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The zebra mussel (Dreissena polymorpha, Pallas) invasion of two rivers in southeast Michigan

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The Zebra Mussel (*Dreissena polymorpha*, Pallas) Invasion of Two Rivers in Southeast Michigan: Interactions with Unionid Bivalves and Patterns of Riverine Dispersal and Colonization

by

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Thesis Committee:

Professor John B. Burch, Chair
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ABSTRACT

The unionid fauna in the Huron River and River Raisin in Southeastern Michigan are threatened by the incipient downstream dispersal of the zebra mussel (*Dreissena polymorpha*) out of infested lakes. I gathered data on unionid species abundance and composition in immediately threatened river segments, assessed patterns of downstream dispersal of *Dreissena* veliger larvae, colonization of unionids, and inferred probable future zebra mussel impact scenarios on unionids in small to mid-sized rivers. Indices of unionid valve fouling by *Dreissena*, veliger flux (Huron only) and recruitment diminished with downstream distance from source populations. Unionid mortality was observed near the source population in the Huron River (124 mussels/unionid) while only 10% of the unionids were fouled 4.5 km downstream (0.1 mussels/unionid). Unionids were less severely fouled in the River Raisin. Little downstream colonization progression occurred in the Huron River between 1995 and 1996 despite an increase in the flux of veligers into the river. Discharge magnitude significantly predicted the slope of downstream attenuation of veliger flux in a 20 km reach of free-flowing channel. The results also indicate that the progeny of riverine *Dreissena* will be swept into downstream impoundments in the Huron and do not pose a threat to unionids in the Huron study reach. In the River Raisin, hydrodynamic factors associated with impoundments, smaller river size, and low-gradients likely have slowed the colonization of lotic habitats. Zebra mussels pose less of an immediate threat to unionids in small-mid sized rivers than in lakes. Short term impacts on unionids are mitigated in small-mid sized rivers by dispersal-hampering hydrodynamic factors associated with moderate gradient and the length of free-flowing channel between a given unionid and the nearest upstream lentic source population. However, prospects for the long-term persistence of riverine unionids in small to mid-sized systems invaded by zebra mussels are uncertain.
Acknowledgments:

Many thanks to the following for assistance and support for this project: The Michigan Department of Natural Resources Natural Heritage Program and Michigan Nature Conservancy for financial support, Renee Sherman for unflagging assistance with fieldwork, to Linda Cope and Karen Lombard for volunteer field assistance, to Jerrine Nichols and Glen Black, and the Great Lakes Science Center, National Biological Service, for lending field equipment (flow meters) and lab space, to the Hudson-Mills Metropark and Bill Anderson for permitting access to study sites on the Huron River, to Ladd Johnson, the University of Michigan Mollusk Division, and Mike Wiley for field and lab equipment.
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Introduction and Literature Review

Freshwater mussels in the family Unionidae are one of the most imperiled faunas in North America. Of 297 species on the continent, 213 (71.1%) are federally listed as either endangered, threatened, or of special concern (Williams et al. 1993). Habitat destruction from dams, siltation, channel modification, and water pollution have contributed to the decline of this fauna. Hastening this decline is the recent introduction and proliferation of the non-indigenous invasive bivalve, the zebra mussel (*Dreissena polymorpha*, Pallas).

Zebra mussels were originally introduced in North America into Lake St. Clair in the mid-1980’s (Herbert et al. 1989), and have since dramatically increased in number in the Great Lakes in a relatively short period of time, reaching densities of up to 750,000 m$^2$ in some locations (Kovalack 1993). Zebra mussels are epizoic, attaching to solid substrates and macrophytes via a byssal apparatus. They are also extremely prolific: adult females can produce up to one million eggs in one season (Sprung 1990). The zebra mussel is renowned as one of the most notorious bio-fouling organisms in the world in freshwater lentic systems amenable to its habitation.

Valves of live native unionids mussels are excellent substrate for zebra mussels. When zebra mussel populations reach high densities, thousands of zebras mussels can be found attached to native mussels (referred to as “fouling”), resulting in death. In Lake Erie, accumulations of up to 10,000 zebra mussels have been found on individual unionids (Mackie 1991), and high zebra mussel densities have corresponded with almost 100% unionid mortality (Schloesser and Nalepa 1994). Unionid mortality has also been strongly correlated with zebra mussel densities in Lake St. Clair (Hunter and Bailey 1991). High unionid mortality (90-100%) has been associated with fouling intensities less than 100 mussels/unionid in the St. Lawrence River (Ricciardi et al 1996). Also, Haag and Garton (1993) showed differential mortality rates between bivalve species and reduced fitness among fouled bivalves in Lake Erie.

While the exact causes of mortality are unclear, Mackie (1991) suggested that extreme levels of *Dreissena* fouling interferes with normal unionid locomotion. Heavily
infested unionids were found to have half the lipid reserves of un-fouled individuals (Herbert et al., 1991). Byrne et al (1995) suggested that competition for suspended food particles is a likely cause of the decline of tissue energy stores in fouled unionids.

Zebra mussels have been steadily expanding their range since their introduction, utilizing a large number of natural and human mediated dispersal vectors (Carlton 1993). Since their arrival in North America, they have dispersed from the Great Lakes into contiguous commercial waterways, into the Chicago Sanitary Ship Canal, the Illinois, and the Mississippi Rivers. Overland dispersal to non-contiguous, isolated inland lakes has occurred at a slower rate, particularly in the Lower Peninsula of Michigan, probably as a result of overland transport by recreational boats (Johnson and Carlton 1993; Marangelo and Johnson 1994; Marangelo 1995).

The downstream dispersal of zebra mussels from inland lakes to lotic habitats is of great interest to the conservation of unionids. North American river systems harbor the vast majority of unionid species on the continent. Research on this issue has been conducted on large commercial river systems (Whitney 1994; Ricciardi 1996), but smaller systems have received little attention. Exceptions are Hunter’s (1994) ongoing work in the Clinton River, a 3rd order system in southeast Michigan, and a study on downstream zebra mussel dispersal dynamics in a 2nd order creek in southwestern Michigan (Horovath 1995).

A critical question concerning riverine unionids is whether zebra mussel can attain densities in rivers sufficient to extirpate native mussels despite less hospitable environmental conditions. European records concerning the abundance of zebra mussels in lotic systems offer only sketchy information, but indicate that densities typically are much higher in impoundments than in downstream lotic stretches of the same system (Kackalova and Sloka 1968). In the large and navigable Dvina River, Kuchina (1968) observed that zebra mussel densities were predominantly low.

The few incipient lotic Dreissena invasions that are currently being studied in the United States also suggests that zebra mussels colonize riverine habitats less acutely than lentic systems (Hunter 1994; Horovath 1995), although substantial unionid impacts have been documented in large lotic systems (Ricciardi 1996). Little is known about the exact nature of the limiting factors of zebra mussels in rivers. As Dreissena’s lifecycle appears to
be best suited to lentic conditions, it is likely that such factors can be attributed to the fundamentally different ecological parameters that exist in lotic systems.

Zebra mussel spawning activity in the spring and summer produces planktonic veliger larvae that remain in the water column for anywhere from 18 to 90 days after fertilization (Ackerman 1994a). Weakly free-swimming veligers disperse in the direction of water currents. Veligers produced by zebra mussel populations in inland lakes will thus disperse into downstream lotic habitats. Under lotic conditions, many factors may potentially effect veliger mortality and recruitment in small to mid-sized river habitats. Turbulence, flow stability, and temperature extremes may exacerbate veliger mortality in flowing water and impair recruitment of larvae. Substrate instability may also stress or limit riverine adult populations of *Dreissena*, and chemical parameters (fluctuations in dissolved oxygen) may serve to stress riverine populations.

Also, little is known about the settling dynamics of zebra mussels in small to mid-sized rivers. Existing experimental data and data from lentic systems indicates that settled adults may provide cues for larval settlement (Baldwin 1994). After settlement, larval pediveligers to juvenile adults actively crawl in the benthos to find suitable substrate (Ackerman 1994a). Laboratory experiments have demonstrated that zebra mussels have difficulty settling in high-velocity flowing water (Ackerman 1994b), but little work has been done on in-situ dynamics of settlement with a variety of settlement substrata. For example, the ability of settling zebra mussel veligers to utilize velocity-sheltered interstitial spaces in substrate with high water velocity and a high proportion of cobble is unknown.

The movement of newly settled post-planktonic veliger larvae and juvenile adults may not be limited to benthic crawling. Martel (1993) observed post-metamorphic re-suspension of early juvenile stages by water currents and waves in Lake Erie. The degree of the manifestation of this types of behavior in rivers may be a critical factor in determining the long-term success of zebra mussel colonization (and hence magnitude of unionid impacts) in lotic systems.

In lentic systems, the exponential population growth that characterizes the early stages of zebra mussel invasion is a result of endogenous recruitment of larvae (in-lake recruitment of veligers that are the progeny of adults in the same lake) into the system’s
adult population. However in rivers, flowing water insures that recruitment of zebra mussel larvae in specific infested channel reaches will be exogenous, a result of the recruitment of veliger progeny of upstream adult populations. A given channel area infested with adult zebra mussels is thus likely to be immune to endogenous recruitment via current-mediated downstream flushing of veligers that occurs during the obligate planktonic phase of the *Dreissena* lifecycle. In unimpounded, free-flowing water conditions, riverine zebra mussel densities and associated unionid impacts will thus mostly be a function of the spawning activity in upstream “source populations” and survivorship and recruitment of zebra mussel veligers under downstream lotic conditions.

Anecdotal evidence suggests a strong relationship between magnitude of discharge and downstream larval dispersal. The Mississippi flood of 1993 appeared to have been responsible for transporting zebra mussels down the Illinois River from Lake Michigan to its confluence with the Mississippi River (Cohen 1994). Similar influences of discharge over the patterns of veliger dispersal may be an important component of the dynamics governing the colonization of lotic habitats in small to mid-sized rivers.

Zebra mussels have now colonized lakes in at least seven major catchments in the Lower Peninsula of Michigan (Marangelo 1995). Investigation of emerging patterns of the colonization of small to mid-sized rivers may provide insights into the potential impact of zebra mussels on unionids in similar small to mid-sized river systems not only in Michigan, but in other North American rivers likely to be invaded by zebra mussels via downstream larval dispersal. This study examines incipient lotic zebra mussel invasions via downstream dispersal in the Huron and Raisin rivers in southeast Michigan, and contrast downstream *Dreissena* colonization patterns and initial unionid impacts in these systems.

For the purposes of this study, unionid impacts may be partitioned into two classes. *Acute* impacts result from severe fouling of live unionids by zebra mussels that results in the death of the animal within 4 - 12 months. *Chronic* impacts result from moderate to low levels of fouling that impart a long-term reduction of fitness in unionids, causing a slow, long-term decline in unionid populations (Whitney 1994). Chronic impact evaluation requires long-term study and hence will not be addressed here. However, chronic impacts
may prove to be more of a long-term threat to unionid persistence in systems colonized by *Dreissena* than acute impacts.

**Zebra Mussel Invasion History**

**Huron River**

Zebra mussels were detected in Portage Lake, Washtenaw County (Fig. 1), a large and popular lake with recreational boaters in the spring of 1994 (R. Sherman, pers. comm.). This lake is part of a series of navigationally contiguous series of lakes connected via the Huron River. Boats passing between these lakes serve as an upstream dispersal vector, and all upstream lakes are now infested with zebra mussels. Hence the discharge of the Huron River at the Baseline Dam (just downstream of the Portage Lake outlet) is composed of water emanating out of infested lakes immediately upstream.

The Huron River Study Reach (HRSR) (Fig. 1) encompasses 22 km of free-flowing channel mainstem directly downstream of Portage and Baseline Lakes, between the Baseline Dam and the Barton Pond impoundment in Ann Arbor. Zebra mussels first colonized upper portions of the HRSR in 1994. Year old adults were found in the river just downstream of the Baseline Dam in the spring of 1995 (estimated density < 1/m²).

**River Raisin**

On the River Raisin, zebra mussels were detected in Vineyard and Clark Lakes (Jackson County) in 1994 (Marangelo 1994). Anecdotal reports suggest that the mussels have been in Vineyard Lake since 1992. The River Raisin Study Reach (RRSR), (Fig. 2; Table 2) consists of the mainstem of the Raisin between Portage Lake and the Sharon Valley Road gauge site near Manchester and the small outlet creek from Clark Lake that joins Goose Creek and the Raisin mainstem in Brooklyn.

Little is known about the present status of unionid fauna of either system. The best historical information exists for the Huron, which was extensively surveyed by van der Shalie (1938). More recently, Scavia and Mitchell (1986) surveyed *Cyclonaias tuberculata* in the HRSR. Unionids once “paved” shoal areas of the HRSR but were heavily impacted by commercial musseling activities and industrial discharge into the river during World-War
II (van der Shalie 1970). Mussels were virtually eliminated from the river downstream of Mill Creek at Dexter during this period.

Historical information for the Raisin is not as extensive. Some early records exist in Goodrich (1932). More recently, Strayer (1979) surveyed a number of mainstem (two of which are in the RRSR) and tributary sites in its watershed.

**System Descriptions**

The portions of the River Raisin threatened with zebra mussel invasion differ substantially from the threatened portion of the Huron mainstem. Vineyard lake is located in the headwaters of the Raisin’s catchment. The mainstem flowing out of the lake is characterized by large low-gradient reaches surrounded by wetland complexes with soft substrate. Water velocity is typically slow, and higher gradient areas have been impounded. Veliger larvae must pass through approximately 3 km of wetland channel before reaching the Brooklyn impoundment. Low gradients/water velocities and three impoundments combine to constitute a study area where the near-endogenous recruitment of veliger progeny of adults in nearby upstream riverine habitats is probable.

A short (approx. 0.5 km) stretch of relatively shallow, gravel bottomed, moderate-velocity channel just downstream of the Brooklyn dam is the only favorable habitat for riverine unionids until the Norvell Dam, 15.7 km downstream from Vineyard Lake. The most productive unionid habitat in the RRSR occurs downstream of this impoundment. The river here is typically shallow (0.1 - 1.0 m at low flow) and narrow (6 - 15 m across) with a substrate of sand and gravel in swifter sections and clay and silt in slower sections. This segment is fragmented by a third impoundment at Sharon Hollow Road.

In contrast to the RRSR, veligers dispersing out of Portage and Baseline Lakes in the HRSR almost immediately enter a 22 km stretch of free-flowing river that flows to the backwaters of the Barton Pond impoundment. The river in the HRSR has been characterized as 37% low gradient run habitat with 63% being fair to excellent gradient with extensive sequences of riffle-run-pool habitat (19% slow-run, 25% fast run-riffle, 29% riffle, and 27% pool; Hay et al 1993). Substrate is mostly cobble and gravel, with some boulders, sand, and marl. The average cross-section is meters at mean discharge of 358 cfs. Water chemistry in
Figure 1: Map of the Huron River Study Reach (HRSR). Numbers correspond to Table 1.
Figure 2: Map of the RRSR. Location numbers correspond to Table 2.
### Table 1: Locations in the Huron River Study Reach. Numbers correspond to Fig. 1

<table>
<thead>
<tr>
<th>#</th>
<th>Site</th>
<th>km downstream</th>
<th>unionid survey</th>
<th>plankton samples</th>
<th>settling plates</th>
<th>stage-discharge</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Portage Lake</td>
<td></td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Portage Outlet</td>
<td></td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Baseline Lake</td>
<td></td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Baseline Dam</td>
<td>0</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>5</td>
<td>-- Bell Road</td>
<td>1.5</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Bell survey site</td>
<td>1.9</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Canoe Camp</td>
<td>3.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>Hudson Mills - Rapids lot</td>
<td>4</td>
<td></td>
<td>x</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>9</td>
<td>Hudson Mills - Island</td>
<td>4.4</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>Powerline</td>
<td>10.2</td>
<td></td>
<td></td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>11</td>
<td>Mill Creek</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>Mast Road</td>
<td>11.6</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>Dexter-Huron</td>
<td>14.8</td>
<td>x</td>
<td></td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>14</td>
<td>-- Delhi West</td>
<td>21.8</td>
<td></td>
<td></td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>15</td>
<td>Delhi Metropark</td>
<td>22.3</td>
<td>x</td>
<td>x</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>16</td>
<td>Barton headwaters</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>17</td>
<td>Barton Pond</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Table 2: Locations in the River Raisin Study Reach. Numbers correspond to Fig. 2

<table>
<thead>
<tr>
<th>#</th>
<th>Mainstem:</th>
<th>km downstream from main source populations</th>
<th>unionid survey</th>
<th>settling plates</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Vineyard outlet</td>
<td>0.05</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>2</td>
<td>Brooklyn Dam</td>
<td>4.0</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>6</td>
<td>Wolf Lake Rd.</td>
<td>11.5</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>7</td>
<td>Norvell Dam</td>
<td>15.7</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>8</td>
<td>Pierce Rd.</td>
<td>21.2</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>9</td>
<td>Sharon Valley Rd.</td>
<td>23.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>Sharon Hollow Rd.</td>
<td>28.9</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>Sharon Valley gauge site</td>
<td>32.4</td>
<td>x</td>
<td>x</td>
</tr>
</tbody>
</table>

### Clark Outlet:

<table>
<thead>
<tr>
<th>#</th>
<th></th>
<th>km downstream</th>
<th>unionid survey</th>
<th>settling plates</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>Clark Outlet</td>
<td>0.05</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>5</td>
<td>Riverside Rd</td>
<td>0.9</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>3</td>
<td>Goose Creek</td>
<td>5.5</td>
<td>x</td>
<td>x</td>
</tr>
</tbody>
</table>
the upper portions of the HRSR is heavily influenced by water in Baseline and Portage Lakes, which are calcareous (171-176 mg/L CaCO$_3$ (Fusilier 1994)) mesotrophic lakes. The HRSR is bounded by glacial till, resulting in groundwater inputs into the system that thermally buffers the water in the river. Temperatures ranged between 22 - 30°C during the late spring and summer of 1995 and 1996, well below the upper temperature tolerance limits of *Dreissena* (Spidle 1995). These factors suggest that physio-chemical parameters will not hinder population development of the zebra mussel.

**Description of Study**

I gathered data to examine the incipient zebra mussel invasion of riverine habitats of both the Raisin and Huron rivers in the context of assessing current impacts on unionids and inferring possible future scenarios of impacts. The three main components of the study were to: 1) assess patterns of downstream riverine dispersal and colonization from upstream lotic source populations of zebra mussels in the study areas; 2) determine the present magnitude of impacts on unionids resulting from these patterns; 3) assess the present state of unionid populations in the study areas to obtain a baseline on pre-*Dreissena* species composition and abundance of unionid fauna; and 4) derive inferences as to the potential magnitude of future unionid impacts in these systems based on prevailing zebra mussel dispersal and colonization patterns. Patterns in the variation of *Dreissena*-fouled unionids in the HRSR and RRSR were compared to gain insights into possible relationships between physical characteristics (flow regimes, discharge, and substrate availability) and relative ability of zebra mussels to colonize these two systems. However, a mechanistic investigation into specific factors that may hinder the colonization of downstream lotic habitats by zebra mussels was beyond the scope of this study.

Larval dispersal was examined in the Huron River to assess the dispersal of *Dreissena* veligers under free-flowing lotic conditions. A conservative estimate of transport time based on pool velocities taken in the HRSR during periods of low discharge between Portage Lake and Barton Pond was 44 hours, which is less than the shortest reported time span (3 - 5 days) of the planktonic veliger stage (Sprung 1993). This suggests that veligers produced by riverine populations of zebra mussels will predominantly be flushed into Barton Pond, and riverine populations will not be able to self-recruit in the HRSR. Data concerning
downstream dispersal of veliger larvae were evaluated against the hypothesis that zebra mussel populations in the HRSR will be the progeny of adult populations in Portage and Baseline lakes, and the entire length of the HRSR may be considered short of the exogenous recruitment flushing distance (ERFD)\(^1\).

Preliminary data was gathered in the summer of 1995 on unionid fauna, downstream veliger dispersal, and zebra mussel recruitment in the Huron River. More extensive data was compiled from both the Huron and Raisin in 1996.

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\(^1\) ERFD refers to the downstream dispersal channel distance between spawning zebra mussels and their settled post-planktonic progeny. ERFD is contingent on water velocity in the river and parameters effecting rate of metamorphosis from fertilized egg to pedi-veliger larvae (veligers ready to settle out of the water column). Minimum ERFD will occur under conditions favorable to rapid metamorphosis (e.g. temperature, food quality) and low-flow conditions (0 - 25% exceedance flow).
Methods

Unionid Surveys

Unionid habitats were stratified into riffle-run and pool habitats. The most productive strata in terms of unionid abundance and diversity (riffle-run) were surveyed to gather pre-invasion data in areas of the greatest conservation interest. Additional unionid survey site selection criteria were:

1) Strategic location to assess the effect of downstream distance from source populations on zebra mussel colonization in downstream areas and related unionid impacts.

2) Survey site accessibility.

At each unionid sampling site, transects were extended across the river. Square meter quadrats were laid out every other meter on a transect, starting at the closest stable substrate to the river bank. Unionids abundances were assessed from 50 to 120 quadrats each site, except for sites where unionid abundance or diversity of unionid species were relatively low (e.g. sites in the Clark Lake outlet creek/Goose Creek in the RRSR), where 10 -15 quadrats were sampled.

Substrate from each quadrat was excavated to a depth of three inches (substrate permitting). Unionids were hand-picked with the aid of a glass bottomed bucket from the excavated material (snorkel gear was used in deeper water). Shallow, low-turbidity water conditions (at low flows) in the HRSR and RRSR maximized the efficiency of this methodology. Transects were randomly located within the predominant habitat type located at the sampling area and were spaced between 2 - 10m apart. Unionids were measured lengthwise, marked, and carefully examined for attached zebra mussels.
On fouled unionids, zebra mussels were counted and measured heightwise (parallel to the hinge axis). Two indices of fouling severity were used: 1) number of zebra mussels/unionid (referred to as fouling intensity) and 2) volume of fouling zebra mussels to unionid volume (volume fouling ratio). The latter fouling index was measured in the field via water displacement with a 1000 ml grad cylinder (volume of fouling zebra mussels = joint $Dreissena$/unionid volume(± 10 ml) - unfouled unionid volume(± 10 ml)). Also, a length-volume regression (see appendix) was used to estimate fouling zebra mussel volume where fouling zebra mussels were too small and/or too few for field volume measurements. Volume fouling ratios were measured with both methods (field displacement and height-volume regression) on a set of heavily fouled unionids at the Baseline Dam in the HRSR to assess their equability.

Similarly, volumes of unionids too large to fit into the graduated cylinder (e.g. $Lampsilis$ ovata, $Lampsilis$ siliquoidea) were estimated with a length-volume regression, with specific regression equations being developed for each species.

Larval Dispersal

Plankton samples were taken in the HRSR to assess the dynamics of lotic veliger production and subsequent downstream dispersal/colonization. 189 1 (50 gallon) samples were bailed with a five gallon bucket through a 63μm plankton net. Three sub-samples were taken at each site in 1995, which was reduced to one sample per site in 1996 on account of sufficiently low variance. Plankton samples were taken at regular intervals (10-14 days in 1995, 7 days in 1996) between early June and early August at five stations (Table 1) strategically located to assess veliger production in Portage (1995 and 1996) and Baseline (‘96 only) lakes and downstream veliger dispersal. Samples were preserved in 30 - 50% ethanol and enumerated in a plankton wheel via cross polarized light microscopy (Johnson 1996) using five 1 - 5 ml subsamples/sample. Veligers that were observed to be empty were included in calculated density estimates and were also enumerated separately to calculate their proportional representation in plankton samples.

Veligers were assumed to be uniformly distributed across the river channel at all sampling sites with the exception of the Baseline Dam site, where veligers entering the river
from the Portage Lake outlet (200 m upstream of the site) produced a plume of veliger concentration on the west bank. At this site, water depth allowing, the river was sampled in thirds along a cross-river transect to estimate veliger density/flux. An additional sample was taken at the normal sampling site on the river's east bank to estimate veliger distribution for dates lacking latitudinal veliger density data.

In 1996, rudimentary stage-discharge relationships were established from three discharge measurements (Bovee and Milhous 1978) with the velocity-area method at three sampling stations in the HRSR. Velocities were measured with a solid cup-type meter. Frequent manipulation of the downstream Baseline Dam sluices made the establishment of a stage-discharge relationship at the Portage Lake outlet prohibitively difficult.

Veliger size-frequency distributions were measured for select sets of plankton samples to help interpret trends in downstream veliger dispersal in the HRSR. Veligers were measured with an optical micrometer under cross polarized light at 50x magnification. A random assortment of veligers from a given sample in a petri dish were sequentially measured height-wise (on an axis parallel to the hinge axis) until 100 measurements/sample were obtained.

**Adult recruitment/river colonization**

Unglazed grooved ceramic quarry tiles (15.3 x 15.3 cm) were secured in cinder blocks and distributed throughout the mainstem (Table 1) of both rivers to assess yearly recruitment of zebra mussels. Tiles were oriented diagonally in cinderblock holes and oriented grooved-side down with the tile edge/block hole facing into the current. Blocks were placed in slow-run or pool areas. Current velocities were taken at each block 10 cm above the substrate in front of the blocks. Four plates/site were deployed with two plates/block, except for all HRSR sites in 1995 and at Clark Creek outlet sites, where two plates/site were deployed. Tiles were set out in early May and retrieved in late September. Zebra mussels on the grooved side of the plates were counted.

The percentage of substrate coverage by zebra mussels colonies was estimated at heavily colonized sites to obtain an approximate measure of riverine colonization severity. The percentage of substrate coverage in 1 m² quadrats spaced every other meter across the
river along cross-river transects was estimated by eye. The mean of all quadrat estimates from five transects spaced 60 m apart down the river at a given site were used to estimate percent substrate coverage.

Where abundant riverine zebra mussel populations existed (>1/m²), zebra mussels were collected from unionids and measured (± 1 mm) to infer information about the demographic status of the population. Comparisons of valve fouling intensities (number of zebra mussels fouling unionid valves) were used to assess overwinter mortality (e.g.; number of mussels/live unionid in the fall vs. spring) at HRSR sites where fouled unionids were found in 1995.
Results

Huron River Study Reach

Zebra Mussel Colonization

Although direct measurements of *Dreissena* density were not taken, a mean of estimates of the percentage of benthic substrate covered by zebra mussels was 31.7% at the Baseline Dam (SD = 20.9, N = 89) in August, 1996, compared to <0.01% in May 1995. In areas with suitable substrate, zebra mussel colonies were approximately 2-5 cm thick on the riverbottom. Qualitative observation indicates that substrate coverage slowly diminished until the rapids at Bell Road Bridge (Fig. 1; Table1), and diminished rapidly in the faster water downstream of the bridge to < 0.5% at a point 1.9 km from Baseline Dam.

Other sites farther downstream had similar low substrate coverage. In 1996, isolated zebra mussels were found on rocky substrate during unionid surveys (estimated density < 1/m²) at all sites downstream of Mill Creek (Mast Rd., Dexter-Huron, and Delhi), indicating that all areas of the HRSR have been lightly colonized. All mussels found in these areas were large (> 14 mm) and hence were from the 1995 cohort.

Zebra Mussel Recruitment

Seasonal recruitment on settling plates diminished with distance from source populations in 1995 and 1996 (Fig. 3). No zebra mussels were found on settling plates downstream of the powerline site (Fig. 1; Table1; 10.2 km from the source population, no plates at this site in 1995). Also, densities on settling plates were greater in 1995 than 1996 at the two sites closest to the Baseline Dam (Bell Rd. and Baseline Dam), with the slope of downstream density attenuation greater in 1995 than 1996 (Fig. 3). This suggests that recruitment was greater in 1995 than in 1996 at these sites.
Figure 3: HRSR seasonal zebra mussel recruitment on settling plates vs. distance from Portage Lake, 1995 and 1996. 1995 densities were greater at upstream sites. No increase in colonization at downstream locations was observed in 1996 over 1995, despite increased flux of veligers into the HRSR. No plates over 10.2 km from Portage Lake were colonized. Note that no settling plates were deployed at 10.2 (the powerline site) km in 1995.
These patterns are contradicted by zebra mussel demographic data. In 1996, young-of-the-year mussels (< 5 mm in late August) comprised 81% of the individuals fouling unionids at Baseline Dam. Moreover, over-winter zebra mussel mortality appeared to be negligible, indicating that recruitment was greater in 1996 than 1995. Comparisons of unionid fouling data at Baseline Dam between fall 1995 and spring of 1996 indicates no reduction in fouling intensity: 9.5 zebra mussels/unionid (n = 93, SD = 11.7; max. = 69) in 1995 vs. 15.6 zebra mussels/unionid (N = 88, SD = 13.9, max. = 36) in 1996, suggesting that the increased percentage of young-of-year zebra mussels in 1996 over 1995 was not an artifact of overwinter mortality in the 1995 cohort.

**Veliger Production in Source Populations**

Veliger production in the Portage Lake source population increased substantially between 1994 and 1996. Limited samples from Portage Lake in 1994 suggest that veliger densities peaked at ~ 4/l. Peak densities in the Portage lake outlet increased to 115/l and 175/l in 1995 and 1996, respectively (Figs. 4a & b). Veliger production in Baseline Lake in 1996 was consistently low in 1996, ranging between 0.4 - 1.4 veligers/l between June 14th and August 6th.

It is likely that veliger flux into the HRSR increased from 1995 to 1996 on account of increased veliger production in Portage Lake. However, estimates of veliger flux out of the Portage outlet were unreliable due to suspected inaccuracy of discharge measurements due to low velocities and macrophyte abundance. The suspect discharge data from the Portage outlet suggests that Portage Lake accounts for between 15 to 33% of the discharge entering the HRSR at the Baseline Dam, with Baseline Lake discharge accounting for the remainder.

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2 This increase in fouling might be attributed to the movement of juveniles off of less stable benthic substrate onto the valves of live unionids over the winter. Alternatively, late summer surveys may have missed late-settling juveniles, thus explaining the increased abundance between the fall and spring.

3 Note that discharge in the Portage Lake outlet is influenced by lake level control structures farther upstream on Portage Creek. So while in a general sense, it can be assumed that there is a close positive correlation between Portage Lake discharge and mainstem discharge, this is not always the case. On one occasion in 1995, water was observed to be flowing into the lake from the Huron River. In this example, no veligers were entering the HRSR from Portage Lake.
Veliger densities entering the HRSR at the Baseline Dam are therefore considerably lower than densities in Portage Lake due to the dilution of Portage Lake veligers by veliger-poor Baseline Lake discharge.

**Downstream Veliger Dispersal**

Veliger flux diminished exponentially with downstream distance from Baseline Dam (Fig. 5) for most of the 1996 sampling dates. The most rapid attenuation occurred in the first 4.5 km of the study area. Deviations from this pattern were observed on two dates in 1996: June 21 and July 17 (Fig. 5). High discharge occurred during the first veliger abundance peak in Portage Lake on June 21 (1300 cfs at Ann Arbor USGS gauge, > 10% exceedance flow; Fig. 4). High flows on this date flushed veligers downstream through the HRSR with minimal, near-linear attenuation compared to other dates (Fig. 5).

Delhi veliger data obtained during the second Portage Lake veliger peak on July 17 under low discharge conditions (193 cfs at the Ann Arbor gauge site, approximately 75% exceedance; Fig. 4) differed from samples from all other dates in 1996 in the following respects: 1) Veliger flux at Delhi (20 km from Baseline Dam) was greater than veliger flux at Hudson Mills (4.5 km) by 479%, while veliger flux decreased between these two points on all other sampling dates in 1996. (Fig. 5); 2) A larger proportion of newly calcified, smaller size class) D-shell veligers were present at Delhi than other dates (Table 3). Also, the difference in percentage of veligers < 95 μm beween Delhi and Baseline Dam was considerably larger than other dates (51% vs. 2 - 5% respectively; Table 3); 3) Five percent of the veligers observed at Delhi on July 17 were empty (Fig. 6), which is considerably lower than the percentage recorded at that site on other dates (33% - 100% empty veligers); and 4) the pattern of the downstream changes in proportion of empty veligers differed from other dates (Fig. 6).
Figures 4 a & b: Portage Lake veliger densities measured in the Portage Lake outlet to the HRSR. Peak densities increased 69% between 1995 (a) and 1996 (b). Two veliger density peaks in Portage Lake in 1996 co-incided alternately with high discharge (June 21; *) and low discharge (July 17; ^), thus providing examples of downstream veliger dispersal under different hydrodynamic conditions.
Figure 5: Veliger flux as a function of distance from Portage Lake in 1996. Anomalous flux patterns recorded on 6-21 and 7-17 can be explained by discharge magnitude. Discharge was below 10% exceedance (the highest of any sampling date) on 6-21 and approximately 75% exceedance on 7-17 at the Ann Arbor gague site.

Figure 6: Proportion of empty veligers in plankton samples plotted against downstream distance. Proportions increased for all dates except July 17, where the proportion decreased between Hudson Mills and Delhi. Proportions for July 3, 25, and 11 Delhi samples were derived from low-density plankton samples (< 1.0 /liter) and are based on sample sizes of less than 15 veligers. All other sample sizes > 40.
Table 3: Percentage of early d-stage veligers (< 95μm) for selected dates. Note the increased proportion at Delhi due to the veliger progeny of riverine adults on 7/17. N = > 100 except for 6/28/96 Delhi sample, where N = 53.

<table>
<thead>
<tr>
<th>Date</th>
<th>7/17/96</th>
<th>7/6/95</th>
<th>6/28/96</th>
<th>7/26/95</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baseline Dam</td>
<td>27%</td>
<td>6%</td>
<td>12%</td>
<td>4%</td>
</tr>
<tr>
<td>Delhi</td>
<td>78</td>
<td>2</td>
<td>14</td>
<td>9</td>
</tr>
</tbody>
</table>

With 1995 and 1996 data pooled, veliger densities at the Portage Lake outlet and discharge at the Ann Arbor USGS gage site are good predictors of veliger density at Delhi (Multiple Linear Regression, $R^2 = 0.649$, n = 12), but only when July 17 data are omitted from the model. Discharge explains only 8.8% of the variance of this relationship when July 17 data are included in the model, but accounts for 22.8% of the variance with the data omitted. The anomalous nature of July 17 Delhi veliger data was interpreted to be a result of the presence of newly-calcified river-spawned veligers in the Delhi plankton samples that were not detected at upstream sites. Thus this data was omitted from the following analyses.

There is a significant negative linear relationship between the slopes of least-squares lines fitted to the veliger flux-downstream distance relationship for each sampling date in 1996 and discharge at the Baseline Dam (Fig. 7; Simple Linear Regression; $R^2 = 0.681$, $p = 0.022$, $\alpha = 0.05$, n = 7; July 17th data omitted), indicating the strength of the influence of discharge magnitude over the degree of veliger attenuation. Also, the degree of influence of discharge over veliger flux diminished with increasing distance from source populations. While the negative relationship between discharge at Baseline Dam and percent decline in veliger flux between Baseline Dam and a site 4.5 km downstream (Hudson Mills) is significant, (Fig. 8; Simple Linear Regression, $R^2 = 0.674$; $p = 0.012$; $\alpha = 0.05$; n = 8) the same relationship between Baseline Dam and a site 20 km downstream (Delhi); is not significant (Fig. 8; $R^2 = 0.298$; $p = 0.205$; $\alpha = 0.05$; n = 7; July 17th data omitted).
Figure 7: The slope of linear least-squares lines of downstream veliger flux attenuation for 1996 sampling dates plotted against Baseline Dam discharge magnitude. The significant relationship ($p=0.022; \alpha=0.05; N=7; y=-34.76+10.056x$) indicates the strength of the influence of discharge over the degree of veliger attenuation.
Figure 8: The relationship between Baseline Dam to Hudson Mills (4.5 km downstream) % veliger flux decline with discharge at Baseline Dam is significant ($R^2 = 0.674$; $p = 0.012$; $\alpha = 0.05$; $N = 7$; July 17 data omitted) while the % flux attenuation between Baseline Dam and Delhi (20 km downstream) is not ($R^2 = 0.298$; $p = 0.205$; $\alpha = 0.05$; $N = 7$; July 17 data omitted). This suggests that the influence of discharge over downstream veliger flux attenuation diminishes with downstream distance, likely due to the instream loss of veligers from either mortality and/or settlement.
Given that veliger fluxes were calculated with density estimates that included empty veligers, a sizable proportion of veliger fluxes at downstream sites were comprised of non-viable veligers. The flux of viable veligers is 33 to 99% (at Delhi) and 6 to 75% (at Hudson Mills) lower than the flux estimates used in Fig. 5.

**Unionid fouling**

Unionid volume fouling ratios and fouling intensity (number of zebra mussels/unionid) were greatest at the Baseline Dam and diminished with downstream distance, with low levels of fouling at Bell Road and Hudson Mills (Fig. 9; Table 4). Fouling indices diminished to zero at Mast Road, 11.6 km downstream of the Baseline Dam. Only one fouled unionid was found in three sampling sites in the lower 12 km of the HRSR (downstream of Mill Creek near Dexter) in 1996. No 1996 young-of-year individuals were found on unionids or other substrata at these downstream sites.

The negative slope of the regression line of natural log of the number of zebra mussels/unionid vs. the natural log of downstream distance was 229% larger in 1996 than 1995 (Fig. 10; irreconcilable variance heteroscedasticity precluded testing the equality of the slopes). Increases in the number of zebra mussels/unionid in 1996 over 1995 was disproportionately greater at upstream sites, accounting for the different slopes in the regression lines. This is consistent with the demographic data that suggests that recruitment was greater in 1996 than 1995 at the Baseline Dam.

At sites downstream of Baseline Dam, fouling indices at Bell Road and Hudson Mills (Fig. 9) translated into only small absolute increases in zebra mussel fouling at these sites in 1996, although the percentage of increase in fouling intensities (numbers of *Dreissena*/unionid) from 1995 to 1996 was substantial at all sites where fouled unionids were found in 1995 (Table 4).

Densities of unionids remained unchanged between 1995 and the spring of 1996 at the Baseline Dam, indicating that no over-winter fouling-induced mortality occurred at this site. However, heavily fouled fresh-dead animals (soft tissues intact) were observed in mid-July. Fresh-dead valves were found in shallows near the riverbank where slower current velocity facilitated higher fouling intensities. Live animals from these areas had 25% higher
volume fouling ratios\(^4\) (mean ratio = 0.55; SD = 0.303; N = 13) than areas away from the riverbanks. The observation of fresh dead animals at this site indicates that fouling-induced mortality has commenced.

Table 4: Zebra Mussel Fouling indices in the HRSR in 1996. All indices diminished with downstream distance (See Fig. 9). Baseline Dam volume fouling ratio is the highest for all sites in the HRSR and RRSR.

<table>
<thead>
<tr>
<th></th>
<th>Baseline Dam</th>
<th>Bell Rd.</th>
<th>Hudson Mills</th>
<th>Dexter-Huron</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>25</td>
<td>135</td>
<td>131</td>
<td>69</td>
</tr>
<tr>
<td>mean volume fouling ratio - SD</td>
<td>0.41 - 0.39</td>
<td>0.02 - 0.04</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>mean zm/unionid - SD</td>
<td>120.5 - 147.6</td>
<td>1.9 - 3.9</td>
<td>0.1 - 0.5</td>
<td>0.01 - 0.1</td>
</tr>
<tr>
<td>increase over 1995 (mean zm/unionid increase - % increase)</td>
<td>104.4 - 770%</td>
<td>1.1 - 229%</td>
<td>0.08 - 500%</td>
<td>na</td>
</tr>
<tr>
<td>% fouled in 1996</td>
<td>100</td>
<td>68.1</td>
<td>11.5</td>
<td>1.4</td>
</tr>
<tr>
<td>km from Baseline Dam</td>
<td>0</td>
<td>1.9</td>
<td>4.5</td>
<td>14.5</td>
</tr>
</tbody>
</table>

Distribution and Abundance of Unionids

Sixteen species of unionids were found in the HRSR in surveys conducted in 1995 and 1996, and one additional species (Alasmidonta viridis) was only found as a dead shell. Overall, 983 animals were retrieved and marked. Densities ranged from 0.99 to 3.83/m\(^2\) (Table 5).

\(^4\) Estimated volume fouling ratios obtained here are based on fouled unionid (unionids and attached zebra mussels) vs. non-fouled field water displacement measurements, adjusted for equivalence to fouling ratios derived from zebra mussel size-volume regression methodology.
Figure 9: Diminishing patterns of HRSR fouling indices with downstream distance. Percentage of fouled unionids declined linearly with downstream channel distance (1995: $p = 0.081; R^2 = 0.984$ and 1996: $p = 0.035; R^2 = 0.997$) and the number of zebra mussels/unionid unionids declined exponentially. Note that the standard deviations for zebra mussels/unionid at Baseline Dam (0.1 km) were 147.6 and 11.7 for 1996 and 1995 respectively. All other zebra mussel/unionid standard deviations were < 4.
Figure 10: Plot of ln (zebra mussels/unionid + 1) vs. ln downstream distance in the HRSR for 1995 ($y = -0.475x + 0.767; R^2 = 0.605; N = 288$) and 1996 ($y = -1.09x + 1.61; R^2 = 0.791; N = 276$). The slope of the 1996 line was 229% greater than 1995. Irreconcilable variance heteroscedasticity precluded testing for equality of slopes. Converging patterns of the regression lines tentatively suggests the existence of a downstream colonization limit beyond which zebra mussel colonization will be negligible.
Table 5: Unionid species composition and abundance in the HRSR. p = present but rare. s = only dead valves detected, no live animals found.

<table>
<thead>
<tr>
<th>Species</th>
<th>Baseline Dam</th>
<th>Bell Road</th>
<th>Hudson Mills</th>
<th>Mast Road</th>
<th>Dexter-Huron</th>
<th>Delhi</th>
<th>Total %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alasmidonta marginata</td>
<td>2.0%</td>
<td>12.7%</td>
<td>11.2%</td>
<td>22.2%</td>
<td>12.8%</td>
<td>26.4%</td>
<td>14.5</td>
</tr>
<tr>
<td>Alasmidonta viridis</td>
<td></td>
<td></td>
<td></td>
<td>s</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyclonaias tuberculata</td>
<td>p 1</td>
<td>61.9</td>
<td>54.5</td>
<td>34.7</td>
<td>40.4</td>
<td>33.5</td>
<td>37.5</td>
</tr>
<tr>
<td>Elliptio dilatata</td>
<td>0.5</td>
<td>3.3</td>
<td>6.3</td>
<td>s</td>
<td>s</td>
<td>1.5</td>
<td>1.9</td>
</tr>
<tr>
<td>Epioblasma triquetra</td>
<td>0.5</td>
<td></td>
<td>s</td>
<td></td>
<td></td>
<td></td>
<td>&gt;0.01</td>
</tr>
<tr>
<td>Lampsis fasciola</td>
<td>17.5</td>
<td>11.6</td>
<td>16.5</td>
<td>27.7</td>
<td>36.7</td>
<td>26.9</td>
<td>22.8</td>
</tr>
<tr>
<td>Lampsis ovata</td>
<td>23.0</td>
<td>1.7</td>
<td>3.1</td>
<td>2.8</td>
<td>1.8</td>
<td>4.6</td>
<td>6.2</td>
</tr>
<tr>
<td>Lampsis siliquioidea</td>
<td>44.0</td>
<td>1.7</td>
<td>2.2</td>
<td></td>
<td>1.0</td>
<td></td>
<td>8.2</td>
</tr>
<tr>
<td>Lasmigona complanata</td>
<td>0.5</td>
<td></td>
<td></td>
<td>1.4</td>
<td></td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>Lasmigona compressa</td>
<td></td>
<td></td>
<td></td>
<td>1.4</td>
<td>p</td>
<td></td>
<td>0.7</td>
</tr>
<tr>
<td>Ligumia recta</td>
<td>3.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.9</td>
</tr>
<tr>
<td>Ptychobranchus fasciolaris</td>
<td>1.0</td>
<td>1.7</td>
<td>3.6</td>
<td>1.4</td>
<td>3.7</td>
<td>4.6</td>
<td>2.6</td>
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<td>Pyganodon grandis</td>
<td>4.5</td>
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<td></td>
<td>1.4</td>
</tr>
<tr>
<td>Strophitus undulatus</td>
<td>1.0</td>
<td>0.5</td>
<td>1.4</td>
<td>s</td>
<td></td>
<td></td>
<td>0.5</td>
</tr>
<tr>
<td>Utterbackia imbecilis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Villosa iris</td>
<td>2.0</td>
<td>5.0</td>
<td>1.8</td>
<td>6.9</td>
<td>1.8</td>
<td>0.5</td>
<td>3.0</td>
</tr>
</tbody>
</table>

| Total unionids density (m²)* | 200 | 181 | 224 | 72  | 109 | 197 | 983 |
| SD                         | 2.57 | 2.53 | 3.83 | 0.99 | 1.37 | 1.46 |
| # of quadrats              | 47  | 74  | 52  | 74  | 78  | 118 |
| Shannon H’                 | 1.59 | 1.31 | 1.47 | 1.58 | 1.26 | 1.54 | 1.68 |

* Density calculations do not include all animals represented in the table.

1 Single animals found by S. J. Nichols, National Biological Service
HRSR unionid fauna can be partitioned into two habitat-based species associations. The section between Baseline Dam and the Bell Road is characterized by lake-quality water discharged from Baseline and Portage Lakes, marl/gravel substrate, slow to moderate water velocity, and is dominated by a species common in lakes (*Lampsilis siliquoidea*). The river downstream of Bell Road is dominated by species more characteristic of rivers, with the possible exception of pool habitats in this reach. Two of the three state listed species present in the HRSR (*Lampsilis fasciola, Cyclonaias tuberculata*, and *Epioblasma triquetra*) are particularly abundant downstream of Bell Road. *Cyclonaias* comprises 45%, and *Lampsilis fasciola* accounts for 23.8% of unionids at sample sites in this area (Table 5). Other bivalves present in the HRSR are the exotic asian clam, *Corbicula fluminea*, and members of the family *Sphaeriidae*. The former species was not noted to be present by Scavia and Mitchell (1986) in the HRSR, and may be a recent invader.

Scavia and Mitchell (1986) surveyed populations of *Cyclonaias tuberculata* in the HRSR using similar methodology. The present study re-surveyed two of the exact locations (Mast Road and Delhi) and two sites in the general proximity (Hudson Mills and Bell Rd.) to Scavia’s survey sites. Comparisons with Scavia’s data indicate that *Cyclonaias* has increased in abundance by 309% to 608% at these sites over the past ten years (Table 6).

<table>
<thead>
<tr>
<th>Site</th>
<th>1986 / (m²)</th>
<th>1996 / (m²)</th>
<th>% increase</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delhi</td>
<td>0.13</td>
<td>0.47</td>
<td>339.43</td>
</tr>
<tr>
<td>Mast Rd.</td>
<td>0.05</td>
<td>0.34</td>
<td>608.11</td>
</tr>
<tr>
<td>Hudson Mills*</td>
<td>0.40</td>
<td>2.35</td>
<td>582.49</td>
</tr>
<tr>
<td>Bell Rd.*</td>
<td>0.22</td>
<td>1.09</td>
<td>490.91</td>
</tr>
</tbody>
</table>

*1996 surveys done in approximate locations of 1986 surveys.

Although dead valves were not counted in this study, it should be noted that the proportion of dead valves to live animals of *Elliptio dilatata* was qualitatively striking in comparison to other species at all sites, and particularly at Baseline Dam. *Elliptio* valves at this site comprised an estimated >70% of all valves found. Few of these valves were
recently dead, but still suggest a marked decline in abundance of this species over the past few years.

**River Raisin Study Reach**

**Zebra Mussel Colonization**

**Unionid Fouling**

The most severely fouled unionids in the RRSR were found at two sites. Downstream of the Brooklyn Dam on the mainstem, zebra mussel volume fouling ratio averaged 0.038 of the unionid volume (SD = 0.089; N = 61; Table 7). The fouling intensity at this site (5.4 zebra mussels/unionid; SD = 7.6; N = 61) was relatively low. The size distribution of zebra mussels suggests that at least three year classes have colonized the river at this site (1994, '95, and '96; Fig. 1ic).

The Clark Lake outlet site nearest to Clark Lake had the highest mean number of zebra mussels/unionid (11.9; SD = 13.6; N = 29). However, the size of fouling zebra mussels were much smaller in this system (Fig. 11a) than at the Brooklyn Dam, thus accounting for the similar volume fouling ratio in the Clark Lake outlet (Table 7). No fouling-induced mortality was apparent at either site.

Both zebra mussel volume fouling ratios and fouling intensities decreased with downstream distance from source populations in the mainstem and the Clark Lake outlet. In the Clark outlet, the decrease in fouling indices occurred within the 0.9 km of channel between sampling sites (Table 7). Similarly, these parameters declined in the Raisin mainstem from the Brooklyn Dam sampling site to the Norvell Dam sampling site (15.7 km downstream from Vineyard Lake), which had negligible fouling indices (1.5 % of unionids fouled). In contrast to the free-flowing HRSR, these patterns were manifested over a reach of channel that hosts two impoundments downstream of the main source population (Vineyard Lake), and whose riverine invasion preceded the onset of colonization in the HRSR by at least one year.

One of the three zebra mussels found fouling unionids at Norvell Dam was 37 mm in length, suggesting that zebra mussels have been present at this site at very low
Figure 11: Size distributions of zebra mussels found at three RRSR sites. Although the distributions in 11a (Clark Lake outlet) and 11b (Clark Lake outlet: Riverside Road) consists of small zebra mussels, both represent at least two year classes of zebra mussels in the Clark Outlet creek, suggesting slow growth and/or high mortality in this small system. Distribution 11c is from the Brooklyn Dam site, which suggests the existence of three year classes (1994: 20 - 36 mm; 1995: 6 - 20 mm; 1996: 0 - 6 mm).
Table 7: Zebra mussel fouling indices in the RRSR. The largest volume fouling ratios are found at the Baseline Dam, while the largest number of zebra mussels/unionid are found at the Clark Outlet site. All fouling incidies diminished with downstream distance from Baseline Dam.

<table>
<thead>
<tr>
<th></th>
<th>Clark Outlet</th>
<th>Clark Outlet: Riverside Rd.</th>
<th>Brooklyn Dam, mainstem</th>
<th>Norvell Dam, mainstem</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>29</td>
<td>28</td>
<td>61</td>
<td>204</td>
</tr>
<tr>
<td>mean volume fouling ratio -SD</td>
<td>0.056 - 0.073</td>
<td>0.004 - 0.007</td>
<td>0.038 - 0.089</td>
<td>&gt; 0.001</td>
</tr>
<tr>
<td>mean zm/unionid -SD</td>
<td>11.9 - 13.6</td>
<td>3.0 - 2.8</td>
<td>5.4 - 7.6</td>
<td>0.014</td>
</tr>
<tr>
<td>% fouled in 1996</td>
<td>100</td>
<td>86.9</td>
<td>84.1</td>
<td>1.47</td>
</tr>
<tr>
<td>km from source population</td>
<td>0.05</td>
<td>0.9</td>
<td>5.5</td>
<td>15.7</td>
</tr>
</tbody>
</table>

densities since the summer of 1994 (or at least since 1995), with little increase in colonization over the past three years.

**Zebra Mussel Recruitment**

Seasonal recruitment diminished with downstream distance in both the Clark Lake outlet and the Raisin mainstem. Settling plate densities diminished 75% over a 0.9 km segment of creek channel between the first two sites in the Clark Lake outlet creek (Fig. 12). Densities on the third set of plates in this system were reduced to negligible levels by probable downstream veliger attenuation in addition to the dilution of veliger concentrations by the discharge of veliger-free Goose Creek. Consistent with patterns observed in the Huron River and the Clark lake outlet, settling plate densities diminished with downstream distance from the Vineyard outlet (Fig. 13) despite a fundamentally different hydrodynamic environment than the free-flowing HRSR.

**Distribution and Abundance of Unionids**

Fifteen unionid species were found in the RRSR (Table 8). The fauna had similar species composition to the HRSR, but differed in terms proportional species abundance and
Figure 12: Seasonal recruitment on settling plates in the Clark Lake outlet. Densities diminished with distance from the source population. Note that Goose Creek densities were diminished by the effects of the confluence of the Clark outlet and Goose Creek. Numbers above the bars represents channel distance from Clark Lake. Error bars = 1 SD.

Figure 13: Seasonal recruitment on settling plates in the RRSR mainstem. Settling plate densities diminished with distance from the Vineyard Lake source population. Plate locations are likely beyond the ERFD due to impoundments and low gradient between sites. Zebra mussels were present at Wolf Lake Rd, but the plates were vandalized. Numbers above bars represent channel distance (in km) from Vineyard Lake. Error bars = 1 SD.
**Table 8**: Unionid species composition and abundance in the RRSE, p = present but rare. s = only dead valves detected.

<table>
<thead>
<tr>
<th>Species</th>
<th>Vineyard Outlet</th>
<th>Clark outlet</th>
<th>Clark: Riverside Road</th>
<th>Goose Creek</th>
<th>Brooklyn Dam</th>
<th>Wolf Lake Road</th>
<th>Norvell Dam</th>
<th>Pierce Rd.</th>
<th>Sharon Valley Rd</th>
<th>Sharon Hollow Rd</th>
<th>Sharon Valley gauge</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Actinonaias ligamentina</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>p</td>
<td>11.7% 0.6%</td>
<td>1.7% 0.8%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>NA</td>
</tr>
<tr>
<td>Alasmidonta marginata</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.1 0.4%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2.2%</td>
</tr>
<tr>
<td>Alasmidonta viridis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.4</td>
</tr>
<tr>
<td>Cyclonaias tuberculata</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6.6 10.0 16.5%</td>
<td>2.8 11.9</td>
<td>6.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elliptio dilatata</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3.1 11.5 20.2</td>
<td>29.2 24.9</td>
<td>19.2</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Fusconaia flava</td>
<td>13.8%</td>
<td>90%</td>
<td>p</td>
<td>2.2%</td>
<td></td>
<td>18.9 58.4 36.7</td>
<td>30.7 19.2</td>
<td>35.7</td>
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<tr>
<td>Lampisilis fasciola</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>p</td>
<td>18.9 58.4 36.7</td>
<td>30.7 19.2</td>
<td>35.7</td>
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<td>Lampisilis ovata</td>
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<td></td>
<td></td>
<td>4.3</td>
<td>7.7 4.2 8.9</td>
<td>3.1 12.7</td>
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<td>Lampisilis siliquioidea</td>
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<td></td>
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<td>13.0 4.3 7.7</td>
<td>4.2 8.9 3.1</td>
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<td></td>
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<td>0.4</td>
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<td>Sirophiplus undulatus</td>
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<td></td>
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<td></td>
<td></td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>Villosa iris</td>
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<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>7.6</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td>6*</td>
<td>29 40 3*</td>
<td>46 6*</td>
<td>194 475 79</td>
<td>73 753 245</td>
<td>1861</td>
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<tr>
<td><strong>Density/m²</strong></td>
<td>NA</td>
<td>2.2 6.7 NA</td>
<td>2.8 0.1</td>
<td>3.7 19.2</td>
<td>1.9 30.1 8.0</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>SD</strong></td>
<td>1.7 4.3</td>
<td>2.4</td>
<td>2.4</td>
<td>2.5 18.6</td>
<td>2.1 12.2 5.0</td>
<td></td>
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</tr>
<tr>
<td><strong>Shannon H</strong>*</td>
<td>0.98 0.38</td>
<td>1.46 0</td>
<td>2.04 1.39</td>
<td>1.63 1.77</td>
<td>1.82</td>
<td>1.93</td>
<td></td>
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</tr>
</tbody>
</table>

*totals include animals found in qualitative surveys.
overall abundance. *Elliptio dilatata* (19.2%) and *Fusconaia flava* (35.7%) were most common overall. Other bivalves present, but not enumerated, were members of the family *Sphaeriidae*.

Mean overall densities in the RRSR ranged from 0.1 to 30.0 unionids/m$^2$ (Table 8). The most productive sites (Sharon Hollow Rd., Pierce Rd., and Sharon Valley Rd.) were most distant from the source populations in the RRSR (Fig. 2; Table 2) and had much higher abundances than the most productive sites in the HRSR. Sites closer to Vineyard Lake (Vineyard Outlet and Wolf Lake Road) were slow-water/soft-substrate habitats with low unionid abundance. Sites in the Clark Lake outlet creek had lower species diversity (Shannon H’) than the most productive sites in the mainstem (Table 8).

<table>
<thead>
<tr>
<th>Table 9: Densities of <em>Cyclonaias tuberculata</em> and <em>Lampsilis fasciola</em> (m$^2$) in the HRSR and RRSR. There is no significant difference for sites where both species were present between study reaches for either species. (t-test: p = 0.64, n = 5 for <em>Cyclonaias</em> and p = 0.36, n = 5 for <em>Lampsilis</em>)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Raisin:</strong></td>
</tr>
<tr>
<td>---------------------------------------------------------------</td>
</tr>
<tr>
<td>Riverside Road</td>
</tr>
<tr>
<td>Wolf Lake Road</td>
</tr>
<tr>
<td>Norvell Dam</td>
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<tr>
<td>Pierce Rd.</td>
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<tr>
<td>Sharon Valley Rd.</td>
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<tr>
<td>Sharon Hollow Rd.</td>
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<tr>
<td>Sharon Valley gauge</td>
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<tr>
<td><strong>range</strong></td>
</tr>
<tr>
<td><strong>Huron:</strong></td>
</tr>
<tr>
<td>Baseline Dam</td>
</tr>
<tr>
<td>Bell Road</td>
</tr>
<tr>
<td>Hudson Mills</td>
</tr>
<tr>
<td>Mast Road</td>
</tr>
<tr>
<td>Dexter-Huron</td>
</tr>
<tr>
<td>Delhi</td>
</tr>
<tr>
<td><strong>range</strong></td>
</tr>
</tbody>
</table>

The state-listed species *Cyclonaias tuberculata* and *Lampsilis fasciola* were present in densities comparable to the HRSR (Table 9). Differences between mean densities for
both *Cyclonaias* and *Lampsilis fasciola* between the two study reaches at sites where the species were present were not significant (*t*-test: $p = 0.64$, $n = 5$ and $p = 0.36$, $n = 5$, respectively). No evidence of the federally endangered *Epioblasma torulosa* was found. Shells of this species were recorded from a tributary of the Raisin by Strayer (1979).

**Unionid Demography: Cyclonaias tuberculata**

Considerable differences in the size distributions of *Cyclonaias* (Figs. 14 a, b & c) were observed between the HRSR and the RRSR, and also between different sections of the HRSR. The RRSR harbors a greater proportion of larger size-class and a smaller proportion of smaller size class *Cyclonaias* than the HRSR. In the HRSR, mean *Cyclonaias* lengths were significantly smaller (Wilcoxon Rank Sum test; $p<0.001$; $n = 231$) at sites downstream of Mill Creek than upstream sites.

**Volume Fouling Ratio Measurement Assessment**

The mean volume fouling ratio (zebra mussel volume/unionid volume) obtained by summing regression-derived volumes of fouling zebra mussels (see appendix) for each unionid was significantly smaller than the mean average volume fouling ratio derived from field volume displacement measurements (*t*-test; $p = 0.02$; $\alpha = 0.05$; $N = 16$) for a set of heavily fouled unionids in the HRSR. Hence, the former more conservative measure was used and all volume fouling ratio measurements derived from the latter method were adjusted for this mean difference (field volume fouling ratio * 0.8179; ($n = 16$; SD = 0.7753)) This adjustment was made for one set of fouled unionids noted earlier.
Figure 14: Size frequency histograms for *Cyclonaiais tuberculata* at a) HRSR upstream of Mill Creek; b) HRSR downstream of Mill Creek; c) RRSR mainstem. *Cyclonaiais* populations in the RRSR were larger than the HRSR. Size classes downstream of Mill Creek (b) were smaller than upstream *Cyclonaiais* populations (a) in the HRSR (Wilcoxon Rank Sum; p<0.001), suggesting that populations downstream of Mill Creek are recovering from past anthropogenic impacts. Note that juvenile size classes may be under-represented.

Figure 15: Huron River hydrograph of UGSG gauge data at the Ann Arbor gauge site for water years 1995-1996 during the seasonal peak of zebra mussel spawning activity. Hydrographs plotted against average monthly maximum, mean, and minimum recorded discharge for water years 1915 - 1995. Note the instances of peak flows that facilitate zebra mussel larval dispersal.
Discussion

Given the patterns of riverine colonization dynamics in this study, the continuum of possible scenarios for unionid impacts in both study reaches is as follows:

1) Zebra mussels heavily colonize all lotic habitats downstream from source populations and all riverine unionids die from acute impacts.

2) Zebra mussels heavily colonize river sections immediately downstream of source populations. Moderate levels of colonization occur in all downstream segments. Unionids succumb to both chronic impacts (downstream areas) and acute impacts (upstream areas).

3) Upstream segments are heavily colonized by zebra mussels, downstream segments are lightly colonized or not colonized at all. Unionids persist in downstream segments.

This continuum can be used as a reference to evaluate the degree of zebra mussel impacts on unionids and to discuss possible future trends in riverine colonization and unionid impacts. It assumes that veliger production in source populations is substantial (> 20/liter during peak abundance). “Source population” is defined here as any zebra mussel-infested lentic or semi-lentic body of water (including impounded backwaters) that produces veligers that disperse into riverine habitats in sufficient numbers to affect unionids in downstream habitats.
**Huron River Study Reach**

**Zebra Mussel Colonization: Unionid Fouling Patterns**

Unionid impact scenario #3 (from above) presently exists in the HRSR. Although not evident in the data, some *Dreissena*-induced unionid mortality has occurred at the Baseline Dam, with unionids residing in low-velocity areas of the river most conducive to zebra mussel settlement being most affected. Given the high volume fouling ratios at this site compared to other sites (Table 4), it is likely that a large number of the animals still alive at this site are highly stressed. A high over-winter mortality rate is a distinct probability in 1997, excluding ~ 6,000 animals that were cleaned of all zebra mussels by the National Biological Service (S. J. Nichols pers. comm.) at this site in the fall of 1996.

Existing unionid fouling and dispersal patterns can be used to form inferences about the probability of progression towards unionid impact scenarios #1 or #2. The converging least-squares lines in Fig. 10 can be explained by a disproportionate increase in 1996 recruitment in upstream sampling sites over 1995 recruitment patterns in response to increased veliger flux into the system. While this is contrary to trends in the settling plate data in Fig. 3, the large percentage of young-of-year zebra mussels (81%) at the Baseline Dam in late August, 1996 confirm that recruitment was indeed larger in 1996 than 1995.

Although more definite conclusions are premature, this tentatively suggests the existence of a downstream colonization distance limit in the HRSR beyond which adult zebra mussel colonization/recruitment is negligible. At present, the colonization limit appears to be approximately 5 km downstream of the Baseline Dam, a point where colonization of unionid valves currently levels off to below 0.1 mussels/unionid (Fig. 9). If the downstream colonization limit proves more or less static, the fouling of unionids below this point may be inconsequential over the long term. In this case, the downstream progression of unionid infestation intensity would diminish over next few years, with a disproportionate proportion of recruitment in the HRSR occurring at upstream sites between Baseline Dam and Hudson Mills (similar to the seasonal recruitment pattern between 1995 and 1996). The exact nature of the downstream colonization limit (static or dynamic) will
be tested over the next few years as the magnitude of veligers entering the HRSR will undoubtedly increase with the development of infestations in source populations.

The unexpected decrease in 1996 seasonal recruitment data from settling plates over 1995 (Fig. 3) may have been caused by settling cues released by benthic masses of *Dreissena*, luring settling veligers away from the settling plates to the benthos. Indeed, *Dreissena* was abundant in the benthos in 1996 but almost non-existant in 1995. Both Baldwin (1994) and Toczyłowski (1996) have found some evidence of the existence of such cues. The role of settling cues also provides an alternate (but not mutually exclusive) explanation of downstream unionid fouling patterns to the downstream colonization limit hypothesis: settling cues may induce increased recruitment in upstream areas already heavily colonized, thus explaining the larger slope of downstream attenuation seen in the 1996 data in Fig 10. Sparse populations of pioneer zebra mussels colonizing a site may provide settling cues in subsequent seasons that facilitate dramatic increases in downstream colonization and related unionid fouling. This effect either may or may not work simultaneously the downstream colonization distance limit hypothesis in explaining patterns of downstream unionid fouling.

Results from another study of the colonization of a 2nd order creek in southwest Michigan from a heavily infested lentic source populations also suggests the existence of a downstream colonization limit. In four field seasons (1993 - 1996), Horvath (pers. comm.) has not found any appreciable adult colonization beyond 1500 m of the outlet of a lentic source population with high magnitudes of veliger production. In contrast, Hunter (1996) has found no relationship between distance from source population and incidence of attachment or mean zebra mussels/unionid in a small 3rd order systems in southeast Michigan, although unionids in this river are persisting longer than unionids in infested lakes bounding the study area on upstream and downstream sides (Hunter, pers. comm.).

It should be noted that the In - In relationship suggested by the lines fitted to the pattern of downstream unionid fouling in Fig. 10 may be influenced by additional variables. In addition to distance from source populations, unionid fouling patterns are likely also to be a function of the gradient at a specific site. For example, in the 1.5 km of channel downstream of Baseline Dam, the HRSR consists of slow-run habitat that pools slightly
before the rapids at the Bell Road bridge. There is an obvious difference (not quantified in this study) between the fairly heavily fouled unionids found in the pooled area upstream of the rapids and the lightly fouled unionids 0.5 km downstream that live in a fast-run habitat. Thus it is likely that average current velocity of a given point plays at least a secondary role in explaining patterns of unionid fouling in addition to downstream distance.

**Downstream Veliger Dispersal**

Exponential patterns of downstream veliger attenuation likely accounts for the observed patterns of downstream unionid fouling (Fig. 10) and the related downstream colonization limit. Hence patterns of veliger attenuation (Fig. 5) provide preliminary evidence for the existence of a similar point of maximal downstream transport (Maximal Distance Transport Point, or MDTP), beyond which larval flux rates are likely to remain at minimal levels compared to flux rates at the point of entry into the system. The distance of the from the source population is influenced by the magnitude of discharge, given the significance of the relationship in Fig. 7. Moreover, the juxtaposition of significant and non-significant regressions in Fig. 8 suggests that the MDTP in the HRSR is situated between Hudson Mills (4.5 km) and Delhi (20 km). If the MDTP was downstream of Delhi (20 km), both relationships in Fig. 8 would be significant. Conversely, both relationships would not be significant if the MDTP were located upstream of Hudson Mills. In addition, the weak negative trend in the Baseline Dam to Delhi % veliger flux decline is heavily influenced by the data point representing high-discharge conditions on June 21, which suggests that Delhi (at 20 km downstream of Baseline Dam) was not beyond the MDTP at flows with an annual 10% exceedance. Thus the reduction of veliger flux beyond the MDTP may be considered negligible except for all but the highest discharge levels.

Given the influence of discharge on downstream veliger flux attenuation, it is probable that distance of both the MDTP and the downstream colonization limit from zebra mussel source populations in the HRSR can shift dynamically within a spawning season. These shifts most likely occur in concert with fluctuations in discharge. Longer term downstream shifts may possibly be precipitated by yearly increases in the magnitude of veliger production in source populations. It is also possible that shifts in the downstream
colonization limit will be maximal during the co-occurrence of high discharge with periods of peak abundance of pedi-veligers (veligers close to settlement) in source populations. Such peaks may occur 1 - 8 days (Ackerman 1994a) after peak numerical veliger abundances in source populations characterized by a predominance of younger d-shell veligers, and will result in the flushing of a large number of veligers that are ready to settle into the river.

Seasonal discharge patterns during zebra mussel spawning season will influence the probability of this co-occurrence. While the period of peak spawning activity is limited to seasonal periods where discharge is typically low (early to mid-summer), sporadic precipitation-mediated runoff events have increased discharge well above mean monthly flow rates in both 1995 and 1996 (Fig. 15). Such future high discharge events may occur during periods of maximal pedi-veliger abundance, thus increasing the distance of the downstream colonization limit and enhancing the probability of substantial increases in recruitment at downstream sites.

Veliger Dispersal Dynamics and the Exogenous Recruitment Flushing Distance

The anomalous nature of the veliger data recorded at Delhi on July 17 can be accounted for by attributing the differences found in these samples to the presence of veligers that are the progeny of the dense colonies of zebra mussels in the HRSR near the Baseline Dam (rather than zebra mussels in source populations), and also to the limitations of cross-polarized light microscopy used to enumerate samples.

Cross polarized light microscopy excels at detecting calcified stages of the veliger's lifecycle, and significantly increases the efficiency in detecting *Dreissena* veligers in plankton samples compared to other methods (Johnson, 1995). However, it cannot detect the un-calcified trochophore larval stage, which persists until anywhere from 6 to 48 hours after fertilization (up to 96 hours in colder water temperatures (Ackerman 1994)). In the HRSR, veligers that are flushed into Barton Pond before a calcified shell is secreted cannot be detected in plankton samples at downstream sampling sites.

Low discharge on July 17 (Fig. 15) delayed the passage of veligers down the Huron River. Also, the dense colonies of zebra mussels near the Baseline Dam in the HRSR likely responded to the same spawning cues that precipitated the peak in veliger abundance noted
in Portage Lake on the 17th (*Dreissena* typically spawns synchronously (Garton and Haag 1993)), producing a slug of water near the Baseline Dam laden with high densities of fertilized eggs. This slug of water was sufficiently delayed in downriver passage by low discharge/water velocity to allow surviving veligers at Delhi to develop D-stage calcified shells\(^5\). Thus these veligers were detected in Delhi plankton samples but not at upstream sites. The smaller proportion of veligers under 95 μm (Table 3) and the smaller proportion of empty veligers observed at Delhi are consistent with this explanation.

Thus the increase in Delhi veliger flux over Hudson Mills flux on July 17 (Fig. 5) can be interpreted as consistent with prevailing patterns of veliger attenuation. The slug of water receiving veligers from the riverine zebra mussel spawn near Baseline Dam had an unknown veliger abundance that was likely considerably higher than the ambient density of veligers in the water moving out of Portage Lake. This slug of water probably had a considerably higher ratio of spawning zebra mussels per unit volume of water than Portage Lake. Veligers in this slug had a much lower potential radius of diffusion from parent mussels than veligers spawned in lakes. Hence this slug of water probably had an extremely high veliger density.

It is probable that the veliger abundance in this slug diminished with downstream distance similar to the patterns in Fig. 5, especially given the low discharge on July 17. The high proportion of viable veligers (viscera intact, Fig 3; Table 6) on this date at Delhi suggests that the MDTP dynamically shifts downstream in response to very high veliger densities in slugs of water flowing downstream, even under low discharges. This shift is most strongly evidenced by the comparatively large overall abundance (Fig. 5) and large abundance of viable veligers (Fig 3; Table 6) observed at Delhi on the 17th that survived passage downstream from the beds of parent mussels in the river near the Baseline Dam. However, the degree of this shift cannot be accurately evaluated given the unknown veliger abundance in the slug at upstream sites.

Elevated veliger abundance at Delhi on July 17th tentatively suggests that over a longer time scale, exponential increases in the number of veligers entering the HRSR from

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\(5\) D-shell veligers are the first calcified stage to develop after the trochophore stage and have been reported to range in size between 70 to 160 μm (Ackerman, 1994a).
source populations may serve to buffer but not stem increases in veliger abundance in downstream areas. Thus the degree of riverine colonization and related unionid impacts may increase in downstream areas only incrementally in response to large increases in the numbers of veligers entering the HRSR from expanding source populations.

The lower proportion of empty veligers at Delhi on July 17 (Fig. 6) is probably related to the newly-calcified status of most of the veligers passing Delhi. Un-calcified veligers that die upstream of Delhi and drift downstream suspended by turbulence will not be detected in plankton samples. If veligers develop calcified shells only a short distance upstream of Delhi (as the small size of these veligers suggests), then the ratio of detectable (calcified) empty veligers to veligers with viscera intact would therefor be expected to be lower than other dates at Delhi than on the 17th.

Pulses of veliger progeny from riverine zebra mussels were also found by Camlin et al (1996) in the Illinois River. These pulses were composed of similar-sized individuals, which is consistent with data from the July 17 Delhi sample.

The likelihood that the small veligers observed in the July 17 plankton sample are the progeny of riverine *Dreissena* colonies supports the hypothesis that the length of the HRSR (22 km) is shorter than the Endogenous Recruitment Flushing Distance under low-discharge conditions. Hence the study reach will be largely immune to endogenous recruitment from the spawning activity of riverine zebra mussels. Delhi is only 2 km upstream of the downstream limits of the HRSR (the backwaters of the Barton Pond impoundment), indicating that all areas of the HRSR will be mostly shielded from the colonization of the progeny of river-dwelling zebra mussels.

July 17 data notwithstanding, the increase in the proportion of empty veligers with increasing downstream distance (Fig. 6) is difficult to interpret. While this trend is certainly due to instream veliger mortality, the presence of empty shells may be more a function of the continued suspension of dead veligers in the river by turbulence and water currents rather than an increased mortality rate caused by factors associated with lotic conditions. Hence the data does not directly indicate that hydrodynamic factors associated with fluvial systems increase veliger mortality rates over rates in lentic systems.
Peak discharge in 1996 followed a peak in veliger abundance (Fig. 4b), suggesting that a large number of settling stage larvae may have been flushed into the HRSR during this period. However, no 1996 young of year were found on unionids in downstream sites, indicating the lack of subsequent increased recruitment and fouling of unionids in sites downstream of Mill Creek. Without specific mechanistic information regarding factors that contribute to veliger settling inhibition or juvenile zebra mussel mortality, recruitment failure in downstream areas in this example is difficult to explain. The scarcity of zebra mussels in downstream areas may result in a lack of settling cues noted by Baldwin (1994) and Toczylowski (1996) that might otherwise induce veligers to settle in downstream areas to a greater extent. However regardless of the mechanism, the lack of downstream colonization during this period is consistent with the phenomenological downstream distance colonization limit hypothesis.

Future Veliger Production

The large proportion of HRSR discharge coming from Baseline Lake gives the lake the potential to surpass the significance of Portage Lake’s potential future levels of veliger contribution to the HRSR. The ability of Baseline Lake to produce veligers will largely be based upon endogenous recruitment-driven population increase of the lake’s adult population. Two factors may serve to minimize endogenous recruitment in the lake. Baseline’s flushing rate is only 14 days (Fusilier, 1994) and moreover, the effective flushing rate given the thermal stratification that develops during the spawning season (mixing and flushing confined to the epilimnion) is approximately 7.4 days, which is less than the duration of the planktonic veliger stage of the zebra mussel’s lifecycle. In addition, the morphometry of the lake appears to minimize eddied or pooled areas of water (the lake is circular in shape, and a line drawn from the inlet to the outlet almost bisects the lake; Fig. 1) that might retain veligers for protracted periods of time. Most veligers are thus swept into the river.

However, the four navigationally connected lakes immediately upstream of Baseline Lake on the Huron mainstem are now either lightly infested or will soon be colonized by zebra mussels via recreational boat traffic. These lakes will produce and export veligers that
will likely increase Baseline’s adult zebra mussel population well above what the lake could achieve via endogenous recruitment. It is under this scenario that Baseline Lake may be able to develop a large spawning population of adult mussels and hence surpass the magnitude of veligers that Portage Lake contributes to the study reach. Hence a dramatic increase in Baseline’s contribution of veligers to the HRSR may be delayed by the lag time required for the series of previously described events leading to a large reproducing adult population in Baseline Lake to occur.

While veliger densities ranged from 1 to 22 veligers/liter at the Baseline Dam in 1996, peak densities could theoretically approach 300 to 500 /liter, similar to peaks abundances recorded in Lake Erie (Nichols 1996; Garton and Haag 1993), assuming sufficient veliger production in Baseline Lake. This would increase the amount of veligers entering the HRSR by 1300 - 1500% over 1996 peak fluxes, assuming an identical discharge regime to 1996. The implications for possible downstream shifting of the downstream colonization limit and the MDTP posed by such large magnitudes of veligers entering the HRSR is unclear, though it is certain that at least some downstream shifting is likely, resulting in an increase in the threat to downstream unionid populations in the HRSR.

Also, the future of the invasion of the Huron River by zebra mussels will likely not be limited to the dynamics of veliger production in Baseline and Portage Lakes and subsequent downstream dispersal. Impoundments and lakes in the upper watershed in Livingston and Oakland Counties (e.g. Pontiac Lake, Union Lake, Kent Lake, Commerce Lake, etc.) are highly susceptible to invasion by zebra mussels in the near future, given the spread of zebra mussels to inland lakes in Oakland County (Marangelo, 1995; Marangelo, 1996). Thus unionids in the upper sections of the river are likely to be threatened with zebra mussel invasion in the near future.

**Unionid Fauna**

The unionid fauna in the HRSR appears to be recovering from prior depletion due to historical anthropogenic impacts noted by van der Shalie (1970). Species distribution and composition of the HRSR has changed little since the last survey in 1932 (van der Shalie 1938). Notable exceptions are the presence of a small number of *Epioblasma triquetra* and
an isolated individual of *Cyclonaias tuberculata* (J. Nichols pers. comm.) downstream of the Baseline dam. The former was considered by van der Shalie to be absent downstream of Baseline Lake and the latter was considered to be absent upstream of Bell Road. Also, the presence of isolated individuals of *Lasmigonia complanata* in the study area differs from van der Shalie’s records in the study site. van der Shalie recorded this species only in the lower section of river in Wayne and Monroe Counties and considered it to be an invader from Lake Erie, suggesting that this species has undergone a range expansion in the Huron watershed over the past few decades. *Alasmidonta viridis* was found as a shell only at Mast Road. This species was considered by van der Shalie to be rare in the Huron mainstem, and may still exist in smaller tributaries and the mainstem near the headwaters. Recent records have confirmed the presence of this species in Fleming Creek (R. Sherman pers. comm.).

Also, neither van der Shalie nor Scavia and Mitchell (1986) recorded the presence of *Corbicula fluminea* from the Huron River. Thus this invasive bivalve is likely a recent invader to the system. In the HRSR, it is most abundant near the Baseline Dam and similar to the distribution of *Dreisena*, diminishes in abundance downstream. It is rare at Hudson Mills (4.5 km) and absent from all other downstream sites. Interestingly, it is the only other bivalve in the HRSR with a veliger larval stage, which may account for this qualitative distribution similarity.

The increase in the abundance of *Cyclonaias tuberculata* since Scavia and Mitchell’s 1986 survey indicates a marked rebound of this species over the past ten years. It also indirectly suggests that other unionid species may have experienced similar increases in abundances, given the river’s history of extreme pollution episodes during World War II and the mussel fishery in the early and mid-20th century (van der Shalie 1970).

van der Shalie’s (1938) 1932 survey provided information on unionid distribution and habitat which suggests that the HRSR provides important habitat for species listed by the state of Michigan as either threatened or of special concern. In 1932, *Cyclonaias* was most abundant in the HRSR when compared to other locations in the Huron where it existed. Given the favored habitat of *Cyclonaias* and its abundance in the HRSR, it is likely that this is still true today. If so, the persistence of this species in the Huron River may rest on its *Dreissena*-influenced fate in the HRSR.
van der Shalie found the state-threatened *Lampsilis fasciola* abundant in the upper watershed of the Huron (including but not limited to the HRSR), and rare downstream of Ann Arbor. If this abundance pattern still exists, the species is unlikely to be extirpated from the river in the near future, even if it is eliminated by zebra mussels from the HRSR. A more comprehensive survey of the watershed above the study reach is needed to determine the present distribution and abundance of this unionid.

The state-endangered *Epioblasma triquetra* was only found by van der Shalie upstream of the HRSR (as well as in the Portage River, which flows into Portage Lake), and was noted to be unusually abundant only at sites near the US 23 underpass (Livingston County) in 1932. In contrast, the present study found a few individuals in the HRSR just downstream of the Baseline Dam. It may still exist as far downstream as Hudson Mills (where a shell was found), but is likely to be extirpated from this area by zebra mussels in the immediate future. Areas upstream of the HRSR need to be re-surveyed to assess the status of this species in the Huron.

**River Raisin Study Reach**

**Zebra Mussel Colonization: Unionid Fouling Patterns**

More than two areas in the RRSR have the potential to become source populations. Other than Vineyard and Clark Lakes, the backwaters of the Brooklyn impoundment, Norvell impoundment and Sharon Valley impoundment either are presently or have the potential to become source populations. Hence the unionid impact scenario continuum can be applied to five river reaches of lotic habitat in the RRSR.

Scenario #3 presently exists in the RRSR downstream of the Brooklyn impoundment and Clark Lake. The fate of unionids in both of these areas is uncertain. While zebra mussels may be fairly abundant on clams near Clark Lake (Table 7), small size distributions possibly maintained by high mortality or low growth rates (Fig. 11 a & b) accounts for the small sub-lethal volume fouling ratio (Table 7). Hydrodynamic factors associated with the size/shallow water of this creek may be inhibiting zebra mussel growth and/or exacerbating mortality. Unionids will probably persist in this system for the immediate future.
The site downstream of Brooklyn Dam appears to have been colonized relatively slowly compared to Baseline Dam in the HRSR, despite being only 4 km downstream of a lake that has likely been infested since 1992. The slow rate of veliger dispersal out of Vineyard lake through the interspersing marshy lotic and impounded backwater habitat has likely slowed this dispersal to the degree that the impounded backwaters of the Brooklyn Dam might be considered the source population for this site.

Unionid mortality may occur within the next few years in the unproductive unionid habitat between Vineyard Lake and the Brooklyn Dam, although the few unionids found in this area had low numbers of zebra mussels attached in 1996 (2 - 15/unionid). The proximity of this site to Vineyard Lake may make it highly susceptible to Dreissena-induced local unionid extirpation. The surprising persistence of unionids here thus far may be due to the low discharge emanating from Vineyard Lake during periods of peak veliger abundance in the early summer and slow water velocity through the marshy channel.

Other potential source populations in the RRSR have yet to develop large zebra mussel populations and hence unionids downstream from these sites will not be subjected to fouling impacts in the near future.

Inferences on Veliger Dispersal in the River Raisin Study Reach

Given that the Clark outlet creek is relatively small (1 - 2.5 m wide, 0.03 - 0.25 cm deep), probable low veliger flux magnitudes indicate that the Clark Lake makes only a minimal contribution of veligers to the mainstem. In comparison, the Raisin mainstem passes directly through Vineyard lake. Thus Vineyard has thus far been the major contributor to the RRSR’s veliger budget.

Veliger dispersal patterns in the RRSR are likely to be much more complex than in the Huron River. Since the Exogenous Recruitment Flushing Distance in the RRSR is likely shorter than the length of the study reach, all veligers entering the system from Vineyard and Clark Lakes that survive to settling stages will recruit in the study reach and may even in turn as adults produce larvae that can also self-recruit in the RRSR. Thus in contrast to the HRSR, the colonization of productive unionid habitats in the RRSR mainstem (areas downstream of the Norvell Dam) will likely be contingent on the ability of zebra mussels to
colonize impounded and slow-water habitats to the extent that these populations can produce enough veligers to heavily colonize the productive unionid habitats downstream of Norvell. Given the abundance of these types of habitats in the RRSR, the study reach has the potential to develop a number of source populations from which downstream areas can be colonized.

Substrate in impounded backwaters and slow-velocity lotic habitats is typically soft muck, and may be a limiting factor than inhibits population development of *Dreissena* in potential source populations. However, zebra mussels have the ability to heavily colonize macrophytes and other aquatic vegetation that are abundant in impounded backwaters (L. Johnson unpub. data). Moreover, soft substrate colonization by *Dreissena* has been observed in Lake Erie (Berkman et al 1995). Such colonization in impoundments and marshy river areas in the RRSR would not bode well for riverine unionids (in particular the productive habitats downstream of the Norvell Dam), given the abundance and distribution of these type of habitats in the RRSR. Soft-substrate colonization would likely occur over a longer time period than the colonization of hard substrates due to the time required for nuclei of zebra mussel soft-substrate dreuses to develop.

Inferences on the aptness of the downstream colonization limit hypothesis to characterize adult colonization patterns in the RRSR cannot be made with the present data due to the lack of veliger dispersal data, lack of a temporal dimension to unionid fouling data, and the heterogeneity of habitat types within the RRSR.

**Unionid Fauna**

To date, the present study represents the most comprehensive known survey of unionids in the upper Raisin mainstem. A limited survey by Strayer (1979) found similar species composition to the present study. The reach between Norvell Dam and Sharon Valley Rd. is highly productive unionid habitat (Table 8), and would be an appropriate area on which to focus unionid conservation efforts on given the abundance of the fauna and the presence of state listed species (*Cyclonaias tuberculata* and *Lampsilis fasciola*). Preliminary data from another survey near the Ives Road Fen downstream of Tecumseh (Mackleburg pers. comm.) indicates that mussel habitat appears to change, with diminished abundances and different species composition (dominating species: *Actinonaiais carinata* and *Fusconaia*
flava with some Amblema plicata). The lack of Cyclonaias tuberculata and Lampsilis fasciola in this area suggests that areas downstream of the Norvell Dam in the RRSR are crucial habitats for the persistence of these species in the River Raisin. More extensive surveys are needed in the Raisin outside of the RRSR to provide more definitive data on the distribution of these species in the watershed.

General Discussion

Unionid Fouling

Data from other studies provide general guidelines for determining the lethal potential of various levels of fouling intensities. Nalepa (1994) found that unionids disappeared in areas of Lake St. Clair with fouling intensities exceeding 55 zebra mussels/unionid. Ricciardi (1996) documented a significant reduction in unionid density when mean fouling intensity approached 10 mussels/unionid in Lake St. Louis (St. Lawrence Seaway drainage). Size differences of fouling Dreissena likely accounted for differences in the mortality threshold of the number of zebra mussels/unionid implied by these studies. Data from this study are consistent with these findings, given the incipient mortality observed at the Baseline Dam site where mean fouling intensities surpassed 55/unionid. In the Clark Outlet creek in the RRSR, fouling intensities are above those documented by Ricciardi (1996) to have imparted mortality, but the small size of the zebra mussels in this system probably indicates that these unionids have a considerably lower volume fouling ratio than the unionids in Lake St. Louis, which supported a small number of large sized mussels. Thus it is unlikely that unionids in the Clark outlet will die from acute impacts in the near future.

This study used patterns of unionid fouling and veliger dispersal to infer future trends in recruitment magnitude on which to base projections of unionid impacts. However, in downstream segments distant from source populations that may be unlikely to develop heavy infestations (over 10 mussels/unionid), volume fouling ratios may approach lethal levels in lotic habitats if growth rates and survivorship among the few zebra mussels that infest unionids are large (Table 10). Ultimate acute (and chronic) impacts on unionids in lightly
infested segments therefore may be a function of the ability of zebra mussels to achieve large sizes sufficient to impart lethal stress in addition to overall seasonal recruitment rates.

**Table 10:** Generalized contingency table for possible range of acute unionid impacts at specific sites in non-navigable small-mid sized river systems. The table is based on differing potentials for rates of zebra mussel recruitment (based on downstream channel distance from source populations) and survivorship/growth (based on the size of a system and likely related limiting physio-chemical parameters) for different lotic sites. Clark Lake outlet sites most closely corresponds to the low growth/survivorship category. The Huron River Baseline Dam site most closely corresponds to the high growth rates/survivorship category.

<table>
<thead>
<tr>
<th>Recruitment</th>
<th>zebra mussel growth rates/survivorship</th>
</tr>
</thead>
<tbody>
<tr>
<td>High (close to source populations)</td>
<td>High (larger rivers)</td>
</tr>
<tr>
<td></td>
<td>fouling intensities: high volume fouling ratios: high high unionid mortality</td>
</tr>
<tr>
<td>Low (distant from source populations)</td>
<td>fouling intensities: low volume fouling ratios: moderate moderate mortality</td>
</tr>
</tbody>
</table>

Long-term unionid impacts may not be related solely to direct interference competition via the fouling of valves by *Dreissena*. Work by Strayer (1996) in the Hudson River in New York suggests that zebra mussels may be able to negatively impact unionids indirectly. Unionids in this system have only been lightly fouled (mean = 2 zebra mussels/unionid) despite overall high zebra mussel densities. Nevertheless, a puzzling unionid decline has been observed, coinciding with the onset of dense zebra mussel colonization, possibly due to usurpation of unionid food sources by zebra mussels. This study suggests that the threat that zebra mussels pose to unionids may be also be related to food competition in addition to the interference competition examined in this study.
**Downstream dispersal/colonization**

It is becoming clear that zebra mussels have differential dispersal/colonization success loosely based on a continuum of stream sizes in lotic systems. Less severe colonization has been observed in smaller systems (Horvath 1994; Hunter pers. comm.), while large scale colonization and heavy unionid impacts have been recorded from large commercial rivers (Whitney 1994; Ricciardi 1996; Miller and Payne 1996). Data from this study appears to be consistent with this pattern, as unionids have been thus far most heavily impacted in the larger HRSR and less impacted in the River Raisin and Clark Outlet Creek despite similar timelines of invasion and zebra mussel population expansion in their respective source populations.

While initial impact of zebra mussels on unionids appears to be governed by the dynamics of source population larval production, subsequent downstream dispersal, and lotic recruitment, the extent of riverine colonization may also be affected by post-metamorphic re-suspension and secondary settlement. Martel (1993) documented the presence of small (0.5 - 2 mm) mussels in the water column re-suspended by storm-mediated turbulence in nearshore areas of Lake Erie, and then speculated that post-metamorphic secondary settling activity may play an important role in the colonization of turbulent systems, including rivers. In the HRSR, this could translate into the downstream movement of juveniles from the heavily colonized area near the Baseline Dam into downstream habitats. It is also possible, however, that re-suspended juveniles would settle out in less turbulent low-velocity pool habitats, where unionids are less abundant.

Future magnitudes of veligers entering the HRSR and RRSR can be expected to track zebra mussel population trends in source populations. Given the likelihood of population decline of *Dreissena* in source populations after the initial “boom” cycle, the magnitude of veliger flux entering downstream reaches will eventually decline after the initial period of exponential increase that typically follows *Dreissena* colonization of lentic source populations. In this sense, the most critical years for determining the fate of riverine unionid populations at least in terms of acute impacts (and possibly for chronic impacts as well) may be the seasons after peak adult densities are achieved in source populations. These periods will likely be marked by a reduction of veliger flux from peak levels into downstream lotic
habitats along with the lingering effects of surviving adult mussels from peak veliger production year cohorts on downstream unionids.

**Listed Species of Unionids**

*Cyclonaias tuberculata* size distribution differences between the RRSR and HRSR and within the HRSR suggests differences in the demographic histories, survivorship, and/or growth rates between these areas (Figs. 14 a, b & c). The lower proportion of smaller size class animals in the RRSR suggests that recruitment has been lacking in the Raisin in recent years. The small size of animals recorded below Mill Creek in the HRSR is consistent with data from *Cyclonaias* abundance comparisons to Scavia and Mitchell’s data (1986; Table 9) that indicates that *Cyclonaias* at these sites has recently increased substantially in abundance. This size distribution (Fig. 14a) is a likely result of new recruitment in an area in which *Cyclonaias* had previously been scarce. This species appears to be rebounding from impacts noted by van der Shalie (1970) in the HRSR. However, some unionid species have been noted to have high year-to-year variation in recruitment (Miller and Payne 1988). Hence without a sufficient temporal dimension, this data must be interpreted with caution. Continued monitoring of these trends is needed to more accurately assess demographic trends in the population of *Cyclonaias* in the Huron and River Raisin.

It should be noted that the methodology employed in unionid surveys may have underestimated true abundances. Hand-picking has the disadvantage of being insensitive to juvenile unionids (although unionids down to 4 mm were detected). It also limits the interpretation of demographic information from size frequency data, since smaller juvenile size classes are either missing or under-represented.

The similarity of abundances of state-listed unionid species (*Lampsilis fasciola* and *Cyclonaias tuberculata*) between the HRSR and RRSR (Table 9) makes it difficult to prioritize the importance of the study sites in these two rivers to the conservation of these species on the basis of abundance. Clearly, both study reaches have ecological conditions well-suited to both these species. For the short term, these unionids are unlikely to be extirpated by zebra mussels from either study reach. Habitats the greatest distance from
present or potential source populations have the greatest probability of long-term persistence.

**Volume fouling ratio measurement assessment**

The most common fouling index used in studies of zebra mussel/unionid interactions has been a mean of the number of zebra mussels/unionid. Attempts to circumvent the biases of this methodology (different size distributions of the same number of mussels/unionid have differential impacts, and stress is likely to be greater for smaller unionids than larger ones for a given number of fouling zebra mussels of a given size distribution) have used measures of a ratio of dry weight biomass of fouling zebra mussels/unionid dry weight. The fouling volume ratio methodology developed for this study has a number of advantages and disadvantages over both these methods. Dry weight biomass measurements are more destructive of unionids and are susceptible to the large variance associated with *Dreissena* spawning condition. Ripe zebra mussels (especially in early spring measurements) are likely to have a much larger dry weight biomass than spawned individuals, thus making such measurements subject to variation not associated with the size of the fouling mussels. Water displacement volume measurements are not destructive and may be especially advantageous when rare species are being studied or when long term studies make consistent dry weight ratios unacceptably destructive of local unionid fauna.

The volume fouling ratio method assumes that all measured bivalves are solid impermeable objects bounded by the animal’s valves. Zebra mussels seldom gape after being immediately removed from water, and thus can be consistently measured via volume water displacement. However this assumption is more severely violated in unionids, as they may or may not gape when removed from the water. Moreover, gaping behavior appears to be species specific (e.g. *Alasmidonta marginata* always gaps when removed from the water, while *Cyclonaias tuberculata* does not). Also, zebra mussels must physically be removed from the unionid (except where the unionid is lightly fouled), making measured individuals unavailable for future cumulative fouling measurements.

Other difficulties with the volume fouling ratio methodology are related to measurement problems. Volumes estimated by field displacement measurements are larger
than ratios obtained via a length-volume regression for zebra mussels due to the retention of water and benthic invertebrates on the surfaces and in interstitial spaces of fouling zebra mussels, and also from sand and gravel adhered to unionid valves via byssal threads. However, fouling intensities measured with zebra mussel volume derived from size-volume regression may not represent the total stress load on a unionid - e.g. the negative effects of byssal threads and adhered organic/inorganic matter will not be accounted for by this method.

Most volume fouling ratio intensities were measured in this study via zebra mussel size-volume regression. This method is advantageous in that it facilitates the measurement of lightly fouled unionids, which are difficult to measure under field conditions due to the small discrepancy between the volume of the fouled unionid and the volume of the unionid with all zebra mussels removed. However, heavily fouled unionids may have hundreds of attached zebra mussels, making the measurement of fouling ratios for a large number of unionids via the length-frequency regression method labor intensive. Field measurements of fouling volume ratios are advantageous under these circumstances, but need to be adjusted by the difference between the two methods to produce unbiased data. It should be noted that the large standard deviation in the volume difference between the two methods indicates that a loss of accuracy accompanies efforts to adjust field measurements volume fouling ratios for equability to regression derived ratios.

Conclusions

Insights provided by this study suggest that lotic habitats may provide at least a temporary and perhaps a long-term refuge for unionids from Dreissena impacts given sufficient free-flowing channel distance from upstream source populations in small to mid-sized rivers. The degree that a given length of channel from upstream sources protects unionids from fouling likely varies with system-specific parameters such as discharge regime, size of the system, and suitability of available lentic or semi-lentic habitats for colonization. This protection will vary in accordance with the habitat and position of a given unionid in the channel - i.e., unionids in eddies, pools, and riverbanks being more susceptible to zebra mussels settlement on account of slower current velocity. The degree to
which such protection is conferred on unionids is likely contingent on the suitability of specific threatened reaches for veliger dispersal and subsequent recruitment.

As zebra mussels disperse throughout river systems that are highly impounded such as the RRSR, the ability of semi-lentic impoundments to harbor large spawning adult populations will be a critical factor in the determining the impacts on unionids downstream. If zebra mussels are successful in heavily colonizing impoundments, the implication is that *Dreissena* will colonize rivers in a stair-step fashion, using dam backwaters as “spawning pools” to send veligers farther downstream while in turn being sustained by upstream veliger production. Under this scenario, only unionids in the most downstream sections of long free-flowing segments might be sheltered from the adverse impacts associated with zebra mussel fouling.

More work needs to be done to evaluate the long-term physiological stress that chronic low to moderate fouling intensities impart on unionids. Many of the interactions between unionid bivalves and zebra mussels in rivers such as the Huron and River Raisin may occur within the context of light to moderate fouling regimes, given the observed patterns of downstream dispersal and colonization. This, coupled with a more complete mechanistic understanding of the downstream colonization dynamics of zebra mussels, will provide a foundation for formulating more specific prognoses for unionids in small to mid-sized systems subject to *Dreissena* invasion.

**Recommendations**

**Dam Removal**

While the exact role of dams in riverine zebra mussel colonization remains somewhat speculative, it is clear that the ability of zebra mussels to colonize impoundments will be a critical factor in assessing the risk that *Dreissena* poses to unionid populations in highly impounded rivers. Rivers such as the Raisin and Huron offer a stair-step of impounded lentic habitat types that may eventually serve as a series of potential “launch pads” for further downstream colonization of unionid-harboring lotic habitats. Despite the uncertainties relating to population development of *Dreissena* in impoundments, removal of superfluous dams (no longer used for recreation, power generation, water supply, or other
industrial uses) are prudent not only for sheltering unionids from zebra mussels, but for the general restoration of fluvial ecosystems.

**Relocations**

Relocating clams to river reaches separated from upstream source populations by as much distance of free-flowing river channel as possible may be useful in protecting individual populations of clams of conservation interest in areas where extirpation is likely. For example, rebounding clam populations in the HRSR downstream of Mill Creek may be augmented by clams relocated from upstream segments closer to the source populations in the HRSR where extirpation by zebra mussels is more likely. Such action would be warranted if emerging infestation patterns in the HRSR suggest that unionids are likely to be extirpated from upstream sites (Bell Road and Hudson Mills). While it would be inappropriate to relocate the unionid fauna upstream of the Baseline Dam to these areas on account of habitat differences, the fauna at Bell Road and Hudson Mills could certainly be relocated given sufficient evidence of the risk of extirpation. Indeed, if zebra mussels succeed in extirpating unionids from these sites, the section on the HRSR downstream of Mill Creek may be the only river segment where species such as *Cyclonaias tuberculata* may persist in large numbers in the Huron.

Inter-basin relocations may be considered if appropriate recipient habitat can be found that has low probability of *Dreissena* invasion. Also, protocols need to be developed to prevent the inadvertent relocation of zebra mussels along with the relocated unionids.

**Interventions**

Large-scale effort to physically remove zebra mussels from clams may prevent extirpation of unionids from specific reaches. One such effort has commenced in the HRSR in 1996 (S. J. Nichols, National Biological Service).

If extensive heavy colonization of all lentic habitats in the HRSR occurs (Scenario #1), it is likely that clam-cleaning efforts may be required to prevent the extirpation of species such as *Cyclonaias tuberculata* and *Lampsilis fasciola* from the HRSR. *Cyclonaias* especially is an appropriate high-priority target due to its concentrated abundance in the HRSR and its Special Concern status. Such efforts may be effective if only limited to years
with elevated magnitudes of dispersal-modulating discharge during July and August. Also, Unionids may be imperiled only during the “boom” years in upstream mussel populations. Hence interventions may only be necessary only during the initial population explosion of zebra mussels in source populations. Watershed associations such as the Huron River Watershed Council may be a source of volunteers for such efforts.

**Future Study**

Continued monitoring of colonization and dispersal patterns in the HRSR and RRSR will yield data that will produce more precise insights into the relationship between veliger production in upstream sources and threats to downstream unionid fauna. Critical among the questions that remain to be addressed is whether a colonization threshold exists at sites such as the HRSR beyond which heavy colonization of the river is unlikely. Also, monitoring of unionid beds at Bell Road and Hudson Mills over an extended period of time may provide insights into the impacts of chronic fouling on unionids.

Sections of the RRSR between Norvell and the Sharon Valley Road gauge site near Manchester should be monitored for the downstream progression of zebra mussel colonization. Given the high unionid abundance of these sites, they should also be targeted as a high-priority area for fluvial system protection/restoration efforts.
Appendices

Survey site descriptions

Huron River

Baseline Dam:

*Unionid transects:* located in an area between 100 - 250 m downstream of the Baseline Dam.

*Settling plates:* located in slow-run habitat in the same area in 1 m of water (low discharge).

*Plankton samples:* taken from private property on north (east) bank of the river and on transects across the river.

*Stage Discharge:* station located in same area.

Bell Road:

*Unionid transects:* located in a riffle-fast run approximately 0.5 km downstream of the bridge on the west side of the downstream half of an island in the river. Maximum depth at low discharge was 0.4 m. Transects were located within a 17.4 x 28.6 m area.

*Settling plates:* located 50m upstream of the bridge on the west bank near the tip of the island in 0.6 meters of water (low discharge) on the edge of a pool.

Canoe Camp, Hudson Mills Metropark:

*Settling plates:* located in a shallow pool area at the center of the river in 0.8 meters of water (low discharge).

Hudson Mills Metropark:

*Plankton samples:* taken at the Rapids parking lot.

*Unionid transects:* located on the west side of the midpoint of an island 1 km downstream of the Rapids parking lot. Transects were taken within a 18 x 20 m area.

*Settling plates:* same as unionid transects, in 0.7 m of water at a velocity of 0.23 m/s 0.1 m above the substrate. The channel was 18 m wide at the transect area.
Stage discharge station: located 30m upstream of the pedestrian bridge at the head of the island.

Power Line area:

Settling plates: in a slow run accessed from a private residence on a subdivision off of Huron River Drive. The plates were in 0.7 m of water.

Mast Road:

Unionid transects: in a shallow riffle area 30 m downstream of the Mast Road Bridge. Transect area: 15.8 x 36.6m.

Dexter-Huron Metropark:

Unionid transects: located just upstream of the rapids adjacent to the picnic shelter. Transect area was located between 35m upstream of the rapids to the onset of the rapids. Maximum water depth was approx. 0.9m at low discharge

Settling plates: in a moderate run adjacent to a Huron River drive pull-off on the east side of the river. Plates were in 0.8 m of water at low discharge.

Delhi West:

Settling plates: were located in the center of the river near the Delhi-West Picnic area in 0.6 m of water.

Delhi:

Unionid transects: located 100m downstream of the rapids in a riffle-fast run area in water with a maximum depth of 0.7 m at low discharge. Substrate was predominantly cobble-gravel-sand with some boulders. The transect area was approximately 40m (channel width) x 25.3m.

Plankton samples / stage discharge station: located in same area.

Barton Pond:

Settling Plates: located in the river just before the slack water area in Barton Pond on the west bank of the river in 0.7 m of water.
River Raisin

Clark Lake outlet sites

Clark outlet:

Unionid transects: located on the east side of the culvert where Clark Lake drains into the outlet. Quadrats taken between 3 and 70 m downstream of the culvert.

Settling plates: located in 0.35 m of water at a deep point in creekbed.

Clark outlet, Riverside Road:

Unionid transects: located between 1 - 50 m downstream of the culvert. Settling plates located in deep water where culvert emerges from under the road.

Goose Creek:

Unionid transects: Next to laundromat on west side of Brooklyn Road.

Settling plates: same location

Mainstem sample sites

Vineyard outlet:

Unionid surveys: conducted between Wamplers Lake Road and the backwaters of the impoundment of the dam in Brooklyn.

Settling plates: located in slow run 15m downstream of the spillway emptying from Vineyard Lake.

Brooklyn Dam:

Unionid surveys: located in the riffle-run habitat between the dam and the municipal park downstream of the dam.

Settling plates: located in slow run 70 m downstream of the bridge in 0.4 m of water.

Wolf Lake Rd:

Unionid transects: conducted within 25m of upstream and downstream sides of the bridge.
Settling plates: located downstream of the bridge (plates were vandalized at this site).

Norvell Dam:

Unionid transects: located between 75 and 125 m downstream of the dam.

Settling plates: located in slack water 25 m past the spillway on south bank.

Pierce Road:

Unionid transects: located on upstream side of bridge above the river segment that parallels the road on the west.

Settling plates: located 30 m upstream of the bridge in slow run habitat.

Sharon Valley Road:

Unionid transects: located between 20 - 120 m downstream of the bridge.

Sharon Hollow Road:

Unionid transects: located 75 - 175 m downstream of the spillway near the Sharon Mills winery.

Sharon Valley Rd, gauge site:

Unionid transects: located on segment of river paralleling road on upstream side of bridge.

Settling plates: located 30 m downstream of the bridge.

**Zebra Mussel Length-Volume Regression:**

\[ \ln(\text{volume}) = 3.046 \times \ln(\text{length}) - 9.324; \quad R^2 = 0.941; \quad p < 0.005; \quad N = 51 \]
Literature Cited


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