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Epizoic Invertebrate Communities on Upper Mississippi River Unionid Bivalves

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ABSTRACT.—Based on the Great Lakes experience with *Dreissena polymorpha*, it is clear that the native freshwater mussel (family Unionidae) fauna will be one of the riverine communities most severely impacted if high zebra mussel densities occur. Negative impacts on unionids will also affect the epizoic invertebrate communities that live on the shells of the unionids. In 1991 and 1992 (prezebra mussel infestation) we determined the composition and density of epizoic invertebrates on individual unionids from the upper Mississippi River. The 1991 samples were from a location with a strong current; the numerically dominant epizoic invertebrates at this location were three species of hydropsychid caddisflies and the chironomid larvae: *Polypedilum convictum*, *P. scalaenum* group, *Rheotanytarsus* sp., *Microtendipes pedellus* group and *Thienemannimyia* group. Strong correlations existed between effective surface area (ESA) (amount of shell surface area above the sediment-water interface) of the individual unionids and: (1) number of epizoic chironomid larvae ($r = 0.81$); (2) number of hydropsychid caddisflies ($r = 0.73$), and (3) total number of epizoic invertebrates ($r = 0.78$). Sampling in a slower current area in 1992 revealed an epizoic composition dissimilar from that observed in 1991. *Glyptotendipes* nr. *lobiferus* was the most abundant epizoic larval chironomid, and, although caddisfly larvae were common, they mostly belonged to families other than the Hydropsychidae. Again, strong correlations existed between ESA of the unionids and: (1) total number of epizoic invertebrates ($r = 0.64$) and (2) number of epizoic chironomid larvae ($r = 0.57$). A strong correlation also existed between the size of the unionids and the number of epizoic taxa present (1991: $r = 0.78$; 1992: $r = 0.77$). Fifty-three invertebrate taxa were collected from the unionids; mean epizoic densities were ca. 9600 and 6400 invertebrates/m² of ESA in 1991 and 1992, respectively. These results indicate that unionids are important substrates for epibenthic invertebrates, especially in rivers in which other large clean substrates are in short supply.

INTRODUCTION

North America's rich unionid (Mollusca: Bivalvia: Unionidae) fauna has suffered from damming, channelization and pollution of the continent's rivers (McMahon, 1991; Stolzenburg, 1992; Williams *et al.*, 1993). More than 25 unionid species are listed as endangered in the United States (McMahon, 1991). Because of their great species richness in North America (one reach of Virginia's Clinch River contains more than three times the number of unionid species reported from the continent of Europe—Stolzenburg, 1992) and the extensive historical losses of unionids from river systems (*see* McMahon, 1991), concerns over further declines in unionid communities are certainly justified. Further reductions in unionid abundance would also affect the epizoic invertebrate fauna which lives on the shells of the bivalves; this epizoic fauna has not been studied previously.

Over 250 yr ago, Jonathan Swift, the English satirist and writer of *Gulliver's Travels*, described an ecological relationship in which:

So, Nat'ralists observe, a Flea
Hath smaller Fleas that on him prey,
And these have smaller Fleas to bite 'em,
And so proceed ad infinitum:

Although the epizoites on unionids don't "bite" their hosts, a conspicuous invertebrate fauna does exist on freshwater unionids. In 1991 and 1992 we identified and quantified epizoic invertebrates present on unionids living in upper Mississippi River (UMR) mussel beds (the UMR is the portion of the Mississippi River between St. Anthony Falls in Minneapolis-St. Paul, Minnesota, and the Mississippi's confluence with the Missouri River near St. Louis, Missouri). In addition to determining what species live on the unionids, and their abundance and densities, we ascertained whether different ambient current velocity conditions produced dissimilar epizoic faunas. We also wanted to determine if there was a correlation between unionid surface area and: (1) the number of epizoic individuals and (2) the number of epizoic taxa.

We were interested in unionids from the UMR for several reasons. Historically, mussel beds in the UMR were severely depleted in the early 1900s by overharvesting for the commercial button industry and the search for pearls (Thiel and Fritz, 1993). Today, harvesting pressures from the cultured pearl industry threaten species such as *Megalomias nervosa* and *Amblyma plicata* (Thiel and Fritz, 1993). In 1990, ca. 6.5 million pounds of unionids with a commercial value of ca. 5.1 million dollars were harvested from the UMR in the states of Minnesota, Wisconsin, Iowa, Illinois and Missouri (Thiel and Fritz, 1993).

Despite historical and contemporary harvesting, diverse and dense unionid beds still occur in the UMR. Intensive sampling of five UMR unionid beds in 1990 and 1991 produced a minimum of 21 and a maximum of 26 unionid species per bed; densities were as high as 80–90 unionids per m² of river bottom in some portions of the beds (Miller and Payne, 1992; 1993). Unfortunately, the zebra mussel *Dreissena polymorpha* (Pallas) has moved from the Laurentian Great Lakes into the Mississippi River drainage. Zebra mussels were first collected from the UMR in 1991 (Moore, 1991) and have now been collected from many locations in the UMR, often attached to native unionids. The colonization of unionids by zebra mussels has had a devastating effect on the unionid community in Lake St. Clair (Mackie, 1991; Hunter and Bailey, 1992), the probable site of the introduction of *Dreissena* into North America (Hunter and Bailey, 1992). Fortunately, at present the density of zebra mussels on unionids in the UMR is low; the potential exists, however, for colonization of UMR unionids by *Dreissena* on the scale observed in Lake St. Clair. Such an occurrence would obviously affect not only the river's unionids, but their epizoic fauna as well. Our study can therefore be viewed as both an examination of the epizoic fauna as it is now, and as a basis for future comparisons if the epizoic fauna changes from a native fauna to one dominated by zebra mussels.

METHODS

Sites and sampling methods.—On 18 July 1991, divers collected 10 unionids for appraisal of their epifauna from a mussel bed located along the river's right descending bank in Pool 12 of the UMR, near Dubuque, Iowa. Water depth at the sampling site was 2.4 to 4.9 m. The divers were instructed to choose the 10 unionids without regard to size or species. The divers carefully removed individual unionids from the river's substrate and placed each in its "own" plastic bag. The top of the bag was knotted underwater to prevent escape of epizoic invertebrates. The bags were brought to the surface and each bag was placed in a separate plastic container. The bags were opened and the unionids, epizoic invertebrates,

and any water in the bags were retained in the plastic containers. The insides of the bags were rinsed into the containers and inspected in order to recover any invertebrates that might have moved from the shells of the bivalves to the inside of the bags. The unionids and their epizoic invertebrates were preserved with a 5–10% buffered formalin solution.

On 2 October 1992, we collected 15 unionids from Pool 8 of the UMR at a point where Crosby Slough (a backwater channel) rejoins the river's main channel (ca. river mile 689.5). These unionids were collected near shore in shallow water (0.9–1.5 m) without regard to size or species, and were obtained by locating the unionids while wading and then briefly going underwater and removing them from the substrate as carefully as possible. We placed each unionid in a zipper-lock bag as it was brought across the air-water interface. Buffered formalin was again used as a preservative.

Laboratory methods.—In general, unionids burrow into the substrate, positioning themselves on an oblique angle, with their hinges up and much of the shell buried beneath the sediment. Consequently, the buried portion of the shell surface is not available for colonization by epizoic invertebrates. The exposed area had animal cases and "aufwuchs" attached, and its coloration was somewhat different from that of the buried portion. In the laboratory we used an electric-powered tool to etch a line on both valves to separate the exposed area from the buried portion. We marked these areas so that we could distinguish them later.

Epizoic invertebrates were dislodged by brushing the exteriors of the shells with a toothbrush. Invertebrates dislodged by brushing, as well as those loose in the plastic sample containers or zipper-lock bags, were collected on a U.S. Standard 60 sieve (openings = 250 μm) and preserved in 70% ethyl alcohol. Chironomids and oligochaetes were mounted on slides using a modification of the method of Beckett and Lewis (1982). All epizoic invertebrates were then identified, generally to the genus or species level. We used the following taxonomic keys in our invertebrate identifications: larval chironomids (Wiederholm, 1983; Epler 1992); annelids (Klemm, 1985; Brinkhurst, 1986); caddisflies (Wiggins, 1977; Schuster and Etnier, 1978); *Stenonema terminatum* (Lewis, 1974); *Dugesia tigrina* (Kenk, 1976); *Muscilium transversum* (Burch, 1975); the remaining taxa (Pennak, 1978; Peckarsky *et al.*, 1990; Thorp and Covich, 1991).

To determine if a relationship existed between available surface area and invertebrate abundance (number of epizoic individuals per unionid), as well as calculate invertebrate densities (number of epizoic individuals per area of shell), we determined the amount of surface area exposed above the sediment-water interface for each collected unionid. We called this area the effective surface area (ESA) since it was the actual surface area available for colonization by epizoic invertebrates. We determined the ESA of each unionid by cutting pieces of aluminum foil such that they fit in a single sheet exactly over the portions of the shell which had been above the sediment-water interface. We also cut out measured squares of aluminum foil from the same roll of foil. We then weighed the aluminum foil specimens on a Mettler balance. Since the weight of the foil is a function of its area, we could calculate the ESA of each unionid using the following ratios:

$$\text{ESA/wt. of foil covering ESA} = \text{area of measured foil/wt. of measured foil}$$

RESULTS

1991 epizoic invertebrates.—Current velocities at our Dubuque sampling site, measured at several points with a meter held slightly below the air-water interface, were between 50 and 75 cm/sec. Seven species were represented among the 10 unionids collected: *Amblema plicata*, *Anodonta grandis* (two specimens), *Arcidens confragosus*, *Fusconaia ebena*, *F. flava*,

TABLE 1.—The effective surface area (ESA), epizoic invertebrate abundance (number of individuals) and density (numbers/m² of unionid ESA), and number of invertebrate taxa, per individual unionid, for samples collected from the upper Mississippi River on 12 July 1991 and 2 October 1992. Total Invert. = total invertebrates, *i.e.*, all epizoic invertebrates. Results for two of the predominant components of total invertebrates, hydropsychid larvae and chironomid larvae, are also shown. "Others" indicates those invertebrates which were not hydropsychid larvae or chironomid larvae. s = standard deviation; max. = maximum; min. = minimum

	ESA (cm ²)	Invertebrate abundance				Total invert. density	No. of taxa
		Total invert.	Hydro- psychid larvae	Chiro- nomid larvae	Others		
1991							
Mean	64.7	74.4	50.6	15.9	7.9	9564	8.7
s	48.6	86.9	65.1	16.6	10.2	6571	5.6
Max.	164.9	277	214	49	29	22,988	16
Min.	11.5	3	2	1	0	583	2
1992							
Mean	55.6	36.7	0.1	24.4	12.3	6367	9.3
s	22.9	27.5	0.3	22.4	6.8	3703	4.4
Max.	99.2	98	1	75	25	15,024	17
Min.	28.4	8	0	4	3	2367	4

Obliquaria reflexa (two specimens) and *Quadrula quadrula* (two specimens). Mean ESA per unionid equaled 64.7 cm² (Table 1).

A *Fusconaia flava* specimen (with an ESA of 120.5 cm²) supported a total of 277 invertebrates, including 214 hydropsychid caddisflies and 49 chironomid larvae. The epizoic density on this bivalve equaled 22,988 invertebrates/m². Epizoic abundance among the collected unionids varied; 277 was the highest number of epizoic invertebrates on one unionid (and produced the highest density), another unionid was colonized by only three invertebrates (density = 583 invertebrates/m²) (Table 1). The mean number of epizoic invertebrates per unionid equaled 74.4 (mean density = 9564 epizoic invertebrates/m² of unionid ESA).

The 277 epifaunal invertebrates collected from the specimen of *Fusconaia flava* represented 14 distinct taxa. While another unionid with fewer invertebrate colonists (121 individuals) supported an even larger number of epizoic taxa (16), the unionid with three invertebrate colonizers had only two epizoic taxa (Fig. 1). A total of 27 epizoic invertebrate taxa were present on the 10 unionids.

Caddisfly larvae belonging to the family Hydropsychidae and chironomid (Diptera: Chironomidae) larvae dominated the 1991 invertebrate collections (Tables 1 and 2). Of the total 744 epizoic invertebrates collected from the unionids, 506 individuals (68%) were hydropsychid larvae and 159 (21%) were chironomid larvae. Slightly over half of the hydropsychids present on the shells were early instars, and were identifiable only to family (Table 2). The later instar hydropsychids were members of three taxa: in order of abundance, *Hydropsyche orris* (61% of the later instar larval hydropsychids), *Potamyia flava* (27%) and *Cheumatopsyche* sp. (12%).

Our 1991 epizoic collection included a total of 10 chironomid taxa. The five most common taxa were members of the *Thienemannimyia* group (gr.) (28% of the larval chiron-

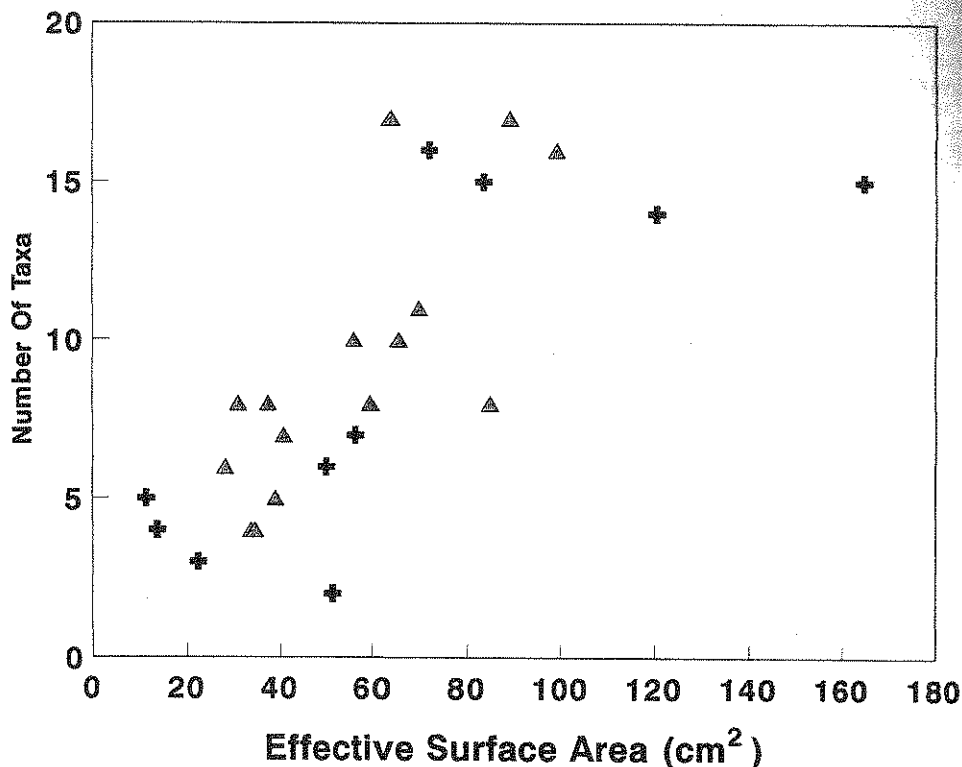


FIG. 1.—Effective surface area and number of epizoic invertebrate taxa on unionids collected from the upper Mississippi River. Data from the collection made on 12 July 1991 from Pool 12 near Dubuque, Iowa, are represented by crosses; data from the collection in Pool 8 on 2 October 1992 are represented by triangles. Correlation analysis of effective surface area and number of epizoic taxa for the 1991 results generated an $r = 0.78$, $P = 0.008$; $r^2 = 0.61$. In 1992 $r = 0.77$, $P = 0.001$; $r^2 = 0.60$.

omids collected), *Polypedilum convictum* (26%), *Microtendipes pedellus* gr. (21%), *Polypedilum scalaenum* gr. (11%) and *Rheotanylarsus* sp. (9%) (Table 2). Each of the remaining five taxa made up approximately 1% of the chironomids present and were represented by only one or two individuals.

The planarian, *Dugesia tigrina*, was relatively common on the unionid shells (a mean of 2.5 per unionid were collected). Other nonhydropsychid, nonchironomid invertebrates found living epizoically, but in small numbers, included the cnidarian *Hydra*, three oligochaete taxa, a leech, the isopod *Caecidotea*, water mites, the mayflies *Caenis* sp. and *Stenonema terminatum*, the riffle beetle *Stenelmis* sp., the dipteran *Hemerodromia* sp. and the fingernail clam *Musculium transversum*.

We used the Pearson product-moment correlation coefficient (r) to determine if significant correlations existed between invertebrate abundance and unionid surface area (ESA) for the 10 unionids collected in 1991. Total invertebrate abundance, as well as its principal constituents—hydropsychid larvae and chironomid larvae—all showed strong, positive correlations with unionid ESA (Table 3, part A).

1992 epizoic invertebrates.—The unionids sampled in 1992 were dominated by *Amblema*

TABLE 2.—Taxonomic composition of the more common epizoic invertebrates present on unionids collected from the upper Mississippi River on 12 July 1991 and 2 October 1992. Mean number per unionid, percentage abundance of that taxon for the 1991 or 1992 collection, and percent frequency of occurrence (Freq.) [(no. of unionids in which the taxon occurred/total no. of unionids collected) × 100] for the two collections are shown. Absence of an entry in the columns indicates that the taxon was not collected on that date. See Appendix for a complete listing of the epizoic taxa collected on the two sampling dates

Taxon	1991			1992		
	Mean	Percent abundance	Freq. (%)	Mean	Percent abundance	Freq. (%)
TURBELLARIA						
<i>Dugesia tigrina</i>	2.5	3.4	30	0.6	1.6	40
OLIGOCHAETA						
Imm. tub. w/o cap. ^a	0.2	0.3	10	0.8	2.2	53
<i>Nais pardalis</i>				0.8	2.2	47
<i>Nais simplex</i>				0.4	1.1	20
<i>Nais variabilis</i>				0.5	1.5	33
Enchytraeidae				0.5	1.3	33
HYDRACARINA	0.7	0.9	10	0.3	0.7	27
EPHEMEROPTERA						
<i>Caenis</i> sp.	0.4	0.5	30	1.5	4.0	67
TRICHOPTERA (Larvae)						
Hydropsychidae						
<i>Cheumatopsyche</i> sp.	2.8	3.8	60			
<i>Hydropsyche orris</i>	14.6	19.6	70	0.1	0.2	7
<i>Potamyia flava</i>	6.5	8.7	90			
Hydropsychidae ei ^b	26.7	35.9	100			
Other Families						
<i>Hydroptila waubesiana</i>				1.9	5.1	73
<i>Nectopsyche</i> sp.				1.2	3.3	47
Leptoceridae ei				0.5	1.3	33
TRICHOPTERA (Pupae)	1.5	2.0	50			
DIPTERA						
Empididae						
<i>Hemerodromia</i> sp.	0.1	0.1	10	0.4	1.1	33
Chironomidae						
<i>Chironomus</i> sp.				0.5	1.3	33
<i>Glyptotendipes</i> nr. <i>lobiferus</i>				21.1	57.5	100
<i>Microtendipes pedellus</i> gr. ^c	3.4	4.6	80			
<i>Polypedilum convictum</i>	4.1	5.5	60			
<i>Polypedilum scalaenum</i> gr.	1.8	2.4	60	0.1	0.2	7
<i>Rheotanytarsus</i> sp.	1.4	1.9	60			
<i>Thienemannimyia</i> gr.	4.5	6.0	100	0.1	0.2	7

^aImm. tub. w/o cap. = immature tubificids without capilliform chaetae

^bei = early instar, not identifiable beyond the indicated level

^cgr. = group, a complex of morphologically similar species or genera

TABLE 3.—Correlation analyses of epizoic invertebrate abundance or density and effective surface areas (ESA) of unionids collected from the Mississippi River. Total invertebrates = all the epizoic invertebrates collected

A. Invertebrate abundance; 1991 samples; analysis includes all unionids collected

Variables: Invertebrate abundance and unionid ESA

Statistic (n = 10)	Total invertebrates	Hydropsychid larvae	Chironomid larvae
r	0.78	0.73	0.81
r ²	0.61	0.54	0.66
P	0.008	0.016	0.004

B. Invertebrate abundance; 1992 samples; analysis includes all unionids collected

Variables: Invertebrate abundance and unionid ESA

Statistic (n = 15)	Total invertebrates	Chironomid larvae
r	0.64	0.57
r ²	0.40	0.32
P	0.011	0.027

C. Invertebrate abundance; 1992 samples; analysis includes only the species *Amblyma plicata*

Variables: Invertebrate abundance and unionid ESA

Statistic (n = 9)	Total invertebrates	Chironomid larvae
r	0.52	0.51
r ²	0.27	0.26
P	0.147	0.162

D. Invertebrate density; 1991 samples; analysis includes all unionids collected

Variables: Invertebrate density and unionid ESA

Statistic (n = 10)	Total invertebrates	Hydropsychid larvae	Chironomid larvae
r	0.44	0.40	0.27
r ²	0.19	0.16	0.07
P	0.207	0.257	0.458

E. Invertebrate density; 1992 samples; analysis includes all unionids collected

Variables: Invertebrate density and unionid ESA

Statistic (n = 15)	Total invertebrates	Chironomid larvae
r	0.17	0.19
r ²	0.03	0.04
P	0.540	0.500

plicata, which made up nine of the 15 unionids collected. The other unionids collected were four *Quadrula quadrula*, and one specimen each of *Fusconaia flava* and *Potamilis alatus*. Current velocities at the collection site near Crosby Slough were much less than those of the 1991 collection site. Although some current was apparent at the 1992 site, its velocity was less than 10 cm per sec.

Chironomid larvae were the numerical dominants on the unionids collected near Crosby Slough, rather than the hydropsychid larvae which were so abundant in the samples collected near Dubuque in 1991 (Table 1). Chironomid larvae made up 66% of the epizoic invertebrates in 1992. The species composition of the Chironomidae in 1992 was dissimilar from that collected in Dubuque. *Glyptotendipes* nr. *lobiferus*, a species not even present in the 1991 collections, contributed 87% of the chironomid larvae collected in 1992 and made up 57.5% of all the epizoic invertebrates (Table 2).

Only a single hydropsychid caddisfly larva was present in the 1992 collections; instead, larval caddisflies in the families Hydroptilidae, Leptoceridae and Polycentropodidae were present (Table 2). *Hydroptila waubesia* and *Nectopsyche* sp. were especially common.

Oligochaetes joined chironomid and caddisfly larvae as numerical dominants in the 1992 collection of epizoic invertebrates, making up 10% of the epizoic fauna. Three oligochaete families were present, including the Enchytraeidae, Tubificidae and Naididae. Naidids were especially diverse on the unionids, with seven species present. *Caenis* sp., *Dugesia tigrina* and larval *Hemerodromia* were also relatively common (Table 2).

Considerable variability in epizoic abundance was evident again in 1992; the maximum number of invertebrates collected from a single unionid was 98, while only eight invertebrates were collected from the shell surface of another unionid (Table 1). The mean number of invertebrates per unionid equaled 36.7 in 1992, with a mean density of 6367 epizoic invertebrates/m² of unionid ESA (Table 1). Mean ESA for the 1992 collection equaled 55.6 cm². Again in 1992, a positive correlation existed between total invertebrate abundance, as well as its principal constituent, larval chironomids and unionid ESA (Table 3, part B).

A total of 39 epizoic taxa were present on the 15 unionids collected in 1992. The maximum number of taxa present on a single unionid equaled 17 (Fig. 1), the minimum number was four, with the mode and median both equal to eight.

Unionid areas and number of epizoic invertebrate taxa.—Since the unionids were each distinct entities, we could view them as "islands in the stream." In the 1991 collection the largest unionid had an ESA that was approximately 14 times that of the smallest (ESA_{max.} = 164.9 cm², ESA_{min.} = 11.5 cm²), and number of epizoic invertebrate taxa varied from a minimum of two taxa to a maximum of 16 (Fig. 1). In 1992 the largest ESA of the unionids was about three times that of the smallest (ESA_{max.} = 99.2 cm², ESA_{min.} = 28.4 cm²), and the number of taxa per unionid varied from a minimum of four to a maximum of 17 taxa (Fig. 1).

We used correlation analyses to determine if ESA and number of epizoic taxa were related. In both 1991 and 1992 a strong positive correlation existed between the size (ESA) of the unionids and the number of taxa that had colonized them ($r = 0.78$ in 1991, $r = 0.77$ in 1992; Fig. 1). Therefore, ca. 61% (r^2) of the variability in the number of epizoic taxa in 1991, and 60% in 1992, was explained by the effect of ESA.

DISCUSSION

The total of 53 epizoic invertebrate taxa collected from the unionids over the two sampling occasions demonstrates their importance as substrates for epibenthic organisms. Human activities have dramatically increased the amount of hard surfaces in large rivers of the Mississippi River drainage. The revetting of riverbanks with riprap or articulated con-

crete mattress, and the placement of rock dikes (called wing dams in the UMR), lock and dam structures, and buoys in river channels have provided additional hard surfaces which are also colonized by epibenthic invertebrates. Before these artificial structures were added to rivers, the surfaces of snags, larger pieces of gravel, and unionids such as those investigated in this study sufficed as the available hard substrates.

The composition of epizoic invertebrates collected at the fast current site (Dubuque—1991) was clearly dissimilar from that collected from the slower waters of Crosby Slough in 1992; e.g., hydropsychid caddisflies dominated the 1991 collections but were almost completely absent from the 1992 samples (Tables 1 and 2). The dominance of hydropsychid caddisflies in fast current areas in large rivers and their absence from slow current areas is consistent with studies of hydropsychids in the UMR (Fremling, 1960), in artificial streams (Edington, 1968; Philipson, 1969), and in a small natural stream (Edington, 1968). Edington (1968) placed a baffle in a small stream, creating a reduced current. Counting the hydropsychid larvae before and after placement of the baffle, he observed a reduction from 125 to four larvae in a 0.19 m² (2 ft²) region behind the baffle in 43 h. In an experiment in the Ohio River, a large river of the Mississippi River drainage, Beckett and Miller (1982) showed that *Hydropsyche orris* larvae (the most common hydropsychid species on the UMR unionids collected in the present study) were abundant on hard substrates in fast currents, but were almost completely absent from identical substrates in slow current. Two of the most common chironomid taxa collected from the unionids in the strong current at Dubuque, *Polypedium convictum* and *Rheotanytarsus* sp., were also shown in the Ohio River experiment to be much more abundant on substrates in fast water than on surfaces in slow current (Beckett and Miller, 1982). Neither of these two chironomid species was present on the unionids collected in Crosby Slough's slack waters; instead, the chironomid *Glyptotendipes* nr. *lobiferus* was an overwhelming dominant. Interestingly, two of us (DCB and SAT) identified chironomid larvae collected in scrapings made in 1991 from the bottoms of boats moored in harbors in the UMR (part of a zebra mussel monitoring program); almost all of the larvae were *G.* nr. *lobiferus*. It is apparent that this chironomid species abundantly colonizes hard surfaces in slack current situations, regardless of whether the surface is the exterior of a unionid or a boat. The composition of the unionid epizoic fauna is therefore largely a function of the current velocities surrounding the unionids.

The unionid epifauna is not restricted to unionids, since these epizoic invertebrates can also be found on rocks, buoys, artificial substrates such as multiplate samplers (Beckett and Miller, 1982), and even boat hulls. However, this lack of faunal uniqueness does not diminish the importance of unionids as epibenthic substrates. As stated earlier, unionids have historically been a primary source of hard, clean substrate for epibenthic animals in our largest rivers, and still provide a large amount of permanently inundated, stable substrate. In rivers with sand or silt bottoms and little or no artificial hard substrates, unionids and snags provide the only appreciable large hard substrates.

The variation in abundance of epizoic invertebrates among unionids is largely a function of the amount of available surface area (ESA). ESA accounted for 61% (r^2 , see Table 3, part A) of the variability in total invertebrate abundance in 1991 and 40% (Table 3, part B) in 1992. Other factors that may account for the remaining variability include the heterogeneity in the shells' contours (some unionid species have pustulose shells, some have ridges and some are fairly smooth), the orientations of the unionids (some individuals are tilted laterally more than others), and the localized effect which may be exerted on current velocities near unionids by other bivalves immediately upstream. Since nine of the 15 unionids collected in 1992 were *Amblema plicata*, we did a correlation analysis between ESA and invertebrate abundance for only those nine animals. Such an analysis would keep shell contour

"constant," and might result in an improvement in r and r^2 . However, this analysis did not improve these statistics. In fact, r was less than it had been for the analysis which considered all the unionids, and was no longer significant at the 0.05 level (Table 3, part C). In this case, therefore, holding shell contour constant did not enhance the accounting for the variability in invertebrate abundance.

Since invertebrate abundance and ESA were strongly correlated in both years, it seemed possible that invertebrate density and ESA could be correlated as well. For example, since some unionids had small surface areas, perhaps arriving invertebrates (via drift) might have packed themselves in more densely. Conversely, it could be hypothesized that unionids with larger ESAs might have a denser epifauna since they tended to have larger overall surface areas and volumes, and would have dug deeper into the substrate; hence, they would be more stable during periods of faster currents associated with elevated river discharges. However, correlation analyses of ESA and total invertebrate density and its principal elements (hydropsychid caddisfly larvae and chironomid larvae in 1991 and chironomid larvae in 1992) revealed no significant relationships (Table 3, parts D and E). Therefore, although invertebrate abundance and ESA were correlated, invertebrate density and ESA were not.

The strong positive correlations between unionid surface area and number of epizoic invertebrate taxa (Fig. 1) are in accord with island biogeography theory (MacArthur and Wilson, 1967, *see also* Beeby, 1993, and Colinvaux, 1993), which postulates a positive relationship between island size and species richness. In island biogeography theory the equilibrium number of species on an island is a function of the size of the island and the distance of the island from the source of its colonists. In our study the effect of distance was nullified (within each sampling effort) since all of the unionid islands were essentially equidistant from the two possible colonization sources: (1) adult female insects swimming down from the surface and ovipositing on a unionid with subsequent instar development taking place on the same unionid, and more likely (2) invertebrates drifting onto the unionids from upstream. A massive number of drifting invertebrates continuously pass over riverine mussel beds (*e.g.*, approximately 400–500 million macroinvertebrates drift past a line across the lower Mississippi River per day, Beckett and Kasul, 1987) and hence no unionid is more distant from the colonization source than another. Our results are in accord with the theory that larger islands should have more species (taxa in our study) because they are bigger targets for immigrants and because extinction rates are lower on them. Certainly, larger unionid islands should be "hit" and then colonized more often by drifting invertebrates. In addition, since smaller unionid islands have fewer colonists, it is more likely that an individual emigrating (rejoining the drift) will cause that taxon to be lost ("become extinct") from that island.

At present the infestation rate of unionids by zebra mussels in the UMR above its confluence with the Illinois River remains low. In 1992 a sampling of unionids in Pools 4 and 13 of the UMR showed that only ca. 1% of the unionids had zebra mussels attached (Tucker *et al.*, 1993). Unfortunately, the percentage of unionids with attached zebra mussels appears to have increased in the UMR from 1992 to the present. In addition, the colonization of unionids by very large numbers of zebra mussels in portions of the Illinois River (K. D. Blodgett, pers. comm.) indicates that unionids in riverine habitats may be just as vulnerable to zebra mussels as they have been in the lacustrine habitats of Lake St. Clair and Lake Erie. Schloesser and Kovalak's (1991) report of a mean density of 6777 attached zebra mussels per unionid in a power plant's intake canal near Lake Erie indicates the potential effects of zebra mussels on the unionids and their epizoic fauna. Similar mean densities of zebra mussels (5496 zebra mussels per unionid) have been observed in parts of Lake St. Clair (Hebert *et al.*, 1991). Our study of epizoic fauna may have been very timely since a

massive colonization of unionids by zebra mussels may soon take place in North America's large rivers. Such an invasion would drastically alter the epizoic community on unionids. These alterations in the epifauna would occur first through competition between the native epizoic fauna and *Dreissena* for space and food, and ultimately, if the example of Lake St. Clair is followed (Hunter and Bailey, 1992), by virtual elimination of the unionid hosts.

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APPENDIX

A listing of all the taxa, and number of individuals in each taxon, present on the ten unionids collected in 1991 and the fifteen unionids collected in 1992 from the upper Mississippi River.

1991. CNIDARIA: *Hydra* sp.—4; TURBELLARIA: *Dugesia tigrina*—25; OLIGOCHAETA: Naididae: *Nais behningi*—1, unidentified naidid—1, Tubificidae: *Limnodrilus hoffmeisteri*—1, *Limnodrilus udekemianus*—1, immature tubificids without capilliform chaetae—2, Hirudinea (very small)—1; ISOPODA: *Caecidotea* sp.—1; HYDRACARINA—7; EPHEMEROPTERA: *Caenis* sp.—4, *Stenonema terminatum*—3, unidentified early instar Ephemeroptera—2; TRICHOPTERA: *Cheumatopsyche* sp.—28, *Hydropsyche orris*—146, *Potamyia flava*—65, early instar hydropsychid larvae—267, *Neotrichia* sp.—1, *Neotrichia* pupa—1, trichopteran pupae—14; COLEOPTERA: *Stenelmis* sp. (larva)—1, early instar elmid larva—2; DIPTERA: Empididae: *Hemerodromia* sp.—1, Chironomidae: *Ablabesmyia rhamphe* gr.—1, *Cryptochironomus* sp.—1, *Microtendipes pedellus* gr.—34, *Nanocladius distinctus*—2, *Nanocladius* nr. *rectinervis*—1, *Nanocladius* sp. (early instar)—1, *Parachironomus* sp.—1, *Polypedilum convictum*—41, *Polypedilum scalaenum* gr.—18, *Rheotanytarsus* sp.—14, *Thienemannimyia* gr.—45; BIVALVIA: *Musculium transversum*—1, very small bivalves—5.

1992. TURBELLARIA: *Dugesia tigrina*—9; OLIGOCHAETA: Naididae: *Nais bretscheri*—2, *Nais communis*—1, *Nais pardalis*—12, *Nais simplex*—6, *Nais variabilis*—8, *Pristina foreli*—2, *Pristina osborni*—1, Tubificidae: *Limnodrilus maumeensis*—1, *Limnodrilus udekemianus*—2, immature tubificids without capilliform chaetae—12, Enchytraeidae—7, unidentified oligochaete—1; Hirudinea: *Placobdella ornata*—1; HYDRACARINA—4; EPHEMEROPTERA: *Caenis* sp.—22, TRICHOPTERA: *Cyrnellus fraternus*—1, *Hydropsyche orris*—1, *Hydroptila waubesiana*—28, *Hydroptila* sp.—1, *Orthotrichia* sp.—2, *Nectopsyche* sp.—18, Leptoceridae early instars—7, *Polycentropus* sp.—1, early instar trichopteran larvae—27; COLEOPTERA: *Stenelmis* sp. (larva)—1, *Stenelmis* sp. (adult)—1; DIPTERA: Empididae: *Hemerodromia* sp.—6, Chironomidae: *Chironomus* sp.—7, *Cladotanytarsus mancus* gr.—4, *Cryptochironomus* sp.—4, *Dicrotendipes modestus*—2, *Dicrotendipes neomodestus*—4, *Dicrotendipes simpsoni*—2, *Endochironomus* sp.—2, *Glyptotendipes* nr. *lobiferus*—317, *Nanocladius distinctus*—1, *Parachironomus pectinatellae*—1, *Parachironomus monochromus*—5, *Paratanytarsus* sp.—1, *Polypedilum halterale* gr.—4, *Polypedilum scalaenum* gr.—2, *Procladius* sp.—1, *Thienemannimyia* gr.—1, early instar Chironominae—5, early instar Orthoclaadiinae—2, early instar Chironomidae—1.

LITERATURE CITED

- BECKETT, D. C. AND M. C. MILLER. 1982. Macroinvertebrate colonization of multiplate samplers in the Ohio River: the effect of dams. *Can. J. Fish. Aquat. Sci.*, 39:1622-1627.
- AND P. A. LEWIS. 1982. An efficient procedure for slide mounting of larval chironomids. *Trans. Am. Microsc. Soc.*, 101:96-99.
- AND R. L. KASUL. 1987. Vertical, horizontal, and diel distribution of invertebrate drift in the lower Mississippi River. Technical Report E-87-5, U.S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi. Available from National Technical Information Service, Springfield, Virginia.

- BEEBY, A. 1993. Applying ecology. Chapman & Hall, London. 441 p.
- BRINKHURST, R. O. 1986. Guide to the freshwater aquatic microdrile oligochaetes of North America. *Can. Spec. Publ. Fish. Aquat. Sci.*, 84:1-259.
- BURCH, J. B. 1975. Freshwater sphaeriacean clams (Mollusca: Pelecypoda) of North America. Malacological Publications, Hamburg, Michigan. 96 p.
- COLINVAUX, P. 1993. Ecology 2. John Wiley & Sons, Inc., New York. 688 p.
- EDINGTON, J. M. 1968. Habitat preference in net-spinning caddis larvae with special reference to the influence of water velocity. *J. Anim. Ecol.*, 37:675-692.
- EPLER, J. H. 1992. Identification manual for the larval Chironomidae (Diptera) of Florida. Florida Department of Environmental Regulation, Tallahassee. 302 p.
- FREMLING, C. R. 1960. Biology and possible control of nuisance caddisflies of the upper Mississippi River. *Agric. Home Econ. Exp. Stn. Iowa State Univ. Res. Bull.*, 483:856-879.
- HEBERT, P. D. N., C. C. WILSON, M. H. MURDOCH AND R. LAZAR. 1991. Demography and ecological impacts of the invading mollusc *Dreissena polymorpha*. *Can. J. Zool.*, 69:405-409.
- HUNTER, R. D. AND J. F. BAILEY. 1992. *Dreissena polymorpha* (zebra mussel): colonization of soft substrata and some effects on unionid bivalves. *Nautilus*, 106:60-67.
- KENK, R. 1976. Freshwater planarians (Turbellaria) of North America. U.S. Environmental Protection Agency, Cincinnati, Ohio. 81 p.
- KLEMM, D. J. (ED.). 1985. A guide to the freshwater Annelida (Polychaeta, naigid and tubificid Oligochaeta, and Hirudinea) of North America. Kendall/Hunt Publishing Co., Dubuque, Iowa. 198 p.
- LEWIS, P. A. 1974. Taxonomy and ecology of *Stenonema* mayflies (Heptageniidae: Ephemeroptera). U.S. Environmental Protection Agency, Cincinnati, Ohio. 81 p.
- MACARTHUR, R. H. AND E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey. 203 p.
- MACKIE, G. L. 1991. Biology of the exotic zebra mussel, *Dreissena polymorpha*, in relation to native bivalves and its potential impact in Lake St. Clair. *Hydrobiologia*, 219:251-268.
- MCMAHON, R. F. 1991. Mollusca: Bivalvia, p. 315-399. In: J. H. Thorp and A. P. Covich (eds.). Ecology and classification of North American freshwater invertebrates. Academic Press, San Diego, Calif.
- MILLER, A. C. AND B. S. PAYNE. 1992. The effects of increased commercial navigation traffic on freshwater mussels in the upper Mississippi River: 1990 studies. Technical Report EL-92-93, U.S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi. Available from National Technical Information Service, Springfield, Virginia.
- AND —. 1993. Effects of increased commercial navigation traffic on freshwater mussels in the upper Mississippi River: 1991 studies. Technical Report EL-93-1, U.S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi. Available from National Technical Information Service, Springfield, Virginia.
- MOORE, S. G. (ED.). 1991. Zebra mussel found in the upper Mississippi River near La Crosse, Wisconsin. *Dreissena polymorpha* Information Review, vol. 2, no. 5:5. Zebra Mussel Information Clearinghouse, New York Sea Grant Extension, Brockport, New York.
- PECKARSKY, B. L., P. R. FRAISSINET, M. A. PENTON AND D. J. CONKLIN, JR. 1990. Freshwater macroinvertebrates of northeastern North America. Cornell University Press, Ithaca, New York. 442 p.
- PENNAK, R. W. 1978. Fresh-water invertebrates of the United States. John Wiley & Sons, Inc., New York. 803 p.
- PHILIPSON, G. N. 1969. Some factors affecting the net-spinning of the caddisfly *Hydropsyche instabilis* Curtis (Trichoptera: Hydropsychidae). *Hydrobiologia*, 34:369-377.
- SCHLOESSER, D. W. AND W. P. KOVALAK. 1991. Infestation of unionids by *Dreissena polymorpha* in a power plant canal in Lake Erie. *J. Shellfish Res.*, 10:355-359.
- SCHUSTER, G. A. AND D. A. ETNIER. 1978. A manual for the identification of the larvae of the caddisfly genera *Hydropsyche* Pictet and *Symphitopsyche* Ulmer in eastern and central North America (Trichoptera: Hydropsychidae). U.S. Environmental Protection Agency, Cincinnati, Ohio. 129 p.
- STOLZENBURG, W. 1992. The mussels' message. *Nature Conservancy*, Nov./Dec. 1992:16-23.

- THIEL, P. A. AND A. W. FRITZ. 1993. Mussel harvest and regulations in the upper Mississippi River system, p. 11-18. *In*: K. S. Cummings, A. C. Buchanan and L. M. Koch (eds.). Conservation and management of freshwater mussels. Proceedings of an Upper Mississippi River Conservation Committee (UMRCC) symposium, 12-14 October 1992, St. Louis, Missouri. Upper Mississippi River Conservation Commission, Rock Island, Illinois.
- THORP, J. H. AND A. P. COVICH (EDS.). 1991. Ecology and classification of North American freshwater invertebrates. Academic Press, Inc., San Diego, Calif. 911 p.
- TUCKER, J. K., C. H. THEILING, K. D. BLODGETT AND P. A. THIEL. 1993. Initial occurrences of zebra mussels (*Dreissena polymorpha*) on freshwater mussels (family Unionidae) in the upper Mississippi River system. *J. Freshwater Ecol.*, 8:245-251.
- WIEDERHOLM, T. (ED.). 1983. Chironomidae of the Holarctic region. Keys and diagnoses. Part 1. Larvae. *Entomol. Scand. Suppl.* 19:1-457.
- WIGGINS, G. B. 1977. Larvae of the North American caddisfly genera (Trichoptera). University of Toronto Press, Toronto, Ontario. 401 p.
- WILLIAMS, J. D., M. L. WARREN, K. S. CUMMINGS, J. L. HARRIS AND R. J. NEVES. 1993. Conservation status of freshwater mussels of the United States and Canada. *Fisheries*, 18:6-22.

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