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Filtration Rates of the Zebra Mussel (*Dreissena polymorpha*) on Natural Seston from Saginaw Bay, Lake Huron

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ABSTRACT. *Filtration rates of the zebra mussel* (Dreissena polymorpha) *on natural seston from two different regions in Saginaw Bay were determined on a monthly basis from April to October in 1992 and 1993. The two regions represent contrasting trophic conditions, with the inner bay more eutrophic than the outer bay. Mean filtration rate was 16.2 mL/mg/h (range 4.0 to 40.7 mL/mg/h) over the entire 2-year period. Filtration rates on seston from the inner bay were significantly lower than rates on seston from the outer bay in 1992, but no differences were apparent in 1993. Lower rates were attributed to higher concentrations of seston (chlorophyll, particulate organic carbon, and total suspended solids) found in the inner bay in 1992. In 1992, overall filtration rates were related to seston concentrations as described by a negative exponential function. In 1993, seston concentrations were uniformly low, and a relationship between filtration rates and concentrations was not observed. Further, filtration rates were not related to seston composition, as determined by the ratio of POC:TSS and chl:TSS. Maximum filtration rates were apparently related to temperature, with highest maximum rates occurring at 10–20°C. Based on measured filtration rates and overall standing stocks, the* Dreissena *population in the inner bay was capable of filtering the volume of the inner bay 1.3 times per day in 1992 and 0.2 times per day in 1993.*

INDEX WORDS: *Filtration rates, suspended solids, chlorophyll, zebra mussels, Lake Huron.*

INTRODUCTION

Because of high filtering rates and often great densities, the zebra mussel, *Dreissena polymorpha,* can play a major role in the movement, circulation, and removal of materials in a given water body (Stanczykowska 1968, 1984; Stanczykowska *et al.* 1976; Reeders *et al.* 1989; Reeders and bij de Vaate 1992; Stanczykowska and Lewandowski 1993). As a suspension feeder, *Dreissena* filters particles from the water column, retaining nearly 100% of the particles > 1 μm (Jorgensen *et al.* 1984). Some of this particulate material is ingested, while a portion is rejected and deposited on the bottom as pseudofeces. Thus, filtering activities of mussels have the potential to shift energy from the pelagic to the benthic region, possibly resulting in major changes in the food web. In order to understand the role of *Dreissena* in energy flow patterns, the filtration rate of the population must be known. Filtration rate, or clearance rate, can be defined as the amount of water cleared of particles per unit time. Because of its fundamental importance in assessing impacts, *Dreissena* filtration rates, and factors affecting these rates, have been measured in a number of different studies (see Reeders *et al.* 1993 for summary table). However, reported rates have varied considerably. Factors that can affect rates are food quantity and quality (Morton 1971, Sprung and Rose 1988, Dorgelo and Smeenk 1988, Walz 1978, Reeders and bij de Vaate 1990), temperature (Reeders and bij de Vaate 1990), and potential artifacts associated with the specific experimental design (Reeders *et al.* 1989).

In this paper, we document filtration rates of *Dreissena* using natural seston from Saginaw Bay. Our main purposes were to determine the extent of spatial and temporal variation in rate measurements and to estimate filtering impacts of mussels on the Saginaw Bay ecosystem. Rates were measured during 1992 and 1993 using seston from two different regions in Saginaw Bay which represented contrasting trophic conditions. The inner bay is a shallow, nutrient-rich, highly-productive system that is influenced by inputs from the Saginaw River, while the outer bay is less productive and influenced by the nutrient-poor waters of Lake Huron. Given measured filtration rates and estimates of population standing stocks (Nalepa *et al.* 1995), filtering impacts of *Dreissena* in Saginaw Bay were determined and assessed relative to observed declines in phytoplankton standing stocks (Fahnenstiel *et al.* 1995a).

METHODS

Clearance rate determinations were conducted on a monthly basis from April to October in 1992 and 1993. On each sampling date, water containing natural seston was collected from just below the surface at Station 5 in the inner bay and at either Station 19, 20, or 21 in the outer bay (Fig. 1). Mussels for the experiments were collected using an epibenthic sled towed behind a small boat. All mussels were collected from Station 5 in the inner bay; however, on two dates in early 1992, mussels from Station 19 in the outer bay were used to determine filtration rates on outer bay seston. Mussels from this site proved difficult to collect consistently, thus all subsequent experiments were conducted with mussels from Station 5. Mussels at this station occur on rocks of various sizes. Small rocks with clusters of 50-200 individuals were selected for the experiments. Clusters were visually examined, and only those not mechanically damaged by the sled were retained. Mussels were placed in coolers and overlaid with wet paper towels for transport to a shore laboratory facility.

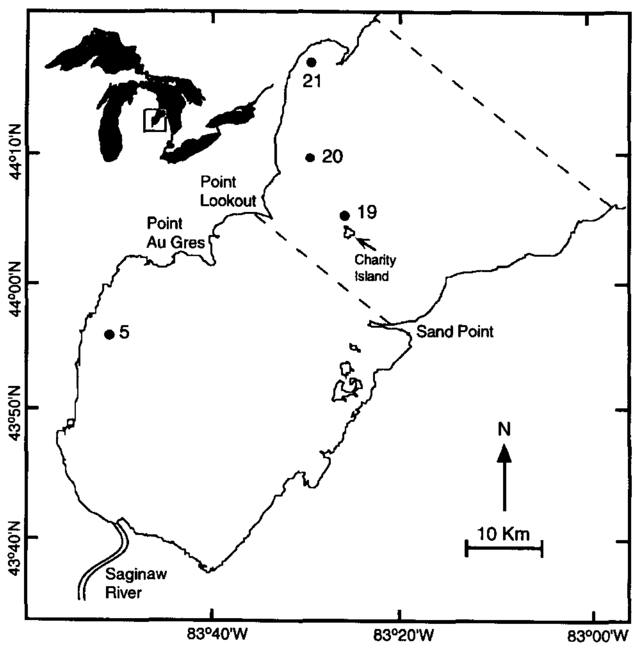

FIG. 1. Location of sampling sites in Saginaw Bay, Lake Huron. Dashed lines differentiate the inner bay from the outer bay and the outer bay from Lake Huron.

At the shore facility, mussel clusters were gently rinsed to remove as much associated particulate matter as possible, and then held in ambient water for at least 0.5 h prior to clearance rate experiments. Overall, experiments were initiated within 2 h after the mussels and water were collected. Experimental vessels consisted of plexiglas aquaria with a capacity of 8 L (20.5 cm high × 21 cm long × 17 cm wide). Water was placed in six aquaria, and the aquaria were then placed in an incubator set at the *in situ* temperature. Natural seston was kept suspended using cascading box filters with filtration media removed. Flow rate was about 3.5 L/min. Preliminary phytoplankton analysis indicated little or no mechanical damage to cells from the impeller circulators (Bob Pillsbury, Bowling Green State University, unpublished data). After water in all aquaria was circulating at the *in situ* temperature, one mussel cluster was placed in each of three aquaria; the remaining three aquaria served as controls (no mussels added). All experiments were conducted in the dark. Experiments were initiated (time zero) when an estimated 90% of the mussels in the cluster were observed to be open and actively filtering. This was consistently only 3-5 min after the mussels were transferred to the aquaria and is similar to the response reported by Bunt *et al.* (1993).

Water was removed by siphon from the middle of the aquaria at 1, 2, 4, and 8 h and immediately filtered for the determination of chlorophyll (chl), particulate organic carbon (POC), and total suspended solids (TSS). Chlorophyll was extracted with 90% acetone following the method of Strickland and Parsons (1972) and determined with a Turner fluorometer. POC was determined using a Perkin-Elmer CHN 2400 Elemental Analyzer, and TSS was determined by filtering the seston on preweighed filters and then drying at 100°C for 48 h.

Filtration rates were determined from the decline in chlorophyll during the experimental period. Chlorophyll proved to be the most sensitive measure of seston concentrations over the wide range of values encountered during the 2-year period. Further, filtration rates of zooplankton in Saginaw Bay were also measured by documenting decreases in chlorophyll over time (Bridgeman *et al.* 1995), making relative filtering impacts of the two invertebrate groups directly comparable.

Filtration rate (FR) was determined by the equation from Coughlan (1969):

$$FR = \frac{Vol\ [(\ln C_0 - \ln C_1) - (\ln C'_0 - \ln C'_1)]}{t}$$

where:

FR = filtration rate of zebra mussel cluster (mL/h)
Vol = volume of lake water in aquaria (mL)
t = time (h)
C_0 = initial chlorophyll concentration in experimental aquaria (μg/L)
C_1 = final chlorophyll concentration in experimental aquaria (μg/L)
C'_0 = inital chlorophyll concentration in control aquaria (μg/L)
C'_1 = final chlorophyll concentration in control aquaria (μg/L)

In this equation, the mean change in control concentrations (without mussels) was subtracted from the change in experimental concentrations (with mussels). Reductions of chlorophyll in controls would likely be attributable to zooplankton grazing and/or pigment degradation. The mean decrease in chlorophyll in control aquaria after 1 h was 0.04 μg/L, which represents a mean decrease of 5.0%. Although seston concentrations were determined several times within 8 h, rates were based on a 1-h exposure period. This time period was adequate to measure clearance rates while minimizing declines in seston concentrations. For all experiments, the final mean concentration of chlorophyll was 69% of the initial concentration after 1 h.

At the end of the experimental period, mussels were removed from the rocks, counted, and measured (shell length) using a digitizer pad. Shell lengths were converted to ash-free dry weights using AFDW:SL regressions determined for each monthly period at the same site (Nalepa *et al.* 1995). Filtration rates were then divided by the total AFDW biomass of the zebra mussel cluster to define filtration rate as mL/mg/h.

As determined, filtration rate is the volume of water cleared of particles per unit time. However, not all particles filtered are retained; some material is rejected as pseudofeces. While pseudofecal material was observed on the aquaria bottom in the immediate vicinity of the cluster on several occasions, some resuspension of low-density pesuodofeces was likely during the experimental period. Thus, some particulate material may have been re-filtered and, as such, measured filtration rates presented herein should be considered conservative estimates. Further, the high rate of water circulation in itself may have contributed to conservative rate estimates. In the marine bivalve *Mytilus*, filtration rates were inversely related to flow velocity (Wildish and Miyares 1990).

RESULTS

Water temperatures and concentrations of chl, POC, and TSS during each of the monthly clearance rate determinations are given in Table 1. For comparable monthly sampling periods, mean concentrations of chl, POC, and TSS were higher in 1992 than in 1993 at both the inner and outer bay sites. Yearly differences were most apparent at the inner bay site. At this site, mean values of each of these parameters declined about 3-fold between 1992 and 1993; chl decreased from 7.4 μg/L in 1992 to 2.2 μg/L in 1993 (paired sample t-test; $p = 0.06$), POC decreased from 1.7 to 0.5 mg/L ($p = 0.02$), and TSS decreased from 8.3 to 2.9 mg/L ($p = 0.09$). Highest concentrations over the entire study period occurred at the inner bay site in September 1992, with maximums of 18.0 μg/L, 3.5 mg/L, and 18.7 mg/L for chl, POC, and TSS, respectively. At the outer bay sites, mean chl decreased from 2.2 to 1.5 μg/L ($p = 0.03$), POC decreased from 0.5 to 0.3 mg/L ($p = 0.02$), and TSS decreased from 2.1 to 0.9 mg/L ($p = 0.08$).

Over the 2-year study period, mean filtration rate was 16.2 mL/mg/h (monthly range: 4.0 to 40.7 mL/mg/h). In both 1992 and 1993, maximum filtration rates on seston from both the inner and outer bay occurred in spring, while minimum rates occurred in late summer (Fig. 2). In 1992, filtration rates on inner bay seston were significantly lower than rates on outer bay seston (paired sample t-test; $P = 0.03$), but in 1993 there was no difference in filtration rates on seston from the two regions (Table 2). For inner bay seston, filtration rates were almost two times higher in 1993 than in 1992, but the difference was not significant; filtration rates on outer bay seston were similar in the 2 years (Table 2).

Filtration rates were examined relative to seston concentration on each sampling date in both 1992 and 1993 (Fig. 3). In both years, filtration rates generally declined as seston concentrations increased. Dates that did not fit this general pattern were September 1992 (inner bay) and April 1993 (outer

TABLE 1. Experimental conditions for each date that filtration rates of Dreissena were determined. Mussels used in the experiments were collected at Station 5 in the inner bay except on 15 June and 20 July 1992 for experiments using outer bay seston when mussels from Station 19 were used. Filtration rates were determined on naturally occurring clusters and the values given are the mean number of mussels, mean shell length, and mean biomass per cluster (three replicates per date). Values for temperature, chlorophyll, particulate organic carbon, and total suspended solids are concentrations at the beginning of the experimental period. Water from the inner bay was collected at Station 5, while water from the outer bay was collected at Station 20 on all dates except 15 June and 20 July 1992 (from Station 19) and 28 April and 21 June 1993 (from Station 21). *Due to problems with analysis of TSS on this date, this value represents TSS on 7 October 1993 from the same site as reported by Nalepa **et al.** ***(in press).***

Date	Mean Number of Mussels	Mean Shell Length Length (mm)	Mean Biomass (mg AFDW)	Temp (°C)	Chl (µg/L)	POC (mg/L)	TSS (mg/L)
Inner Bay							
15 Apr 92	116	4.8	158.2	6.0	3.8	1.3	5.6
27 May 92	178	5.8	340.9	15.0	0.6	0.5	2.5
15 Jun 92	157	6.8	211.5	21.5	2.1	1.1	9.9
21 Jul 92	136	5.8	133.8	22.0	7.8	1.7	5.0
10 Aug 92	88	7.7	114.4	25.0	11.9	2.4	7.9
9 Sep 92	195	5.5	138.3	19.0	18.0	3.5	18.7
8 Oct 92	139	6.0	93.0	15.0	2.9	0.9	4.0
27 Apr 93	78	8.8	207.5	7.0	0.6	0.4	2.4
17 May 93	124	5.3	112.2	13.0	0.8	0.3	1.0
22 Jun 93	126	7.5	210.7	19.0	2.2	0.2	1.1
14 Jul 93	72	7.9	143.2	23.0	1.9	0.6	7.0
9 Aug 93	104	9.0	267.3	21.0	2.5	0.8	3.4
8 Sep 93	114	8.3	85.2	19.5	4.9	0.8	2.4
Outer Bay							
22 Jun 92	126	6.6	217.9	18.0	1.2	0.6	2.8
20 Jul 92	89	8.1	248.8	22.0	3.2	0.7	2.3
13 Aug 92	102	6.0	74.6	21.0	2.2	0.4	1.5
16 Sep 92	121	5.8	100.0	21.0	2.5	0.6	2.3
7 Oct 92	92	8.3	143.7	15.0	2.3	0.5	1.8
28 Apr 93	140	7.9	291.8	9.0	1.8	0.4	6.3
19 May 93	80	7.6	153.0	13.0	3.3	0.4	1.5
21 Jun 93	117	6.3	140.5	19.0	1.0	0.2	0.6
12 Jul 93	71	7.9	140.2	22.0	2.3	0.5	1.4
10 Aug 93	81	9.1	217.6	19.5	1.2	0.3	1.4
5 Oct 93	108	8.7	97.2	12.0	1.6	0.2	0.7*

bay). Seston on these dates was collected during a storm event, and high amounts of particulate material, even sand grains, were observed in the experimental vessels. If these dates could be considered atypical and not included in the data set, the relationship between filtration rate and seston concentration can be described by the negative exponential function $Y = ae^{bx}$, where Y = filtration rate and x = 1 h mean seston concentration. The relationship was significant for all three measures of seston concentration in 1992, but was significant only for POC in 1993 (Table 3). In either year, there was no relationship between filtration rates and food composition as defined by POC:TSS or chl:TSS (linear regression; P >0.20) (Fig. 4).

There was wide variation in filtration rates for a given temperature, but the relationship between maximum filtration rate and temperature generally

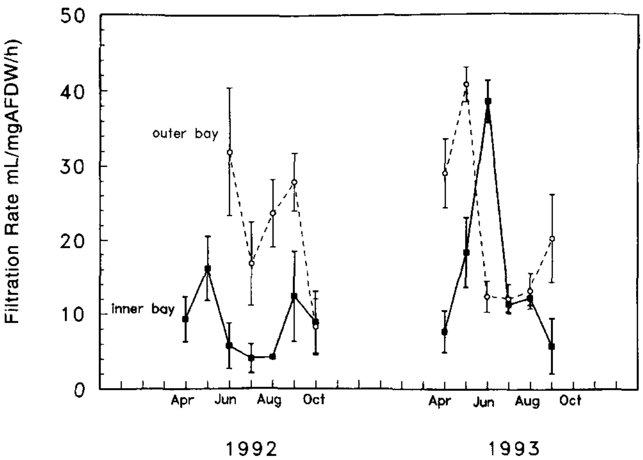

FIG. 2. Mean (± SE) filtration rates for **Dreissena polymorpha** *on each sampling date in 1992 and 1993 on seston from a site in the inner bay and a site in the outer bay of Saginaw Bay.*

TABLE 2. Mean filtration rates (mL/mg/h) in two regions of Saginaw Bay (inner bay and outer bay) in 1992 and 1993. SD = standard deviation; n = number of sampling dates

Region	Mean	SD	n
Year:1992			
Inner Bay	8.6	4.5	7
Outer Bay	21.7	9.4	5
Year:1993			
Inner Bay	15.6	12.0	6
Outer Bay	21.2	11.5	6

followed a normal curve with an optimum between 10°C and 20°C (Fig. 5). The peak filtration rate of 46 mL/mg/h occurred with outer bay seston when the temperature was 13°C.

DISCUSSION

Observed spatial (inner and outer bay) and temporal (year and season) differences in filtration rates during the 2-year sampling period were best explained by variations in seston concentrations. Filtration rates were lowest on inner bay seston in 1992 when concentrations were at a maximum, but were higher and not significantly different from filtration rates on outer bay seston in 1993 when seston concentrations were lower. Seston concentrations, as measured by chl, POC, and TSS, declined in Saginaw Bay between 1991 and 1993 as *Dreissena* became established and increased in density (Fahnenstiel *et al.* 1995a, Nalepa *et al.* 1995, Johengen *et al.* 1995). A relationship between filtration rate and food concentration has often been demonstrated for *Dreissena* and many other filter-feeding bivalves, with filtration rates declining exponentially as a function of increasing food concentration when concentrations are above an incipient limiting concentration (Winter 1973, Foster Smith 1975, Walz 1978, Sprung and Rose 1988, Dorgelo and Smeenk 1988, Reeders and bij de Vaate 1990). When food concentrations are below this incipient level, filtration rates were reportedly independent of food concentrations. For *Dreissena,* incipient levels derived under controlled conditions have varied widely. In laboratory experiments using unialgal cultures as a food source, Walz (1978) found that the incipient limiting concentration for *Dreissena* feeding on *Nitzschia* was 2.0 mg/L POC, while Sprung and Rose (1988) reported a limiting concentration of 16,000 cells/mL of *Chlamydomonas*, or about 2.7 mg/L POC (assuming 0.17×10^{-3} μg POC per cell), and Dorgelo and Smeenk (1988) reported a limiting concentration at about 81,000 cells/mL of *Chlamydomonas*, or about 14 mg/L POC. Of the three measures of seston concentrations in our experiments, filtration rates were best described as a functional response to concentrations of POC (Table 3). Our finding of a significant negative exponential relationship between filtration rates and POC over the entire range of POC concentrations in both years (0.2–3.5 mg/L POC) suggests that, if an incipient limiting concentration did exist, the level was much lower than reported in these previous studies. However, it is difficult to compare our findings with those of previous works because we used natural seston while others, as noted, used unialgal cultures. For filter-feeding bivalves, consumption models based on natural seston are more accurate predictors than models based on algal monocultures (Doering and Oviatt 1986). For the Asiatic clam, *Corbicula*, filtration rates were highest when measured at natural food concentrations and with particles representative of the size ranges found *in situ* (Way *et al.* 1990). Despite the number of studies examining the relationship between filtration rate and food concen-

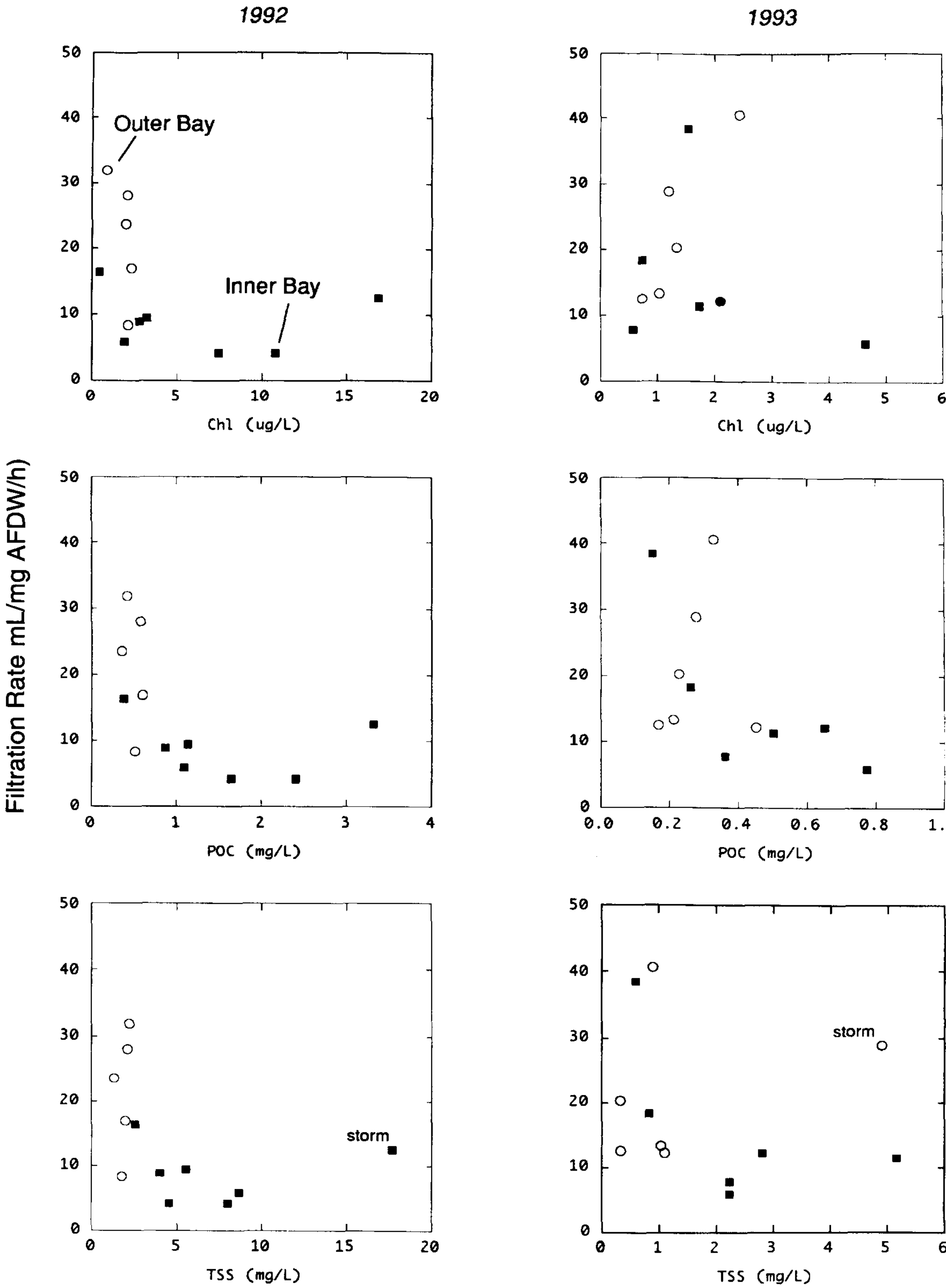

FIG. 3. Relationship between filtration rate and seston concentration for Dreissena polymorpha *on each sampling date in 1992 and 1993 at a site in the inner bay and outer bay of Saginaw Bay. chl = chlorophyll ; POC = particulate organic carbon; TSS = total suspended solids.*

TABLE 3. Relationship between filtration rate and three measures of seston concentrations (chlorophyll, particulate organic carbon, and total suspended solids) in 1992 as fitted to the inverse exponential equation $Y = ae^{bx}$, where Y = filtration rate (mL/mg/h), and X = seston concentration. The relationship was derived from all filtration rate experiments on inner and outer bay seston on each date with the exception of September 1992 (inner bay) and April 1993 (outer bay). Seston conditions on these dates were considered atypical because of storm events. P = significance level (two-tail).

Variable	log a	b	R^2	P
Year :1992				
Chl (µg/L)	2.980	–0.170	0.505	0.014
POC (mg/L)	3.280	–0.946	0.654	0.003
TSS (mg/L)	3.268	–0.217	0.560	0.008
Year :1993				
Chl (µg/L)	2.909	–0.129	0.061	0.464
POC (mg/L)	3.357	–1.805	0.369	0.048
TSS (mg/L)	2.999	–0.195	0.219	0.147

tration in *Dreissena*, only Reeders and bij de Vaate (1990) have described the relationship using natural seston. For various lakes in the Netherlands, they found a negative exponential relationship between filtration rates and seston concentrations over the range of 5-79 mg/L (dry matter content). Thus, our finding of a negative exponential relationship between filtration rates and natural seston from Saginaw Bay is consistent with their results, even though our range of seston concentrations were far lower.

Reeders *et al.* (1989) and Reeders and bij de Vaate (1990) noted that filtration rates were unrelated to seston composition; that is, rates were a function of the dry matter content despite great differences in algal species composition, silt content, or nutritional status. In this study, filtration rates were unrelated to two measures of seston composition, POC:TSS and chl:TSS, but the exact role of food quality in affecting filtration rates is not clear since phytoplankton species composition was not determined. For example, high seston concentrations found in late summer 1992 in the inner bay were apparently associated with relatively high abundances of cyanophytes, particularly *Microcystis* sp. (Soon-Jin Hwang, personal communication, Kent State University). Both Gardner *et al.* (1995) and Lavrentyev *et al.* (1995) reported diminished filtering by *Dreissena* when cyanophytes were present in Saginaw Bay seston. Thus, lower filtration rates observed during this period may partly be attributed to the phytoplankton species present. Similarly, Shevtsova (1989) found that filtration rates of *Dreissena* were lower during a cyanophyte bloom, but it was not clear whether rates were lower because of the algae itself or because of the high particulate content of the water during the bloom period.

Maximum filtration rates for a given temperature generally followed a normal curve with greatest rates between 10°C and 20°C (Fig. 5). Because of the strong relationship between filtration rate and seston concentrations, the functional relationship between filtration rate and temperature was only apparent on dates when food concentrations were low and filtration rate was at a maximum. All maximum filtration rates found within the temperature range of 10-20°C occurred with the lower seston concentrations found in the outer bay with the exception of one maximum rate which occurred with inner bay seston. This latter rate occurred on a date when seston concentrations in the inner bay were at the lowest levels of the 2-year period (June 1993). Although maximum filtration rates were found only on dates with lower seston concentrations, filtration rates on many dates with similar temperatures and seston concentrations were much lower. At any rate, the observed relationship between maximum filtration and temperature is consistent with other inves-

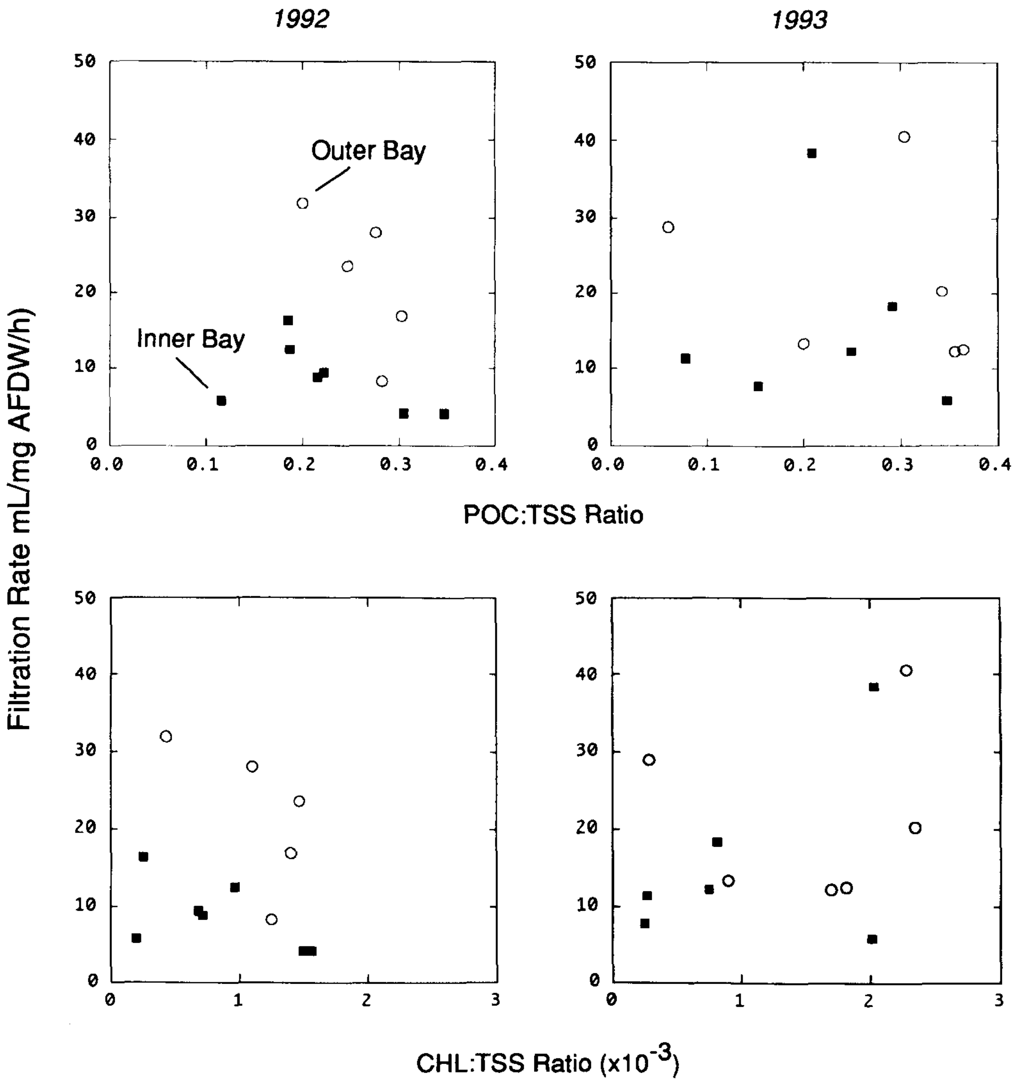

FIG. 4. Relationship between filtration rate and seston composition for **Dreissena polymorpha** *on sampling date in 1992 and 1993 at a site in the inner bay and outer bay of Saginaw Bay. Seston composition is defined as the proportion of particulate organic carbon in the total material suspended (POC:TSS) and as the proportion of chlorophyll in the total material suspended (chl:TSS).*

tigators. When food concentrations were kept constant at low levels, Walz (1978) found that ingestion rates in *Dreissena* varied as a function of temperature, and the relationship was best described by a normal curve with an optimum ingestion rate at 12.5°C. Also, Reeders and bij de Vaate (1990) showed that maximum filtration rates fit a normal curve with an optimum at about 14°C. Because of the wide variation between filtration rates at a given temperature in the temperature range of 10-20°C, they proposed a model showing optimum filtration rate within this entire temperature range. However, variations in filtration rates for a given temperature was likely a result of varying seston concentrations since rates were determined at *in situ* concentrations.

Summary tables of *Dreissena* filtration rates have been provided by a number of different investiga-

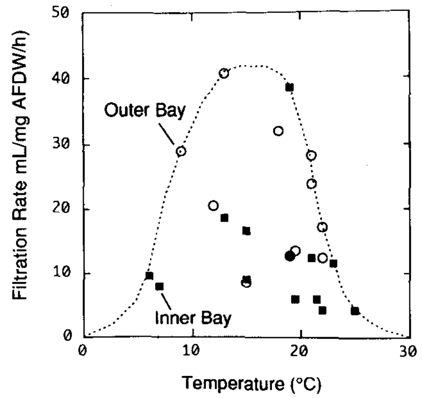

FIG. 5. Relationship between filtration rate and temperature for* Dreissena polymorpha *on each sampling date in 1992 and 1993 at a site in the inner bay and outer bay of Saginaw Bay. The dashed line is fitted to maximum filtration rates over the range of seasonal temperatures.

tors (Bunt *et al.* 1993, Kryger and Riisgard 1988, Reeders *et al.* 1993). Most previous determinations of filtration rates for *Dreissena* have used individuals of varying size classes that had been removed from their natural substrate. Filtration rates were then related to size based on the allometric equation $FR = ax^b$, where FR is individual filtration rate, and x is the soft tissue weight or shell length. Since our intention was to measure filtration rates under the most natural conditions possible, rates were determined on entire clusters of mussels that remained as found *in situ*. This design kept disturbance to a minimum and accounted for the influence that mussels may have on each other when in close proximity and competing for food resources. However, since filtration rates of individuals within the cluster could not be determined, this design precluded us from developing an allometric equation for filtering rate vs. shell length or tissue weight, and thus prevented the direct comparison of our measured rates to rates previously reported. Therefore, for purposes of comparison, we estimated filtration rates for each individual in the cluster using the various allometric equations reported by others for filtering rate vs shell length and weight vs length, or filtering rate vs weight, and then summed the values to determine the theoretical filtration rate per unit weight of the cluster. That is, reported individual-based filtration rates in other studies were recalculated based on the size-frequency distributions found in our experimental clusters. The mean filtration rate in our experiments were generally comparable to most other previously reported rates (Table 4).

Filtering impacts of mussels in the bay can be determined from estimates of mussel standing stocks and measured filtration rates. Total biomass of the mussel population in the inner bay was estimated by determining mean biomass of mussels on the two dominant substrate types in the inner bay (sand/cobble and silt), multiplying by the total bottom area covered by the two substrates, and summing the two values. Mean biomass for the two substrate types, and the proportion of the inner bay bottom with either sand/cobble or silt are given in Nalepa *et al.* (1995). Given a mean filtration rate of 8.6 in 1992 and 15.6 mL/mg/h in 1993, and assuming mussels filter 17 h per day (Walz 1978), the *Dreissena* population in the inner bay filtered 6.4

TABLE 4. Filtration rates of* Dreissena *from various studies. Comparisons are limited to those studies for which a relationship between filtration rate and weight or length was provided since all rates were applied to the size-frequency distribution of individuals found in the clusters of this study.

Reference	Food	Temperature (C)	Filtration Rate (mL/mg AFDW/h)
This study	Natural Seston	6–25	16.2
Kryger and Riisgard (1988)	*Chorella*	20	16.5
Reeders and bij de Vaate (1990)	Natural Seston	10–21	4.3
Kondratev (1963)		16–17	16.4
Alimov (1969)	Clay particles	18–20	14.3
Micheev (1966)	Natural Seston	20–22	3.2

m³/m²/day and 0.9 m³/m²/day in the 2 years, respectively. With water volume of the inner bay estimated at 7.9×10^9 m^3 (Nalepa *et al.* 1995), the population was theoretically capable of filtering the entire inner bay 1.3 times per day in 1992 and 0.2 times per day in 1993 during the April-October period. The lower impact in 1993 occurred despite overall higher filtration rates because population biomass declined 14-fold between 1992 and 1993 (Nalepa *et al.* 1995). Filtering impacts calculated for the entire inner bay seem justified since the inner bay is shallow and well-mixed, allowing mussels access to seston throughout the water column. Stratification during the study period was minimal (Nalepa *et al.* 1995). Given phytoplankton growth rates in the inner bay of 0.25 per day in 1992 and 0.20 per day in 1993 (G. Fahnenstiel, unpublished data), filtering activities of the mussel population can account for the decline in chlorophyll and increase in water clarity in the inner bay between 1991 and 1993 (Fahnenstiel *et al.*1995a).

Filtering impacts of *Dreissena* in Saginaw Bay are generally comparable to impacts calculated for other water bodies. Hebert *et al.* (1991) estimated that *Dreissena* could filter the volume of Lake St. Clair twice a day at densities of 6,000/m². MacIsaac *et al.*(1992) estimated that mussels at a reef site in western Lake Erie were capable of filtering the water column directly over the reef at rates of 3.5 and 18.8 times per day, depending on the literature source of the filtration rate. These relatively high impact estimates were site-specific and not likely applicable to the entire western basin. Impacts were based on a population density of about 260,000/m², which is far greater than densities found in most other areas of the western basin (Dermott and Munawar 1993, Garton and Haag 1993). Reeders *et al.* (1989) determined that *Dreissena* was capable of filtering the entire volume of two lakes in the Netherlands in 11 and 18 days, respectively.

The intent of this study was to determine the extent of variability in filtration rates and to estimate filtering impacts under the specific conditions found in Saginaw Bay. Our rate measurements can be used to assess potential ecosystem level impacts of *Dreissena* such as changes in water clarity (Fahnenstiel *et al.* 1995a), and phytoplankton dynamics (Fahnenstiel *et al.* 1995b), or to compare relative impacts of *Dreissena* to phytoplankton grazers such as zooplankton (Bridgeman *et al.* 1995) . However, these filtration rates cannot be used to assess ingestion since pseudofeces was not quantified. Even at low seston concentrations, pseudofeces is produced (Walz 1978, Reeders and bij de Vaate 1992). Because *Dreisenna* is selective of material ingested (Ten Winkel and Davids 1982), both filtration and ingestion rates need to be examined to determine the potential for long-term growth of populations in the bay. Given differences in growth and survival of *Dreissena* in the inner and outer regions of Saginaw Bay (Nalepa *et al.* 1995), future studies will examine energy budgets of mussels in the two regions, emphasizing the role of food quality in determining actual rates of ingestion.

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