The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata

Anthony Ricciardi, Fred G. Whoriskey, and Joseph B. Rasmussen

Abstract: We examined the importance of the Eurasian zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata in the Great Lakes – St. Lawrence River system. An experiment using artificial substrata (i.e., cement bricks with either a layer of living zebra mussels, a layer of intact empty shells that mimicked living mussels, or with no added layer) showed that macroinvertebrate abundance is enhanced in the presence of zebra mussels and that macroinvertebrate responses to physical versus biological attributes of mussel beds (e.g., spatial habitat created by clumped shells; biodeposition) vary among taxa. Moreover, densities of zebra mussels and associated epifauna have increased severalfold at various sites in the Great Lakes – St. Lawrence River system within the past decade; changes in community composition were similar to those observed in our artificial substrate experiment. Our results suggest that dense zebra mussel colonization alters macroinvertebrate communities on hard substrata by enhancing conditions for deposit-feeding organisms, small gastropods, and small predatory invertebrates, and by displacing large gastropods and certain large filterers. In the St. Lawrence River, these effects were associated with zebra mussel densities of 1500–4000 individuals/m^2, which are likely to be supported by most waterbodies in North America.

Résumé : Nous avons examiné l'importance de la moule zébrée eurasienne (*Dreissena polymorpha*) dans la structuration des communautés de macroinvertébrés sur des substrats durs dans le réseau des Grands Lacs et du Saint-Laurent. Une expérience faisant appel à des substrats artificiels (c.-à-d., des briques de ciment soit couvertes d'une couche de moules zébrées vivantes, soit portant une couche de coquilles vides intactes ressemblant à des moules vivantes, soit sans recouvrement) a révélé que l'abondance de macroinvertébrés est accrue en présence de moules zébrées, et que les taxons de macroinvertébrés varient en fonction des attributs physiques ou des attributs biologiques des gisements de moules (p. ex., habitat spatial créé par les coquilles entassées; nourriture fournie par le dépôt de matières organiques). En outre, les densités des moules zébrées et de l'épifaune associée ont augmenté plusieurs fois à divers sites du réseau des Grands Lacs et du Saint-Laurent au cours de la dernière décennie; les changements dans la composition des communautés étaient similaires à ceux que nous avons observés pendant notre expérience sur les substrats artificiels. Nos résultats font ressortir que la colonisation par les moules zébrées modifie les communautés de macroinvertébrés sur les substrats durs en stimulant les conditions favorables aux organismes déposivores, aux petits gastropodes et aux petits invertébrés prédateurs, et en déplaçant les gros gastropodes et certains filtreurs de grande taille. Dans le Saint-Laurent, ces effets étaient associés à des densités de moules zébrées de 1500–4000 individus/m^2, qui sont susceptibles d'être observées dans la plupart des masses d'eau de l'Amérique du Nord.
[Traduit par la Rédaction]

Introduction

Sessile fouling organisms have been shown to play important roles in structuring benthic communities (e.g., Paine 1974; Suchanek 1979, 1986; Ban and Nelson 1987; Matsumasa 1994). On marine rocky shores, mussels form spatially complex patches (mussel beds) that provide habitat for a diverse assemblage of organisms (e.g., Tsuchiya and Nishihira 1986; Jacobi 1987; Ong Che and Morton 1992; Lintas and Seed

A. Ricciardi.[1] Département de biologie (GIROQ), Université Laval, Ste-Foy, QC G1K 7P4, Canada.
F.G. Whoriskey. Department of Natural Resource Sciences, McGill University, Ste-Anne-de-Bellevue, QC H9X 3V9, Canada.
J.B. Rasmussen. Department of Biology, McGill University, Montreal, QC H3A 1B1, Canada.

[1] Author to whom all correspondence should be addressed.
    e-mail: anthony.ricciardi@giroq.ulaval.ca

1994; Seed 1996) but may also reduce or displace other benthic fauna (Paine 1974; Griffiths et al. 1992; Hockey and van Erkom Schurink 1992). Dramatic changes in marine benthic communities have followed invasions by competitively dominant mussels (Rao and Rao 1975; Griffiths et al. 1992; Hockey and van Erkom Schurink 1992; Abdel-Razek et al. 1993).

The introduction of the Eurasian zebra mussel (*Dreissena polymorpha*) to the Laurentian Great Lakes in the mid-1980s (Hebert et al. 1989) added the first epifaunal mussel to North American freshwater communities, which generally have evolved without dominant macrofouling organisms. Therefore, the potential impacts of this invasion on benthic fauna and food webs have fueled much speculation (e.g., Hebert et al. 1991; Cooley 1991; Bruner et al. 1994). Although the zebra mussel has been established in Europe for almost two centuries (Stanczykowska 1977), and several European studies provide anecdotal evidence that zebra mussels influence benthic macroinvertebrate abundance (e.g., Sebestyen 1937; Dusoge 1966; Wiktor 1969; Izvekova and Lvova-Katchanova 1972; Lyakhnovich et al. 1982; Maslowski 1992; Burlakova 1995), there is little quantitative information available in the

European literature that could be used to predict the mussel's impacts on North American benthic fauna. Within the last few years, the deleterious effects of zebra mussels on native North American freshwater mussel (Unionidae) populations have become well documented (e.g., Gillis and Mackie 1994; Schloesser and Nalepa 1994; Ricciardi et al. 1995a, 1996), but impacts on epifaunal communities have only recently begun to be evaluated.

During the past decade, substantial changes in the composition and abundance of benthic macroinvertebrate fauna occurred in the lower Great Lakes (Griffiths 1993; Stewart and Haynes 1994; Wisenden and Bailey 1995), where zebra mussel population densities were among the highest ever recorded ($\sim 10^5$ mussels/m^2, 100-fold higher than in most European habitats; cf. Stanczykowska 1977). It is unclear whether the coincident development of dense zebra mussel populations in the region was the direct cause of these changes, but it has been suggested that the physical and biological attributes of zebra mussel beds (e.g., interstitial habitat provided by clumped mussel shells and byssal threads; filtration currents; food provided by mussel feces and pseudofeces) play important roles in structuring benthic communities (Griffiths 1993; Stewart and Haynes 1994). However, the relative importance of these attributes for macroinvertebrate assemblages on hard substrata has not been tested.

In the early 1990s, the zebra mussel expanded its range into the St. Lawrence River (Mellina and Rasmussen 1994) and subsequently invaded several other large rivers outside of the Great Lakes watershed (e.g., the Hudson, Illinois, Mississippi, Ohio, and Tennessee rivers) (Ludyanskiy et al. 1993). Because the zebra mussel is expected to become established in most North American drainages (Strayer 1991; Ramcharan et al. 1992), information on the response of St. Lawrence River benthic communities to this invasion will help predict the mussel's impacts in riverine ecosystems that have not yet been extensively colonized. In this study, we tested the hypothesis that zebra mussel colonization alters the abundance and composition of macroinvertebrates on hard substrata. Specifically, we examined the effect of zebra mussels on macroinvertebrate community development in the St. Lawrence River using deployed substrata and field surveys and evaluated the relative importance of physical and biological attributes of mussel colonies in structuring these communities.

Methods

Artificial substrate experiment

Artificial substrata (plain cement bricks individually measuring $21.5 \times 11 \times 6.5$ cm) were used to (*i*) test whether zebra mussel beds have a significant effect on macroinvertebrate colonization and (*ii*) distinguish the relative importance of the physical structure of zebra mussel beds versus their biological characteristics in influencing macroinvertebrate abundance and composition on hard substrata. Clusters of byssally attached zebra mussels (collected from various sites in the St. Lawrence River and maintained in laboratory aquaria) were rinsed thoroughly to remove any epizoic animals and then allowed to attach to one broad (21.5×11 cm) surface of each of 10 bricks in aquaria; in some cases, the attachment was reinforced by the use of a thin nylon thread permanently tying the cluster to the brick. In this way, 10 bricks were covered with a layer of 128 ± 3.8 (mean $\pm$ SE) living zebra mussels (length 22.1 ± 0.6 mm). Ten additional bricks were similarly covered with a monolayer of 134 ± 3.5

intact, empty mussel shells of the same size range used in the previous treatment. For this treatment, individual mussels were eviscerated and the shells were dried at an ambient temperature of 20°C for several days; they were subsequently glued (using silicone aquarium sealant cured in air for 5 days) to one broad (21.5×11 cm) surface of each brick so as to mimic a living zebra mussel bed. In both treatments, >90% of this surface was covered by the zebra mussel layer, resulting in a net increase of ~60% of exposed surface area on the top face of the brick (assuming the bases of attached mussel shells to be uncolonizable surfaces). Thus, the first set of bricks (treatment 1) was intended to provide invertebrate colonizers with habitat structure (mussel shells), food (mussel biodeposits), and other advantages associated with a living mussel bed, while the second set of bricks (treatment 2) provided only habitat structure. Finally, 10 additional bricks were left bare to control for the effects of both treatments.

On May 19, 1995, the bricks were transported in buckets of water to a shallow (<2 m depth), protected littoral site on Lake St. Louis, an enlargement of the St. Lawrence River at Lachine, Que. Natural substrate at this site consisted of a dense layer of cobble on silty sand, and the local zebra mussel density was 451 ± 53 individuals/m^2 of rock surface. The 30 bricks were haphazardly deployed by a diver within an area of 10 m^2. They were placed on the cobble, with the zebra mussel cluster facing upward. After 9 weeks (on July 21, 1995), the bricks were located, carefully bagged underwater, and transported to the laboratory. All (20) of the treatment bricks and seven of the control bricks were recovered. Over 90% of zebra mussels on each of the bricks used for treatment 1 were still attached and alive at the time of recovery. Three bricks used for treatment 2 were found damaged (most of the mussel shells had become detached) and were therefore omitted from our analysis. Changes in zebra mussel numbers caused by larval settlement on the bricks during the experiment were negligible (<2% of original total). All macroinvertebrates were removed from the bricks using forceps and spray from a water bottle, washed onto a 500-µm sieve, and sorted. They were identified to at least their family level (generic level in most cases) following Merritt and Cummins (1984), Pennak (1989), and Thorp and Covich (1991). These taxa were subsequently assigned to their respective functional feeding groups (sensu Cummins 1973) based primarily on information provided by Merritt and Cummins (1984) and Thorp and Covich (1991), with the exception that all gastropods were placed within the same functional group (i.e., scrapers). The amphipod *Gammarus fasciatus* feeds on a range of food items but prefers fine particulate organic material (Delong et al. 1993) and therefore was classified as a deposit feeder.

The significance of the macroinvertebrate community response to experimental treatment was determined by multivariate analysis of variance (MANOVA) of abundance data (numbers of individuals per brick), which were $\log_{10}(x + 1)$ transformed to achieve normality and stabilize variance (Draper and Smith 1981). For individual taxa, the effects of different treatments were tested at the 0.05 level using Tukey's Studentized range test. Relationships between macroinvertebrate taxa and treatment were further analyzed by principal components analysis (PCA). The two factors that explained the most variance in the data were used as axes to ordinate the taxonomic groups that responded significantly to treatment. These and all other statistical analyses were done using SAS procedures (SAS Institute Inc. 1991).

Field survey

Macroinvertebrates were sampled at four sites that are part of the fluvial corridor of the upper St. Lawrence River (Fig. 1). Two sites were on Lake St. Louis: one was on a jetty at Lachine, Que., and the other was on the east shore of Ile Madore, an island at the confluence of the Ottawa and St. Lawrence rivers. The two remaining sites were located on the eastern end of the Soulanges Canal at Pointe-des-Cascades, Que., and on Lake St. François at Cornwall, Ont. Each of these four sites supported rich macroinvertebrate communities on

Fig. 1. Location of St. Lawrence River sampling sites (1, Lake St. Louis at Lachine; 2, Lake St. Louis at Ile Madore; 3, Soulanges Canal at Pte-des-Cascades; 4, Lake St. François at Cornwall).
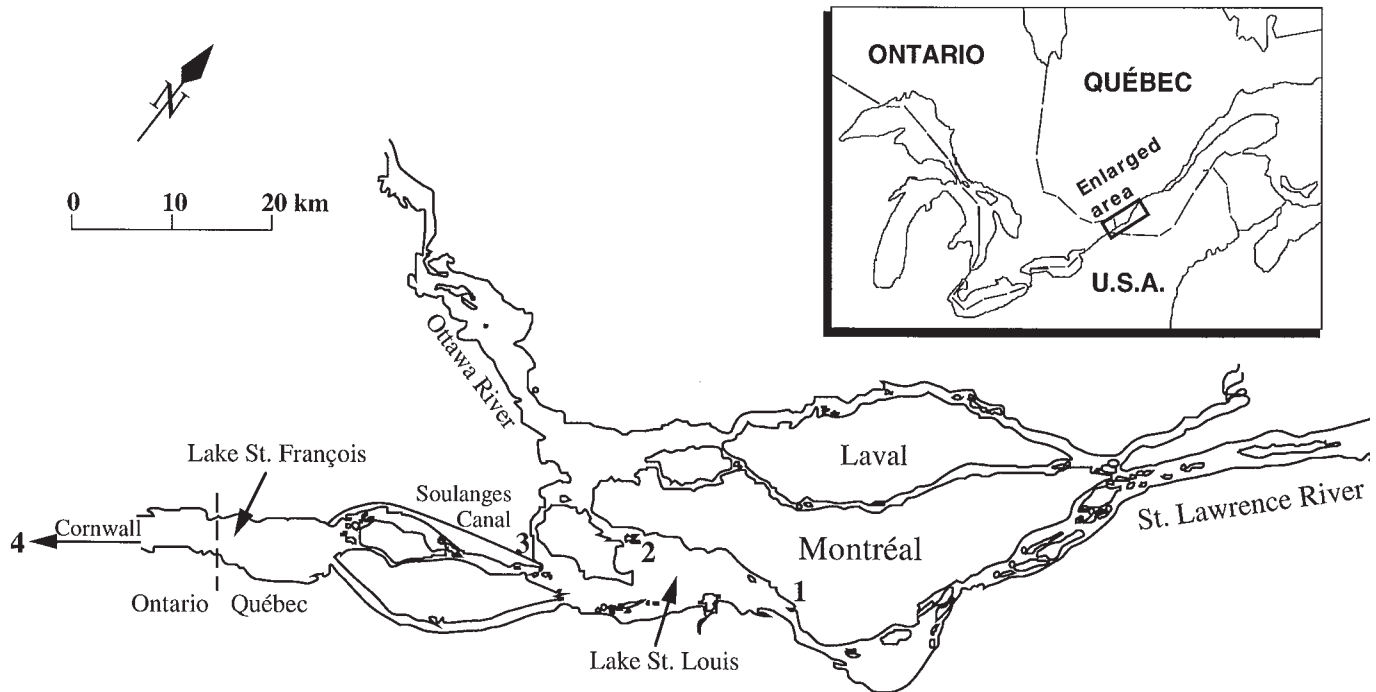
abundant cobble and was invaded by zebra mussels in 1990–1991 (A. Ricciardi, personal observations). We sampled each site in September 1992, when zebra mussel densities were relatively low, and resampled them in September 1994 (September 1995 for the Lachine site) following the develpment of dense zebra mussel populations in the river (Mellina and Rasmussen 1994; A. Ricciardi and F. Whoriskey, personal observations). On each sampling occasion, 10 stones were collected randomly from <2-m depths by wading or snorkeling (except at the Soulanges Canal, where they were collected from ~6 m depth by a SCUBA diver) within an area of 10 m^2 and placed in individual plastic buckets or enamel trays. The surface area of each stone was estimated from its three orthogonal dimensions (length, width, breadth) by an equation that determines the area of an ellipsoidal shape (Dall 1979):

(1)   Surface area $= \dfrac{\pi}{3}$ (length × width + length × breadth

$$+ \text{width} \times \text{breadth})$$

At each site, the mean surface area of stones did not vary by more than 3% between sampling occasions. The mean stone surface areas for Lachine, Ile Madore, Soulanges Canal, and Cornwall were 554, 381, 535, and 342 cm^2, respectively. All visible macroinvertebrates were removed from the stones with the aid of forceps, a bristle brush, and spray from a water bottle and were then washed onto a 500-µm sieve before being sorted and identified.

To construct a Great Lakes – St. Lawrence River data set that provided quantitative information on macroinvertebrate abundances (numbers per square metre of rock surface) before and after zebra mussel invasion, we combined our field data (Table 1) with literature data for Lake St. Clair (Griffiths 1993) and Lake Ontario (Stewart and Haynes 1994) (Table 2). Data from Wisenden and Bailey (1995) were not included in this synthesis because their experimental design (which involved the transfer of precolonized rocks between waterbodies) was not comparable with the other studies. The macroinvertebrate groups chosen a priori for analysis were three functional feeding groups (deposit feeders, scrapers, and predators) and four principal taxa (gammarid amphipods, chironomid larvae, snails, and turbellarian flatworms); these groups were chosen because they were well represented at each site in our data set before zebra mussels became abundant and are considered to be important components of epibenthic communities that have been altered by zebra mussel invasion (Dermott et al. 1993; Griffiths 1993; Stewart and Haynes 1994; Botts et al. 1996).

We tested the significance of observed changes in macroinvertebrate communities using a multivariate approach. Replicated data for St. Lawrence River sites were used to construct a robust PCA model describing macroinvertebrate community structure prior to the establishment of dense zebra mussel populations. Densities of functional or taxonomic groups sampled at the time when zebra mussel abundance was low (i.e., "before" data) for each St. Lawrence River site were normalized by $\log_{10}(x + 1)$ transformation and ordinated using PCA (SAS Institute Inc. 1991). The principal component (PC) that explained the most variance was used to generate scores from before (baseline) and "after" (post-invasion) data for each site (including Great Lakes sites; because raw replicated before data from the Great Lakes were unavailable to us, the St. Lawrence River model was applied to all sites). Each score represented a linear sum of the products of PCA loadings and macroinvertebrate densities. The differences between before and after site scores were then tested at the 0.05 level of significance using paired-comparison t tests. We excluded Ile Madore from this comparison, because it was the only site in our data set where zebra mussels did not settle in large numbers during our sampling period; the zebra mussel population density was only 73 individuals/m^2 in 1994, which is an order of magnitude lower than the lowest densities at which significant community changes associated with zebra mussel invasions have been reported. Differences between sites were not tested, as we were primarily interested in how macroinvertebrate community structure had changed over time in densely colonized areas of the Great Lakes – St. Lawrence River system. Bonferroni-corrected t tests were used on $\log_{10}$-transformed

Table 1. Macroinvertebrate densities on rocks at St. Lawrence River sites.

	Lake St. Louis, Lachine, Que.		Lake St. Louis, Ile Madore		Lake St. François, Cornwall, Ont.		Soulanges Canal, Pte-des-Cascades, Que.	
	1992	1995	1992	1994	1992	1994	1992	1994
Mollusca								
Bivalvia								
Dreissenidae	176 (22)	3876 (96)	6.8 (3.7)	73.0 (17.3)	82.7 (14.1)	1502 (157)	504 (48)	3185 (228)
Gastropoda								
Ancylidae	—	—	—	—	—	—	35.0 (11.1)	178.5 (30.0)
Hydrobiidae	23.7 (8.4)	406.6 (38.9)	—	—	—	—	—	—
Pleuroceridae	9.4 (6.4)	0	2.5 (1.7)	6.2 (3.4)	11.3 (5.9)	8.2 (5.7)	8.4 (3.1)	1.6 (1.6)
Bithyniidae	12.8 (5.1)	42.7 (11.1)	49.0 (11.1)	82.1 (22.3)	21.5 (6.8)	36.0 (11.7)	80.4 (15.1)	223.4 (34.2)
Valvatidae	0	28.1 (10.1)	—	—	—	—	—	—
Planorbidae	16.5 (5.1)	258.4 (29.0)	25.8 (10.1)	21.7 (9.0)	7.0 (5.3)	34.0 (14.3)	7.6 (4.9)	1.6 (1.6)
Physidae	—	—	12.0 (9.3)	57.8 (26.3)	12.0 (6.3)	19.9 (10.0)	4.1 (2.7)	48.9 (14.4)
Lymnaeidae	3.6 (2.4)	1.6 (1.6)	—	—	—	—	15.4 (6.9)	25.6 (5.2)
Crustacea								
Amphipoda	77.2 (19.9)	1634 (113)	11.4 (4.8)	16.3 (7.7)	62.3 (12.1)	642.5 (64.8)	176.5 (24.5)	1097 (131)
Isopoda	5.1 (2.9)	28.4 (9.5)	6.8 (3.7)	1.6 (1.6)	—	—	9.5 (4.6)	90.3 (22.2)
Insecta								
Trichoptera								
Helicopsychidae	—	—	48.4 (7.5)	91.4 (18.8)	41.0 (9.4)	54.0 (11.3)	—	—
Leptoceridae	26.3 (10.3)	113.4 (34.6)	11.4 (5.2)	22.8 (9.3)	15.2 (6.9)	41.4 (11.8)	—	—
Polycentropodidae	—	—	—	—	19.4 (5.9)	12.9 (6.8)	13.4 (4.0)	0
Ephemeroptera								
Heptageniidae	12.8 (4.7)	57.5 (15.7)	43.6 (9.3)	29.2 (9.1)	23.3 (8.7)	61.1 (15.4)	41.3 (13.2)	105.1 (20.5)
Baetidae	57.1 (18.3)	227.1 (35.4)	—	—	—	—	—	—
Coleoptera								
Psephenidae	—	—	29.7 (8.6)	15.5 (7.1)	—	—	—	—
Elmidae	—	—	9.5 (5.1)	26.1 (11.5)	—	—	—	—
Diptera								
Chironomidae	281 (31.2)	1946 (111)	20.0 (7.3)	27.9 (7.6)	53.7 (13.4)	431.1 (37.2)	195.5 (26.3)	696.1 (92.1)
Turbellaria								
	54.1 (9.1)	624.3 (22.4)	38.5 (11.1)	72.1 (19.6)	23.2 (5.7)	104.9 (24.9)	46.7 (12.4)	332.0 (43.3)
Annelida								
Hirudinea								
Glossiphoniidae	8.0 (3.4)	75.0 (18.2)	5.8 (4.4)	18.5 (15.2)	13.4 (4.8)	49.3 (15.4)	10.7 (38)	100.4 (22.7)
Erpobdellidae	—	—	—	—	1.7 (1.7)	5.0 (3.4)	—	—
Oligochaeta								
Naididae	22.4 (11.5)	310.5 (39.0)	—	—	4.3 (3.0)	71.9 (24.7)	45.5 (16.7)	263.4 (53.3)
Spongillidae								
	34.9 (18.5)	55.7 (18.9)	—	—	—	—	35.0 (18.2)	62.2 (29.3)
Ectoprocta								
Plumatellidae	371.2 (110)	54.4 (24.8)	—	—	—	—	—	—
Total no.[a]	610 (99.9)	5753 (315)	314.4 (38.3)	489.4 (41.5)	309.3 (47.6)	1572 (179)	690.0 (85.2)	3164 (396)

Note: Values are mean numbers of individuals/m^2 of substrate (for sponges and ectoprocts, values represent colony area in cm^2/m^2 of substrate), with standard errors in parentheses.

[a] Excluding *Dreissena*, sponges, and ectoprocts.

data to test changes in the densities of zebra mussels and associated macroinvertebrates.

Results

Artificial substrate experiment

In our artificial substrate experiment, macroinvertebrate numbers varied significantly among treatments (Wilks' $\lambda = 0.0045$, $p < 0.0001$). The mean total number of invertebrates (excluding zebra mussels) on bricks declined across the three treatment levels and was about fourfold higher in the presence of live mussels than on bare substrate (Fig. 2). Individual taxa that responded to treatment (F tests, $p < 0.05$) were ordinated along two PCs that cumulatively explained 75% (PC1 = 57.6%, PC2 = 17.3%) of the standardized variance (Fig. 3). The first principal component (PC1) apparently describes an organism's affinity for mussel beds (treatments 1 and 2) compared with bare substrate (control), reflecting the general trend shown in Fig. 2 (i.e., live mussels > dead shells >> control). Groups that loaded positively on this axis (i.e., deposit feeders

Table 2. Densities (mean no./m^2) of principal macroinvertebrate taxa and functional feeding groups at Great Lakes sites.
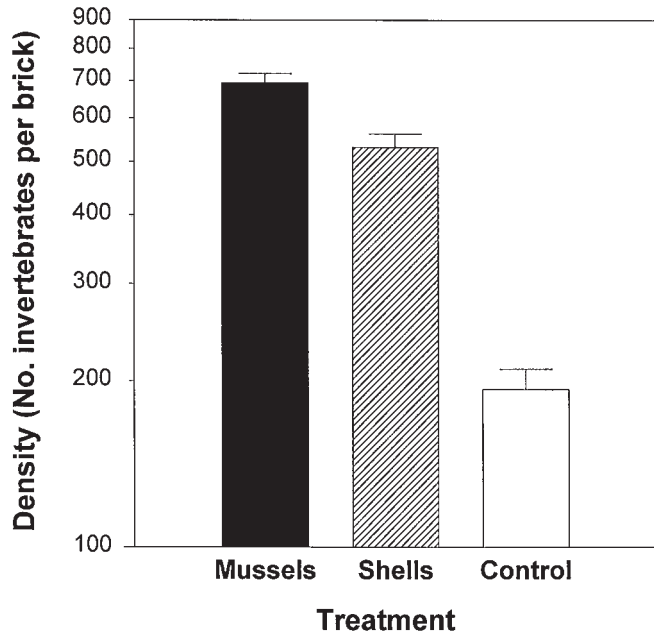
Site	*Dreissena*	*Gammarus*	Chironomids	Snails	Flatworms	Deposit feeders	Scrapers	Predators	Total[a]
				Lake St. Clair[b]					
May 1983	0	<1	280.0	20.0	<1	260.0	20.0	240.0	800.0
June 1991	20 520	400	360.0	340.0	300.0	5440.0	340.0	460.0	6500.0
				Lake Ontario[c]					
Cobble site									
Aug. 1983	0	357.8	6.0	48.1	12.0	391.5	55.3	23.7	531.0
Aug. 1992	20 773	2095.1	67.0	1311.1	29.3	3506.1	1313.4	69.5	4971.0
Reef site									
Aug. 1983	0	669.9	2.4	197.6	6.0	672.3	201.2	7.2	881.9
Aug. 1992	30 597	1524.4	12.1	363.3	25.6	1703.6	364.5	39.0	2115.8

[a] Excluding *Dreissena*.

[b] Data are from Griffiths (1993).

[c] Data are from Stewart and Haynes (1994
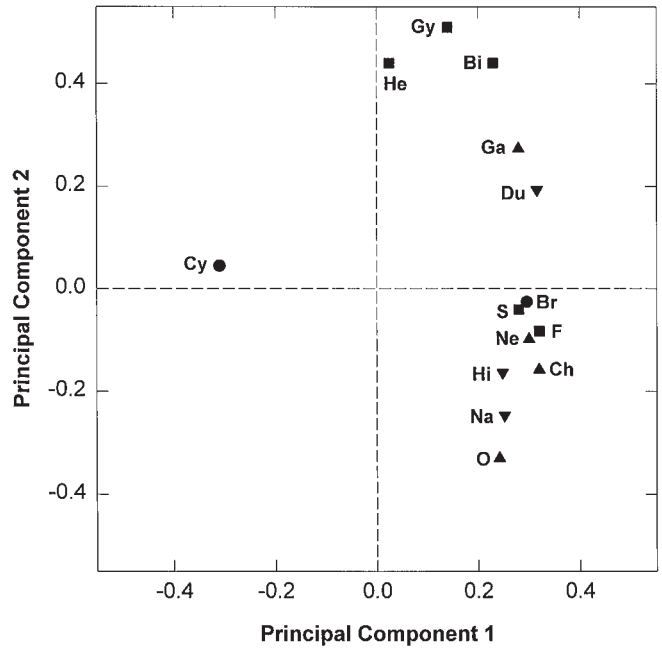
Fig. 2. Mean macroinvertebrate densities (± 1SE; excluding zebra mussels) after 9 weeks of colonization on experimental treatment bricks (with living mussels or with shells only) and control bricks.

Fig. 3. Ordination of macroinvertebrate groups that responded significantly to treatment in the artificial substrate experiment. The first two principal components are shown. We interpret principal component 1 as a reflection of macroinvertebrate response to mussel-covered substrata (treatments 1 and 2) versus controls and principal component 2 as a response to substrate covered with dead shells (treatment 2) versus living mussels (treatment 1) or controls. Data are coded according to their functional feeding group: scrapers (■), deposit feeders (▲), filterers (●), and predators (▼). He, *Helicopsyche* (caddisfly); Gy, *Gyraulus* (snail); Bi, *Birgella* (snail); F, *Ferrissia* (limpet); S, *Stenonema* (mayfly); Ga, *Gammarus* (amphipod); Ne, *Nectopsyche* (caddisfly); Ch, chironomids; O, ostracods; Cy, *Cyrnellus* (caddisfly); Br, *Brachycentrus* (caddisfly); Du, *Dugesia* (flatworm); Hi, leeches; Na, naidid oligochaetes (primarily *Chaetogaster*).

and predators) colonized bricks with living zebra mussels in substantially greater densities than on control bricks (Fig. 4). *Gammarus* differed from other deposit feeders (Fig. 5) by responding only to mussel structure (aggregated shells of living or dead mussels). Predators (e.g., leeches, flatworms, and *Chaetogaster*) and commensal organisms (e.g., *Brachycentrus*) were found on live mussels in greater numbers than on dead shells or bare substrate (Fig. 5). Conversely, the large filter-feeding caddisfly *Cyrnellus* loaded negatively on the PC1 axis (Fig. 3).

The second principal component (PC2) appears to describe an organism's preference for surfaces with dead shells (treatment 2) compared with living mussel beds or bare substrate. The weak positive response by *Cyrnellus* on PC2, coupled with its strong negative response on PC1, indicates an aversion to surfaces covered with living mussels and an indifference

towards dead mussel shells (Fig. 5). Most scrapers (i.e., *Helicopsyche, Gyraulus, Birgella*) loaded positively on PC2. *Helicopsyche*'s preference for surfaces with dead shells and indifference toward living mussels (Fig. 5) is refected by its

Fig. 4. Mean density (±1 SE) of functional feeding groups on treatment bricks in the artificial substrate experiment. Bars having different letters above them differ significantly (Tukey's range test).
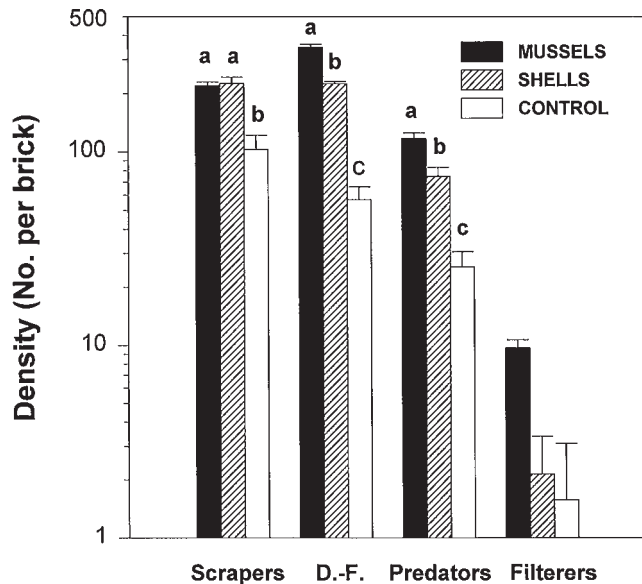
strong positive score on PC2 and its trivial score on PC1 (Fig. 3). By contrast, deposit-feeding chironomids and ostracods were enhanced in the presence of living mussels, but did not respond to dead shells, and therefore scored negatively on PC2. The treatment response of these organisms was mirrored by their predators (Fig. 5).

In summary, almost all taxa increased in abundance on substrata covered with mussels (living or dead), and most achieved higher densities in the presence of living mussels compared with dead shells.

Field survey

Zebra mussel densities on rocks at St. Lawrence River study sites increased 14-fold, on average, over the 2–3 year period between sampling dates (Fig. 6). At every site, densities of associated macroinvertebrates increased by 1.6 to 8.4 times initial values. The smallest increase in macroinvertebrate density was observed at Ile Madore, which had the smallest zebra mussel population (73 individuals/m^2); at all other sites, macroinvertebrate density increased at least fivefold. Paired comparisons of PCA site scores for communities sampled before and after the establishment of dense zebra mussel populations at Great Lakes – St. Lawrence River sites indicate that macroinvertebrate community structure was altered substantially ($t = 8.68$, $p < 0.0003$, using taxonomic group data and a PC that accounted for 80% of the variance; $t = 5.37$, $p < 0.003$, using functional group data and a PC that accounted for 77% of the variance). The direction and magnitude of changes in dominant functional feeding groups (Fig. 7) and taxonomic groups (Fig. 8) were similar among the three St. Lawrence River sites, where final dreissenid densities were ~1500–3900 mussels/m^2, and agreed with the results of our artificial substrate experiment.

Following the establishment of dense zebra mussel populations, deposit-feeding organisms (e.g., amphipod and isopod crustaceans, chironomid larvae) dominated benthic assemblages

at Great Lakes and St. Lawrence River sites. Populations of *G. fasciatus* increased dramatically, particularly in Lake St. Louis at Lachine, where their density multiplied by a factor of 20 between 1992 and 1995. Turbellarian flatworms and small gastropods also became highly abundant at most sites (Tables 1 and 2).

Only a few taxa responded negatively to zebra mussel colonization at St. Lawrence River sites. In the Soulanges Canal, larvae of the polycentropodid caddisfly *Cyrnellus* sp. were eliminated from rocks that became densely covered with zebra mussels. Large pleurocerid snails (*Elimia livescens*) declined at each of the three mussel-infested St. Lawrence River sites; they were virtually eliminated at the Lachine and Soulanges Canal sites, although smaller gastropods (hydrobiids, physids, limpets, etc.) increased substantially (Table 1). The plumatellid bryozoan *Plumatella fungosa*, which historically dominated cobble at the Lachine site, was reduced to a few small colonies on zebra mussel shells and on surrounding substrate; areal coverage by this species declined by 85%. By contrast, areal coverage by sponges (*Eunapius fragilis* and *Ephydatia muelleri*), which became abundant on mussel shells in 1994–1995, did not change significantly (Table 1).

Discussion

Comparison of field and experimental studies

Our findings strongly support the view that dense zebra mussel populations have a profound impact on the structure of macroinvertebrate communities on hard substrata, as claimed in earlier studies (e.g., Dusoge 1966; Griffiths 1993; Dermott et al. 1993; Stewart and Haynes 1994). Parallel changes in macroinvertebrate abundance and composition at Great Lakes and St. Lawrence River sites suggest that habitat differences had less influence on community structure than the presence of dense zebra mussel beds. These changes were characterized by multifold increases in macroinvertebrate densities, and the development of mussel bed communities dominated by *Gammarus*, turbellarian flatworms, and chironomid larvae.

The results of our before and after field comparisons and artificial substrate experiment were remarkably similar. The direction and magnitude of the change in abundance of deposit feeders, predators, and scrapers on rocks at Great Lakes – St. Lawrence River sites mirrors observed differences in community structure on bricks with and without zebra mussels. After 9 weeks, the treatment bricks developed mussel-associated communities that were remarkably similar to those observed at the Great Lakes – St. Lawrence River sites 4 years after colonization by zebra mussels. The mean density of living zebra mussels on the treatment bricks (1450 individuals/m^2) was 50% lower than the mean density on stones at our St. Lawrence River sites in 1994–1995 (2854 mussels/m^2). Zebra mussel densities in the St. Lawrence River were ~10-fold lower than those observed at the Great Lakes sites, yet resulted in similar changes to the macroinvertebrate community, which suggests that these changes may be better correlated with zebra mussel biomass or that they may be provoked by moderate zebra mussel densities. The zebra mussel density at Ile Madore (73 mussels/m^2) was evidently insufficient to cause significant community changes like those that occurred at the other St. Lawrence River sites. However, the

2602

Can. J. Fish. Aquat. Sci. Vol. 54, 1997

Fig. 5. Mean density (±1 SE) of invertebrates (sorted by functional feeding group) on treatment bricks in the artificial substrate experiment. He, *Helicopsyche*; Gy, *Gyraulus*; Bi, *Birgella*; F, *Ferrissia*; S, *Stenonema*; Ga, *Gammarus*; Ne, *Nectopsyche*; Ch, chironomids; O, ostracods; Cy, *Cyrnellus*; Br, *Brachycentrus*; Du, *Dugesia* (flatworm); Hi, leeches; Na, naidid oligochaetes (primarily *Chaetogaster*).
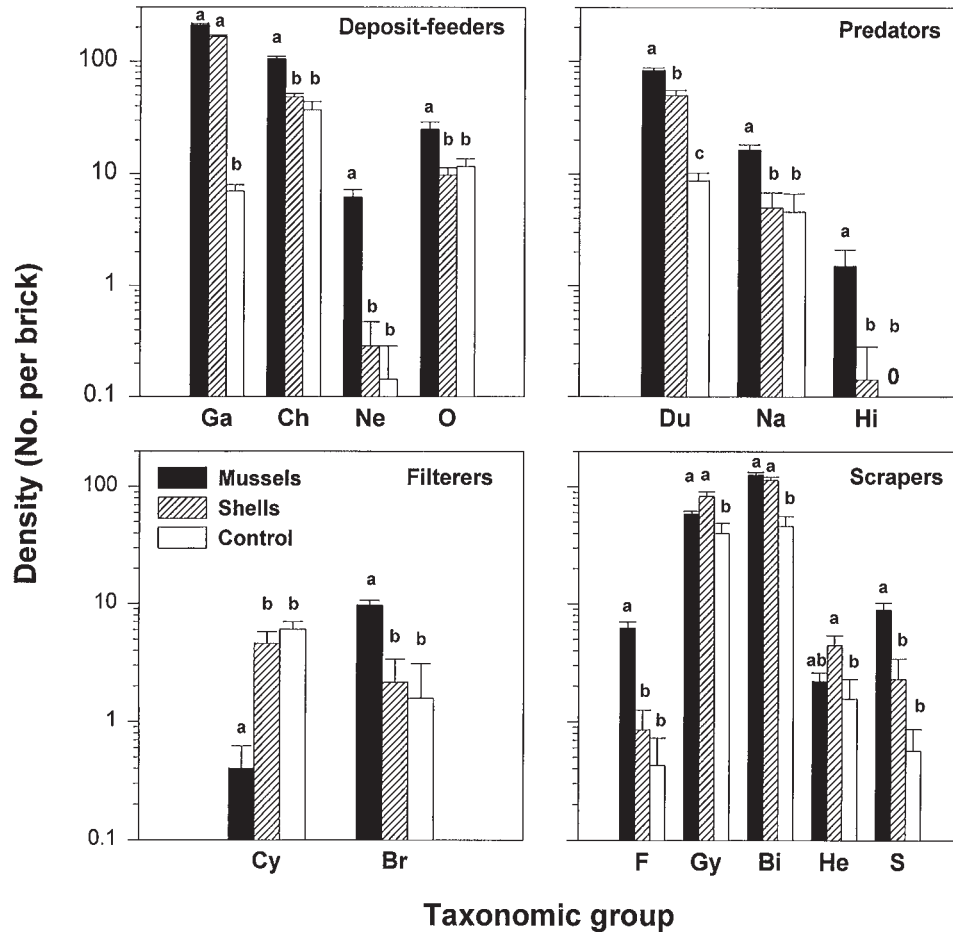
range of densities at which significant changes were observed (e.g., 1500–4000 mussels/m^2) are likely to occur in most lakes and rivers in North America (Strayer 1991; Ramcharan et al. 1992; Mellina and Rasmussen 1994).

Characteristics of zebra mussel aggregations that influence invertebrate response

Zebra mussels have a suite of physical and biological attributes that may influence the structure of their macroinvertebrate assemblages. Through efficient filtration, zebra mussel populations can remove large amounts of particulate organic matter from the water column and deposit these on sediments as agglutinated mussel feces and pseudofeces (Izvekova and Lvova-Katchanova 1972; Stanczykowska and Planter 1985). Mussel biodeposits are a nutrient-rich and easily assimilated food source (Izvekova and Lvova-Katchanova 1972), and the organic enrichment of substrata by mussel biodeposition can alter the local distribution and abundance of benthic invertebrates (Sephton et al. 1980). Zebra mussel biodeposition is assumed responsible for increased abundances of deposit-feeding chironomids and oligochaetes in Lake St. Clair (Griffiths 1993) and in European lakes (Lyakhnovich et al. 1982; Smit et al. 1993). In our field survey, we found 5- to 10-fold increases in abundances of deposit feeders at the St. Lawrence

River sites where dense (>1500 mussels/m^2) zebra mussel populations became established (Fig. 7). However, our artificial substrate experiment suggests that this response was provoked by both physical and biological attributes of zebra mussels.

Mussel beds increase the surface area and spatial heterogeneity of benthic substrata, thereby creating habitat for a diverse group of associated organisms (Suchanek 1979, 1986; Jacobi 1987; Seed 1996). Spatially complex surfaces tend to support richer faunal communities (e.g., Abele 1974; Hart 1978; Minshall 1984; O'Connor 1991), presumably because they provide a greater number of niches and resources. Clumped mussels have an abundance of interstitial spaces that may serve as refugia from disturbance and predation for small organisms (Gosselin and Chia 1995), a role played by other biological substrata (e.g., Brock 1979; Gillinsky 1984; Ban and Nelson 1987; Holmlund et al. 1990; Matsumasa 1994). These spaces also trap sediments and biodeposits (Jacobi 1987; Yager et al. 1993), thus benefiting deposit-feeding organisms. The interaction between interstitial habitat and sedimentation makes it difficult to determine the primary mechanism(s) by which mussel beds enhance populations of associated fauna. Slepnev et al. (1994) found that invertebrate colonization was three times higher in the presence of living

Fig. 6. Mean density (±1 SE) of zebra mussels (*Dreissena*) and associated macroinvertebrates on stones at St. Lawrence River sites. *, $p < 0.005$.
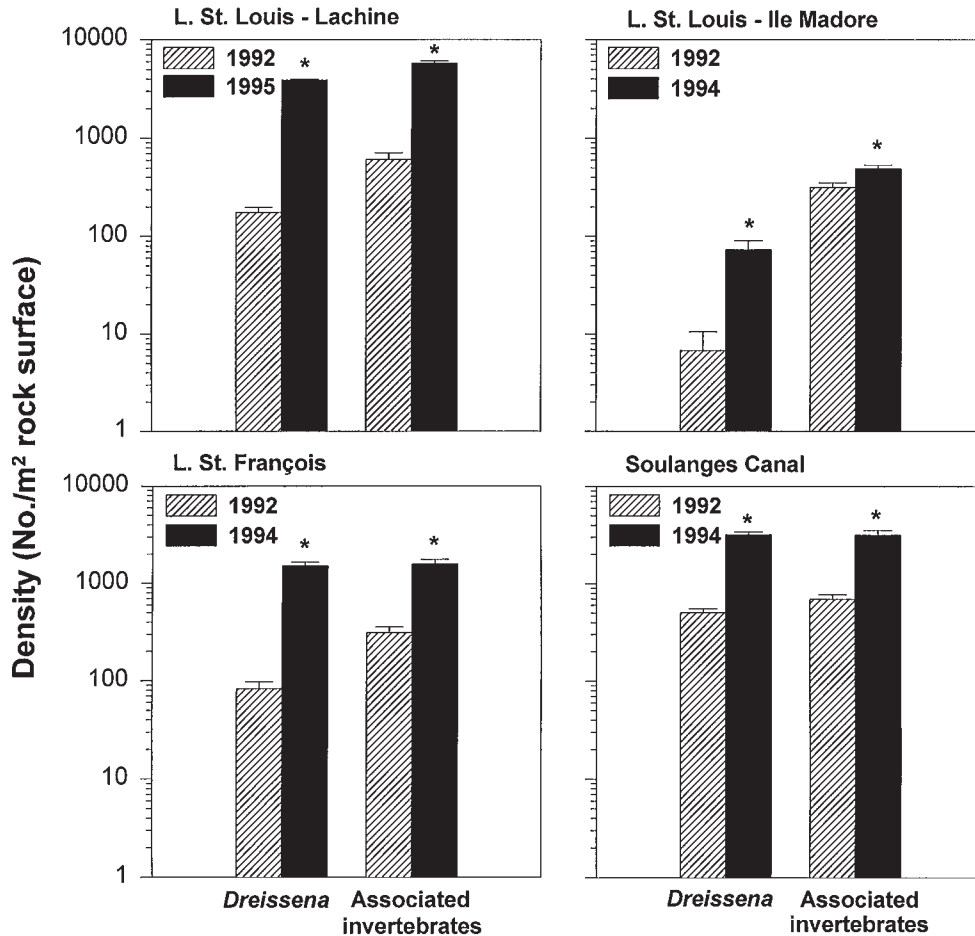
zebra mussels than in the presence of rubber models; they attributed this difference to both the accumulation of biodeposits among living mussels and the more complex spatial structure of natural mussel aggregations. However, Suchanek (1979) showed that artificial mussel beds contained faunal communities virtually identical to those of real *Mytilus* beds. The PCA of data from our artificial substrate experiment (Fig. 3) indicated that although general trends exist, taxa within the same functional feeding group responded differently to treatment, suggesting that they responded to more than just a trophic effect. For several taxa, the effect of mussel structure on abundance was stronger than the various biotic effects associated with living mussels (Figs. 4 and 5). Therefore, although biological attributes of living zebra mussels played significant roles, we believe that the enhancement of substrate complexity by zebra mussel beds was generally the most important factor controlling the changes in macroinvertebrate composition and abundance at our St. Lawrence River sites.

Several previous studies have documented an increased abundance of gammarid amphipods on substrata densely colonized by zebra mussels (Protasov and Afanasyev 1990; Dermott et al. 1993; Griffiths 1993; Stewart and Haynes 1994; Wisenden and Bailey 1995; Botts et al. 1996). Our analysis of field data confirms a general multifold increase in *G. fasciatus* densities coinciding with the development of dense zebra

mussel populations in the Great Lakes – St. Lawrence River system. The results of our artificial substrate experiment suggest that this increase is a response to enhanced substrate complexity, which is consistent with published observations that *Gammarus* preferentially colonizes interstitial habitat (Gee 1982; Olyslager and Williams 1993).

Zebra mussels may colonize soft substrata by settling on "seed" surfaces, i.e., individual shells or stones that serve as foci for aggregations of byssally attached mussels (Hunter and Bailey 1992). These aggregations act as islands of firm substrate for epifauna such as hydroids, sponges, bryozoans, turbellarians, gastropods, and leeches, in habitats where hard substrata are scarce (Maslowski 1992; Smit et al. 1995; Botts et al. 1996). However, the dense colonization of mussel-covered bricks by a rich macroinvertebrate community in the presence of abundant bare cobble at our experimental site, coupled with a density enhancement (~400%; Fig. 2) that is disproportionate with the net increase in surface area created by mussel beds (~60%), suggests that zebra mussels provide additional advantages for epibenthic animals.

Filtration currents generated by zebra mussels may be exploited by small organisms such as young sponge colonies and filter-feeding caddisfly larvae (e.g., *Brachycentrus*), which normally attach themselves to the posterior margins of the mussel shell in close proximity to the siphons (A. Ricciardi, personal observation). A similar commensal relationship

2604

Can. J. Fish. Aquat. Sci. Vol. 54, 1997

Fig. 7. Mean density (±1 SE) of functional feeding groups on stones at St. Lawrence River sites. Scr, Scrapers; Dep, deposit feeders; Pre, predators. *, $p < 0.05$.
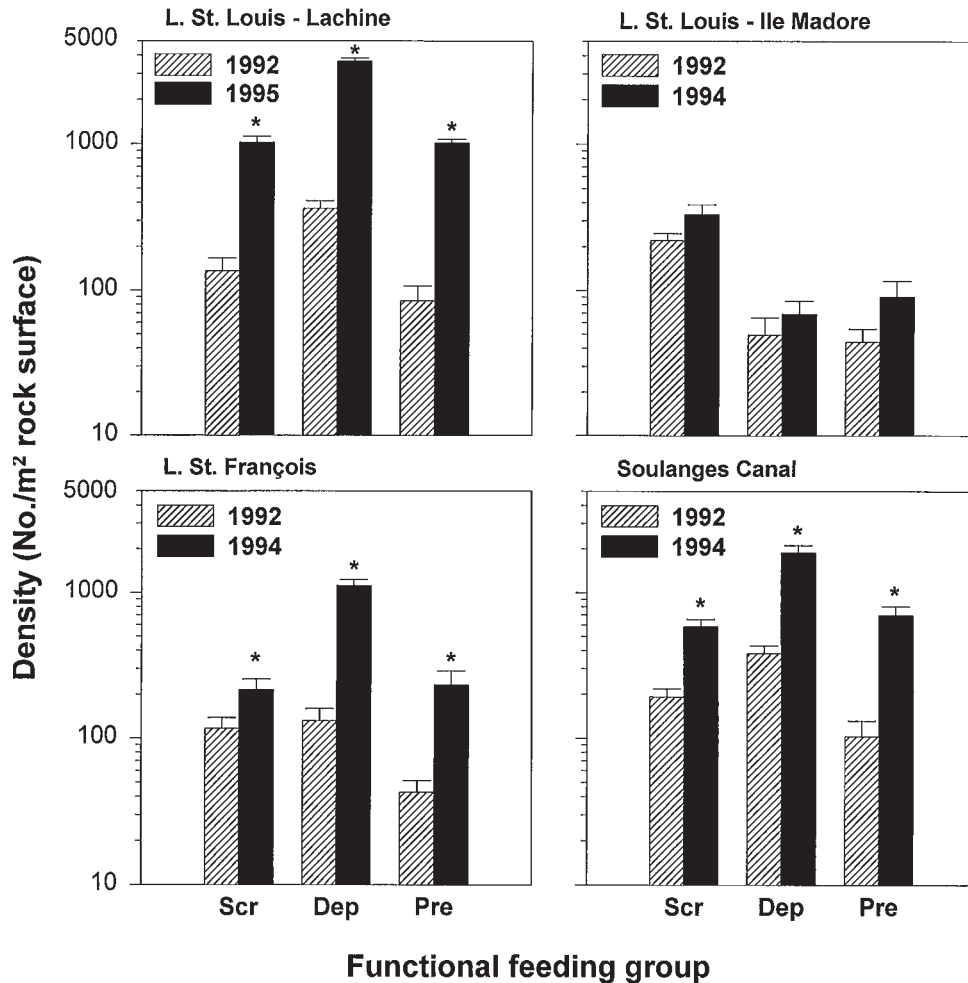

involving blue mussels (*Mytilus edulis*) and barnacles (*Balanus improvisus*) has been documented; barnacles tend to attach to the siphonal regions of mussels, and those that attach to living mussels grow faster than those on empty shells (Laihonen and Furman 1986). *Brachycentrus* larvae orient themselves so that the anterior opening of their case is exposed to the zebra mussel's filtration current; in this position, the larvae appear capable of scavenging incoming food partices. Their preference for living zebra mussels as attachment sites was clearly demonstrated in our artificial substrate experiment (Fig. 5). Furthermore, *Brachycentrus* larvae have densely colonized zebra mussel beds in sections of the St. Lawrence River where they were historically absent (Conn and Conn 1993; D.B. Conn, University of Sewanee, Sewanee, Tenn., personal communication). Sponges are also common epibionts of zebra mussels in the St. Lawrence River (Ricciardi et al. 1995*b*), but their aerial coverage of hard substrata does not appear to be affected by dense zebra mussel colonization (Table 1).

Another organism commensally associated with zebra mussels in our artificial substrate experiment and field studies was the limpet *Ferrissia rivularis* (Ancylidae). Densities of *Ferrissia* in the Soulanges Canal increased fivefold between 1992 and 1994 (Table 1) and were more abundant on zebra mussel

shells than on surrounding substrate. Conn and Conn (1993) also found *F. rivularis* occurring in large numbers on zebra mussel beds. *Ferrissia* may benefit from grazing on mussel shell surfaces, which are often covered with attached diatoms (A. Ricciardi, personal observation), the preferred food item for limpets (Thorp and Covich 1991). Because limpets appear to have higher oxygen requirements than most other gastropods (Pennak 1989), they may also benefit from being in close proximity to currents generated by mussel siphons. In our substrate experiment, *Ferrissia* colonized living mussels in larger numbers than either dead mussel shells or bare substrate. By contrast, other scrapers (i.e., *Helicopsyche, Birgella, Gyraulus*) did not differentiate between living and dead mussels, but colonized mussel-covered bricks more densely than bare bricks (Figs. 3 and 5). The depuration of nutrients (N, P) from living and dead zebra mussel shells (Stanczykowska and Planter 1985) could conceivably stimulate periphyton growth and thus attract scrapers.

Zebra mussels may also enhance local invertebrate abundance by acting as prey (e.g., for leeches), or as hosts for parasites and internal commensals. Leeches, particularly glossiphoniids, are common in zebra mussel aggregations (this study; Lewandowski 1976; Griffiths 1993; Dermott et al. 1993; Stewart and Haynes 1994) and may prey on zebra

Fig. 8. Mean density (±1 SE) of principal invertebrate taxa at St. Lawrence River sites. Gam, *Gammarus*; Chir, chironomids; Turb, turbellarian flatworms; Gast, snails and limpets. *, $p < 0.05$.
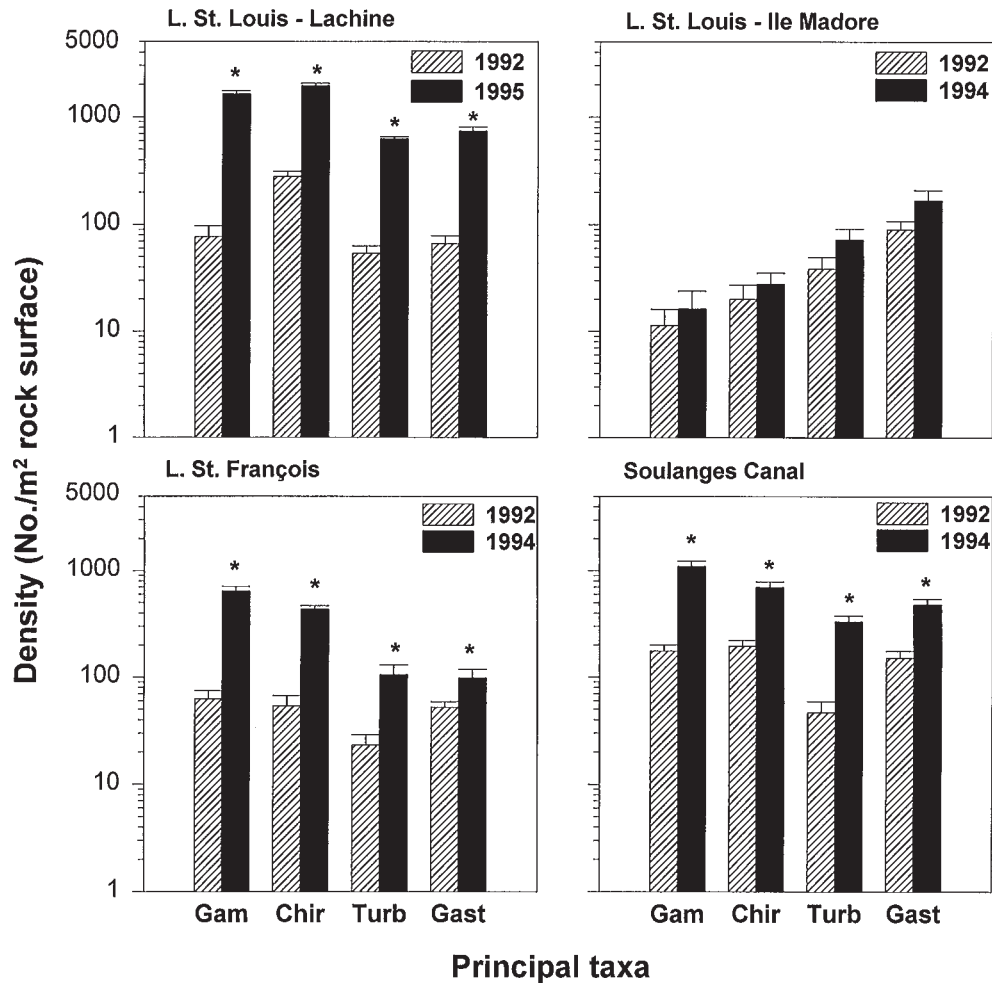
mussels (Smit et al. 1993) or their associated invertebrates (Pennak 1989). The predatory oligochaete *Chaetogaster limnaei* is a facultative parasite of zebra mussels (Conn et al. 1996) and may also be abundant in zebra mussel beds (this study; Piesik 1983; Stewart and Haynes 1994). Larval chironomids of *Paratanytarsus* sp. live commensally in the mantle cavity of zebra mussels, where they are provided with food (in the form of pseudofeces and mucus secretions) and spatial refuge (Ricciardi 1994).

Negative responses to zebra mussels

Contrary to most previous studies (Griffiths 1993; Dermott et al. 1993; Stewart and Haynes 1994), our results suggest that dense coverage of hard surfaces by zebra mussels may reduce or displace certain species. Large net-spinning caddisfly larvae (Polycentropodidae) declined after the establishment of zebra mussel populations at our field sites (Table 1) and avoided substrata covered by living zebra mussels in our artificial substrate experiment (Fig. 5). Competition for food and space limits the distribution and abundance of net-spinning caddisflies on stones (Lancaster et al. 1990; Hemphill 1988). We believe that these larvae cannot exploit zebra mussel filtration currents as can smaller caddisflies (e.g., *Brachycentrus*). Large net-spinning caddisflies are territorial and space themselves to

avoid receiving water previously filtered by their neighbors (A. Ricciardi, personal observation; Hemphill 1988). Zebra mussels may compete with polycentropodid caddisflies for optimal positions on substrate, and their filtration activity may produce local flow patterns that interfere with polycentropodid feeding (cf. Johnson 1990).

The decline of the ectoproct bryozoan *Plumatella fungosa* at our Lachine site is unusual given that this species was abundant at this site in previous years (Ricciardi and Reiswig 1994; A. Ricciardi, personal observation) and that plumatellids can use zebra mussels as substrate (e.g., Maslowski 1992). However, because *P. fungosa* builds massive spreading colonies on smooth surfaces in the St. Lawrence River (A. Ricciardi, personal observation), its growth may be limited by the small cavities and discontinuous shell surfaces of clumped mussels. Competition with zebra mussels for local particulates may have also occurred. Conversely, the decline may have been caused by a factor unrelated to zebra mussels, such as a change in water quality (see Ricciardi and Reiswig 1994, and references therein).

The displacement of large snails (i.e., individuals comparable in size with zebra mussels) from substrata densely colonized by zebra mussels has been reported previously (Dusoge 1966; Wisenden and Bailey 1995). Gizinski and Wolnomiejski

2606

Can. J. Fish. Aquat. Sci. Vol. 54, 1997

(1982) noted a reduction in native molluscs coinciding with the development of shoals of zebra mussels in a Polish reservoir but did not speculate on mechanisms linking the two events. Although zebra mussels may negatively impact large gastropods by fouling their shells (Tucker 1994), mussels rarely attached to snails at our study sites and probably did not reduce their abundance through increased mortality. Large snails may be inefficient at grazing on interstitial surfaces and thus may have been outcompeted for food and space by smaller gastropods (cf. Harman 1968). We suggest that the alteration of hard substrata by zebra mussel aggregations increases the abundance of snails but limits their mean size, analogous to the effect that marine mussel beds have on gastropods (Jacobi 1987; Griffiths et al. 1992). However, in littoral areas of lakes invaded by zebra mussels, gastropods of all sizes could increase in abundance outside of mussel beds in response to higher benthic algal growth resulting from the enhanced light penetration and nutrient deposition associated with zebra mussel filtration activity (Griffiths 1993; Stewart and Haynes 1994).

Implications for food webs

We expect that higher abundances of *Gammarus*, chironomids, and small gastropods will increase prey availability for benthivorous fishes such as yellow perch (*Perca flavescens*), which feed preferentially on these organisms (Boisclair and Leggett 1989). Examination of the digestive tracts of yellow perch and rock bass (*Ambloplites rupestris*) from the Soulanges Canal at Pointe-des-Cascades, Que., has shown that these fish consumed proportionally more *Gammarus* in the summer of 1995 than in previous years (A. Ricciardi, unpublished data). Moreover, a European study found that the production of benthivorous fish in a lake doubled within 6 years following zebra mussel invasion; this was attributed to both direct predation by fish on zebra mussels and indirect predation on mussel-associated organisms (Karataev and Burlakova 1995). Based on the assumption that mussel biodeposits stimulate *Gammarus* production, Bruner et al. (1994) hypothesized that zebra mussels increase the bioaccumulation of organic contaminants through aquatic food chains (e.g., seston – mussel feces – *Gammarus* – fish – bird). However, their assumption is not supported by the results of our study (Fig. 5) and Botts et al. (1996), both of which suggest that gammarid populations are enhanced by habitat structure rather than mussel biodeposits. It remains to be tested whether gammarids or other deposit feeders that live in zebra mussel beds have higher contaminant concentrations than those living outside of mussel beds.

Conclusions

Our findings indicate that zebra mussel invasions cause rapid transformations of epilithic communities into assemblages dominated by zebra mussels, amphipods, chironomids, flatworms, and small gastropods. Data suggest that larger fauna adapted to smooth substrate (e.g., pleurocerid snails, certain net-spinning caddisflies and bryozoans) may be reduced or eliminated by dense zebra mussel colonization. A number of physical and biological characteristics of mussel beds (e.g., accumulations of biodeposits; filtration currents) may contribute to these changes, but an important factor is the formation of an

interstitial shell matrix that provides refuge, traps sediment, and enhances substrate complexity. Multifold increases in the abundance of mussel-associated fauna may occur at zebra mussel densities as low as 1500 individuals/m^2 within a few years of invasion. Given that most lakes and rivers on this continent are physically and chemically suitable for the establishment of these mussel densities (Ramcharan et al. 1992; Mellina and Rasmussen 1994), we predict widespread restructuring of North American freshwater benthic communities and food webs as the zebra mussel continues to invade new drainages.

Acknowledgements

References

Abdel-Razek, F.A., Chiba, K., Kurokura, H., Okamoto, K., and Hirano, R. 1993. Distribution of *Limnoperna fortunei kikuchii* in Shonai Inlet, Lake Hamana. Suisan Zoshoku, **41**: 89–95.

Abele, L.G. 1974. Species diversity of decapod crustaceans in marine habitats. Ecology, **55**: 156–161.

Ban, S.M., and Nelson, W.G. 1987. Role of *Diopatra cuprea* Bosc (Polychaeta: Onuphidae) tubes in structuring a subtropical infaunal community. Bull. Mar. Sci. **40**: 11–21.

Boisclair, D., and Leggett, W.C. 1989. Among-population variability of fish growth: II. Influence of prey type. Can. J. Fish. Aquat. Sci. **46**: 468–482.

Botts, P.S., Patterson, B.A., and Schloesser, D.W. 1996. Zebra mussel effects on benthic invertebrates: physical or biotic? J. N. Am. Benthol. Soc. **15**: 179–184.

Brock, R.E. 1979. An experimental study of the effects of grazing by parrotfishes and role of refuges in benthic community structure. Mar. Biol. **51**: 381–388.

Bruner, K.A., Fisher, S.W., and Landrum, P.F. 1994. The role of the zebra mussel, *Dreissena polymorpha*, in contaminant cycling: II. Zebra mussel contaminant accumulation from algae and suspended particles, and transfer to the benthic invertebrate, *Gammarus fasciatus*. J. Great Lakes Res. **20**: 735–750.

Burlakova, L. 1995. The relationship between *Dreissena polymorpha* and other benthic animals. *In* Proceedings of the 5th International Zebra Mussel and Other Aquatic Nuisance Organisms Conference. Ontario Hydro, Toronto, Ont. pp. 23–29.

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 3rd International Zebra Mussel Conference. *Edited by* J.L. Tsou. Electric Power Research Institute, Palo Alto, Calif. pp. 223–234.

Conn, D.B., Ricciardi, A., Babapulle, M.N., Klein, K.A., and Rosen, D.A. 1996. *Chaetogaster limnaei* (Annelida: Oligochaeta) as a parasite of the zebra mussel *Dreissena polymorpha* and the quagga mussel *Dreissena bugensis* (Mollusca: Bivalvia). Parasitol. Res. **82**: 1–7.

Cooley, J.M. 1991. Zebra mussels. J. Great Lakes Res. **17**: 1–2.

Cummins, K.W. 1973. Trophic relations of aquatic insects. Annu. Rev. Entomol. **18**: 183–206.

Dall, P.C. 1979. A sampling technique for littoral stone dwelling organisms. Oikos, **33**: 106–112.

Delong, M.D., Summers, R.B., and Thorp, J.H. 1993. Influence of

food type on the growth of a riverine amphipod, *Gammarus fasciatus*. Can. J. Fish. Aquat. Sci. **50**: 1891–1896.

Dermott, R., Mitchell, J., Murray, I., and Fear, E. 1993. Biomass and production of zebra mussels (*Dreissena polymorpha*) in shallow waters of northeastern Lake Erie. *In* Zebra mussels: biology, impacts, and control. *Edited by* T.F. Nalepa and D.W. Schloesser. Lewis Publishers, Boca Raton, Fla. pp. 399–413.

Draper, N.R., and Smith, H. 1981. Applied regression analysis. J. Wiley, New York.

Dusoge, K. 1966. Composition and interrelations between macrofauna living on stones in the littoral of Mikolajskie Lake. Ekol. Pol. Ser. A, **14**: 755–762.

Gee, J.H.R. 1982. Resource utilization by *Gammarus pulex* (Amphipoda) in a Cotswold stream: a microdistribution study. J. Anim. Ecol. **51**: 817–832.

Gillinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology, **65**: 455–468.

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.

Gizinski, A., and Wolnomiejski, N. 1982. Zoobenthos of Koronowo Dam reservoir in its 10th and 15th year of existence. Acta Univ. Nicolai Copernici Pr. Limnol. **13**: 35–50.

Gosselin, L.A, and Chia, F.S. 1995. Distribution and dispersal of early juenile snails: effectiveness of intertidal microhabitats as refuges and food sources. Mar. Ecol. Prog. Ser. **128**: 213–223.

Griffiths, C.L., Hockey, P.A.R., van Erkom Schurink, C., and Le Roux, P.J. 1992. Marine invasive aliens on South African shores: implications for community structure and trophic functioning. S. Afr. J. Mar. Sci. **12**: 713–722.

Griffiths, R.W. 1993. Effects of zebra mussels (*Dreissena polymorpha*) on the benthic fauna of Lake St. Clair. *In* Zebra mussels: biology, impacts, and control. *Edited by* T.F. Nalepa and D.W. Schloesser. Lewis Publishers, Boca Raton, Fla. pp. 414–437.

Harman, W.N. 1968. Interspecific competition between *Bithynia* and pleurocerids. Nautilus, **81**: 77–83.

Hart, D.D. 1978. Diversity in stream insects: regulation by rock size and microspatial complexity. Verh. Int. Ver. Theor. Angew. Limnol. No. 20. pp. 1376–1381.

Hebert, P.D.N., Muncaster, B.W., and Mackie, G.L. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. Can. J. Fish. Aquat. Sci. **46**: 1587–1591.

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.

Hemphill, N. 1988. Competition between two stream dwelling filter-feeders, *Hydropsyche oslari* and *Simulium virgatum*. Oecologia, **77**: 73–80.

Hockey, P.A.R., and van Erkom Schurink, C. 1992. The invasive biology of the mussel *Mytilus galloprovincialis* on the southern African coast. Trans. R. Soc. S. Afr. **48**: 123–139.

Holmlund, M.B., Peterson, C.H., and Hay, M.E. 1990. Does algal morphology affect amphipod susceptibility to fish predation? J. Exp. Mar. Biol. Ecol. **139**: 65–83.

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.

Izvekova, E.I., and Lvova-Katchanova, A.A. 1972. Sedimentation of suspended matter by *Dreissena polymorpha* Pallas and its subsequent utilization by Chironomidae larvae. Pol. Arch. Hydrobiol. **19**: 203–210.

Jacobi, C.M. 1987. The invertebrate fauna associated with intertidal beds of the brown mussel *Perna perna* (L.) from Santos, Brazil. Stud. Neotrop. Fauna Environ. **22**: 37–72.

Johnson, A.S. 1990. Flow around phoronids: consequences of a neighbor to suspension-feeders. Limnol. Oceanogr. **35**: 1395–1401.

Karataev, A.Y., and Burlakova, L.E. 1995. The role of *Dreissena* in lake ecosystems. Russian J. Ecol. (Engl. Transl. Ekol.), **26**: 207–211.

Laihonen, P., and Furman, E.R. 1986. The site of attachment indicates commensalism between blue mussel and its epibiont. Oecologia, **71**: 38–40.

Lancaster, J., Hildrew, A.G., and Townsend, C.R. 1990. Competition for space by predators in streams: field experiments on a net-spinning caddisfly. Freshwater Biol. **20**: 185–193.

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

Lintas, C., and Seed, R. 1994. Spatial variation in the fauna associated with *Mytilus edulis* on a wave-exposed rocky shore. J. Molluscan Stud. **60**: 165–174.

Ludyanskiy, M.L., McDonald, D., and MacNeill, D. 1993. Impact of the zebra mussel, a bivalve invader. BioScience, **43**: 533–544.

Lyakhnovich, U.P., Gavrilov, S.I., Karataev, A.Y., Karataeva, I.V., and Myakhaeva, T.I. 1982. Long-term changes in the macrobenthos of the Lukoml'skoe Lake. Vyestsi Akad. Navuk. BSSR Syer. Biyal. Navak, 1982: 91–93. (Translated from Russian by New York Sea Grant Extension, Brockport, NY.)

Maslowski, J. 1992. Bottom macrofauna of the Szczecin Lagoon (north-western Poland). Acta Hydrobiol. **34**: 253–274.

Matsumasa, M. 1994. Effect of secondary substrate on associated small crustaceans in a brackish lagoon. J. Exp. Mar. Biol. Ecol. **176**: 245–256.

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.

Merritt, R.W., and Cummins, K.W. 1984. An introduction to the aquatic insects of North America. 2nd ed. Kendall-Hunt, Dubuque, Iowa.

Minshall, G.W. 1984. Aquatic insect–substratum relationships. *In* The ecology of aquatic insects. *Edited by* V.H. Resh and D.M. Rosenberg. Praeger Publishers, New York. pp. 358–400.

O'Connor, N.A. 1991. The effects of habitat complexity on macroinvertebrate colonization of wood substrates in a lowland stream. Oecologia, **85**: 504–512.

Olyslager, N.J., and Williams, D.D. 1993. Microhabitat selection by the lotic amphipod *Gammarus pseudolimnaeus* Bousfield: mechanisms for evaluating local substrate and current suitability. Can. J. Zool. **71**: 2401–2409.

Ong Che, R.G., and Morton, B. 1992. Structure and seasonal variations in abundance of the macro-invertebrate community associated with *Septifer virgatus* (Bivalvia: Mytilidae) at Cape d'Aguilar, Hong Kong. Asian Mar. Biol. **9**: 217–233.

Paine, R.T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia, **15**: 93–120.

Pennak, R.W. 1989. Fresh-water invertebrates of the United States. Protozoa to Mollusca. 3rd ed. John Wiley & Sons, New York.

Piesik, Z. 1983. Biology of *Dreissena polymorpha* (Pall.) settling on stylon nets and the role of this mollusc in eliminating the seston and the nutrients from the water-course. Pol. Arch. Hydrobiol. **30**: 353–361.

Protasov, A.A., and Afanasyev, S.A. 1990. Principal types of *Dreissena* communities in periphyton. Hydrobiol. J. **26**(5): 15–23.

Ramcharan, C.W., Padilla, D.K., and Dodson, S.I. 1992. Models to predict potential occurrence and density of the zebra mussel, *Dreissena polymorpha*. Can. J. Fish. Aquat. Sci. **49**: 2611–2620.

Rao, K.V., and Rao, K.H. 1975. Macro- and micro-faunal associates of the fouling dreissenid *Mytilopsis sallei* (Recluz) in the Visakhapatnam Harbour. Bull. Dep. Mar. Sci. No. 7. University of Cochin, Cochin, India. pp. 623–629.

2608

Can. J. Fish. Aquat. Sci. Vol. 54, 1997

Ricciardi, A. 1994. Occurrence of chironomid larvae (*Paratanytarsus* sp.) as commensals of dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*). Can. J. Zool. **72**: 1159–1162.

Ricciardi, A., and Reiswig, H.M. 1994. Taxonomy, distribution, and ecology of the freshwater bryozoans (Ectoprocta) of eastern Canada. Can. J. Zool. **72**: 339–359.

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

Ricciardi, A., Snyder, F.L., Kelch, D.O., and Reiswig, H.M. 1995*b*. Lethal and sublethal effects of sponge overgrowth on introduced dreissenid mussels in the Great Lakes – St. Lawrence River system. Can. J. Fish. Aquat. Sci. **52**: 2695–2703.

Ricciardi, A., Whoriskey, F.G., and Rasmussen, J.B. 1996. Impact of the *Dreissena* invasion on native unionid bivalves in the upper St. Lawrence River. Can. J. Fish. Aquat. Sci. **53**: 1434–1444.

SAS Institute Inc. 1991. SAS/STAT user's guide, release 6.03 edition. SAS Institute Inc., Cary, N.C.

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.

Sebestyen, O. 1937. Colonization of two new fauna-elements of Pontus-origin (*Dreissena polymorpha* Pall. and *Corophium curvispinum* G.O. Sars *forma devium* Wundsch) in Lake Balaton. Verh. Int. Ver. Theor. Angew. Limnol. No. 8. pp. 169–182.

Seed, R. 1996. Patterns of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. J. Mar. Biol. Assoc. U.K. **76**: 203–210.

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

Slepnev, A.Y., Protasov, A.A., and Videnina, Y.L. 1994. Development of a *Dreissena polymorpha* population under experimental conditions. Hydrobiol. J. **30**(1): 26–33.

Smit, H., bij de Vaate, A., Reeders, H.H., van Nes, E.H., and Noordhuis, R. 1993. Colonization, ecology, and positive aspects of zebra mussels (*Dreissena polymorpha*) in the Netherlands. *In* Zebra mussels: biology, impacts, and control. *Edited by* T.F. Nalepa and D.W. Schloesser. Lewis Publishers, Boca Raton, Fla. pp. 55–77.

Smit, H., Reinhold-Dudok Van Heel, H.C., and Wiersma, S.M. 1995. Sublittoral macrozoobenthic assemblages in the enclosed sediment-polluted Rhine–Meuse delta; their relationship to environmental conditions. Neth. J. Aquat. Ecol. **29**: 31–47.

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

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

Stewart, T.W., and Haynes, J.M. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena*. J. Great Lakes Res. **20**: 479–493.

Strayer, D.L. 1991. Projected distribution of the zebra mussel, *Dreissena polymorpha*, in North America. Can. J. Fish. Aquat. Sci. **48**: 1389–1395.

Suchanek, T.H. 1979. The *Mytilus californianus* community: studies on the composition, structure, organization and dynamics of a mussel bed. Ph.D. thesis, University of Washington, Seattle.

Suchanek, T.H. 1986. Mussels and their role in structuring rocky shore communities. *In* The ecology of rocky coasts. *Edited by* P.G. Moore and R. Seed. Columbia University Press, New York. pp. 70–96.

Thorp, J.H., and Covich, A.P. 1991. Ecology and classification of North American freshwater invertebrates. Academic Press, San Diego, Calif.

Tucker, J.K. 1994. Windrow formation of two snails (families Viviparidae and Pleuroceridae) colonized by the exotic zebra mussel, *Dreissena polymorpha*. J. Freshwater Ecol. **9**: 85–86.

Tsuchiya, M., and Nishihira, M. 1986. Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization. Mar. Ecol. Prog. Ser. **31**: 171–178.

Wiktor, J. 1969. The biology of *Dreissena polymorpha* (Pall.) and its ecological importance in the Firth of Szczecin. Stud. Mat. Morsk. Inst. Ryb. Gdynia Ser. A, **5**: 1–88.

Wisenden, P.A., and Bailey, R.C. 1995. Development of macroinvertebrate community structure associated with zebra mussel (*Dreissena polymorpha*) colonization of artificial substrates. Can. J. Zool. **73**: 1438–1443.

Yager, P.L., Nowell, A.R.M., and Jumars, P.A. 1993. Enhanced deposition to pits: a local food source for benthos. J. Mar. Res. **51**: 209–236.