

## Species and epilimnion/hypolimnion-related differences in size at larval settlement and metamorphosis in *Dreissena* (Bivalvia)

**Abstract**—Recently settled postlarval quagga mussels (*Dreissena bugensis*) and zebra mussels (*D. polymorpha*) were examined using optic microscopy to determine planktonic shell growth and size at settlement and metamorphosis from two habitats in Eastern Lake Erie: nearshore epilimnion and offshore hypolimnion. Postlarvae (shell length  $\sim 400$ – $2000$   $\mu\text{m}$ ) were collected from various substrates between 1992 and 1995. Planktonic shell growth and size at settlement and metamorphosis were determined by measuring height of the prodissoconch I (PI) and prodissoconch II (PII) on right valves. Mean PI height was 79.07 (SD = 4.64) and 79.62  $\mu\text{m}$  (SD = 4.28) for the quagga and zebra mussel, respectively, and did not differ between species or across habitats. There was, however, a distinct between-species difference in size at settlement and metamorphosis (PII size), with larvae of the quagga mussel settling at significantly larger sizes than those of the zebra mussel (nearshore/epilimnion data: quagga PII means, 256–284  $\mu\text{m}$ ; zebra PII means, 236–249  $\mu\text{m}$ ). In addition, quagga mussel larvae settled at a greater size in the offshore hypolimnion habitat (PII mean = 313.64  $\mu\text{m}$ , SD = 24.69,  $n = 320$ ) compared to nearshore epilimnion habitat (mean = 261.89  $\mu\text{m}$ , SD = 19.41,  $n = 207$ ). The additional 28% of larval shell (PII) secreted by offshore hypolimnion quagga mussels may be linked to several factors, including a prolonged planktonic period. This study is the first to document the relationship between offshore distance and size at settlement in a bivalve.

The larvae of bivalves constitute a significant component of the plankton of many marine and estuarine communities during the breeding and recruitment seasons (Thorson 1946; Loosanoff et al. 1966). In contrast, in freshwater ecosystems, few lamellibranch taxa display planktonic larval development and free-swimming planktotrophic larvae (Ackerman et al. 1994). Among those that do are mollusks of the family Dreissenidae, a group of bivalves originating from the Caspian Sea and Black Sea regions (Stańczykowska 1977; Rosenberg and Ludyanskiy 1994). Like many marine bivalves with planktotrophic larval development, a *Dreissena* larva spends many days feeding, developing, and dispersing over great distances until it is competent to settle, metamorphose, and begin the benthic byssate life of the adult (Sprung 1989; Ackerman et al. 1994; Martel et al. 1995). This taxonomic group includes several highly invasive species that have been accidentally introduced via human activities to many rivers and large lakes in Europe and more recently in North America (Hebert et al. 1991; Mackie 1991). Free-swimming larvae of dreissenid bivalves have become an important component of the planktonic community of the Laurentian Great Lakes, with summer larval densities commonly in the range of  $10^3$ – $10^5$   $\text{m}^{-3}$  (Garton and Haag 1993; Martel et al. 1994).

Although similar in appearance and basic life history, the quagga mussel, *Dreissena bugensis*, differs from the zebra

mussel, *D. polymorpha*, in a number of traits, including shell morphology, physiology, and reproduction, as well as habitat requirements (May and Marsden 1992; Dermott and Munawar 1993; Domm et al. 1993, Claxton and Mackie 1998). Unlike zebra mussels, which are typically found on hard substrates in nearshore habitats, the quagga mussel can colonize soft-bottom substrates found within offshore deep water habitats of large lakes (Dermott and Munawar 1993; Mills et al. 1993, 1996; Claxton and Mackie 1998). Dermott and Munawar (1993) reported that in Eastern Lake Erie quagga mussels outnumbered zebra mussels by 14 to 1 in the hypolimnion ( $\sim >20$  m) and had successfully colonized soft substrates beyond 40 m. In Lake Ontario, Mills et al. (1993) collected quagga mussels at a depth of 130 m, and larvae and adults of the quagga mussel also occur in shallow water substrates in Eastern Lake Erie (Mitchell et al. 1996).

The potential effect of inshore versus offshore and other related physical conditions on the morphology and ecology of planktotrophic larvae of benthic invertebrates has received little attention, with only one study on a marine gastropod (Robertson 1994). Previous studies have documented that bivalve larval size at settlement and metamorphosis as well as the duration of the planktonic period can vary greatly (Bayne 1965; Pechenik 1984, 1985). This can be observed in the larval shell of bivalves with planktotrophic larval development, which acts as a skeletal record of the growth and developmental history (e.g., size at settlement and metamorphosis) of the animal (Ockelmann 1965; Lutz and Jablonski 1978; Lutz et al. 1984; Martel et al. 1995). This is evident in the larval shell, which is composed of two distinct regions, the D-shaped prodissoconch I (PI) and the prodissoconch II (PII) (Martel et al. 1995). However, little is known about the morphological, behavioral, or ecological response of planktotrophic larvae of benthic invertebrates along natural environmental gradients (but see Lutz and Jablonski 1978). The recent successful colonization of *Dreissena* spp. in the lower Laurentian Great Lakes, including the ecological success of the quagga mussel both in the offshore hypolimnion and the nearshore epilimnion habitats of Lake Erie, provides an opportunity to distinguish the influence of physical environments on the larval development of a benthic invertebrate. In this study, using light microscopy and field-collected postlarval specimens from benthic and buoy samples, we first compare the morphometry of prodissoconch I and II of the quagga mussel with that of the zebra mussel. Second, we demonstrate notable differences in planktonic larval shell growth and size at metamorphosis between quagga mussels settling in nearshore epilimnion and offshore hypolimnion environments. The observed differences in size at settlement and metamorphosis (PII) reported herein could reflect on important differences in larval ecol-

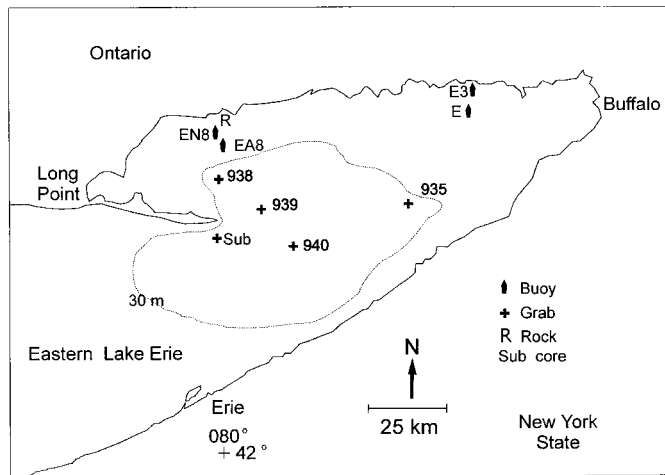


Fig. 1. Sampling sites in Eastern Lake Erie, during 1992–1995. Nearshore epilimnion (~2 m) sites: near Nanticoke, buoys EN8 and a rocky reef (R). Near Port Colborne, buoys E and E3. Offshore hypolimnion benthic samples were collected at Fisheries and Oceans water quality sites in the Eastern Basin of Lake Erie, including sites 935 (35 m), 938 (36 m), 939 (45 m), and 940 (57 m), as well as station sub collected using a submersible (50 m).

ogy between species as well as within species between habitats.

**Materials and methods**—Mussels were collected as part of limnological studies designed to examine the distribution and the impact of *Dreissena* spp. on native benthic invertebrates and on food webs in the Great Lakes (Wormington et al. 1995; Dermott et al. 1998). Early juvenile mussels (shell length ~400–2000  $\mu\text{m}$ ) were collected from the nearshore shallow water and offshore deep water habitats in Eastern Lake Erie (Schertzer et al. 1987) (Fig. 1). Sites were located east of the Long Point area, near the towns of Nanticoke (area of buoys EN8 and EA8) and Port Colborne (area of buoys E and E3), Ontario (Fig. 1). Each sample of postlarvae came from a different site within that habitat and was considered a replicate, with no consideration given to the year of collection (1992–1995).

A total of six hypolimnion benthic samples were collected at irregular intervals during the period 1993–1995 at five sampling sites (one sample per site, except for site 938, which was sampled twice) in the offshore hypolimnion waters of Eastern Lake Erie (Fig. 1). For 1993 and 1994, samples were collected using a petite Ponar grab (0.022 m<sup>2</sup>). Site number (depth) and date of collection were: site 935 (35 m) on 14 June 1993, site 938 (36 m) and 939 (45 m) on 15 June 1993, as well as site 938 (36 m) and site 940 (47 m) on 13 September 1994. Grab samples were sieved through a 0.15-mm net, and the retained residue preserved in buffered (1.3 g CaCO<sub>3</sub> L<sup>-1</sup>; pH range 6.6–7.0) 8% formalin for later analysis (Dermott and Munawar 1993). Within ~2 weeks the formalin was replaced with 70% ethanol. This preservation procedure, although not ideal for shelled mollusks, allows a detailed examination of the PI, PII, and D regions of the early shells of settling *Dreissena* spp.

On 13 July 1995, an additional offshore benthic sample

was obtained during a dive with the Canadian submersible SDL-1 (Dermott et al. 1998). A core sample was taken at a depth of 50 m, near Long Point, northwest of site 940 (Fig. 1). The core sediment was sieved using a 0.15-mm mesh and the residue preserved directly in 70% ethanol.

Postlarval or early juvenile dreissenids from nearshore epilimnion sites were collected from navigation buoys (quagga mussels and zebra mussels) and rocks (quagga mussels only) during 1992, 1993, and 1994. Buoys were removed from Lake Erie at the end of the navigation shipping season between the last week of November and the second week of December (Wormington et al. 1995). The distinctive number on each buoy determined its exact position in the lake. Four buoys were sampled (approx. water depth at each location: E3 = 10 m, E = 18 m, EN8 = 11 m, EA8 = 15 m) (Fig. 1). The *Dreissena* on the underwater part of the buoys, particularly the ballast rings (depth = 2 m below the water surface), were scraped off and dried. The dried material was passed through a 1-mm screen and the finer material examined for the presence of newly settled mussels. During October 1994, rocks (ca. 15–30 cm) were collected from a nearshore shoal (<2 m deep) (Fig. 1) using a dipnet. Extraction was conducted in the laboratory by scraping off mussels with a knife. Small quagga mussels (shell length ~400–2000  $\mu\text{m}$ ) were preserved in 70% ethanol for examination of the larval shell portion.

Both *Dreissena* species were present in Lake Erie. The quagga mussel, *D. bugensis*, was commonly found in hypolimnion habitat, whereas the zebra mussel was rare or absent at sites deeper than 30 m (Dermott et al. 1998). Discrimination between *D. bugensis* and *D. polymorpha* in their early postlarval or juvenile stage ( $\geq 300$ –400  $\mu\text{m}$ ) was resolved using early dissoconch morphology as per the study by Claxton et al. (1997).

Morphometric analysis of the larval shell was conducted by taking height measurements of the prodissoconch I (PI) and prodissoconch II (PII), using a modification of the methodology described by Martel et al. (1995) for the zebra mussel. PI and PII of postlarvae were examined from either wet (70% ethanol for brittle specimens) or dry preparations. In the wet preparation method, individual postlarvae were placed in a 5-cm glass petri dish that contained ~1 mm of ultrafine sand covered by ~3 mm of 70% ethanol to allow postlarvae to be oriented in various ways. Dry-preserved postlarvae or wet specimens whose shells were strong enough to be manipulated with fine forceps were placed in thin troughs made on a 1 to 2 mm thick layer of gray colored plasticine on a microscope glass slide. Postlarvae were placed side by side into the fine sand or the plasticine (umbo pointing upward) and lifted to an angle varying from 20° to 70° depending on the size of the specimen. This technique allowed direct observation with a stereomicroscope of the precise outline of either the PI or the PII in full view (plane view). Measurements of the height (PI and PII) of each of the two larval shell portions were taken from the right valve using a Jandel/SigmaScan digitizer and an Olympus SZH (7.5–128 $\times$ ) dissecting stereomicroscope equipped with a drawing attachment. The distance between the drawing attachment tube and the surface of the digitizer was set at 47

Table 1. Results of the prodissoconch I (PI) morphometric analysis for quagga mussel (*Dreissena bugensis*) and zebra mussel (*D. polymorpha*) postlarvae collected at different locations within the nearshore epilimnion habitat and the offshore hypolimnion habitat of Eastern Lake Erie during 1992–1995.

Prodissoconch I (PI) Species, habitat, site	PI height ( $\mu\text{m}$ )				
	Mean	SD		<i>N</i>	
Zebra/nearshore EN8	80.11	3.74		8	
Zebra/nearshore E3	79.11	4.98		8	
Quagga/nearshore Rock	78.43	5.66		9	
Quagga/nearshore EN8	79.33	3.59		8	
Quagga/nearshore E3	79.56	3.22		7	
Quagga/offshore 938	78.54	5.38		8	
Quagga/offshore 939	80.74	3.93		7	
Quagga/offshore sub	78.14	5.99		8	
Nested ANOVA (mixed model)					
Zebra nearshore vs. Quagga nearshore					
	<i>df</i>	SS	MS	<i>F</i>	<i>P</i>
Source of variation					
Among species	1	2.5	2.5	0.76	0.451
Among sites	3	9.9	3.3	0.17	0.916
Residual	35	680	19.4		
Quagga nearshore vs. Quagga offshore					
Source of variation					
Among habitats	1	0.011	0.011	0.001	0.973
Among sites	4	34.6	8.7	0.373	0.828
Residual	41	955	23.3		

cm to reduce the error in replicate measurements (critical when measuring PI).

The present study used the conventional terminology of marine bivalve larvae to describe dimensions of the larval shell (cf. Loosanoff et al. 1966; Chanley and Andrews 1971) and used the larval shell *height* (i.e., the dimension termed length in Martel et al.'s 1995 study on *Dreissena polymorpha*) to determine larval (prodissoconch) size. This conventional larval shell height (cf. marine literature) refers to the longest distance across the larval shell starting from the umbo, measured perpendicular or from the middle of the larval hinge line (provinculum) in the early larval stages. Shell height is not the longest dimension in early D-shaped stages, but it is close to or is the greatest in late larval stages (see Loosanoff et al. 1966).

To compare means of prodissoconch I and II heights among species, habitats (nearshore vs. offshore), and sites we performed two-level nested ANOVAs (mixed model) and one-way ANOVAs (model II). Morphometrical analysis of PI (i.e., size of first larval or D-shape stage) showed that the latter did not significantly vary among species, habitats, or sites within a habitat (Table 1). A nested ANOVA revealed that mean PI height of early postlarval quagga mussels that settled in the offshore hypolimnion habitat did not significantly differ from that of mussels that settled in the nearshore epilimnion (range of PI means for quagga offshore, 78.14–80.74  $\mu\text{m}$ ; quagga nearshore, 78.43–79.56  $\mu\text{m}$ ) (Table 1). The examination of the PI of zebra mussels that had settled on the nearshore shallow water substrates displayed similar means of PI heights to those of quagga mussels from the same substrate (PI means for zebra

nearshore: 79.11–80.11  $\mu\text{m}$ ) (Table 1). In this study PI is thus assumed to be a constant (overall mean: 79.21  $\mu\text{m}$ ). No postlarval zebra mussels were observed in the offshore hypolimnion samples examined.

**Results**—Morphometric analysis of prodissoconch II: The morphometric analysis of the prodissoconch II region of early postlarval *Dreissena* spp. (~400–2000  $\mu\text{m}$ ) from the nearshore epilimnion habitat of Eastern Lake Erie revealed that mean size of larvae at settlement and metamorphosis, as determined from the height of the larval shell at the PII-D boundary, was significantly greater in quagga mussels (range of PII means = 256.30–284.81  $\mu\text{m}$ , SD = 11.43–21.43) than in zebra mussels (range of PII means = 236.19–248.74  $\mu\text{m}$ , SD = 14.46–23.07) from the same substrate or site (nested ANOVA,  $P < 0.0081$ ) (Table 2, Fig. 2). For both the quagga mussel and the zebra mussel, highest mean sizes at settlement and metamorphosis at nearshore sites were observed at buoy EA8 ( $Q = 275.8 \mu\text{m}$ , SD = 11.4;  $Z = 248.7 \mu\text{m}$ , SD = 14.4  $\mu\text{m}$ ) and buoy E ( $Q = 283.8 \mu\text{m}$ , SD = 16.9;  $Z = 246.9 \mu\text{m}$ , SD = 23.1) (Fig. 2). These two buoys were located farther from the shore than other epilimnion sites (Fig. 1).

Mean size at settlement and metamorphosis (PII height) of quagga mussels settling in the offshore hypolimnion habitat was consistently greater than that of individuals of the same species settling in the nearshore epilimnion habitat (nested ANOVA,  $P < 0.001$ ) (Table 2) (Fig. 2). Ranges of means for size at settlement and metamorphosis were 310.69–322.81  $\mu\text{m}$  (SD = 21.57–25.69) for settlers in the

Table 2. Results of nested ANOVAs (mixed model) for the prodissoconch II (PII) morphometric analysis for quagga mussel (*Dreissena bugensis*) and zebra mussel (*D. polymorpha*) postlarvae collected in the nearshore epilimnion habitat and the offshore hypolimnion habitat of Eastern Lake Erie during 1992–1995.

Nested ANOVA (PII)	df	SS	MS	F	P
Quagga nearshore vs. Quagga offshore					
Source of variation					
Among habitats	1	219,394.1	219,394.1	96.84	<0.0001
Among sites	9	20,389.6	2,265.5	4.64	0.0001
Residual	516	251,669.5	487.7		
Zebra nearshore vs. Quagga nearshore					
Source of variation					
Among species	1	35,889.6	35,889.6	13.41	0.0081
Among sites	7	18,735.1	2,676.4	9.18	0.0001
Residual	349	101,774.6	291.6		

offshore hypolimnion and 256.30–283.81  $\mu\text{m}$  (SD = 11.43–21.43) for settlers in the nearshore epilimnion (total of 527 individuals) (Fig. 2).

Frequency distributions of PII height for quagga mussels from the offshore hypolimnion and the nearshore epilimnion habitats are shown on Fig. 3. Pooled means were 313.64  $\mu\text{m}$  (SD = 24.69,  $n = 320$ ) and 261.89  $\mu\text{m}$  (SD = 19.41,  $n = 207$ ) for the offshore hypolimnion and nearshore epilimnion, respectively. On average, quagga mussels settled in the hypolimnion at a size that was 20% larger than that of individuals that settled within the nearshore epilimnion sites. Using size classes that represented 2% or more of the size frequencies, the pooled data indicated a range of size at settlement and metamorphosis of 270–360  $\mu\text{m}$  for quagga mussels at offshore sites. In contrast, the range was 230–295  $\mu\text{m}$  for quagga in the nearshore sites (Fig. 3).

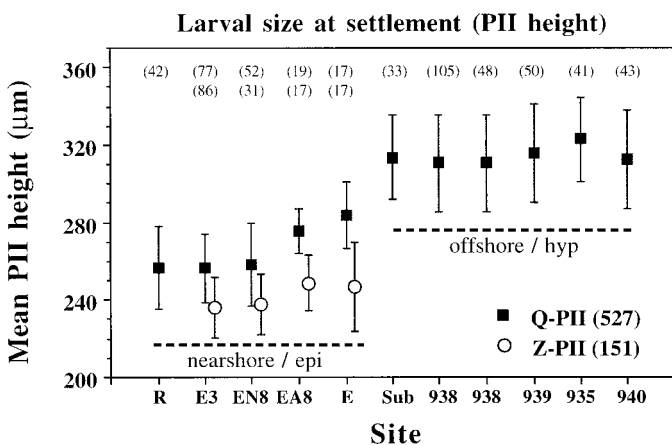


Fig. 2. Mean larval size at settlement and metamorphosis, as determined by the prodissoconch II (PII) height ( $\mu\text{m}$ ), from different sites in two types of habitat in Eastern Lake Erie during 1992–1995; filled squares, quagga mussel (*Dreissena bugensis*) postlarvae from offshore hypolimnion (right) or from nearshore epilimnion (left) sites; open circles, zebra mussel (*D. polymorpha*) postlarvae from nearshore epilimnion sites. Vertical bars represent  $\pm 1$  standard deviation of the mean. Numbers above each bar represent sample size (totals: 527 measurements for the quagga mussel and 151 for the zebra mussel). Sites listed under each type of habitat are presented starting with nearest to farthest from shore (see Fig. 1).

**Discussion**—Three salient points relating to size at settlement and metamorphosis as well as to recruitment success of *Dreissena* spp. in Eastern Lake Erie arise from this study. First, quagga mussels (*D. bugensis*) settle at larger size than zebra mussels (*D. polymorpha*) (prodissoconch II sizes of zebra mussels from this study compare with values reported by Martel et al. 1995). The difference in mean size at settlement between the two species could be explained by a longer planktonic development time, a superior ability to delay settlement, or a faster larval growth rate in the quagga mussel. This could represent an ecological separator for these two introduced bivalves in the Great Lakes region. The second point is that zebra mussels recruit successfully in Eastern Lake Erie only in nearshore habitats. This may be caused by a reduced flexibility in pattern of larval development in that species. The third salient point is that size at settlement and metamorphosis in quagga mussels is greater offshore (hypolimnion) than in nearshore (epilimnion) habitats (Figs. 2, 3). For four consecutive years (1992–1995) the

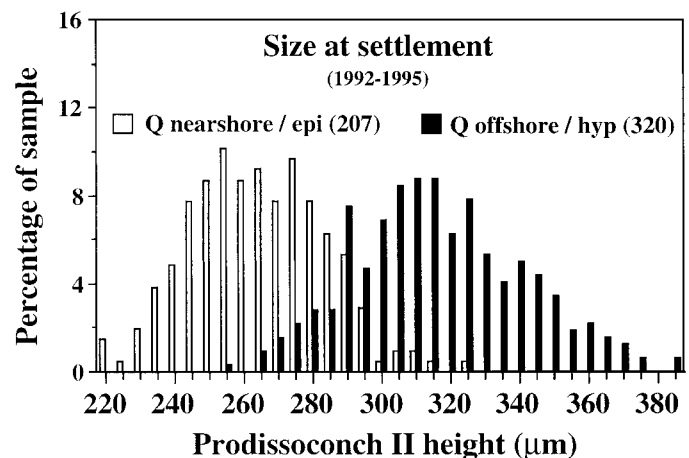


Fig. 3. Pooled size-frequency distributions of prodissoconch II (PII) height ( $\mu\text{m}$ ) (size at settlement and metamorphosis) of *Dreissena bugensis* obtained from postlarval specimens (ca. 500–2,000  $\mu\text{m}$  shell length) collected from the offshore hypolimnion and nearshore epilimnion habitats of Eastern Lake Erie during 1992–1995. Number in parentheses represents total number of PII measurements.



examination of the PII height from recently settled postlarvae showed that quagga mussel larvae settling and metamorphosing in the offshore deep water habitat had secreted a significantly larger larval shell compared to those settling in nearshore shallow waters. By subtracting the value of PI (shown to be a constant at  $\sim 79 \mu\text{m}$ ) from the mean of PII (pooled data), it is estimated that quagga larvae settling in the deep hypolimnetic habitat of Eastern Lake Erie deposited, on average,  $235 \mu\text{m}$  of larval shell (PII) during their planktonic life. This contrasts with  $183 \mu\text{m}$  of planktonic larval shell secretion for quagga larvae settling in the nearshore shallow water habitat (the value is  $160 \mu\text{m}$  for the zebra mussel). This represents a 28.4% greater increment in planktonic larval shell secretion for quagga mussels settling in offshore hypolimnion by comparison to quagga mussels settling in nearshore epilimnion.

This study was limited by the number of sites and samples for prodissoconch morphometry analysis, and samples for both habitats spanned different years and seasons. However, several lines of evidence point toward habitat effects as the leading source of variance affecting size at settlement and metamorphosis of quagga mussel larvae in this system, overriding variance originating from differences in locality within a habitat or that among years. First, there was no significant difference in mean PII height of quagga postlarvae among the six benthos samples (33–105 PII measurements per site; total, 320) collected in the offshore hypolimnion habitat (one-way ANOVA,  $P > 0.05$ ), despite samples originating from different sites and collected during a time period that spanned 3 yr (1993–1995). Second, results from the two-level nested ANOVA testing for the effect of habitat (nearshore vs. offshore) and that of site within a habitat on PII height of quagga mussels yielded a high  $F$  value for the habitat factor [ $F(\text{habitat}) = 96.84$ ,  $df = 1, 9$ ], with a  $P$  value  $< 0.0001$  (Table 2). Thus, the differences in PII means observed among the two types of habitats are significant above and beyond differences among sites within habitats. Finally, a nearshore/offshore effect is also suggested when comparing PII size of both the quagga mussel and the zebra mussel that settled on buoys within the nearshore epilimnion habitat (Fig. 2). Indeed, for the quagga mussel, the smallest PII heights were observed from postlarvae sampled from sites closest to shore, i.e., the rocks, buoy E3, and buoy EN8 (see Figs. 1, 2), and there was no significant difference among PII height means for this group of samples (one-way ANOVA,  $P > 0.05$ ). A similar trend was observed for zebra mussel settlers (Fig. 2).

This study is the first to provide firm evidence that bivalve larvae show developmental flexibility across a spatial/environmental gradient, herein documenting a correlation between offshore distance (nearshore/epilimnion versus offshore/hypolimnion) and larval morphometry, and hence larval ecology, in a bivalve. A number of possible explanations, not necessarily mutually exclusive, could explain the observed difference in size at settlement and metamorphosis between quagga mussels colonizing offshore hypolimnion habitats and nearshore epilimnion habitats. First, quagga mussel larvae may grow faster in the offshore/hypolimnion habitat. One could argue, however, that larvae developing and settling in the deep water environment should, at least for the latter part of their planktonic larval

development, experience a lower temperature regime as they begin searching for a favorable substrate (assuming that a thermocline exists at that time). This would result in lower growth rates and consequently a smaller larval size after a given time period in the plankton (Bayne 1965). A second scenario is that only larger (i.e., faster growing) larvae may survive the time period required to drift offshore and settle on substrates; smaller larvae may die (starvation?) or may be more vulnerable to predation. A third possible explanation is that early postmetamorphic natural selection may drive the size differences noted here between the two habitats. This postsettling size selection could be tested through comparisons of size distributions of advanced (competent) dreissenid larvae collected from the plankton in conjunction with size distributions of postlarvae collected from nearby substrates.

Another hypothesis that may explain the observed difference in size at settlement of quagga mussel larvae between the two types of habitats is that of delayed settlement and metamorphosis. The ability of bivalve larvae to prolong the planktonic period and delay settlement and metamorphosis is well documented in the marine literature (e.g., Bayne 1965; Pechenik 1985) and has also been suggested for *Dreissena polymorpha* (Sprung 1989; Haag and Garton 1992). Long planktonic periods or delay of metamorphosis result in greater sizes at settlement, hence a positive correlation between PII size and time spent in the plankton (Bayne 1965; Lutz and Jablonski 1978). As competent dreissenid larvae drift offshore delaying settlement and metamorphosis and secreting a large PII ( $\sim 300$ – $350 \mu\text{m}$ ) they may not be capable of remaining in the plankton longer, especially if they are positive geotactic and/or if their velum, which allows for both feeding and swimming, begins to degenerate (ref. study on *Mytilus* by Bayne 1965). Quagga mussel larvae found in offshore waters would then progressively sink to the bottom and eventually colonize the offshore deep water habitat of the lake. Moreover, during periods when the lake is stratified, quagga larvae spending a significant portion of their development in the cold, deep water layer may further extend their planktonic life and display larger PII, since a strong inverse correlation between size at larval settlement and water temperature has been well documented for bivalves (Myidae, Lutz and Jablonski 1978; Mytilidae, Bayne 1965; Pectinidae, Hodgson and Bourne 1988). It is noteworthy that for sites located in the nearshore epilimnion habitat, for both the quagga mussel and the zebra mussel, the highest PII means were observed from buoys located the farthest from the shore. This observation is consistent with the hypothesis of delayed settlement and metamorphosis among dreissenid larvae collected offshore.

The timing of spawning of quagga mussels in Lake Erie may also influence the mean size of larvae at settlement and metamorphosis. This timing will determine the temperature regime and temperature stratification of the water column within which larvae will develop in the plankton. Year-round low temperature regimes prevailing within the deep hypolimnion could lead to significantly lower larval growth rates, a prolonged planktonic period as well as a greater size at settlement and metamorphosis for quagga larvae developing within that environment (see Bayne 1965; Lutz and Jablonski 1978).

The origin of quagga mussel larvae settling into the deep

hypolimnion habitats is unknown. Larvae may immigrate from nearshore shallow water populations or from aut recruitment from deep water populations. The higher density (Mitchell et al. 1996) and fecundity (Claxton and Mackie 1998) of nearshore populations favor immigration as the likely source. This question, along with others raised in this study, will remain unresolved until further field studies on the reproduction and larval ecology of deep water populations of quagga mussels are conducted.

André L. Martel<sup>1</sup>

Research and Collections Division, Canadian Museum of Nature  
P.O. Box 3443, Station D  
Ottawa, Ontario, Canada, K1P 6P4;  
also Bamfield Marine Station,  
Bamfield, British Columbia, Canada, V0R 1B0

Brad S. Baldwin

Biology Department, St. Lawrence University  
Canton, New York 13617

Ronald M. Dermott

Department of Fisheries and Oceans, Great Lakes Laboratory  
P.O. Box 5050  
Burlington, Ontario, Canada, L7R 4A8

Richard A. Lutz

Institute of Marine and Coastal Sciences, Rutgers University  
New Brunswick, New Jersey 08903

## References

- ACKERMAN, J. D., B. SIM, S. J. NICHOLS, AND R. CLAUDI. 1994. A review of the early life history of zebra mussels (*Dreissena polymorpha*): Comparisons with marine bivalves. *Can. J. Zool.* **72**: 1169–1179.
- BAYNE, B. L. 1965. Growth and the delay of metamorphosis of the larvae of *Mytilus edulis* (L.) *Ophelia* **2**: 1–47.
- CHANLEY, P., AND J. D. ANDREWS. 1971. Aids for identification of bivalve larvae of Virginia. *Malacologia* **11**: 45–119.
- CLAXTON, W. T., AND G. L. MACKIE. 1998. Seasonal and depth variations in gametogenesis and spawning of *Dreissena polymorpha* and *Dreissena bugensis* in eastern Lake Erie. *Can. J. Zool.* **76**: 2010–2019.
- , A. MARTEL, R. M. DERMOTT, AND E. G. BOULDING. 1997. Discrimination of field-collected juveniles of two introduced dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) using mitochondrial DNA and shell morphology. *Can. J. Fish. Aquat. Sci.* **54**: 1280–1288.
- 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.
- , ———, AND J. LORIMER. 1998. Submersible confirmation of the profuse abundance of *Dreissena* on sediments in Lake Erie: Implications to food web. *Verh. Int. Verein. Limnol.* **26**: 2044–2047.
- DOMM, S. R., R. W. MCCAULEY, E. KNOTT, AND J. D. ACKERMAN. 1993. Physiological and taxonomic separation of two dreissenid mussels in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* **50**: 2294–2297.
- GARTON, D. W., AND W. R. HAAG. 1993. Seasonal reproductive cycles and settlement patterns of *Dreissena polymorpha* in western Lake Erie, p. 415–437. *In* T. F. Nalepa and D. W. Schloesser [eds.], *Zebra mussels: Biology, impacts and control*. Lewis.
- HAAG, W. R., AND D. W. GARTON. 1992. Synchronous spawning in a recently established population of the zebra mussel, *Dreissena polymorpha*, in western Lake Erie, USA. *Hydrobiologia* **234**: 103–110.
- HEBERT, P. D. N., C. C. WILSON, M. H. MURDOCH, AND R. LAZAR. 1991. Demography and ecological impacts of the invading mollusc *Dreissena polymorpha*. *Can. J. Zool.* **69**: 405–409.
- HODGSON, C. A., AND N. BOURNE. 1988. Effect of temperature on larval development of the spiny scallop, *Chlamys hastata* Sowerby, with a note on metamorphosis. *J. Shellfish Res.* **7**: 349–357.
- LOOSANOFF, V. L., H. C. DAVIS, AND P. E. CHANLEY. 1966. Dimensions and shapes of larvae of some marine bivalve mollusks. *Malacologia* **4**: 351–435.
- LUTZ, R. A., AND D. JABLONSKI. 1978. Larval bivalve shell morphology: A new paleoclimatic tool? *Science* **202**: 51–53.
- , ———, AND R. D. TURNER. 1984. Larval development and dispersal at deep-sea hydrothermal vents. *Science* **226**: 1451–1454.
- MACKIE, G. L. 1991. Biology of the exotic zebra mussel, *Dreissena polymorpha*, in relation to native bivalves and its potential impact in Lake St. Clair. 1991. *Hydrobiologia* **219**: 251–268.
- MARTEL, A., T. M. HYNES, AND J. BUCKLAND-NICKS. 1995. Prodissoconch morphology, planktonic shell growth, and size at metamorphosis in *Dreissena polymorpha*. *Can. J. Zool.* **73**: 1835–1844.
- , A. F. MATHIEU, C. S. FINDLAY, S. J. NEPSZY, AND J. H. LEACH. 1994. Daily settlement rates of the zebra mussel, *Dreissena polymorpha*, on an artificial substrate correlate with veliger abundance. *Can. J. Fish. Aquat. Sci.* **51**: 856–861.
- MAY, B., AND J. E. MARSDEN. 1992. Genetic identification and implications of another invasive species of dreissenid mussel in the Great Lakes. *Can. J. Fish. Aquat. Sci.* **49**: 1501–1506.
- MILLS, E. L., R. M. DERMOTT, E. F. ROSEMAN, D. DUSTIN, E. MEL-LINA, D. B. CONN, AND A. P. SPIDLE. 1993. Colonization, ecol-

<sup>1</sup> Corresponding author (amartel@mus-nature.ca).

## Acknowledgements

We are grateful to D. Pathy for her kind assistance with laboratory work. A. Wormington and C. Timmins collected the *Dreissena* samples from the navigation buoys. We thank S. Smith, B. Giles, and the crew of the DFO-CSS *Limnos* for help collecting benthos samples from offshore sites in Eastern Lake Erie. We thank the captain and crew of HMCS *Cormorant* and the pilots of the submersible SDL-1 for retrieving the core sample, and D. Graham and M. Lewis of the Bedford Institute of Oceanography, who arranged the opportunity to sample during the Great Lakes Dive Program. Earlier versions of the manuscript benefited greatly from critical discussions and written comments from graduate students and researchers at the Bamfield Marine Station, including, R. Akester, D. Arsenaault, L. Auffrey, L. Boulding, J. Holmes, R. Koss, D. Levitan, D. Renfrew, R. Rochette, B. Wilson, S. Zaklan, and two anonymous reviewers. We are grateful to the directors and staff at the Canadian Museum of Nature (CMN) and at the Bamfield Marine Station (BMS) for support and access to facilities during this research. We thank the Digital/Compaq Cie for providing computer assistance and hardware support to A.M. at CMN and BMS. This research was in part supported by a CMN-RAC (RSABAA7) grant to A.M., a DFO Great Lakes Action Plan grant to R.D., and a Sea Grant (NA36-RG0505) to B.B. and R.L.

- ogy, and population structure of the “quagga” mussel (Bivalvia: Dreissenidae) in the lower Great Lakes. *Can. J. Fish. Aquat. Sci.* **50**: 2305–2314.
- , G. ROSENBERG, A. P. SPIDLE, M. LUDYANSKIY, Y. PLIGIN, AND B. MAY. 1996. A review of the biology and ecology of the quagga mussel (*Dreissena bugensis*), a second species of freshwater Dreissenid introduced in North America. *Am. Zool.* **36**: 271–286.
- MITCHELL, J. S., R. C. BAILEY, AND R. W. KNAPTON. 1996. Abundance of *Dreissena polymorpha* and *Dreissena bugensis* in a warmwater plume: Effects of depth and temperature. *Can. J. Fish. Aquat. Sci.* **53**: 1705–1712.
- OCKELMANN, K. W. 1965. Developmental types in marine bivalves and their distribution along the Atlantic coast of Europe, p. 25–35. *In* L. R. Cox and J. F. Peak [eds.], *Proceedings of the First European Malacological Congress*. Conchological Society of the Great Britain and Ireland and the Malacological Society of London.
- PECHENIK, J. A. 1984. The relationship between temperature, growth rate, and duration of planktonic life for larvae of the gastropod *Crepidula fornicata* (L.). *J. Exp. Mar. Biol. Ecol.* **74**: 241–257.
- . 1985. Delayed metamorphosis of marine molluscan larvae: Current status and directions for future research. *Am. Malacol. Bull. Spec. Ed.* **1**: 85–91.
- ROBERTSON, R. 1994. Protoconch size variation along depth gradients in a planktotrophic *Epitonium*. *Nautilus* **107**: 107–112.
- ROSENBERG, G., AND M. L. LUDYANSKIY. 1994. A nomenclatural review of *Dreissena* (Bivalvia: Dreissenidae), with identification of the quagga mussel as *Dreissena bugensis*. *Can. J. Fish. Aquat. Sci.* **51**: 1474–1484.
- SCHERTZER, W. M., J. H. SAYLOR, F. M. BOYCE, D. G. ROBERTSON, AND F. ROSA. 1987. Seasonal thermal cycle of Lake Erie. *J. Gt. Lakes Res.* **13**: 468–486.
- SPRUNG, M. 1989. Field and laboratory observations of *Dreissena polymorpha* larvae: Abundance, growth, mortality and food demands. *Arch. Hydrobiol.* **115**: 537–561.
- STAŃCZYKOWSKA, A. 1977. Ecology of *Dreissena polymorpha* (Pallas) (Bivalvia) in lakes. *Pol. Arch. Hydrobiol.* **24**: 461–530.
- THORSON, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. *Medd. Kom. Dan. Fisk. Havunders.*, Plankton **4**: 1–523.
- WORMINGTON, A., C. A. TIMMINS, H. JOHNSTON, AND R. M. DERMOTT. 1995. Distribution of zebra mussels on Canadian navigation buoys on the Great Lakes, December 1993. *Can. Manuscr. Rep. Fish. Aquat. Sci.* **2281**.

Received: 14 June 2000

Accepted: 21 December 2000

Amended: 17 January 2001

*Limnol. Oceanogr.*, 46(3), 2001, 713–718  
© 2001, by the American Society of Limnology and Oceanography, Inc.

## A preliminary assessment of the geochemical dynamics of Issyk-Kul Lake, Kirghizstan

**Abstract**—Issyk-Kul Lake is one of the largest brackish water lakes in the world. Being a closed-basin lake, it is susceptible to volume changes caused by natural climatic variability, as well as human-induced water diversion from the basin. Long-term lake level records indicate that lake levels are declining and that salinity is increasing because of evapoconcentration. We present the first trace element data for this important lacustrine system and, using both ours and previously published data, investigate the geochemical dynamics within the watershed.

Issyk-Kul Lake, lying between 76° and 78°15'E and 42°10' and 42°40'N, is the deepest lake in central Asia (maximum depth of 668 m) and the fourth largest saline/brackish water lake in the world. The lake is located in the northeast portion of the country of Kirghizstan (Fig. 1). The lake basin occupies a depression in the northern Tien Shan Mountains at an altitude of 1,609 m, making it the second largest mountain lake in the world (Grosswald et al. 1994). The lake basin was formed during the Carboniferous period, and the lake, in its present form, is at least as old as the Late Pliocene (Tsigelnaya 1995). It is very much a “superlative” lake in the same way as Lake Baikal (Weiss et al. 1991).

Although the biology of the lake (especially its fisheries) has been investigated since the 1920s, there is much less information regarding the lake's physical and chemical characteristics, and only since 1992 have there been results published in the western literature (Savvaitova and Petr 1992;

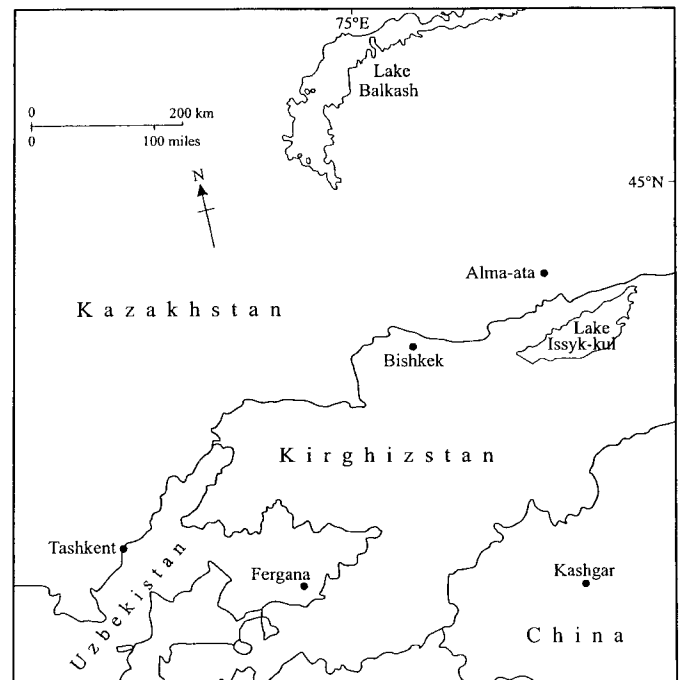


Fig. 1. Map of Central Asia.