Characteristics of a refuge for native freshwater mussels (Bivalvia: Unionidae) in Lake St. Clair

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ABSTRACT

The Lake St. Clair delta ($\sim$100 km^2) provides an important refuge for native freshwater mussels (Unionidae) wherein 22 of the $\sim$35 historical species co-occur with invasive dreissenids. A total of 1875 live unionids representing 22 species were found during snorkeling surveys of 32 shallow ($\sim$1 m) sites throughout the delta. Richness and density of unionids and zebra mussel infestation rates varied among sites from 3 to 13 unionid species, 0.02 to 0.12 unionids/m^2, and <1 to 35 zebra mussels/unionid, respectively. Zebra mussel infestation of unionids in the delta appears to be mitigated by dominant offshore currents, which limit densities of zebra mussel veligers in nearshore compared to offshore waters (13,600 vs. 28,000/m^3, respectively). Glycogen concentrations in the tissues of a common and widespread species in the delta (*Lampsilis siliquoidea*) suggest that zebra mussels may be adversely affecting physiological condition of unionids in a portion of the Lake St. Clair delta. Physiological condition and community structure of unionids within the delta may also be influenced by differences in food quantity and quality resulting from the uneven distribution of water flowing from the St. Clair River. The delta likely supports the largest living unionid community in the lower Great Lakes and includes several species that have been listed as Endangered or Threatened in Canada and/or the state of Michigan, making it an important refuge for the conservation of native unionids.

Introduction

In the Great Lakes, declines in native unionids due to the impacts of zebra mussels (*Dreissena polymorpha* Pallas, 1771) have been well-documented (e.g., Schloesser and Nalepa 1994, Nalepa et al., 1996, Schloesser et al., 2006). However, several "refuge" sites for unionids have been found in nearshore wetland habitats of Lake Erie where zebra mussels are present, but at low densities. A viable community of 21 species was found in Metzger Marsh along the south shore of Lake Erie in 1996 (Nichols and Wilcox, 1997), and a community of 15 species was found in nearby Crane Creek Marsh in 2001 (Bowers and de Szalay 2004). Thompson Bay, the outer harbor of Presque Isle Bay,

supports a smaller community of only nine species, and annual monitoring between 1992 and 2006 suggests that the community is stable (E.C. Masteller, Pennsylvania State University. pers. comm. 2008). The locations, characteristics, and ultimate significance of these refuges are of considerable interest for unionid conservation.

Zanatta et al. (2002) discovered an important refuge for unionids in the Lake St. Clair delta, where 22 of $\sim$35 historical species were found alive between 1999 and 2001. This refuge falls mainly within the territory of the Walpole Island First Nation. Eight of the species found are designated as Endangered or Threatened in Canada and/or Michigan and a ninth species, the Northern Riffleshell (*Epioblasma torulosa rangiana* Lea, 1838), is listed as Endangered in the US, Canada and Michigan (COSEWIC, 2007a; Michigan DNR, 2007; U.S. Fish and Wildlife Service 2007). Densities of unionids in the Lake St. Clair delta are low, ranging from 0.03 to 0.07 unionids/m^2 (Zanatta et al. 2002), compared to an average density of 2 unionids/m^2 reported for offshore waters of Lake St. Clair before the zebra mussel invasion in 1986 (Nalepa and Gauvin 1988). However, the Lake St. Clair refuge is much larger than any of the other refuge sites discovered to date in

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Lake Erie (~ 100 km^2 vs. 1 to 3 km^2) and, as such, it sustains some of the largest remaining populations of unionids in the lower Great Lakes. For example, the estimated size of the *Villosa iris* (Lea, 1829) population in the delta is >190,000 individuals (COSEWIC, 2006).

Infestation rates of zebra mussels on unionids in the Lake St. Clair delta are variable and generally higher than those found in other refugia in Lake Erie. Average rates (# zebra mussels/unionid) were <1 in Metzger Marsh (Nichols and Amberg 1999), zero in Thompson Bay (Schloesser and Masteller 1999) and 4 in Crane Creek Marsh (Bowers and de Szalay 2004), whereas average infestation rates in the delta ranged from 3 to 47 (Zanatta et al. 2002). In Metzger Marsh, the limited infestation rates are likely due to the presence of soft sediments, which allow unionids to burrow, thereby smothering any attached zebra mussels (Nichols and Wilcox 1997). The low infestation rates in Thompson Bay and Crane Creek Marsh are attributed to water-level fluctuations that expose zebra mussels and cause them to either release voluntarily from unionids or perish (Schloesser and Masteller 1999, Bowers and de Szalay 2005). Zanatta et al. (2002) speculated that low infestation rates of unionids in the nearshore waters of Lake St. Clair delta, relative to those recorded in the open waters of the lake (Gillis and Mackie 1994), may be the result of fluctuations in the number of zebra mussel veligers reaching and settling in the shallow areas of the delta due to variations in wind direction, currents and water levels.

Although the zebra mussel infestation rates reported in the delta by Zanatta et al. (2002) are well below the lethal threshold of 100 zebra mussels/unionid reported by Ricciardi et al. (1995) and Schloesser et al. (1996), a subsequent study determined that significant declines in unionid density can occur when the mean infestation rate exceeds 10 zebra mussels/unionid (Ricciardi et al., 1996). Unionid mortality in some systems has also been attributed to increased competition for food resources by zebra mussels (Strayer and Smith, 1996). Assessing the effects of low levels of zebra mussel infestation on the physiological condition of unionids may help to determine if these remnant Great Lakes populations are stable.

Effects of stressors, like zebra mussels, may adversely affect the relative condition of unionids at levels that are lower than those that cause mortality. Thus, researchers often look to sublethal measures, such as those influencing physiology, biochemistry and reproduction, because these measures may be predictive of future mortality. Glycogen is the principal storage form of carbohydrates in many aquatic invertebrates (Stetten and Stetten 1960, De Zwaan and Zandee 1972, Hummel et al. 1989) and has been used as an indicator of physiological condition in unionids. For example, glycogen has been used as an indicator of stress resulting from emersion (Greseth et al. 2003), parasitic infestations (Jokela et al. 1993), relocation and quarantine (Patterson et al. 1997, Naimo et al. 1998), and zebra mussel infestation (Haag et al. 1993, Hallac and Marsden 2000).

Changes in total lipid and/or individual fatty acid concentrations in organisms can reveal broad scale changes in ecosystem function (Hebert et al. 2006, 2008). Fatty acids have been successfully used as trophic markers (reviewed in Dalsgaard et al., 2003). Because many fatty acids found in the diet are conserved within the tissues of consumers they have seen widespread use as biomarkers of feeding both in the short (e.g. Brett et al. 2006; Iverson in press) and long term (e.g. Hebert et al. 2008). Traditional methods for determining diet (e.g., gut content analyses, behavioral studies) are time consuming, labor intensive and generally do not integrate the effects of feeding temporally and/or spatially. Fatty acids are helpful in this respect because they integrate the effects of feeding over time. They have also been extensively used as indices of condition in a wide range of aquatic organisms (Arts and Wainman 1999, Schlechtriem et al. 2008) and, occasionally, in marine mussels (Hellou and Law 2003, Alkanani et al. 2007). Although total lipid content has been used to assess the condition of unionids (Haag et al. 1993), using specific fatty acids in such contexts has not been done before.

The Walpole Island First Nation and Environment Canada's Water Science and Technology Directorate formed a 3-year partnership in 2003 to develop and implement an action plan to conserve and recover unionid communities of the Lake St. Clair delta. The objectives were to: a) document the composition of unionid communities throughout the shallow (<1.5 m) waters of the Lake St. Clair delta, b) determine the spatial distribution and abundance of zebra mussels veligers, c) evaluate the effects of water currents on the distribution of zebra mussel veligers and, d) examine variation in the physiological condition of unionids across the delta as they relate to the rate of zebra mussel infestation.

Methods

Study area

The Lake St. Clair delta is located at the mouth of the St. Clair River where it enters the northeast end of Lake St. Clair (Fig. 1). The delta is bisected by the Canada/US border between the Province of Ontario and the State of Michigan. The Canadian portion of the delta falls mainly within the territory of the Walpole Island First Nation (WIFN), which contains >12,000 ha of wetlands and is one of the largest wetland complexes in the Great Lakes Basin (The Nature Conservancy 1995). More than 50 plant and animal species listed as Canadian Species at Risk occur on the lands and in the waters of the WIFN (Bowles 2005). In contrast, the US portion of the delta is highly urbanized with hardened shorelines (Jaworski and Raphael 1976). Average annual discharge of the St. Clair River is ~5000 m^3/s (Lake St. Clair Canadian Watershed Coordination Council 2005). The flow of water from the river is divided into three main channels in the upper part of the delta and a number of secondary channels in the lower delta. The eastern (Canadian) section of Lake St. Clair receives only 8% of the inflow from the St. Clair River (Environment Canada, et al. 1994). A dredged navigation channel crosses the lake along the international border, and water masses on either side of the channel rarely mix (Lake St. Clair Canadian Watershed Coordination Council 2005). The south-eastern (Canadian) water mass is warmer and more productive, whereas the northwestern (US) water mass, which receives most of its water from Lake Huron, is cooler and less productive (Leach 1980).

Assessment of unionid communities in the delta

Thirty two sites were surveyed for unionids, 18 quantitatively and 14 semi-quantitatively (Fig. 1). Surveys were conducted at depths of 0.5 to 1.5 m where previous surveys showed most live unionids would be found (Zanatta et al. 2002). Individual sites were selected for survey using several criteria. First, quantitative sampling was repeated at nine sites that had been previously surveyed by Zanatta et al. (2002). The other 9 quantitative sites and the 14 semi-quantitative sites were selected to distribute sampling effort across the shallow bays of the delta and in a few instances were based on aboriginal knowledge of areas known to support unionids. Only locations where live unionids were observed were selected for intensive quantitative surveys. Given that sites were not chosen randomly, these data should not be viewed as representative of the entire delta. Quantitative surveys were conducted from July 21 to August 8, 2003 at nine sites in Canadian waters (Sites 1–7, 15 and 18) and nine sites in US waters (Sites 8–14 and 16–17) using the following "circle-plot" sampling technique devised by Zanatta et al. (2002). At each site, three transects spaced ~25 m apart perpendicular to shore were searched by a two-person team consisting of a snorkeler and a helper. The snorkeler swam until a live unionid was encountered, at which point the helper pounded an iron stake into the substrate next to the unionid; a U-bolt attached to a 4.55 m length of rope was slipped over the stake, and the snorkeler held the other end of the rope and extended it to its maximum length. The snorkeler then swam around the stake in circles
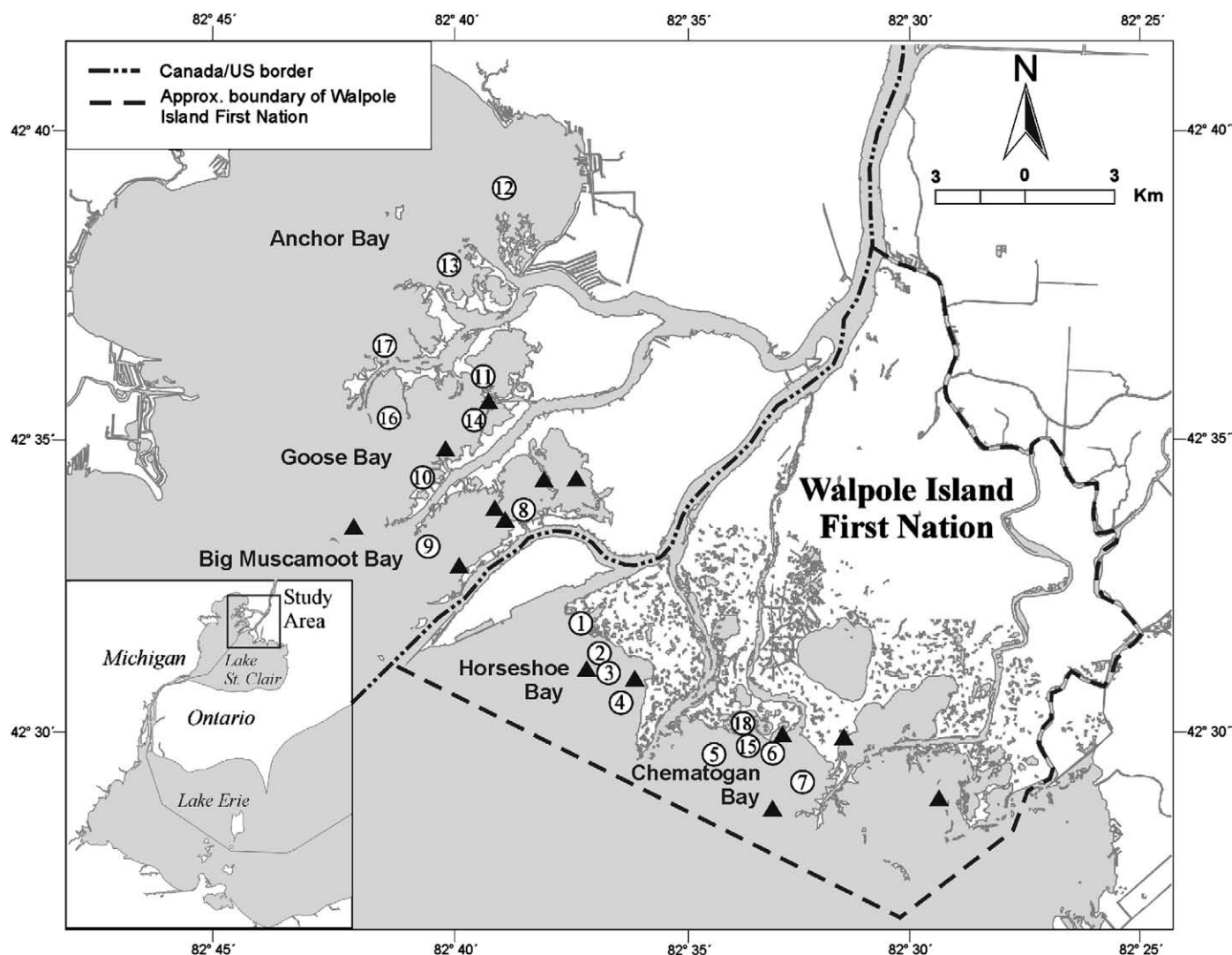
Fig. 1. Locations of 32 sites surveyed for unionids in the Lake St. Clair delta in 2003 and 2005. Sites surveyed quantitatively ($n = 18$) are indicated by circles containing the site number; sites surveyed semi-quantitatively ($n = 14$) are indicated by black triangles.

of decreasing diameter until the entire 65 m² area had been searched and all visible live unionids had been collected and placed in a mesh bag for examination. This procedure was repeated until each team had surveyed 10 plots along each transect. At sites where unionid densities were very low, some or all snorkelers were unable to survey their full 10 plots before either reaching shore or entering waters that were too deep to search effectively, resulting in smaller search areas at these sites (Table 2). Locations of transects were marked using a hand-held GPS unit. The unionids collected were identified to species, counted and then maximum shell lengths were measured to the nearest mm using vernier calipers. Zebra mussels were removed from three randomly selected individuals of each unionid species from each site and counted to estimate the infestation rate. Shell lengths of zebra mussels were also measured.

The "circle-plot" technique would likely overestimate the actual density of unionids at a site if the unionids were exhibiting an aggregated distribution in the rather uniform "sand flat" habitat of the delta. On the other hand, the technique may also *underestimate* densities at a site because it does not detect burrowed adults and juveniles. As unionid densities are very low in the delta, this method generated data with a reasonable amount of effort and established a baseline from which future surveys using the same method could be directly compared.

Semi-quantitative surveys were conducted from July 21 to August 8, 2003 and August 9 and 10, 2005 at six sites in Canadian waters and

eight sites in US waters using a timed search technique. Surveys involved one to four snorkelers who spread out and randomly searched the area for unionids for times ranging from 0.25 to 4 person-hours. Live unionids were identified to species, measured to the nearest mm, and counted. Data from all 32 quantitative and semi-quantitative sites were combined only to establish the number and composition of species in the delta. All other analyses were performed using the data obtained from the 18 quantitative survey sites. All unionids collected during these surveys were returned to the lake alive except for those sacrificed for physiological condition analyses.

The role of water movement in transport of zebra mussel veligers

The rates of zebra mussel infestation on unionids depend, in part, on the number of zebra mussel veligers to which the unionids are exposed (Martel et al. 1994). Unionids continue to survive in the delta long after they were extirpated from the offshore waters of the lake sometime between 1994 and 1997 (Nalepa et al. 2001), suggesting that the number of veligers reaching and/or settling in the delta are low. To test this hypothesis, four transects were established in different areas of the delta (Fig. 2). Veligers were collected from stations with water depths of 4 m (offshore), 2 m (intermediate), and <1 m (nearshore) along each transect on seven occasions between
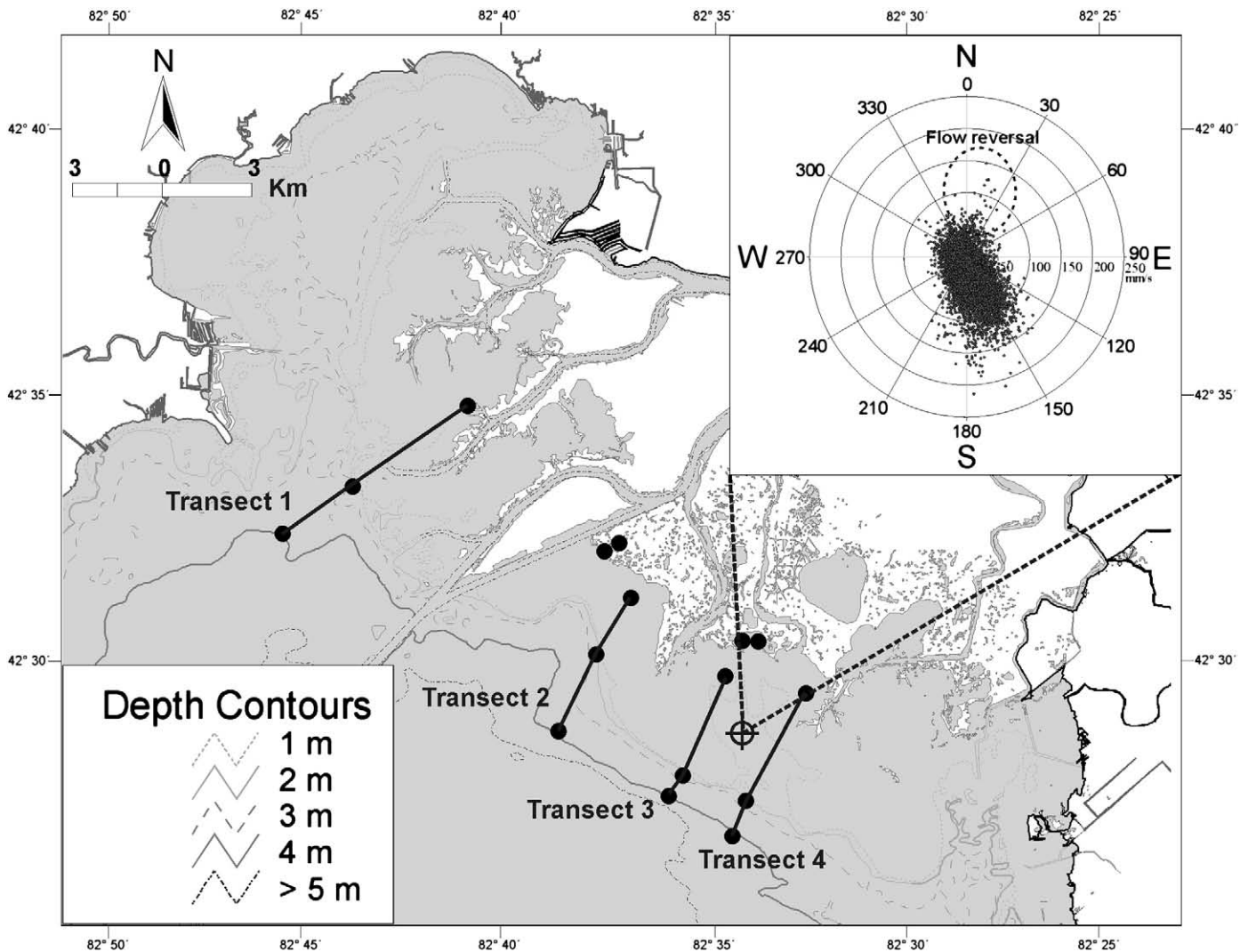
Fig. 2. Locations of stations sampled for zebra mussel veligers in the water column in 2003 and 2004. The installation site for the acoustic Doppler current profiler (ADCP) and optical backscatter sensors is also shown. Inset: magnitude and direction of water currents in the Lake St. Clair delta as measured by the ADCP. The ellipse highlights periods of flow reversal. Each dot represents an individual measurement of current direction and magnitude.

June 3 and August 27, 2003. In 2004, veligers were collected on six occasions between June 3 and August 11 at the same stations along transects 2 and 3 and at four additional inshore stations near Sites 1 and 18 where the highest densities of unionids had been found in 2003 (see Fig. 2). Samples were collected in triplicate from each of the stations using a 12 L capacity Schindler-Patalas trap with 40 μm mesh and preserved in ~70% ethanol. In the lab, a 50–90 ml aliquot of each sample was poured into a square-gridded Petri dish. Six to 12 of the 36 1-cm^2 squares were randomly selected, and all veligers within each square were enumerated and sorted into size classes representing the five stages of the veliger life cycle, including the three planktonic forms: pre-D form (<80 μm), D form (81–150 μm), and veliconcha (151–250 μm) and the two settling forms: pediveliger (251–300 μm) and plantigrade (>300 μm). Veliger counts were averaged by station for each year and log-transformed for statistical analyses.

An acoustic Doppler current profiler (ADCP) and three optical backscatter sensors (OBS) with data loggers were installed on the nearshore side of a sandbar off Walpole Island (Fig. 2) to investigate the role of water movement in transporting zebra mussel veligers into the delta. The ADCP measured current velocity and direction while the OBS measured turbidity to indicate sediment re-suspension events. The equipment was deployed by SCUBA divers at 2.0 m depth on August 22, 2003, and remained operational until it was

removed on November 17, 2003. ADCP data were plotted to illustrate current magnitude and direction during the 62 day monitoring period. Meteorological data (water temperature, barometric pressure, wave height and period, and wind speed) were obtained from Environment Canada ODAS weather buoy # 45147 in Lake St. Clair to monitor storm events over the same 62 day period. The weather buoy is located in the centre of the lake approximately 11 km from the location of the ADCP.

Physiological condition analyses

Foot and mantle tissues were collected from 54 male *Lampsilis siliquoidea* (Barnes, 1823) at 14 of the 18 quantitatively-surveyed sites in 2003. Tissues were collected from four specimens at each site except for Sites 12 and 15 where only three animals were found. *L. siliquoidea* was not present at Sites 2, 5, 6, and 7. Tissues were immediately frozen on dry ice and stored at −80 °C until they could be analyzed. *L. siliquoidea* was selected because it is widely distributed in the delta, and males were chosen to minimize variation due to reproductive condition. Foot and mantle tissues were combined for all physiological condition analyses. These data were used to assess relationships between physiological condition indicators (glycogen or fatty acids) and the rate of zebra mussel infestation on unionids, and

to determine if there were differences in the relative condition of mussels across the delta.

Glycogen

For most samples, a 10.0 ± 2.0 mg aliquot of tissue was analyzed for glycogen using the alkaline digestion and phenol-sulfuric acid spectro-photometric method (Naimo et al. 1998, Naimo and Monroe 1999, Monroe and Newton 2001). About 3% of samples were smaller, so a 5.0 ± 2.0 mg aliquot was used in order to leave sufficient material for quality assurance and quality control. The accuracy of glycogen determinations was quantified by the use of procedural blanks, replicates of an in-house reference material (Naimo et al. 1998), triplicate analyses of four aqueous calibration standards, triplicate analyses of randomly selected tissue samples, and triplicate analyses of known additions. As a measure of precision, the relative standard deviation of triplicate analyses of either known additions or tissue samples was estimated according to APHA et al. (1995). The relative standard deviation of 10 triplicate known additions averaged ($\pm$ SD) 19 $\pm$ 9%. Bias associated with glycogen determinations was estimated by recovery of known additions (APHA et al., 1995). Mean recovery in 10 composite samples was $67 \pm 16\%$. Our recovery estimates are similar to those of Naimo and Monroe (1999), who reported 70–75% recovery of known addition samples. The lower recoveries may be related to the use of known additions, where background concentrations in non-spiked samples are considerably more variable, than in matrix standards where variation is reduced due to the use of a standardized tissue sample.

Fatty acids

Analysis included three procedures: gravimetric extraction, deri-vitization, and quantification on a gas chromatograph (GC) following the methods described in Zellmer et al. (2004). Fatty acid methyl esters (FAME) were identified using Supelco's 37 component FAME standard (#47885-U) by comparing peak retention times between samples and standards. The FAME standard was run as a 4-point standard curve with each set of twenty samples. This standard curve was used also to quantify the amount of each fatty acid in a sample. Also, an internal standard (5 α-cholestane; Sigma-Aldrich; #C8003) was added to the tissue before extraction to estimate percent recovery. Additional single fatty acid standards were used to expand the range of quantifiable FAME to include other important fatty acid (i.e., docosapentaenoic acid; 22:5n-3) not included in the 37 component FAME standard. Fatty acid results were reported as μg FAME/mg dry mass of tissue.

Statistical analyses

For each of the three most common species, differences in length-frequency distributions between individuals collected in Canadian and US waters were tested using a two-sample Kolmogorov–Smirnov test. Differences in the number of zebra mussels attached to unionids at quantitatively surveyed sites were assessed using one-way ANOVA. Differences in the densities of zebra mussel veligers both among and within transects were assessed using two-way ANOVA with post-hoc Tukey pairwise comparisons. Relationships between unionid density and average zebra mussel infestation at a site and between glycogen or fatty acid concentrations in *L. siliquoidea* and the number of zebra mussels attached to their shells were assessed using Pearson correla-tions. Differences in the slope of the relationship between zebra mussel infestation rate and glycogen concentration in *L. siliquoidea* between Canadian and US waters were assessed using 2-way ANOVA. The distribution of fatty acid markers in *L. siliquoidea* across the delta was investigated using discriminant analysis to identify the best subset of fatty acid markers needed to separate unionids among the major bays of the delta. All analyses were conducted using SYSTAT® v. 11 and, where necessary, data were transformed using the natural logarithm to meet the assumptions of normality.

Results

Assessment of unionid communities in the delta

Unionid surveys

A total of 1875 unionids of 22 species were found at 32 sites in the St. Clair delta in 2003 and 2005 (Table 1). Eight of these species are listed as Endangered or Threatened in one or more jurisdictions. Members of the sub-families Lampsilinae and Ambleminae comprised 76% and 22%, respectively, of all unionids collected, whereas members of the sub-family Anodontinae accounted for only 2%. *Lampsilis siliquoidea* was the most abundant and frequently encountered

Table 1
Relative abundance and percent occurrence of unionid species found at 32 sites in the Lake St. Clair delta in 2003 and 2005

Species	Subfamily	Relative abundance (%)	Percent occurrence
Lampsilis siliquoidea (Barnes, 1823)	Lampsilinae	47.49	90.6
Fusconaia flava (Rafinesque, 1820)	Ambleminae	12.82	68.8
Lampsilis cardium (Rafinesque, 1820)	Lampsilinae	12.07	78.1
Pleurobema sintoxia (Rafinesque, 1820)[a]	Ambleminae	6.84	34.4
Villosa iris (Lea, 1829)[a]	Lampsilinae	4.86	50.0
Potamilus alatus (Say, 1817)	Lampsilinae	4.81	59.4
Ligumia nasuta (Say, 1817)[a]	Lampsilinae	4.43	25.0
Amblema plicata (Say, 1817)	Ambleminae	1.98	31.3
Leptodea fragilis (Rafinesque, 1820)	Lampsilinae	0.75	21.9
Pyganodon grandis (Say, 1829)	Anodontinae	0.64	15.6
Elliptio dilatata (Rafinesque, 1820)	Ambleminae	0.59	21.9
Obovaria subrotunda (Rafinesque, 1820)[a,b]	Lampsilinae	0.59	18.8
Lampsilis fasciola (Rafinesque, 1820)[a,d]	Lampsilinae	0.53	18.8
Lasmigona costata (Rafinesque, 1820)	Anodontinae	0.43	12.5
Anodontoides ferussacianus (Lea, 1834)	Anodontinae	0.27	6.3
Ligumia recta (Lamarck, 1819)	Lampsilinae	0.27	6.3
Strophitus undulatus (Say, 1817)	Anodontinae	0.21	12.5
Alasmidonta marginata (Say, 1818)	Anodontinae	0.16	9.4
Ptychobranchus fasciolaris (Rafinesque, 1820)[a]	Lampsilinae	0.11	6.3
Quadrula pustulosa (Lea, 1831)	Ambleminae	0.05	3.1
Quadrula quadrula (Rafinesque, 1820)[c]	Ambleminae	0.05	3.1
Truncilla donaciformis (Lea, 1829)[a]	Lampsilinae	0.05	3.1

[a] Endangered in Canada.
[b] Endangered in Michigan.
[c] Threatened in Canada (Great Lakes–Western St. Lawrence population).
[d] Threatened in Michigan.

Table 2
Number of unionid species, mean density of unionids, mean zebra mussel infestation rate, and size class distribution of zebra mussels attached to unionids at 18 sites surveyed quantitatively in US and Canadian waters of the Lake St. Clair delta in 2003

Site	Area searched (m²)	Number of species	Mean density (#/m² ± SE)	Infestation rate (#/unionid ± SE)	% of zebra mussels in each length class (mm)		
					1–12	13–24	25–40
US waters							
12	1755	5	0.032 ± 0.003	11 ± 3	19	81	0
13	1950	6	0.042 ± 0.004	13 ± 3	9	81	10
17	1950	6	0.048 ± 0.003	2 ± 0.5	4	83	13
16	1950	4	0.043 ± 0.007	9 ± 3	70	28	2
11	1950	6	0.027 ± 0.004	15 ± 2	28	55	17
14	1950	8	0.081 ± 0.010	27 ± 5	28	67	5
10	1950	7	0.030 ± 0.003	24 ± 3	16	82	2
9	1040	6	0.039 ± 0.010	7 ± 2	35	65	0
8	1235	7	0.045 ± 0.010	29 ± 4	23	62	15
Canadian waters							
1	1950	13	0.096 ± 0.022	0.7 ± 0.2	–[1]	–	–
2	260	3	0.021 ± 0.005	8 ± 4	10	83	7
3	1950	11	0.075 ± 0.008	15 ± 2	13	73	14
4	1690	8	0.033 ± 0.008	7 ± 2	14	66	20
5	1950	6	0.035 ± 0.002	13 ± 3	48	42	10
18	1950	12	0.120 ± 0.020	9 ± 2	29	54	17
15	1950	6	0.023 ± 0.003	27 ± 6	53	38	9
6	1950	6	0.021 ± 0.005	35 ± 15	58	37	5
7	910	6	0.023 ± 0.004	21 ± 4	17	80	3

Sites arranged from west to east.
[1] Zebra mussels not measured.

species, followed by *Fusconaia flava* (Rafinesque, 1820), *Lampsilis cardium* (Rafinesque, 1820) and *Pleurobema sintoxia* (Rafinesque, 1820). Species richness at the 18 quantitative sites ranged from 3 to 13 species/site, and mean density ranged from 0.02 to 0.12 unionids/m² (Table 2).

Unionid community structure varied throughout the study area. There were differences in species composition among sites in Canadian and US waters. Sites in Canadian waters supported more species than sites in US waters (19 vs. 13), although average species richness did not differ (*t*-test; $p = 0.154$) between Canadian and US waters (8 vs. 6). Canadian waters also supported a 16% higher overall density of unionids (0.050/m² vs. 0.043/m²) and more Endangered and Threatened species (100 specimens of 5 species vs. 77 specimens of 3 species). Unionids from Canadian sites were also larger than those from US sites, based on comparisons of the three most common species. Mean lengths were 59 vs. 55 mm for *L. siliquoidea* ($n = 310$ and 501, respectively), 83 vs. 71 for *L. cardium* ($n = 154$ and 26, respectively) and 41 vs. 36 for *F. flava* ($n = 186$ and 48, respectively); the length distributions were significantly different in Canadian and US waters for each species ($p < 0.001$).

Zebra mussel infestation

A total of 4605 zebra mussels were removed from the shells of ~20% of unionids collected from the quantitative sites. Overall, the mean infestation rate (± SE) across all sites was 15 ± 1 zebra mussels/ unionid. Infestation rates differed significantly among sites ($F_{17,282} = 14.8$; $p < 0.001$), ranging from <1 at Site 1 to 35 at Site 6 (Table 2) but did not differ between Canadian and US waters ($F_{1,16} < 0.01$; $p = 0.993$). There was a negative, marginally significant, correlation between mean density of unionids and mean rate of zebra mussel infestation ($n = 18$; $r = -0.419$; $p = 0.084$). The lengths of individual zebra mussels removed from unionids ranged from 2 to 38 mm. The size class distribution of attached zebra mussels, categorized into three length ranges (1–12, 13–24, and 25–40 mm), varied considerably across the delta (Table 2).

The role of water movement in transport of zebra mussel veligers

Zebra mussel veligers were present in the water column over the entire study period in both 2003 and 2004. Significant differences were observed in total veliger densities among the offshore, intermediate and nearshore stations in the delta in 2003 ($F_{2,73} = 10.0$; $p < 0.001$) and 2004 ($F_{3,42} = 7.9$; $p < 0.001$) and also among transects in 2003 and 2004 ($F_{3,73} = 4.5$; $p = 0.004$ and $F_{1,42} = 9.7$; $p = 0.001$ respectively). Veliger densities at offshore stations in 2003 (28,000 ± 5042 larvae/ m³) were significantly higher than those at the intermediate (13,408 ± 3152/m³) and nearshore stations (13,581 ± 2720/m³), which did not differ from each other (Fig. 3). In 2004, veliger densities were significantly higher at the offshore stations than the intermediate, nearshore, and inshore stations. Planktonic D-form and veliconcha veligers made up the largest proportion of the total veligers over the sampling period in both 2003 (90%) and 2004 (87%), while only 7% of the veligers in 2003 and 10% in 2004 were settling stage pediveligers.

Shallow areas of the delta exhibited periods of high turbidity that often coincided with storm events. The direction of water flow was generally toward the south to southeast, with a mean magnitude
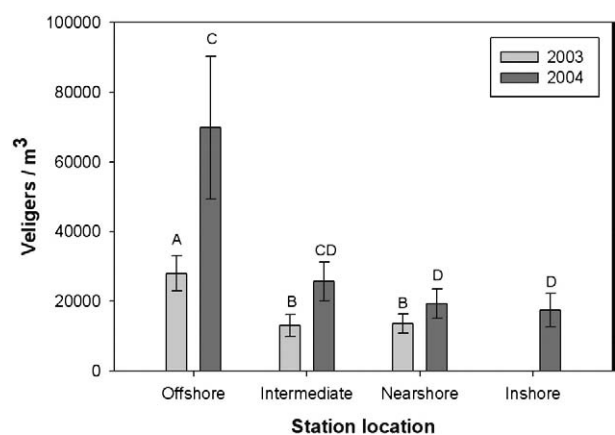

Fig. 3. Mean densities (#/m³ ± SE) of zebra mussel veligers in water samples collected from offshore, intermediate, nearshore and inshore stations in the Lake St. Clair delta during the summers of 2003 ($n = 28$ at each location) and 2004 ($n = 10$ at offshore, intermediate, and nearshore stations and $n = 15$ at the inshore stations). Locations not connected by the same letter had significantly different veliger densities. Differences between years were not assessed.
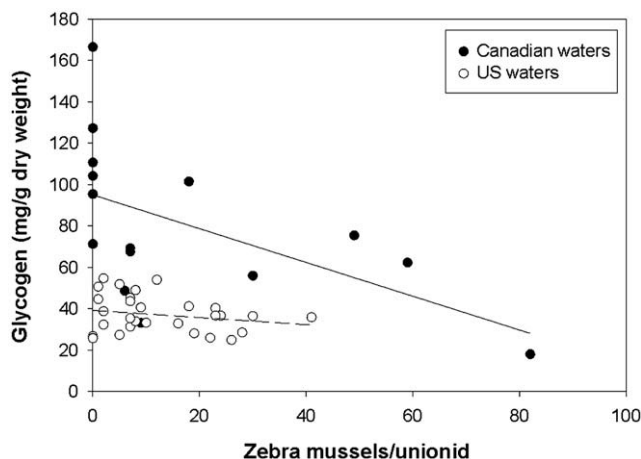
Fig. 4. Relationships between glycogen concentrations (mg/g dry weight) in combined foot and mantle tissues of individual male *Lampsilis siliquoidea* collected from the Lake St. Clair delta in 2003 and the number of zebra mussels attached to their shells. Lines represent regressions for specimens collected from Canadian sites (solid line) and US sites (dashed line).
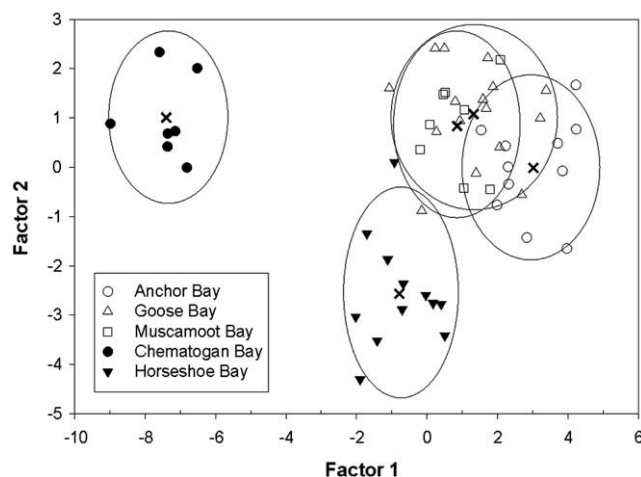

Fig. 5. Canonical scores plot derived from a discriminant analysis of the concentrations of 9 fatty acids in the foot and mantle tissues of male *Lampsilis siliquoidea* grouped by the bay in which they were collected from the Lake St. Clair delta in 2003. Filled symbols are from animals collected in Canadian waters of the delta and hollow symbols from animals collected from US waters. The centroid for each 75% confidence ellipse is denoted by an X.

($\pm$ SD) of 51.1 ± 31.7 mm/s (Fig. 2). The OBS data showed an increase in turbidity when current magnitude exceeded 150 mm/s in combination with extended periods of high wind from the northeast, or when the direction of the wind was from the south to southeast and persisted long enough to reverse the direction of water flow. Flow reversal events were rare, occurring only 3% of the time.

Physiological condition analyses

Glycogen

Glycogen concentrations in *L. siliquoidea* ranged from 18 to 167 mg/g across the delta (Fig. 4). Highest mean glycogen concentrations observed were in specimens collected from Site 1 (125 ± 14.3 mg/g) and Site 18 (82.5 ± 13.0 mg/g)—sites which also supported the most diverse and abundant unionid communities. Across the delta, there was a negative, marginally significant, correlation between mean glycogen concentration and zebra mussel infestation rate ($r = -0.258$; $p = 0.084$). However, there was a significant difference in the mean concentrations of glycogen in *L. siliquoidea* at Canadian sites (75.9 ± 6.1 mg/g; $n = 19$) compared to US sites (40.0 ± 10.1 mg/g; $n = 35$) (t-test; $p < 0.001$) and differences were also apparent in the slope of the relationship between glycogen concentration and zebra mussel infestation rate in Canadian vs. US sites ($F_{1,42} = 10.4$; $p = 0.002$) (Fig. 4). At Canadian sites, there was a negative correlation between zebra mussel infestation rate and glycogen concentration ($r = -0.667$; $p = 0.007$), whereas at US sites the relationship was not significant ($r = 0.079$; $p = 0.672$).

Table 3
Canonical discriminant coefficients of the 9 fatty acids retained in the discriminant analysis of the fatty acid composition of *Lampsilis siliquoidea* in the Lake St. Clair delta in 2003

Common Name	Molecular formula	Canonical discriminant coefficients	
		Factor 1	Factor 2
Pentadecanoic acid	15:0	2.8	8.6
Palmitoleic acid	16:1n-7	8.1	4.7
Heptadecanoic acid	17:0	−3.0	9.8
Oleic acid	18:1n-9	−13.2	6.2
Linoleic acid	18:2n-6	−2.1	−32.5
α-linolenic acid (ALA)	18:3n-3	−12.8	24.7
Arachidonic acid (ARA)	20:4n-6	−15.8	−10.1
Eicosapentaenoic acid (EPA)	20:5n-3	18.3	−12.6
Docosahexaenoic acid (DHA)	22:5n-3	20.5	2.1

Fatty acids

Mean total lipid levels (% dry weight) in *L. siliquoidea* ranged from 3.8 to 9.0%. Total lipid content of unionids was not correlated with zebra mussel infestation ($r = -0.020$; $p = 0.856$) at sites across the delta. There was no significant correlation between zebra mussel infestation and any individual fatty acid. However, because of the established role of diet as a key factor influencing fatty acid profiles, the spatial distribution of fatty acid profiles in unionids across the delta was investigated. Individual *L. siliquoidea* were grouped based on their occurrence in one of the five major bays of the delta (Fig. 1). Nine fatty acids were retained in the discriminant analysis (Table 3). The first two factors accounted for 94% of the dispersion and clearly separated unionids from the two Canadian bays (Horseshoe and Chematogan) from each other and from the three US bays (Anchor, Goose, and Muscamoot), which grouped together (Fig. 5).

Discussion

Live unionids were found at all but one of the 32 sites surveyed in the shallow waters (<1.5 m) of the Lake St. Clair delta. Unionid densities averaged $0.05 \pm 0.007/m^2$ at the 18 quantitatively surveyed sites, which is the same as the average density of $0.05/m^2$ reported for the delta in 2001 (Zanatta et al. 2002). Unionid densities have been reported for only one other Lake Erie refuge. Bowers and de Szalay (2004) reported a mean density of $0.01/m^2$ in Crane Creek Marsh; however, in their study densities were determined using sampling plots dispersed randomly throughout an area deemed to contain suitable habitat for unionids. Given the difference in the sampling method used in their study, a direct comparison with the densities in the Lake St. Clair delta is not possible.

The three most abundant species in 2003 and 2005 (*L. siliquoidea*, *F. flava* and *L. cardium*) were also the most abundant in 1999–2001 (Zanatta et al. 2002). In the present study, the proportion of the unionid community in each of the subfamilies Lampsilinae, Amblemiinae and Anodontinae was 76%, 22% and 2%, respectively, which is similar to the 80% Lampsilinae, 14% Amblemiinae, and 6% Anodontinae reported by Nalepa and Gauvin (1988) for offshore waters of Lake St. Clair prior to the establishment of zebra mussels. As Lampsiline and Anodontine mussels are thought to be more affected by zebra mussel infestation than Amblemines (Schloesser et al. 1998), the dominance of Lampsilines in the unionid community of the shallow waters of the

delta suggests that this community has been sheltered from the most severe effects of zebra mussels.

The rates of zebra mussel infestation of unionids in refugia in Lake Erie are near zero either because unionids are able to shed their load of attached zebra mussels actively by burrowing in soft sediments (Nichols and Wilcox 1997; Schloesser et al. 1997) or the zebra mussels are killed or released from unionids when water-level fluctuations cause them to be exposed (Schloesser and Masteller 1999; Bowers and de Szalay 2005). The average number of zebra mussels attached to unionids declined from 61 in 1999 to 31 in 2000 to 17 in 2001 (Zanatta et al. 2002), and to 15 in this study, a trend which is consistent with observed declines in the density of zebra mussels at other sites in Lake St. Clair between 1994 and 1997 (Nalepa et al. 2001). Although declining, infestation rates in the delta are still higher than those observed in the Lake Erie refugia. Only the unionids at Site 1 showed evidence of periodic shedding of attached zebra mussels, i.e., unionids at this site had almost no zebra mussels attached to them but most had the remnants of byssal threads on their shells. It was noted that substrates at Site 1 were less consolidated than at other sites and were easily disturbed during snorkeling; thus, it seems likely that unionids at this location may be able to burrow and rid themselves of attached zebra mussels. At most other sites in the delta, the majority of zebra mussels attached to unionids were <24 mm in length and thus were either in their first or second year of life based on the growth estimates for Lake St. Clair (Mackie 1991). Zebra mussels with lengths >24 mm, which would likely be >2 years old (Mackie 1991), were found attached to unionids at all but three of the sites surveyed quantitatively. The presence of zebra mussels from several age classes attached to unionids, suggests that unionids were not periodically shedding zebra mussels over much of the delta area and that some other mechanism(s) are likely responsible for the low rates of infestation in the delta.

The direction and rate of water flow in the delta may be limiting zebra mussel infestation of unionids. Densities of zebra mussel veligers were consistently lower at sites nearest the shore in 2003 and 2004. Lower densities of veligers in the water column have been shown to result in lower settlement rates of zebra mussels onto artificial substrates (Martel et al. 1994); thus, zebra mussel veliger settlement rates in the delta are likely lower in waters <1.5 m deep where live unionids occur. The direction of water flow and predominant wind direction are both from the north-west, tending to move water and particulate matter, including planktonic veligers, out of the delta. This flow pattern reverses when the wind direction changes and blows from the south or southeast and persists long enough to push water into the delta, coinciding with re-suspension of sediments (as measured by increased turbidity). During such events in Lake Erie, Martel (1993) demonstrated increased drift and settlement of postmetamorphic zebra mussels, which were also re-suspended into the water column. Postmetamorphic zebra mussels are thought to have a better chance of survival as they have already made the transformations necessary for the transition to benthic life (Martel 1993). Flow reversal events are one mechanism by which zebra mussel veligers and/or postmetamorphic zebra mussels could enter the shallow areas of the delta where the unionids are found, but the low frequency of these flow reversals likely limits the exposure of unionids to zebra mussels.

There were differences in the unionid communities found in Canadian and US waters of the delta. The unionid community in US waters was less diverse and was dominated (>90% of abundance) by three species (*L. siliquoidea*, *V. iris* and *F. flava*), whereas the unionid community in Canadian waters was more diverse, with five species (*L. siliquoidea*, *F. flava*, *L. cardium*, *Ligumia nasuta* (Say, 1817) and *P. sintoxia*) making up 90% of the community by abundance. Unionid densities, species richness, and the number of Endangered and Threatened species were also greater in Canadian waters of the delta. It is speculated that these differences are due, at least in part, to

differences in productivity and land use on either side of the delta. The shipping channel, which bisects Lake St. Clair along the border, effectively splits the lake into less productive (US) and more productive (Canada) water masses (Leach 1980).

Although zebra mussel infestation rates in the delta are low, there is evidence that unionids may be experiencing some negative effects. There was a weak negative correlation between unionid density and zebra mussel infestation rate. There was also a significant negative correlation between glycogen concentration in *L. siliquoidea* and the number of attached zebra mussels in Canadian waters of the delta. A similar pattern has been seen in other systems. For example, specimens of *Amblema plicata* (Say, 1817) and *Quadrula pustulosa* (Lea, 1831) obtained from a heavily infested (>350 zebra mussels/m^2) reach of the Ohio River had significantly lower glycogen levels than specimens obtained from a lightly infested (<5 zebra mussels/m^2) reach (Patterson et al. 1997). Unlike in Canadian waters, the slope of the relationship between glycogen and zebra mussel infestation rate in US waters was not significantly different from zero, indicating that *L. siliquoidea* in US waters had similar, low glycogen concentrations regardless of the rate of zebra mussel infestation. Although increased stress has been clearly linked with reductions in energy stores as glycogen in unionids, the reductions in glycogen have not resulted in increased mortality (Haag et al. 1993, Newton et al. 2001). The inconsistency between glycogen concentration and the rate of zebra mussel infestation in Canadian and US waters may result from the ability of unionids to slowly utilize stored glycogen during periods of food limitation and to maintain glycogen levels above 25% (on a dry wt basis) for ~200 days without food (Ellis and Calvin 1936). However, due to the lack of definitive physiological thresholds, it cannot be determined if unionids in US waters have reached a critical, low threshold glycogen value that results in mortality.

Concentrations of total lipid and of individual fatty acids in *L. siliquoidea* were not significantly correlated with zebra mussel infestation, but fatty acids do provide a possible explanation for differences in glycogen concentrations on either side of the Canada-US border. Unionids from sites in US waters had higher levels of palmitoleic acid (16:1n-7) and eicosapentaenoic acid (20:5n-3) in their tissues, suggesting that they consume a diet rich in diatoms. Unionids collected from Chematogan Bay on the Canadian side of the delta had higher concentrations of α-linolenic acid (18:3n-3) and linoeic acid (18:2n-6), which is indicative of a diet rich in green algae and cyanobacteria, respectively (Napolitano 1999). These results suggest that diatoms are more abundant in less productive US waters, which receive most of the water flowing out of Lake Huron, whereas green algae and cyanobacteria make up larger portions of the planktonic community in the more eutrophic Canadian waters. Zebra mussels have been shown to have significant effects on the community structure of phytoplankton (Heath et al. 1995, Smith et al. 1998); thus, zebra mussels may indirectly influence food resources for unionids. However, as there was no difference in rates of zebra mussel infestation on either side of the delta, apparent differences in potential food resources for unionids between US and Canadian waters cannot be solely explained based on zebra mussel infestation. It is speculated that differences in diet are more likely due to the differences in productivity across the delta resulting in lower food availability in US waters as unionids and zebra mussels would be competing for food from a smaller resource pool. However, diatoms are a more nutritious food source than filamentous green algae and cyanobacteria (Reeders et al. 1992), suggesting a quantity/quality tradeoff. Unionids in US waters, although consuming higher quality food, may be food limited, resulting in lower stored glycogen in their tissues as compared to unionids in Canadian waters. Food limitation in combination with cooler ambient water temperatures may also explain the observed differences in shell length between US and Canadian waters, which suggest that unionids grow more slowly in US than Canadian waters.

The unionid communities of the Lake St. Clair delta appear relatively stable over the 6 year interval since Zanatta et al.'s (2002) study. However, 6 years is a very short time interval for an animal that may live for several decades, so continued sampling of this potentially important refuge is needed to evaluate long term trends in population dynamics. The dominant offshore currents in the delta may prevent planktonic zebra mussel veligers from achieving high densities in shallow waters and this may be a factor limiting zebra mussel infestation of unionids in the delta. Even at the low rates of infestation observed, zebra mussels appear to be adversely affecting energy stores (as glycogen) in unionids from Canadian waters of the delta. The lack of a trend in concentrations of glycogen in unionids from US waters over the same gradient of infestation as seen in Canadian waters suggests that additional factors are affecting energy storage in unionids in the delta. Fatty acids in unionids indicate that there may be important differences in food quantity in the US vs. Canadian waters. This seems plausible since the source waters for the US side of the delta stem immediately from the more oligotrophic and diatom-rich waters of Lake Huron.

The goal of this study was to characterize the refuge for native freshwater mussels in the Lake St. Clair delta and not to make direct comparisons between US and Canadian waters. However, it is interesting to note that in almost every measure, whether it be unionid density, species richness, maximum shell length, or the concentration of glycogen and fatty acid composition of unionid tissues, there were differences between US and Canadian sites. Reasons presented here to explain differences in measures of physiological condition are speculative and more in-depth studies of the inter-relationships between glycogen and fatty acid concentrations in unionids, zebra mussels, and food type/availability are required.

With an area of ~100 km^2, the refuge in the delta of Lake St. Clair is 30 to 100× larger than the other known Great Lakes refugia, all of which are in Lake Erie. Based on the large size of this refuge, it is apparent that the delta supports the largest and richest unionid community remaining in the lower Great Lakes. The refuge also supports several species that are listed as Endangered and Threatened in Canada and/or Michigan, including significant populations of *P. sintoxia*, *Obovaria subrotunda* (Rafinesque, 1820), and *L. nasuta*. The populations of these species are likely the largest remaining in Canada (COSEWIC, 2003, 2004, and 2007b). Conserving the unionid communities of the Lake St. Clair delta will be critical to efforts aimed at preserving the highly imperiled unionid fauna of the Great Lakes.

Acknowledgments

References

Alkanani, T., Parrish, C.C., Thompson, R.J., McKenzie, C.H., 2007. Role of fatty acids in cultured mussels, *Mytilus edulis*, grown in Notre Dame Bay, Newfoundland. J. Exp. Mar. Biol. Ecol. 348, 33–45.

APHA [American Public Health Association, American Water Works Association, and Water Environment Federation], 1995. Standard Methods for the Examination of Water and Wastewater, 19th ed. American Public Health Association, Washington DC., p. 993.

Arts, M.T., Wainman, B.C. (Eds.), 1999. Lipids in Freshwater Ecosystems. Springer-Verlag, New York, p. 319. ISBN: 0-387-98505-0.

Bowers, R., de Szalay, F.A., 2004. Effects of hydrology on unionids (Unionidae) and zebra mussels (Dreissenidae) in a Lake Erie Coastal Wetland. Am. Midl. Nat. 151, 286–300.

Bowers, R., de Szalay, F.A., 2005. Effect of water level fluctuations on zebra mussel distribution in a Lake Erie coastal wetland. J. Freshw. Ecol. 20, 85–92.

Bowles, J.M. 2005. Walpole Island Ecosystem Recovery Strategy (Draft 8). Prepared for the Walpole Island Heritage Centre, Environment Canada, and The Walpole Island Recovery Team: 45 pp.

Brett, M.T., Müller-Navarra, D.C., Ballantyne, A.P., Ravet, J.L., Goldman, C.R., 2006. *Daphnia* fatty acid composition reflects that of their diet. Limnol. Oceanogr. 51, 2428–2437.

COSEWIC [Committee on the Status of Endangered Wildlife in Canada], 2003. COSEWIC assessment and update status on the Round Hickorynut *Obovaria subrotunda* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vi + 31 pp.

COSEWIC [Committee on the Status of Endangered Wildlife in Canada], 2004. COSEWIC assessment and status report on the Round Pigtoe *Pleurobema sintoxia* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vi + 33 pp.

COSEWIC [Committee on the Status of Endangered Wildlife in Canada], 2006. COSEWIC assessment and status report on the Rainbow mussel *Villosa iris* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 38 pp. http://www.sararegistry.gc.ca/status/status_e.cfm.

COSEWIC [Committee on the Status of Endangered Wildlife in Canada], 2007a. Canadian Species at Risk: September 2007. http://www.cosewic.gc.ca/eng/sct0/rpt/rpt_csar_e.pdf.

COSEWIC [Committee on the Status of Endangered Wildlife in Canada], 2007b. COSEWIC assessment and status report on the Eastern Pondmussel *Ligumia nasuta* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 34 pp.

Dalsgaard, J., St. John, M.A., Kattner, G., Müller-Navarra, D.C., Hagen, W., 2003. Fatty acid trophic markers in the pelagic marine environment. Adv. Mar. Biol. 46, 225–340.

De Zwaan, A., Zandee, D.I., 1972. The utilization of glycogen and accumulation of some intermediates during anaerobiosis in *Mytilus edulis* L. Comp. Biochem. Physiol. B 43, 47–54.

Ellis, M.M., Calvin, D.B., 1936. Glycogen content of freshwater mussels during prolonged starvation. Proc. Soc. Exp. Biol. Med. 34, 222–225.

Environment Canada, U.S. Environmental Protection Agency, Ontario Ministry of Environment and Michigan Department of Natural Resources, 1994. The St. Clair River Remedial Action Plan: Stage 1 Environmental Conditions in the St. Clair River Area of Concern up to 1994; http://www.friendsofthestclair.ca.

Gillis, P.L., Mackie, G.L., 1994. Impact of the zebra mussel, *Dreissena polymorpha*, on populations of Unionidae (Bivalvia) in Lake St. Clair. Can. J. Zool. 72, 1260–1271.

Greseth, S.L., Cope, W.G., Rada, R.G., Waller, D.L., Bartsch, M.R., 2003. Biochemical composition of three species of unionid mussels after emersion. J. Molluscan Stud. 69, 101–106.

Haag, W.R., Berg, D.J., Garton, D.W., Farris, J.L., 1993. Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in western Lake Erie. Can. J. Fish. Aquat. Sci. 50, 13–19.

Hallac, D.E., Marsden, J.E., 2000. Differences in tolerance to and recovery from zebra mussel (*Dreissena polymorpha*) fouling by *Elliptio complanata* and *Lampsilis radiata*. Can. J. Zool. 78, 161–166.

Heath, R.T., Fahnenstiel, G.L., Gardner, W.S., Cavaletto, J.F., Hwang, S.J., 1995. Ecosystem-level effects of zebra mussels (*Dreissena polymorpha*): an enclosure experiment in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21, 501–516.

Hebert, C.E., Arts, M.T., Weseloh, D.V.C., 2006. Ecological tracers can quantify food web structure and change. Environ. Sci. Technol. 40, 5618–5623.

Hebert, C.E., Weseloh, D.V.C., Idrissi, A., Arts, M.T., O, Gorman, R., Gorman, O.T., Locke, B., Madenjian, C.P., Roseman, E.F., 2008. Restoring piscivorous fish populations in the Laurentian Great Lakes causes seabird dietary change. Ecology 89, 891–897.

Hellou, J., Law, R.J., 2003. Stress on stress response of wild mussels, *Mytilus edulis* and *Mytilus trossulus*, as an indicator of ecosystem health. Environ. Pollut. 126, 407–416.

Hummel, H., De Wolf, L., Zurburg, W., Apon, L., Bogaards, R.H., Van Ruitenburg, M., 1989. The glycogen content in stressed marine bivalves: the initial absence of a decrease. Comp. Biochem. Physiol. B 94, 729–733.

Iverson, S.J. in press. Tracing aquatic food webs using fatty acids: from qualitative indicators to quantitative determination. In Lipids in Aquatic Ecosystems, eds. M.T. Arts, M.T. Brett and M. Kainz, New York: Springer, (in press).

Jaworski, E., Raphael, C.N., 1976. Modification of coastal wetlands in southeastern Michigan and management alternatives. Mich. Acad. 8, 303–317.

Jokela, J., Uotila, L., Taskinen, J., 1993. Effects of the castrating trematode parasite *Rhipidocotyle fennica* on energy allocation of fresh-water clam *Anodonta piscinalis*. Funct. Ecol. 7, 332–338.

Lake St. Clair Canadian Watershed Coordination Council, 2005. The Lake St. Clair Canadian watershed draft technical report: An examination of current conditions. 76 pp.

Leach, J.H., 1980. Limnological sampling intensity in Lake St. Clair in relation to distribution of water masses. J. Great Lakes Res. 6, 141–145.

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. Hydrobiol. 219, 251–268.

Martel, A., 1993. Dispersal and recruitment of zebra mussel (*Dreissena polymorpha*) in a nearshore area in west-central Lake Erie: the significance of postmetamorphic drifting. Can. J. Fish. Aquat. Sci. 50, 3–12.

Martel, A., Mathieu, A.F., Findlay, C.S., Nepszy, S.J., Leach, J.H., 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.

Michigan DNR [Department of Natural Resources], 2007. Endangered and Threatened Species. http://www.state.mi.us/orr/emi/admincode.asp?AdminCode=Single&Admin_Num=29901021&=NR&RngHigh=. Accessed October 2008.

Monroe, E.M., Newton, T.J., 2001. Seasonal variation in physiological condition of *Amblema plicata* in the Upper Mississippi River. J. Shellfish Res. 20, 1167–1171.

Naimo, T.J., Monroe, E.M., 1999. Variation in glycogen concentrations within mantle and foot tissues in *Amblema plicata plicata*: implications for tissue biopsy sampling. Am. Malacol. Bull. 15, 51–58.

Naimo, T.J., Damschen, E.D., Rada, R.G., Monroe, E.M., 1998. Nonlethal evaluation of the physiological health of unionid mussels: methods for biopsy and glycogen analysis. J. North. Am. Benthol. Soc. 17, 121–128.

Nalepa, T.F., Gauvin, J.M., 1988. Distribution, abundance, and biomass of freshwater mussels (Bivalvia: Unionidae) in Lake St. Clair. J. Great Lakes Res. 14, 411–419.

Nalepa, T.F., Hartson, D.J., Gostenik, G.W., Fanslow, D.L., Lang, G.A., 1996. Changes in the freshwater mussel community of Lake St. Clair from Unionidae to *Dreissena polymorpha* in eight years. J. Great Lakes Res. 22, 354–369.

Nalepa, T.F., Hartson, D.J., Fanslow, D.L., Lang, G.A., 2001. Recent population changes in freshwater mussels (Bivalvia: Unionidae) and zebra mussels (*Dreissena polymorpha*) in Lake St. Clair, U.S.A. Am. Malacol. Bull. 16, 141–145.

Napolitano, G.E., 1999. Fatty acids as trophic and chemical markers in freshwater ecosystems. In: Arts, M., Wainman, B.C. (Eds.), Lipids in Freshwater Ecosystems. Springer-Verlag, New York, pp. 21–44.

Newton, T.J., Monroe, E.M., Gutreuter, S.J., Kenyon, R., Thiel, P.A., Welke, K.I., 2001. Evaluation of relocation of unionid mussels into artificial ponds. J. North. Am. Benthol. Soc. 20, 468–485.

Nichols, S.J., Wilcox, D.A., 1997. Burrowing saves Lake Erie clams. Nature 389, 921.

Nichols, S.J., Amberg, J., 1999. Co-existence of zebra mussels and freshwater unionids: population dynamics of *Leptodea fragilis* in a coastal wetland infested with zebra mussels. Can. J. Zool. 77, 423–432.

Patterson, M.A., Parker, B.C., Neves, R.J., 1997. Effects of quarantine times on glycogen levels of native freshwater mussels (Bivalvia: Unionidae) previously infested with zebra mussels. Am. Malacol. Bull. 14, 75–79.

Reeders, H.H., Bij de Vaate, A., Noordhuis, R., 1992. Potential for zebra mussel (*Dreissena polymorpha*) for water quality management. In: Nalepa, T.F., Schloesser, D.W. (Eds.), Zebra Mussels. Biology, Impacts, and Control. Lewis Publishers, pp. 440–451.

Ricciardi, A., Whoriskey, F.G., Rasmussen, J.B., 1995. Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density. Can. J. Fish. Aquat. Sci. 52, 1449–1461.

Ricciardi, A., Whoriskey, F.G., Rasmussen, J.B., 1996. Impact of the *Dreissena* invasion on native unionid bivalves in the upper St. Lawrence River. Can. J. Fish. Aquat. Sci. 53, 1434–1444.

Schlechtriem, C., Arts, M.T., Johannsson, O.E., 2008. Effect of long term fasting on the use of fatty acids as trophic markers in the opossum shrimp *Mysis relicta*—a laboratory study. J. Great Lakes Res. 34, 143–152.

Schloesser, D.W., Nalepa, T.F., 1994. Dramatic decline of unionid bivalves in offshore waters of western Lake Erie after infestation by the zebra mussel, *Dreissena polymorpha*. Can. J. Fish. Aquat. Sci. 51, 2234–2242.

Schloesser, D.W., Masteller, E.C., 1999. Mortality of unionid bivalves (Mollusca) associated with dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) in Presque Isle Bay, Lake Erie. Northeast. Nat. 6, 341–352.

Schloesser, D.W., Nalepa, T.F., Mackie, G.L., 1996. Zebra mussel infestation of unionid bivalves (Unionidae) in North America. Am. Zool. 36, 300–310.

Schloesser, D.W., Smithee, R.D., Longton, G.D., Kovalak, W.P., 1997. Zebra mussel induced mortality of unionids in firm substrata of western Lake Erie and a habitat for survival. Am. Malacol. Bull. 14, 67–74.

Schloesser, D.W., Kovalak, W.P., Longton, G.D., Ohnesorg, K.L., Smithee, R.D., 1998. Impact of zebra and quagga mussels (*Dreissena* spp.) on freshwater unionids (Bivalvia: Unionidae) in the Detroit River of the Great Lakes. Am. Midl. Nat. 140, 299–313.

Schloesser, D.W., Metcalfe-Smith, J.L., Kovalak, W.P., Longton, G.D., Smithee, R.D., 2006. Extirpation of freshwater mussels (Bivalvia: Unionidae) following the invasion of dreissenid mussels in an interconnecting river of the Laurentian Great Lakes. Am. Midl. Nat. 155, 307–320.

Smith, T.E., Stevenson, R.J., Caraco, N.F., Cole, J.J., 1998. Changes in phytoplankton community structure during the zebra mussel (*Dreissena polymorpha*) invasion of the Hudson River (New York). J. Plankton Res. 20, 1567–1579.

Stetten, D., Stetten, M.R., 1960. Glycogen metabolism. Physiol. Rev. 40, 505–537.

Strayer, D.L., Smith, L.C., 1996. Relationships between zebra mussels (*Dreissena polymorpha*) and unionid clams during the early stages of the zebra mussel invasion of the Hudson River. Freshw. Biol. 36, 771–779.

The Nature Conservancy, 1995. Significant Areas of Biological Diversity in the Great Lakes Basin, Ontario. The Nature Conservancy Midwestern Regional Office, Minneapolis, Minnesota and Great Lakes Programs Office, Chicago, Illinois.

U.S. Fish and Wildlife Service, 2007. Federally Endangered, Threatened, and Candidate Species in Michigan. http://www.fws.gov/midwest/Endangered/lists/state-mi.pdf. Accessed September 2007.

Zanatta, D.T., Mackie, G.L., Metcalfe-Smith, J.L., Woolnough, D.A., 2002. A refuge for native freshwater mussels (Bivalvia: Unionidae) from the impacts of the exotic zebra mussel (*Dreissena polymorpha*) in Lake St. Clair. J. Great Lakes Res. 28, 479–489.

Zellmer, I.D., Arts, M.T., Abele, D., Humbeck, K., 2004. Evidence of sublethal damage in *Daphnia* (Cladocera) during exposure to solar UV radiation in subarctic ponds. Arc. Antarct. Alp. Res. 36, 370–377.