Deepwater population structure and reproductive state of quagga mussels (*Dreissena bugensis*) in Lake Erie

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Abstract: Quagga mussel (*Dreissena bugensis*) population structure and reproductive status were assessed at deepwater (37 and 55 m) sites in eastern Lake Erie during July 1996. Mussels occupied ~70% of soft substrates at 37-m sites and between 63 and 90% at 55-m sites. Shell length and dry mass frequency distributions were similar at both sites, although recruits ≤5 mm comprised a larger proportion of the population at the deeper site. The population surveyed here allocated disproportionately less mass to shell and more to soft tissues relative to zebra mussels (*Dreissena polymorpha*) from shallow-water sites in eastern Lake Erie and from Lake St. Clair. The population at 55 m was slightly skewed toward male mussels (58%). Female mussels that were examined for reproductive state contained mature oocytes (80%) or had spent gonads (20%). Because water temperature at the site was only 4.8°C, this survey provides the first evidence of gonadal development and spawning by quagga mussels at low temperature. These findings contrast with most reports of spawning by congeneric zebra mussels at temperatures ≥12°C but are consistent with distributions of the species in different basins of the lake.

Résumé : La structure de la population et l'état génésique des moules quaggas (*Dreissena bugensis*) ont été estimés à des sites en eau profonde (37 et 55 m) dans l'est du lac Érié en juillet 1996. Les moules occupaient environ 70 % du fond là où le substrat était mou (37 m de profondeur) et entre 63 et 90 % aux sites par 55 m de profondeur. Les distributions de fréquence selon la longueur des coquilles et la masse sèche étaient semblables aux deux sites, même si les recrues de ≤5 mm composaient une proportion plus importante de la population au site plus profond. La population étudiée ici présentait, de façon disproportionnée, moins de masse de coquilles et plus de tissus mous comparativement à la moule zébrée (*Dreissena polymorpha*) provenant de sites en eau moins profonde dans la partie orientale du lac Érié et dans le lac Sainte-Claire. La population à 55 m était légèrement biaisée en faveur des mâles (58 %). Les femelles examinées contenaient à 80 % des ovocytes matures et à 20 % des gonades vides. Étant donné qu'au site, la température de l'eau n'était que de 4,8°C, l'étude fournit la première preuve du développement des gonades et de la fraye chez des moules quaggas à de basses températures. Ces conclusions sont contraires à la plupart des rapports sur sa congénère la moule zébrée, qui frayerait à des températures ≥12°C, mais sont conformes aux distributions de l'espèce dans différents bassins du lac.
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Introduction

Zebra mussels (*Dreissena polymorpha* (Pallas)) were discovered in Lake St. Clair in 1988, although the colonization event may have occurred as early as 1985 (Hebert et al. 1989). Quagga mussels (*Dreissena bugensis* Andrusov) were discovered in eastern Lake Erie in 1989 (May and Marsden 1992; Rosenberg and Ludyanskiy 1994; Mills et al. 1996). While the distribution of the former species has since expanded to include major river systems and numerous inland lakes throughout temperate eastern North America (Ram and McMahon 1996), the latter is restricted primarily to the central and eastern basins of Lake Erie and Lake Ontario (Mills et al. 1993, 1996). Zebra and quagga mussels attach via byssal threads to either solid substrates in shallow, turbulent waters or to soft sediments in areas where wave disturbance is low (Dermott

and Munawar 1993; Mills et al. 1993; S. Roe, personal observation). The species differ morphologically, physiologically, genetically, and, frequently, with respect to depth distributions (reviewed in Mills et al. 1996). Zebra mussels are restricted primarily to epilimnetic waters whereas quagga mussels occur in both littoral and profundal areas (reviewed in Mackie et al. 1989; Dermott and Munawar 1993; Mills et al. 1993).

Growth and reproduction of *Dreissena* living in the hypolimnion of large lakes may be constrained by low water temperatures. For example, although distinct gonad growth in *D. polymorpha* occurred at temperatures as low as 2–4°C, spawning was restricted to periods during which temperature was ≥12°C (Borcherding 1991). Similarly, Sprung (1987, 1995) reported that gonad size of *D. polymorpha* could increase during periods when lakes were ice-covered if sufficient food was available, but fertilization of eggs occurred only when water temperature exceeded 10°C. Possibly owing to its far more limited distribution in Europe relative to *D. polymorpha*, virtually nothing is known about the thermal biology of *D. bugensis*, particularly its effect on reproduction. To date, no studies have assessed the reproductive status of *D. bugensis* in deep, cold-water environments. We surveyed population size structure and reproductive status of *D. bugensis* from deepwater (37 and 55 m) sites in eastern Lake Erie.

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Materials and methods

Dreissena bugensis was collected on 15 July 1996 in eastern Lake Erie at sites on the north (42°37.378′N, 80°00.56′W) and south (42°27.13′N, 80°07.37′W) sides of Long Point, Ontario. Depths at the sites were 37 and 55 m, respectively. Mussels and sediment cores were collected from three adjacent locations (<200 m apart) at each depth using a shovel and corer, respectively, attached to an articulated arm of an SDL-1 submersible (Canadian Forces). Samples were stored separately in external compartments on the submarine. Water temperature was recorded with a Hobo temperature logger fastened to the exterior of the submarine.

Upon return to the surface, mussel samples were wrapped in aluminum foil and frozen at –20°C. Half of one sample from a 55-m site was frozen, while the other half was stored live wrapped in wet paper towels for later assessment of the reproductive state of the population (Nichols 1993). Live animals were placed on ice during transport to the laboratory and transferred to an aquarium containing dechlorinated (ROpure) filtered tap water (Sybron/Barnstead, Dubuque, Iowa) at 5°C. The following morning, live mussels were measured (±0.1 mm) using Manostat vernier calipers and weighed (±1 mg) using an A/D model FX-200 electronic balance. The reproductive–digestive tract was removed from 70 individuals with ≥15 mm shell length and examined at 100× magnification with a compound microscope using a squash mount preparation. Reproductive state of female mussels was categorized according to the developmental stage of oocytes: <50% of eggs with visible germinal vesicle, >50% of eggs with visible germinal vesicle, and spent (spawned) reproductive tissues (Nichols 1993). Presence of a visible germinal vesicle is characteristic of mature eggs (Nichols 1993). Diameter of 10 eggs from each of 10 randomly selected females (≥15 mm) was measured with an ocular micrometer (±10 μm). Reproductive state of male mussels was not categorized.

Frozen mussels were thawed, blotted dry with a paper towel, shell length measured, and eviscerated. Samples from the 37- and 55-m sites contained (±SE) 109 ± 11 and 162 ± 12 individuals, respectively. Soft tissues and shells were weighed separately. Soft tissues of all mussels from two randomly selected samples (one from each depth) were individually placed on preweighed aluminum weigh boats, dried for 24 h at 60°C, and reweighed. To test for constancy of dry mass, the dried sample from 55 m was reassessed following 48 h of exposure at 60°C; mass of all individuals remained constant (±1 mg). The relationship between dry soft mass and shell length was fitted separately for each dried sample using nonlinear regression analysis (Systat Inc. 1992) and subsequently used to estimate dry soft mass of mussels in the other two samples from the same depth. Differences in shell length and dry soft mass distributions of mussels collected at each of the depths were assessed using Kolmogorov–Smirnov two-sample tests.

Bottom coverage by *D. bugensis* was monitored at four positions at the 55-m site using a Sony 537A Beta Cam SP equipped with a Figinon lens. Video images were downloaded to a personal computer using a Targa+ frame grabber. Percent bottom coverage was determined digitally by comparing relative area of mussel coverage to area of exposed substrate (Mocha 1.2 software, Jandel Scientific).

Results

Water temperature was 6 and 4.8°C for the 37- and 55-m sites, respectively. Both sites had relatively flat topography devoid of hard substrates. Benthic substrates at both sites were composed of silt and clay (J.J.H. Ciborowski, Biology Department, University of Windsor, Windsor, Ont, personal communication).

Dreissena bugensis was widely distributed at each location at the 37-m depth. Because of colony patchiness, bottom coverage averaged ~70% at the three locations. Dense colonies

were observed in some sediment troughs but not on crests. The distribution at 55 m was similar to that at 37-m depths. Image analysis of four image frames revealed mean coverage of 76.4% (range 63–90%). As at the 37-m sites, dense colonies were also observed in sediment troughs (100% coverage).

Shell length of *D. bugensis* ranged from 3.8 to 25.3 mm ($\bar{x} = 13.6$ mm) at 37 m depth and from 2.0 to 25.7 mm ($\bar{x} = 11.8$ mm) at 55 m depth (Figs. 1 and 2). Mussel allometry was very similar at both depths (Table 1). For example, neither shell length nor dry soft mass distributions differed between sites ($P > 0.05$; Kolmogorov–Smirnov tests), although large (>22 mm) mussels from the deeper site had substantially higher mass than those from 37 m (Figs. 1 and 2). Relationships between dry soft mass and shell length were also very similar at both depths (Fig. 3).

Female mussels comprised 42% of the population surveyed at the 55-m depth. All female mussels ≥15 mm that were censused were sexually mature. Of these individuals, 56% had eggs of which >50% contained a visible germinal vesicle, and 24% had eggs of which <50% contained a visible germinal vesicle. Oocyte diameter averaged 78 ± 3 μm in these females. The remaining 20% of females had already spawned.

Discussion

Most surveys of *Dreissena* distribution have examined populations inhabiting solid substrates (e.g., Stańczykowska 1977; Lewandowski and Stańczykowska 1986; Wisniewski 1990; Mellina and Rasmussen 1994; Martel 1995; Nalepa et al. 1995; MacIsaac 1996a; Mitchell et al. 1996). Despite this pattern, both *D. polymorpha* and *D. bugensis* have been reported as resident on soft substrates including sand, silt, and mud (Hunter and Bailey 1992; Dermott and Munawar 1993; Mills et al. 1993). *Dreissena* may be precluded from soft-bottom substrates in shallow water owing to wave-associated disturbance (Lewandowski and Stańczykowska 1986; Nalepa et al. 1995; MacIsaac 1996a; Mills et al. 1996). In this study, we observed quagga mussels that formed extensive, nearly continuous colonies on soft substrates at 37- and 55-m depths in eastern Lake Erie. Colonies at these depths are unlikely to be affected by factors such as waves, ice scour, and waterfowl predation that may influence population distribution, size structure, and density in shallow-water habitats (see MacIsaac 1996b). The presence of mussels in troughs but not on crests of sediment undulations suggests that near-bottom currents (~2 cm·s⁻¹; H. MacIsaac, personal observation) may influence the delivery of larval settlers.

Dreissena bugensis of all sizes collected at both depths were very fragile, with thin and brittle shells. Some individuals were accidentally crushed during shell length measurements, a problem never encountered during manipulation of conspecifics from surface waters near Nanticoke, Ont., or of *D. polymorpha* from western Lake Erie (H. MacIsaac, personal observation). Deepwater *D. bugensis* appear to allocate very little energy to shell formation, possibly reflecting the low degree of turbulence encountered at depth in eastern Lake Erie (Table 1; Fig. 4). For example, relative to *D. polymorpha* from shallow water in eastern Lake Erie, deepwater *D. bugensis* allocate more energy to soft tissues and less to shell; this difference was more pronounced with large than with small mussels (Fig. 4). The strength of mollusc shells has important implications

Fig. 1. Mean (+SE) length frequency distribution of *D. bugensis* from 37- and 55-m depths in eastern Lake Erie.
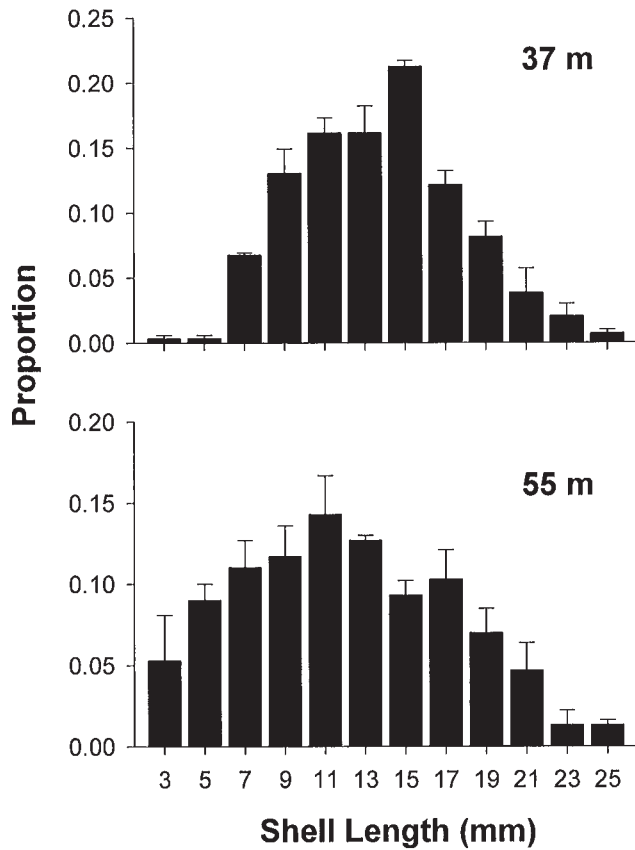
Fig. 2. Mean (+SE) dry soft mass frequency distribution of *D. bugensis* from 37- and 55-m depths in eastern Lake Erie.
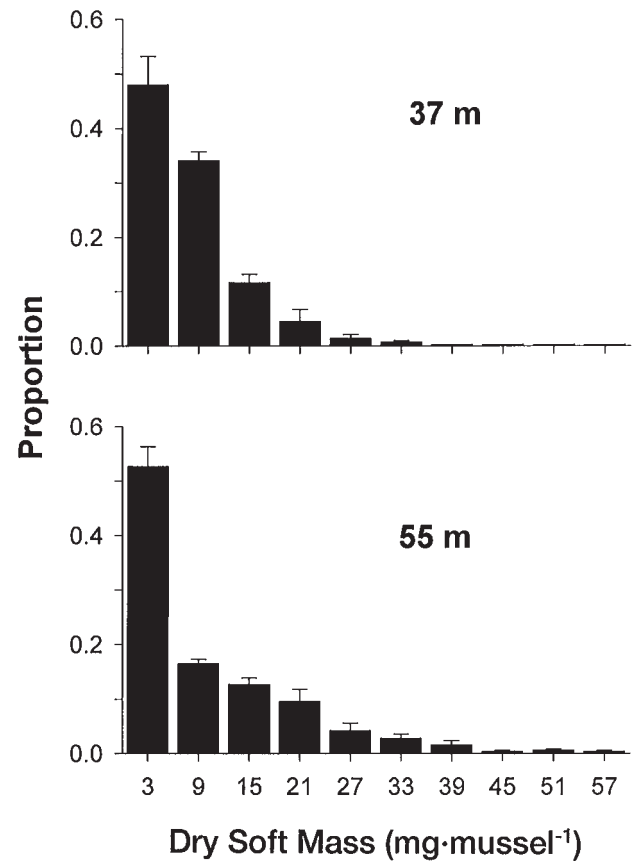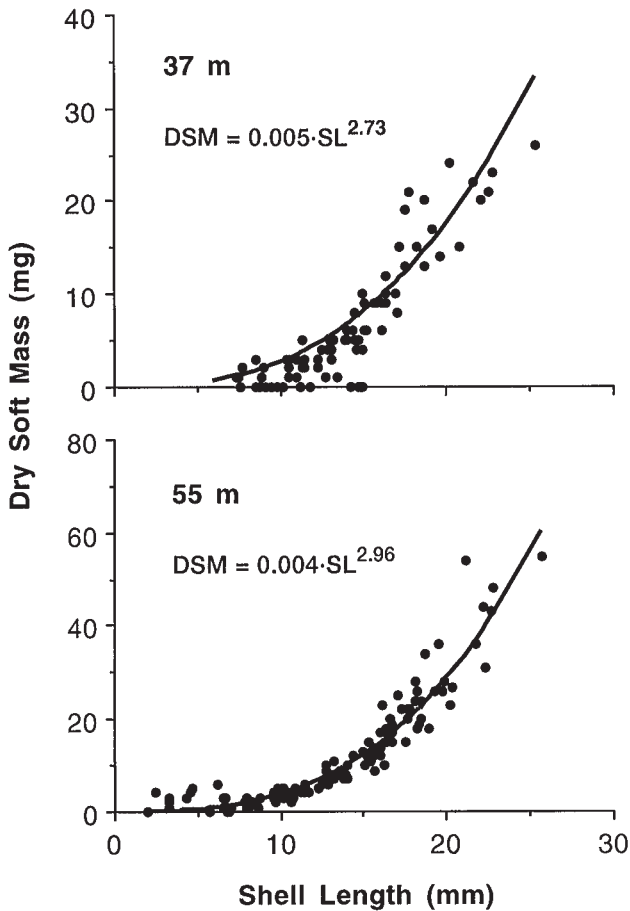

Table 1. Allometric relationships between mussel mass (mg) and shell length (mm).

Species	Location	Depth (m)	Mass type	*a*	*b*	Reference
D. bugensis	Lake Erie (east)	37	DSM	0.005	2.725	This study
D. bugensis	Lake Erie (east)	55	DSM	0.004	2.964	This study
D. polymorpha	Lake Erie (east)	3	DSM	0.040	2.198	Dermott et al. 1993*
D. polymorpha	Lake St. Clair	<2	DSM	0.007	2.982	Mackie 1991
D. polymorpha	Slesinskie Lake	NS	DSM	0.015	2.406	Stańczykowska 1977
D. polymorpha	Lichenskie Lake	NS	DSM	0.012	2.576	Stańczykowska 1977
D. polymorpha	Patnowskie Lake	NS	DSM	0.014	2.520	Stańczykowska 1977
D. polymorpha	Neusiedler Lake	NS	DSM	0.022	2.355	Stańczykowska 1977
D. polymorpha	Mikolajskic Lake	NS	DSM	0.005	2.931	Stańczykowska 1977
D. polymorpha	Taltowisko Lake	NS	DSM	0.061	1.937	Stańczykowska 1977
D. bugensis	Lake Erie (east)	37	WSM	0.044	2.831	This study
D. bugensis	Lake Erie (east)	55	WSM	0.034	2.966	This study
D. polymorpha	Lake Erie (east)	3	WSM	0.135	2.695	Dermott et al. 1993*
D. bugensis	Lake Erie (east)	37	TWM	0.064	2.911	This study
D. bugensis	Lake Erie (east)	55	TWM	0.054	3.002	This study
D. bugensis	Zaporozh'ye Reservoir	NS	TWM	0.064	3.32	Zolotareva 1976
D. polymorpha	Lake Erie (east)	3	TWM	0.244	2.663	Dermott et al. 1993*
D. bugensis	Dneiper-Krivoy Rog Canal	NS	TM	0.244	2.687	Shevstova 1971
D. polymorpha	Dneiper-Krivoy Rog Canal	NS	TM	0.278	2.701	Shevstova 1971
D. bugensis	Lake Erie (east)	55	SM	0.035	2.877	This study
D. bugensis	Lake Erie (east)	55	SM:DSM	1.604	0.603	This study

Note: Regressions were of the form mass = a(shell length)^b. Key: NS, not specified; DSM, dry soft mass; WSM, wet soft mass; TWM, total wet mass (shells plus viscera); SM, dry shell mass; TM, total mass.

*Equation format modified from original form.

Fig. 3. Relationship between mussel dry soft mass (DSM) and shell length (SL) for *D. bugensis* from 37- and 55-m depths in eastern Lake Erie.
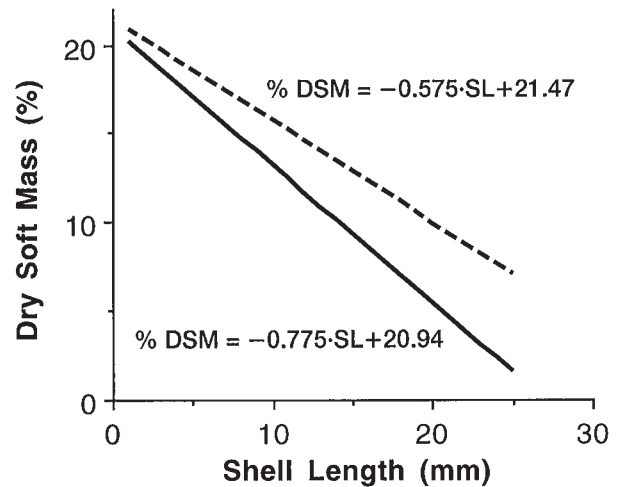

Fig. 4. Allocation to soft tissues, as a percentage of total dry mass, of *D. polymorpha* (solid line) and *D. bugensis* (broken line) in eastern Lake Erie. *Dreissena polymorpha* was surveyed at a shallow (3 m) site near the north shore of the lake (Dermott et al. 1993), while *D. bugensis* was collected at 55 m.

regarding the types and sizes of predators capable of preying on the mussel (Appleton and Palmer 1988; MacIsaac 1994). *Dreissena polymorpha* has weaker shells than other bivalves (Miller et al. 1994). Thus, deepwater *D. bugensis* may be more vulnerable to predators than other *Dreissena* populations. Alternatively, thinner shells of deepwater *Dreissena* may be a result of lower predation pressure (Appleton and Palmer 1988) or may reflect reduced calcium carbonate availability in deepwater environments.

Deepwater *D. bugensis* has lower total wet mass than other *Dreissena* populations from other locations. For example, total wet mass (shell plus viscera) of individuals from 37- and 57-m depths was much less than total wet mass of similar sized *D. polymorpha* from shallow water in eastern Lake Erie (Table 1; Dermott et al. 1993). Moreover, total wet mass increased at a lower rate with increasing shell length for *D. bugensis* from eastern Lake Erie relative to conspecifics from the Zaporozh'ye Reservoir, Ukraine (Table 1; Zolotareva 1976).

Thermal effects on reproductive development of *D. bugensis* are unknown. Gonad growth and development of *D. polymorpha* is cued by changes in temperature (Stańczykowska 1977; Walz 1978; Borcherding 1991). Consistent low temperatures may delay or prevent the onset of sexual maturity in *D. polymorpha*. For example, oocyte growth rate of zebra mussels from

Lake Constance maintained in water from 60 m depth was less than half that of oocytes from mussels maintained in surface water, even though maximum diameter of oocytes did not differ between the two groups (Walz 1978). Mean oocyte diameter for *D. bugensis* reported in this study is well within the published range for mature oocytes of *D. polymorpha* (40–85 μm; Nichols 1993), although temporal sampling is necessary to determine rate of growth. Borcherding (1995) found that oocytes did not mature in *D. polymorpha* from the Fühlinger See maintained at 5°C whereas they did mature in 36 and 100% of females maintained at 12 and 19°C, respectively. The presence of mature oocytes in *D. bugensis* from cold, deep waters clearly demonstrates a lower thermal limit for gonadal growth and development than has been reported for *D. polymorpha*.

Synchronization of gamete release to thermal cues has been suggested for *D. polymorpha* and the blue mussel (*Mytilus edulis*) (Sprung 1983). In a review of 18 European and North American studies of *D. polymorpha* populations, Nichols (1996) reported a 10°C minimum threshold for the appearance of larvae, although temperatures commonly ranged between 12 and 15°C or higher. If thermal cues of this scale are important to spawning initiation in *D. bugensis*, individuals inhabiting deepwater sites in eastern Lake Erie possibly would never be exposed to appropriate cues; near-bottom temperatures rarely exceed 7–8°C during summer months and only approach 10–11°C during fall turnover (Schertzer et al. 1987). Mills et al. (1993) questioned whether temperature had any effect on the reproductive success of *Dreissena* in Lake Ontario given that hypolimnetic temperature rarely exceeds 5°C. Walz (1978) also dismissed a direct role of temperature in reproduction after observing *D. polymorpha* spawn at low temperature in Lake Constance (4.5–5.5°C) and Grosse Plöner See (2.6°C), Germany (N. Walz, Department of Lowland Rivers and Shallow Lakes, Berlin, Germany, personal communication). These studies, and the presence of spawned and gravid females in eastern Lake Erie observed in this study, suggest that factors

other than temperature may influence spawning. Ram and Nichols (1993) proposed a model in which spawning is triggered initially by chemicals associated with phytoplankton, followed by further stimulus by chemicals associated with gametes. A heat-stable metabolite released by phytoplankton has been demonstrated to trigger spawning in *M. edulis* (Starr et al. 1990).

The presence of gravid and spent female *D. bugensis* near the deepest section of Lake Erie suggests that local recruitment may not depend on advective transport of larvae from adjacent littoral areas. However, further work is required before it can be concluded that the gravid and spent female mussels observed in this survey reproduce successfully or contribute to local recruitment of mussel populations in deep water in eastern Lake Erie.

Acknowledgements

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