

# Lethal and sublethal effects of sponge overgrowth on introduced dreissenid mussels in the Great Lakes – St. Lawrence River system

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**Abstract:** Freshwater sponges in the Great Lakes – St. Lawrence River system overgrow and kill introduced zebra (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*) on solid substrates. Sponges overgrow and smother mussel siphons, thereby interfering with normal feeding and respiration. We tested the significance of sponge-enhanced mussel mortality by repeated sampling at several sites where both organisms were abundant in the upper St. Lawrence River and on an artificial reef in central Lake Erie. A small proportion (<10%) of the dreissenid population at each site was overgrown by sponge. Mussel colonies that were completely overgrown for 1 or more months invariably contained a significantly greater proportion of dead mussels than local uncovered populations. Mussels that survived prolonged periods (4–6 months) of overgrowth suffered significant tissue weight losses. Laboratory experiments and field observations suggest that dreissenids are not able to colonize sponges; therefore, sponges should always dominate competitive overgrowth situations. The overall impact of sponges on dreissenid populations in the Great Lakes – St. Lawrence River system will probably be negligible because of the high rate of mussel recruitment and the environmental constraints on sponge growth; however, our results suggest that sponges may control mussel abundance locally.

**Résumé :** Dans le réseau du fleuve Saint-Laurent et des Grands Lacs, des éponges d'eau douce recouvrent et tuent les bivalves introduits que sont la moule zébrée (*Dreissena polymorpha*) et la moule couagga (*Dreissena bugensis*) sur des substrats solides. Les éponges recouvrent et obstruent les siphons des moules, nuisant ainsi à leur alimentation et à leur respiration. Nous avons mesuré l'importance de la mortalité des moules due aux éponges à l'aide d'échantillonnages répétés à plusieurs sites du fleuve Saint-Laurent et sur un récif artificiel du lac Érie, où ces deux organismes étaient abondants. Une petite proportion (moins de 10%) de la population de dreissenidés de chaque site était recouverte par les éponges. Les colonies de moules qui étaient complètement recouvertes pendant 1 ou plusieurs mois contenaient invariablement une proportion significativement plus élevée de moules mortes que les populations locales non recouvertes. Les moules qui ont survécu à des périodes de recouvrement prolongées (4–6 mois) présentaient des diminutions significatives de poids des tissus. Des expériences en laboratoire et des observations in situ suggèrent que les dreissenidés ne sont pas capables de coloniser les éponges; par conséquent, les éponges devraient toujours l'emporter dans les situations de compétition pour le recouvrement. L'impact global des éponges sur les populations de dreissenidés du réseau du fleuve Saint-Laurent et des Grands Lacs sera probablement négligeable à cause du fort taux de recrutement des moules et des contraintes environnementales limitant la croissance des éponges; toutefois, nos résultats suggèrent que les éponges pourraient limiter localement l'abondance des moules.

[Traduit par la Rédaction]

Received February 23, 1995. Accepted June 20, 1995.  
J12794

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## Introduction

It is well documented that competition for space significantly affects the abundance and distribution of sessile organisms in marine rocky intertidal habitats and reef environments (Connell 1961; Dayton 1971; Paine 1974; Jackson 1977; Russ 1982; Quinn 1982; Hirata 1987). By contrast, competitive interactions among organisms that occupy hard substrates in freshwater systems have only recently gained attention (e.g., McAuliffe 1984; Lancaster et al. 1988; Hemphill 1988; Dudley et al. 1990). Prior to the introduction of the European zebra mussel (*Dreissena polymorpha*) to the Great Lakes in the mid-1980s (Hebert et al. 1989), macrofouling organisms were not prominent and rarely had ecological or economic impacts in North American freshwater habitats (but see Tenney and Woolcott 1964; Frost 1978; Greenland et al. 1988). Zebra mussel are dominant competitors for space on hard substrates in the Great Lakes – St. Lawrence River system, where they occur in densities of up to  $10^3/\text{m}^2$  and are a significant component of the benthos (Leach 1993; Griffiths 1993; Dermott et al. 1993; A. Ricciardi, personal observations). A second species of *Dreissena* introduced to the Great Lakes – St. Lawrence River system, the quagga mussel (*Dreissena bugensis*), also contributes to dreissenid encrustation on solid surfaces, but to a much smaller degree because it is less abundant in shallow waters (Mills et al. 1993; Dermott and Munawar 1993).

Byssally attached dreissenid mussels compete for space on a wide variety of substrates, including the exposed shells of native unionid bivalves. Massive dreissenid encrustations kill unionids by smothering their siphons and preventing normal feeding and respiration (Haag et al. 1993) and may thus cause severe local reductions in unionid abundance and species richness (Gillis and Mackie 1994). Dreissenid mussel beds have altered the surficial structure of reefs that are used as spawning areas by sport fishes in the Great Lakes, but negative impacts on spawning have not been observed (Leach 1993). These mussel beds provide interstitial habitat and refugia for smaller invertebrates (Dermott et al. 1993; Griffiths 1993; Ricciardi 1994), but may displace other epibenthic fauna such as large grazing snails (Dusoge 1966) and net-spinning caddisfly larvae (A. Ricciardi, personal observations).

There are very few documented cases of spatial competition between the zebra mussel and other benthic fauna in which the mussel is outcompeted. Conn and Conn (1993) found a cluster of adult zebra mussels overgrown and killed by the bryozoan *Pectinatella magnifica* in a tributary of the St. Lawrence River, but this interaction has not yet been observed at other localities in the St. Lawrence where both species are common, despite intensive sampling (A. Ricciardi, personal observation). In Europe, the filter-feeding amphipod *Corophium curvispinum* builds muddy tubes that foul zebra mussel and render hard substrata unsuitable for their settling larvae; consequently, the invasion of the Rhine River by *C. curvispinum* has precipitated a substantial decline in the resident zebra mussel population (Van den Brink et al. 1991; Van der Velde et al. 1994). Sebestyen (1938) reported the rapid overgrowth and subsequent death of zebra mussel colonies by freshwater

sponges in Lake Balaton (Hungary), a competitive interaction similar to that which occurs between encrusting sponges and epifaunal bivalves in marine coastal habitats (Pequegnat 1964; Jackson 1977; Hirata 1987; Perera et al. 1990). These examples suggest that encrustation by dreissenids is not necessarily a terminal condition for hard substrata in freshwater habitats.

In this study, we report the first case of a native organism (freshwater sponge) consistently outcompeting *Dreissena* for solid substrate in North American aquatic habitats. To assess the potential for freshwater sponges to control dreissenid abundance, we examined the frequency and impact of sponge overgrowth on zebra and quagga mussels at selected sites in the Great Lakes – St. Lawrence River system. For the purposes of this study, we define overgrowth as sponge growth resulting in the complete occlusion of mussel siphons.

## Methods

Using self-contained underwater breathing apparatus (SCUBA), we examined substrates at a total of seven sites where both sponges and dreissenids were abundant. Six sites were located on the upper St. Lawrence River near the Island of Montréal: Lake St. Louis (45°26'N, 73°42'W), two sites on Lake St. François (outflow of the Raisin River, 45°10'N, 74°50'W, and a small bay at Les Cèdres, 45°18'N, 74°03'W), the Lachine Canal (45°26'N, 73°40'W), and two sections of the Soulanges Canal ("east" and "west," ca. 45°20'N, 73°58'W). The remaining site was an artificial concrete reef in the central basin of Lake Erie near Lorain, Ohio (41°28'N, 82°12'W). These were selected on the basis of preliminary observations of sponge overgrowth and previous surveys which showed that sponges and dreissenid mussels contributed substantially (sponges 5–60%, mussels >40%) to benthic invertebrate biomass at each site (unpublished data). To examine the frequency of occurrence of sponges on the shells of living dreissenids, random samples of 200 mussels were scraped from rocks at 1–2 m depths in Lake St. Louis and from the walls (at <2 m depths) of the Lachine Canal; these two sites had the highest sponge biomass per unit area among all St. Lawrence River sites.

To examine the effect of sponge overgrowth on mussel mortality, we collected samples from the St. Lawrence River sites (in conjunction with other studies) from May to October 1992–1994, by SCUBA and wading. Samples from the Lorain artificial reef in Lake Erie were collected in August and September of 1993 and 1994 at 6–8 m depths using SCUBA. At each site, dense sponge growths were probed and scraped with a knife to determine if they covered mussels. Sponge colonies were generally probed near their center, where colony growth was oldest and thickest. Sponge-covered mussels were brought to the surface, removed from the sponge, and examined for signs of vitality. The number of empty shells covered by sponge was recorded, whereas the remaining mussels were left undisturbed on an enamel tray for several seconds and watched for emersion response. Under most conditions, dreissenids gape slightly when emersed but will shut their valves quickly when disturbed (Ricciardi et al. 1995). If no

**Table 1.** Frequency of occurrence of freshwater sponges on dreissenid mussels ( $n = 200$ ) randomly collected from the Lachine Canal and Lake St. Louis.

Sponge species	Lachine Canal		Lake St. Louis	
	No.	%	No.	%
<i>Eunapius fragilis</i>	41	20.5	24	12
<i>Ephydatia muelleri</i>	23	11.5	4	2
<i>Spongilla lacustris</i>	11	5.5	3	1.5
<i>Heteromeyenia tubisperma</i>	—	—	1	0.5
<i>Trochospongilla horrida</i>	3	1.5	—	—
Proportion of mussels with one or more sponge epibionts	65	32.5	31	15.5

response was observed after several seconds, we attempted to lightly pry open the shells with a scalpel, and judged valve resistance to indicate whether the mussel was alive. Nonencrusted mussels in the vicinity of overgrown specimens were also collected. Using a Yates-corrected chi-square contingency test (Zar 1984), we compared the mortality (indicated by the proportion of dead mussels in a population) of dreissenids covered by sponge with that of uncovered dreissenids occupying the same substrate or similar local substrates. Sponge samples were preserved in 70% ethanol and later identified following Ricciardi and Reisinger (1993).

Sponge-covered mussels found alive in October 1994 in the Lachine Canal (the site where overgrowth was most extensive) were taken to the laboratory within 2 h of collection. Their tissues were removed with a scalpel, stored in a freezer at  $-20^{\circ}\text{C}$  for at least 24 h, and then dried for 48 h at  $-50^{\circ}\text{C}$  using a Labconco model 45 freeze drier; after drying, the tissues were weighed to the nearest milligram on an electronic balance. Dry tissue weights were similarly determined for a random sample of 30 uncovered (control) mussels occupying the same substrate as the sponge-covered mussels. Shell length – dry tissue weight ( $\log_{10}$  transformed) regressions were constructed for sponge-covered and control mussels, and these regression equations were compared by analysis of covariance (ANCOVA) using SAS procedures (SAS Institute Inc. 1988).

Mechanisms of sponge overgrowth were examined by repeated sampling over the spring, summer, and autumn of 1994 at particular sites in the St. Lawrence River, and by comparing images of mussel-covered substrate on the Lorain artificial reef between 1992 and 1993 using underwater VHS video operated by SCUBA divers.

Dreissenids colonize an immense variety of substrates, including soft substrates such as algal filaments, mud, silt, and sand (Kuchina 1964; Lyakhov and Mikheev 1964; Hunter and Bailey 1992; Maslowski 1992; Dermott and Munawar 1993; A. Ricciardi, personal observations). We thus, a priori, considered it likely that they may attach to, and subsequently overgrow, freshwater sponges. To investigate this possibility, we tested the tendency of dreissenids to attach byssally to sponges in the laboratory and in field

**Table 2.** Frequency of occurrence of sponges involved in overgrowth situations at Lake Erie and St. Lawrence River sites.

Sponge species	Frequency			
	By sample <sup>a</sup>		By site <sup>b</sup>	
	No.	%	No.	%
<i>Eunapius fragilis</i>	29/40	72.5	6/7	85.7
<i>Ephydatia muelleri</i>	6/40	15	1/7	14.3
<i>Spongilla lacustris</i>	5/40	12.5	2/7	28.6

<sup>a</sup>The number of sampled sponge colonies found overgrowing mussels.

<sup>b</sup>The number of sites in which these samples were collected.

situations. In the laboratory, three sponge colonies (each approximately 80 cm<sup>2</sup> in area and 1–2 cm in thickness) and an assortment of alternative substrates (limestone rocks and unionid shells) were placed in each of three 32-L aquaria with aerated water maintained at an ambient laboratory temperature of 20°C. Colonies of the sponges *Ephydatia muelleri*, *Spongilla lacustris*, and *Eunapius fragilis* were scraped from the walls of the Lachine Canal and transported in plastic bags to the laboratory for these experiments. Zebra mussels belonging to three age-classes (determined from length–frequency distributions of summer populations in the Lachine Canal) were carefully placed on each sponge; each sponge thus served as initial substrate for three young-of-the-year mussels (5–10 mm length), three 1-year-old mussels (15–20 mm length), and one 2-year-old mussel (25–29 mm length). Similar mixtures of mussels were placed on the other objects in the aquaria, and acted as controls. The aquaria were inspected every day for up to a week to determine if the mussels had attached to the sponges or translocated to new substrates. The sponge colonies remained intact and healthy for the duration of these experiments. A similar series of experiments using quagga mussels was run simultaneously.

## Results and discussion

### Frequency of sponge growth on dreissenids

Five of the seven species of freshwater sponge known to occur in the Great Lakes – St. Lawrence River system (Gee 1937; Lukaszewicz 1978; Ricciardi and Reisinger 1993) were found growing on the shells of living zebra and quagga mussels collected in this study. The majority of these species were found at Lake St. Louis and the Lachine Canal (Table 1), where sponges covered up to 25 and 55%, respectively, of available hard substrate at 0–2 m depths. By contrast, only three species (*Eunapius fragilis*, *Ephydatia muelleri*, and *Spongilla lacustris*) were involved in overgrowth situations; these were the only species among the seven found to produce massive, spreading colonies (often larger than 1 cm thickness and 100 cm<sup>2</sup> area) that completely covered the largest mussels. *Eunapius fragilis* occurred more frequently on dreissenids (Table 1), and was involved in more overgrowth situations (Table 2), than any other species.

**Table 3.** Mean percentages of dead mussels in sponge-covered and control (uncovered) populations in the Great Lakes – St. Lawrence River system.

Site	Dead mussels				Chi-square
	Sponge-covered		Control		
	%	No.	%	No.	
Lachine Canal	57.4	39/68	6.3	5/80	43.5
Lake St. Louis	75.8	75/99	17.3	14/81	58.6
Soulanges Canal					
East site	75.0	27/36	13.8	11/80	39.5
West site	61.1	22/36	15.0	3/20	9.27
Lake St. François					
Raisin River outflow	82.4	14/17	6.7	2/30	24.4
Les Cèdres	100	11/11	0	0/16	23.0
Lake Erie (Lorain reef)	39.1	9/23	2.5	1/40	12.1

Note: All chi-square statistics are significant ( $p < 0.0005$ ).

We observed sponge overgrowth of dreissenid mussels on stones, cobbles, pier pilings, wood timbers, concrete walls, unionid shells, and macrophytes (*Elodea canadensis* and *Myriophyllum spicatum*). In the upper St. Lawrence River, dreissenids were overgrown as early as May (at water temperatures near 10°C) and remained covered for up to 6 months; sponges subsequently degenerated in late autumn. Overgrowth occurred by two mechanisms: (i) rapidly spreading sponge colonies grew laterally from adjacent substrate onto byssally attached zebra mussels, and (ii) conspecific sponge larvae settled on dreissenid shells and established pioneer colonies that grew over the mussel individually, or by fusing with other colonies to rapidly form a confluent mat over the mussel. In either case, certain sponge colonies produced an adherent patch of gemmules (overwintering structures) in the autumn that formed a new colony on the mussel in the following year. Mussels (if they survived) were thus subject to annual overgrowth from successive generations of sponge. The first mechanism of overgrowth was observed at all sites, whereas the second mechanism was observed primarily in areas where mussel coverage of the substrate was extensive (e.g., Soulanges Canal and Lake Erie). A comparison of substrate images made over a 2-year period using underwater video showed larval-derived sponges (primarily *Eunapius fragilis*) spreading and forming confluent patches over zebra mussel beds on the Lorain reef in Lake Erie. This type of overgrowth probably also occurred in Lake Balaton, where sponges colonized dense zebra mussel beds soon after the mussel became established in the lake (Sebestyen 1938). Dreissenid mussels apparently have no mechanism to prevent fouling overgrowth, but their high recruitment rate (Sprung 1990), tendency to aggregate in large numbers (Wiktor 1963; Stanczykowska 1977), and ability to exploit a wide range of substrata (Stanczykowska 1977; A. Ricciardi, personal observations), appears to give them a compensatory advantage in spatial competition. While overgrowth by sponge was observed at each of our sites, only a small proportion of the dreissenid population (<10% at all sites) was affected. At some sites, however, a

larger proportion of the population (e.g., 33% at the Lachine Canal; Table 1) bore sponge tissues or gemmules on their shells; thus, the potential for overgrowth at these sites was higher than what was observed during our study.

#### Lethal effects of overgrowth

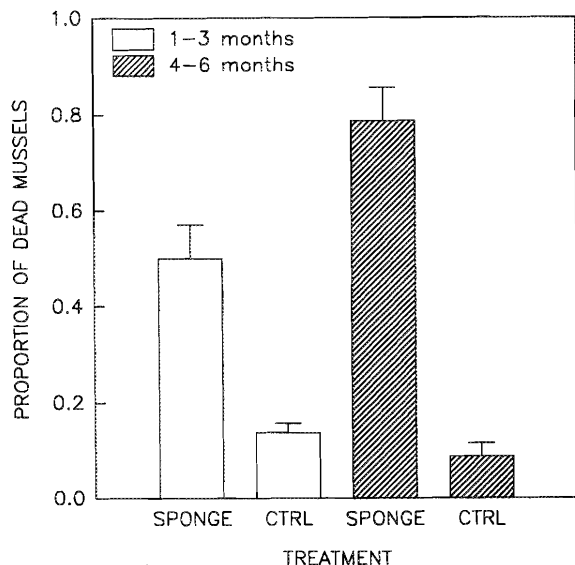
At every site, dreissenid colonies that had been overgrown by sponges for 1 or more months contained a higher proportion of dead mussels than the local uncovered population (Table 3). The proportion of dead mussels in colonies overgrown for 4–6 months was higher than in colonies overgrown for 1–3 months (chi-square test,  $p < 0.005$ ). From 38.5 to 61.1% (mean 49.9%) of sponge-covered (overgrown) mussels were dead after 1–3 months, whereas 39.1–100% (mean 78.7%) were dead after 4–6 months (Fig. 1). Of a total of 290 sponge-covered mussels examined in this study, 197 (67.9%) were found dead. Shell lengths ( $\log_{10}$  transformed) of living and dead mussels overgrown by sponge were not significantly different ( $t$  test,  $p > 0.05$ ), nor was there a difference between proportions of dead zebra mussels and dead quaggas (chi-square test,  $p > 0.20$ ).

The large percentage of dead mussels found overgrown by sponges on substrate otherwise covered with clusters of healthy zebra mussels is compelling evidence of enhanced mortality. We considered that, if most dead shells immediately fall away from their substrates, the encapsulation of mussels by sponges may bias the mortality of overgrown mussels relative to uncovered mussel populations over time by retaining shells long after the mussels have died. However, our observations suggest that this is not a factor because dead shells usually remain bound by the byssal threads of neighbouring mussels within a cluster. Furthermore, we could easily distinguish recently dead mussels by their shell integrity and the quality of the periostracum.

#### Sublethal effects of overgrowth: tissue degrowth

We hypothesized that prolonged overgrowth would result in tissue weight loss because of metabolic stress. We therefore compared the dry tissue weights of mussels covered by

**Fig. 1.** Proportion of dead mussels (with standard error bars) in sponge-covered (SPONGE) populations versus neighbouring uncovered (CTRL) populations, after 1–3 and 4–6 months of overgrowth, respectively.



sponge for approximately 5 months with those of uncovered (control) mussels in the Lachine Canal (Fig. 2). The relationship between dry tissue weight (DTW, in milligrams) and shell length ( $L$ , in millimetres) was described by the following allometric exponential equations for sponge-covered (eq. 1) and control mussels (eq. 2), respectively:

$$[1] \quad \text{DTW} = 0.00611 \times L^{2.809}$$

$$R^2 = 0.903, p < 0.0001, N = 16$$

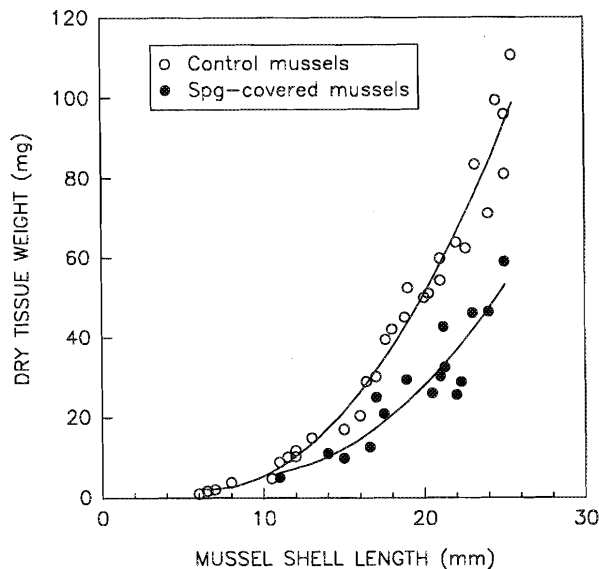
$$[2] \quad \text{DTW} = 0.00597 \times L^{3.011}$$

$$R^2 = 0.988, p < 0.0001, N = 30$$

These two classes of mussels had different dry weight – shell length relationships (ANCOVA using  $\log_{10}$  transformations of both equations,  $F = 112.2$ ,  $p < 0.0001$ ). Sponge-covered mussels (eq. 1) had lower tissue weights per unit shell length than control mussels (eq. 2), suggesting that they suffered nutritional stress as a result of overgrowth. The mean percent weight loss for these mussels was 43%.

Weight losses in zebra mussels have previously been attributed to, among other causes, intraspecific competition. Zebra mussels from high-density populations in lakes tend to have a lower dry tissue weight per unit shell length than mussels from low-density populations (Stanczykowska 1979; Nalepa et al. 1993). It seems likely that interference competition from other suspension feeders would produce a similar effect. Furthermore, because sponges filter particles as small as bacteria (Frost 1980a), sponge overgrowth may negatively affect mussel fecundity by limiting food availability to the mussels (Sprung and Borcharding 1991; Borcharding 1995). Sponge overgrowth may also physically interfere with gamete release. These effects may have a greater impact on local mussel densities than mortality, and deserve further study.

**Fig. 2.** Relationships between dry tissue weight and shell length for sponge-covered and control mussels from the Lachine Canal. See text for regression equations.



#### Can dreissenids overgrow sponges?

Zebra and quagga mussels placed on sponge colonies in laboratory aquaria failed to lay down byssal threads, even after several days, although greater than 90% of the mussels on other objects in the aquaria were byssally attached. Furthermore, a substantial proportion (38–48%) of zebra mussels (primarily young-of-the-year mussels) moved from the sponges to relocate and attach onto other substrates (Table 4). Similarly, dreissenids were never found overgrowing or attached to sponges at any of our field sites, even though densely packed mussel clusters were occasionally found immediately adjacent to, or in peripheral contact with, large encrusting sponge colonies. Similar avoidance of sponges by dreissenids has been observed in southern Lake Michigan (T. Lauer, Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907, personal communication), Lake Ontario (R. Serrouya, Department of Natural Resource Sciences, McGill University, Montréal, QC H9X 1V9, personal communication), Lake St. Clair (R.W. Griffiths, Ontario Ministry of Environment and Energy, London, ON N6E 1V3, personal communication), and western Lake Erie (Nalepa and Schloesser 1993, plate 18). Indeed, freshwater sponges are apparently immune to overgrowth or extensive fouling even from common epibenthic organisms such as bryozoans, net-spinning caddisfly larvae, and filamentous algae (Frost 1976; A. Ricciardi, personal observations). Similarly, marine sponges have a low susceptibility to fouling, and this has been attributed to the secretion of inhibitory toxins (Goodbody 1961; Green 1977; Proksch 1994). For these reasons, we hypothesize that dreissenids cannot colonize sponges. Therefore, to the extent that competitive ability is indicated by the capacity of a species to overgrow or to resist overgrowth by other species (Russ 1982), overgrowth competition in freshwater communities should always favor the sponge.

**Table 4.** Results of experiments that tested dreissenid attachment to sponges; 21 mussels were placed on sponges in each of three aquaria and examined for attachment every day for 7 days.

	Duration of experiment		
	1 day	3 days	7 days
No. of zebra mussels remaining on sponges	19±0.6	13±0.6	12.3±0.7
No. of zebra mussels attached to sponges	0	0	0
No. of quagga mussels remaining on sponges	21	20.3±0.7	20.3±0.7
No. of quagga mussels attached to sponges	0	0	0

Note: Values are given as the mean ± standard error.

Overgrowth is considered to be an evolved response by sponges to spatial competition, where fast-growing species overgrow, and often suffocate, their slower growing neighbours (Ruetzler 1970; Jackson 1977; Russ 1982). Freshwater sponges have previously been observed to cover 40–60% of available hard substrate (Rader and Winget 1985; Pronzato and Manconi 1991; A. Ricciardi, personal observations), and overgrow and kill bryozoans (Bushnell 1966; Frost 1991; Ricciardi and Reiswig 1994). Encrusting marine sponges overgrow and kill a wide variety of epifaunal invertebrates, including bivalves (Pequegnat 1964; Jackson 1977; Hirata 1987; Perera et al. 1990), and are successful competitors for space in rocky intertidal and reef habitats (Jackson 1977; Russ 1982; Quinn 1982; Nandakumar et al. 1993). This competitive ability may have been a characteristic of freshwater sponges that was previously inconspicuous in the absence of a significant macrofouling competitor like the zebra mussel. Both freshwater and marine intertidal sponges are successful competitors for space on hard substrates because they exhibit indeterminate growth that allows continuous lateral substrate expansion without requiring intervening stages of sexual reproduction and larval settlement, and because they are relatively insusceptible to fouling and overgrowth by other organisms (Jackson 1977; Frost 1991). The freshwater sponge *Eunapius fragilis*, which is common in large lakes and rivers throughout North America (Frost 1991; Ricciardi and Reiswig 1993), is a superior competitor for space because of its rapid growth, massive colony size, and adherent gemmules that effectively conserve substrate (including mussel shell space) after sponge dieback in the autumn. Simultaneous hatching of *Eunapius fragilis* gemmules at low water temperatures (4–5°C; Fell 1990), followed by tissue fusion and subsequent rapid growth, produces a large sponge colony early in the spring, before dreissenid spawning and larval settlement have occurred (Stanczykowska 1977). Attached gemmules also insure successive annual generations of *Eunapius fragilis* colonies on mussel shells and other hard substrates (Ricciardi and Reiswig 1993).

#### Can sponge overgrowth limit dreissenid abundance?

Although Stanczykowska (1977) found no evidence that competing organisms limit *Dreissena* abundance in Polish lakes, there are examples of the zebra mussel encountering significant competition for substrate in other European

habitats. The recent range expansion of the tube-dwelling amphipod *Corophium curvispinum* has apparently caused a severe reduction in dreissenid densities in the lower Rhine River (Van der Velde et al. 1994). *Corophium curvispinum* builds a fouling mass of mud tubes on hard substrate, including dreissenid shells, resulting in overgrowth effects similar to those caused by sponges. Sebestyen (1938) described the rapid overgrowth of young-of-the-year and adult zebra mussels by freshwater sponges (*Eunapius fragilis* and *Eunapius carteri*); she also provided photographs of dead mussels embedded in sponge colonies. Similarly, Arndt (1937) described the overgrowth of dreissenids by freshwater sponges (*Ochridaspongia rotunda*) at 30–40 m depths in Lake Ochrid; although Arndt found living and dead mussels embedded in the sponge, he did not comment on the effects of overgrowth. Our results indicate that overgrowth by sponges results in tissue degrowth and increased local mortality of dreissenids. However, intolerance to siltation tends to restrict competitive sponge growth to vertical, overhanging, and cryptic surfaces (Bakus 1968; Jackson 1977). Therefore, sponge growth is rarely sufficient to displace organisms beyond a local scale; this is reflected by the small proportion of dreissenids that were overgrown by sponges at each of our sites. Consequently, sponges are unlikely to have a significant impact on the total dreissenid biomass within most lakes or river systems, but they may control dreissenids in local habitats that support prolific sponge growth. Our observations suggest that freshwater sponges, like their marine relatives, grow prolifically on vertical surfaces and therefore may affect dreissenid abundance on canal walls and other artificial substrates.

One question that deserves further study is whether zebra mussel activity enhances sponge growth, thereby increasing the potential for competitive interaction. Increased sponge growth has been observed in areas of Lake Michigan (T. Lauer, personal communication), Lake Erie (F.L. Snyder and D.O. Kelch, personal observations), and Lake St. Clair (R.W. Griffiths, personal communication), where zebra mussels have established dense populations. There are several possible reasons for this. In some sponges, growth is substantially enhanced by the presence of algal symbionts (Frost and Williamson 1980; Frost 1991; Sand-Jensen and Pedersen 1994) and therefore may respond favorably to increased light intensity resulting from zebra mussel filtration activity in lentic habitats (Holland 1993;

Leach 1993; Griffiths 1993). Intense grazing pressure from zebra mussels may also cause algal populations to shift toward smaller cell sizes (cf. Sterner 1989; Mellina et al. 1995); this may benefit sponge growth by removing the larger size fraction of seston that is not processed efficiently (and is normally rejected) by sponges (Frost 1980a) or that fouls sponge pores (cf. Bakus 1968), in favor of a smaller size fraction of particles (e.g., bacteria) that are selectively ingested by sponges (Frost 1980a, 1980b, 1981). Furthermore, bacterial suspensions associated with large deposits of mussel feces and pseudofeces (Izvekova and Lvova-Katchanova 1972) may nourish sponges. Finally, the ability of dreissenids to colonize soft substrates, including sand and mud (Kuchina 1964; Lyakhov and Mikheev 1964; Hunter and Bailey 1992; Maslowski 1992), should facilitate subsequent colonization of these habitats by freshwater sponges by providing hard secondary substrate. For example, zebra mussel colonization of the sandy areas of the Szczecin Lagoon in northwestern Poland was accompanied by increased abundance of the sponge *Ephydatia fluviatilis*, which normally could not colonize soft substrates (Maslowski 1992). For these reasons, we hypothesize that sponge growth will become prolific in standing waters that support high densities of zebra mussels.

Competition between macrofouling invertebrates structures epifaunal communities in rocky intertidal habitats (Connell 1961; Dayton 1971; Russ 1982), and may have a similar impact in freshwater systems. Given that sponges and zebra mussels provide habitat for unique assemblages of invertebrates (Dusoge 1966; Roback 1968; Konopacka and Sicinski 1985; Kharchenko et al. 1989; Ricciardi and Reisinger 1993; Conn and Conn 1993; Dermott et al. 1993; Griffiths 1993; Ricciardi 1994), the colonization and subsequent overgrowth of zebra mussel beds by sponges should result in a concomitant transformation of the local epifaunal community. Dreissenid colonies, therefore, may not necessarily represent a final successional stage for epifaunal communities in North American freshwater habitats.

## Acknowledgements

We gratefully acknowledge F. Whoriskey for his diving assistance at the St. Lawrence River sites. We also thank T. Frost, R. Griffiths, and T. Lauer for providing valuable discussions. Funding for the St. Lawrence River portion of this study was provided by the Government of Québec (Fonds pour la formation de chercheurs et l'aide à la recherche). The Lake Erie portion of this study was sponsored by the Ohio Sea Grant College Program, project A/EP/1 under grant NA90AA-D-SG496 of the National Sea Grant College Program, National Oceanic and Atmospheric Administration (U.S. Department of Commerce).

## References

- Arndt, W. 1937. *Ochridaspongia rotunda* n.g. n.sp., ein neuer Süsswasserschwamm aus dem Ochridasee. Arch. Hydrobiol. 31: 636–677.
- Bakus, G.J. 1968. Sedimentation and benthic invertebrates of Fanning Island, Central Pacific. Mar. Geol. 6: 45–51.
- Borcherding, J. 1995. Laboratory experiments on the influence of food availability, temperature and photoperiod on gonad development in the freshwater mussel *Dreissena polymorpha*. Malacologia, 36: 15–27.
- Bushnell, J.H. 1966. Environmental relations of Michigan Ectoprocta and dynamics of natural populations of *Plumatella repens*. Ecol. Monogr. 36: 95–123.
- Conn, D.B., and D.A. Conn. 1993. Parasitism, predation and other biotic associations between dreissenid mussels and native animals in the St. Lawrence River. In Proceedings of the Third International Zebra Mussel Conference, Toronto, Ont., February 23–26, 1993. Edited by J.L. Tsou. Electric Power Research Institute, Palo Alto, Calif. pp. 223–234.
- Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle, *Chthamalus stellatus*. Ecology, 42: 710–723.
- Dayton, P.K. 1971. Competition, disturbance and community organisation: the provision and subsequent utilisation of space in a rocky intertidal community. Ecol. Monogr. 41: 351–389.
- Dermott, R., and M. Munawar. 1993. Invasion of Lake Erie offshore sediments by *Dreissena*, and its ecological implications. Can. J. Fish. Aquat. Sci. 50: 2298–2304.
- Dermott, R., J. Mitchell, I. Murray, and E. Fear. 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.
- Dudley, T.L., C.M. D'Antonio, and S.D. Cooper. 1990. Mechanisms and consequences of interspecific competition between two stream insects. J. Anim. Ecol. 59: 849–866.
- Dusoge, K. 1966. Composition and interrelations between macrofauna living on stones in the littoral of Mikolajskie lake. Ecol. Pol. Ser. A, 14: 755–762.
- Fell, P.E. 1990. Environmental factors affecting dormancy in the freshwater sponge *Eunapius fragilis* (Leidy). Invertebr. Reprod. Dev. 18: 213–219.
- Frost, T.M. 1976. Investigations of the aufwuchs of freshwater sponges. I. A quantitative comparison between the surfaces of *Spongilla lacustris* and three aquatic macrophytes. Hydrobiologia, 50: 145–149.
- Frost, T.M. 1978. The impact of the freshwater sponge *Spongilla lacustris* on a sphagnum bog pond. Verh. Int. Ver. Theor. Angew. Limnol. 20: 2368–2371.
- Frost, T.M. 1980a. Clearance rate determinations for the freshwater sponge *Spongilla lacustris*: effect of temperature, particle type and concentration, and sponge size. Arch. Hydrobiol. 90: 330–356.
- Frost, T.M. 1980b. Selection in sponge-feeding processes. In Nutrition in the lower Metazoa. Edited by D.C. Smith and Y. Tiffon. Pergamon Press, Oxford, U.K. pp. 33–44.
- Frost, T.M. 1981. Analysis of ingested materials within a freshwater sponge. Trans. Am. Microsc. Soc. 100: 271–277.
- Frost, T.M. 1991. Porifera. In Ecology and classification of North American freshwater invertebrates. Edited by J.H. Thorp and A.P. Covich. Academic Press, New York. pp. 95–124.
- Frost, T.M., and C.E. Williamson. 1980. In situ determination of the effect of symbiotic algae on the growth of the freshwater sponge *Spongilla lacustris*. Ecology, 61: 1361–1370.
- Gee, N.G. 1937. Canadian fresh-water sponges. Trans. R. Can. Inst. 21: 285–296.
- Gillis, P.L., and G.L. Mackie. 1994. Impact of the zebra mussel, *Dreissena polymorpha*, on populations of Unionidae (Bivalvia) in Lake St. Clair. Can. J. Zool. 72: 1260–1271.
- Goodbody, I. 1961. Inhibition of the development of a marine sessile community. Nature (London), 190: 282–283.



- Green, G. 1977. Ecology of toxicity in marine sponges. *Mar. Biol.* (Berlin), 40: 207–215.
- Greenland, D.C., S.H. Newton, and R.F. Faucette. 1988. Effects of cage encrustation by the bryozoan *Plumatella casmiana* on production of channel catfish. *Prog. Fish-Cult.* 50: 42–45.
- 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.
- Haag, W.R., D.J. Berg, D.W. Garton, and J.L. Farris. 1993. Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in western Lake Erie. *Can. J. Fish. Aquat. Sci.* 50: 13–19.
- Hebert, P.D.N., B.W. Muncaster, and G.L. Mackie. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. *Can. J. Fish. Aquat. Sci.* 46: 1587–1591.
- Hemphill, N. 1988. Competition between two stream dwelling filter-feeders, *Hydropsyche oslari* and *Simulium virgatum*. *Oecologia*, 77: 73–80.
- Hirata, T. 1987. Succession of sessile organisms on experimental plates immersed in Nabeta Bay, Izu Peninsula, Japan. II. Succession of invertebrates. *Mar. Ecol. Prog. Ser.* 38: 25–35.
- Holland, R.E. 1993. Changes in planktonic diatoms and water transparency in Hatchery Bay, Bass Island area, western Lake Erie since the establishment of the zebra mussel. *J. Great Lakes Res.* 19: 617–624.
- Hunter, R.D., and J.F. Bailey. 1992. *Dreissena polymorpha* (zebra mussel): colonization of soft substrata and some effects on unionid bivalves. *Nautilus*, 106: 60–67.
- Izvekova, E.I., and A.A. Lvova-Katchanova. 1972. Sedimentation of suspended matter by *Dreissena polymorpha* Pallas and its subsequent utilization by Chironomidae larvae. *Pol. Arch. Hydrobiol.* 19: 203–210.
- Jackson, J.B.C. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *Am. Nat.* 111: 743–767.
- Kharchenko, T.A., A.V. Lyashenko, and O.A. Davydov. 1989. A fresh-water sponge consortium in the Dnieper–Donbass Canal. *Hydrobiol.* J. 23: 32–36.
- Konopacka, A., and J. Sicinski. 1985. Macrofauna inhabiting the colonies of the sponge *Spongilla lacustris* (L.) in the River Gać. *Verh. Int. Ver. Theor. Angew. Limnol.* 22: 2968–2973.
- Kuchina, E.S. 1964. Distribution of the mollusk *Dreissena polymorpha* Pallas in the Northern Dvina River. In *Biology and control of Dreissena*. Edited by B.K. Shtegman. Tr. Inst. Biol. Vnutr. Vod Akad. Nauk SSSR, 7: 25–31.
- Lancaster, J., A.G. Hildrew, and C.R. Townsend. 1988. Competition for space by predators in streams: field experiments on a net-spinning caddisfly. *Freshwater Biol.* 20: 185–193.
- Leach, J.H. 1993. Impacts of the zebra mussel (*Dreissena polymorpha*) on water quality and fish spawning reefs in western Lake Erie. In *Zebra mussels: biology, impacts, and control*. Edited by T.F. Nalepa and D.W. Schloesser. Lewis Publishers, Boca Raton, Fla. pp. 381–397.
- Lukasiewicz, J. 1978. *Eunapius fragilis* (Porifera: Spongillidae): a report of fresh-water sponges in Lake Huron. *J. Great Lakes Res.* 4: 103.
- Lyakhov, S.M., and V.P. Mikheev. 1964. The population and distribution of *Dreissena* in the Kujbyshev reservoir seven years after its construction. In *Biology and control of Dreissena*. Edited by B.K. Shtegman. Tr. Inst. Biol. Vnutr. Vod Akad. Nauk SSSR 7: 1–14.
- Maslowski, J. 1992. Bottom macrofauna of the Szczecin Lagoon (north-western Poland). *Acta Hydrobiol.* 34: 253–274.
- McAuliffe, J.R. 1984. Competition for space, disturbance, and the structure of a benthic stream community. *Ecology*, 65: 894–908.
- Mellina, E., J.B. Rasmussen, and E.L. Mills. 1995. Impact of zebra mussel (*Dreissena polymorpha*) on phosphorus cycling and chlorophyll in lakes. *Can. J. Fish. Aquat. Sci.* 52: 2553–2573.
- Mills, E.L., R.M. Dermott, E.F. Roseman, D. Dustin, E. Mellina, D.B. Conn, and A.P. Spidle. 1993. Colonization, ecology, and population structure of the “quagga” mussel (Bivalvia: Dreissenidae) in the lower Great Lakes. *Can. J. Fish. Aquat. Sci.* 50: 2305–2314.
- Nalepa, T.F., and D.W. Schloesser. (Editors). 1993. *Zebra mussels: biology, impacts, and control*. Lewis Publishers, Boca Raton, Fla.
- Nalepa, T.F., J.F. Cavaletto, M. Ford, W.M. Gordon, and M. Wimmer. 1993. Seasonal and annual variation in weight and biochemical content of the zebra mussel, *Dreissena polymorpha*, in Lake St. Clair. *J. Great Lakes Res.* 19: 541–552.
- Nandakumar, K., M. Tanaka, and T. Kikuchi. 1993. Interspecific competition among fouling organisms in Tomioka Bay, Japan. *Mar. Ecol. Prog. Ser.* 94: 43–50.
- Paine, R.T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, 15: 93–120.
- Pequegnat, W.E. 1964. The epifauna of a California siltstone reef. *Ecology*, 45: 272–283.
- Perera, M., M. Ballesteros, and X. Turon. 1990. Estudio de los organismos epibiontes en un cultivo de bivalvos marinos del delta del Ebro. *Cah. Biol. Mar.* 31: 385–399.
- Proksch, P. 1994. Defensive roles for secondary metabolites from marine sponges and sponge-feeding nudibranchs. *Toxicon*, 32: 639–655.
- Pronzato, R., and R. Manconi. 1991. Colonization, life cycles and competition in a freshwater sponge association. In *Fossil and recent sponges*. Edited by J. Reitner and H. Keupp. Springer-Verlag, Berlin. pp. 432–444.
- Quinn, J.F. 1982. Competitive hierarchies in marine benthic communities. *Oecologia*, 54: 129–135.
- Rader, R.B., and R.N. Winget. 1985. Seasonal growth rate and population dynamics of a freshwater sponge. *Hydrobiologia*, 123: 171–176.
- 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 H.M. Reiswig. 1993. Freshwater sponges (Porifera, Spongillidae) of eastern Canada: taxonomy, distribution and ecology. *Can. J. Zool.* 71: 665–682.
- Ricciardi, A., and H.M. Reiswig. 1994. Taxonomy, distribution, and ecology of the freshwater bryozoans (Ectoprocta) of eastern Canada. *Can. J. Zool.* 72: 339–359.
- Ricciardi, A., R. Serrouya, and F.G. Whoriskey. 1995. Aerial exposure tolerance of zebra and quagga mussels (Bivalvia: Dreissenidae): implications for overland dispersal. *Can. J. Fish. Aquat. Sci.* 52: 470–477.
- Roback, S.S. 1968. Insects associated with the sponge *Spongilla fragilis* in the Savannah River. *Not. Nat. Acad. Nat. Sci. Philadelphia*, 412: 1–10.
- Ruetzler, K. 1970. Spatial competition among Porifera: solution by epizoism. *Oecologia*, 5: 85–95.
- Russ, G.R. 1982. Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. *Oecologia*, 53: 12–19.



- Sand-Jensen, K., and M.F. Pedersen. 1994. Photosynthesis by symbiotic algae in the freshwater sponge, *Spongilla lacustris*. *Limnol. Oceanogr.* 39: 551–561.
- SAS Institute Inc. 1988. SAS/STAT user's guide, release 6.03 edition. SAS Institute Inc., Cary, N.C.
- Sebestyen, O. 1938. 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.* 8: 169–182.
- Sprung, M. 1990. Costs of reproduction: a study on metabolic requirements of the gonads and fecundity of the bivalve *Dreissena polymorpha*. *Malacologia*, 32: 267–274.
- Sprung, M., and J. Borcharding. 1991. Physiological and morphometric changes in *Dreissena polymorpha* (Mollusca; Bivalvia) during a starvation period. *Malacologia*, 33: 179–191.
- Stanczykowska, A. 1977. Ecology of *Dreissena polymorpha* (Pall.) (Bivalvia) in lakes. *Pol. Arch. Hydrobiol.* 24: 461–530.
- Stanczykowska, A. 1979. Size and weight of *Dreissena polymorpha* from European lakes. *Hydrobiol. J.* 13: 20–23.
- Sterner, R.W. 1989. The role of grazers in phytoplankton succession. *In* Plankton ecology: succession in plankton communities. Edited by U. Sommer. Springer-Verlag, Berlin. pp. 107–170.
- Tenney, W.R., and W.S. Woolcott. 1964. A comparison of the responses of some species of fishes to the toxic effect of the bryozoan *Lophodella carteri* (Hyatt). *Va. J. Sci. (New Ser.)*, 15: 16–20.
- van den Brink, F.W.B., G. van der Velde, and A. bij de Vaate. 1991. Amphipod invasion on the Rhine. *Nature (London)*, 352: 576.
- van der Velde, G., B.G.P. Paffen, F.W.B. van den Brink, A. bij de Vaate, and H.A. Jenner. 1994. Decline of zebra mussel populations in the Rhine: competition between two mass invaders (*Dreissena polymorpha* and *Corophium curvispinum*). *Naturwissenschaften*, 81: 32–34.
- Wiktor, J. 1963. Research on the ecology of *Dreissena polymorpha* Pall. in the Szczecin lagoon (Zalew Szczecinski). *Ekol. Pol. Ser. A*, 11: 275–280.
- Zar, J.H. 1984. *Biostatistical analysis*. 2nd ed. Prentice-Hall Inc., Englewood Cliffs, N.J.