Nalepa et al 1991

Hydrobiologia **219**: 239–250, 1991.
M. Munawar & T. Edsall (eds),
Environmental Assessment and Habitat Evaluation of the Upper Great Lakes Connecting Channels.

Phosphorus cycling by mussels (Unionidae : Bivalvia) in Lake St. Clair

T.F. Nalepa, W.S. Gardner & J.M. Malczyk
Great Lakes Environmental Research Laboratory, 2205 Commonwealth Blvd., Ann Arbor, MI 48105, USA

Key words: nutrients, excretion, biodeposition, *Lampsilis*, phosphorus budget

Abstract

The role of mussels in cycling phosphorus in Lake St. Clair during the May–October period was examined by measuring concentrations in the water column and in mussel tissue, and by measuring rates of biodeposition and excretion. Mean rates of biodeposition and excretion for *Lampsilis radiata siliquoidea*, the most abundant species, were 6.3 μg P (g shell-free dry wt)$^{-1}$ h^{-1} and 1.3 μg P (g shell-free dry wt)$^{-1}$ h^{-1}, respectively; body tissue phosphorus content was 2.7 percent of dry wt. Seasonal changes in excretion rates appeared to be related to the gametogenic cycle of the organism, but seasonal changes in biodeposition rates were not apparent. Phosphorus assimilation efficiency for this species was about 40 percent. Overall, the mussel population in Lake St. Clair filtered about 210 MT of phosphorus, or about 13.5 percent of the total phosphorus load for the May–October study period. Of this amount, about 134 MT was sedimented to the bottom via biodeposition. Mussel biodeposition may be an important source of nutrients to other biotic components in the lake such as macrophytes and invertebrate deposit-feeders.

1. Introduction

Through their feeding and burrowing activities, benthic invertebrates can play an important role in the cycling of nutrients. In addition to mixing nutrient-rich pore waters with overlying waters, these organisms ingest organic material and excrete remineralized nutrients in forms readily available to phytoplankton. For example, in near-shore Lake Michigan, phosphorus excretion by benthic invertebrates was comparable to amounts released from the sediments (Gardner *et al.*, 1981). Of the various invertebrate groups, unionid bivalves (mussels) in particular can have a significant impact on nutrient cycling (Lewandowski & Stanczykowska, 1975; Walz, 1978; Stanczykowska & Planter, 1985; Kasprzak, 1986; James, 1987). These large filter-feeders have the capacity to remove great amounts of particulate material from the water column. Some of this material is assimilated and used for growth, metabolism, and the production of offspring, but a large portion is voided through pseudofeces, feces, and inorganic excretion.

The purpose of this study was to examine the role of mussels in the cycling of phosphorus in Lake St. Clair. Mussels are the dominant macroinvertebrate in the lake, with standing stocks about four times greater than that of all other benthic invertebrates combined (Nalepa & Gauvin, 1988). A phosphorus budget through the mussel population was estimated from measurements of concentrations in the water column and in mussel tissue, and from rate measurements of biodeposition and excretion. Since material deposited on the bottom by mussels along with

naturally-sedimented material may play a role in the cycling of phosphorus, rates of phosphorus release from the sediments were also determined.

2. Description of study site

Lake St. Clair lies at the center of the 125 km long waterway between Lake Huron and Lake Erie. The main inflow is from the St. Clair River, which has a flow rate of 5 100 $m^3 s^{-1}$ and contributes 98 percent of the flow into the lake. The only outflow is through the Detroit River. Hydraulic retention time in the lake is about 9 days. The lake has an area of 1 110 km^2, a volume of 3.4 km^3, and a mean depth of 3 m. Because of its high flow-through rate and shallow depth, the lake is well-mixed; thermal stratification does not occur and oxygen concentrations remain close to saturation. Two distinct water masses have been distinguished within the lake: a northwestern mass, which consists primarily of low-nutrient water flowing into the lake from Lake Huron via the St. Clair River, and a southeastern mass, which consists of more stable water enriched by nutrient loadings from Ontario tributaries (Leach, 1980). As a result of these two distinct water masses, biological (chlorophyll *a* and zooplankton) and chemical (carbon, phosphorus, nitrogen, chloride, and total alkalinity) features of the water column tend to increase on a gradient from northwest to southeast (Leach, 1972, 1973). Because of the high inflow of low-nutrient water from Lake Huron, the water quality of Lake St. Clair has remained relatively good despite extensive shoreline development and agricultural land use in the watershed. The lake has been classified as mesotrophic, with overall nutrient concentrations lying between the low values of the upper lakes and the high values found in western Lake Erie (Herdendorf *et al.*, 1986).

3. Methods and materials

Mussels were collected at one site (Station 73) on five different dates in 1985 and two sites

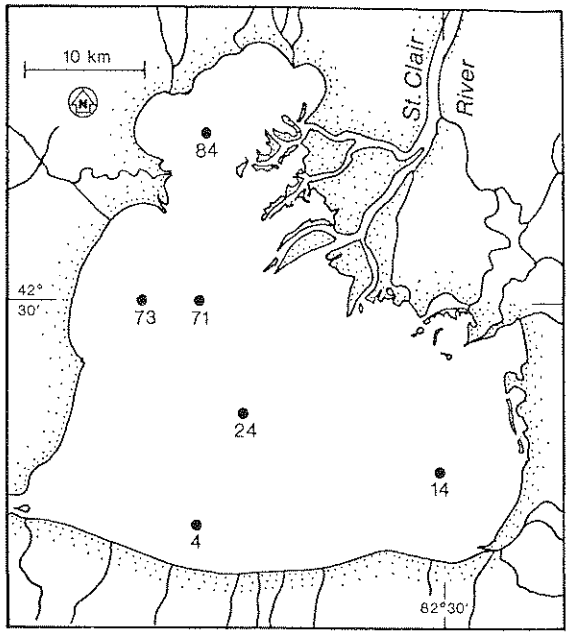

Fig. 1. Location of sampling stations in Lake St. Clair. Mussels were collected at Stations 73 and 24 and intact sediment cores were collected at Stations 84, 71, 24, 4, and 14. Station designations are the same as used by Nalepa & Gauvin (1988).

(Stations 73 and 24) on six dates in 1986 (Fig. 1). The two collection sites in 1986 had different substrate types; sandy silt was dominant at Station 73, while silt was dominant at Station 24. Also, submergent macrophytes were present only at the former site during the summer months. Mussels were collected with an epibenthic sled, except in May and September 1985 when mussels were collected by divers. In the first year, excretion rates were determined on the first five to seven individuals collected, regardless of species. However, in the second year excretion was measured on only one species, *Lampsilis radiata siliquoidea*. This species is the dominant mussel in Lake St. Clair; it is distributed throughout the lake and accounts for 45 percent of the entire mussel population (Nalepa & Gauvin, 1988).

After collection, individual mussels were gently scrubbed and immediately placed in polyethylene containers having 2 liters of low-nutrient, particle-free, culture water (Lehman, 1980). The containers were placed in large coolers and the cul-

ture water was maintained at the *in situ* temperature. The incubation period lasted 4 hours with 1 ml samples for phosphorus and ammonia determinations drawn at 0, 2, and 4 h. Mussels began to filter water within 30 min after being placed in the containers. Phosphate (PO_4–P) concentrations in the culture water were determined with an autoanalyzer (Gardner & Malczyk, 1983) and ammonium (NH_4–N) was measured after reaction with o-phthalaldehyde (Gardner, 1978). In 1986, the biodeposition rate was determined by drying and weighing the fecal and pseudofecal material produced during the 4-h incubation period. Phosphorus content of this material was determined with an autoanalyzer after block digestion with mercuric acid, sulfuric acid, and potassium sulfate (Malczyk & Eadie, 1980). Dry weights of the mussels (soft tissue) were determined after drying at 60 °C for at least 48 h. After weighing, the soft tissue was ground to a fine powder and phosphorus content was measured as for the biodeposited material. The nutrient excretion rate of each individual was determined from the slope of a regression line between time and concentration during the 4-h time series. Since both excretion and biodeposition rates were determined on individuals placed in a non-food medium, these rates might be considered conservative estimates.

On most sampling dates in 1986, water samples were taken about 1 meter above the bottom with a Van Dorn water bottle. Total phosphorus, total particulate phosphorus, and total dissolved phosphorus were individually determined in these samples; the particulate fraction was separated by filtering the water through a glass-fiber filter (Malczyk & Eadie, 1980).

Intact cores for measurements of phosphorus flux out of the sediments were collected by divers at five sites in May and September 1985 (Fig. 1). The core tubes (4.2 cm dia. and 10 cm long) were inserted into the sediment about 5 cm, stoppered at both ends, and carefully brought to the surface. The core samples, which contained sediments along with bottom waters immediately overlying the sediments, were kept upright in a cooler during transport to the laboratory and were then placed in an incubator set at the *in situ* temperature. Aeration lines were placed through the top stopper and air was slowly bubbled into the overlying waters. This procedure kept the water well-mixed and also kept dissolved oxygen concentrations at near-saturation levels. All core tubes and aeration lines were made of high-density linear polyethylene to minimize phosphorus adsorption. Samples for phosphorus determinations were taken every 3 to 4 days by drawing out 1 ml of overlying water through a sampling port in the top stopper. Phosphorus levels in lake-water controls were also measured on each sampling day. The volume of overlying water was kept constant by adding 1 ml of lake water after each sample was drawn. The incubation period lasted between 65 and 70 days.

A total of 6 to 8 sediment cores were collected at each site on each sampling date. Since Lake St. Clair is shallow and bottom sediments are easily resuspended, the impact of resuspension on sediment phosphorus release was estimated by mixing the top 1 cm of sediment of one-half of the replicates at the beginning of the incubation period. This created a sediment slurry with the overlying waters. The sediments were mixed again every 10 days until the end of the incubation period. Phosphorus release rates in these mixed cores were compared to release rates in cores that were left undisturbed.

The rate of phosphorus release from the sediments was determined from the slope of a regression line between sampling day and phosphorus concentration in the overlying waters during the incubation period. If the regression was not significant at the 0.05 level, the release rate was considered to be zero. In many cases, phosphorus concentrations increased rapidly at the beginning of the incubation period and then remained relatively constant thereafter. Consequently, a maximal phosphorus release rate was also determined for each replicate core. This rate was calculated using concentrations at the beginning and end of the time period (within each incubation period) when phosphorus concentrations increased most rapidly.

Table 1. Phosphorus content of near-bottom waters at each of the two stations sampled in 1986. TSM = total suspended matter ($mg\,l^{-1}$); TDP = total dissolved phosphorus ($\mu g\,l^{-1}$); TPP = total particulate phosphorus ($\mu g\,l^{-1}$); TP = total phosphorus ($\mu g\,l^{-1}$).

Sampling Date	Station 73				Station 24			
	TSM	TDP	TPP	TP	TSM	TDP	TPP	TP
Apr 30	4.8	–	5.9	8.5	–	–	–	–
May 19	4.6	3.9	5.9	10.0	8.2	7.0	14.8	21.9
Jul 10	6.5	6.0	11.0	13.8	5.2	6.7	9.9	17.0
Aug 4	3.6	4.2	3.2	6.4	–	–	–	–
Sep 16	10.5	6.3	9.7	16.1	10.2	6.1	13.0	20.0
Oct 15	8.8	5.6	10.0	15.2	25.5	5.1	24.2	28.1

4. Results

4.1. Phosphorus content of near-bottom waters

In general, more phosphorus was present at Station 24 than at Station 73. (Table 1). The former station was located farther south than the latter and, as mentioned, nutrient concentrations in the water column increase on a gradient from northwest to southeast. Also, the finer sediments present at Station 24 were more likely to be resuspended in the water column; the greatest difference in particulate phosphorus between the two stations occurred in October during the period of frequent storms. The percentage of particulate phosphorus in the seston ranged from 0.09 to 0.19 percent and was highest in spring/early summer at both stations (Fig. 2). This peak likely reflected a large biotic fraction in the water column at this time; chlorophyll *a* concentrations in Lake St. Clair are highest between April and June (Leach, 1972).

4.2. Mussel nutrient excretion

Mean rates of phosphorus and ammonia excretion by *Lampsilis radiata siliquoidea* in 1985 and 1986 are given in Table 2. Since excretion rates of individuals from Stations 73 and 24 were not significantly different (t-test; $P < 0.05$) on any of the sampling dates, only a mean value for the two stations is given. Seasonal trends in both phosphorus and ammonia excretion were similar for the two years. Phosphorus excretion in the summer declined from spring values to reach a minimum, and then increased to a peak in the fall;

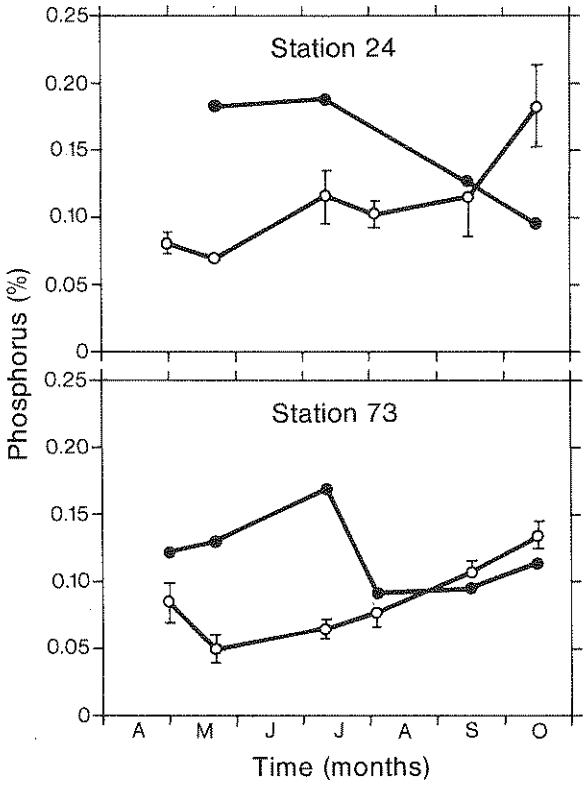

Fig. 2. Seasonal fluctuations in the phosphorus content (mean ± SE) of suspended material in the water column (•—•) and in mussel biodeposits (○—○) at the two sampling stations.

Table 2. Mean (± SE) excretion rates of PO_4–P and NH_4–N by *Lampsilis radiata siliquoidea* in Lake St. Clair in 1985 and 1986. Rates given in μg (g dry wt)$^{-1}$ h^{-1}.

Sampling Date	Temp (°C)	*n*	Mean Dry Wt (g)	Excretion Rate	
				PO_4–P	NH_4–N
1985					
May 14	13.0	1	5.1	0.3	8.4
Jul 16	22.5	5	3.3	<.1 ± <.1	22.3 ± 1.4
Sep 3	21.0	2	1.6	1.9 ± 0.1	9.7 ± 3.5
Sep 19	–	4	2.8	1.9 ± 0.6	12.3 ± 1.6
1986					
Apr 30	10.0	9	1.7	1.1 ± 0.3	10.5 ± 1.0
May 19	12.0	4	1.8	0.6 ± 0.1	9.4 ± 1.8
Jul 10	22.0	9	2.3	0.5 ± 0.1	22.6 ± 1.7
Aug 4	22.7	10	1.9	1.5 ± 0.3	23.6 ± 3.8
Sep 16	17.0	10	1.9	1.9 ± 0.4	18.4 ± 2.8
Oct 15	12.0	10	1.8	1.9 ± 0.4	9.6 ± 1.0

conversely, ammonia excretion was low in the spring and fall but reached a maximum in summer. Excretion rates of other mussel species were similar to those of *L. r. siliquoidea*, but seasonal trends were not as pronounced (Table 3). Reasons for the strong seasonal trends in excretion rates of *L. r. siliquoidea* are not clear, but are likely related to changes in the gametogenic cycle of the organism. *L. r. siliquoidea* is a long-term breeder (Clarke, 1981) in which gametes are formed in late spring/early summer, fertilized and deposited in the brood pouch in late summer/early fall, and glochidia expelled the following spring/early summer (Coker *et al.*, 1921). Spawning condition affects phosphorus excretion, since a greater portion of assimilated material would be used for the production of gametes and not for metabolism. In the marine mussel *Modiolus*, sexually mature individuals retained more phosphorus during the spawning season (thereby excreting less, given the same food source) than individuals in the spent condition (Kuenzler, 1961). Dramatic

Table 3. Mean (± SE) excretion rates of PO_4–P and NH_4–N by various species of mussels in Lake St. Clair in 1985. Rates given in μg (g dry wt)$^{-1}$ h^{-1}.

Sampling Date	Temp (°C)	*n*	Mean Dry Wt (g)	Excretion Rate	
				PO_4–P	NH_4–N
1985					
May 7	13.0	5[a]	2.4	0.9 ± 0.1	11.1 ± 1.7
May 14	13.0	6[b]	8.0	1.0 ± 0.4	5.3 ± 1.0
Jul 16	22.5	4[c]	2.4	1.8 ± 0.5	16.4 ± 1.1
Sep 3	21.0	5[d]	2.3	4.7 ± 1.0	12.1 ± 0.9
Sep 19	–	3[e]	5.5	2.1 ± 0.8	12.6 ± 4.9

[a] *Leptodea fragilis*, 1 *Anodonta grandis*, 1 *Proptera alata*
[b] 2 *L. fragilis*, 1 *Elliptio complanata*, 1 *Lampsilis ovata*, 1 *Ligumea recta*, 1 *P. alata*
[c] 1 *Amblema plicata*, 1 *L. fragilis*, 1 *A. grandis*, 1 *P. alata*
[d] 3 *P. alata*, 2 *L. fragilis*
[e] 1 *A. grandis*, 1 *L. fragilis*, 1 *P. alata*

seasonal trends in the phosphorus content of *L. r. siliquoidea* were not apparent; yet, although differences were not significant, mean content was highest in late spring when gamete production supposedly occurs (Fig. 3). The increase in ammonia excretion in the summer also corresponds to the period of gamete production. Active protein catabolism (and hence increased ammonia excretion) occurs when the glycogen normally used for metabolism is used instead for gamete production (Gabbott & Bayne, 1973; Bayne & Scullard, 1977). The time lag between minimal phosphorus excretion (May) and maximal ammonia excretion (July) may have been a period of gradually increasing protein catabolism. Seasonal trends in food supplies tend to confirm increased phosphorus retention in mid-summer; the proportion of particulate phosphorus in the total seston was actually highest during the mid-summer period when phosphorus excretion rates were minimal (Fig. 2). Of course, this difference may also mean that the particulate phosphorus present in the water in late spring/early summer is more readily retained than that present at other times.

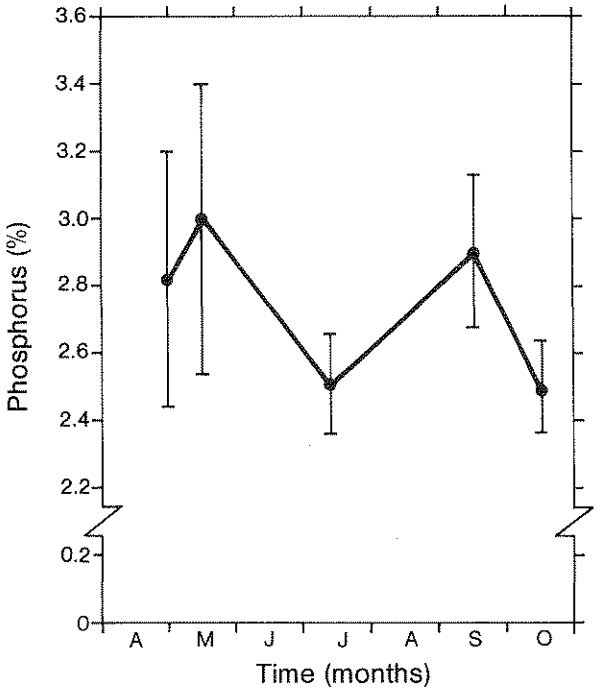

Fig. 3. Seasonal fluctuations in the phosphorus content (mean ± SE) of the body tissue of *Lampsilis r. siliquoidea.*

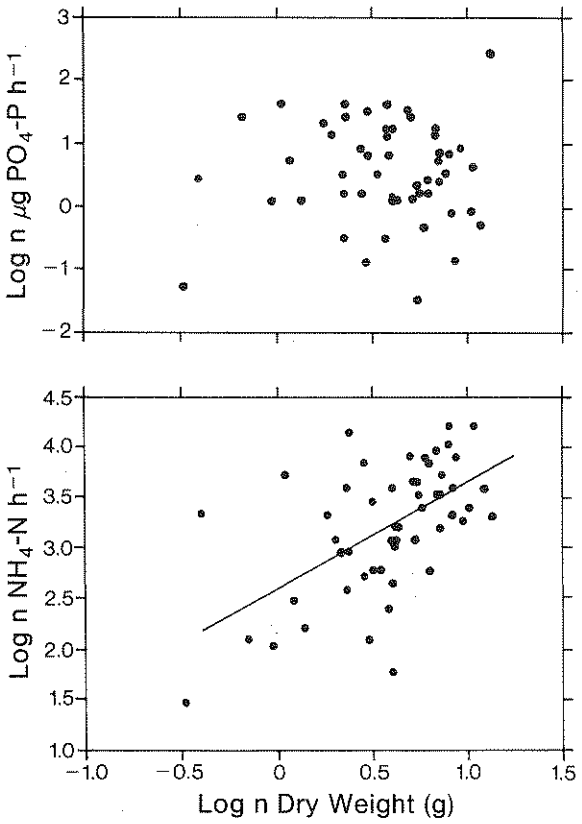

Fig. 4. Relationship between phosphorus (upper) and nitrogen (lower) excretion vs. dry-weight body tissue of *Lampsilis r. siliquoidea.* Regression coefficients (a, b) were 0.69 and −0.42 for phosphorus and 2.6 and 1.03 for nitrogen. Correlation coefficients (r) were 0.16 (non-significant; $P < 0.05$) and 0.63 (significant; $P < 0.05$) for the two nutrients, respectively.

The relationship between ammonia excretion and tissue dry weight followed the general allometric equation $y = ax^b$, where y = excretion, x = shell-free dry weight, and a and b are regression coefficients, but a similar relationship for phosphorus excretion was not apparent (Fig. 4). This lack of a relationship for phosphorus contrasts to other studies of bivalve excretion which found both phosphorus and nitrogen excretion related to tissue dry weight (James, 1987; Lauritsen & Mozley, 1989). Overall, weight-specific excretion rates were somewhat lower than those found for other bivalves (Table 4).

Table 4. Mean (± SE) excretion rates of PO_4–P and NH_4–N by some bivalve species. Estimates are for an animal of about 1 gram. Rates given in μg (g dry wt)$^{-1}$ h^{-1}.

Benthic Organism	Excretion Rate		Source
	PO_4–P	NH_4–N	
Freshwater:			
Lampsilis r. siliquoidea	1.3	16.2	This study
Hyridella menziesi		41.0	James (1987)
Marine:			
Mytilus californianus		23.9	Bayne *et al.* (1976)
Mytilus edulis		19.7	Bayne & Scullard (1977)
*Geukensia demissa**		38.0	Jordan & Valiela (1982)
Modiolus demissus	2.7		Kuenzler (1961)

* *Geukensia demissa* = *Modiolus demissus.*

4.3. Mussel biodeposition

Mussel biodeposition is the sum of pseudofeces (material filtered but not ingested) and feces (material ingested but not assimilated) production. Generally, the phosphorus content of pseudofeces does not change relative to the material filtered (Stanczykowska & Planter, 1985). A comparison of phosphorus content of seston to the phosphorus content of biodeposited material showed that differences were most apparent in late spring/early summer (Fig. 2). At this time, phosphorus concentrations in the seston were high, while phosphorus concentrations in the biodeposited material were low. This further reflects the great efficiency of phosphorus retention during this period.

The mean rate of phosphorus biodeposition was 6.3 μg P g^{-1} h^{-1} and varied from 3.1 to 11.7 μg P g^{-1} h^{-1} (Table 5). Differences between the two stations were not significant on any of the sampling dates (t-test, $P < 0.05$). The rates tended to be higher at both stations in the fall. This trend corresponded to the general tendency for rates to be positively related to amounts of particulate phosphorus in the water column (Fig. 5).

Table 5. Mean (± SE) rates of phosphorus biodeposition by *Lampsilis r. siliquoidea* on each of the sampling dates in 1986. Rates given in μg P (g dry wt)$^{-1}$ h^{-1}.

Sampling Date	Phosphorus Biodeposition	
	Station 73	Station 24
Apr 30	5.8 ± 2.1	4.8 ± 1.8
May 19	3.5 ± 0.5	3.1
Jul 10	5.6 ± 1.7	7.2 ± 2.1
Aug 4	5.4 ± 1.5	4.5 ± 0.7
Sep 16	8.5 ± 1.9	11.7 ± 0.9
Oct 15	6.2 ± 1.2	8.8 ± 3.2

4.4. Phosphorus release from sediments

Phosphorus release from the sediments at each of the five stations on the two sampling dates is given

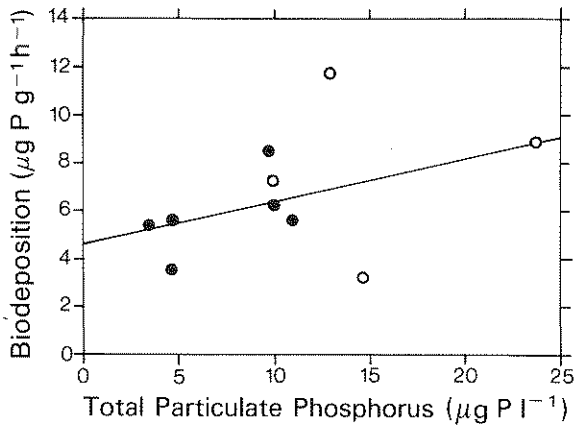

Fig. 5. Relationship between biodeposition rates of phosphorus and total particulate phosphorus in the water column ($r = 0.39$). Closed circles are Station 73 and open circles are Station 24.

Table 6. Mean (± SE) rates of PO_4–P release from Lake St. Clair sediments at each of the stations on the two sampling dates in 1985. Maximum mean release rates are given in parentheses. Rates are given as $\mu g\ P\ m^{-2}\ d^{-1}$. Phosphorus release from sediments at Station 14 in September occurred early in the incubation period and then declined.

Station	Sampling Date	
	May[1]	September[2]
4	32.8 ± 4.7 (51.7)	11.0 ± 6.3 (37.6)
14	14.0 ± 7.4 (68.3)	0.0 ± 0.0 (78.2)
24	29.4 ± 9.9 (51.4)	9.6 ± 6.2 (62.8)
71	2.5 ± 0.9 (21.6)	0.4 ± 0.4 (10.5)
84	5.8 ± 2.7 (15.8)	3.1 ± 3.1 (32.6)

[1] Water temperature = 13 °C.
[2] Water temperature = 22 °C.

in Table 6. Mean release rates in this table include values from all replicates at a given station since there were no significant differences (t-test; $P < 0.05$) between release rates of mixed and unmixed cores at any of the five stations.

Release rates at the two sites in the northwestern portion of the lake (Stations 71 and 84) tended to be lower than rates at the three sites farther south (Stations 4, 14, and 24), which follows the trend of greater overall nutrient concentrations from northwest to southeast. Overall, release rates were higher in May than in September, despite the lower water temperatures during the former month. This difference can likely be attributed to the settling and subsequent mineralization of the spring phytoplankton bloom.

The net release of phosphorus from Lake St. Clair sediments was generally lower than sediment release rates in other areas of the Great Lakes. The mean release rate in this study was 11 $\mu g\ P\ m^{-2}\ d^{-1}$ and the mean maximal release rate was 43 $\mu g\ P\ m^{-2}\ d^{-1}$. In comparison, release rates of 170–570 $\mu g\ P\ m^{-2}\ d^{-1}$ were reported from nearshore Lake Michigan (Quigley & Robbins, 1986) and 30–800 $\mu g\ P\ m^{-2}\ d^{-1}$ were reported from Lake Ontario (Bannerman *et al.*, 1974). Because Lake St. Clair is relatively shallow, wave-induced resuspension occurs quite frequently (4 to 6 resuspension events per month in the spring and fall and 1 to 2 events per month in the summer; N. Hawley, pers. com.). Resuspension diminishes the potential for phosphorus release from the sediments by keeping the upper sediments well oxidized; under such conditions phosphorus tends to remain strongly sorbed to the sediments (Syers *et al.*, 1973). In addition, frequent resuspension of the upper sediments reduces pore-water gradients and thus the potential for release through diffusive flux (Quigley & Robbins, 1986).

5. Discussion

The cycling of phosphorus through the mussel population of Lake St. Clair during the May–October period can be estimated from the determined values of concentrations and flux rates (Fig. 6). Values determined for *L. r. siliquoidea*, which was the dominant and most widespread species, were assumed to be representative of the entire mussel population. Phosphorus removal from the water column by mussels is the product of concentrations in the water, filtration rates, time spent filtering, and density. The mean concentration of particulate phosphorus 1 m above the bottom was 10.7 $\mu g\ l^{-1}$ (Table 1), the filtration rate was 460 $ml\ g^{-1}\ h^{-1}$ (Vanderploeg *et al.*, in prep.), and the mean biomass of the mussel population in the lake was 4.4 g (shell-free dry wt) m^{-2} (Nalepa & Gauvin, 1988). Removal

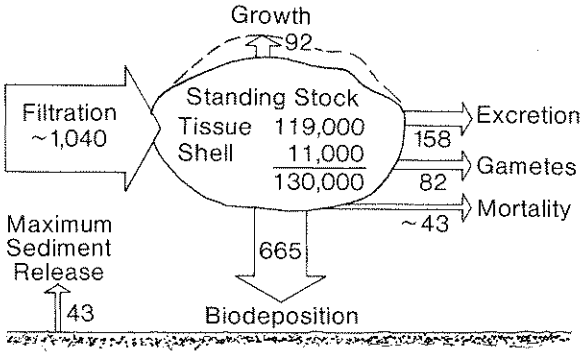

Fig. 6. Phosphorus flow through the mussel population in Lake St. Clair for the May–October 1986 period. Units are in $\mu g\ P\ m^{-2}\ d^{-1}$ except for standing stock which is in $\mu g\ P\ m^{-2}$.

rates of phosphate phosphorus and dissolved organic phosphorus were not considered since phosphate uptake comprises only a small fraction of total uptake (0.6% of particulate phosphorus uptake; Kuenzler, 1961) and the use of dissolved organic phosphorus by mussels has not been proved. The filtration rate of *L. r. siliquoidea* was determined in October 1987 and compares favorably to filtration rates of other mussel species of comparable size (Alimov, 1969; Lewandowski & Stanczykowska, 1975; Paterson & Cameron, 1985). The proportion of time spent filtering by individuals during the determination of their filtration rates was assumed to be equal to the proportion of time spent filtering by *in situ* populations. Given all the above values, the removal rate of phosphorus by mussels in Lake St. Clair was 520 μg P m^{-2} d^{-1}. However, in examining other measured components of phosphorus flux through the population, the amount of phosphorus filtered should have been much higher. For instance, the mean excretion rate was 158 μg P m^{-2} d^{-1} and the biodeposition rate was 665 μg P m^{-2} d^{-1}, giving a total of 823 μg P m^{-2} d^{-1} or an amount 1.6 times higher than that filtered only for these two budget components. A possible reason for this discrepency is that amounts of phosphorus in the water column at 1 m above the bottom are not the same as amounts occurring at a few centimeters above the bottom where the mussels are actually filtering. Indeed, although Lake St. Clair is well mixed, amounts of suspended material are about two times higher at 0.4 m above the bottom than at 1 m (Hamblin *et al.*, 1987). Therefore, a more accurate estimate of the amount of phosphorus actually filtered would be at least 1040 μg P m^{-2} d^{-1}, or two times the amount originally calculated, assuming a similar proportional increase in the amount of particulate phosphorus. Since biodeposition equaled 665 μg P m^{-2} d^{-1}, about 375 μg P m^{-2} d^{-1} or 36 percent of that assumed to be filtered is assimilated by the population. This proportion is generally comparable to that found for other bivalve species from a variety of habitats. For example, the freshwater mussel *Dreissena polymorpha* assimilated 49 percent of the phosphorus filtered in some Polish lakes (Stanczykowska & Planter, 1985) and *Hyridella menziesi* assimilated 80 percent in an oligotrophic lake in New Zealand (James, 1987). The estuarine species *Corbicula japonica* assimilated 41 percent in a poikilohaline lagoon (Fuji, 1979). In contrast, the marine mussel *Mytilus* effectively assimilated only 6 percent of the phosphorus filtered in a Georgia salt marsh (Kuenzler, 1961). This proportion is likely more a function of the quality and quantity of seston, and subsequently the amount of pseudofeces produced, rather than of great differences in assimilation efficiencies. Typically, as amounts of seston increase, the amount lost as pseudofeces also increases (Tenore & Dunstan, 1973; Fuji, 1979; Stanczykowska & Planter, 1985). Particulate phosphorus concentrations were ten times higher in the Georgia salt marsh (44 μg l^{-1}) than in the New Zealand lake (4 μg l^{-1}).

Of the phosphorus assimilated by the Lake St. Clair mussel population, 158 μg m^{-2} d^{-1} or 42 percent was excreted, with the remainder used by the population for production of biomass and generative elements, or lost through mortality during the period. The amount incorporated into standing stocks of the population can be estimated from growth rates and average content in the body and shell fractions. Production of *L. r. siliquoidea* in Lake St. Clair is 0.2 g m^{-2} y^{-1} and mean biomass is 1.5 g m^{-2} (Nalepa & Gauvin, 1988). Extrapolated over the entire population, the mussel production rate in the lake is equal to 0.57 g m^{-2} y^{-1}. Considering that most all growth in mussels occurs during the warmer months (Isely, 1914; Coker *et al.*, 1921), production during the May–October period was about 3.1 mg m^{-2} d^{-1}. Mean phosphorus content of mussel tissue was 2.7 percent, so the amount stored in the body fraction equals 119,000 μg P m^{-2} and the rate of incorporation into the body equals 84 μg P m^{-2} d^{-1}. The standing stock of shells was 55.5 g m^{-2} (Nalepa unpublished). Assuming that the phosphorus content of the shell fraction is equal to 0.02 percent (Kuenzler, 1961) and that phosphorus is incorporated into the shell fraction at the same

rate as into the body fraction, phosphorus contained in the shells equaled 11 100 μg P m^{-2} and incorporation into the shell fraction was 8 μg P m^{-2} d^{-1}. Thus, the total amount of phosphorus incorporated into growth for the period was 92 μg P m^{-2} d^{-1}.

The amount of phosphorus lost from the population in gametes can be inferred from the decrease in phosphorus content of the population over the study period (Kuenzler, 1961). Mean phosphorus content of the soft tissue was 2.82 percent on the first sampling date (April 30) and 2.48 percent on the last sampling date (October 15). Therefore, the net loss for the May–October period was 82 μg P m^{-2} d^{-1}. Overall, the amount incorporated into biomass and generative elements was equal to 174 μg P m^{-2} d^{-1}, or 17 percent of the amount filtered; this compares to the 12 percent estimated for the freshwater mussel *Dreissena polymorpha* (Stanczykowska & Planter, 1985).

The sum of biodeposition, growth, excretion, and gamete loss over the period, all measured independently, equaled 997 μg P m^{-2} d^{-1}. This sum is very similar to the estimated filtration rate of 1040 μg P m^{-2} d^{-1}. The difference of 43 μg P m^{-2} d^{-1} may be shown in Fig. 6 as mortality loss, which is the remaining pathway for phosphorus flux through the population during the period. This loss seems reasonable since mortality in adult mussels is generally low. The estimate of phosphorus loss due to mortality was 0.03 percent of the phosphorus contained in standing stocks (tissue and shell), whereas this loss was 0.06 percent in the marine mussel *Modiolus demissus* (Kuenzler, 1961).

As noted, total biodeposition by the mussels equaled 665 μg P m^{-2} d^{-1}. This amount is potentially available for further use by deposit-feeding benthic invertebrates along with material that has been deposited on the bottom through natural sedimentation. Release from the sediments averaged 11 μg P m^{-2} d^{-1} with a mean maximal release rate of 43 μg P m^{-2} d^{-1}. Because additional phosphorus was not released when the sediments were resuspended, the difference between sediment input and sediment release is phosphorus which either remains bound to sediment particles and is transported out of the system or buried, or which is incorporated into standing stocks of macrophytes or other benthic invertebrates besides the mussels. Accumulation in the sediments is not likely because wave-induced resuspension of the upper sediments is intense and phosphorus concentrations in the upper sediments are quite low (0.01% to 0.07%; Upper Great Lakes Connecting Channels Study – Sediment Workgroup, unpublished report). In addition, estimates of phosphorus loads and losses are not significantly different, indicating no apparent sources or sinks within the lake (Lang *et al.*, 1988).

The role of mussels in cycling phosphorus in Lake St. Clair can be evaluated by comparing rate measurements to total loading from outside sources. The total mean load of phosphorus into the lake is about 3100 MT (metric tons) y^{-1} or 1550 MT for the May–October period (Lang *et al.*, 1988). Over this same period, mussels filtered 210 MT of phosphorus, or 13.5 percent of the total load. Part of the phosphorus is incorporated into biomass or excreted, but a large amount, 134 MT, is sedimented to the bottom via biodeposition. Thus, it appears that the primary role of mussels is to increase the retention of phosphorus in the lake by removing particles from the water column and depositing them on the bottom. Small suspended particles that may not easily settle to the bottom are made available as a food resource to other benthic components, thereby stimulating benthic productivity. Standing stocks of deposit-feeders are generally higher in areas with mussels than in areas without them (Sephton *et al.*, 1980; Radziejewska, 1986). Also, mussel biodeposits can stimulate the growth of aquatic macrophytes, presumably by enhancing nutrient levels in the sediments (Bertness, 1984). Phosphorus uptake by macrophytes in Lake St. Clair has been estimated at 219 MT y^{-1} (Lang *et al.*, 1988). Mussel biodeposition may be especially important in enhancing nutrient availability in Lake St. Clair considering the high frequency of resuspension in the lake and the low rate of natural sedimentation.

6. Acknowledgements

We would like to thank M. Duquet of the R/V Bluewater for his outstanding support during field operations, J. Cavaletto for her help in making the nutrient determinations, and M. Quigley for his insightful comments on the manuscript.

Note added in proof

This article was completed before the discovery and subsequent population increase of the zebra mussel, *Dreissena polymorpha* in Lake St. Clair. Since the phosphorus budget in this article is based on the activities of the unionid population only, all estimates of the role of the entire mussel population in the Lake must now be considered as minimum values.

References

Alimov, A. F., 1969. Nekotorye obscie zakonomernosti processa filtracii u dvustvorcatych molljuskov. Z. Obsc. Biol. 30: 621–631.

Bannerman, R. T., D. E. Armstrong, G. C. Holdren & R. F. Harris, 1974. Phosphorus mobility in Lake Ontario sediments (IFYGL), Proc. 17th Conf. Great Lakes Res., pp. 158–178.

Bayne, B. L. & C. Scullard, 1977. Rates of nitrogen excretion by species of *Mytilus* (Bivalvia: Mollusca). J. Mar. Biol. Assoc. U.K. 57: 355–369.

Bayne, B. L., C. J. Bayne, T. C. Carefoot & R. J. Thompson, 1976. The physiological ecology of *Mytilus californianus* Conrad. 1. Metabolism and energy balance. Oecologia 22: 211–228.

Bertness, M. D., 1984. Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh. Ecology 65: 1794–1807.

Clarke, A. H., 1981. The Freshwater Molluscs of Canada. Ntnl. Mus. Can., Ottawa.

Coker, R. E., A. F. Shira, M. W. Clarke & A. W. Howard, 1921. Natural history and propagation of fresh-water mussels. Bull. U.S. Bur. Fish. 37: 79–181.

Fuji, A., 1979. Phosphorus budget in natural population of *Corbicula japonica* Prime in poikilohaline lagoon, Zyusan-ko. Bull. Fac. Fish. Hokkaido Univ. 30: 34–49.

Gabbott, P. A. & B. L. Bayne, 1973. Biochemical effects of temperature and nutritive stress on *Mytilus edulis* L. J. Mar. Biol. Assoc. U.K. 53: 269–286.

Gardner, W. S., 1978. Microflurometric method to measure ammonium in natural waters. Limnol. Oceanogr. 23: 1069–1072.

Gardner, W. S. & J. M. Malczyk, 1983. Discrete injection flow analysis of nutrients in small-volume water samples. Anal. Chem. 55: 1645–1647.

Gardner, W. S., T. F. Nalepa, M. A. Quigley & J. M. Malczyk, 1981. Release of phosphorus by certain benthic invertebrates. Can. J. Fish. Aquat. Sci. 38: 978–981.

Hamblin, P. F., F. M. Boyce, J. Bull, F. Chiocchio & D. Robertson, 1987. Report to UGLCCS Work Groups. Ntnl. Wat. Res. Inst. Burlington, Ontario. Contrib. 87–87.

Herdendorf, C. E., C. N. Raphael & E. Jaworski, 1986. The ecology of Lake St. Clair wetlands: a community profile. U.S. Fish Wild. Serv. Biol. Rep. 85(7.7), Washington D.C.

Isely, F. B., 1914. Experimental study on the growth and migration of freshwater mussels. U.S. Bur. Fish. Doc. 7922, Washington, D.C.

James, M. R., 1987. Ecology of the freshwater mussel *Hyridella menziesi* (Gray) in a small oligotrophic lake. Arch. Hydrobiol. 3: 337–348.

Jordan, T. E. & I. Valiela, 1982. A nitrogen budget of the ribbed mussel, *Geukensia demissa*, and its significance in nitrogen flow in a New England salt marsh. Limnol. Oceanogr. 27: 75–90.

Kasprzak, K., 1986. Role of Unionidae and Sphaeriidae (Mollusca, Bivalvia) in the eutrophic Lake Zbechy and its outflow. Int. Rev. Ges. Hydrobiol. 71: 315–334.

Kuenzler, E. J., 1961. Phosphorus budget of a mussel population. Limnol. Oceanogr. 6: 400–415.

Lang, G. A., J. A. Morton & T. D. Fontaine, 1988. Total phosphorus budget for Lake St. Clair: 1975–80. J. Great Lakes Res. 14: 257–266.

Lauritsen, D. D. & S. C. Mozley, 1989. Nutrient excretion by the Asiatic clam *Corbicula fluminea*. J. North Amer. Benthol. Soc. 8: 134–139.

Leach, J. H., 1972. Distribution of chlorophyll *a* and related variables in Ontario waters of Lake St. Clair. Proc. 15th Conf. Great Lakes Res., pp. 80–86.

Leach, J. H., 1973. Seasonal distribution, composition and abundance of zooplankton in Ontario waters of Lake St. Clair. Proc. 16th Conf. Great Lakes Res., pp. 54–64.

Leach, J. H., 1980. Limnological sampling intensity in Lake St. Clair in relation to distribution of water masses. J. Great Lakes Res. 6: 141–145.

Lehman, J. H., 1980. Release and cycling of nutrients between planktonic algae and herbivores. Limnol. Oceanogr. 25: 620–632.

Lewandowski, K. & A. Stanczykowska, 1975. The occurrence and role of bivalves of the family Unionidae in Miklajskie Lake. Ekol. Pol. 23: 317–334.

Malczyk, J. M. & B. J. Eadie, 1980. Collection, preparation, and analysis procedures employed and precision achieved in the chemical field program, 1976–79. Open File Report No. 226. Great Lakes Env. Res. Lab., Ann Arbor, MI.

Nalepa, T. F. & J. M. Gauvin, 1988. Distribution, abundance, and biomass of freshwater mussels (Bivalvia:

Unionidae) in Lake St. Clair. J. Great Lakes Res. 14: 411–419.

Paterson, C. C. & I. F. Cameron, 1985. Comparative energetics of two populations of the unionid, *Anodonta cataracta* (Say). Freshwat. Invertebr. Biol. 4: 79–90.

Quigley, M. A. & J. A. Robbins, 1986. Phosphorus release processes in nearshore southern Lake Michigan. Can. J. Fish. Aquat. Sci. 43: 1201–1207.

Radziejewska, T., 1986. On the role of *Mytilus edulis* aggregations in enhancing meiofauna communities off the southern Baltic coast. Ophelia (Suppl. 4): 211–218.

Sephton, T. W., C. G. Paterson & C. H. Fernando, 1980. Spatial interrelationships of bivalves and nonbivalve benthos in a small reservoir in New Brunswick, Canada. Can. J. Zool. 58: 852–859.

Stanczykowska, A. & M. Planter, 1985. Factors affecting nutrient budget in lakes of the R. Jorka watershed (Masurian Lakeland, Poland) X. Role of the mussel *Dreissena polymorpha* (Pall.) in N and P cycles in a lake ecosystem. Ekol. Pol. 33: 345–356.

Syers, J. K., R. F. Harris & D. E. Armstrong, 1973. Phosphate chemistry in lake sediments. J. Env. Qual. 2: 1–14.

Tenore, K. R. & W. M. Dunstan, 1973. Comparison of feeding and biodeposition of three bivalves at different food levels. Mar. Biol. 21: 190–195.

Walz, V. N., 1978. Die Produktion der Dreissena-Population und deren Bedeutung im Stoffkreislauf des Bodensees. Arch. Hydrobiol. 82: 482–499.