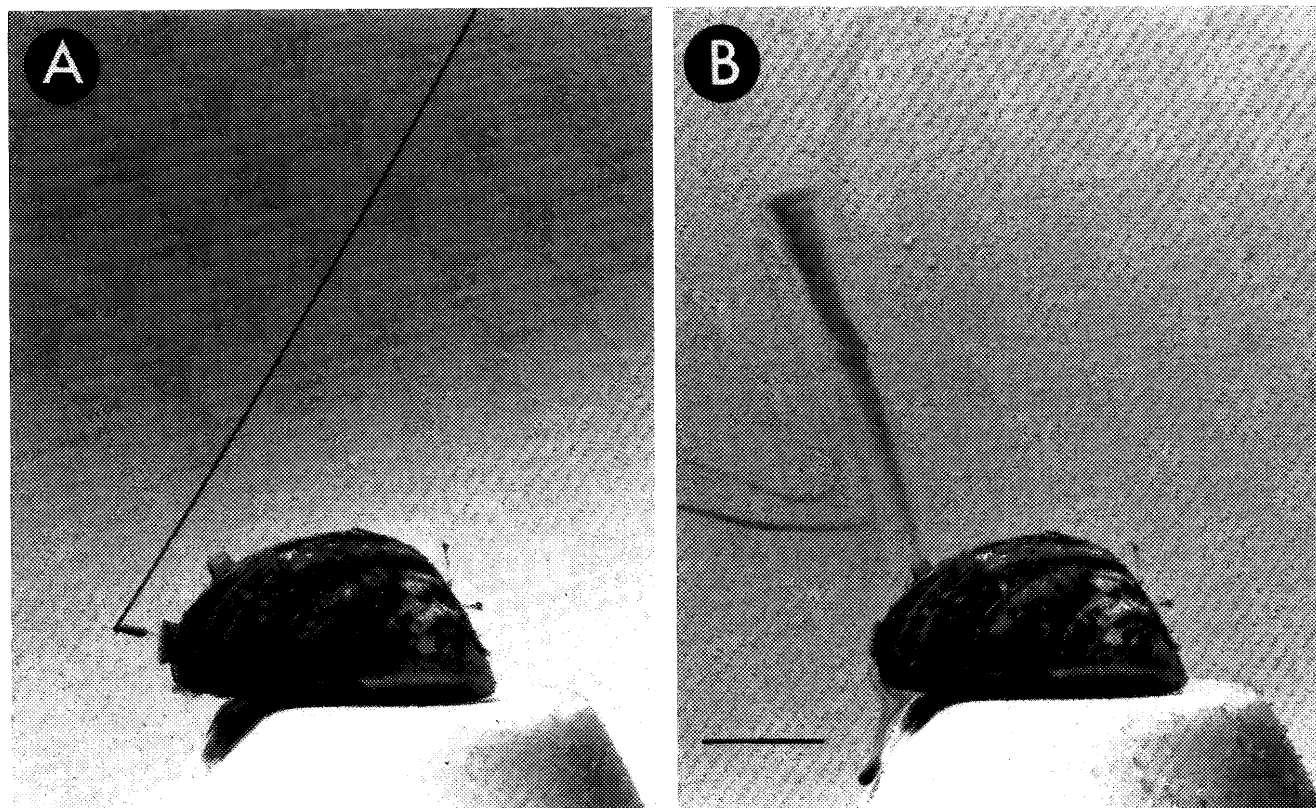


FIG. 2. (A) Dye inhalation into the mantle cavity of a zebra mussel and (B) the subsequent linear and laminar exhalation of the dye. Note the distinct leading edge of the exhalant plume. Bar = 5 mm.

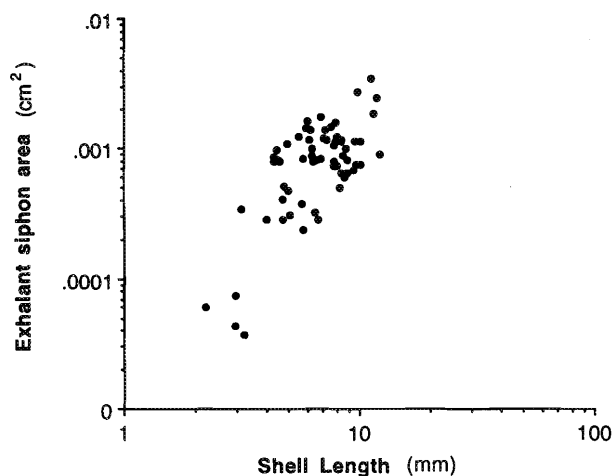


FIG. 3. Exhalant siphon aperture surface area as a function of shell length (Pearson's correlation, $r = 0.57$, $p < 0.0001$, $n = 65$).

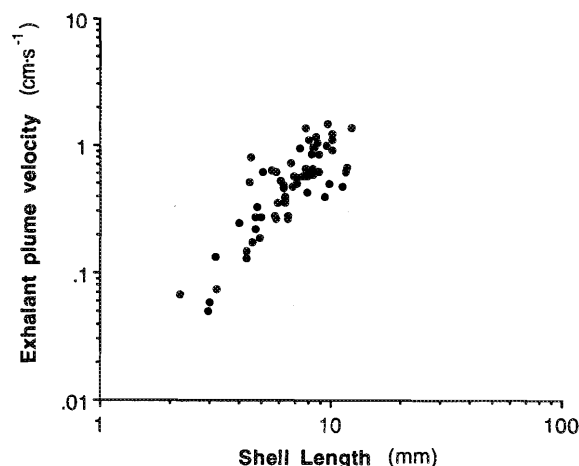


FIG. 4. Exhalant plume velocity determined from video footage of mussels (2–11 mm) pumping dye (Pearson's correlation, $r = 0.71$, $p < 0.0001$, $n = 65$).

both exhalant siphon surface area (Pearson's correlation, $r = 0.57$, $p < 0.0001$, $n = 65$; Fig. 3) and exhalant plume velocity (Pearson's correlation, $r = 0.71$, $p < 0.0001$, $n = 65$; Fig. 4) were positively correlated with mussel shell length. These findings were not surprising, as MacIsaac et al. (1991) reported that exterior inhalant siphon diameter and shell length were positively correlated in *D. polymorpha*. Moreover, the amount of water processed by siphonate bivalves (e.g., *Corbicula*, *Dreissena*) can increase with mussel shell length

(Morton 1971; Leff et al. 1990; Reeders and Bij de Vaate 1990) (Fig. 5) only if exhalant siphon cross-sectional area and/or plume velocity increase concomitantly. Jørgensen et al. (1988) observed that the pumping rate of *Mytilus edulis* was positively correlated with siphon area and was maximal when valves were fully gaped and siphons fully extended.

Pumping rate, determined as the product of exhalant siphon surface area and exhalant plume velocity, was also related to *D. polymorpha* shell length (Fig. 5). The mechanistic basis for

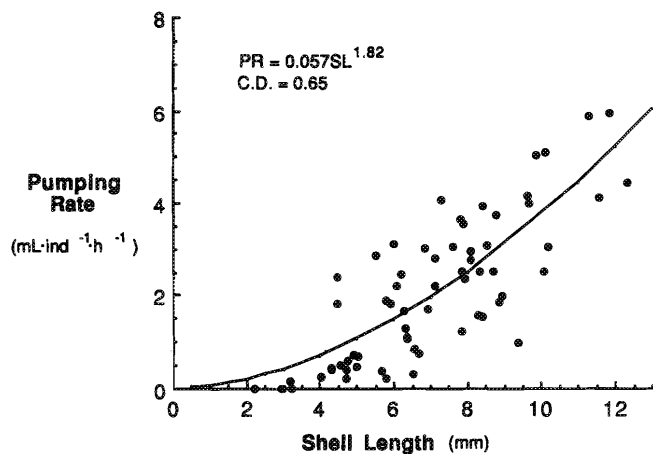


FIG. 5. Relationship between pumping rate and shell length of *D. polymorpha* (2–11 mm shell length) as determined by the dye pumping process. The nonlinear least squares regression line is shown (ANOVA, regression coefficient = 1.82, $p < 0.0005$, $n = 65$). PR = pumping rate, SL = shell length, and C.D. = coefficient of determination.

this nonlinear relationship is not clear, although Bayne et al. (1976) suggested that it may result from an underlying association between gill area or gill ostia area and animal dry weight.

Our study is the first to assess pumping rate capabilities of Lake Erie *D. polymorpha* < 7 mm. Animals between 2 and 7 mm may process up to 0.2 and 2.0 mL·ind⁻¹·h⁻¹, respectively (Fig. 5). These values are at least an order of magnitude lower than those of large (>20 mm) *D. polymorpha* (Kryger and Riisgård 1988) (see Fig. 6) but are equal to or greater than individual clearance (= filtering) rates of *Daphnia galeata mendotae* and *D. retrocurva* (0.03–0.47 mL·ind⁻¹·h⁻¹ for animals 0.49–1.54 mm in body length), the primary suspension-feeding zooplankters in western Lake Erie (Wu and Culver 1991).

If *D. polymorpha* are 100% efficient at clearing particles >4 μm from suspension, as suggested by Jørgensen et al. (1984), then clearance rate should equal pumping rate. We superimposed our pumping rates on Kryger and Riisgård's (1988) compilation of clearance rate data; similarities and differences exist between the various studies (Fig. 6). For example, our measured and extrapolated pumping rates for individuals between 10 and 12.5 mm shell length are between those of large mussels as measured by Micheev (1966) and Morton (1971) but are considerably lower than those measured by Kondratev (1963), Alimov (1969), and Kryger and Riisgård (1988) for *D. polymorpha* of comparable size (Fig. 6).

Variation in reported clearance rates (Fig. 6) is extensive and possibly the result of a number of factors including temperature (Hinz and Scheil 1972; Jørgensen et al. 1988; Reeders and Bij de Vaate 1990), food type and concentration (Ten Winkel and Davids 1982; Sprung and Rose 1988; Reeders et al. 1989; Reeders and Bij de Vaate 1990), and perhaps experimental method (see review, Kryger and Riisgård 1988). For example, Kryger and Riisgård (1988) speculated that studies conducted with suspensions of graphite particles may have underestimated filtration rate by virtue of the high particle densities used, inefficient retention of particles, or particle unpalatability.

Disturbance associated with handling of mussels prior to experimentation can also affect resultant filtration rates. Reeders et al. (1989) reported that clearance rates continued to

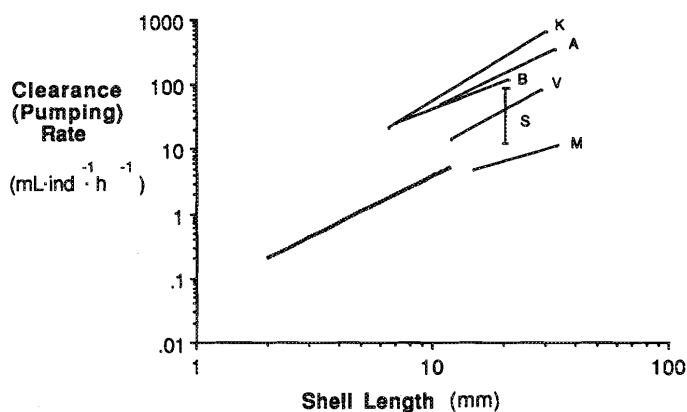


FIG. 6. Regression relationships between adult *D. polymorpha* clearance rate (solid lines) (see Kryger and Riisgård 1988), juvenile *D. polymorpha* pumping rate (broken line; Fig. 5), and shell length. Modified from Kryger and Riisgård (1988). K = original Kryger and Riisgård (1988) data, A = Alimov (1969), B = Kondratev (1963), V = Micheev (1966), S = Stańczykowska (1976) with SE bars, and M = Morton (1971).

increase for at least 24 h after disturbance. This finding contradicts our observation of a rapid response by disturbed mussels. In most instances, experimental animals appeared to fully open valves and extend siphons within minutes (approximately <2–5 min) of disturbance. Coughlan and Ansell (1964) stated that fully extended siphons provide a good indication of pumping characteristics of undisturbed animals. Disturbance (e.g., intensity of culture aeration) during the acclimation period prior to experimentation could influence animal sensitivity during subsequent handling and testing, but its effect has not been addressed. Furthermore, it remains to be determined whether each of the above-mentioned factors, explored with adult *D. polymorpha*, applies to juvenile individuals as well.

Potential Juvenile Mussel Filtering Impact

By combining mean size–frequency distribution data from three reefs in Lake Erie's western basin with the allometric equation for pumping rates ($PR = 0.057 \cdot SL^{1.82}$), it is possible to estimate the potential effect that the previously unstudied juvenile mussels have on phytoplankton abundance and, indirectly, on water clarity. Based on observed 1990 densities, *D. polymorpha* with shell lengths between 2 and 11 mm were capable of processing a water column equivalent to the mean depth (approximately 7 m) of western Lake Erie between 0.39 and 0.96 times daily (Table 1). The filtering impact of juvenile and adult *D. polymorpha* should be maximized in western Lake Erie because of the basin's unique morphometry. For example, benthic suspension-feeders probably have access to phytoplankton stocks throughout most of the water column at most times during spring, summer, and fall because the basin rarely stratifies, and stratification only persists for brief intervals when it does occur (Schertzer et al. 1987). The short residence time and shallow mean depth would further serve to minimize the localization of *D. polymorpha* induced phytoplankton depletion to benthic waters. The recent decline in chlorophyll *a* concentration and increase in water clarity (Leach 1992) are consistent with our predictions. While adult mussels probably play a greater role in these changes (MacIsaac et al. 1992), the potential filtering rate of juvenile mussels is considerable and

TABLE 1. Mean density of juvenile *D. polymorpha* (2–11 mm) on three reefs in the western basin of Lake Erie (October 22, 1990) and the potential number of times the entire water column ($\bar{x} = 7$ m) can be pumped daily (i.e., turnover rate) according to $PR = 0.057 \cdot SL^{1.82}$, where $PR =$ pumping rate ($\text{mL} \cdot \text{ind}^{-1} \cdot \text{h}^{-1}$) and $SL =$ shell length (mm). Mean *D. polymorpha* densities in each 1-mm size class were multiplied by size-specific pumping rates and then summed to yield total potential impact.

Reef	Sites sampled (n)	Mean <i>D. polymorpha</i> density ($\text{ind} \cdot \text{m}^{-2}$)	Water column turnover rate (d^{-1})
Sunken Chicken Is.	8	310 700	0.96
Chickenolee Is.	8	102 550	0.39
Hen Is.	9	226 375	0.82

should not be ignored. These findings are in contrast with those of Wu and Culver (1991) who concluded that *Daphnia* has a greater effect on water clarity and edible algal concentration than *Dreissena*. Our maximum population filtering rate of $0.96 \cdot \text{d}^{-1}$ for juvenile *D. polymorpha* inhabiting Sunken Chicken Island Reef (Table 1) is 1.1–4.0 times the maximum 1989 offshore ($0.855 \cdot \text{d}^{-1}$) and nearshore ($0.24 \cdot \text{d}^{-1}$) rates, respectively, of *Daphnia* (fig 4a and 4b in Wu and Culver 1991). The effects of *Daphnia* grazing are also likely to be far more transient than those of juvenile *D. polymorpha* because of the ephemeral nature of *Daphnia* populations in Lake Erie (Wu and Culver 1991). On the other hand, *Daphnia* residing in the plankton clearly have the potential to influence surface waters whereas the impact of settled *Dreissena* depends on the extent of water column mixing and whether all animals in a colony have full access to the water column.

Other authors have also documented strong filtering impacts of benthic *D. polymorpha* populations. For example, Stańczykowska et al. (1976) reported that littoral populations of *D. polymorpha* at densities of $300 \text{ ind} \cdot \text{m}^{-2}$ were able to filter the epilimnion of Mikolajskie Lake in Poland twice annually. Moreover, *D. polymorpha* populations in Lakes Stregiel and Taltowisko, Poland, were capable of filtering epilimnetic waters in approximately 5 and 22 d, respectively (Stańczykowska 1968). Hebert et al. (1991) estimated that *D. polymorpha* could filter the entire water column of Lake St. Clair twice daily if densities averaged $6000 \text{ animals} \cdot \text{m}^{-2}$. Reeders et al. (1989) reported that zebra mussel populations orders of magnitude smaller than those in western Lake Erie were able to filter the water columns of two lakes in The Netherlands in 11 and 18 d. Indeed, rather than being perceived as nuisance organisms, zebra mussels are employed in The Netherlands in programs designed to restore water quality in eutrophic lakes (Reeders and Bij de Vaate 1990). Perhaps the closest analog to *D. polymorpha* filtering capacities in Lake Erie comes from *Mytilus* populations in a Danish fjord; Jørgensen (1980) suggested that these mollusc aggregations were capable of filtering the water column 10 times per day. However, because thermal and salinity stratification precluded thorough water column mixing, these mussels were probably limited to refiltering benthic waters many times per day.

We conclude that juvenile *D. polymorpha* have a great potential to filter phytoplankton from, and increase the transparency of, the water column of western Lake Erie. This potential results from the enormous mussel densities in western Lake Erie and from the modest per capita pumping rates of individuals between 2 and 11 mm.

Acknowledgements

This study was supported financially by a postdoctoral fellowship (H.J.M.) and operating grant (W.G.S.) from the Natural Sciences and Engineering Research Council of Canada, by a Renewable Resources grant from the Ontario Ministry of Natural Resources (to W.G.S. and H.J.M.), and by the Great Lakes University Research Fund from Environment Canada. We are grateful to Philip van Wassenaeer and Stephanie Phan for technical assistance, Tom McDougal and Dave Johnson for field assistance, Dr. Nick Collins for the use of his video equipment, Dr. Joe Leach for *D. polymorpha* size–frequency data, and Darren Browning for his photography expertise. Dr. David Culver made some helpful comments on the manuscript, and Dr. Joe Leach saved us the embarrassment of publishing results derived from erroneous computations.

References

- ALIMOV, A.E. 1969. Nekotorye obschie zakonomernosti processa filtracii u dvustvorcatych molljuskov. Zh. Obshch. Biol. 30: 621–631.
- BAYNE, B.L., R.J. THOMPSON, AND J. WIDDOWS. 1976. Physiology: I, p. 135. In B.L. Bayne [ed.] Marine mussels: their ecology and physiology. Cambridge University Press, Cambridge, England.
- COUGHLAN, J. 1969. The estimation of filtering rate from the clearance of suspensions. Mar. Biol. 2: 356–358.
- COUGHLAN, J., AND A.D. ANSELL. 1964. A direct method for determining the pumping rate of siphonate bivalves. J. Perm. Cons. Int. Explor. Mer 29: 205–213.
- GRIFFITHS, R.W., D.W. SCHLOESSER, J.H. LEACH, AND W.P. KOVALAK. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. 48: 1381–1388.
- HEBERT, P.D.N., C.C. WILSON, M.H. MURDOCH, AND R. LAZAR. 1991. Demography and ecological impacts of the invading mollusc *Dreissena polymorpha*. Can. J. Zool. 69: 405–409.
- HINZ, W., AND H.G. SCHEIL. 1972. Zur Filtrationsleistung von *Dreissena*, *Spaerium* und *Pisidium*. Oecologia (Berl.) 11: 45–54.
- JØRGENSEN, C.B. 1980. Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effects on the benthic community. Oikos 34: 68–76.
- JØRGENSEN, C.B., T. KJØRBOE, F. MOHLENBERG, AND H.U. RIISGÅRD. 1984. Ciliary and mucus net filter feeding, with special reference to fluid mechanical characteristics. Mar. Ecol. Prog. Ser. 15: 283–292.
- JØRGENSEN, C.B., P.S. LARSEN, F. MOHLENBERG, AND H.U. RIISGÅRD. 1988. The mussel pump: properties and modelling. Mar. Ecol. Prog. Ser. 45: 205–216.
- KONDRATEV, G.P. 1963. O nekotorye osobennostjah filtracii u presnovodnyh molljuskov. Nauchn. Dokl. Vyssh. Shk. Biol. Nauki 1: 13–16.
- KRYGER, J., AND H.U. RIISGÅRD. 1988. Filtration rate capacities in 6 species of European freshwater bivalves. Oecologia 77: 34–38.
- LEACH, H.J. 1992. Impacts of the zebra mussel, *Dreissena polymorpha*, on water quality and spawning reefs in western Lake Erie. In T. Nalepa and D. Schloesser [ed.] Zebra mussels: biology, impacts and control. Lewis Publishers, Chelsea, MI.
- LEFF, L.G., J.L. BURCH, AND J.V. MCARTHUR. Spatial distribution, seston removal, and potential competitive interactions of the bivalves *Corbicula fluminea* and *Elliptio complanata*, in a coastal stream. Freshwater Biol. 24: 409–416.
- MACISAAC, H.J., W.G. SPRULES, O.E. JOHANNSSON, AND J.H. LEACH. 1992. Filtering impacts of larval and sessile zebra mussel (*Dreissena polymorpha*) in western Lake Erie. Oecologia.
- MACISAAC, H.J., W.G. SPRULES, AND J.H. LEACH. 1991. Ingestion of small-bodied zooplankton by zebra mussels (*Dreissena polymorpha*): can cannibalism on larvae influence population dynamics? Can. J. Fish. Aquat. Sci. 48: 2051–2060.
- MICHEEV, V.P. 1966. O skorosti fil tracii vody Drejssenoj. Tr. Inst. Biol. Vodokhran Akad. Nauk SSSR 12: 134–138.
- MORTON, B. 1971. Studies on the biology of *Dreissena polymorpha* Pall. v. Some aspects of filter-feeding and the effect of microorganisms upon the rate of filtration. Proc. Malacol. Soc. Lond. 39: 289–301.
- REEDERS, H.H., AND A. BIJ DE VAATE. 1990. Zebra mussels (*Dreissena polymorpha*): a new perspective for water quality management. Hydrobiologia 200/201: 437–450.
- REEDERS, H.H., A. BIJ DE VAATE, AND F.J. SLIM. 1989. The filtration rate of *Dreissena polymorpha* (Bivalvia) in three Dutch lakes with reference to biological water quality management. Freshwater Biol. 22: 133–141.

- SCHERTZER, W.M., J.H. SAYLOR, F.M. BOYCE, D.G. ROBERTSON, AND F. ROSA. 1987. Seasonal thermal cycle of Lake Erie. *J. Great Lakes Res.* 13: 468-486.
- SPRULES, W.G., L.B. HOLTBY, AND G. GRIGGS. 1981. A microcomputer-based measuring device for biological research. *Can. J. Zool.* 59: 1611-1614.
- SPRUNG, M., AND U. ROSE. 1988. Influence of food size and food quantity on the feeding of the mussel *Dreissena polymorpha*. *Oecologia* 77: 526-532.
- STAŃCZYKOWSKA, A. 1968. Możliwości filtracyjne populacji *Dreissena polymorpha* Pall. w różnych jeziorach jako czynniki wpływające na obieg materii w jeziorze. *Ekol. Pol. Ser. B* 14: 265-270.
- STAŃCZYKOWSKA, A., W. LAWACZ, J. MATTICE, AND K. LEWANDOWSKI. 1976. Bivalves as a factor effecting the circulation of matter in Lake Mikołajskie (Poland). *Limnologica* 10: 347-352.
- TEN WINKEL, E.H., AND C. DAVIDS. 1982. Food selection by *Dreissena polymorpha* Pallas (Mollusca: Bivalvia). *Freshwater Biol.* 12: 553-558.
- WALZ, N. 1978. The energy balance of the freshwater mussel *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance. I. Pattern of activity, feeding and assimilation efficiency. *Arch. Hydrobiol. Suppl.* 55: 83-105.
- WU, L., AND D.A. CULVER. 1991. Zooplankton grazing and phytoplankton abundance: an assessment before and after invasion of *Dreissena polymorpha*. *J. Great Lakes Res.* 17: 425-436.