ZEBRA MUSSEL COLONIZATION AND GROWTH IN THE RICHELIEU RIVER BETWEEN 1997 AND 2000

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Zebra Mussel Colonization and Growth in the Richelieu River Between 1997 and 2000

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Management Perspective

This report presents the results of a study conducted under the Biodiversity component of the federal-provincial St. Lawrence Vision 2000 Action Plan (SLV 2000). One of its objectives was to monitor the introduction of exotic species and their impact on the aquatic ecosystems of the St. Lawrence River. The results presented here report on the presence and spatial distribution of zebra mussels along the Richelieu River, a major tributary of the St. Lawrence. It is recommended that a quantitative sampling program, coupled with specific ecological studies, be conducted on an ongoing basis in order to assess and monitor the abundance of zebra mussels in the Richelieu River and their impact on the river's ecosystem.

Perspective de gestion

Ce rapport présente les résultats d'une étude réalisée dans le cadre du volet Biodiversité du plan d'action fédéral-provincial Saint-Laurent Vision 2000 (SLV 2000). Un des objectifs de ce volet visait à suivre l'introduction et les impacts des espèces exotiques sur les écosystèmes aquatiques du Saint-Laurent. Les résultats de la présente étude font état de la présence et de l'extension de la répartition spatiale de la Moule zébrée le long de la rivière Richelieu, l'un des principaux tributaires du fleuve Saint-Laurent. La mise sur pied d'un programme d'échantillonnage quantitatif, couplé à des études spécifiques sur la Moule zébrée, est recommandée afin d'assurer le suivi des populations de Moules et l'évaluation de ses impacts sur l'écosystème de la rivière Richelieu.

Acknowledgments

Our most sincere and warmest thanks go to the many volunteers who took part in the three clean-up operations of 1998, 1999 and 2000. We would like to express our sincere gratitude to Marcel Comiré, co-ordinator of the Comité de Conservation et de Valorisation du Bassin de la Rivière Richelieu (COVABAR – Richelieu River Watershed Conservation and Enhancement Committee) and instigator of the clean-up days, as well as everyone who works for COVABAR and the Conseil Régional de l'Environnement de la Montérégie (CREM – Montérégie Regional Environment Council). Those days provided tangible evidence that a group effort is required to tackle environmental issues.

Abstract

The advancing colonization of the Richelieu River by zebra mussels was assessed during intensive clean-up operations at different sites on the riverbed every September for four years, from 1997 to 2000. The objects removed from the water were examined and the number of zebra mussels attached to each was recorded. The following information was also noted: type of object (bottle, tire, unionid, etc.), type of substrate (glass, plastic, metal, etc.), size of object and percentage of colonizable surface. The zebra mussels were taken back to the laboratory for morphometric assessment (length and weight). Quantitative sampling in quadrats was also done in a parallel study conducted at six sites in 1998. The results of that study showed that the upper Richelieu was clearly more colonized than the lower Richelieu, downstream of the Chambly Basin. The colonization rate on objects upstream varied from 47 to 63% between 1997 and 1998, whereas downstream it was only 2 to 3% during the same period. Though downstream sites were still only lightly colonized in 1999 and 2000, zebra mussel numbers increased there nonetheless. The zebra mussels showed no significant preference for any particular substrate, whether unionids (large native freshwater mussels) or inert objects. An analysis of the size structure of zebra mussels revealed the presence of one or more cohorts, depending on the site and the year, reflecting major spatial and temporal variability in recruitment. Furthermore, an estimate of the potential impact of zebra mussels on the biological components of the river, based on relative mussel biomass by location and year, suggests that the impact on the upper Richelieu since 1997 has been between 10 and 100 times greater than on the lower Richelieu. Long-term monitoring of zebra mussel colonization of the Richelieu River and its potential impact is therefore strongly recommended.

Résumé

La progression de la colonisation par la Moule zébrée dans la rivière Richelieu a été évaluée grâce à des activités de nettoyage intensif du lit de la rivière effectuées à différents sites en septembre de 1997 à 2000. Les objets retirés de l'eau étaient examinés et le nombre de Moules zébrées attachées à chacun était noté. Les informations suivantes étaient aussi notées: nature de l'objet (bouteille, pneu, moules Unionides indigènes, etc.), type de substrat (verre, plastique, métal, etc.), dimensions de l'objet, pourcentage de surface colonisable. Les Moules zébrées ont été ramenées au laboratoire pour fins de mesures morphométriques (longueur et poids). Une récolte quantitative par quadrats a été réalisée parallèlement en 1998 à six sites. Les résultats ont montré que le secteur du haut Richelieu (amont) était nettement plus colonisé que le secteur du bas Richelieu en aval du bassin de Chambly. Les pourcentages de colonisation d'objets entre 1997 et 1998 variaient de 47 à 63 % en amont alors qu'ils n'étaient que de 2 à 3 % en aval. Bien qu'encore faiblement colonisés en 1999 et 2000, on constate une progression de la colonisation des sites en aval. La Moule zébrée n'a montré aucune préférence significative pour un type de substrat, y compris entre les mulettes (grosses moules Unionides indigènes) et les objets inertes. L'analyse de la structure de taille des Moules zébrées a révélé la présence d'une ou plusieurs cohortes selon les sites et les années, traduisant ainsi une variabilité spatio-temporelle importante dans le recrutement. Par ailleurs, une estimation de l'impact potentiel des Moules zébrées sur les composantes biologiques de la rivière, fondée sur la biomasse relative des moules par secteur et par année, suggère que le haut Richelieu aurait été soumis à un impact de 10 à 100 fois plus élevé que le bas Richelieu depuis 1997. Un suivi à long terme de la colonisation de la rivière Richelieu par la Moule zébrée et de son impact potentiel est donc fortement recommandé.

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1 Introduction

Rivers are pathways for the transport and dispersal of aquatic organisms and help structure regional biological communities. This role is particularly evident when exotic species are introduced, and may in fact contribute to the problem of the dispersal of nuisance species. Introduced into the Great Lakes in the mid-1980s, the zebra mussel (Dreissena polymorpha) quickly spread through many bodies of water in eastern North America (Claudi and Leach, 2000). The invasion and rapid dispersal of the species over so vast a territory were largely attributed to its relatively long planktonic larval stage (15–25 days) (Claudi and Mackie, 1993), which means it can be carried long distances by the current. Rivers and canals are thus major vectors of transportation of zebra mussels from one region to another and their subsequent colonization of other ecosystems. Spread of the zebra mussel from the Great Lakes watershed to that of the Hudson River is assumed to have occurred via the Erie Canal and the Mohawk River in the state of New York (Mills et al., 2000). Once in the Hudson, the species then invaded Lake Champlain in 1993 (Eliopoulos and Stangel, 1999), finally reaching the Richelieu River in 1996 (de Lafontaine and Cusson, 1997). This example illustrates the key role of rivers and other waterways in colonization by zebra mussel populations and in the eventual homogenization of aquatic biodiversity as a result of the introduction of a non-native species (Gido and Brown, 1999).

A preliminary estimate of the degree of colonization and spatial distribution of the zebra mussel in the Richelieu was done in September 1997, during sampling carried out as part of a riverbed clean-up campaign organized by the Conseil Régional de l'Environnement de la Montérégie (CREM – Montérégie Regional Environment Council) (Cusson and de Lafontaine, 1998). The results highlighted a spatial distribution pattern characterized by a noticeable decrease in zebra mussel abundance between the inlet and outlet of Chambly Basin. The unimodal size distribution, corresponding to one-year-old mussels, seemed to suggest that colonization of the river was in its initial stages and that it depended mainly on the production of larvae in Lake Champlain (de Lafontaine and Cusson, 1997). The colonization process has much in common

with the "downstream march" model defined by Horvath et al. (1996), which has also been observed in the Hudson (Strayer et al., 1996), the Illinois (Stoeckel et al., 1997) and the Rhine (Borcherding and de Ruyter van Steveninck, 1992) rivers. This preliminary observation gave rise to the recommendation that similar sampling be repeated in subsequent years to monitor the situation (Cusson and de Lafontaine, 1998).

Given the speed at which the zebra mussel propagates in the bodies of water that it infests, samples must be taken every year to determine the extent of its spread. Clean-up operations carried out in 1998, 1999 and 2000 afforded an opportunity to monitor zebra mussel populations along the Richelieu. The sampling method used in 1997 was essentially semiquantitative and based on examination of objects (bottles, tubes, pieces of metal or pottery, unionids, etc.) taken from the water by divers, thus making it impossible to arrive at an accurate estimate of mussel density in a given surface area (square metre). Quantitative sampling in quadrats, done in parallel with the semiquantitative sampling of objects, was suggested as a means of assessing the validity of the sampling approach for purposes of monitoring the zebra mussel in the Richelieu.

The goal of our study was to bring information on zebra mussel abundance and spatial distribution in this waterway up to date and validate the sampling technique for quantitative purposes. The specific objectives were thus to (1) assess changes in the degree of zebra mussel colonization of the Richelieu River since 1997, (2) determine the validity of abundance estimates made by examining objects in comparison with a quantitative assessment by quadrats and (3) determine the extent of zebra mussel colonization of unionids. Morphometric data on specimens gathered in 1998 also served to determine the length-weight ratio of individuals in the Richelieu zebra mussel population; this information will be useful in future estimates of biomass and production for the purpose of assessing the impact of zebra mussels.

2 Materials and Methods

2.1 SAMPLING

Sampling campaigns were conducted on September 20, 1998, September 19, 1999, and September 17, 2000, as part of the annual clean-up of the Richelieu riverbed organized by CREM, the Comité de Mise en Valeur de la Vallée du Richelieu (CMVVR – Richelieu Valley Enhancement Committee) and the Comité de Conservation et de Valorisation du Bassin de la Rivière Richelieu (COVABAR - Richelieu River Watershed Conservation and Enhancement Committee). In 1998, work was done at 5 of the 12 sites examined in 1997 (Figure 1, Table 1). One site (Saint-Jean-sur-Richelieu) was located upstream of the Chambly Basin and the other four were downstream. In 1999, the only two sites selected for clean-up were downstream (Saint-Marc-sur-Richelieu and Saint-Ours), while in 2000, five sites, all downstream of the Chambly Basin, were selected. Only the Saint-Marc-sur-Richelieu site was sampled each year. The choice of sites was determined by the clean-up organizers on the basis of their needs and objectives and not with regard to a zebra mussel sampling strategy. The sampling sites in a given municipality varied each year so that unexplored adjacent areas (within 1 km) could be cleaned up and thus more objects would be picked up. The sites downstream of the Chambly Basin turned out to be well chosen, because they made it possible to monitor the progress of the zebra mussel through an area little colonized in 1997.

The sampling technique was essentially the same as the one used in 1997 (Cusson and de Lafontaine, 1998). Anthropogenic objects and debris were taken from the water by divers, then examined by volunteers, who counted the number of attached zebra mussels. The divers were also asked to pick up unionids (native freshwater mussels) when they found them. The diving and clean-up took an average of four hours at each site and was concentrated within a strip of less than 15 m from the shore. The total area inspected by the divers varied, depending on the number of objects and the number of divers at each site. When there were too many objects at some sites to examine them all exhaustively and in detail, objects were randomly selected from the batches brought up by the divers. The information noted was type of object examined (for

example, bottle or tire), and in the case of unionids, whether they were alive or dead; type of substrate (glass, plastic, metal, wood, etc.); size (length, width, height) in centimetres; colonizable surface (i.e., percentage of surface of object that was not buried in sediment at the bottom of the river); and number of zebra mussels attached. The zebra mussels were removed and placed in a plastic bag identified with a code corresponding to the site and object number. When there were a great many zebra mussels or it was impossible to examine the entire object, only a fraction of the total surface of the object was examined. In this case, the percentage of the surface area actually examined was calculated.

In 1998, quantitative sampling was also done at each of the five clean-up sites as well as next to the Chambly wharf and marina, in the Chambly Basin (Figure 1). Two divers would place a quadrat measuring one square metre randomly on the riverbed, in an area that had not yet been cleaned up, so that they would not be disturbed by higher turbidity. Three or four quadrats were sampled at each site. All the zebra mussels as well as the unionids in each of the quadrats were gathered and placed in a net bag, then taken to the surface. The zebra mussels were placed in a plastic bag identified with a code corresponding to the site and quadrat number.

At each site, only two or three specimens of various species of unionids were kept for identification purposes. The other specimens, once examined, were placed in a basin of water and then later put back on the riverbed by the divers. All the samples of zebra mussels were placed in a freezer (-20°C) at the end of the day, while the unionids were cleaned and dried or preserved in a solution of 70% (v/v) denatured ethanol.

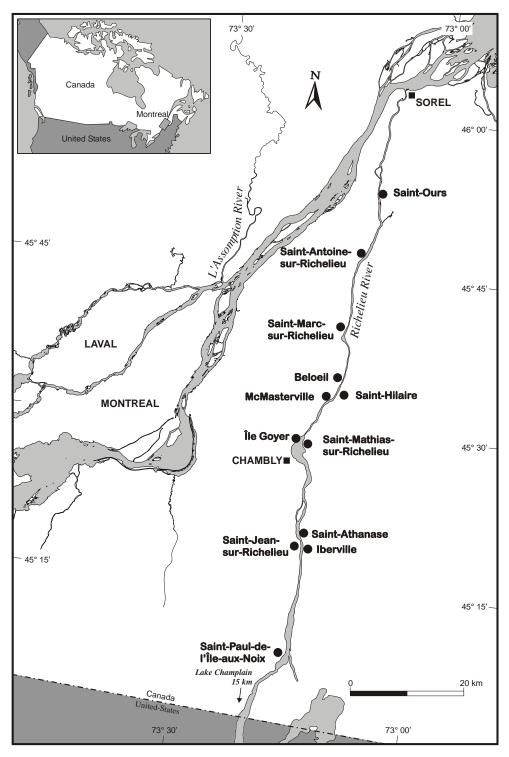


Figure 1 Location of sampling sites on the Richelieu River

2.2 LABORATORY ANALYSES

Zebra mussels from all samples were identified and counted in the St. Lawrence Centre laboratory. Zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*) were distinguished on the basis of morphological characteristics (Domm et al., 1993; Claxton et al., 1997). The shell length of each of up to 300 mussels per site was measured using digital vernier callipers (± 0.01 mm).

All the zebra mussels gathered during the quantitative sampling (by quadrat) were identified and measured (length, width, height) using digital vernier callipers (± 0.01 mm). Each mussel was then dissected to separate the soft tissue from the shell. The soft tissue and the shell were oven dried at 105°C for 24 h then weighed (dry weight) using a Mettler electronic scale (± 0.0001 g).

The objects gathered and examined were divided into two main categories: anthropogenic objects and unionids. The anthropogenic objects were grouped by 12 main types of substrate: glass, metal, plastic, rubber, cement, wood, cloth, fibreglass, paper, organic matter, polypropylene and pottery/clay. The glass objects were chiefly bottles, the rubber objects chiefly tires and the metal objects chiefly aluminum beer or soft-drink cans or steel car or bicycle frames. The unionids were identified as live or dead (empty shells) in most cases. The surface area of each object was calculated from measurements of length, width and height, taking into account the object's geometric form.

The data gathered were all entered into computer files (Microsoft Excel, version 7.0). The statistical calculations were done using SAS software and all tests were applied with a level of significance set at 0.05.

3 Results

3.1 DISTRIBUTION AND ABUNDANCE

A total of 6231 objects, including 1616 unionids, were examined, and 5661 zebra mussels were gathered at the seven sites sampled at least twice between 1997 and 2000 (Table 1). All the specimens gathered were of the species *Dreissena polymorpha*; no quagga mussel (*Dreissena bugensis*) has yet been found in samples from the Richelieu River.

The presence of zebra mussels was confirmed at all sites from Saint-Paul-de-l'Île-aux-Noix to Saint-Ours (Figure 1, Table 1). As the number of objects examined varied greatly from site to site and from year to year, the percentage of objects colonized by the zebra mussels was calculated to compare the relative intensity of colonization (Figure 2). The colonization rate at the Saint-Jean-sur-Richelieu site on the upper Richelieu (upstream of Chambly Basin) was 63.4% in 1997 and 47.2% in 1998—much higher than the overall downstream rate of 2.4%. In 1998, more than 3000 zebra mussels (or 99.1% of the total number of mussels taken) were gathered at Saint-Jean-sur-Richelieu, while the numbers were quite low (between 0 and 18 mussels per site) at the four sites on the lower Richelieu, downstream of the Chambly Basin (Saint-Marc-sur-Richelieu, Beloeil, Saint-Hilaire and Saint-Mathias). Although there were few zebra mussels at downstream sites in 1999 and 2000, colonization has gradually increased over the years (Table 1, Figure 2).

At the same time, the relative abundance of zebra mussels, estimated by the mean number of mussels per object, was also lower at the downstream sites (0 to 2 mussels per object) than on the upper Richelieu (12 to 13 mussels per object) (Table 1). The abundance index increased tenfold between 1997 and 2000 downstream and the greatest progression was recorded at the Saint-Ours site between 1997 and 1999.

Table 1

Number of objects examined, including unionids, and zebra mussel abundance at seven sites sampled at least twice between 1997 and 2000

Municipality	Site	Year	Number of objects examined	Number of objects colonized	Number of zebra mussels gathered	Mean number of zebra mussels per object	Mean number of zebra mussels per colonized object
Upstream						-	-
Saint-Jean-sur-Richelieu	2	1997	145	92	1,844	12.72	20.04
		1998	250	118	3,101	12.40	26.28
Downstream							
Saint-Mathias	6	1997	218	3	7	0.03	2.33
		1998	442	10	18	0.04	1.80
		2000	178	3	3	0.02	1.00
Saint-Hilaire	8	1997	183	0	0	0	0
		1998	560	0	0	0	0
		2000	208	21	46	0.22	2.19
Beloeil	9	1997	285	3	3	0.01	1.00
		1998	866	1	1	0.00	1.00
		2000	242	20	36	0.15	1.80
Saint-Marc-sur-Richelieu	10	1997	77	5	5	0.06	1.00
		1998	542	9	9	0.02	1.00
		1999	300	42	57	0.19	1.36
		2000	254	21	43	0.17	2.05
Saint-Antoine	11	1997	227	2	12	0.05	6.00
		2000	374	27	37	0.10	1.37
Saint-Ours	12	1997	664	13	14	0.02	1.08
		1999	216	76	425	1.97	5.59
Downstream Total	l	1997	1654	26	41	0.02	1.58
		1998	2410	20	28	0.01	1.40
		1999	516	118	482	0.88	4.08
		2000	1256	93	165	0.12	1.79

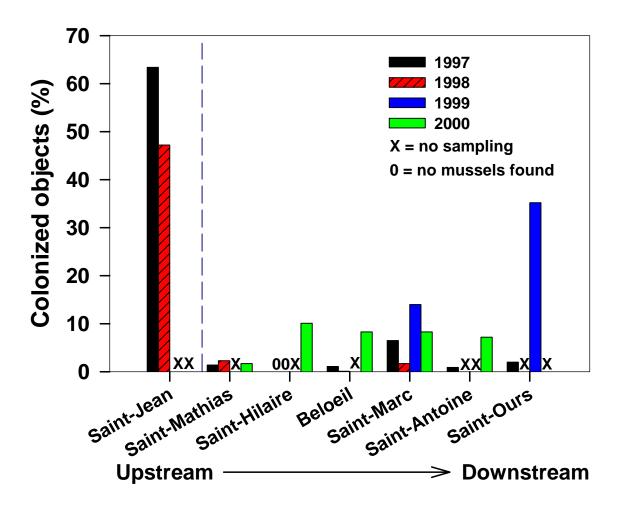


Figure 2 Zebra mussel colonization rates along the Richelieu River between 1997 and 2000

Quantitative sampling by 1 m² quadrats in 1998 found zebra mussels only at St. Jean sur Richelieu, where densities varied between 15 and 161 mussels/m² (n = 4, mean = 88, SD = 59). No mussel was found in the quadrats at the four sites along the lower Richelieu or at Chambly, where underwater exploration by two diver biologists turned up no sign of them, either on the natural riverbed or on the walls of the wharf and lock.

3.2 EFFECT OF SUBSTRATE TYPE

The zebra mussels attached to objects of different types and to various species of unionids (see list of species in Appendix 1). The degree of colonization of unionids was not significantly different from that of anthropogenic objects as a whole (all sites and years combined) (t test = -0.0799; p = 0.94, n = 23) (Table 2). Despite the huge differences between the number of unionids and the number of objects examined, the intensity of colonization of the two types of substrates was very similar for each sector and year. The gradient between the colonization rates of the areas upstream and downstream of Chambly Basin was very clear both for inert objects and unionids (Table 2).

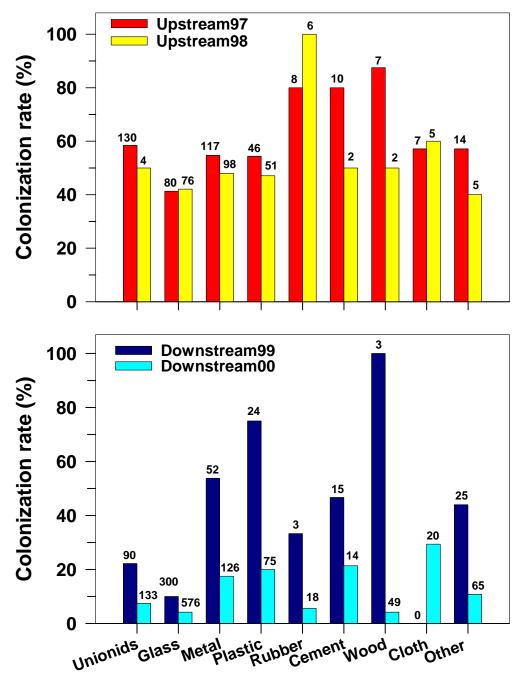
Location	Year	Number of sites	Inert objects		Unionids	
			п	%	n	%
Upstream	1997	4	293	59.7	131	49.6
	1998	1	246	47.2	4	50.0
Downstream	1997	7	1399	1.8	843	0.6
	1998	4	2000	0.9	410	0.5
	1999	2	426	23.0	90	22.2
	2000	5	1117	7.4	139	7.2

Table 2Zebra mussel colonization rate of inert objects and unionids
in the Richelieu River between 1997 and 2000

The colonization rates observed for the various types of substrate showed that zebra mussels have no significant preference for any particular type of substrate (*G* test likelihood ratio = 8.213, p = 0.314) (Figure 3). This was particularly apparent at the upstream sites, where there was greater colonization. When the analysis was restricted to glass, metal and plastic substrates, for which high enough numbers of objects were examined (n > 50), colonization of

glass substrates was found to be slightly lower than for metal or plastic, but not significantly so (G test = 3.9, p = 0.14). Nonetheless, this tendency to lesser colonization of glass objects was more noticeable using the mean number of mussels per category of substrate (Figure 4). Zebra mussel abundance on glass objects (9.9 mussels ± 2.4 in 1997; 9.3 ± 1.9 in 1998) was on average half to a quarter of that on metal objects (22.8 mussels ± 5.6 in 1997; 32.8 mussels ± 10.8 in 1998) or plastic (21.3 mussels ± 6.4 in 1997; 35.0 mussels ± 19.2 in 1998).

The surface area of the objects examined varied between 0.004 and 1 m², but for the most part between 0.01 and 0.1 m² (Figure 5). The overall results showed no significant relationship between zebra mussel abundance and object surface area (correlation test, p > 0.05). Yet a significant relationship (correlation test, r = 0.52, p < 0.001) was found when only colonized objects (number of mussels > 0) from the Saint-Jean-sur-Richelieu site were considered for both years combined (1997 and 1998). The weak relationship (27% of variance explained) made it pointless to use a correction factor that would take into account the size of the objects in calculating the colonization differences associated with the type of substrate.



Figures above or inside bars indicate number of objects examined.

Figure 3 Colonization rates of various types of substrate in upstream and downstream stretches of the Richelieu River between 1997 and 2000

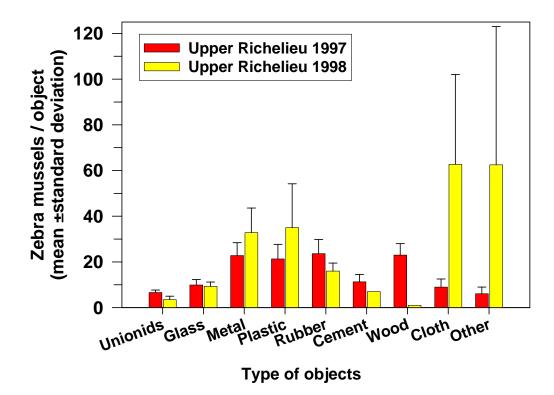


Figure 4 Mean number (and standard deviation) of zebra mussels on different types of substrate gathered at upstream sites along the Richelieu River in 1997 (4 sites) and 1998 (1 site)

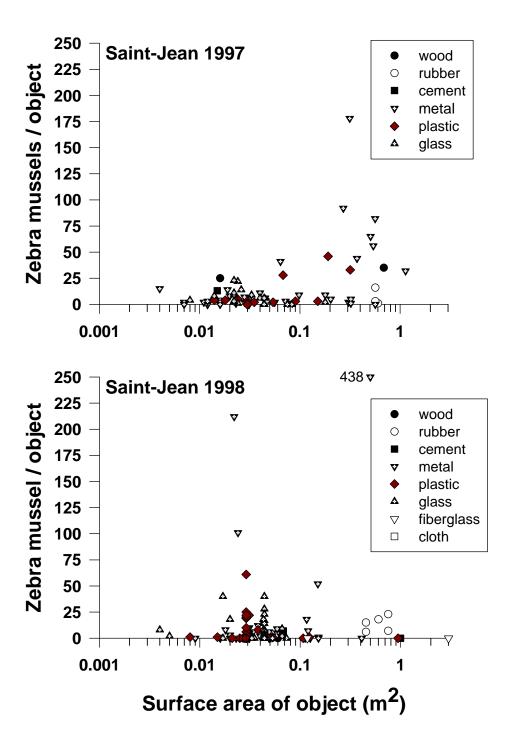


Figure 5 Number of zebra mussels as a function of colonizable surface area of objects grouped by type of substrate, at Saint-Jean-sur-Richelieu in 1997 and 1998

The colonization rate of live and dead unionids was very similar for upstream and downstream sites and from year to year (Table 3). The difference between upstream and downstream colonization rates and the disproportionate number of live versus dead unionids in the two sectors and from year to year made statistical analysis of the results impossible. Although the cumulative results suggest a zebra mussel colonization rate three times higher for live unionids than dead (10.7% vs. 3.5%), the findings in the downstream stretch of the river, combined for all four years, show no significant difference in colonization rates of live and dead unionids. This finding supports observations made upstream in 1997 (Table 3).

		Live unionids			Dead unionids	
Location/ Year	Examined	Colonized	Colonization rate (%)	Examined	Colonized	Colonization rate (%)
Upstream 1997	125	71	56.8	6	5	83.3
Upstream 1998	4	2	50.0	—	—	—
Downstream 1997	458	4	0.9	385	1	0.26
Downstream 1998	167	2	1.2	227	2	0.88
Downstream 1999	31	8	25.8	59	12	20.3
Downstream 2000	72	5	6.9	63	6	9.5
Downstream Total	728	19	2.6	734	21	2.8
Total	857	92	10.7	740	26	3.5

Table 3

Zebra mussel colonization rate of live and dead unionids at upstream and downstream sites between 1997 and 2000

3.3 SIZE OF ZEBRA MUSSELS AND COHORT ANALYSIS

The shell length of zebra mussels varied from 3.4 to 33.3 mm (n = 1307). The size distribution and mean length of the mussels was significantly different between the upstream and downstream sites and from year to year (Figure 6) (Kolmogorov-Smirnov *D* test, p < 0.0001; ANOVA: F = 12.27, p < 0.001). Fisher's least significant difference test (multiple comparison of pairs) indicated significant differences in mussel length between 1997 and 1998 for the upstream sites, and between 1999 and 2000 for the downstream sites.

At Saint-Jean-sur-Richelieu (upstream), the 1997 zebra mussel population consisted of a single cohort with a size range from 7.4 to 20.3 mm and a mode of 15 mm (Figure 6). In 1998, the size distribution of upstream mussels ranged from 6.8 to 26.6 mm and was characterized by two distinct cohorts with modal values of 11 and 19 mm. Specimens under 15 mm in length (threshold value separating the two cohorts) represented 56.7% of all zebra mussels measured in 1998.

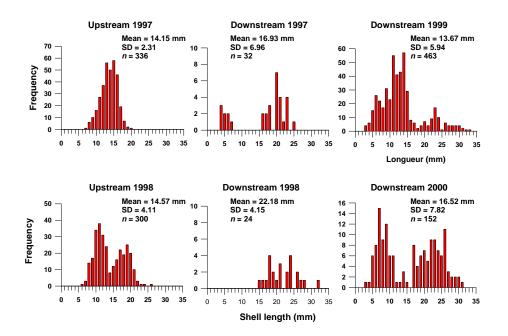


Figure 6 Size distribution of zebra mussels in the Richelieu River upstream and downstream of the Chambly Basin between 1997 and 2000

The very low numbers of zebra mussels gathered at the downstream sites in 1997 (n = 32) and 1998 (n = 24) produce truncated size distributions and cannot be used to determine with any accuracy the number of cohorts that make up the populations. All the mussels measured more than 15 mm long, except for eight specimens gathered at a site in 1997, which were between 4 and 7 mm in length. Despite the low numbers, the size distributions of mussels downstream were significantly different from those upstream in 1997 (K-S: D = 0.588, p < 0.001) and in 1998 (K-S: D = 0.643, p < 0.001). In 1999 and 2000, the size distribution changed radically and was clearly multimodal, indicating that there were two (or even three) distinct zebra mussel cohorts. The proportion of individuals under 15 mm was 73.4% in 1999 and 45.4% in 2000. The size distributions in those two years differed significantly (K-S: D = 0.354, p < 0.001).

In 1999, the size distribution was characterized by a principal mode between 11 and 14 mm and secondary modes of 6 mm and 23 mm. In 2000, the size distribution was largely dominated by mussels smaller than 10 mm, while the proportion of mussels between 12 and 16 mm was very small, in contrast with earlier observations both upstream and downstream. Despite slight variations in the numbers of mussels, multimodal size distribution was observed among the mussels gathered at the various sites.

Compared with observations of objects taken from the water, the size distribution of zebra mussels in the quantitative samples (quadrat method) gathered at Saint-Jean-sur-Richelieu in 1998 was characterized by a greater mean length (16.6 mm) and the dominance of a principal cohort with a modal size of 17 mm (Figure 7). The proportion of mussels under 15 mm was 19.1% in the quadrat samples, as opposed to 56.7% on the sample objects.

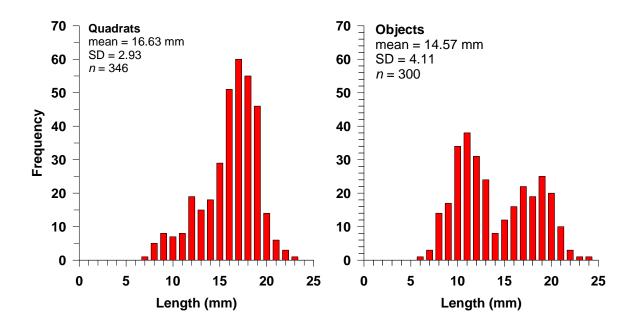


Figure 7 Comparison of shell length of zebra mussels gathered in quadrats and attached to objects at Saint-Jean-sur-Richelieu in 1998

Based on the premise that each cohort corresponds to a different annual recruitment peak, cohort analysis allows us to estimate the strength of annual colonization. Attribution of cohorts to years of larval production depends, however, on the presumed growth rate of the mussels. Given the lack of information on individual growth of zebra mussels in the Richelieu River, our analysis is based on the results of population growth in other bodies of water. In their review of the literature, Jantz and Neumann (1992) state that the mean length of zebra mussels at the end of the first growth season (0+ cohort) varied between 4 and 7 mm, while the mean length of one year olds (1+ cohort) was 13 to 17 mm. Bigger specimens were older. After examining samples gathered in three consecutive years from the Hudson River, Strayer et al. (1996) reported

multimodal size distributions in which each mode corresponded to a different production year. The size of newly settled juveniles (settled during the current year) varied from 4 to 8 mm in September, while a second mode of about 15 mm corresponded to mussels produced the preceding year (Strayer et al., 1996). Two-year-old mussels measured more than 20 mm long. Nalepa et al. (1995) also reported cohorts of very similar size for zebra mussels beginning to colonize Lake Huron. In northern Lake Champlain near the Richelieu River, Eliopoulos and Stangel (1999) observed that the mean length of juvenile mussels attached to artificial substrates varied between 3 and 7 mm (mean 5 mm) in mid-October, a month later than our sampling in the Richelieu. In experiments involving colonization of artificial substrates, zebra mussels gathered in late October in the St. Lawrence were under 5 mm in length (mean 3 mm, de Lafontaine et al., 2002).

In light of this information, it would seem plausible to consider that most of the zebra mussels gathered in mid-September in the Richelieu would be at least a year old: those under 15 to 17 mm would be a year old (1+ cohort) and the larger ones would be two or more years old (2+ cohort). It could also be deduced that zebra mussels produced in the current year (0+ cohort) in the Richelieu would be no longer than 5 or 6 mm. Except for four small mussels gathered at the Saint-Ours site (downstream) in 1997 (Figure 6), specimens of the 0+ cohort appear to be few and far between. The number of mussels born in the current year (0+ cohort) would therefore appear to be negligible in our samples. The relative abundance of annual recruitment of zebra mussels in the Richelieu has been estimated from the product of the relative proportion of mussels in each cohort and an estimate of mussel abundance (Table 4). Upstream, 1997 recruitment (7.02) represented 57% of that calculated for 1996 (12.34). The low recruitment in 1997 is even more remarkable upon analysis of the size structure of mussels in the quadrats (Figure 7). This distribution is probably more representative of the population established in the river (at the Saint-Jean-sur-Richelieu site) in 1998, given that the site had been visited the year before and that various debris had been removed. Downstream, recruitment was very low in 1996 and 1997. On the other hand, 1998 recruitment at the downstream sites appeared to be much

higher than that of 1999 and 1997 (Table 4) and largely contributed to the first significant colonization by zebra mussels in the lower Richelieu.

Table 4

samj	pled at upstream a	and downs	tream sites along	the Richeli	eu River
Location/Year	Abundance (mussels/object)	<i>l</i> + cohort		2+ cohort	
		%	Abundance	%	Abundance
Upstream 1997	12.72	97.0	12.34	3.0	0.38
Upstream 1998	12.40	56.6	7.02	43.3	5.38
Downstream 1997	0.025	12.5	0.003	62.5	0.016
Downstream 1998	0.012	4.2	0.0005	95.8	0.0115
Downstream 1999	0.88	81.4	0.716	18.5	0.163

0.055

53.9

0.065

46.1

Relative proportion of various cohorts defined by length classes of zebra mussels sampled at upstream and downstream sites along the Richelieu River

3.4 ALLOMETRIC RELATIONSHIPS

0.12

Downstream 2000

The relationship between the length and height of zebra mussel shells at the Saint-Jeansur-Richelieu site in 1998 was comparable to that calculated in 1997 (Table 5). The relationship between total dry weight and shell length of the zebra mussel was typically allometric (Figure 8), with an exponent close to 3, which is generally to be expected for this type of biological relationship (Peters, 1984). The relationship between dry weight of soft tissue and length is also allometric, with a coefficient of 2.88. The predictive model for this relationship explains 84.7% of the variance. A coefficient between 2.6 and 2.9 was also observed between the weight of soft tissue and shell length in earlier studies (Roe and MacIsaac, 1997). On the other hand, the dry tissue weight varied linearly or proportionally with the dry shell weight (Figure 8, Table 5).

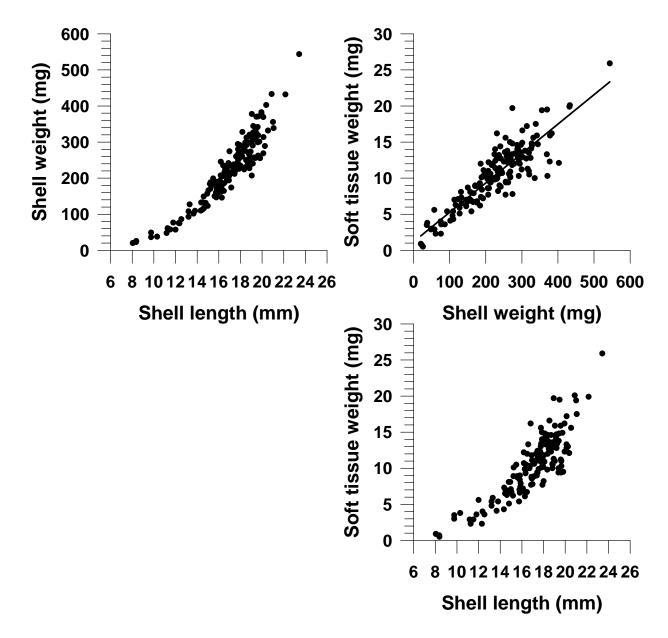


Figure 8 Relationship between weight and shell length of zebra mussels from the Richelieu River in September 1998

Table 5

Empirical relationships between various morphometric measurements of zebra mussels from the Richelieu River in 1997 and 1998

Site	Year	n	Relationship	r^2
Richelieu (12 sites)	1997	942	$\ln (\text{height}) = -0.400 + 0.924 \ln (\text{length})$	0.940
Saint-Jean-sur-Richelieu	1997	336	$\ln (\text{height}) = -0.441 + 0.938 \ln (\text{length})$	0.887
	1998	157	$\ln (\text{height}) = -0.3196 + 0.886 \ln (\text{length})$	0.890
	1998	157	$\ln (\text{total dry weight}) = -3.145 + 3.016 \ln (\text{length})$	0.951
	1998	157	$\ln (dry tissue weight) = -5.899 + 2.884 \ln (length)$	0.847
	1998	157	$\ln (dry shell weight) = -3.225 + 3.0028 \ln (length)$	0.952
	1998	157	dry tissue weight = $0.0407 + 1.187$ dry shell weight	0.780

4 Discussion

Annual monitoring of zebra mussels as part of Richelieu River clean-up campaigns from 1997 to 2000 found mussels at all the sampling sites between Saint-Paul-de-l'Île-aux-Noix and Saint-Ours, which is most of the length of the river (Cusson and de Lafontaine, 1998; this study). Spatial distribution of zebra mussels was not uniform, but characterized by a steep gradient between the areas upstream and downstream of the Chambly Basin. The upper Richelieu (upstream of the Chambly Basin) was clearly and significantly more colonized than the lower Richelieu, both in the degree of colonization and the relative abundance of mussels per object (Table 1). Downstream, mussel abundance and distribution gradually increased between 1997 and 2000 (Table 1, Figure 2), which suggests that zebra mussel populations are still in the process of invading and establishing colonies in this area. These findings support Cusson and de Lafontaine's conclusion (1998) that zebra mussel colonization of the Richelieu follows a pattern similar to the downstream march defined by Horvath et al. (1996). According to this model, zebra mussel colonization along a river mainly depends on the larval production of upstream source populations. Invasion of the entire length of a river is conditional upon the establishment of stable, abundant breeding populations all along the waterway. In all likelihood, zebra mussels have propagated in the same way in the Hudson (Strayer et al., 1996), the Illinois (Stoeckel et al., 1997) and the Rhine (Borcherding and de Ruyter van Steveninck, 1992). Similarly, the colonization by zebra mussels of the lower course of the Rideau River has rapidly extended downstream from a source point that provided the inoculum for the production of larvae that drift downstream, where they settle (Martel, 1995).

The Chambly Basin seems to play a key role in determining the observed difference between upstream and downstream sites in terms of colonization rates and relative abundance of zebra mussels. The physical and chemical characteristics of the waters of the Richelieu are significantly different downstream of the basin: greater flow rate, turbidity, conductivity, major nutrients (N, P) for primary producers and agricultural contaminant loads (Piché and Simoneau, 1998). These changes are associated with two tributaries (the L'Acadie and Des Hurons rivers)

that run through farmland and empty into the Richelieu at the Chambly Basin. Yet except for the rate of flow, variations in which may influence the transportation of zebra mussel larvae, all the factors mentioned are unlikely, given the small variations observed, to explain the differences in colonization upstream and downstream from the basin. Levels of calcium, crucial to zebra mussel growth (Claudi and Mackie, 1993), do not vary much between upstream and downstream, and were between 16.34 and 20.82 mg/L in 1998 (Y. de Lafontaine, unpublished data). These values, though relatively low and not optimal for zebra mussels, are still above 11 mg/L, the level deemed critical for survival, growth and reproduction (McMahon, 1996). According to Mellina and Rasmussen (1994), high zebra mussel densities generally develop in water with calcium levels above 21 mg/L. Eliopoulos and Stangel (1999) have shown, however, that ambient concentrations of between 14 and 20 mg/L had no negative effect on zebra mussels in Lake Champlain. In our opinion, this conclusion also applies to Richelieu River populations. The speed of the current in the lower Richelieu could act as a limiting factor on zebra mussel colonization, although once again, observed values (0.6-1.0 m/sec, see Piché and Simoneau,1998) are below the critical levels reported in the literature (Claudi and Mackie, 1993). Thus, while the possibility cannot be totally excluded, it seems unlikely that the physical-chemical conditions and quality of the water of the Richelieu are the cause of the pronounced gradient in zebra mussel colonization between the stretches upstream and downstream of the Chambly Basin.

The low abundance of zebra mussels downstream of Chambly Basin would appear to be attributable, rather, to weak recruitment stemming from translocation of larvae. Zebra mussel colonization of the upper Richelieu (upstream of the Chambly Basin) seems to result chiefly from larval drift from Lake Champlain (de Lafontaine and Cusson, 1997). Sampling in 1996 and 1997 showed that the density of veliger larvae dropped by more than 90% between the upper and lower Richelieu (de Lafontaine and Cusson, 1997; Cusson and de Lafontaine, 1997; Y. de Lafontaine, unpublished data), which would mean lower colonization potential downstream. Recent studies have shown that zebra mussels in rivers do not usually reach abundance levels comparable to those of upstream lakes and do not generally dominate lotic

habitats (Horvath et al., 1999; Toczylowski et al., 1999). The situation in the Richelieu, with its upstream-downstream gradient of zebra mussel densities, thus seems typical of the dynamics of this species in rivers. Our current findings, however, do not allow us to conclude whether the present spatial gradient is a stable situation or whether it will be attenuated over time. According to the downstream march model (see above, Horvath et al., 1996), colonization and abundance of zebra mussels in the lower Richelieu could increase over time, once upper Richelieu populations have become well established and achieved high enough densities to ensure sustained and abundant larval production. Long-term monitoring, coupled with specific studies focusing on larval production and drift and on colonization by juveniles, is required to shed light on the dynamics of colonization and dispersal of zebra mussels from the upper to the lower Richelieu.

The variability of the size structure of mussels in the two parts of the river and from year to year reveals a variability in time and place of recruitment of zebra mussels in the Richelieu (Table 4). Massive colonization of the upper Richelieu probably occurred in 1996, with significant colonization of the lower Richelieu not taking place until two years later, in 1998. A number of findings suggest that recruitment and colonization in 1997 were relatively weaker than in 1996 or 1998. First, mussel abundance per object upstream of the Chambly Basin remained stable (~12 mussels/object) between 1997 and 1998 (Table 1), while the size distribution clearly indicated the presence of two cohorts in 1998 as opposed to just one in 1997 (Figure 6). Second, the absence of mussels smaller than 15 mm downstream (though there were some upstream) in 1998 also suggests very low recruitment in 1997. Similarly, the low proportion of mussels in the 2+ cohort (> 15 to 17 mm) in 1999 may well be indicative of low recruitment in 1997 and earlier. Yet each year there was a very small proportion of mussels in the 0+ cohort. This situation may be due to (1) late colonization of the Richelieu by zebra mussels or (2) volunteers' difficulty detecting very small mussels (< 3 mm) on objects. It seems unlikely that our attribution of various size groups of mussels to production years might be erroneous and that mussels between 7 and 15 mm might belong to the 0+ cohort, as that would mean a growth rate far superior to that observed in populations in Lake Champlain and other sites at the same latitude. In our opinion, the environmental conditions of the Richelieu River could not support such a high growth rate.

Table 6

Mean flow (m³/s) of the Richelieu River in June, July and August, between 1995 and 2000

Year	June Mean (SD) Min-Max	July Mean (SD) Min-Max	August Mean (SD) Min-Max
1995	241 (51) 155–321	125 (15) 96–157	171 (29) 104–214
1996	729 (106) 573–940	504 (24) 458–563	383 (67) 284–495
1997	465 (104) 275–632	269 (24) 224–311	204 (14) 175–225
1998	469 (62) 384-631	661 (63) 508-741	451 (36) 396–523
1999	226 (59) 139-328	122 (15) 102–164	89 (9) 63–103
2000	677 (101) 505-873	390 (52) 309–504	273 (31) 224–334

In species characterized by planktonic larval drfit, the transportation of larvae is a determining factor in the spatial extent of colonization from year to year. In a river, the flow may carry larvae downstream, where the juveniles eventually settle. The mean flow rates of the Richelieu in summer (July and August) have been highly variable in the last few years, depending on the rainfall (Table 6). The highest mean flows in July, which is the peak period for veliger larvae in the river (Cusson and de Lafontaine, 1997; de Lafontaine and Cusson, 1997), were recorded in 1998 (661 m^3/s). This flow, two to five times higher than in other years, could have transported more larvae downstream and been responsible for the greater colonization of the lower Richelieu in 1998, as evidenced by the size of the 1+ cohort observed during the clean-ups in 1999 (Table 4). It is also interesting to note that the mean flows were also very high in July 1996 (504 m³/s) at the time when the initial colonization of the upper Richelieu probably occurred. On the other hand, the very low flows recorded in the summer of 1999 (Table 6) probably led to less downstream colonization than the year before (Table 4). We therefore hypothesize a causal link between river flow fluctuations and strength of recruitment and colonization of zebra mussels in the Richelieu. Although many earlier studies have noted the importance of the larval supply on zebra mussel recruitment in lotic systems (Borcherding and de Ruyter van Steveninck, 1992; Martel, 1995; Nichols, 1996; Stoeckel et al., 1997), the effect of fluctuations in flow on controlling recruitment was still very speculative. Confirmation of this hypothesis and the development of an empirical model of the relationship between summer flow and zebra mussel recruitment in the Richelieu would require long-term monitoring of mussel colonization along the river. Monitoring of this type must include an analysis of size and annual growth of mussels in order to determine the structure of zebra mussel cohorts.

According to Ackerman et al. (1994), recruitment of zebra mussels is a two-stage process: (1) attachment of pediveliger larvae followed by metamorphosis into juveniles and (2) movement of juvenile or adult mussels (also called translocators) to new areas. It has already been demonstrated that juveniles can be translocated when the water plants to which they are attached are pulled up and carried away by the current (or by boats) (Lewandowski, 1982; Johnson and Carlton, 1996). While the first mechanism seems to have largely contributed to the colonization of the upper Richelieu through the transportation of larvae from Lake Champlain (de Lafontaine and Cusson, 1997), the second process might explain the presence of large mussels (> 20 mm) downstream in the first two years (1997 and 1998). Large mussels were rarely found at the upstream sites, but were more abundant downstream. The lack of a continuum of relative proportions of the various mussel cohorts along the Richelieu may suggest that translocation is at work. It is nevertheless impossible to specify whether the transportation (i.e., by boat trailers, Johnson and Carlton, 1996). This method of spreading zebra mussel populations in the Richelieu appears to be less significant than colonization by larval drift.

4.1 MONITORING: BY CLEAN-UP OPERATION OR QUADRAT?

As a means of determining the presence of zebra mussels at the various sites, the sampling of quadrats turned out to be much less efficient than the intensive collection done during the clean-up operations. The monitoring by clean-up crews was very effective in confirming the presence of zebra mussels at a given site and comparing degrees of colonization at different sites. In 1998, zebra mussels were reported in the quadrats at only one highly colonized site (Saint-Jean-sur-Richelieu) and no mussel was found in the quadrats at downstream sites,

despite their presence on objects at the same sites. On the other hand, gathering zebra mussels from objects did not allow us to obtain sufficiently precise density estimates. In fact, the lack of significant relationship between the surface area of the objects examined and the number of mussels attached (Figure 5) poses a serious problem for quantitative estimating of mussel abundance through monitoring in clean-up campaigns. Furthermore, our findings have shown lower colonization of glass than metal or plastic substrates (Figures 3 and 4), as noted earlier in experimental studies (Kilgour and Mackie, 1993; Marsden and Lansky, 2000). If monitoring is to be continued in conjunction with clean-ups, it will be essential to note the type of objects examined so that colonization from year to year and site to site can be better compared with respect to type of substrate.

Quadrat sampling gave a preliminary quantitative estimate of zebra mussel densities for the Richelieu. Abundance rates of 15 to 160 mussels/m² in the upper Richelieu in 1998 were lower than the densities (500 to 7500 mussels/m²) reported for populations already established for some time in a lake or river (Ramcharan et al., 1992; Nalepa et al., 1995; Martel, 1995; Strayer et al., 1996). Densities in the Hudson River fluctuated between 1000 and 10 000 mussels/m² barely three years after the initial invasion (Strayer et al., 1996), while those in the Rideau were as high as 3500 mussels/m² four years after they were discovered. Considering that the initial colonization of the Richelieu River by zebra mussels probably took place in 1996, we recommend that systematic quantitative sampling be carried out *without further delay* at various sites along the entire length of the river in order to obtain a precise estimate of relative densities and spatial distribution of the zebra mussel in this waterway. It is imperative to conduct a quantitative assessment of this kind when colonization is just beginning, in order to establish a baseline for future estimates of the potential impact of the zebra mussel.

4.2 POTENTIAL IMPACT

Aside from their impact on the economic and recreational use of waterways, zebra mussels have perceptible abiotic and biotic effects on various trophic levels of aquatic ecosystems (Effler et al., 1996; MacIsaac, 1996). These effects remain to be demonstrated for the

Richelieu. One of the most quickly observable direct biotic effects is the decline in native unionid populations (Lewandowski, 1976; Ricciardi et al., 1995; Nalepa et al., 1996; Schloesser, 1996; Schloesser et al., 1998). The impact on unionids is highly variable, however, depending on the degree of infestation by zebra mussels, which in turn depends on environmental conditions and habitat type (Tucker, 1994; Nichols and Amberg, 1999; Toczylowski et al., 1999; Horvath et al., 1999; Hart et al., 2001). It has recently been shown that unionids were not colonized by zebra mussels any more than were various other solid substrates and that zebra mussel densities on unionids were similar to those measured on rigid substrates in the same area (Toczylowski and Hunter, 1997; Toczylowski et al., 1999). Our findings tend to confirm this, as they reveal no significant difference in degree of colonization of unionids in comparison to inert objects in the Richelieu (tables 2 and 3), which suggests that in the early stages of colonization, zebra mussel attachment is essentially related to availability of a rigid substrate, without preference for unionids. In our study, the mean level of infestation of unionids was under 10 zebra mussels per unionid, which is still much lower than the levels reported in other rivers heavily colonized by zebra mussels (>100 mussels/unionid, Tucker, 1994; Ricciardi et al., 1995). According to observations by Hart et al. (2001), the degree of colonization of unionids observed in the Richelieu in 1998 was too low to have a significant negative effect on unionid survival rates. According to the model proposed by Ricciardi et al. (1995), high unionid mortality rates are to be expected when colonization reaches about 100 zebra mussels per unionid. Considering that the infestation rate on Unionidae went from 10 to 100 zebra mussels per unionid in four years in the Mississippi River (Hart et al., 2001), it is imperative to reassess the degree of colonization of unionids in the upper Richelieu as soon as possible. The ratio of the number of live and dead unionids could provide an indication of the impact of zebra mussel colonization on unionids in the Richelieu and be compared with data accumulated during the last four clean-up operations.

Despite the imprecise estimates of zebra mussel abundance in the Richelieu, we have attempted to establish a preliminary assessment of the relative potential impact of the invasion of the river by zebra mussels. Based on size distribution (Figure 6) and predictive relationships between shell length and dry soft tissue weight (Table 5), we established a frequency distribution

of dry weights for each area and each year. From the product of this weight frequency distribution and estimates of abundance on objects (Table 1), we calculated an index of potential impact in terms of relative biomass for the upper and lower stretches of the river for each year (Table 7). The index is expressed in terms of biomass rather than number because most metabolic processes vary exponentially with the weight of the organism (filtration, respiration and assimilation rates, Effler et al., 1996; McMahon, 1996). Given the heterogeneous spatial distribution of zebra mussels along the river, the upper Richelieu would appear to have suffered, since 1997, an impact 10 to 100 times greater than the lower Richelieu between 1997 and 2000. Despite the relative stability in the abundance of zebra mussels in the upper Richelieu between 1997 and 1998, the index suggests a 21% increase in the potential impact in the second year, due to the mussels' growth in size. On the other hand, the increase in colonization rates in the lower river between 1998 and 1999 probably multiplied the potential impact thirtyfold, though this is still far below estimates for the upper river. These estimates assume that the quantity of substrates available for colonization by zebra mussels is similar both upstream and downstream from the Chambly Basin.

between 1997 and 2000				
Location/Year	Abundance (mussels/object)	Relative potential impact [standardized biomass of soft tissue (dry weight)]		
Upstream 1997	12.72	77.86		
Upstream 1998	12.40	94.32		
Downstream 1997	0.02	0.26		
Downstream 1998	0.01	0.23		
Downstream 1999	0.88	7.24		
Downstream 2000	0.12	1.73		

Table 7

Abundance and relative potential impact of zebra mussels by location and year

5 Conclusion

The overall findings from the clean-up campaigns conducted in the Richelieu River in early autumn each year have allowed us to confirm and document the spread of zebra mussels all along the river since the first invasion in 1996. Four years later, the spatial distribution of the zebra mussel remained very heterogeneous and characterized by a steep abundance gradient between the stretches of the river upstream and downstream of the Chambly Basin. The population dynamics and recruitment of this invasive species are complex and often characterized by strong variations in abundance in the short and long term (Ramcharan et al., 1992; Stanczykowska and Lewandowski, 1993; van der Velde et al. 1994; Nalepa et al., 1995). The populations of zebra mussels in the Richelieu River may also be subject to strong variations caused by larval translocation controlled by the force of the flow of the river in summer (July). Monitoring between 1997 and 2000 revealed that zebra mussel colonization is increasing and out of balance with its surrounding environment: the impact has not yet been fully defined and measured.

To date, the Richelieu River is the only tributary of the St. Lawrence that has been invaded and colonized by zebra mussels. The impact of any future translocation of mussels from the Richelieu to the St. Lawrence has not been assessed, but should be fairly moderate and confined mainly to the south shore of Lake Saint-Pierre. It is important to keep in mind, however, that colonization of the Richelieu by zebra mussels increases the risk of the species spreading to other bodies of water in Quebec. The Richelieu is heavily used by pleasure craft, and some of them may frequent other inland waters. In this regard, the implementation and application of a prevention program should be a high priority in order to reduce the risk of propagation of the zebra mussel and other undesirable species.

References

- Ackerman, J.D., B. Sim, and R. Claudi. 1994. A review of the early life history of zebra mussels (*Dreissena polymorpha*): Comparisons with marine bivalves. *Can. J. Zool.* 72: 1169–1179.
- Borcherding, J. and E.D. de Ruyter van Steveninck. 1992. "Abundance and Growth of Dreissena polymorpha Larvae in the Water Column of the River Rhine during Downstream Transportation." In D. Neumann and H.A. Jenner (eds.), The Zebra Mussel Dreissena polymorpha: Ecology, Biological Monitoring and First Applications in Water Quality Management. pp. 29–44.Gustav Fischer, Stuttgart.
- Claudi, R. and J.H. Leach (eds.). 2000. Nonindigenous Freshwater Organisms: Vectors, Biology, and Impacts. CRC Press Inc., Lewis Publishers, Boca Raton, Florida. 464 pp.
- Claudi, R. and G.L. Mackie. 1993. *Practical Manual for Zebra Mussel Monitoring and Control*. CRC Press Inc., Lewis Publishers, Boca Raton, Florida. 227 pp.
- Claxton, W.T., A. Martel, R.M. Dermott, and E.G. Boulding. 1997. Discrimination of fieldcollected juveniles of two introduced dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) using mitochondrial DNA and shell morphology. Can. J. Fish. Aquat. Sci. 54: 1280–1288.
- Cusson, B. and Y. de Lafontaine. 1997. Présence et abondance des larves de Moules zébrées dans la rivière Richelieu et le Saint-Laurent en 1996. Scientific and Technical Report ST-143. Environment Canada – Quebec Region, Environmental Conservation, St. Lawrence Centre. 58 pp.
- Cusson, B. and Y. de Lafontaine. 1998. *Distribution spatiale des Moules zébrées dans la rivière Richelieu en 1997.* Scientific and Technical Report ST-167. Environment Canada – Quebec Region, Environmental Conservation, St. Lawrence Centre. 38 pp.
- de Lafontaine, Y., G. Costan, and F. Delisle. 2002. Testing a new anti-zebra mussel coating with a multi-plate sampler: Confounding factors and other fuzzy features. *Biofouling* (in press).
- de Lafontaine, Y. and B. Cusson. 1997. Veligers of zebra mussels in the Richelieu River: An intrusion from Lake Champlain? *Proceedings of the Second Northeast Conference on Nonindigenous Aquatic Nuisance Species*, April 18–19, 1997, Burlington, Vermont.
- Domm, S., R.W. McCauley, E. Kott, and J.D. Ackerman. 1993. Physiological and taxonomic separation of two Dreissenid mussels in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* 50: 2294–2297.

- Effler, S.W., C.M. Brooks, K. Whitehead, B. Wagner, S.M. Doerr, M. Perkins, C.A. Siegfried, L. Walrath, and R.P. Canale. 1996. Impact of zebra mussel invasion on river water quality. *Water Environ. Res.* 68: 205–214.
- Eliopoulos, C. and P. Stangel. 1999. *Lake Champlain 1998 Zebra Mussel Monitoring Program*. Vermont Department of Environmental Conservation, Waterbury, Vermont. 32 pp.
- Gido, K.B. and J.H. Brown. 1999. Invasion of North American drainages by alien fish species. *Freshwater Biology* 42: 387–399.
- Hart, R.A., M. Davis, J.W. Grier, and A.C. Miller. 2001. Survival of unionids following removal of attached zebra mussels. *J. Freshwater Ecology* 16: 29–34.
- Horvath, T.G., K.M. Martin, and G.A. Lamberti. 1999. Effect of zebra mussels, *Dreissena* polymorpha, on macroinvertebrates in a lake-outlet stream. *Am. Midl. Nat.* 142: 340–347.
- Horvath, T.G., G.A. Lamberti, D.M. Lodge, and W.L. Perry. 1996. Zebra mussel dispersal in lake-stream systems: Source-sink dynamics? *J.N. Am. Benthol. Soc.* 15: 564–575.
- Jantz, B. and D. Neumann. 1992. "Shell Growth and Aspects of the Population Dynamics of Dreissena polymorpha in the River Rhine." In D. Neumann and H.A. Jenner (eds.), The Zebra Mussel Dreissena polymorpha. Ecology, Biological Monitoring and First Applications in Water Quality Management. pp. 48–66.Gustav Fischer, Stuttgart.
- Johnson, L.E. and J.T. Carlton. 1996. Post-establishment spread in large-scale invasions: Dispersal mechanisms of the zebra mussel *Dreissena polymorpha*. *Ecology* 77: 1686–1690.
- Kilgour, B.W. and G.L. Mackie. 1993. "Colonization of Different Construction Materials by the Zebra Mussel (*Dreissena polymorpha*)." In T.F. Nalepa and D.W. Schloesser (eds.), Zebra Mussels: Biology, Impacts, and Control. pp. 167–173. Lewis Publishers, Boca Raton, Florida.
- Lewandowski, K. 1976. Unionidae as a substratum for Dreissena polymorpha Pall. Polskie Archiwum Hydrobiologii 23: 409–420.
- Lewandowski, K. 1982. The role of early developmental stages in the dynamics of *Dreissena polymorpha* (Pall.) (Bivalvia) populations in lakes. II. Settling of larvae and the dynamics of settled individuals. *Ekol. Pol.* 30: 223–286.
- MacIsaac, H.J. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. *Amer. Zool.* 36: 287–299.

- Marsden, J.E. and D.M. Lansky. 2000. Substrate selection by settling zebra mussels, *Dreissena* polymorpha, relative to material, texture, orientation, and sunlight. Can. J. Zool. 78: 787–793
- Martel, A. 1995. Demography and growth of the exotic zebra mussel (*Dreissena polymorpha*) in the Rideau River (Ontario). *Can. J. Zool.* 73: 2244–2250.
- McMahon, R.F. 1996. The physiological ecology of the zebra mussel, *Dreissena polymorpha*, in North America and Europe. *Amer. Zool.* 36: 339–363.
- Mellina, E. and J.B. Rasmussen. 1994. Patterns in the distribution and abundance of zebra mussel (*Dreissena polymorpha*) in rivers and lakes in relation to substrate and other physicochemical factors. *Can. J. Fish. Aquat. Sci.* 51: 1024–1036.
- Mills, E.L., J.R. Chrisman, and K.T. Holeck. 2000. "The Role of Canals in the Spread of Nonindigenous Species in North America." In R. Claudi and J.H. Leach (eds.), Nonindigenous Freshwater Organisms: Vectors, Biology and Impacts. pp. 347–380. CRC Press Inc., Lewis Publishers, Boca Raton, Florida.
- Nalepa, T.F., J.A. Wojcik, D.L. Fanslow, and G.A. Lang. 1995. Initial colonization of the zebra mussel (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron: Population recruitment, density, and size structure. J. Great Lakes Res. 21: 417-434.
- Nalepa, T.F., D.J. Hartson, G.W. Gostenik, D.L. Fanslow, and G.A. Lang. 1996. Changes in the freshwater mussel community of Lake St. Clair: From Unionidae to Dreissena polymorpha in eight years. J. Great Lakes Res. 22: 354–369.
- Nichols, S.J. 1996. Variations in the reproductive cycle of *Dreissena polymorpha* in Europe, Russia, and North America. *Am. Zool.* 36: 311–325.
- Nichols, S.J. and J. Amberg. 1999. Co-existence of zebra mussels and freshwater unionids: Population dynamics of *Leptodea fragilis* in a coastal wetland infested with zebra mussels. *Can. J. Zool.* 77: 423–432.
- Peters, R.H. 1984. *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, U.K. 329 pp.
- Piché, I. and M. Simoneau. 1998. "Le bassin de la rivière Richelieu: Profil géographique, sources de pollution, intervention et assainissement et qualité des eaux." In *Le bassin versant de la rivière Richelieu: l'état de l'écosystème aquatique 1995*. Ministère de l'Environnement and de la Faune, Direction des écosystèmes aquatiques, Quebec. Envirodoq No. EN980604, rapport EA-13, section 1.

- Ramcharan, C.W., D.K. Padilla, and S.I. Dodson. 1992. A multivariate model for predicting population fluctuations of *Dreissena polymorpha* in North American lakes. *Can. J. Fish. Aquat. Sci.* 49: 150–158.
- Ricciardi, A. F.G. Whoriskey, and J.B. Rasmussen. 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.
- Roe, S.L., and H.J. MacIsaac. 1997. Deepwater population structure and reproductive state of quagga mussels (*Dreissena bugensis*) in Lake Erie. *Can. J. Fish. Aquat. Sci.* 54: 2428– 2433.
- Schloesser, D.W. 1996. Mitigation of unionid mortality caused by zebra mussel infestation: Cleaning of unionids. N. Am. J. Fish. Man. 16: 942–946.
- Schloesser, D.W., W.P. Kovalak, G.D. Longton, K.L. Ohnesorg, and R.D. Smithee. 1998. Impact of zebra and quagga mussels (*Dreissena* spp.) on freshwater unionids (Bivalvia: Unionidae) in the Detroit River of the Great Lakes. Am. Midl. Nat. 140: 299–313.
- Stanczykowska, A. and K. Lewandowski. 1993. "Thirty Years of Dreissena polymorpha Ecology in Mazurian Lakes of Northeastern Poland." In T.F. Nalepa and D.W. Schloesser (eds.), Zebra Mussels: Biology, Impacts and Control. pp. 3–33.Lewis Publishers, Boca Raton, Florida.
- Stoeckel, J.A., D.W. Schneider, L.A. Soeken, K.D. Blodgett, and R.E. Sparks. 1997. Larval dynamics of a riverine metapopulation: Implications for zebra mussel recruitment, dispersal, and control in a large-river system. J. N. Am. Benthol. Soc. 16: 586–601.
- Strayer D.L., J. Powell, P. Ambrose, L.C. Smith, M.L. Pace, and D.T. Fischer. 1996. Arrival, spread, and early dynamics of a zebra mussel (*Dreissena polymorpha*) population in the Hudson River estuary. *Can. J. Fish. Aquat. Sci.* 53: 1143–1149.
- Toczylowski, S.A. and R. D. Hunter. 1997. "Do Zebra Mussels Preferentially Settle on Unionids and/or Adults Conspecifics?" *In* F. D'Itri (ed.), *Zebra Mussels and Aquatic Nuisance Species*. pp. 125–140.Ann Arbor Press Inc., Chelsea, Michigan.
- Toczylowski, S.A., R. D. Hunter, and L.M. Armes. 1999. The role of substratum stability in determining zebra mussel load on unionids. *Malacologia* 41:151–162.
- Tucker, J.K. 1994. Colonization of unionid bivalves by the zebra mussel, *Dreissena polymorpha*, in Pool 26 of the Mississippi River. J. Freshwater Ecology 9: 129–134.
- Van der Velde, G., B.G.P. Paffen, and F.W.B. van den Brink. 194. Decline of Zebra mussel populations in the Rhine. *Naturwissenchaften* 81: 32–34.

Appendixes

Site (Year)	Species	
Saint-Paul-de-l'Île-aux-Noix (1997)	Lampsilis radiata Elliptio complanata	
Iberville (1997)	Lampsilis radiata Lampsilis cardium Ligumia recta Elliptio complanata Pyganodon grandis	
Saint-Jean-sur-Richelieu (1997)	Lampsilis radiata Elliptio complanata	
Saint-Athanase (1997)	Lampsilis radiata Elliptio complanata Elliptio sp. Ligumia recta Pyganodon cataracta	
Saint-Mathias (1997)	Lasmigona costata Elliptio complanata Lampsilis radiata Leptodea fragilis Ligumia recta	
Île Goyer (1997)	Lampsilis radiata Elliptio complanata Leptodea fragilis	
McMasterville (1997)	Lampsilis radiata Elliptio complanata Elliptio dilatata Leptodea fragilis Alasmidonta undulata Lampsilis cardium Lasmigona costata Ligumia recta Elliptio crassidens Strophitus undulatus	

1 Unionid Species Gathered in the Richelieu River during Clean-up Operations

Site (Year)	Species
Saint-Hilaire (1997)	Lampsilis cardium Lampsilis radiata Ligumia recta Elliptio complanata Leptodea fragilis
Beloeil (1997)	Lampsilis radiata Leptodea fragilis
Saint-Marc-sur-Richelieu (1997)	Elliptio complanata Elliptio crassidens Elliptio sp. Lampsilis radiata Lampsilis cardium
Saint-Antoine-sur-Richelieu (1997)	Leptodea fragilis Ligumia recta Elliptio complanata Lampsilis radiata Lampsilis cardium
Saint-Ours (1997)	Elliptio complanata Lampsilis radiata Lampsilis cardium Alasmidonta undulata Ligumia recta Elliptio dilatata Strophitus undulatus Pyganodon grandis
Saint-Mathias (1998)	Lampsilis cardium Pyganodon sp. Pyganodon cataracta Lampsilis radiata Elliptio complanata Leptodea fragilis Elliptio dilatata Ligumia recta Elliptio sp. Lasmigona costata

Site (Year)	Species	
Saint-Hilaire (1998)	Lampsilis radiata Elliptio dilatata Elliptio complanata Ligumia recta Alasmidonta undulata Lampsilis cardium	
Beloeil (1998)	Elliptio dilatata Elliptio complanata Pyganodon grandis Lampsilis radiata Alasmidonta undulata	
Saint-Marc-sur-Richelieu (1998)	Lampsilis radiata Ligumia recta Lampsilis ventricosa Leptodea fragilis Pyganodon cataracta Elliptio crassidens Elliptio sp.	
Saint-Marc-sur-Richelieu(1999)	Elliptio complanata Ligumia recta Lampsilis radiata Lampsilis cardium Leptodea fragilis Pyganodon cataracta	
Saint-Ours (1999)	Lampsilis cardium Lampsilis radiata Elliptio complanata Ligumia recta Elliptio dilatata Elliptio crassidens	