Differences in tolerance to and recovery from zebra mussel (*Dreissena polymorpha*) fouling by *Elliptio complanata* and *Lampsilis radiata*

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Abstract: Zebra mussels (*Dreissena polymorpha*) in Lake Champlain have colonized the shells of many native unionids, causing declines in their abundance. Periodically cleaning zebra mussels from unionids may be an effective conservation technique, if unionids can recover from the stress induced by zebra mussels. Efforts will need to target species that are most vulnerable to fouling and subsequent energetic losses. We used glycogen as a biochemical indicator of energetic stores to assess species-specific differences in tolerance to zebra mussels. There was no evidence that glycogen levels decreased as dreissenid/unionid mass ratios increased in *Elliptio complanata*. However, dreissenid/unionid mass ratios as low as 0.25 in *Lampsilis radiata* were correlated with a significant decline in glycogen content. The ability of these species to recover glycogen after zebra mussel removal and replacement in situ was also evaluated. Mussels were cleaned of zebra mussels and replaced in situ. After 10 weeks, cleaned, heavily fouled, and never-fouled (control) mussels were collected. Glycogen levels in fouled mussels were lower than in the control mussels, while glycogen levels in cleaned mussels did not differ from the control mussels. Results suggest that heavily fouled *E. complanata* and *L. radiata* can recover glycogen levels if cleaned of zebra mussels and that cleaning may be a viable option for unionid conservation.

Résumé : Les Moules zébrées (*Dreissena polymorpha*) du lac Champlain ont colonisé les coquilles de plusieurs unionidés, causant ainsi des diminutions importantes de leur abondance. Le nettoyage périodique des unionidés pour y enlever les Moules zébrées peut être une technique efficace de conservation si les unionidés peuvent se remettre de leur stress. Les efforts de nettoyage devront être concentrés sur les espèces les plus vulnérables à l'encrassement et aux pertes énergétiques qui en résultent. Nous avons utilisé le glycogène comme indicateur des réserves énergétiques pour évaluer les différences entre les espèces quant à leur tolérance aux Moules zébrées. Nous n'avons pas constaté de diminution des concentrations de glycogène quand le rapport entre la masse des dreissénidés et celle des unionidés augmente chez *Elliptio complanata*; cependant, même si ce rapport a une valeur aussi faible que 0,25 chez *Lampsilis radiata*, il se produit une diminution importante du contenu en glycogène. La capacité de ces moules de récupérer le glycogène perdu après l'enlèvement des Moules zébrées et la réinsertion in situ a été évaluée. Des moules ont été nettoyées et replacées in situ. Après 10 semaines, des moules très encrassées, des moules nettoyées et des moules jamais encrassées (moules témoins) ont été récoltées. Les concentrations de glycogène des moules encrassées étaient plus faibles que celles des moules témoins, mais celles des moules nettoyées ne différaient pas de celles des moules témoins. Les résultats indiquent que les moules *E. complanata* et *L. radiata* encrassées peuvent récupérer leur glycogène si elles sont nettoyées des Moules zébrées; le nettoyage est une opération prometteuse pour la conservation des unionidés.

[Traduit par la Rédaction]

Introduction

Zebra mussels (*Dreissena polymorpha*) have been linked to recent declines in native unionid mussel abundance and species diversity in North America (Gillis and Mackie 1994; Nalepa 1994; Schloesser and Nalepa 1994; Schloesser et al. 1996). Typical declines occur rapidly (1–3 years) following heavy colonization of unionids by zebra mussels. Ricciardi et al. (1996) suggested that all populations of unionids carrying a mean zebra mussel mass equal to their own mean mass are likely to become extirpated. Eventually all fouled unionid species exhibit mortality. However, some species experience higher initial mortality rates than do others. Survey results from western Lake Erie suggest that members of the subfamily Lampsilinae suffer from glycogen loss and endure higher mortality rates than members of the subfamily Ambleminae when fouled by zebra mussels (Haag et al. 1993). Characterization of those species most at risk is important for establishing priorities when developing conservation strategies.

Because over 70% of the 297 species of freshwater mussels in North America are regarded as endangered, threatened, or of special concern, the additional stress of zebra mussel infestation has prompted immediate action from resource managers (Williams et al. 1993). Translocation, which involves moving threatened species to new areas, has

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been the primary conservation strategy used. Over 80% of all fisheries conservation plans for threatened and endangered fish include translocation (Williams et al. 1988). Unionid conservation plans for species threatened by zebra mussels aim to relocate species to refugia, i.e., areas that have very low probabilities of future zebra mussel infestation. However, the number of possible refugia is decreasing, as the zebra mussel continues to invade new bodies of water in North America.

Translocation involves a number of potentially stressful steps and requires an evaluation of possible translocation sites. In addition, long-term survival of translocated unionids may be difficult to estimate because monitoring relocated populations can be difficult in the field. A recent review of 33 mussel relocations described overall survival as being poor (Cope and Waller 1995).

Cleaning unionids is an alternative to translocation and has been used to increase survival of fouled unionids in western Lake Erie (Schloesser 1996). A periodic cleaning strategy simply requires collection and removal of all zebra mussels, perhaps once a year or less, from select populations of unionids. This approach allows unionids to remain in their original habitat and minimizes stress.

Regardless of the conservation method, heavy zebra mussel fouling may induce sufficient stress so that recovery even under optimal conditions is unlikely. Biochemical indicators are useful when determining relative measures of physiological condition in unionids in quarantine or the field. Bivalves use glycogen as the primary storage nutrient (Martin 1966). Glycogen content has been used as a bioindicator of condition in many bivalves (Hummel et al. 1989; Haag et al. 1993; Lauer 1997). We used glycogen as an indicator to examine differences in stress induced by zebra mussels and recovery from zebra mussel removal in two unionid species in Lake Champlain, Vt.

Zebra mussels first appeared in the south end of Lake Champlain in 1993 and spread rapidly to all areas of the lake (Eliopoulos and Stangel 1998). In recognition of the threat facing unionids in Vermont, the Lake Champlain Native Mussel Working Group was formed in 1996 to evaluate and carry out management plans. An unsuccessful translocation effort in 1997 and the need for quick action warranted a short-term assessment of a cleaning application. The purpose of this study was to assess zebra mussel induced mortality of two common unionid species (*Elliptio complanata* and *Lampsilis radiata*), examine which of the species is most vulnerable to energetic losses induced by zebra mussel fouling, determine the levels of fouling at which energetic loss occurs, and examine their ability to recover after cleaning of the heavy zebra mussel infestations.

Methods

Species-specific analysis

The relationship between the magnitude of zebra mussel fouling and glycogen content was determined for *E. complanata* and *L. radiata* in Lake Champlain, Vt. These two species are the most abundant unionids in Lake Champlain (Fiske and Levy 1996). The magnitude of fouling was expressed using the dreissenid/unionid mass ratio (Ricciardi et al. 1996), which was determined by dividing the blotted wet mass of the removed zebra mussels by the blotted wet mass of the unionid. Dreissenid/unionid mass ratios were obtained using 56 *E. complanata* and 92 *L. radiata* during the 1st week of July from Button Bay. An additional 29 *E. complanata* and 18 *L. radiata* were collected for glycogen analysis from Button Bay during the first 2 weeks of August 1997, using SCUBA (Fig. 1). Collections were made 100 m west of the boating access ramp in 0.5–1.5 m of water. Efforts were made to collect unionids that exhibited a range of zebra mussel fouling. Unionids were sacrificed after zebra mussel removal and a sample of mantle tissue, lining the mantle cavity, was removed. We examined the relationship between observed dreissenid/unionid mass ratios and glycogen content with a Spearman's rank correlation (Zar 1984). After plotting glycogen data, a post hoc analysis was used to determine the fouling threshold at which glycogen content began to significantly decline. A Welch's t test was used to examine differences between selected groups.

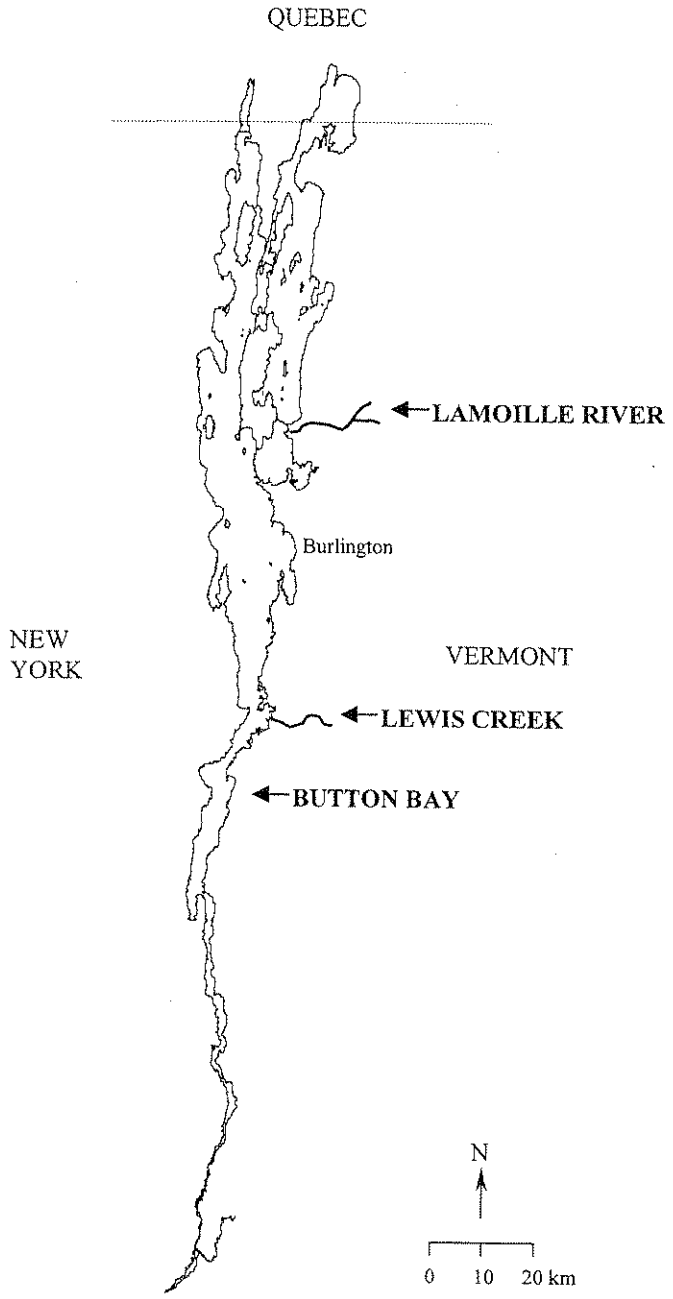
Mortality data for *E. complanata* and *L. radiata* were collected from Button Bay and the Lamoille River delta using 0.5-m^2 quadrats (Fig. 1). Surveyors used SCUBA or snorkel gear depending on water depth and visibility. A quadrat was randomly placed upon the substrate and all dead and living mussels were excavated from the substrate down to 15 cm below the sediment–water interface. In an effort to collect only recently dead mussels, they were only counted as dead if the hinge ligament was present and connecting both valves. The percentage of live mussels was calculated for each species at both sites and analyzed using the Kruskal–Wallis ANOVA on ranks followed by Dunn's procedure for multiple comparisons (Zar 1984).

Cleaning experiment

To determine the ability of *L. radiata* and *E. complanata* to recover glycogen after zebra mussel removal, a cleaning experiment was performed at the Lewis Creek delta on July 15, 1997, in an area where heavily fouled mussels were observed (Fig. 1). The experimental area was located ~100 m west of the mouth. SCUBA was used to collect 35 heavily fouled *E. complanata* and 35 *L. radiata* individuals from the sand–silt substrate in 1–2 m of water. All zebra mussels were removed and each unionid shell was thoroughly scrubbed with a small brush. The dreissenid/unionid mass ratio was obtained for each cleaned unionid. Mussels were individually marked by scribing through the periostracum with a dental pick. The mussels were replaced in a 4-m^2 open-topped chicken wire pen that was secured to the substrate with eight rebar stakes. The diameter of the chicken wire (25 mm) and open top allowed normal water flow through the area. The pen was inspected every 2 weeks for dead mussels. All mussels were removed from the pen on September 30, 1997, and an equivalent number of zebra mussel fouled unionids of each species was collected in close proximity to the pen. During the same week, 20 *E. complanata* and 20 *L. radiata* were collected from the Lamoille River delta, approximately 30 miles (48 km) north of Lewis Creek. Zebra mussels were not present at the Lamoille River delta, so this sample represented unionids living in a delta environment that had never been fouled by zebra mussels.

Never-fouled, fouled, and cleaned mussels were sacrificed and mantle tissue was sampled for glycogen content analysis on the same day of collection. Because the glycogen content data could not be normalized via standard transformations and did not meet homogeneity of variance assumptions, analysis for species- and treatment-specific differences was accomplished using pairwise Welch's t tests with a Bonferroni adjustment for multiple comparisons (Zar 1984). Comparisons were made between mean glycogen levels for all species-treatment combinations. To control for Type I experimentwise error between these 15 comparisons, Bonferroni significance levels for Welch's t tests were considered significant at the 0.05 level, with P values less than 0.003.

Fig. 1. Mussel collection sites at the Lamoille River, Button Bay and Lewis Creek, Lake Champlain, Vt.



Glycogen analysis

All mantle tissues were preserved in 95% ethanol after biopsy. The glycogen content of preserved mantle tissue was analyzed with an enzymatic method using amyloglucosidase (Keppler and Decker 1974), as modified by Patterson et al. (1997). Samples were held for no longer than 30 days prior to analysis.

Results

Species specific analysis

Mean dreissenid/unionid mass ratios for *E. complanata* and *L. radiata* at Button Bay were 0.24 ± 0.11 and 0.23 ± 0.18, respectively. Fouling was negatively correlated with glycogen content in *L. radiata* from Button Bay (Fig. 2) but not in *E. complanata* (Fig. 3).

Fig. 2. Glycogen content in zebra mussel fouled *Lampsilis radiata* collected from Button Bay. The dreissenid/unionid mass ratio is the blotted wet mass of the zebra mussels relative to the mass of the unionid.

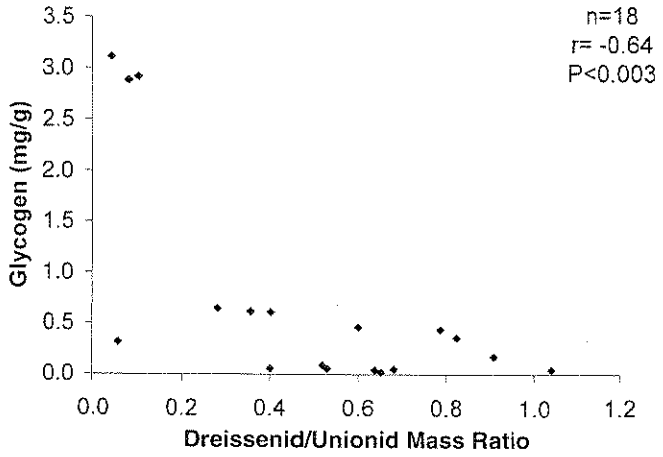
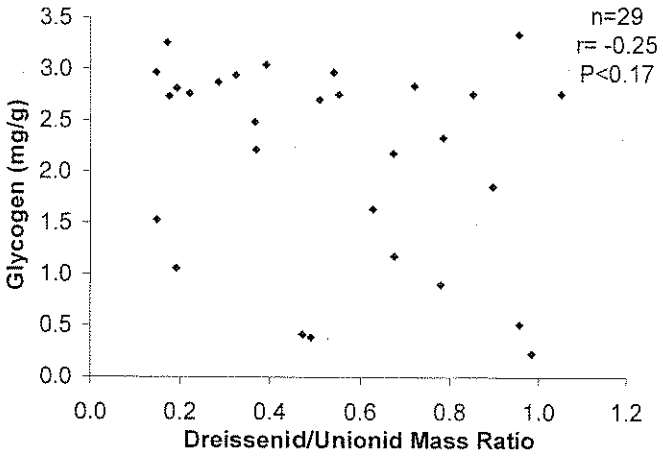


Fig. 3. Glycogen content in zebra mussel fouled *Elliptio complanata* collected from Button Bay. The dreissenid/unionid mass ratio is the blotted wet mass of the zebra ussels relative to the mass of the unionid.



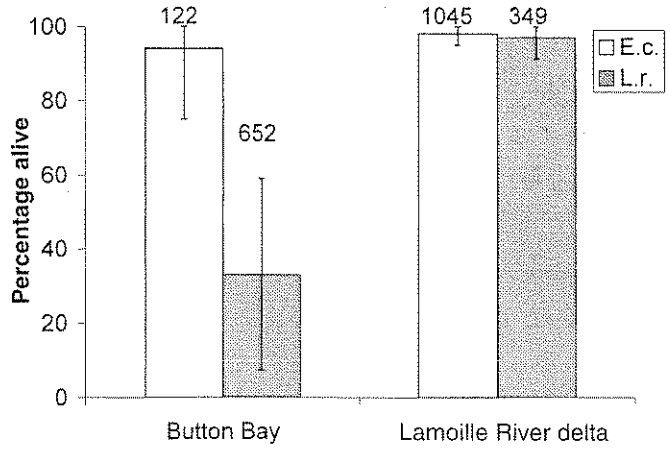
Post hoc determination of threshold fouling levels at which glycogen content declined was accomplished by assigning specimens to a fouling group. Because *L.radiata* specimens with dreissenid/unionid mass ratios below 0.25 appeared to have higher glycogen content than mussels with higher fouling, they were grouped into the following according to the dreissenid/unionid mass ratios: group 1 (0–0.25), group 2 (0.26–0.5), group 3 (0.51–0.75), and group 4 (0.76–1.0) (Table 1). We tested the mean glycogen content for group 1 against groups 2, 3, and 4 combined. This analysis was performed separately for each species. Glycogen content in group 1 *L. radiata* was significantly higher ($P < 0.001$) than all other groups combined (2.3 ± 1.33 vs. 0.26 ± 0.24 mg/g). In contrast, glycogen content in group 1 *E. complanata* was not significantly different ($P < 0.36$) than all other groups combined (2.44 ± 0.81 vs. 2.06 ± 1.00 mg/g).

Table 1. Glycogen content in post hoc assigned fouling groups in *Elliptio complanata* and *Lampsilis radiata*.

	Fouling group			
	0.0–0.25	0.26–0.50	0.51–0.75	0.76–1.0
Glycogen content (mg/g)				
L. radiata	2.3±1.33 (4)	0.48±0.28 (4)	0.16±0.17 (5)	0.18±0.19 (5)
E. complanata	2.44±0.81 (7)	2.0±1.16 (7)	2.32±0.68 (7)	1.83±1.16 (8)

Note: Fouling groups are based on dreissenid/unionid mass ratios. Values are given as the mean ± SD and numbers in parentheses show the number of individuals of each species in each fouling group.

Fig. 4. Percentage of live *E. complanata* (E.c.) and *L. radiata* (L.r.) at Button Bay and the Lamoille River delta counted in 100 quadrats. Zebra mussels are present at Button Bay and absent from the Lamoille River delta. Error bars represent SD.



At Button Bay, a mean of 94 ± 19% (mean ± SD) of the *E. complanata* surveyed were alive, while only 33 ± 26% of the *L. radiata* surveyed were alive. At the Lamoille River delta, 98 ± 0.03% of the *E. complanata* and 97 ± 0.06% of the *L. radiata* were found alive (Fig. 4). The percentage of live *E. complanata* in Button Bay was not significantly different than at the Lamoille River delta, but the percentage of live *L. radiata* was significantly lower than that for *E. complanata* at Button Bay ($P < 0.05$) and for both species at the Lamoille River delta ($P < 0.05$).

Cleaning experiment

After 10 weeks, one *L. radiata* was found dead and one was missing from the pen in Lewis Creek. Three *E. complanata* were missing. Missing mussels presumably escaped under the border of the chicken wire pen. One large adult zebra mussel was found on one *L. radiata*. Small juveniles (<2 mm) were present on all cleaned mussels. The dreissenid/unionid mass ratio for cleaned *E. complanata* and *L. radiata*, prior to cleaning, was 1.49 ± 0.51 and 1.40 ± 0.64, respectively. Dreissenid/unionid mass ratios for fouled *E. complanata* and *L. radiata* found outside the pens were 1.84 ± 0.52 and 1.70 ± 0.90, respectively.

Significant differences in the glycogen content of mantle tissue were found among the six groups of unionids (Table 2). In *L. radiata*, cleaned and never fouled mussels had significantly higher glycogen levels than fouled mussels ($P < 0.001$ for both comparisons). Fouled *E. complanata* had lower glycogen levels than cleaned mussels (1.81 ± 0.95 vs. 2.30 ± 0.79 mg/g), but the difference was not significant ($P < 0.005$). With comparable levels of fouling, *E. complanata* had significantly higher ($P < 0.001$) glycogen content than *L. radiata*. The glycogen content in cleaned *E. complanata* and *L. radiata* was not significantly different ($P < 0.54$). Additionally, glycogen content in never-fouled *E. complanata* and *L. radiata* was similar ($P < 0.84$).

Table 2. Differences in glycogen content among never-fouled, cleaned, and fouled *E. complanata* and *L. radiata* from the Lewis Creek and Lamoille River deltas.

		Glycogen content (mg/g)	
Treatment	*n* per species	*E. complanata*	*L. radiata*
Never fouled	20	2.52±0.36*a*	2.56±0.26*a*
Cleaned	32	2.30±0.78*ab*	2.40±0.81*ab*
Fouled	32	1.81±0.95*b*	0.46±0.38*c*

Note: Values are given as the mean ± SD and groups sharing the same letter are not significantly different from each other at the $\alpha = 0.003$ level, after a Bonferroni adjustment for multiple comparisons.

Discussion

Results from this study show that a species in the subfamily Lampsilinae (*L. radiata*) experienced greater mortality and suffered greater losses of glycogen than a species from the subfamily Ambleminae (*E. complanata*) when fouled by zebra mussels. Similar results were found by Haag et al. (1993) using *Amblema plicata* and *L. radiata*. In contrast, results from Lake St. Clair implied that lampsilines were less vulnerable to zebra mussel infestation than species of Ambleminae (Hunter and Bailey 1992). Strayer and Smith (1996) found that in the presence of zebra mussels, condition, recruitment, and density of *E. complanata* were less severely affected than *Anodonta implicata* (Anodontinae) and *Leptodea ochracea* (Lampsilinae). In Lake St. Clair, Gillis and Mackie (1994) found that another related species, *Elliptio dilatata*, did not experience a large decline after infestation.

The reason for these species-specific differences in tolerance is still largely unknown but may be due to breeding characteristics and (or) shell morphology. Certain species may be able to better assimilate particles, detritus, or even zebra mussel feces and pseudofeces than others. Metabolic arrest mechanisms are important in marine bivalves and gastropods for surviving periods of environmental stress (Storey 1993). Although this adaptation is speculative, certain spe-

cies of unionids may have a greater ability to down regulate the activity of certain glycolytic enzymes during periods of stress. The capacity to control metabolic rate when fouled would not make any species immune to zebra mussel induced stresses but merely prolong the wasting and dying process.

Species-specific differences in tolerance to zebra mussel fouling may also be an effect of breeding strategies. When fouled by zebra mussels, bradytictic glochidia brooders with light shells have experienced greater mortality than tachytictic glochidia brooders with heavier shells in Lake St. Clair (Nalepa 1994). After zebra mussels were present in 1993, 87% of the living unionids surveyed on the nearshore contours of Lake Erie were tachytictic brooders (Schloesser et al. 1997). Bradytictic unionids, such as *L. radiata*, maintain developing glochidia in marsupia throughout the year. Consequently, the energetic cost of sustaining glochidia may cause gravid females to be more susceptible to energetic declines when fouled by zebra mussels. In contrast, tachytictic unionids, such as *E. complanata*, complete the development and release of glochidia during the spring and summer. Therefore, females do not experience the persistent energetic costs that bradytictic species suffer and may be more capable of sustaining energetic stores.

Clearly, *E. complanata* is relatively tolerant of zebra mussel fouling, and massive mortality has not yet been documented at any site on Lake Champlain. In contrast, zebra mussels have caused notable glycogen declines and mortality in *L. radiata*. Nevertheless, we observed considerable variation in glycogen content in *E. complanata* that was not attributable to fouling intensity. Glycogen content variation of this magnitude, and greater, has been measured in unionids in the Ohio River (Patterson et al. 1997) and may be attributed to reproductive state or temporal proximity to major movement or migration in the substrate.

At Button Bay, dreissenid/unionid mass ratios above 0.25 were correlated with low glycogen content in *L. radiata*, while a fouling threshold at which *E. complanata* experienced significant glycogen declines was not reached. These glycogen and mortality data support the conclusions of Ricciardi et al. (1996) that species with mean dreissenid/unionid ratios of 1.0 will likely be extirpated, and moreover, suggests that this estimate may be a liberal one. For certain species, as demonstrated in this study with *L. radiata*, dreissenid/unionid mass ratios as low as 0.25 may cause significant energetic impacts. Fouling thresholds will likely vary by species, season, reproductive state, and aquatic system. Therefore, fouling thresholds must be measured empirically and may not be useful as an indicator of relative stress for unionids populations.

The most encouraging results of this study indicate that unionids, relieved of a chronic stress, can recover glycogen stores over a period of only 10 weeks. This study provides clear evidence of short-term energetic recovery when unionids are cleaned and replaced in situ, and differs markedly from cleaning when used in combination with translocation. Survival of cleaned unionids was significantly higher (42 vs. 0%) than fouled unionids after translocation from lentic to lotic habitat and held in suspended cages in Lake Erie (Schloesser 1996). Cleaning and replacement in situ may have resulted in better survival of unionids in Lake Erie because replacing unionids in the exact habitat they were removed from may minimize stress.

Although unionids were cleaned for this study in July, unionid cleaning for conservation should ideally be performed after maximum veliger settlement in June–August to prevent massive refouling. Additionally, unionids must be cleaned early enough during the summer or fall to allow for sufficient energetic recovery. Without adequate recovery time, unionids may not have the ability to secure energetic stores for the winter, which may be a period of great environmentally induced stress (Ricciardi et al. 1996).

Unionids in this study were collected from shallow sandy and silty bays where unionid shells comprise the majority of hard surface area for zebra mussel veligers to settle on. These types of areas are ideal for cleaning strategies because low overall densities of zebra mussels in the immediate area make local nutrient depletion unlikely. In the Hudson River, the density of unionids decreased by 56% and condition declined by 20–50% between 1991 and 1995, in an environment where only 30% of unionids were fouled (Strayer and Smith 1996). Strayer and Smith (1996) concluded that zebra mussels might affect unionids through competition for food along with, and perhaps in the absence of, fouling. We suggest that potential for unionid recovery should be assessed in individual lakes or rivers prior to establishment of a conservation strategy, and most importantly, not be used in a system where possible food depletion exists.

This demonstration of recovery attests to the ability of stressed unionids to recover after removal of the stressor and reveals that, under the appropriate conditions, salvaging even heavily fouled unionids is not a useless effort. Many of the unionids cleaned in this study, *L. radiata* in particular, were probably near death. Most of the unionids had zebra mussels covering both valves almost completely. Fouling had apparently caused posterior valve irregularities that were observed on almost all shells where zebra mussels occurred inside the mantle cavity. These mussels may not have survived the additional energy loss that can occur during quarantine.

Cleaning populations is not a permanent solution to zebra mussel fouling. Populations may need to be cleaned as frequently as once every year to maintain low fouling levels. In areas where the bottom substrate is covered with zebra mussels, cleaning and leaving unionids may not be effective owing to movement of zebra mussels onto unionids after cleaning. However, periodically cleaning unionids and leaving them in situ may secure the necessary time needed to identify more effective quarantine procedures, specific habitat requirements, and interpopulation differences; all of which are involved in translocations. More research is needed to determine the long-term efficacy, frequency, and cost of periodic cleaning.

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