Impact of the *Dreissena* invasion on native unionid bivalves in the upper St. Lawrence River

A. Ricciardi, F.G. Whoriskey, and J.B. Rasmussen

Abstract: Introduced Eurasian mussels (*Dreissena polymorpha* and *Dreissena bugensis*) colonized native unionid bivalves in the upper St. Lawrence River in the early 1990s. From 1992 to 1995, we examined the infestation and impact of *Dreissena* on unionids at several sites near the Island of Montréal. Unionids suffered heavy (90–100%) mortality at sites where *Dreissena* occurred in high densities (i.e., 4000 – 20 000/m^2). Mean infestations (<100 dreissenids/unionid) were 10–100 times lower than those reported for infested unionid populations in Lake Erie and Lake St. Clair, yet resulted in similarly high mortality levels. At two St. Lawrence River sites, significant declines in unionid density were first observed when mean infestations exceeded 10/unionid. North American data suggest that populations of unionids that carry, on average, a mass of *Dreissena* nearly equal to or greater than their own mass will become extirpated. We hypothesize that dreissenid infestation enhances unionid mortality primarily by interfering with normal activity (feeding, respiration, locomotion) in such a way as to cause the unionid to expend energy reserves required for surviving winter.

Résumé : Au début des années 1990 dans le cour supérieur du Saint-Laurent, des moules eurasiennes (*Dreissena polymorpha* et *Dreissena bugensis*) introduites ont colonisé des bivalves de la famille des unionidés, indigènes dans ces eaux. De 1992 à 1995, nous avons étudié l'infestation et évalué l'impact des *Dreissena* chez les unionidés de diverses stations situées à proximité de l'île de Montréal. Là où la densité des *Dreissena* était élevée (c'est à dire de 4000 à 20 000 m^{-2}), la mortalité a été très forte chez les unionidés (90–100%). Les infestations moyennes (<100 *Dreissena*/unionidé) étaient 10–100 fois moindres que celles qui ont touché les populations d'unionidés des lacs Érié et Saint-Clair, mais la mortalité a atteint des valeurs à peu près aussi élevées. Dans deux stations du fleuve Saint-Laurent, la densité des unionidés a baissé dans une mesure significative lorsque l'infestation moyenne a dépassé 10 *Dreissena*/unionidé. D'après les données recueillies en Amérique du Nord, lorsque la masse des *Dreissena* est, en moyenne, presque égale ou supérieure à la masse de la population d'unionidés hôte, cette dernière est destinée à disparaître. Selon notre hypothèse, l'infestation de *Dreissena* fait augmenter la mortalité chez les unionidés principalement en nuisant aux activités normales (alimentation, respiration, locomotion) de son hôte, celui-ci devant puiser dans les réserves énergétiques qui lui permettrait normalement de survivre en hiver.

[Traduit par la Rédaction]

Introduction

Biological invasions may substantially alter pre-existing communities by displacing native species through predation, hybridization, or competitive interactions (Elton 1958; Mooney and Drake 1986; Lodge 1993). The invasion of North American inland waters by Eurasian macrofouling bivalves, the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*Dreissena bugensis*), has provoked considerable concern about their potential impact on native mussels (families Unionidae and Margaritiferidae) because of *Dreissena*'s ability to colonize virtually all solid surfaces, including the shells of other molluscs (Mackie 1990; Schloesser and Kovalak 1991). The negative impact of exotic macrofouling mussels on other bivalves has been documented in the marine literature: invasive mytilids *Mytilaster lineatus* and *Musculista senhousia*

may overgrow and kill other bivalves (Zhadin 1965; Willan 1987), and dense colonies of the dreissenid *Mytilopsis sallei* may smother oyster beds (Morton 1989). Unlike their marine relatives, unionid mussels have evolved in the absence of dominant fouling organisms and may be particularly sensitive to *Dreissena* infestation.

Several European studies have described the infestation of unionid mussels by *Dreissena* (Behning 1928; Wagner 1936; Sebestyen 1935, cited in Lewandowski 1976; Biryukov et al. 1964; Wolff 1969; Lewandowski 1976) but provide virtually no information on changes in unionid abundance following *Dreissena* invasion. In North America, published quantitative information concerning the impacts of *Dreissena* on unionids is limited to a few studies in the Great Lakes. Heavy infestation of unionids by *Dreissena* is considered to be the major cause of recent severe declines in the unionid populations of Lake Erie and Lake St. Clair (Gillis and Mackie 1994; Schloesser and Nalepa 1994; Nalepa 1994), although a large die-off of mussels in Lake St. Clair had already occurred before *Dreissena* invaded the lake (Nalepa and Gauvin 1988), and unionids have been declining in western Lake Erie for several decades (Nalepa et al. 1991). The history of infestation and unionid mortality in these two lakes has been used to forecast the impact of *Dreissena* on other North American unionid populations (Biggins 1992; Schloesser and Nalepa 1994). However, it is not known whether these predictions apply to lotic habi-

A. Ricciardi and J.B. Rasmussen.[1] Department of Biology, McGill University, Montréal, QC H3A 1B1, Canada.
F.G. Whoriskey. Department of Natural Resource Sciences, Macdonald Campus of McGill University, Ste-Anne-de-Bellevue, QC H9X 3V9, Canada.

[1] Author to whom all correspondence should be addressed. e-mail: jrasmu@bio1.lan.mcgill.ca

tats, which generally have lower *Dreissena* densities (Stanczykowska 1977; Mellina and Rasmussen 1994) and infestation intensities (Ricciardi et al. 1995), or whether the unusually high *Dreissena* densities recorded in the Great Lakes (10^4–10^5 mussels/m^2; Mackie 1990; Griffiths et al. 1991) are necessary to cause significant unionid mortality.

Since its introduction to North America ca. 1986, *Dreissena* has invaded several large rivers, including the St. Lawrence, Hudson, Mississippi, Illinois, Ohio, Tennessee, and Arkansas rivers. Large North American rivers and their tributaries contain most of the endemic species of freshwater mussels in the world, and many of these species are threatened with extinction (Biggins 1992; Williams et al. 1993). The ability to predict the ecological impacts of *Dreissena* on unionid populations in large rivers would allow us to make informed management decisions and effectively focus conservation efforts to mitigate these impacts. Thus far, our predictive power has been limited by the lack of quantitative data on *Dreissena*–unionid interactions in rivers.

In the early 1990s, the St. Lawrence became the first large North American river to be colonized by *Dreissena* (Griffiths et al. 1991; Conn and Conn 1993; Mellina and Rasmussen 1994), and thus provides an important source of predictive information for large rivers that have not yet been invaded or heavily colonized. Dreissenid mussels were first observed on unionids in the international section of the St. Lawrence River in 1991 (Conn and Conn 1993), but their impact has not been previously examined. In this study, we quantitatively assessed the infestation and impact of *Dreissena* on unionids in the upper St. Lawrence River and tested the prediction that unionid diversity and abundance will decline as *Dreissena* abundance increases in the river.

Methods

From 1992 to 1995, unionid and dreissenid mussels were collected by divers on various dates from nine sites on the upper St. Lawrence River near Montréal, Quebec. From east to west along the river, these sites were located on Lake St. Pierre (three sites), Port of Montréal (one site), Lake St. Louis at Lachine (two sites), and Lake St. François at Les Cèdres (one site), and in two sections (denoted east and west) of the Soulanges Canal at Pointe-des-Cascades (approx. 45°20′N, 73°58′W). Our most intensive sampling was done at the east section of the Soulanges Canal, which empties into a branch of the lower Ottawa River near Île Perrot. The depth of the canal is 6.0 m and the bottom substrate consists primarily of mud and silt. The concrete canal walls and unionid shells provide most of the colonizable hard substrate for dreissenids. One-year-old and young-of-the-year *D. polymorpha* (age estimated by shell length, following Mackie 1990) were first observed on the walls and bottom substrates (including unionid shells) by divers in the autumn of 1991 (F.G. Whoriskey, personal observation); therefore, we estimate that *Dreissena* became established in this section of the river in late 1990 or early 1991. *Dreissena* and unionids were abundant when we began our investigation in 1992. Long-term changes in the abundance and infestation history of unionids in the Soulanges Canal (east section) were monitored by collections made during the summers (June–September) of 1992–1994 and in May 1995. Water quality parameters during these sampling periods were as follows: water temperature (at 1 m depth), 12–23°C; pH, 7.8–8.4; chlorophyll *a* concentration (mean ± SE), 0.32 ± 0.04 μg/L; CaCO$_3$ hardness, 59 ± 4 mg/L; and dissolved oxygen (near the sediments), 6.1 ± 0.4 mg/L. In 1991, *Dreissena* became established in Lake St. Louis (A. Ricciardi, personal observation),

where its rate of population growth lagged noticeably behind that in the Soulanges Canal and thus served as a useful comparison for our long-term infestation and mortality monitoring. Two sites in Lake St. Louis at Lachine were sampled between 1992 and 1995: site 1 was a shallow (<2 m depth), wave-swept embayment with a substrate of abundant large cobble over a mixture of silt and sand; site 2 was located at the Iroquois Yacht Club in Lachine and had a mean depth of ca. 3 m and a muddy substrate.

The other St. Lawrence River sites were sampled incidentally. The west section of the Soulanges Canal was sampled only in July 1994 and September 1995. Lake St. François (at Les Cèdres) was sampled in July 1992 and September 1995. The Port of Montréal was sampled once in July 1994. Each of the three Lake St. Pierre sites was sampled on a single occasion: site 1 (located at the north end of the lake near Grande-Riviere-du-Loup) was sampled in September 1995, while sites 2 and 3 (located near the river channel at the southwestern part of the lake) were sampled in October 1995.

All unionids, including empty shells, were removed by hand from a 1-m^2 polyvinyl chloride quadrat cast randomly on the bottom substrate by a scuba diver. The upper 10 cm of sediment within the quadrat was probed by hand, aided by an underwater light when necessary, to locate living and dead individuals buried immediately beneath the surface. We decided a priori to use at least five replicated 1-m^2 quadrats at each site because this was expected to yield a precision of ±20% when sampling unionid densities of 10–30 mussels/m^2 (Downing and Downing 1992). At the Port of Montréal, unionid and dreissenid densities were not sampled but living and freshly killed unionids were randomly collected by a diver. Freshly killed unionids were distinguished from older shells by their intact hinge ligament and uneroded nacre; our previous experience suggested that these characteristics were reliable in identifying individuals that had been dead for less than a few months. Some freshly killed specimens were easily recognized by their decaying tissues. Unionid species were identified following Clarke (1981) and McMahon (1991).

Dreissenid densities were estimated by removing mussel-covered substrates from random 1-m^2 quadrats (five replicates). Smaller (25 × 25 cm, or 0.0625-m^2) quadrats were used at the densely colonized Soulanges Canal sites, where dreissenids were scraped from the walls at 3–5 m depths with a knife. Unionids and dreissenids were stored in a cooler and taken to the laboratory within 2 h of collection. Dreissenids were removed from unionid shells and other substrates using forceps and a bristle brush and then were washed through a 1-mm mesh sieve, weighed on an electronic balance to determine their fresh mass, and counted under a dissecting microscope. For each unionid population, we determined the mean infestation intensity (i.e., mean number of dreissenids per unionid host, all unionids considered).

Unionids were weighed and their shell length was measured with dial calipers. Their tissues were scraped from the shells with a scalpel, stored in a freezer at –20°C for approximately 48 h, and then dried for another 24 h at –50°C using a freeze-drier (Labconco model 45). Unionid shells were blotted and allowed to dry in ambient air at 20°C for at least 24 h. After drying, the tissues and shells were weighed. Shell length – dry tissue mass (log$_{10}$ transformed) regression equations were constructed for samples from lightly infested (1992 and 1993) and heavily infested (1994) populations of *Elliptio complanata* (the dominant unionid species) at the Soulanges Canal. These relationships were compared by analysis of covariance (ANCOVA) using SAS procedures (SAS Institute Inc. 1988). We used sample sizes of 24, 64, and 12 unionids for 1992, 1993, and 1994 populations, respectively. The caloric content of freeze-dried mussel tissues was determined by an oxygen bomb calorimeter (Parr model 1341). We examined temporal trends in the caloric content of unionids and dreissenids in the Soulanges Canal (August 1992 – September 1994) using Spearman rank correlation.

Using linear regression (Proc GLM; SAS Institute Inc. 1988) on data from this study, supplemented with data from the literature and unpublished data from other researchers, we related the ratio of the

1436

Can. J. Fish. Aquat. Sci. Vol. 53, 1996

fresh mass of dreissenids and their unionid hosts ($\log_{10}$ transformed) to the proportion of freshly killed unionids (transformed as arcsin $x^{0.5}$) in each of 13 North American populations. Because of temporal replication at certain sites, the final data set contained 22 records.

Densities (number per square centimetre) of *Dreissena* on living unionids and the concrete walls of the Soulanges Canal were compared using a *t* test on $\log_{10}$-transformed data. The amount of unionid shell surface area available for colonization was estimated using a surface area – shell length regression equation that we developed previously (Ricciardi et al. 1995). Because unionids in the canal were normally buried with only their posterior shell region exposed, we assumed that the exposed surface area would be about one half of the total surface area.

Results

Infestation and mortality of unionids in the upper St. Lawrence River

In 1992, *Dreissena* in the Soulanges Canal had a population density of 1990/m² (97% *D. polymorpha*, 3% *D. bugensis*) on the canal walls and outnumbered unionids (21/m²) by two orders of magnitude. Three unionid species (*E. complanata*, *Lampsilis radiata*, *Pyganodon* (*Anodonta*) *cataracta*) were common in 1992 (another species, *Ligumia recta*, was encountered alive on only one occasion in 1993). Seventy-four percent of unionids had *Dreissena* attached to their shells, and the mean infestation for the entire unionid population was 3.1/unionid (Fig. 1). Smaller mean infestations were recorded for Lake St. François (1.2/unionid) and Lake St. Louis (0.8/unionid and 1.3/unionid, at two sites) in the summer of 1992, but the *Dreissena* field density at each of these sites was less than 10% of that of the Soulanges Canal. Unionid densities at St. Lawrence River sites in 1992 varied from 3 to 120/m² with a median value of 21/m² (Table 1).

In 1993, 95% of unionids in the Soulanges Canal were infested with 1–75 dreissenids (96% *D. polymorpha*), and the mean infestation for the population (9.9/unionid) tripled from that of the previous year (Fig. 1). Unionids were carrying, on average, more than 36% of their own mass in attached dreissenids. Small unionids (<30 mm length), mostly juveniles, carried infestations equivalent to 2.3 times their own mass. The density of dreissenids on the walls of the Soulanges Canal (1819/m²) did not significantly change from the previous year, but the biomass increased by almost 70% (from 1568 g/m² in 1992 to 2624 g/m²). Unionid biomass in the canal declined by 52% (from 904 to 433 g/m²) over this period.

In the spring of 1994, there was a significant increase in the number of freshly killed unionids, all heavily infested with *Dreissena* (Figs. 1–3). Freshly killed unionids were often buried near the sediment–water interface with a cluster of living dreissenid mussels attached to their posterior end, which indicated that they were alive when heavily colonized. Most of the dead unionids belonged to *Lampsilis radiata*, which was absent from all collections of living unionids after the winter of 1993–1994 (Fig. 2). *Pyganodon cataracta* was absent from our autumn 1994 collection of unionids, although a few freshly killed specimens were found. However, both *Lampsilis radiata* and *P. cataracta* were still common at Lake St. Louis site 1, where mean infestation (<10/unionid) and field density (ca. 1300/m²) were comparable to 1993 Soulanges Canal values (Fig. 1). In July 1994, the density and biomass of dreissenids in the Soulanges Canal were near 4000/m² and 6000

Fig. 1. Mean (±1 SE) density of living unionid bivalves and infestation (number of *Dreissena* per unionid) at (*a*) a low infestation site (Lake St. Louis site 1) and (*b*) a high infestation site (Soulanges Canal, east section), 1992–1995.
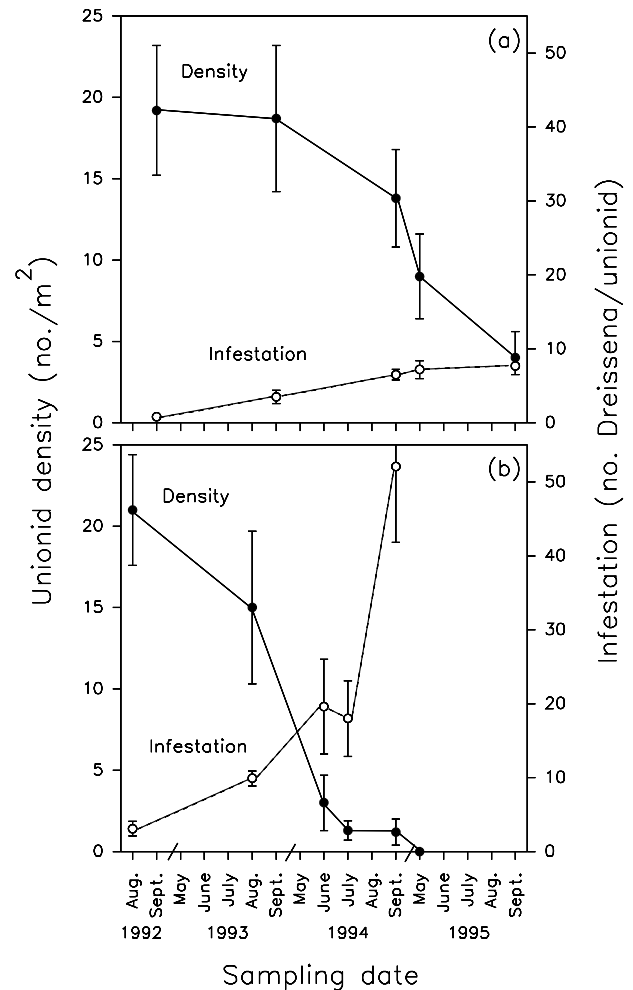
g/m², respectively. Infestation levels continued to rise from the previous year: 100% of unionids were colonized, and the mean infestation level grew from 19/unionid in the spring to 52/unionid in the autumn, 17 times greater than the level recorded in 1992 (Fig. 3). By September 1994, we found a few living unionids and several dead individuals with more than 100 attached dreissenids. Unionids were carrying 87% of their own mass in attached dreissenids (Fig. 4), and their density (1.2/m²) had declined to less than 10% of its level in 1992 (Fig. 1).

In the early spring of 1995, no living unionids were found in the east section of the Soulanges Canal, despite intensive sampling (eight 1-m² quadrats, 45 min search time). There was, however, an abundance of freshly killed unionids (predominantly *E. complanata*) whose shells were covered with dreissenids around their siphonal end (mean 42/unionid; Fig. 3). In September, we searched the west section of the canal for 30 min and found no living unionids. We collected only a few dead shells (*Lampsilis radiata*, *E. complanata*, and *P. cataracta*), which carried 25–134 dreissenids (43.8 ± 9.2/unionid). The mean density of *Dreissena* on the canal walls at this site was 19 140 ± 3512/m².

Table 1. Infestation and mortality data for unionid populations in the upper St. Lawrence River and associated *Dreissena* densities.

Site	Unionid density (no./m²) Past	Unionid density (no./m²) Present	% freshly killed	*Dreissena* density (no./m²) Past	*Dreissena* density (no./m²) Present	Infestation Mean	Infestation Max.	Source
Lake St. Pierre								
Site 1		10	8		<10	0.7	14	This study
Site 2		11				6.4	18	This study; MEF (Quebec),[a] unpublished data
Site 3			22			47.7	92	This study; MEF (Quebec), [a] unpublished data
Port of Montréal								
(1994)			39			23	42	This study
Lake St. Louis								
Site 1	19.2	4	29	101	1 068	7.7	21	This study
Site 2	48	0	100	123	3 876	34[b]	81[b]	This study
Soulanges Canal								
East site	21	0	100	1990	4 223 (1994)	23.3 (1994)	91	This study
West site	5.3 (1994)	0	100 (1994)	2944 (1994)	19 140	43.8 (1994)	134	This study
Lake St. François	120	5	33	165	2 272	26.4	58	This study; St. Lawrence Centre,[c] unpublished data
Prescott, Ont.	3	<1	>80		~5 000	62	77	D.B. Conn,[d] unpublished data
Brockville, Ont.	42	<1	>80			<100		D.B. Conn,[d] unpublished data
Grasse River, N.Y.								
(river mouth)		<1 (1993)	>80 (1993)			<100 (1993)		D.B. Conn,[d] unpublished data
Kingston, Ont.		<1 (1994)	>90 (1994)	~5000		<100 (1994)		R. Serrouya,[e] personal communication

Note: Past values are from 1992, and present values (including infestation and mortality data) are from 1995, unless otherwise indicated in parentheses.

[a]F. Cotton, Ministère de l'Environnement et de la Faune, Québec, Que.

[b]Values from dead unionids.

[c]L. Lapierre, St. Lawrence Centre, Environment Canada, Montreal, Que.

[d]Department of Biology, University of the South, Sewanee, Tenn.

[e]Department of Natural Resource Sciences, McGill University, Montréal, Que.

Dreissena density (1068/m²) and infestation (7.7/unionid) at Lake St. Louis site 1 did not change significantly, but the unionid density (4.0 ± 1.6/m²) was 80% lower than its value in 1992 (Fig. 1). *Dreissena* density at Lake St. Louis site 2 (Iroquois Yacht Club) grew to 3876/m² by the autumn of 1995. At site 2, we recorded a unionid density of 48/m² and a mean infestation of 1.3/unionid in 1992; in September 1995, several dead unionids encrusted with *Dreissena* were found in every quadrat, but no living specimens were collected.

In Lake St. Pierre, unionid mortality increased along a gradient of mean infestation that spanned three orders of magnitude across all three sites. In Lake St. François near Les Cèdres, mean infestation increased by 22 times and unionid density declined by 96% between 1992 and 1995. In general, the St. Lawrence River sites with the highest mean infestations had the fewest living unionids (Table 1). Mean infestation ($\log_{10}$ transformed) explained 52% ($F = 16.1$, $p < 0.0008$) of the variance in the proportion of freshly killed unionids ($\text{arcsin}^{0.5}$ transformed) in St. Lawrence River populations.

Preferential colonization of unionids by *Dreissena*
After 1992, *Dreissena* colonized living unionids to a greater

extent than the walls of the Soulanges Canal (*t* test, $p < 0.01$), even though the walls provided most of the available hard substrate (Fig. 5). Mean dreissenid densities on unionids in 1993 (0.6/cm²) and 1994 (1.5/cm²) were approximately 3.5 times greater than densities on the walls. On a per square metre basis, the mean *Dreissena* density on unionids in 1994 ($15\ 067 \pm 2368$/m²) was similar to the densities reported on rocky substrates in western Lake Erie and Lake St. Clair in the late 1980s (Mackie 1990; Griffiths et al. 1991). Although both living and dead unionids were colonized, greater numbers of *Dreissena* were found on living unionids in 1992 and 1993 (*t* tests, $p < 0.05$). However, as unionids began to suffer heavy mortality after 1993, differences in infestation on living and freshly killed specimens became insignificant (Fig. 3).

Change in condition and caloric content of Soulanges Canal unionids following infestation
The 52% reduction in unionid biomass without a concomitant decline in unionid density suggests that either large individuals suffered a die-off or unionids became emaciated in 1993. A plot of dry tissue mass against shell length for *E. complanata*, the dominant unionid in the Soulanges Canal, supports both of

1438

Can. J. Fish. Aquat. Sci. Vol. 53, 1996

Fig. 2. Mean (±1 SE) density of principal unionid taxa in the Soulanges Canal (east section).

Fig. 4. Mean (±1 SE) mass ratio of infesting dreissenid mussels and their unionid hosts in the Soulanges Canal, 1992–1994.
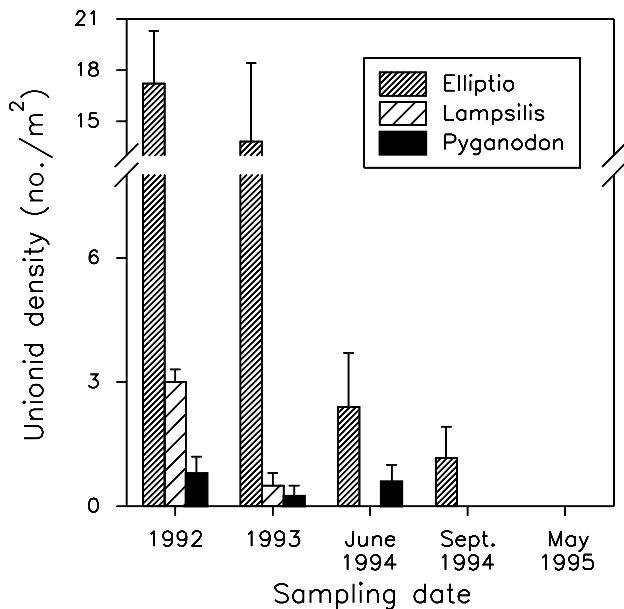
Fig. 3. Mean (±1 SE) infestation levels on living and dead unionids in the Soulanges Canal (east section).
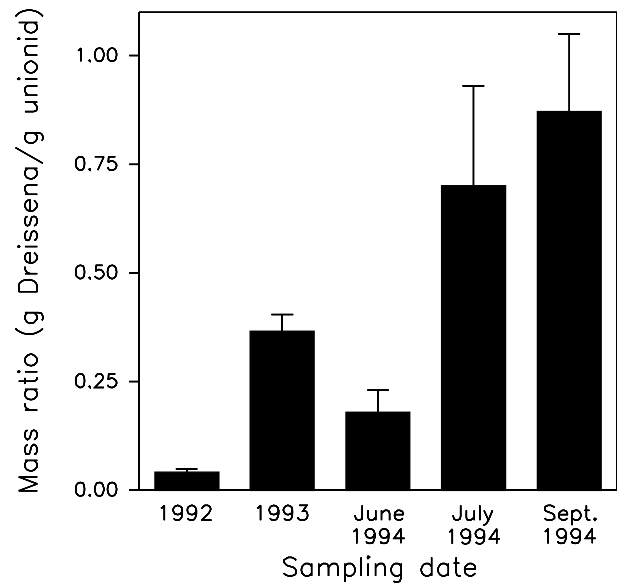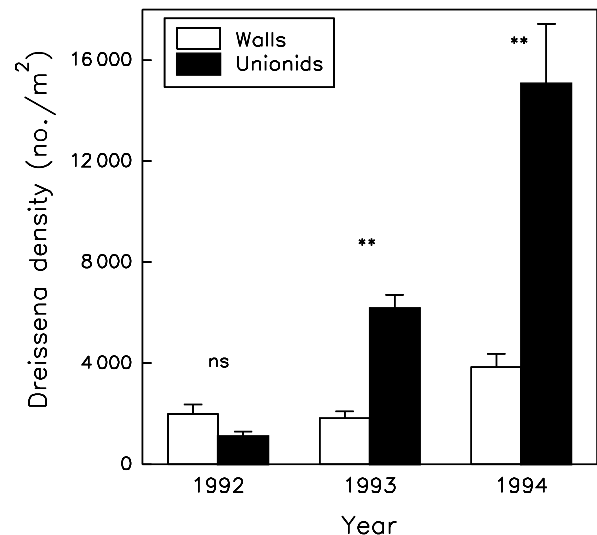

Fig. 5. Difference in *Dreissena* population density on the concrete walls and the shells of living unionids in the Soulanges Canal, 1992–1994. **, $p < 0.01$; ns, not significant.

these hypotheses (Fig. 6). The 1992 dry mass – shell length regression ($\log_{10}$ mass = 2.86 $\log_{10}$ length – 5.31, r^2 = 0.90) was significantly different (ANCOVA, $F = 52.0$, $p < 0.0001$) from those of 1993 ($\log_{10}$ mass = 2.97 $\log_{10}$ length – 5.75, r^2 = 0.91) and 1994 ($\log_{10}$ mass = 3.79 $\log_{10}$ length – 7.24, r^2 = 0.81). Regressions for 1993 and 1994 were not different from each other (ANCOVA, $F = 3.9$, $p > 0.40$). The decline in unionid condition between 1992 and 1993 corresponded with a ninefold increase in the dreissenid–unionid mass ratio (Fig. 4). Living specimens of *E. complanata* with shell lengths >70 mm were more abundant in 1992 than in 1993 and 1994 (*t* tests on $\log_{10}$-transformed data, $p < 0.05$).

There was no correlation between unionid caloric content and infestation intensity (number and mass of *Dreissena* per unionid) within any given year. However, there was a declining trend in unionid caloric content from August 1992 to September 1994 (Spearman rank correlation, $r = -0.89$, $p < 0.007$). By contrast, *D. polymorpha* caloric content did not change significantly over this time period (Spearman, $r = -0.48$, $p > 0.13$) and appeared to fluctuate around a mean value of 5100 cal/g dry tissue mass (1 cal = 4.19 J) (Fig. 7). Unionid caloric content reached its lowest value (3505 cal/g) in September 1994.

A small number of heavily infested unionids at our St. Lawrence River sites had conspicuous shell damage along the valve edges of the siphonal region, where dense *Dreissena*

Fig. 6. Dry tissue mass versus shell length for *Elliptio complanata* from the east section of the Soulanges Canal, 1992–1994.

Fig. 7. Caloric content (cal/g dry tissue mass) of unionid and dreissenid mussels in the east section of the Soulanges Canal, 1992–1994.
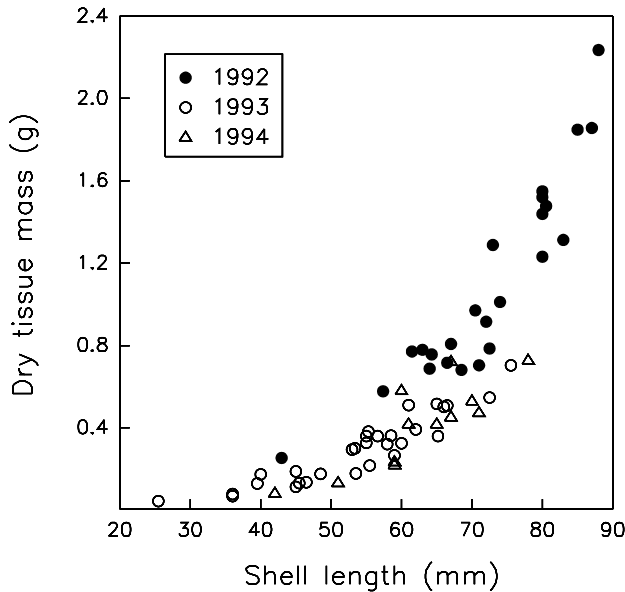
attachment occurred. This damage involved a bent or indented shell margin resulting in an irregular gape. In the west section of the Soulanges Canal, where the mean infestation on living unionids was 43.8/unionid (maximum 134), 7% (1/15) of living unionids and 13% (3/23) of dead unionids had deformed shells. In the east section of the canal in 1994, where the mean infestation was 23/unionid (maximum 91), the frequency of shell deformities was 2.8% (1/36) among living unionids and 5% (4/80) among freshly killed unionids. Virtually no shell deformities were observed in the Soulanges Canal prior to 1994. Less than 5% of unionids collected at each of the other St. Lawrence River sites had deformities.

### Correlation between dreissenid–unionid mass ratio and unionid mortality

Mean dreissenid–unionid mass ratios for Great Lakes – St. Lawrence River populations spanned two orders of magnitude (Table 2) and explained 73% ($F = 54.3$, $p < 0.0001$) of the variance in the proportion of freshly killed unionids among these populations (Fig. 8). By comparison, mean infestation explained 61% ($F = 30.2$, $p < 0.0001$) of this variance. Mean mass ratios for the St. Lawrence River varied from 0.03 to 0.87 and explained 68% ($F = 33.7$, $p < 0.0001$) of the variance in unionid mortality.

Discussion

Comparison of infestation and mortality rates in the St. Lawrence River, Great Lakes, and European habitats

Unionids are preferred substrates for settling *D. polymorpha* larvae in the St. Lawrence River (Fig. 5; Conn and Conn 1993; Mellina and Rasmussen 1994) and the Great Lakes (Mackie 1990). Infestation rates in the upper St. Lawrence River are similar to those reported from small lakes and rivers in Europe, where infestations are generally much lower than 100/unionid (Behning 1928; Kuchina 1964; Lewandowski 1976). In Lake Balaton (Hungary), however, infestations of several hundred
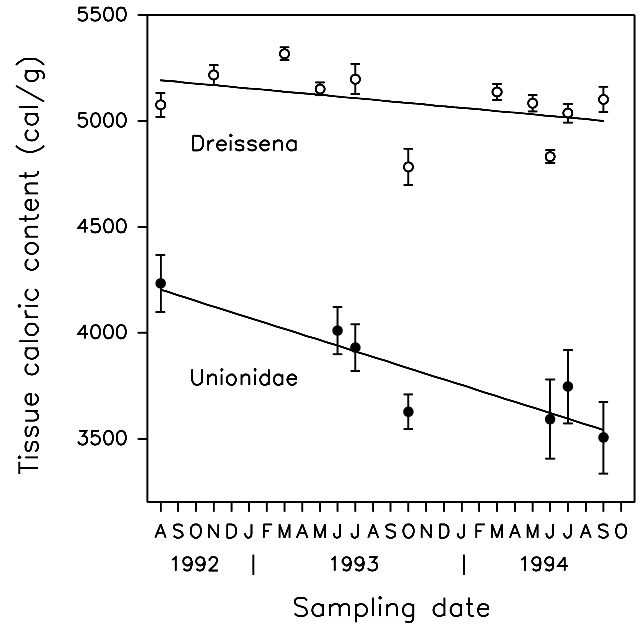
to a thousand *D. polymorpha* per unionid have been observed (Sebestyen 1938, cited in Lewandowski 1976; Wagner 1936). Similarly, mean infestations reported from the lower Great Lakes are in the range of 200–7000/unionid (Schloesser and Kovalak 1991; Hebert et al. 1991; Haag et al. 1993; Schloesser and Nalepa 1994; Nalepa 1994; Gillis and Mackie 1994), one or two orders of magnitude higher than in the St. Lawrence River. Some individual unionids from the Great Lakes have been found to carry more than 10 000 dreissenids (Hebert et al. 1991; Schloesser and Kovalak 1991; Schloesser and Nalepa 1994). These infestations were composed primarily of juvenile mussels <5 mm long (Schloesser and Kovalak 1991; Gillis and Mackie 1994; Schloesser and Nalepa 1994). Because mean infestation is strongly correlated with local *Dreissena* density (Ricciardi et al. 1995), the difference in infestation between populations in the St. Lawrence River and the Great Lakes is probably related to the difference in the abundance and survivorship of settling *Dreissena* larvae in these habitats. *Dreissena* densities in the Great Lakes were on the order of 10^4–10^5 mussels/m^2 when the above infestations were recorded (Hebert et al. 1991; Griffiths et al. 1991). The highest European infestation was observed in Lake Balaton, where *Dreissena* density exceeded 30 000/m^2 at some sites (Wagner 1936). By contrast, *Dreissena* densities are generally below 5000/m^2 in other European habitats (Stanczykowska 1977) and St. Lawrence River sites (Mellina and Rasmussen 1994; A. Ricciardi, unpublished data). High-density populations of *Dreissena* in the St. Lawrence and other large rivers are usually found near navigation locks, marinas, basins, and canals (Biryukov et al. 1964; Wolff 1969; Mellina and Rasmussen 1994; A. Ricciardi and F.G. Whoriskey, personal observations), which have slow or negligible current and extensive artificial surface area for colonization. These areas probably serve as point sources for veliger larvae that colonize local and downstream unionid populations.

1440

Can. J. Fish. Aquat. Sci. Vol. 53, 1996

Table 2. Dreissenid–unionid mass ratios, infestations, and mortality for various unionid populations.

Site	Mean mass ratio	Mean infestation	% freshly killed unionids	Source
Lake St. Pierre, 1995				
Site 1	0.04 (0.02)	0.7 (0.3)	8.2	This study
Site 2	0.07 (0.01)	6.4 (0.9)	11.1	This study
Site 3	0.04 (0.003)	47.7 (4.0)	22.0	This study
Port of Montréal, 1994	0.58 (0.08)	23.1 (2.8)	39.0	This study
Lake St. Louis				
Site 1, 1992	0.03 (0.005)	0.8 (0.2)	9.5	This study
Site 2, 1992	0.04 (0.01)	1.3 (0.4)	27.3	This study
Site 1, 1993	0.04 (0.01)	3.5 (0.9)	13.3	This study
Site 1, 1994	0.18 (0.02)	6.5 (0.7)	17.2	This study
Site 1, May 1995	0.09 (0.02)	7.2 (1.2)	14.9	This study
Site 1, Sept. 1995	0.21 (0.04)	7.7 (1.2)	28.9	This study
Soulanges Canal				
East site, 1992	0.04 (0.01)	3.1 (0.6)	16.6	This study
East site, 1993	0.37 (0.04)	9.9 (0.9)	25.0	This study
East site, June 1994	0.18 (0.52)	19.6 (6.4)	57.1	This study
East site, July 1994	0.70 (0.23)	18.0 (5.1)	72.5	This study
East site, Sept. 1994	0.87 (0.18)	52.1 (10.3)	76.7	This study
West site, 1994	0.49 (0.11)	43.8 (9.2)	60.0	This study
Lake St. François, 1992	0.06 (0.02)	1.2 (0.04)	14.7	This study
Lake St. François, 1995	0.24 (0.07)	26.4 (5.2)	33.3	This study
Western Lake Erie, 1989	3.0	6805 (623)	84.0	Schloesser and Nalepa 1994
Detroit River, 1992	0.7		90.0	Ohnesorg et al. 1993
Lake St. Clair, 1990	1.2	300	83.1	Gillis and Mackie 1994; Nalepa 1994
Lake Wawasee , 1994	0.49	130	30.0	D.W. Garton, unpublished data

Note: Values in parentheses are standard errors.

One of the most significant observations of this study is the change in unionid abundance at mean infestations as low as ca. 10/unionid at the Lake St. Louis and Soulanges Canal sites. Unionid density declined by 80% in the Soulanges Canal (east section) between 1993 and 1994, after the mean infestation exceeded 10/unionid. Similarly, a significant decline in Lake St. Louis unionids was first observed when the mean infestation approached 10/unionid (Fig. 1). This is the lowest mean infestation at which an impact has been documented and is undoubtedly related to the relatively large size of dreissenids attached to St. Lawrence River unionids. For example, in a power plant canal in western Lake Erie, unionids were infested with a mean number of nearly 7000 dreissenids (mean length <5 mm), which equaled 74% of their mass (Schloesser and Kovalak 1991); in the Soulanges Canal, unionids had a mean infestation of only 52/unionid but carried 87% of their own mass in attached dreissenids. Our observations also showed that a few large dreissenids may impair unionids by interfering with valve closure; 1993 Soulanges Canal collections revealed a small number of unionids whose valves were blocked from fully opening or closing by a only a few (one to five) large *D. polymorpha* byssally attached within, or across, the gape. This type of infestation interferes with the unionid's filtering ability (Gillis 1993), exposes the tissues to predators and parasites, and allows sediment into the interior of the shell (A. Ricciardi, personal observation).

Shell deformities observed in this study are similar to those found in infested unionids in Lake St. Clair (Hunter and Bailey 1992), Lake Mikolajskie (Lewandowski 1976), and the lower Rhine River (Wolff 1969). Shell damage was observed in 2%

of unionids collected from populations that had mean infestations of 20–52 *Dreissena*/unionid in Lake Mikolajskie (Lewandowski 1976), and in 78% of unionids (primarily *Lampsilis siliquoidea*) in southeastern Lake St. Clair in 1990 (Hunter and Bailey 1992), which had mean infestations of ca. 500/unionid (Nalepa 1994). Shell deformities were found in less than 5% of unionids in Lake St. Louis, Lake St. François, Lake St. Pierre, and Port of Montréal populations, all of which had mean infestations similar to those of Lake Mikolajskie (Table 1).

Previous studies found unionids to be a dominant component of benthic communities in the upper St. Lawrence River (Magnin 1970; Magnin and Stanczykowska 1971; Levasseur 1977), even in highly disturbed or contaminated areas (Haynes and Makarewicz 1982; Jacquaz 1995). Unionid densities in Lake St. Louis at Lachine (19.2/m^2) and the Soulanges Canal (21/m^2) in 1992 were similar to densities (ca. 25/m^2) reported from around the Island of Montréal over 25 years ago (Magnin 1970; Magnin and Stanczykowska 1971). The recent severe declines of previously stable populations at the Soulanges Canal (Figs. 1 and 2) and Lake St. Louis site 2 are remarkable given the short time frame during which they occurred. These rapid declines were associated with concomitant increases in *Dreissena* density over 2 to 3 years. The slow rate of decline in unionid abundance at Lake St. Louis site 1 and Lake St. François is paralleled by relatively slow increases in local *Dreissena* density. The extremely low *Dreissena* density (<10/m^2) at Lake St. Pierre site 1 in 1995 is coupled with the lowest unionid mortality (8%) observed among all St. Lawrence River sites. *Dreissena* densities at sites where un-

ionids suffered >90% mortality were near or above 5000/m^2 (Table 1), which does not differ greatly from our predicted threshold density of 6000/m^2 (Ricciardi et al. 1995).

Qualitative reports by divers in 1994–1995 suggest that unionid populations at other locations in the upper St. Lawrence River have been severely affected by *Dreissena* infestation (Table 1). Heavy infestation and mortality have been observed for unionids at the mouth of the Grasse River, a south shore tributary of the St. Lawrence in New York state (D.B. Conn, Department of Biology, University of the South, Sewanee, Tenn., personal communication), as well as for populations at Kingston (R. Serrouya, Department of Natural Resource Sciences, McGill University, Montréal, Que., personal communication), Brockville, and Prescott, Ontario (D.B. Conn, personal communication). At Prescott, where unionids were abundant in 1992, large numbers of freshly killed specimens encrusted with *D. polymorpha* were found in the summer of 1995; the few living unionids that were encountered had infestations (ca. 40–80/unionid) similar to those recorded at Soulanges Canal prior to extirpation (D.B. Conn, unpublished data).

The 4-year interval between the establishment of *Dreissena* and the extirpation of several unionid populations in the upper St. Lawrence River parallels time lags observed in Lake St. Clair (Nalepa 1994; Gillis and Mackie 1994), the Detroit River (Ohnesorg et al. 1993), and Lake Balaton (Wagner 1936; Sebestyen 1935, cited in Lewandowski 1976). In the Soulanges Canal, we observed a substantial increase in unionid mortality approximately 2 years after initial infestation. Similar observations were made after 2 years in Lake Balaton (Wagner 1936; Sebestyen 1935, cited in Lewandowski 1976), Lake St. Clair (Nalepa 1994), western Lake Erie (Schloesser and Nalepa 1994), and Lake Wawasee, a small isolated lake in Indiana (Garton 1994). The consistency of these results strongly implicate *Dreissena* as the major cause of unionid mortality in these habitats. Because mortality is correlated with local *Dreissena* density (Ricciardi et al. 1995), the observed temporal patterns may reflect the time required to establish a large *Dreissena* population in the invaded habitat.

Potential causes of unionid mortality resulting from *Dreissena* infestation

Several causal mechanisms of *Dreissena*-enhanced mortality of unionids have been proposed. Heavy infestations may impair unionids by smothering their siphons, generating metabolic wastes, preventing valve opening and closure, interfering with normal feeding and burrowing activity, and weighing down the unionid shell, thus unbalancing it or causing it to sink into soft sediments (Mackie 1990; Schloesser and Kovalak 1991; Haag et al. 1993; Schloesser and Nalepa 1994). While these mechanisms are quite plausible, there is little evidence to clearly demonstrate that any of them, acting alone or in concert, causes mortality.

Infested unionids in the Soulanges Canal suffered an 80% reduction in density over the winter of 1993–1994 and were subsequently extirpated during the winter of 1994–1995 (Fig. 1). A similar winter die-off of unionids at a heavily infested site in western Lake Erie in 1989–1990 resulted in a 70% decline (Schloesser and Nalepa 1994). In both Lake St. Clair and Lake Balaton, where native mussel populations were decimated 4 years after *D. polymorpha* became established in

these lakes, the greatest number of freshly killed unionids were observed in early spring (Wagner 1936; Nalepa 1994). These die-offs are attributed to a lack of energy stores required to survive winter stress (Schloesser and Nalepa 1994; Nalepa 1994), a view supported by studies that have correlated energetic losses in unionids with mean infestation levels. Hebert et al. (1991) found that lipid content tended to be lower in unionids carrying larger masses of zebra mussel on their shells. In field experiments, Haag et al. (1993) found no relationship with lipid content but showed that glycogen levels in unionids were inversely related to the number of attached *D. polymorpha*. We did not find a significant correlation between tissue caloric content and infestation for unionids in the Soulanges Canal within any given year, but the decline in tissue caloric content between 1992 and 1994 occurred with a concomitant increase in infestation (Fig. 7). Unionids in the canal reached their lowest caloric values before the winter of 1994–1995 when the population was extirpated. The change in the dry tissue mass – shell length relationship for *E. complanata* after 1992 showed that unionids became emaciated, possibly from increased stress (Russell-Hunter 1985). These energy losses may have resulted from impaired unionid feeding and locomotion caused by attached *D. polymorpha*.

Nalepa (1994) suggested that heavily infested unionids may be more susceptible to winter stress, not only as a result of their failure to secure adequate energy stores, but also because the large *Dreissena* cluster may prevent them from burrowing into sediments before the onset of winter (Amyot and Downing 1991). Conversely, heavily infested unionids may inadvertently sink below the sediment surface under the weight of attached dreissenids (Schloesser and Nalepa 1994; A. Ricciardi, personal observation). The concentration of attached zebra mussels on the exposed posterior region (typically one half to one third) of a unionid in soft sediments (Mackie 1990; Schloesser and Kovalak 1991; Hunter and Bailey 1992; Gillis and Mackie 1994; A. Ricciardi, personal observation) is also hypothesized to change the unionid's center of gravity and thus force the mussel to expend energy to maintain the proper orientation required for feeding, respiration, or excretion (Haag et al. 1993).

Dreissenid–unionid mass ratio: a predictor of unionid mortality?

Haag et al. (1993) predicted that heavy-shelled unionids would be less affected by additional mass on their shell and, as a population, would suffer lower mortality from infestation. Heavily infested unionids (*Anodonta piscinalis*) in Lake Mikolajskie (Poland) had significantly heavier shells per unit length than unionids with little or no infestation (Lewandowski 1976), which may reflect increased survivorship among thick-shelled individuals. Thick-shelled unionids may have a more stable center of gravity and stronger musculature such that their locomotion is less encumbered by *Dreissena* infestation. Studies in Lake Erie (Haag et al. 1993) and Lake St. Clair (Nalepa 1994; Gillis and Mackie 1994) have found that unionid taxa that have lighter shells and brood larvae over an extended period (e.g., *Lampsilis*, *Pyganodon*) suffer greater mortality during infestation than heavy-shelled, short-term brooders (e.g., *Amblema*, *Elliptio*). This differential mortality may be related to both the long-term expenditure of reproductive energy in unionids like *Lampsilis*, and the relative suscep-

tibility of unionids to encumbrance from *Dreissena* infestation.

The encumbrance inflicted by infestation may be better represented by the ratio of the mass of attached dreissenids to that of their unionid host. The highest mass ratio (grams *Dreissena* per gram unionid, fresh mass) recorded for individual unionids in the southeastern portion of Lake St. Clair increased from ca. 2.5 in 1989 (Hebert et al. 1991) to 8.5 in 1990 (Nalepa 1994), when a high incidence of unionids with deformed shells (Hunter and Bailey 1992) and heavy mortality (Gillis and Mackie 1994; Nalepa 1994) was observed. The mean mass ratio for unionids in Lake St. Clair 2 years prior to their extirpation was 1.2 (Nalepa 1994). At one site in western Lake Erie, a mean mass ratio near 3.0 preceded a 40% increase in unionid mortality over the winter of 1989–1990; by the end of the following summer, the local population was completely eliminated (Schloesser and Nalepa 1994). The mean mass ratio of surviving unionids at the Lake Erie site was reduced to ca. 0.5 in the spring of 1990 (Schloesser and Nalepa 1994). Similarly, the mean mass ratio for unionids in the Soulanges Canal dropped from 0.37 to 0.18 after 80% of the unionids died over the winter of 1993–1994 (Fig. 4). These results suggest that unionids with heavy burdens suffer greater mortality. In fact, the relationship between the mean mass ratio of living mussels and the proportion of freshly killed unionids in a given population is highly significant (Fig. 8). Given the differences in species composition, habitat type, and the geographic location of unionid populations used to generate this regression model, and other sources of stress that may contribute to mortality (Havlik and Marking 1987; Williams et al. 1993), the proportion of variance explained by the mass ratio (73%) is quite substantial and is larger than the value we obtained (61%) using the mean infestation level (number of *Dreissena* per unionid) as a predictor. For St. Lawrence River sites the mean mass ratio and mean infestation explained 68 and 52%, respectively, of the variance in unionid mortality.

The highest mass ratio recorded prior to the extirpation of the Soulanges Canal unionid population was 0.87 ± 0.18, which is slightly higher than the value for the Detroit River population (Ohnesorg et al. 1993) but lower than the values recorded in Lake St. Clair and Lake Erie (Fig. 4). In the Soulanges Canal the distribution of mean mass ratios over time is bimodal (Fig. 4), with the first peak (0.37) preceding the elimination of *Lampsilis radiata* and older individuals of *E. complanata*, and the subsequent peak (0.87) preceding the elimination of the remaining individuals of *E. complanata* (Fig. 2). Because of the apparent differences in sensitivity among unionid taxa to *D. polymorpha* infestation, it is difficult to define precise thresholds of infestation tolerance that may result in enhanced mortality. However, mean mass ratios near or above 1.0 were associated with heavy (90–100%) unionid mortality in the Soulanges Canal (this study), the Detroit River (Ohnesorg et al. 1993), Lake Wawasee (D.W. Garton, Department of Biological and Physical Sciences, Indiana University, Kokomo, Ind., personal communication), Lake Erie (Schloesser and Nalepa 1994), and Lake St. Clair (Nalepa 1994).

In summary, *Dreissena* infestation has substantially enhanced unionid mortality in the upper St. Lawrence River. Heavily infested unionid populations were extirpated, or on the verge of extirpation, at several sites in 1995. Significant

Fig. 8. Relationship between the proportion of freshly killed unionids (y) and the mean mass ratio of living unionids (x) for populations in the Great Lakes – St. Lawrence River system: $\sin^{-1}(y^{0.5}) = 0.449 \log_{10}x + 0.973$ ($r^2 = 0.73$, $p < 0.0001$, $SE_{est} = 0.16$). Data are from Table 2.
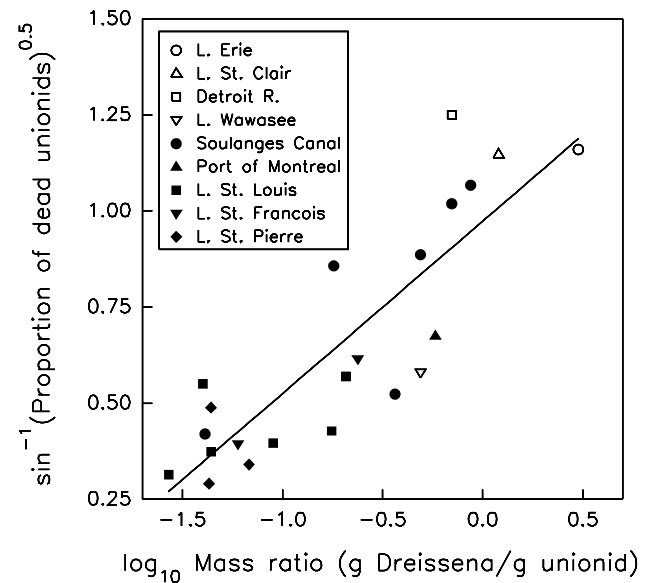
mortality resulting in these extirpations occurred at *Dreissena* infestations and densities one or two orders of magnitude lower than those reported from the Great Lakes. Mass ratios (grams *Dreissena* per gram unionid) associated with heavy mortality are similar for infested unionid populations in the St. Lawrence River, Detroit River, and Lake St. Clair. Mass ratios explain 73% of the variance in the proportion of freshly killed unionids in North American habitats invaded by *Dreissena*. Heavy mortality (>90%) occurs in populations of unionids that are carrying, on average, a mass of *Dreissena* equal to or greater than their own mass. Unionid mortality in the St. Lawrence River appears to result primarily from the failure of heavily infested unionids to secure adequate energy stores for overwintering. Because mortality can occur at relatively low infestation levels, unionid populations in other large North American rivers are at risk of extirpation as *Dreissena* continues to invade new drainages.

Acknowledgments

References

Amyot, J.P., and Downing, J.A. 1991. Endo- and epibenthic distribution of the unionid mollusc *Elliptio complanata*. J. North Am. Benthol. Soc. **10**: 280–285.

Behning, A. 1928. Das Leben der Wolga. *In* Die Binnengewasser. Vol. 5. Thienemann, Stuttgart, Germany.

Biggins, R.G. 1992. Threat of the nonindigenous zebra mussel, *Dreissena polymorpha*, to the native freshwater mussel fauna of North America: urgency for research and management strategies. Minutes of a zebra mussel workshop sponsored by the U.S. Fish and Wildlife Service, 20–21 May 1992, National Fisheries Research Center, Ann Arbor, Mich. Available from the National Fisheries Research Center, Ann Arbor, Mich.

Biryukov, I.N., Kirpichenko, M.Y., Lyakhov, S.M., and Segeeva, G.I. 1964. Living conditions of the mollusk *Dreissena polymorpha* Pallas in the Babinskii backwater of the Oka River. *In* Biology and control of *Dreissena*. Edited by B.K. Shtegman. Tr. Inst. Biol. Vnutr. Vod Akad. Nauk. SSSR, **7**(10): 32–38.

Clarke, A.H. 1981. The freshwater Mollusca of Canada. National Museums of Canada, Ottawa, Ont.

Conn, D.B., and Conn, D.A. 1993. Parasitism, predation and other biotic associations between dreissenid mussels and native animals in the St. Lawrence River. *In* Proceedings of the Third International Zebra Mussel Conference, Toronto, Ont., February 23–26, 1993. *Edited by* J.L. Tsou. Electric Power Research Institute, Paolo Alto, Calif. pp. 223–234.

Downing, J.A., and Downing, W.L. 1992. Spatial aggregation, precision, and power in surveys of freshwater mussel populations. Can. J. Fish. Aquat. Sci. **49**: 985–991.

Elton, C.S. 1958. The ecology of invasions by animals and plants. Methuen, London.

Garton, D.W. 1994. Impact of fouling by *Dreissena polymorpha* on unionids of Lake Wawasee, Indiana. *In* Abstracts of the Fourth International Zebra Mussel Conference, Madison, Wis., March 7–10, 1994. University of Wisconsin Sea Grant Institute, Madison, Wis.

Gillis, P.L. 1993. Impact of *Dreissena polymorpha* on populations of Unionidae and their effect on the host unionid's filtration capacity and growth rate in Lake St. Clair. M.Sc. thesis, University of Guelph, Guelph, Ont.

Gillis, P.L., and Mackie, G.L. 1994. Impact of the zebra mussel, *Dreissena polymorpha*, on populations of Unionidae (Bivalvia) in Lake St. Clair. Can. J. Zool. **72**: 1260–1271.

Griffiths, R.W., Schloesser, D.W., Leach, J.H., and Kovalak, W.P. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. **48**: 1381–1388.

Haag, W.R., Berg, D.J., Garton, D.W., and Farris, J.L. 1993. Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in western Lake Erie. Can. J. Fish. Aquat. Sci. **50**: 13–19.

Havlik, M.E., and Marking, L.L. 1987. Effects of contaminants on naiad mollusks (Unionidae): a review. U.S. Fish Wildl. Serv. Resour. Publ. No. 164.

Haynes, J.M., and Makarewicz, J.C. 1982. Comparison of benthic communities in dredged and undredged areas of the St. Lawrence River, Cape Vincent, N.Y. Ohio J. Sci. **82**: 165–170.

Hebert, P.D.N., Wilson, C.C., Murdoch, M.H., and Lazar, R. 1991. Demography and ecological impacts of the invading mollusc, *Dreissena polymorpha*. Can. J. Zool. **69**: 405–409.

Hunter, R.D., and Bailey, J.F. 1992. *Dreissena polymorpha* (zebra mussel): colonization of soft substrata and some effects on unionid bivalves. Nautilus, **106**: 60–67.

Jacquaz, B. 1995. Analyse d'échantillons de benthos provenant du lac Saint-Louis. Rapp. Sci. Tech. nº ST–10. Centre Saint-Laurent, Environnement Canada, Montreal, Que.

Kuchina, E.S. 1964. Distribution of the mollusk *Dreissena polymorpha* Pallas in the Northern Dvina River. *In* Biology and control of *Dreissena*. Edited by B.K. Shtegman. Tr. Inst. Biol. Vnutr. Vod Akad. Nauk SSSR, **7**(10): 25–31.

Levasseur, H. 1977. Étude du benthos du fleuve Saint-Laurent. Rapp. Tech. No. 10. Soumis au comité d'étude du fleuve Saint-Laurent par les services de protection de l'environnements du Québec. L'Editeur officiel du Québec, service de la reprographie.

Lewandowski, K. 1976. Unionidae as substratum for *Dreissena polymorpha*. Pol. Arch. Hydrobiol. **23**: 409–420.

Lodge, D.M. 1993. Biological invasions: lessons for ecology. Trends Ecol. Evol. **8**(4): 133–136.

Mackie, G.L. 1990. Early biological and life history attributes of the zebra mussel, *Dreissena polymorpha* (Bivalvia: Dreissenidae), and impacts on native bivalves in Lake St. Clair. *In* Proceedings of the Technology Transfer Conference, Toronto, Ont., November 19–20, 1990. pp. 215–231.

Magnin, E. 1970. Faune benthique littorale du Lac Saint-Louis près de Montréal (Québec) I. Quelques données générales. Ann. Hydrobiol. **1**: 179–193.

Magnin, E., and Stanczykowska, A. 1971. Quelques données sur la croissance, la biomasse et la production annuelle de trois mollusques Unionidae de la region de Montréal. Can. J. Zool. **49**: 491–497.

McMahon, R.F. 1991. Mollusca: Bivalvia. *In* Ecology and classification of North American freshwater invertebrates. *Edited by* J.H Thorp and A.P. Covich. Academic Press, New York. pp. 315–399.

Mellina, E., and Rasmussen, J.B. 1994. Patterns in the distribution and abundance of zebra mussels (*Dreissena polymorpha*) in rivers and lakes in relation to substrate and other physicochemical factors. Can. J. Fish. Aquat. Sci. **51**: 1024–1036.

Mooney, H.A., and Drake, J.A. 1986. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York.

Morton, B. 1989. Life history characteristics and sexual strategy of *Mytilopsis sallei* (Bivalvia: Dreissenacea), introduced into Hong Kong. J. Zool. (Lond.), **219**: 469–485.

Nalepa, T.F. 1994. Decline of native unionid bivalves in Lake St. Clair after infestation by the zebra mussel, *Dreissena polymorpha*. Can. J. Fish. Aquat. Sci. **51**: 2227–2233.

Nalepa, T.F., and Gauvin, J.M. 1988. Distribution, abundance, and biomass of freshwater mussels (Bivalvia: Unionidae) in Lake St. Clair. J. Great Lakes Res. **14**: 411–419.

Nalepa, T.F., Manny, B.A., Roth, J.C., Mozley, S.C., and Schloesser, D.W. 1991. Long-term decline in freshwater mussels (Bivalvia: Unionidae) of the western basin of Lake Erie. J. Great Lakes Res. **17**: 214–219.

Ohnesorg, K.L., Smithee, R.D., Longton, G.D., Kovalak, W.P., and Schloesser, D.W. 1993. Impact of zebra mussels (*Dreissena polymorpha*) on native mussels (Unionidae) in the Detroit River. *In* Abstracts of the Third International Zebra Mussel Conference, Toronto, Ont., February 23–26, 1993. Electric Power Research Institute, Palo Alto, Calif.

Ricciardi, A., Whoriskey, F.G., and Rasmussen, J.B. 1995. Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density. Can. J. Fish. Aquat. Sci. **52**: 1449–1461.

Russell-Hunter, W.D. 1985. Physiological, ecological and evolutionary aspects of molluscan tissue degrowth. Am. Malacol. Bull. **3**: 213–221.

SAS Institute Inc. 1988. SAS/STAT user's guide, release 6.03 edition. SAS Institute Inc., Cary, N.C.

Schloesser, D.W., and Kovalak, W. 1991. Infestation of unionids by *Dreissena polymorpha* in a power plant canal in Lake Erie. J. Shellfish Res. **10**: 355–359.

Schloesser, D.W., and Nalepa, T.F. 1994. Dramatic decline of unionid bivalves in offshore waters of western Lake Erie after infestation by the zebra mussel, *Dreissena polymorpha*. Can. J. Fish. Aquat. Sci. **51**: 2234–2242.

Stanczykowska, A. 1977. Ecology of *Dreissena polymorpha* (Pall.) (Bivalvia) in lakes. Pol. Arch. Hydrobiol. **24**: 461–530.

Wagner, H. 1936. Die Wandermuschel (*Dreissensia*) erobert den Platten-See. Nat. Volk, **66**: 37–41.

Willan, R.C. 1987. The mussel *Musculista senhousia* in Australasia: another aggressive alien highlights the need for quarantine at ports. Bull. Mar. Sci. **41**: 475–489.

Williams, J.D., Warren, Jr., M.L., Cummings, K.S., Harris, J.L., and Neves, R.J. 1993. Conservation status of freshwater mussels of the United States and Canada. Fisheries, **18**(9): 6–22.

Wolff, W.J. 1969. The Mollusca of the estuarine region of the rivers Rhine, Meuse and Scheldt in relation to the hydrography of the area. II. The Dreissenidae. Basteria, **33**: 93–103.

Zhadin, V.I. 1965. Molluscs of fresh and brackish waters of the U.S.S.R. Keys to the fauna of the U.S.S.R. No. 46. Academy of Sciences of the U.S.S.R., Moscow. (Translated by the Israel Program for Scientific Translation, Jerusalem.)