

NOTE

Comparative Growth and Survival of *Dreissena polymorpha* and *Dreissena bugensis*, Exotic Molluscs Introduced to the Great Lakes

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ABSTRACT. Zebra (*Dreissena polymorpha*) and quagga mussels (*D. bugensis*) are among the most recent species to invade the Great Lakes. This study explored growth rates of two size classes (5 and 15 mm) of each species reciprocally transplanted into western and eastern Lake Erie, and in laboratory experiments in which environmental temperature and food concentration were varied. Both species and size classes experienced high survival rates in western (>95%) and eastern ($\geq 85\%$) Lake Erie. Length- and mass-specific growth rates varied significantly between locations and mussel size classes, but not by species. Mussels incubated in the warm, western basin of Lake Erie exhibited growth (length and mass), whereas those in the cooler eastern basin did not. In a laboratory experiment, temperature and size were the most important determinants of growth, though species differences were evident. Growth of both species was greater at 15°C than at 6°C. Specific growth rates of zebra mussels were greater than those of quagga mussels, except with respect to mass growth of smaller mussels at the higher temperature. Large mussels of both species experienced no mortality, whereas small quagga mussels experienced a significantly higher rate of mortality (50%) at the higher temperature than did small zebra mussels (10%). Results of the present study indicate that mussel growth of both species corresponds with initial size and environmental temperature, and that the distribution of quagga mussels in the Great Lakes is unlikely to be determined by high water temperature.

INDEX WORDS: *Dreissena*, zebra mussel, quagga mussel, growth, survival, Lake Erie,

INTRODUCTION

The Laurentian Great Lakes have been highly receptive to exotic species, with more than 140 species successfully introduced during the past two centuries (Mills *et al.* 1993a). The vast majority of these species have caused no apparent economic or ecological damage, though approximately 10% of introduced species have caused serious problems (Mills *et al.* 1993a). Two species of dreissenid mussel with tremendous potential for food web alterations and economic damage have recently become established in the Great Lakes. Zebra mussels (*Dreissena polymorpha*) were first introduced into Lake St. Clair and western Lake Erie in 1986 (Hebert *et al.* 1989, Grif-

fiths *et al.* 1991). Zebra mussel distribution subsequently expanded extremely rapidly, and now includes all of the Great Lakes and numerous river systems and inland lakes in the eastern United States and Canada. The quagga mussel (*D. bugensis*), first observed in Lake Erie in 1989, is limited principally to Lake Ontario, central and eastern Lake Erie, and the St. Lawrence River (Mills *et al.* 1993b).

Zebra and quagga mussels appear to have divergent spatial distributions; the former is found primarily in warm, eutrophic, shallow waters, whereas populations of the latter extend from shallow, warm water to deep, oligotrophic, cold water (Mills *et al.* 1993b; pers. obs.). In regions of Lakes Ontario and

Erie where the species co-occur, quagga mussels tend to be larger than zebra mussels (Mills *et al.* 1993b). The only exception to this pattern occurred along the border of western and central Lake Erie, at the proximate distribution limit of the quagga mussel, where zebra mussels tended to be larger than quagga mussels (Mills *et al.* 1993b). At present, it is not clear what factors contribute to differences in distributions and size-frequency patterns of the two species. However, temperature and food availability may be factors. Zebra mussels have achieved densities as high as 3.4×10^5 individuals m^{-2} in Lake Erie (Leach 1992). This has resulted in chlorophyll depletion ($< 1 \mu g L^{-1}$) and possible food limitation in the boundary layer above mussel beds (MacIsaac *et al.* 1991, 1992).

The purpose of this study was to determine whether environmental factors affect the growth, and thus the potential distribution, of *Dreissena polymorpha* and *Dreissena bugensis* in western and eastern Lake Erie. In addition to field studies, laboratory experiments were conducted in which growth rates of the two species were studied under different combinations of temperature, food concentration, initial mussel size, and potential competition (inter- vs. intraspecific).

METHODS

Source of Mussels

Quagga and zebra mussels for all experiments were respectively collected from a raw water intake line ($\sim 9^\circ C$; 3 June 1993) located at Ontario Hydro's generating plant at Nanticoke, Ontario, in eastern Lake Erie, and from rocks in a littoral area adjacent to Middle Sister Island in western Lake Erie. Mussels were transported to the laboratory in chilled coolers and maintained in separate 66-L aquariums at $4^\circ C$. Aquarium water, which originated from the shipping channel in southwest Lake St. Clair, was filtered through $0.7 \mu m$ (retention) borosilicate microfibre filters (Micro Filtration Systems), aerated, and supplemented with a small quantity ($\sim 1 mg$ dry mass $L^{-1} day^{-1}$) of dried *Chlorella* (Acta Pharmaceutical, Sunneyvale, CA; Nichols 1992).

Field Transplant Experiment

Growth experiments were conducted at each of three sites (ca. 1 km apart) in eastern and western Lake Erie (Fig. 1). Experiments consisted of placing 20 zebra mussels and 20 quagga mussels together into 1.9-L plastic cages tethered on anchored

lines in each basin. Each cage had two opposing 74-cm^2 rectangular windows covered with $400\text{-}\mu m$ Nitex-mesh to permit passage of water and seston. Two cages were tethered per line, each containing either 5-mm or 1%mm mussels. Lines were maintained 1.5 m off the lake bed by deployment of buoys 1 m above the tethered cages and at the surface.

Prior to experimentation, right valve shell length was measured to the nearest 0.2 mm using a Zeiss Technival II dissecting microscope, and wet mass was determined to the nearest 0.1 mg using a Cahn electrobalance. Because it was expected that bottom water temperature in western Lake Erie at the time of mussel deployment would exceed $15^\circ C$, experimental mussels destined for this basin were removed from the $4^\circ C$ environment chamber and placed in 3.8-L glass jars at $16^\circ C$ 4 days prior to deployment. Similarly, mussels incubated in eastern Lake Erie were transferred to and maintained at $6^\circ C$ for 4 days prior to deployment. Water temperature and oxygen profiles were obtained at each site when cages were deployed and recovered.

Cages were recovered following 55 (29 June-23 August) and 56 (8 July-2 September) days incubation (July and August) in western and eastern Lake Erie, respectively. One tethered line was not recovered in western Lake Erie, and mesh windows of one cage of a second line had been slightly damaged. Cages and animals were placed in sealed

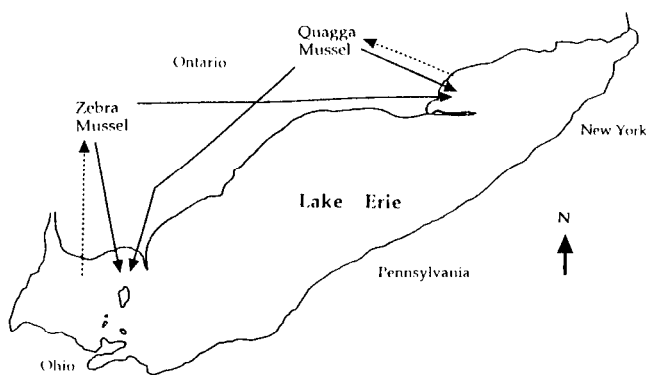


FIG. 1. Sites of reciprocal transplant experiment in western and eastern basins of Lake Erie. Zebra and quagga mussels originated (dotted lines) in western and eastern Lake Erie, respectively. In situ growth chambers were placed on tethered lines (solid lines) 1.5 m off the lake bed at three locations in each basin; two lines were recovered in western Lake Erie.

plastic bags and placed on ice for transport to the laboratory. Mussels were measured (length, wet mass) and placed in a 105°C oven for 24 hr prior to determination of dry weight (tissue and shell). Wet mass was highly correlated with dry mass for both 5 mm ($r^2 = 0.87$) and 15 mm ($r^2 = 0.90$) individuals. Mean wet mass and right valve length was computed for each mussel species in each cage before and after incubation in the lake. Length- and wet mass-specific growth rates were computed assuming exponential growth as:

$$G = 100 * (\ln W_2 - \ln W_1) / T$$

where G is length- or mass-specific growth rate (day^{-1}), W_2 and W_1 are mean final and initial right valve lengths or wet masses, and T is time in days (Winberg 1971).

Differences in length-specific and wet mass-specific rates of growth were compared for different species, size classes and lake basins using 3-way ANOVA; differences in mean specific growth rates of different mussel size classes in different basins were assessed using Bonferroni multiple comparisons tests.

Laboratory Experiment

Effects of temperature, food concentration, and potential competition between species on growth of two size classes of zebra and quagga mussels were determined in a complete factorial design experiment. Treatments consisted of placing two con- or hetero-specific mussels of the same length (5-mm or 15-mm) on a small piece of screen mesh in 500-mL glass jars with 435 mL of *Chlorella*-supplemented Lake St. Clair water, in constant environment chambers at 5 or 16°C. Mussels were acclimated to test conditions for 3 days prior to the outset of the experiment. Immediately prior to the experiment, each mussel was measured (right valve length, wet mass) and the right valve was color-marked for subsequent identification.

Lake water was initially prefiltered (see methods above) to remove virtually all particles within the established zebra mussel food spectrum (Sprung and Rose 1988). Either 5 mg dry mass L^{-1} (low food) or 10 mg dry mass L^{-1} (high food) of *Chlorella* powder was added to 20-L carboys of filtered lake water. This suspension was thoroughly mixed and refiltered through Whatman 41 (retention to 20-25 μm) filter paper. The resulting filtrate, which retained 62% of suspended *Chlorella* mass, provided ca. 3.1 and 6.2 mg L^{-1} *Chlorella* for mus-

sels in low and high food treatments, respectively. Food levels were selected to exceed minimum maintenance requirements for *D. polymorpha* (Walz 1978b).

Mussel survival was assessed daily when cultures were replenished with water by replacing 400 mL with an equal volume of fresh medium. Temperature of fresh medium was equilibrated with experimental conditions prior to use. Mussels were transferred to new jars containing fresh medium once per week. Five replicates were conducted per treatment. Right valve length, wet mass, and dry mass were determined for each mussel when the experiment was terminated after 34 days. Differences in length-specific and mass-specific rates of growth were compared for different species, size classes, and temperatures using 3-way ANOVA. Differences in survival frequencies of small zebra mussels and quagga mussels were tested at both temperatures using Fisher's Exact Test (Zar 1984).

RESULTS

Specific growth rates of mussels incubated in Lake Erie varied significantly among lake basins and among initial mussel size classes, though species differences were not detected (Table 1; Figs. 2, 3). In general, both measures of growth (length and mass) provided similar results. Each species and size class of mussel grew well in western Lake Erie and poorly in eastern Lake Erie; the interaction between initial mussel size and deployment location was also significant (Table 1; Figs. 2, 3). Growth rates of small (5-mm) mussels, pooled across species, were significantly greater than large (15-mm) individuals in western Lake Erie ($p < 0.05$). However, length and wet mass growth rates of large and small mussels incubated in eastern Lake Erie did not differ significantly ($p > 0.05$). Small zebra and quagga mussels incubated in the western basin increased in mean length by 118% and 108%, and in wet mass by an average of 742% and 873%, respectively. Small individuals incubated in the eastern basin decreased in wet mass by 11% and 6%, respectively. Small zebra mussels experienced mean shell degrowth of 70%, and quagga mussels grew by 1%. Growth of large zebra and quagga mussels was very similar in both basins, except for wet biomass increase in western Lake Erie (49% vs. 88%, respectively).

Both species and size classes of mussels experienced high survival when incubated in western Lake Erie. Small and large zebra mussels averaged 90% and 100% survival, respectively; comparable

TABLE 1. Results of tests (ANOVA) to determine effects of lake basin (location), initial mussel size (size), and mussel species (species) on mean length-specific (right valve) growth rate (shell growth), and mean wet mass-specific growth rate (mass growth) of *Dreissena* in Lake Erie. Probabilities lower than 0.007 are significant at an experimentwise error rate of 0.05.

Factor	df	Shell Growth		Mass Growth	
		F	P<	F	P<
Location	1, 12	707	0.0001	376	0.0001
Size	1, 12	288	0.0001	133	0.0001
Species	1, 12	<1	0.6222	1	0.3257
Location*Size	1, 12	193	0.0001	134	0.0001
Location*Species	1, 12	2	0.1989	2	0.1958
Species*Size	1, 12	1	0.3227	<1	0.8778
Location*Species*Size	1, 12	3	0.1301	<1	0.6201

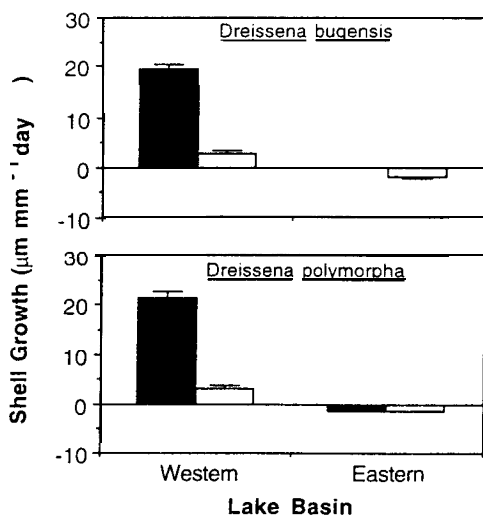


FIG. 2. Mean (+ S.E.) shell growth rate ($\mu\text{m mm}^{-1} \text{ day}^{-1}$) of 5-mm (solid) and 15-mm (open) quagga and zebra mussels incubated in western and eastern basins of Lake Erie.

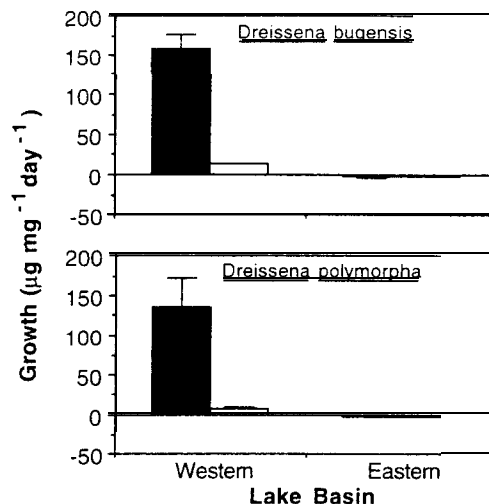


FIG. 3. Mean (+ S.E.) mass growth rate ($\mu\text{g mg}^{-1} \text{ day}^{-1}$) of 5-mm (solid) and 15-mm (open) *D. bugensis* and *D. polymorpha* incubated in western and eastern basins of Lake Erie.

rates for quagga mussels were 100% and 98%, respectively ($n = 2$ cages for each). Survival rates were slightly lower in eastern Lake Erie; mean rates for small and large zebra mussels in this basin were 85% and 90%, respectively, while quagga mussels averaged 98% and 85% survival, respectively ($n = 3$ cages each). Overall, no significant survival differences between species, sizes of species, or basins were detected (ANOVA, $p > 0.10$) though small sample sizes limited statistical power and the ability to discern differences.

Differences in mussel growth in western and eastern Lake Erie correspond with physical differences between sites. Western Lake Erie was warm and isothermal when field cages were deployed in late-June and retrieved in late-August (Fig. 4a,b). Water column oxygen concentrations in the west basin were at or close to saturation on both sampling dates, except at maximum depth at one sampling location in August (Fig. 4a,b). By contrast, eastern Lake Erie was thermally stratified when sampled in early July and in early September (Fig.

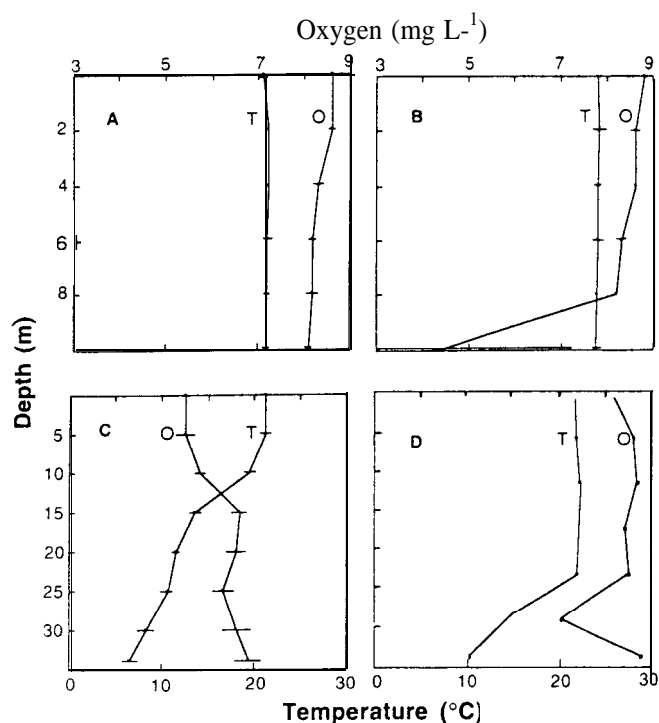


FIG. 4. Mean (2 S.E.) temperature (T) and Oxygen (O) concentration (mg L^{-1}) profiles at the time experimental cages were deployed (a,c) and recovered (b,d), in western (a,b) and eastern (c,d) Lake Erie.

4c,d): oxygen concentration increased slightly with depth in July, but values were generally lower than those recorded in early September.

Laboratory growth experiments generally corroborated field results, though growth rates were considerably lower than those observed in western Lake Erie. Growth rates were affected most by incubation temperature, mussel size, and by a temperature-mussel size interaction (Table 2). Preliminary analyses indicated that neither food concentration nor competitor species affected mussel growth (ANOVA, $p > 0.10$). Length and mass growth were significantly ($p < 0.0001$; Table 2) greater at 15°C than at 6°C (Figs. 5, 6). Small mussels had higher degrowth than larger individuals at low temperature, but also experienced higher growth rates at the higher environmental temperature. Small individuals of both species decreased in length and lost mass when incubated at 6°C (Figs. 5, 6), whereas large individuals experienced shell degrowth but a gain in wet weight. Shell length and

mass of both species increased at 15°C except for shell growth of large quagga mussels.

Differences between species growth rates were also evident (Table 2). Zebra mussels had lower length losses and higher mass gains at 6°C than quagga mussels, and experienced greater mass and length growth at 15°C except biomass growth of small individuals at 15°C (Table 2; Figs. 5, 6). For example, wet-mass losses of small zebra and quagga mussels averaged 6% and 13%, respectively, at 6°C though the species gained 14% and 26% of initial mass at 15°C .

Zebra and quagga mussels also experienced different mortality rates in laboratory cultures. Whereas no large individuals of either species died during the experiment, mortality of small quagga mussels (15 of 30) at 15°C was significantly greater than that of small zebra mussels (3 of 30) ($p = 0.0015$).

DISCUSSION

In situ growth rates of quagga and zebra mussels in Lake Erie were strongly size- and basin-dependent. Mean growth rates for 15-mm zebra (0.05 mm day^{-1}) and quagga (0.04 mm day^{-1}) mussels were much lower than respective values for 5-mm individuals (0.13 and 0.12 mm day^{-1}) in western Lake Erie. Growth of 15mm mussels was comparable, however, to that reported for 6.3-mm *D. polymorpha* in the laboratory (0.02 mm day^{-1}) and in Lake Maarsseveen, Netherlands (0.05 mm day^{-1}) (Dorgelo and Smeenk 1988). Growth of 5-mm *D. polymorpha* in the Lower Rhine River ranged between 0 and 0.15 mm day^{-1} and was strongly related to spring and autumn water temperature but decoupled from summer temperature (Smit *et al.* 1992). Smit *et al.* (1992) suggested that the allocation of energy to reproduction may result in the decoupling of growth and water temperature.

Mussels incubated in eastern Lake Erie typically experienced shell degrowth and mass loss. These findings are generally consistent with those from an exhaustive series of laboratory and field experiments conducted by Walz (1978a-c) that identified mussel size, temperature, and food supply as determinants of zebra mussel growth. Growth was inversely related to mussel size, optimal between 10°C and 15°C and maximal at an algal concentration of -2 mg C L^{-1} ($4 \text{ mg dry mass L}^{-1}$). Mussels incubated for 2 years at 60 m depth in Lake Constance, Germany, where temperature varied between 4.5° to 5.5°C , experienced an exponential decline in body mass, protein, and carbon, though

TABLE 2. Results of tests (ANOVA) to determine the effects of environmental temperature (temp.), mussel species (species), and initial mussel size (size) on length-specific growth rates (shell growth) and mass-specific growth rates (mass growth) of *Dreissena* in laboratory experiments. Probabilities lower than 0.007 are significant at an experimentwise error rate of 0.05.

Factor	df	Shell Growth		Mass Growth	
		F	P<	F	P<
Temp.	1, 211	55	0.0001	93	0.0001
Size	1, 211	32	0.0001	<1	0.7751
Species	1, 211	26	0.0001	<1	0.9852
Temp.*Size	1, 211	45	0.0001	44	0.0001
Temp.*Species	1, 211	1	0.2398	8	0.0066
Species*Size	1, 211	1	0.2845	1	0.3723
Temp.*Species*Size	1, 211	<1	0.9836	8	0.0045

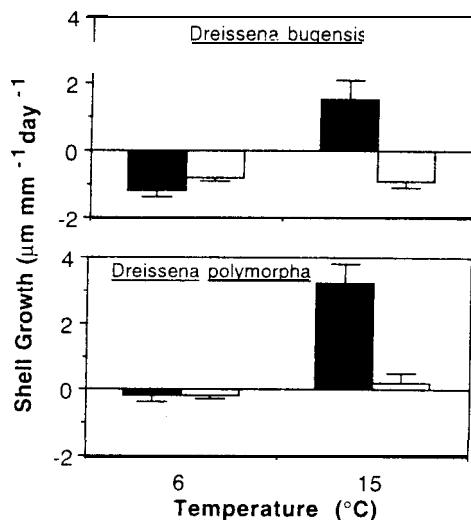


FIG. 5. Mean (+ S.E.) shell growth rate ($\mu\text{m mm}^{-1} \text{day}^{-1}$) of 5-mm (solid) and 15mm (open) *D. bugensis* and *D. polymorpha* in laboratory experiments.

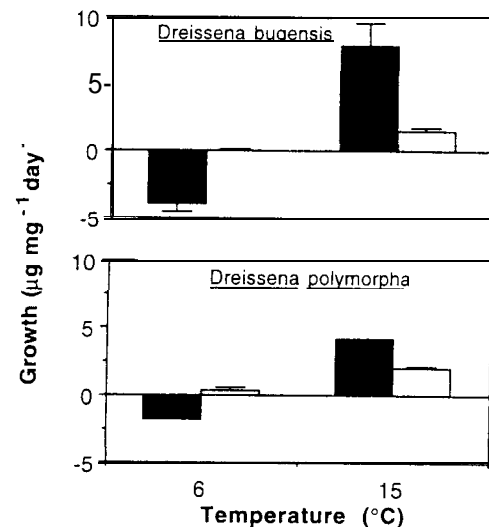


FIG. 6. Mean (+ S.E.) mass growth rate ($\mu\text{g mg}^{-1} \text{day}^{-1}$) of 5-mm (solid) and 15-mm (open) *D. bugensis* and *D. polymorpha* in laboratory experiments.

shell length remained constant (Walz 1978~). Morton (1969) observed that growth of *D. polymorpha* in a London, England reservoir was restricted to periods when water temperature exceeded 11°C. This value agrees with a 10-12°C growth threshold for *D. polymorpha* in Lake St. Clair (Mackie 1991) but contrasts with the 3°C threshold reported by Smit *et al.* (1992). It seems unlikely, however, that low temperature in eastern Lake Erie was responsible for observed growth patterns because quagga mussels were found in abundance at the site and postveliger mussels settled and grew on non-mesh exterior surfaces of experimental cages. The release of gametes could potentially account for mass loss,

but hypolimnetic water temperature ($\leq 10^\circ\text{C}$) was below that (12°C) reported to initiate spawning in European *D. polymorpha* (Borcherding 1991).

Growth differences in eastern and western Lake Erie may have resulted from differences in food concentration and water flow rates. Vertically-integrated, uncorrected, chlorophyll a concentration was usually lower at study sites in eastern ($X = 1.8 \mu\text{g L}^{-1}$) than in western ($X = 4.8 \mu\text{g L}^{-1}$) Lake Erie during summer 1993 (E. S. Millard, Department of Fisheries and Oceans, Burlington, ON, pers. comm.). However, chlorophyll a depletion in near-bottom water may have reduced the magnitude of food concentration differences experienced by mus-

sels incubated at these sites (e.g., see MacIsaac *et al.* 1992). Water flow rates over the lake bed could also affect food concentration experienced by mussels. Flow rates tend to be lower at depth in eastern (5.2 cm sec⁻¹) than in western (7.0 cm sec⁻¹) Lake Erie during July and August (Saylor and Miller 1987). A higher rate of water renewal through containers incubated in western Lake Erie may have reduced the severity of "local" seston depletion. Grizzle *et al.* (1992) observed that growth of the hard clam *Mercenaria mercenaria* was positively correlated with current speed, and speculated that the potential for seston depletion would decrease as water flow speed increased from no-flow conditions up to the animal's pumping speed. While pumping rates of small *D. polymorpha* are lower than benthic flow rates in eastern and western Lake Erie, those of larger individuals almost certainly exceed flow rates in at least the eastern basin (Bunt *et al.* 1993, Saylor and Miller 1987).

Quagga and zebra mussels incubated in Lake Erie had very similar growth and survival rates (Figs. 2, 3). By contrast, some species effects were evident in the laboratory experiments (Figs. 5, 6), as zebra mussels tended to grow faster and, for small individuals at 15°C survive longer than quagga mussels. It is unlikely that these species differences are ecologically meaningful because both species experienced high survival and good growth in western Lake Erie, where temperatures were higher and potentially more stressful than those in laboratory tests. The slightly better survival of zebra mussels in laboratory experiments is consistent with the results of Domm *et al.* (1993), who reported that acute thermal tolerance of quagga mussels was lower than that of zebra mussels.

IMPLICATIONS FOR SPECIES DISTRIBUTIONS

A number of factors may account for differences in the distribution of zebra and quagga mussels, including different times and locations of introduction, different mechanisms or rates of dispersal, and different physiological tolerances. Introduction dates cannot be ascertained, but based on dates the species were first reported and the sizes of presumed founding individuals (Hebert *et al.* 1989, Griffiths *et al.* 1991, Mills *et al.* 1993b), zebra mussels may have been introduced 1 or 2 years prior to quagga mussels. Identification of the initial quagga mussel founding site has not been made, though it is unlikely that the species was introduced with the zebra mussel because a *Dreissena* allozyme survey conducted on Lake St. Clair individuals failed to detect

the presence of quagga mussels during 1988 (Hebert *et al.* 1989; P. D. N. Hebert, University of Guelph, pers. comm.). Therefore, it seems plausible that the quagga mussel was introduced at a site lower in the Great Lakes than where the zebra mussel was introduced, and that the former is still in the process of colonizing upstream sites. This view is consistent with the excellent growth and survival of both large and small quagga mussels in western Lake Erie and indicates that the species is physiologically capable of tolerating summer conditions in the basin. Quagga mussels are also found in abundance at shallow water sites in the eastern basin near Nanticoke, Ontario, where summer surface temperature $\geq 21^\circ\text{C}$ (pers. obs.; Schertzer *et al.* 1987).

Dispersal differences may contribute to disparities in zebra and quagga mussel distributions. However, it has not been established whether veligers produced by benthic quagga mussels overlap spatially with those of littoral zebra mussels, nor whether potential dispersal mechanisms (currents, ballasting or trailered boats, waterfowl) (Carlton 1992) effect dispersal of the species equally. Any factor that differentially affects dispersal of larvae or adults of these species could impact rates at which their geographic distributions expand.

CONCLUSIONS

Growth rates of zebra and quagga mussels incubated in Lake Erie varied by basin of incubation and initial mussel size, though species differences were not detected. Survival of transplanted zebra and quagga mussels was high in both western and eastern Lake Erie. Laboratory experiments generally corroborated field results, as temperature and initial mussel size were the best predictors of mussel growth. *In situ* growth and survival rates of quagga mussels in western Lake Erie indicate that the species is physiologically tolerant of mid-summer environmental conditions in the basin. The absence of quagga mussels from most of the western basin may relate more to the timing and location of introduction than to physiological constraints.

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