Aerial exposure tolerance of zebra and quagga mussels (Bivalvia: Dreissenidae): implications for overland dispersal

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Abstract: We examined the effects of ambient temperature (10, 20, and 30°C) and relative humidity (10, 50, and 95% RH) on the aerial exposure tolerance of adult zebra mussel (*Dreissena polymorpha*) and quagga mussel (*D. bugensis*) collected from the St. Lawrence River. Survivorship of mussels in air significantly increased with increasing RH, decreasing temperature, and increasing mussel size. At 20°C and 50% RH (early temperate summer conditions), large (21–28 mm) *D. polymorpha* survived more than 5 days exposure, whereas small (10–18 mm) *D. polymorpha* survived 1–3 days. Seventy-three percent of large *D. polymorpha* and 10% of small *D. polymorpha* survived 10 days exposure at conditions considered optimal for survivorship (10°C and 95% RH). Survivorship of *D. bugensis* was tested at 20°C and was 15–100% lower than that of *D. polymorpha* at all RH levels combined with exposures less than 5 days. *Dreissena bugensis* also suffered significantly higher percent weight losses because of desiccation than *D. polymorpha*. The differences in the desiccation tolerance of zebra and quagga mussels reflect their relative depth distribution in lakes. Our results suggest that, given temperate summer conditions, adult *Dreissena* may survive overland transport (e.g., on small trailered boats) to any location within 3–5 days' drive of infested waterbodies.

Résumé : Nous avons examiné les effets de la température ambiante (10, 20 et 30°C) et de l'humidité relative, (10, 50 et 95% HR) sur la tolérance à l'exondation de moules zébrées (*Dreissena polymorpha*) et de moules quaggas (*D. bugensis*) adultes prélevées dans le Saint-Laurent. Le taux de survie des moules exposées à l'air augmentait de façon significative en fonction de la croissance de HR, de la baisse de la température et de l'augmentation de la taille des coquillages. À 20°C et 50% HR (conditions tempérées du début de l'été), les *D. polymorpha* de grande taille (21–28 mm) ont survécu à une exondation de plus de cinq jours, tandis que celles de petite taille (10–18 mm) ont survécu de un à trois jours seulement. À des conditions considérées comme optimales pour la survie (10°C et 95% HR), 73% des *D. polymorpha* de grande taille et 10% de celles de petite taille ont survécu à une exondation de dix jours. Le taux de survie de *D. bugensis* a été testé à 20°C et se trouvait de 15–100% inférieur à celui de *D. polymorpha* à tous les niveaux de HR combinés à des exondations de moins de cinq jours. Les *Dreissena bugensis* ont aussi subi des pertes de poids en pourcentage, dues à la déshydratation, nettement supérieures à celles de *D. polymorpha*. Les différences dans la tolérance à la déshydratation chez les moules zébrées et quaggas reflètent leurs distributions relatives en profondeur dans les lacs. Nos résultats permettent de penser que, dans des conditions estivales tempérées, les *Dreissena* adultes peuvent survivre au transport terrestre (par exemple si elles sont fixées à la coque de petits bateaux transportés par remorque) en n'importe quel point situé à 3–5 jours de distance des plans d'eau infestés.

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Introduction

Since its initial introduction in Lake St. Clair ca. 1986 (Hebert et al. 1989), the exotic zebra mussel (*Dreissena polymorpha*) has spread rapidly throughout the Great Lakes and into several major river systems (e.g., the St. Lawrence, Hudson, Ohio, Mississippi, and Tennessee rivers) and has caused substantial economic and ecological impacts (e.g., Schloesser and Kovalak 1991; Kovalak et al. 1993; Lepage 1993; MacIsaac et al. 1993; Holland 1993). Its rapid expansion has been linked to its possession of planktonic veliger larvae, byssal threads (for attachment to hard surfaces), and high rates of growth and recruitment (Stanczykowska 1977; Carlton 1993). A second dreissenid recently found in the Great Lakes, the quagga mussel (*Dreissena bugensis*), is also expanding its range (Mills et al. 1993) and may have negative impacts on profundal fauna (Dermott and Munawar 1993).

Because *Dreissena* can potentially colonize most of the major lakes and rivers on the continent (Strayer 1991; Ramcharan et al. 1992), it is important to determine the factors that allow the mussels to spread into new habitats. The principal downstream dispersal vector in river systems is larval drift (Griffiths et al. 1991), but humans may spread zebra mussels considerable distances upstream on the hulls of commercial barges (Keevin et al. 1992) and to isolated lakes and rivers through fishing and boating activity (Carlton 1993; McNabb 1993). The potential for overland transport of byssally attached mussels on trailored boats has also been strongly emphasized (Griffiths et al. 1991; Neary and Leach 1992; Johnson and Carlton 1993; Carlton 1993). Dreissenid mussels may attach to boat hulls or to aquatic vegetation that is caught on boating equipment and trailers; up to 25% of recreational boat trailers departing certain Michigan boat ramps are estimated to be carrying adult zebra mussels (Johnson and Carlton 1993). The movement of mussel-fouled chains, fishing nets, buoys, boat docks, and other fishing and boating equipment between water basins may also help disperse dreissenids (Carlton 1993). The successful overland transport of dreissenid mussels by these vectors will depend primarily on their ability to tolerate periods of aerial exposure (desiccation).

References to the desiccation tolerance of *Dreissena* in the literature are generally anecdotal and lack quantitative information on air temperature or relative humidity conditions. Some authors refer vaguely to the ability of *Dreissena* to tolerate aerial exposure for periods of "a few days" (O'Neill 1990) to "several days" (Neary and Leach 1992). Mussels attached to a car pulled out of Lake Erie survived 4 days in air (Griffiths et al. 1991). In a laboratory study, Alyakrinskaya (1978) observed that *D. polymorpha* remained alive out of water for 4 days at temperatures of 20–22°C and variable relative humidity. Wisniewski (1992) noted that 96% of *D. polymorpha* placed on moist sand in a Polish reservoir survived 3 days exposure to air. Conversely, *D. polymorpha* survived 14 days in the cool, moist interior of an unused water pipe (Hoestland and Lassabliere 1959). McMahon and Paine (1992) found that both relative humidity and temperature had a significant effect on the survivorship of emersed mussels. No previous study has assessed the effects of mussel size on the aerial exposure tolerance of *D. polymorpha*, and there are no published data on the aerial exposure tolerance of *D. bugensis*. This information would help predict the rate of overland spread of *Dreissena* and aid in the development of methodologies to control mussel dispersal.

We examined the effects of temperature, relative humidity, exposure period, and mussel size on the survivorship of *D. polymorpha* and *D. bugensis* in air. Given that *D. bugensis* is typically found at greater depths in lakes than *D. polymorpha* (Mills et al. 1993), we hypothesized that it is less adapted (i.e., less tolerant) to aerial exposure.

Methods

Dreissenid mussels (*D. polymorpha* and *D. bugensis*) were collected in the summer and autumn of 1992 by SCUBA at Soulanges Canal, a section of the St. Lawrence River southwest of the Island of Montreal (45°20′N, 73°58′W); the mean summer density and biomass of dreissenids at this site were 1990 mussels/m^2 and 1568 g (fresh wt., including shells)/m^2, respectively (A. Ricciardi, unpublished data). *Dreissena bugensis* (distinguished by the convex ventral margin of its shell) occurred in the collections in small numbers (1 of 100 dreissenids) and were separated from *D. polymorpha*. These collections were used to establish laboratory colonies for use in our experiments.

Prior to experimentation, the mussels were kept in aerated aquaria at 20°C and fed daily with dried *Chlorella* or with phytoplankton produced in separate aquaria. To determine if smaller *D. polymorpha* desiccate at a faster rate than larger mussels, two size classes (SC) were used: 10–18 mm (SC1: mean length ± SE = 15.0 ± 1.4 mm) and 21–28 mm (SC2: mean length ± SE = 24.0 ± 1.2 mm); in the upper St. Lawrence River in summer, these size classes generally correspond to 1- and 2-year old *D. polymorpha*, respectively (determined by size–frequency distributions; A. Ricciardi, unpublished data). Groups of 10 live mussels belonging to one size class were placed in desiccating chambers (glass jars approximately 3 L in volume, with screw-on lids) and subjected to treatment combinations of three temperatures (10, 20, 30°C), three relative humidities (RH = 10, 50, 95%), and three exposure periods (1, 3, 5 days). The exposure periods were chosen based on reports of zebra mussel tolerance to drying in situ. Temperatures and relative humidities were chosen to represent ranges comparable to those experienced in the St. Lawrence River valley during the ice-free periods of the year. The 10°C treatments were conducted in an incubator (Sherer model CEL255-6); 20°C treatments were conducted in the laboratory (controlled ambient air temperature of 19–21°C); 30°C treatments were conducted in a heated circulating water bath. Graded solutions of sodium hydroxide were prepared as desiccants, following Madge (1961). Individual mussels were removed from their aquaria, blotted dry on tissue paper, numbered with a permanent marker, measured for maximum length (using callipers), and weighed (wet weight, i.e., shell + meat + internal water) before each treatment. The mussels were then placed in an uncovered Petri dish which was elevated at least 3 cm above the desiccating solution by plastic supports. A relative humidity of approximately 95% was obtained by using distilled water

Table 1. Mean percent survivorship of *D. polymorpha* in air at three different exposures (1, 3, 5 days) of combinations of three levels of relative humidity (10, 50, 95%) and ambient temperature (10, 20, 30°C).

	Mussel length, 10.0–18.0 mm									Mussel length, 21.0–28.0 mm								
	10°C			20°C			30°C			10°C			20°C			30°C		
%RH	1 d	3 d	5 d	1 d	3 d	5 d	1 d	3 d	5 d	1 d	3 d	5 d	1 d	3 d	5 d	1 d	3 d	5 d
10	93.3	26.7	0*	66.7*	3.3	0	0*	0	0	93.3	36.7	25.0*	96.7*	13.3	0	60.0*	0	0
	(6.7)	(16.7)	(0)	(12.0)	(3.3)	(0)	(0)	(0)	(0)	(3.3)	(8.8)	(5.0)	(3.3)	(6.7)	(0)	(0)	(0)	(0)
50	93.3	90.0	3.3**	72.5*	3.3**	0	0**	0	0	100	100	100**	96.7*	73.3**	16.7	77.5**	0	0
	(6.7)	(0)	(3.3)	(7.5)	(3.3)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(3.3)	(13.3)	(12.0)	(8.5)	(0)	(0)
95	96.7	90.0	73.3*	96.7	70.0*	13.3*	33.3*	0	0	100	100	100*	100	100*	47.5*	100*	3.3	0
	(3.3)	(5.8)	(6.7)	(3.3)	(0)	(8.8)	(17.6)	(0)	(0)	(0)	(0)	(0)	(0)	(0)	(11.1)	(0)	(3.3)	(0)

Note: Standard errors are in parentheses. Asterisks indicate significant differences between size classes: *, $p < 0.05$; **, $p < 0.01$.

Table 2. Mean percent survivorship of dreissenid mussels after prolonged (10, 15 d) exposure in air in cool, moist (10°C, 95% RH) conditions.

Size class	Exposure (days)	PWL	% survivorship
	D. polymorpha		
I	10	41.2 (1.2)	6.7 (3.3)
II	10	12.5 (1.3)	73.3 (12.0)
I	15	44.7 (0.1)	0 (0)
II	15	36.5 (0.5)	0 (0)
	D. bugensis		
I	10	44.0	0
II	10	17.6	40.0
II	15	43.0	0

Note: Except for *D. bugensis*, all values are averages of three replicates; standard errors are in parentheses. PWL, percent weight loss.

alone. Relative humidity levels were monitored daily by inserting a hygrometer probe (Climomaster model 6511) into the desiccating chamber, and blocking the opening with a plastic bag while reading the hygrometer. Each chamber was opened briefly each day to check the relative humidity and to make necessary adjustments by adding either NaOH solution or distilled water. Average daily temperature and relative humidity fluctuations were ±2.0°C and ±5%, respectively.

The treatment chambers were sampled by a gas chromatograph to determine if oxygen was in sufficient supply. Five-millilitre samples of air were taken at the beginning of a trial and again 24 h later. The air samples were analyzed using a Fischer-Hamilton model-28 gas partitioner, which indicated that the oxygen concentration within the chambers (both before and after 24 h) was not significantly different from the atmospheric concentration. Air was replenished in the chambers every 24 h when they were opened briefly to check relative humidity levels.

Each treatment was replicated two to four times. Controls consisted of mussels (SC1) immersed in aerated, plankton-free water at 10, 20, and 30°C, for 1-, 3-, and 5-day exposures and were replicated three times. At the end of each treatment, mussels were reweighed, and their viability determined by 24 h reimmersion in a 1-L flask of aerated water maintained at 20°C and containing phytoplankton. If, after 24 h, the mussel did not extend its siphon, move its valves, lay down byssi, or respond to prodding, it was considered dead. During treatment inspections, mussels that showed obvious signs of death (e.g., extended shell gape) were immediately removed from the desiccating chamber.

The same protocol was used to determine the aerial exposure tolerances of *D. bugensis*; however, fewer trials were run, because of the scarcity of quaggas in our collections. Quaggas were tested at each relative humidity – exposure period combination at 20°C. We used specimens belonging to one size class with a length range of 12.0–18.0 mm (mean ± SE = 16.0 ± 1.1 mm).

In a separate set of experiments using similar protocols, the prolonged aerial exposure tolerance of both size classes

Table 3. Mean percent survivorship and percent weight loss of *D. bugensis* in air at three different exposures (1, 3, 5 days) and relative humidities (10, 50, 95% RH) at 20°C.

	% survivorship			% weight loss		
%RH	1 d	3 d	5 d	1 d	3 d	5 d
10	35.0	0	0	43.5	62.3	62.0
	(15.0)	(0)	(0)	(0.3)	(0.1)	(1.9)
50	40.0	0	0	42.7	59.0	63.5
	(5.8)	(0)	(0)	(2.4)	(1.8)	(1.2)
95	85.0	10.0	0	8.3	15.7	41.7
	(15.0)	(10.0)	(0)	(0.2)	(0)	(6.7)

Note: Standard errors are in parentheses.

of *D. polymorpha* was determined for 10 and 15 days exposure in optimal conditions (10°C, 95% RH); three replicates were run for each exposure period. The survivorship of SC2 *D. polymorpha* exposed for 10 days at 20°C and 95% RH was also tested (three replicates). The survivorship of *D. bugensis* in prolonged (10 and 15 days) exposure was tested at 10°C and 95% RH for two size classes (12.0–18.0 and 21.0–24.0 mm); because of the insufficient number of available mussels, these experiments could not be replicated.

Results were analyzed by ANOVA (General Linear Models procedure; SAS Institute Inc. 1988), and Bonferroni-adjusted *t*-tests were used in multiple comparisons of treatment effects.

Results

Survivorship of *D. polymorpha* in air

Temperature, RH, and exposure period explained 95% of the observed variance in survivorship of small (SC1) *D. polymorpha* (ANOVA, $p < 0.0001$, df = 79). At 10°C, 100% mortality occurred within 3–5 days at 10% RH and within 5–10 days at 50–95% RH (Table 1). At 20°C, 100% mortality occurred within 3–5 days at 10–50% RH and 5–6 days at 95% RH. At 30°C, 100% mortality occurred in less than 24 h at 10–50% RH and within 1–3 days at 95% RH. The mean percent survivorship after 10 days exposure at 10°C and 95% RH was 6.7%; no mussel survived 15 days exposure (Table 2).

Temperature, RH, and exposure period explained 96% of the observed variance in survivorship of large (SC2) *D. polymorpha* (ANOVA, $p < 0.0001$, df = 78). At 10°C, 100% mortality occurred within 5–10 days at 10–50% RH and within 10–15 days at 95% RH (Tables 1 and 2). At 20°C, 100% mortality occurred within 3–5 days at 10% RH and 5–7 days at 50–95% RH. At 30°C, 100% mortality occurred within 1–3 days at 10–50% RH and within 3–5 days at 95% RH. Survivorship of SC2 *D. polymorpha* at 10°C and 95% RH was 73% after 10 days but declined sharply thereafter to reach 0% at 15 days (Table 2). Although 21% of SC2 mussels survived 5 days exposure at 20°C and 95% RH, all mussels died within 10 days of prolonged exposure in these conditions.

Table 4. Mean percent weight loss of *D. polymorpha* in air at all desiccation treatments.

	Mussel length, 10.0–18.0 mm									Mussel length, 21.0–28.0 mm								
	10°C			20°C			30°C			10°C			20°C			30°C		
%RH	1 d	3 d	5 d	1 d	3 d	5 d	1 d	3 d	5 d	1 d	3 d	5 d	1 d	3 d	5 d	1 d	3 d	5 d
10	22.7**	42.7*	51.2	32.9**	58.2**	62.0*	39.4**	60.2	60.3	12.2**	34.0*	41.7	20.4**	43.8**	55.7*	29.7**	50.8	60.2
	(1.8)	(1.6)	(5.5)	(1.2)	(0.2)	(0.9)	(0.5)	(0.4)	(0.8)	(0.4)	(2.5)	(0.7)	(0.5)	(0.6)	(1.6)	(2.0)	(3.8)	(1.1)
50	11.5*	24.6	46.1*	21.2*	48.5**	61.4**	40.0**	60.6	63.8	8.4*	16.7	29.3*	12.2*	28.2**	35.4**	25.8**	55.0	57.0
	(0.8)	(3.1)	(6.9)	(2.4)	(3.9)	(1.1)	(2.3)	(0.3)	(0.6)	(0.5)	(0.2)	(1.8)	(0.8)	(0.9)	(1.4)	(1.3)	(3.2)	(2.2)
95	4.9	6.9	11.6	6.6	13.7	19.1	21.5	52.1	61.4*	4.3	5.1	9.8	5.4	9.1	20.9	14.2	40.6	46.3*
	(1.1)	(1.0)	(1.8)	(1.8)	(1.8)	(1.3)	(4.8)	(1.0)	(1.6)	(0.7)	(0.8)	(0.4)	(1.2)	(1.4)	(3.4)	(1.3)	(9.8)	(3.4)

Note: Standard errors are in parentheses. Asterisks indicate significant differences between size classes: *, $p < 0.05$; **, $p < 0.01$.

Overall, experimental treatment (temperature, RH, exposure period, mussel size) explained 86% of variation in survivorship ($p < 0.0001$) of *D. polymorpha* when both size classes were combined.

Survivorship of *D. bugensis* in air

Relative humidity and exposure period explained 92% of the observed variation in survivorship of *D. bugensis* (12–18 mm shell length) at 20°C (ANOVA, $p < 0.0001$, df = 20). Survivorship of *D. bugensis* for 24 h in air was similar at 10 and 50% RH; all mussels died within 3 days (Table 3). At 95% RH, only 10% of *D. bugensis* survived 3 days exposure (none survived 5 days), contrasting with the high survivorship (70–100%) of *D. polymorpha* over the same period. Under cool, humid conditions (10°C, 95% RH), large *D. bugensis* (21–24 mm shell length) survived at least 10 days aerial exposure but with lower survivorships than large zebra mussels (Table 3). Mean survivorship of small *D. bugensis* (12–18 mm shell length) was compared with that of small *D. polymorpha* (SC1) at 20°C using *t*-tests and was found to be lower ($p < 0.05$) at all RH combined with exposures less than 5 days.

Weight loss of zebra and quagga mussels because of desiccation

In general, the percent weight loss (PWL) of dreissenids because of desiccation was directly proportional to temperature and exposure period, and inversely proportional to RH (Tables 3 and 4). Experimental treatments explained 94 and 97% of the variation in the PWL of *D. polymorpha* and *D. bugensis*, respectively. However, a wide range of mean weight loss was observed for *D. polymorpha* at 0% mortality (3.6–30.9 PWL; mean = 12.3 ± 1.2) and 100% mortality (16.5–64.4 PWL; mean = 53.4 ± 1.3). No individual zebra mussel survived a weight loss greater than 48%.

Dreissena bugensis suffered higher PWLs than SC1 and SC2 *D. polymorpha*, at treatment combinations of 20°C, all RH, and exposures less than 5 days (multiple *t*-tests, $p < 0.05$). PWLs of *D. bugensis* at different exposures were not significantly different at 10% and 50% RH (Table 3).

Discussion

Our results suggest that the successful overland dispersal of byssally attached dreissenid mussels exposed to air for a short period of time (days) is highly probable. We found that large *D. polymorpha* (length >20 mm) may survive 5 days in still air in environmental conditions typical of an early temperate summer (20°C, 50% RH). This compares favourably with reports of *D. polymorpha* surviving 3–4 days emersion in natural (and variable) conditions (Griffiths et al. 1991; Wisniewski 1992). Mussels may survive 10–15 days out of water in the cool, humid conditions (10°C, 95% RH) that often occur in late autumn or early spring (Table 2).

Despite different methodologies (desiccation procedure, temperature, and RH regimes), the tolerance times observed for *D. polymorpha* in our study were similar to those reported by McMahon and Paine (1992). McMahon and Paine (1992) found that 100% mortality of *D. polymorpha* (size range not specified) occurred between 15 and 20 days at low temperature (5°C) over a RH range of 5–75%. By contrast, no mussels in our experiments survived 15 days exposure at a combination of low temperature (10°C) and high RH (>95%), but differences in acclimation and treatment temperatures may account for this disparity.

Causes of mortality

Iwanyzki and McCauley (1993) found that 10–20 mm *D. polymorpha* (corresponding approximately to our SC1 length range) that were acclimated at 20°C survived less than 3 days in water at 30°C, and survivorship rapidly declined with every degree increase above 30°C. None of our SC1 *D. polymorpha* (also acclimated at 20°C) survived 24 h aerial exposure at 30°C and RH ≤ 50%, indicating that mortality was not due to thermal stress alone. The small percentage of SC2 mussels that survived more than 3 days exposure at 30°C and 95% RH suggests that desiccation resistance and thermal tolerance may increase with mussel size. Smaller *D. polymorpha* have a higher tissue surface area to volume ratio and thinner shells (with possibly higher permeability), and therefore may lose water more rapidly when desiccated (cf. Schaefer et al. 1968; Byrne et al. 1988; Thivakaran and Kasinathan 1990). Differences in survivorship between the zebra mussel size classes were most pronounced at 20°C (Table 1), while differences in PWL were most pronounced at temperatures of 10–20°C and 10–50% RH. Differences in PWL tended not to be significant at 95% RH.

The observed change in mussel weight over the treatment period was assumed to represent a combination of (*i*) evaporative water loss (tissue water + water in the mantle cavity) due to desiccation and (*ii*) resorption of energy stores because of starvation and stress. The difference in mussel weight loss at low (10% RH) and high (95% RH) relative humidities became more pronounced at lower temperatures; at 10°C, the PWL at 10% RH was three to six times greater than at 95% RH, whereas at 30°C, it was generally one-half to three-quarters that at 95% RH (Table 4). In our experiments, groups of mussels that experienced similar weight losses did not always suffer similar mortalities, suggesting that evaporative (water) loss because of desiccation was not the sole cause of mortality. Other causes may include depletion of energy reserves, acidosis, toxic buildup of anaerobic metabolites, or a combination of these factors (Byrne et al. 1990). Alyakrinskaya (1978) found that *Dreissena* buffered a biochemically driven shift in acidity during desiccation by releasing calcium ions through shell dissolution, but it is not known whether this mechanism would be effective during prolonged aerial exposure. In our study, *D. polymorpha* and (to a lesser extent) *D. bugensis* were observed to periodically gape (i.e., partially open their valves and expose their mantle tissue) during aerial exposures at high RH (≈50–95%), but rarely at low RH (≈10%); gaping behaviour for *D. polymorpha* was also noted by McMahon and Paine (1992). This behaviour suggests that the mussels were maintaining an aerobic metabolism that may delay the lethal buildup of anaerobic endproducts during emersion; however, metabolites such as ammonia may accumulate to toxic levels during prolonged aerial exposure (as in *Corbicula*, cf. Byrne et al. 1990).

Effects of microhabitat selection and mussel clustering on aerial exposure tolerance

Mussel survival may increase within a cluster, which would retain water vapour, reduce exposed surface area, and provide shelter from convective air currents. Multilayered *D. polymorpha* clusters are common wherever populations have had adequate time to establish high densities (Wiktor 1963; Morton 1969; Stanczykowska 1977; Hebert et al. 1989). The tendency for dreissenids to aggregate along seams and in crevices (Mellina and Rasmussen 1994; A. Ricciardi, personal observation), where they retain moisture and are sheltered from direct sunlight and wind, should enhance their aerial exposure tolerance. In the St. Lawrence River estuary, mussel colonies occur in crevices on the surface of boulders exposed to direct sunlight at low tide (Mellina and Rasmussen 1994). The microclimate within these colonies may retain moisture and expose internal occupants to higher humidity levels. Conversely, this benefit may be offset by adverse conditions created by densely packed multilayered clusters, e.g., lower oxygen tension and higher ammonia levels; a dense cluster may trap and accumulate ammonia, and mussels byssally bound by their neighbours may be prevented from effectively gaping.

Griffiths et al. (1991) noted that densely packed mussels attached to the exterior of a car pulled out of Lake Erie survived 4 days in summer weather, but he did not mention the proportion of surviving mussels. For short periods of time, the benefits of clumping probably outweigh the costs; differences in the aerial exposure tolerance for a monolayered bed of mussels (very common in nature where substrate is not limiting; A. Ricciardi, personal observation) versus a multilayered cluster may be important. The monolayer may retain water within its interstices, and perhaps increase boundary-layer resistance to desiccation by convection, but probably would not suffer the adverse effects associated with multilayered clumping. Therefore, we expect that a small aggregation, or monolayer, of mussels would survive longer periods of overland dispersal than mussels in multilayered clumps.

Individual mussels within clumps of vegetation may also be protected against enhanced desiccation from sunlight and wind. *Dreissena* attaches to vegetation in lakes (Lewandowski 1982; UW Sea Grant Institute 1993), and vegetation is commonly transported between lakes on boating equipment (e.g., Johnstone et al. 1985). Furthermore, *D. polymorpha* has been found on aquatic weeds caught on boat trailers departing from the Great Lakes, and many boaters travel between the Great Lakes and inland waterbodies on a daily or weekly basis (Johnson and Carlton 1993; Gunderson 1994); successful interlake dispersal is highly probable over these short time periods (Table 1).

Mitigation strategies based on aerial exposure

Dreissena polymorpha is a common fouling organism on the walls of reservoirs (Oldham 1930; Morton 1969; Wisniewski 1992) and may be periodically exposed by drawdown. From our data, 100% mortality of mussels on reservoir walls could be achieved by drawdown for 5–10 days at temperatures greater than 20°C. Because *D. polymorpha* occurs in greatest densities at depths of 2–4 m (Stanczykowska 1977), controlled drawdown of reservoirs in midsummer could eradicate the majority of the mussels, and confine the remaining mussels to unfavorable habitats (e.g., anoxic hypolimnia). This method has been advocated as a control for another invader of reservoirs, the Asiatic clam *Corbicula fluminea* (White 1977; Byrne et al. 1988). For mussels infesting the cool interior of a water pipe, 100% mortality would require at least 15 days after dewatering (assuming >95% RH), but desiccation could be accelerated by convective drying with heated air (cf. Jenner and Janssen-Mommen 1993).

Aerial exposure tolerance as a factor governing the depth distribution of dreissenids

Dreissena polymorpha's tolerance of short periods of emersion may be an important factor governing its ability to colonize hard substrate in shallow waters. Zebra mussels are most abundant in the littoral and sublittoral zones of lakes and reservoirs (Stanczykowska 1977), and also occur in intertidal areas (Strayer and Smith 1993; Mellina and Rasmussen 1994) where they must be endure periodic exposure to the air and sun. By contrast, *D. bugensis* is the dominant dreissenid in deep waters in the Laurentian Great Lakes (up to 130 m, cf. Mills et al. 1993) and in profundal areas of reservoirs along the Dnieper River in the Ukraine (Pligin 1984), and therefore might be expected to be less adapted to desiccation. The lower aerial exposure tolerance of *D. bugensis* observed in our experiments supports this hypothesis. The patterns we observed are analogous to those of intertidal marine bivalves and other invertebrates whose depth distribution is inversely correlated with their desiccation resistance (Kensler 1967; Landenberger 1969; Foster 1971). Ussery and McMahon (1994), working independently from us, recently compared the desiccation tolerance of *D. polymorpha* and *D. bugensis* at 15°C under a variety of RH and found that *D. bugensis* suffered greater mortality than *D. polymorpha* at >50% RH; these results lend further support to the contention that the deeper water dreissenid is less likely to survive prolonged aerial exposure during overland dispersal.

Conclusions

The factors contributing to the successful establishment of exotic species in new habitats have not been fully elucidated (Elton 1958; Lodge 1993). If invasion success depends on the size of the introduced (pioneer) population, then the overland transport of highly fecund adults may have greater invasion potential than the transport of larvae across short geographic distances. Since many recreational boaters use the Great Lakes and smaller inland lakes within the same week (Johnson and Carlton 1993; Gunderson 1994), the successful overland dispersal of adult dreissenid mussels from established Great Lakes populations is highly probable. Our results indicate that, given average summer weather conditions, *D. polymorpha* could be transported overland to any location within a radius of 5 days' drive of infested areas. There have been sightings of adult dreissenids in water bodies isolated from the Great Lakes system and which required overland transport for colonization; these include several inland lakes in Michigan, Indiana, Ohio, and New York (Marangelo and Johnson 1993; University of

Wisconsin Sea Grant Institute 1994). There is also evidence that *Dreissena* was introduced into the Hudson River at Catskill, New York State, by humans rather than by larval drift from the Erie Canal (Strayer and Powell 1992); this may have been accomplished by an infested boat. The probability of an isolated lake being colonized by dreissenid mussels transported overland on boat trailers should increase substantially as the distance between the mussel's range and the lake decreases, enhancing the conditions for successful overland dispersal. Water bodies in close proximity to major highways (allowing greater traffic between invaded and uninvaded sites) should be considered particularly vulnerable to invasion by overland dispersal.

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