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Effects of drought on freshwater mussels and instream habitat in Coastal Plain tributaries of the Flint River, southwest Georgia (July-October, 2000)

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Executive Summary

Habitat conditions (water depth, water temperature, dissolved oxygen and flow velocity) and mussel survivorship were monitored weekly at nine locations in the lower Flint River Basin during extreme drought conditions (June-October 2000). Sites ranged in size from d-link magnitudes of 23 to 617.

Stream habitat and mussel population responses to drought were not uniform across study sites. At sites on Spring and Chickasawhatchee creeks, water flow ceased, or the stream bed dried, and dissolved oxygen concentrations were extremely low (< 5 mg/L) for extended periods. Weekly mussel mortality as high as 76% was observed at these locations. In contrast, sites on Muckalee and Ichawaynochaway creeks experienced less severe reductions in flow and dissolved oxygen, and mussel mortality was correspondingly low (i.e., weekly mussel mortality averaged 2.8% during the entire survey period).

Flow velocity and dissolved oxygen were highly correlated to mussel mortality. Unionid mortality increased when flow velocity at the substrate surface fell below 0.01 m/s or when dissolved oxygen concentrations fell below 5 mg/L. *Elliptio crassidens*, *Lampsilis subangulata*, *Medionidus pencilatus* and *Pleurobema pyriforme* experienced highest mortality under hypoxic conditions (i.e., DO<5mg/L). *Elliptio complanata* and *Villosa vibex* had lowest mortality under hypoxia and withstood long-term (>20 d) emersion. Overall, riffle-dwelling and rare mussel species experienced greater mortality in relation to drought conditions than widespread, common species.

We observed higher habitat impairment at sites with lower d-link magnitudes, i.e., generally smaller streams. Smaller streams also demonstrated a decrease in diversity, evenness and richness during the study period.

Observed mussel behavioral responses to drought (i.e., movement and mantle exposure behavior) suggest that several habitat factors might act to mediate the effects of drought on mussel mortality. Among these is the presence of large woody debris in streams, which may create small, well-shaded depressions that could serve as mussel micro-refugia during drought. In addition, instream aquifer discharge may be key to providing water, cooler stream temperatures, or increasing flow stability during drought conditions.

These results strongly underscore the need for instream flow protection that not only ensures proper water levels in stream channels, but also considers minimum dissolved oxygen and flow velocity conditions. The presence of diverse mussel assemblages observed in medium sized sites coupled with the high levels of mortality observed at these sites suggest that moderately sized stream reaches (i.e., d-link magnitudes from 80 to 130) may be priority areas for mussel conservation and protection efforts in the region.

These data also highlight new avenues for research that may be key to management concerns for mussel fauna throughout the Southeast. In particular, we recommend further research to determine minimum flow and dissolved oxygen requirements for sensitive taxa, and studies to determine the independent effects of low flow velocity and low dissolved oxygen conditions on mussel mortality. Additional effort should also be focused on quantifying non-lethal effects of drought, such as reduced reproductive capacities, reduced glycogen stores, and lowered growth rates. Potentially,

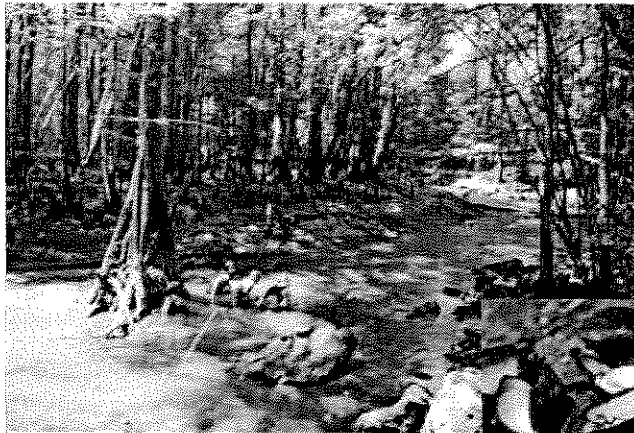
these drought-related responses could affect the viability of mussel populations in the lower Flint River Basin. Finally, studies designed to assess post-drought responses of mussel populations are critical to more fully understanding the long-term effects of drought on these assemblages.



Spring Creek unionids
June, 2000



Low flow conditions in
Kinchafoonee Creek near Preston, GA
July, 2000



Stagnant stream reach
Chickasawhatchee Creek
Baker County, GA
July, 2000

Elliptio crassidens
found dead during monitoring
Chickasawhatchee Creek
Baker County, GA,
July, 2000



Emersed mussel survey quadrat
(corners marked by yellow flags)
Spring Creek near Damascus, GA
August, 2000

Live *Medionidus pencilatus*
Chickasawhatchee Creek
near Albany, GA
July, 2000



Mussel trails
July, 2000



Introduction

Streams and rivers of the southeastern US were the center of unionid speciation and radiation 150 million years ago (Butler 1989) and today are home to the most diverse assemblages of freshwater mussels found anywhere in the world (Bogan 1993). However, unionids are now among the most endangered of North American fauna, with about 70% of the group considered endangered, threatened or extinct (Neves et al. 1997).

The tributary streams of the Coastal Plain portion of the Flint River Basin (lower FRB), southwest Georgia, historically had a diverse mussel fauna, including at least 14 genera and 29 species, six of which were endemic to (i.e., found only in) the Flint River basin (Clench and Turner 1956, Johnson 1970). Surveys conducted during the past decade have found that only 22 native bivalve species persist in the FRB (Brim Box and Williams 2000). Of these, three species are federally Endangered (*Lampsilis subangulata*, *Medionidus pencillatus*, *Pleurobema pyriforme*), one species is federally Threatened (*Elliptio sloatianus*), and an additional six taxa (*Elliptio arctata*, *Elliptio purpurella*, *Lampsilis straminea claibornensis*, *Pyganadon cataracta*, *Quincuncina infucata*, *Villosa villosa*) have been identified as special concern species (Brim Box and Williams 2000).

Deforestation, intensive upland agricultural development, river impoundments, and declines in native fish species have adversely affected mussel diversity and abundance in the lower FRB (Brim Box and Williams 2000). Infrequent natural disturbances such as floods and droughts may further affect mussels by causing physiological stress or death to individuals or populations already stressed by habitat alteration.

During the 1999 and 2000 water years (October 1998-September 2000), south Georgia experienced record drought conditions (USGS 2000). Numerous streams and rivers in the region flowed at record-low levels, and many previously perennial stream segments were dried completely or reduced to intermittent chains of pools. Human use of aquatic resources in the region is thought to have compounded the problems associated with unusually low precipitation levels. In particular, underground aquifer water withdrawals may have exacerbated streambed drying during drought, especially where stream baseflow was predominantly fed by shallow aquifer discharge (Phillip N. Albertson and Lynn J. Torak, Hydrologists, U.S. Geological Survey, Atlanta, Georgia, written communication, 2000).

Extended drought causes changes in stream water depth, velocity, dissolved oxygen (DO), and water temperature. Drought impacts on physical habitat are frequently incremental and prolonged, requiring mussels to endure extended exposure to suboptimal conditions. Early in a drought cycle, decreases in water depth and flow velocity affect food and oxygen delivery to mussels and expose them to high concentrations of organic and inorganic pollutants, normally diluted by greater flow volume. As drought conditions persist, mussels face greater predation pressures, hypoxia (low levels of dissolved oxygen in water, i.e., < 5mg/L), increasing water temperature, and ultimately, anoxia (no dissolved oxygen in water) or emersion (stranding out of water and exposure to air). Despite adaptations to a wide range of environmental conditions, including periodic changes in substrate stability, water turbidity, temperature, dissolved oxygen, and water depth, most mussels are considered sensitive to pollution, intolerant of extreme

disturbance, and unable to withstand low DO and high temperature levels (for summary, see Fuller 1974).

Mussels may suffer lethal and non-lethal impacts from drought-related habitat change. Increases in stream temperature may shorten the period of glochidial encystment (attachment of larval mussels to fish gills); slow righting, burrowing and movement responses; and increase oxygen consumption (Young 1911, Bartsch et al. 2000). Low oxygen concentration impairs respiration, slows growth, reduces glycogen stores and may inhibit reproduction (for summaries, see Fuller 1974). Decreased flow velocity during drought may be insufficient to suspend glochidia (larval mussels) and superconglutinates (larval mussel masses), resulting in reproductive failure (M. Freeman, personal communication). In addition, reduced flow conditions may result in mussel stranding and emersion. Mortality during drought may result from respiratory failure, desiccation of soft tissues, predation, or the accumulation of toxic levels of anaerobic metabolic wastes (Holland 1991, Byrne and McMahon 1994).

Several mechanisms for enduring drought-related environmental change have evolved among the Unionidae. Some freshwater bivalves have the capacity to lower metabolic activity in response to temporary temperature changes and dissolved oxygen stress (e.g., *Elliptio complanata*, *Utterbackia imbecilis*, *Pyganadon grandis*) (McMahon 1991, Bayne 1967, Sheldon and Walker 1989, Burky 1983). At least one freshwater species, *Anodonta implicata*, can produce metabolic oxygen in sufficient quantities to survive anoxic surroundings (Eddy and Cunningham 1934). Upon emersion, other Unionidae may respire through “mantle exposure behavior” (MEB), a gaping behavior that permits the exchange of aerial gases through a mucus-sealed mantle margin (McMahon 1991). Others are able to switch from aerobic to anaerobic respiration during times of anoxia (Holland 1991). A final unionid adaptation is the ability to rapidly migrate deep into sediments to avoid emersion (White 1979).

The objective of this study was to assess the effects of the 2000 drought on unionid mortality in the lower FRB by quantifying mussel community and habitat changes at selected stream sites. We sought to identify habitat factors related to mussel mortality, and assess the differential impacts of habitat changes on individual species and mussel functional groups. We believe this study to be the first broad-scale assessment of unionid community responses to record drought.

Methods

1.) Study Site and Climatic Conditions

The lower FRB lies predominantly in the Dougherty Plain district of the Coastal Plain physiographic province, a region underlain by a shallow carbonate aquifer. Water exchange between stream and aquifer systems in the Dougherty Plain is frequent, but extremely variable in time and space (Hicks et al. 1987, Albertson and Torak 2000). Typically, aquifer discharge supplies the majority of base flow during summer months, when evapotranspiration substantially reduces overland flow into streambeds (Hicks et al. 1987). Because of the high degree of exchange between aquifer and stream systems, large-scale aquifer withdrawals have the potential to reduce drought-period streamflow in the region (Torak and McDowell 1996).

During May-October, 2000, statewide streamflow levels averaged 50% of normal (i.e., 25th percentile of historic flows). The lowest flows occurred in the lower FRB, where water levels were 1-34% of historic average monthly flows (i.e., in 0.05-17th percentile of historic flows). During this period, all USGS stream-gauging stations in the lower FRB reported new monthly minimums for one or more months during the period (USGS 2000). At numerous locations throughout the basin, reaches of normally perennially flowing streams dried completely.

2.) Survey Methods

Between July 1 and October 31, 2000, unionid survivorship, water temperature, water depth, and dissolved oxygen (DO) were tracked at nine survey sites in tributary streams of the lower FRB (Figure 1). Sites represented a gradient of functional stream sizes, from d-link magnitudes of 23 to 617.

Drought monitoring sites were initially selected to include three stream segments from each of three categories of sensitivity to groundwater pumping, as designated in a study by the U.S. Geological Survey (Phillip N. Albertson and Lynn J. Torak, Hydrologists, U.S. Geological Survey, Atlanta, Georgia, written communication, 2000). Later revisions to these classifications altered the balance of our study design, and further analysis of the impacts of water withdrawals were not undertaken.

Sites represented a gradient of functional stream sizes, from d-link magnitudes of 23 to 617. D-link magnitude was determined by counting the number of first-order streams draining into the point immediately below the first confluence downstream from each survey reach (Osborne and Wiley 1992). First order streams were counted using 1:100,000 Digital Line Graphs (DLGs, US Geological Survey). (D-link magnitude was selected as a measure of stream size, because unlike stream order or link magnitude metrics, this metric approximates the functional size of a stream by adjusting for the effect of adjacent waterways. For example, the d-link magnitude for streams draining directly into large rivers is the sum of the link magnitude of that stream plus the link magnitude of the adjacent large river.)

All survey sites were located at stream segments with predominantly lotic conditions (i.e., flowing water and stream habitat) during 1999 surveys, and were not observed to have standing water or lentic (i.e., lake-like) conditions prior to 2000. Baseline habitat data on stream canopy cover, incision, and substrate types were collected during summer and fall 1999 as part of a basin-wide study of mussel communities (Johnson in prep.).

In July 2000, 3 to 5 4-m² quadrats were established at high-density mussel areas within each of the monitoring sites. Quadrats were placed 100-300 m upstream from bridge crossings. At the start of the monitoring period, all dead mussels were removed from the quadrats, and all live mussels within the quadrats were identified and counted. In some instances, in order to increase the number of study subjects in the survey quadrats, additional mussels, found in similar habitats adjacent to the quadrats, were moved into the quadrats.

Sites were surveyed every 7 to 11 days, at which time unionid counts, DO, and water depth measurements were made at each quadrat. Mussels were found by visually searching and grubbing (i.e., sediments to a depth of 15 cm were sieved with fingers). All live and dead mussel shells were counted and identified to species, except *Elliptio*

complanata and *Elliptio icterina*. These species were classed together as *E. complanata/icterina* because of the difficulty in distinguishing them in the field. Dead shell material was classified as "dead-no apparent injury" if the shell was intact upon finding it, or "dead-eaten by animal" if the shell had been cracked or crushed. Live mussels were returned to the substrate in the quadrat. Survey time per quadrat varied, depending on the effort required to thoroughly search the substrate. Cobble substrate and high or rapid flow conditions generally required longer search times. Water depth and dissolved oxygen were measured using a standard surveying rod and a Sentry Oxygen Meter (Sentry Products, Milton, DE) at the corners and center of every quadrat. Water velocity was initially visually assessed and assigned to one of four categories: no flow, slow, moderate, or fast. Beginning in late August, observations of water flow were replaced by electronic flowmeter (FLO-MATE, Marsh-McBirney, Inc., Frederick, MD) velocity measurements at the streambed and near the water surface of every quadrat. Temperature was recorded at each site every two hours throughout the study period using HOBO XT temperature loggers (Onset Instruments, Pocasset, MA). Observational data on water clarity/turbidity, mussel predation, movement patterns, and depth distributions were also recorded.

3.) *Data Analysis*

Two measures of unionid community mortality were employed for the following analyses. "Weekly unionid mortality" was calculated as the ratio of dead mussels (having no apparent injury; therefore presumed to have died from causes other than predation) to all live and dead unionids found per site (in all survey quadrats) for each survey date. The "cumulative unionid mortality" for each survey date was calculated as the cumulative total of dead (no injury) mussels found in all survey quadrats (i.e., all dead mussels up to and including the current survey date) divided by the sum of all live mussels found in the survey quadrat on the current survey date plus the cumulative total of dead.

a.) Habitat conditions and mussel mortality across monitoring sites

Quadrat habitat data and mussel mortality rates were assessed at each site using graphical analysis. Average quadrat habitat measurements (temperature, bottom velocity, DO and water depth) were determined for each survey date. Line graphs of mean habitat values were then superimposed on a bar graph of weekly unionid mortality on successive survey dates to assess the effects of different environmental factors on mussel survivorship. An additional plot comparing habitat data and the number of live, injured and non-injured dead animals was also prepared for each site. Scatterplots of selected habitat parameters were also visually assessed to identify correlated variables and patterns of relationships among habitat variables.

b.) Unionid responses to dissolved oxygen, depth, velocity and temperature fluctuations

Scatterplots were used to visually ascertain the relationship of weekly unionid mortality to water depth, DO, temperature, and bottom velocity measurements. Water depth, DO, temperature, and bottom velocity data used for the scatterplots represented mean values of the quadrat measurements for each survey site and date.

The relationship of DO and individual species mortality was assessed by comparing weekly mortality associated with DO concentrations below 5 mg/L and above

5 mg/L for each species. A 5 mg/L threshold was selected because graphical analysis suggested increasing mortality below this level. Wilcoxon rank-sum tests were used to detect significant differences in mortality between the two DO concentration levels.

Ten taxa were omitted from species-level analyses of hypoxia responses.

Observational counts of these species were too low (*Villosa villosa*, *Lampsilis teres*, *Elliptoides sloatianus*, *Pyganadon cataracta*, *Strophitus subvexus*, *Megalonais nervosa*, *Elliptio arctata*), or study specimens were only exposed to DO conditions above 2 mg/L, precluding assessment of mortality under a full range of hypoxic conditions (*Elliptio purpurella*, *Quincuncina infucata*, *Lampsilis straminea claibornensis*).

To compare DO and mortality among different mussel functional groups, all species found during the study were grouped according to assemblage types (i.e., riffle, pool, rare and common species, *sensu* Johnson in prep.) and Wilcoxon rank-sum tests were again used to compare differences in mortality between DO levels above and below 5 mg/L.

c.) *Habitat and mortality differences among stream size classes*

ANOVA (Proc ANOVA, SAS Institute 1985) was used to test differences in habitat conditions among three stream size classes. Sites were evenly distributed among the stream size classes based on their d-link magnitudes. Parameters tested included flow stability (the maximum water level difference during the study period / average mid-channel depth), bottom velocity, cumulative mussel mortality, dissolved oxygen, and temperature. Species were also grouped according to habitat association types and mussel assemblage mortality, and changes in relative abundance were compared among sites in each size category using bar graphs.

Results

1.) *Habitat conditions and mussel mortality across monitoring sites*

Sites represented a range of geomorphic types found in the lower FRB (Table 1). Sand, cobble and clay composed most of the substrate at the study sites, which ranged in average mid-channel depth from 0.4 to 1.17 m. Stream segments varied in size and canopy openness, and represented deeply incised streams as well as shallow, broad streams with large adjacent floodplains (Table 1).

A total of 19 unionid species were observed during the study period. All sites supported relatively diverse species assemblages during the 1999 surveys (Table 2), although the number of species observed in the 2000 study quadrats at each site ranged from 2 to 9 species. The predominant assemblage types at the survey sites included riffle, common and rare taxa. A few pool-inhabiting individuals were found during the study, however their numbers did not exceed 1 or 2 individuals per study site. During the survey period, the number of unionids observed at each monitoring site averaged 116 and ranged from 16 to 302 mussels. A site by site summary of habitat conditions and weekly mussel mortality during the survey period is provided in Appendix 1 and Figures A1-A9.

Site habitat conditions and mussel survivorship varied widely in response to drought (Tables 2-3). Several large-stream sites on Ichawaynochaway and Muckalee creeks (e.g., sites 91-009, 91-020, 99-003) experienced lower than average flow conditions, but DO, bottom velocity and water temperatures apparently did not reach

critical limits for mussels, and cumulative unionid mortality was relatively low, ranging from 13 to 27% (Table 2). Conversely, sites on Chickasawhatchee (site 91-010) and Spring Creek (sites 92-070 and 97-090) were exposed to extreme habitat fluctuations, including dessication, standing water, hypoxia, and high water temperatures (up to 29.5 °C). Cumulative mortality at these sites ranged from 14 to 93% (Table 2).

There was a strong nonlinear relationship between bottom velocity and dissolved oxygen (Figure 2). Dissolved oxygen dropped below 5 mg/L when bottom velocity approached 0 m/s ($r^2 = 0.75$; $p < 0.0001$). Other habitat variables were not significantly correlated.

2.) Unionid responses to dissolved oxygen, depth, velocity and temperature fluctuations

Unionid communities demonstrated a range of responses to changes in measured habitat parameters. Water depth and temperature did not appear to be related to unionid survival (Figures 3 & 4). Mussels, both live and dead, were most commonly found at depths between 20 and 40 cm, accounting for the somewhat higher mortality levels in the middle depth ranges (Figure 3). The unusual peak in mortality at water temperatures between 24 and 26 °C was likely an artifact of concentrated mortality during early summer months, when temperatures typically fluctuated in that range (Figure 4).

Flow velocity at the substrate surface was strongly related to unionid survival. Weekly unionid mortality increased dramatically when flow velocity dropped below 0.01 m/s (Figure 5).

Low DO, which occurred during low flow periods (Figure 2), was also associated with high weekly unionid mortality (Figure 6). Between 0 and 3 mg/L, mortality ranged from 0 to 76%. Between oxygen concentrations of 3 and 5 mg/L, mortality fluctuated between 0 and 24%. At DO levels above 5 mg/L, mortality ranged from 0 to 13%.

Species-level mortality under declining DO conditions varied greatly among species. Two species, *Elliptio complanata/icterina* and *Villosa vibex* survived complete emersion for at least 20 days, and were observed live in hypoxic water for up to 110 days (Table 4). In contrast, one species, *Elliptio crassidens*, experienced an average mortality rate of 82% under hypoxia.

The Wilcoxon test for differences in individual species mortality between DO concentration levels above and below 5 mg/L demonstrated a strong relationship between hypoxia ($DO < 5 \text{ mg/L}$) and elevated mortality (Table 4) in several species. Average species mortality ranged from 0% to 82% when DO concentrations were below 5 mg/L, while mortality ranged from 0.5% to 27% when DO was above 5 mg/L. The species with the highest mortality when exposed to DO concentrations below 5 mg/L included two federally Endangered species (*Lampsilis subangulata*, *Medionidus pencillatus*) and one riffle-dwelling species, *E. crassidens*. A third Endangered species, *Pleurobema pyriforme*, demonstrated moderate, but significantly higher, average mortality (15%) when DO was below 5 mg/L. Several taxa (*E. complanata/icterina*, *V. vibex*, *Villosa lienosa*) had significantly higher mortality at DO concentrations below 5 mg/L, but average mortality was always less than 10%. Mortality rates in two species (*Toxolasma paulus* and *Uniomermis carolinianus*) were not related to DO.

Among assemblage types, riffle-dwelling species (including *E. crassidens*, *Elliptio arctata*, *Megalonais nervosa*) demonstrated the highest average mortality (53%) in relation to hypoxia (Table 5, Figure 7). As a group, rare species (*Lampsilis straminea*

claibornensis, *L. subangulata*, *P. pyriforme*, *M. pencilatus*, *Elliptio purpurella*, *Quincuncina infucata*) mortality averaged almost 35% under DO levels below 5 mg/L, and common species (*E. complanata/icterina*, *T. paulus*, *U. carolinianus*, *V. vibex*) average mortality was approximately 9%.

3.) *Habitat and mortality differences among stream size classes*

Habitat conditions and mortality were not significantly different among stream size categories (Table 6, Figure 8). However, streams generally demonstrated trends of greater habitat impairment with smaller stream size (Figure 8); dissolved oxygen was lower and flow stability decreased as stream size decreased. Cumulative unionid mortality was not significantly different among stream size categories, but was generally higher in larger streams.

Unionid mortality demonstrated strong patterns of response when mussels were grouped by assemblage types (Figure 9). Rare assemblage type cumulative mortality declined from small to large streams. No riffle-type species were found in small streams, but the medium-sized stream experienced much higher cumulative riffle species mortality than large streams. Common species cumulative mortality was highest in large sites and lowest in small sites.

Shifts in assemblage composition from the start to the end of the survey period varied among size categories (Figure 10). At medium-sized sites, common species relative abundance significantly increased, concomitant with a general decrease in rare species and a significant decrease in riffle species relative abundance. At small and large sites, changes in relative abundances of species groups during the monitoring period were not significantly different. Overall, diversity, evenness and richness appeared to decline at medium and small sites during the study period, while increasing slightly at large sites (Figure 11).

4.) *Observational notes*

We observed several mussel behavioral responses to drought conditions. Critical DO (< 5 mg/L) and temperature (28-30 °C) levels triggered adaptive responses such as mantle exposure behavior and burial. Similar conditions increased mussel movements, as evidenced by numerous mussel trails circling in small, isolated pools or side channels where flow had ceased. Occurring concurrently were greater fluctuations in quadrat species composition and abundance. (These events were noted particularly at sites 92-070 and 97-090.) We believe that these behaviors were evidence of mussel movements in search of favorable habitat conditions. Mussel trails were rarely observed when habitat conditions were stable; at such times, quadrat species composition was more constant, presumably because we were observing the same individuals week after week.

We also found that during drying conditions (particularly at site 92-070) mussels tended to converge in small, well-shaded pool depressions created by large woody debris. Some species seemed more likely to bury deeply (e.g., *T. paulus*, *Lampsilis teres*, *U. carolinianus*) in response to unfavorable conditions. Other species remained on the substrate surface when dissolved oxygen dropped below 3-4 mg/L (e.g., *L. subangulata*, *L. straminia claibornensis*). On several occasions, we observed these mussels submerged in water, exposing mucus-sealed mantle surfaces in what appeared to be mantle exposure

behavior. (Mussels did not clamp shut when handled by observers, but the adductor muscle was still holding shells firmly in place.)

We observed one specimen of *L. subangulata* extruding a superconglutinate that lay settled on the substrate surface. Flow velocity appeared to be inadequate to suspend the superconglutinate, making it unlikely that the appropriate host fish, largemouth bass (*Micropterus salmoides*), would strike at it.

At sites where stream flow decreased rapidly, we noted the greatest mortality in shallow side channels and on topographic highs in the streambed. At several sites, we also observed a pulse in mortality following rainfall events that suddenly raised water levels and flow velocity.

In some locations, raccoon predation was extremely high when water became shallow and mussels were easily visible from the surface (especially sites 97-090 and 91-020). Raccoons tended to prey upon thin-shelled smaller species such as *V. lienosa* and *V. vibex*, attacking mussels by cracking the shell at the mantle margin of the posterior end and consuming the soft internal organs.

We also noted that the presence of high densities of nonnative *Corbicula spp.* seemed to exacerbate hypoxic conditions (most notably at site 91-010). *Corbicula* die relatively quickly in hypoxic water and are considered intolerant to hypoxia (McMahon 1979). In sufficient quantities, bacterial decay of soft organs may have driven dissolved oxygen levels down lower or more quickly than would have occurred in the absence of *Corbicula*. In addition, under hypoxic conditions, *Corbicula* may compete with unionids for limited supplies of dissolved oxygen.

Finally, in addition to observing large variability in mussel mortality among sites, we recorded high spatial variability in mortality within sites. Frequently, mussels located near springs or in flowing sections of stream survived drought conditions better than those found in shallow, isolated beds on stream margins, or in stagnant pools.

Discussion

Drought during summer and fall, 2000, had significant impacts on observed mussel populations in the lower Flint River Basin. However, survey sites experienced great variability in habitat conditions, and impacts to mussel communities ranged from minimal apparent change to high mussel mortality. The most stressful period for mussels at all sites occurred during early June through mid-July, when streamflows were at their lowest, and ambient air temperature, evapotranspiration, and water use were at their highest levels. During this period, we observed weekly mussel mortality as high as 76%. At least-impacted sites, weekly mussel mortality averaged 2.8% during the entire survey period. Differences in drought impacts among sites may be due to differences in stream size, precipitation, groundwater removal, aquifer flow, and surface water removal.

Neither water temperature nor water depth was strongly related to mussel mortality under drought conditions. The lack of correlation between water depth and mortality may be because depth of flow does not directly affect mussel physiology. However, water depth can affect susceptibility to predators, water temperature, velocity and dissolved oxygen levels, and therefore may play an indirect role in mussel survival. Water temperature likely played an indirect role in mussel survival by regulating dissolved oxygen levels.

Across survey sites, unionids demonstrated patterned responses to changes in flow velocity and dissolved oxygen. Mortality among freshwater mussels increased as flow velocity at the substrate approached 0 m/s. This response is likely due to the lack of sufficient flow conditions to properly aerate gill surfaces and aerate stream water. As demonstrated in Figure 2, dissolved oxygen conditions drop below 5 mg/L when flow velocity is near 0 m/s.

Dissolved oxygen was the habitat variable most strongly correlated to weekly unionid mortality during the 2000 drought in the lower FRB. As DO levels fell below 5 mg/L, the upper range of weekly unionid mortality increased steadily (Figure 6). Maximum recorded mortality during one survey visit was 76%, occurring when DO measured 1.13 mg/L. The broad range in weekly mussel mortality (0-76%) observed under low DO conditions may be related to adaptive responses such as mantle exposure behavior, burial, and anaerobic respiration, which varied by mussel species. Moreover, the mussel community at each site comprised different species, each of which had different sensitivities to hypoxia and other physical and chemical conditions. For example, site 97-090 on Spring Creek consisted of species of the common assemblage type, and experienced much lower mortality than site 91-010 on Chickasawhatchee Creek, which contained a large proportion of rare assemblage species at the beginning of the drought. Both sites experienced severe drought conditions. Quadrats located at site 97-090 on Spring Creek fluctuated between drying and hypoxic and anoxic standing water through most of the drought, and cumulative unionid mortality was only 46%. Quadrats at site 91-010 on Chickasawhatchee Creek were located in anoxic and hypoxic water 30-60 cm deep through most of the drought, but cumulative unionid mortality was 93%. Thus, differences in unionid mortality at sites experiencing similar drought conditions could be attributed to the differences in species composition at the survey sites.

Assessments of species-specific responses to DO fluctuations demonstrate that the three Endangered species in the lower FRB, *Lampsilis subangulata*, *Medionidus pencillatus*, and *Pleurobema pyriforme*, and one riffle species, *Elliptio crassidens*, suffered the highest mortality under low DO conditions (Table 4). Species that suffered the lowest mortality under low DO conditions included *Elliptio complanata/icterina*, *Villosa lienosa*, *Villosa vibex* and *Uniomerous carolinianus*. Since we did not observe all species responses to a range of DO, our data still leave gaps in understanding species response to hypoxia. In particular, we were not able to assess the relationship of DO fluctuations to special concern species, *Elliptio purpurella* and *Quincuncina infucata*, or rare species such as *Strophitus subvexus* and *Elliptoides sloatianus*.

Analysis of streamflow and mussel community response among stream size categories demonstrated trends of increasing unionid habitat impairment (ie., lower velocity, lower DO) with decreasing stream size (Figure 8). Patterns in unionid mortality across stream size classes indicate a trajectory of changes in mussel community structure that may arise from drought impacts. It appears that drought-related effects may drive mussel community composition toward greater relative abundance of common species and lower relative abundance of riffle and rare species (as was observed at medium sized sites in this study), and decreased richness, diversity and evenness (as was observed at small and medium sites; Figures 9-11). Changes may be most acute in moderately sized streams, because these sites were marked by high diversity mussel communities and

significant drought-related instream habitat changes. Conversely, mussel communities at large sites may not have been impacted as greatly because instream changes were less severe. And at small sites, where instream changes were significant, mussel community composition did not demonstrate significant shifts in relative abundance and composition because species composition at the onset of monitoring consisted predominantly of drought-tolerant common species types.

These data indicate that differences among species responses to drought conditions may partially explain regional patterns of species distributions. Byrne and McMahon (1994) have suggested that the adaptation of freshwater mussels to short-term emersion was key to the evolution of unionids, which invaded freshwater from marine, intertidal and estuarine systems. The local taxa observed to have the greatest hypoxia and emersion tolerance were those identified as common, widespread species (especially *E. complanata/icterina*, *V. vibex*, *V. lienosa*, *U. carolinianus*) during our 1999 survey of lower Flint Basin streams. These taxa were typical in highly degraded, intermittent or headwater streams, the only species found in low diversity sites, and frequently the most abundant species found at our survey sites. In addition, we observed that under extreme hypoxia, a diverse mussel assemblage gradually narrows to one consisting predominantly of these species (i.e., Chickasawhatchee, Site 91-010).

The results of lower FRB drought, habitat and distribution studies suggest that emersion/hypoxia tolerance may be key to successful mussel establishment in local intermittent and headwater streams where repeated drying or hypoxic conditions may occur. The most widespread mussels are those that demonstrate greatest hypoxia tolerance, emersion resistance, and persistence in small stream reaches. Conversely, rare and sensitive species demonstrate intolerance to hypoxia and gradual declines in medium sized stream reaches impacted by drought. Intolerance to hypoxia may explain some species' (e.g., *L. stramina claibornensis*, *E. sloatianus*) preferences for larger stream bodies and stream reaches not heavily organically polluted, which are less likely to experience dessication or hypoxia. The impacts of drought on mussel community structure across stream sizes also offer a potential explanation for observed increases in mussel abundance and diversity with increasing stream size (Strayer 1993, Johnson in prep.).

This study indicates that several habitat factors might act to mediate the effects of drought on mussel mortality. Among these is the presence of large woody debris in streams, which may create small, well-shaded depressions that could serve as mussel micro-refugia during drought. In addition, springs and aquifer discharge may be key to providing water, cooling stream temperatures, and/or increasing flow stability during drought conditions. *Corbicula* densities may affect competition for limited food and dissolved oxygen, as well as bacterial oxygen consumption rates. The absence of *Corbicula*, therefore, might mean the difference between life and death for mussels enduring extreme drought conditions. Finally, the predominant assemblage types present in a stream reach have an important effect on unionid mortality in an area. Streams populated by widespread, common species will likely survive drought with a limited population of mussels, while streams with diverse assemblages consisting of rare and riffle dwelling species will tend to exhibit much higher mortality rates.

This research provides insight into the mechanisms through which lower FRB mussel communities are being shaped. Although the effect of regional aquifer

withdrawals requires further study, hypoxia-sensitivity appears to play an important role in the distribution and conservation status of unionid species in the region. Drought conditions, including dissolved oxygen levels below 5 mg/L and bottom velocity below 0.01 m/s increased mussel mortality. We also observed multiple non-lethal drought impacts to mussels, as demonstrated by mantle exposure behavior, increased mussel movements, and settled superconglutinates. These results strongly underscore the need for instream flow protections that not only ensure proper water levels in stream channels, but also account for minimum dissolved oxygen and flow velocity conditions. The presence of diverse mussel assemblages coupled with the high levels of mortality observed at medium sized sites suggest that these reaches may be priority areas for mussel conservation and protection efforts in the region.

These data also highlight new avenues for research that may be key to management concerns for mussel fauna throughout the Southeast. In particular, we recommend further research to determine minimum flow and dissolved oxygen requirements for sensitive taxa, and studies to determine the independent effects of low flow velocity and low dissolved oxygen conditions on mussel mortality. Additional effort should also be focused on quantifying non-lethal effects of drought, such as reduced reproductive capacities, reduced glycogen stores, and lowered growth rates. Potentially, these drought-related responses could affect the viability of mussel populations in the lower Flint River Basin. Finally, studies designed to assess post-drought responses of mussel communities are critical to more fully understanding the long-term effects of drought on these communities.

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Tables

Table 1. Survey site locations and pre-drought reach habitat descriptors.

Stream Size Class *	D-link magnitude *	Site ID **	Creek Name and Location	Incision (bankful width: bankful depth) **	% Canopy Openness **	Dominant Substrate	Mean Depth (m) **
Small	23	97-090	Spring Creek @ GA Rt. 200	20.66	14	sand	0.4
	53	92-070	Spring Creek @ US Rt. 27	12.72	15	sand	0.45
	60	97-115	Chickasawhatchee Creek @ GA Rt. 234	27.17	0.5	clay-sand	0.50
Medium	84	91-010	Chickasawhatchee Creek @ Baker CR 121	15.12	18	cobble	0.76
	124	99-003	Muckalee Creek @ GA Rt. 118	14.85	30	clay-sand	0.51
	129	91-020	Ichawaynochaway Creek @ GA Rt. 37	10.79	23	sand	1.17
Large	155	97-132	Muckalee Creek @ GA Rt. 32	10.30	59	clay-sand	1.10
	278	91-009	Ichawaynochaway Creek @ GA Rt. 216	15.41	84	cobble	1.02
	617	92-149	Mill Creek @ GA Rt. 300	6.05	50	sand	0.62

* Alberston and Torak 2000; ** Johnson in prep.

Table 2. Descriptors of mussel assemblage composition at survey reaches and within survey quadrats, July-October 2000.

Site ID	species richness at survey reach (1999)**	predominant assemblage types **	species richness in survey quads		number of unionids in survey quadrats			cumulative mussel mortality (injured and non-injured)	cumulative mussel mortality (non-injured shells)
			max	min	average	min	max		
91-009	6	Riffle	4	1	270	231	302	25%	21%
91-010	9	Common, Rare, Riffle	6	2	41	16	157	94%	93%
91-020	11	Common, Rare, Riffle	9	7	51	41	69	48%	13%
92-070	7*	Common, Rare	7	6	113	88	127	17%	14%
92-149	11	Common, Rare	6	4	260	230	291	45%	40%
97-090	4	Common	6	2	40	31	54	49%	46%
97-115	9	Common, Rare	7	3	96	44	137	53%	31%
97-132	7	Common, Rare	8	7	92	87	106	57%	48%
99-003	9	Common, Rare	8	6	83	67	108	39%	27%

*total number of species found in survey quadrats during 2000 monitoring; this reach was not surveyed in 1999; ** Johnson in prep.

Table 3. Habitat conditions at survey sites, July-October 2000.

Site ID	water depth (cm)		dissolved oxygen (mg/L)		flow velocity (cm/s)			water temperature (°C)	
	average	max	min	max	average	max	min	average	max
91-009	46.2	73.8	18.7	7.3	9.7	5.6	0.3	24.6	29.4
91-010	44.6	61.3	31.0	2.6	4.9	0.1	0.0	21.8	25.6
91-020	52.7	83.0	23.9	7.3	8.7	6.5	1.7	24.2	28.9
92-070	43.6	59.6	34.5	4.7	7.5	2.0	0.0	22.6	25.8
92-149	53.8	64.5	48.3	7.6	8.5	6.4	5.7	24.6	28.5
97-090	16.1	39.7	0.0	2.3	6.0	0.0	0.0	22.6	25.4
97-115	46.7	85.2	21.6	6.1	7.3	2.8	1.7	22.7	28.1
97-132	50.1	98.5	30.3	7.4	8.8	6.0	4.3	23.6	28.2
99-003	46.5	90.6	24.0	6.9	8.1	5.7	14.0	23.2	27.3

Table 4. Summary of mussel species mortality and survivorship under observed DO conditions and results of Wilcoxon Rank-Sum tests comparing mortality differences between DO concentration levels of <5 mg/L and >5 mg/L.

assemblage type*	species	conservation status in Flint River Basin**	range of recorded DO exposure (mg/L)	length of emergence (d)	Weekly Mortality when DO<5mg/L		Number of observations of DO<5 mg/L associated with species	Weekly Mortality when DO>5mg/L		Number of observations of DO>5 mg/L associated with species	Wilcoxon Rank-Sum statistic	p>Z
					mean	std. error		mean	std. error			
Rimble	<i>Elliptio crassidens</i>	stable	0.1-9.7	-	82%	9%	13	1%	0.3%	28	4.62	0.0001
					9%	2%		2%	0.5%			
Common	<i>Elliptio complanata /icterina</i>	stable	0.0-8.2	20	9%	2%	41	2%	0.5%	87	2.2	0.01
	<i>Toxolasma paulus</i>	stable	0.0-8.2	-	23%	12%	11	27%	5%	43	-1.09	0.14
	<i>Unio merous carolinianus</i>	stable	0.0-8.7	-	0%	0%	3	1%	2%	31	-0.21	0.42
	<i>Villosa itenosa</i>	stable	0.0-8.8	-	9%	5%	22	0.5%	0.3%	74	2.51	0.006
	<i>Villosa vibex</i>	stable	0.0-8.8	20	3%	1%	36	1%	0.6%	86	1.49	0.07
	<i>Medionidus pencilatus</i>	endangered	0.1-7.1	-	50%	29%	3	3%	2%	12	1.94	0.03
Rare	<i>Pleurobema pyriforme</i>	endangered	1.1-8.8	-	15%	7%	18	1%	1%	25	1.46	0.07
	<i>Lampsilis subangulata</i>	endangered	0.0-9.7	-	28%	10%	19	1%	0.7%	70	3.94	0.0001

* Johnson in prep.,** Brim Box and Williams 2000

Table 5. Results of Wilcoxon Rank-Sum tests comparing mortality differences among assemblage types at DO concentrations of <5 mg/L and >5 mg/L.

Assemblage Type	Weekly Mortality when DO<5mg/L		Number of observations of DO<5 mg/L associated with species	Weekly Mortality when DO>5mg/L		Number of observations of DO>5 mg/L associated with species	Wilcoxon Rank-Sum statistic	pr>Z
	mean	std. error		mean	std. error			
Rare	24.87%	7.82%	24	3.58%	1.05%	89	1.35	0.09
Common	8.80%	1.94%	41	2.70%	0.39%	87	2.75	0.003
Riffle	53.45%	8.97%	15	1.02%	0.33%	28	3.86	<0.0001

Table 6. Mean habitat values for sites within flow sensitivity categories. ANOVA analysis found no significant difference ($p>0.10$) among habitat values in each flow sensitivity category.

Stream Size Class	Flow Stability		Flow Velocity (cm/s)		Temperature (C)		Dissolved Oxygen (mg/L)		Water Depth	
	mean	std. dev	mean	std. dev	mean	std. dev	mean	std. dev	mean	std. dev
Large	0.47	0.19	10.20	0.30	24.27	0.58	7.43	0.15	0.91	0.26
Medium	0.74	0.50	13.63	11.86	23.07	1.21	5.60	2.61	0.81	0.33
Small	0.94	0.36	5.10	5.41	22.63	0.06	4.37	1.92	0.45	0.05

Figures

Figure 1. Mussel monitoring sites in lower Flint River Basin, summer 2000.

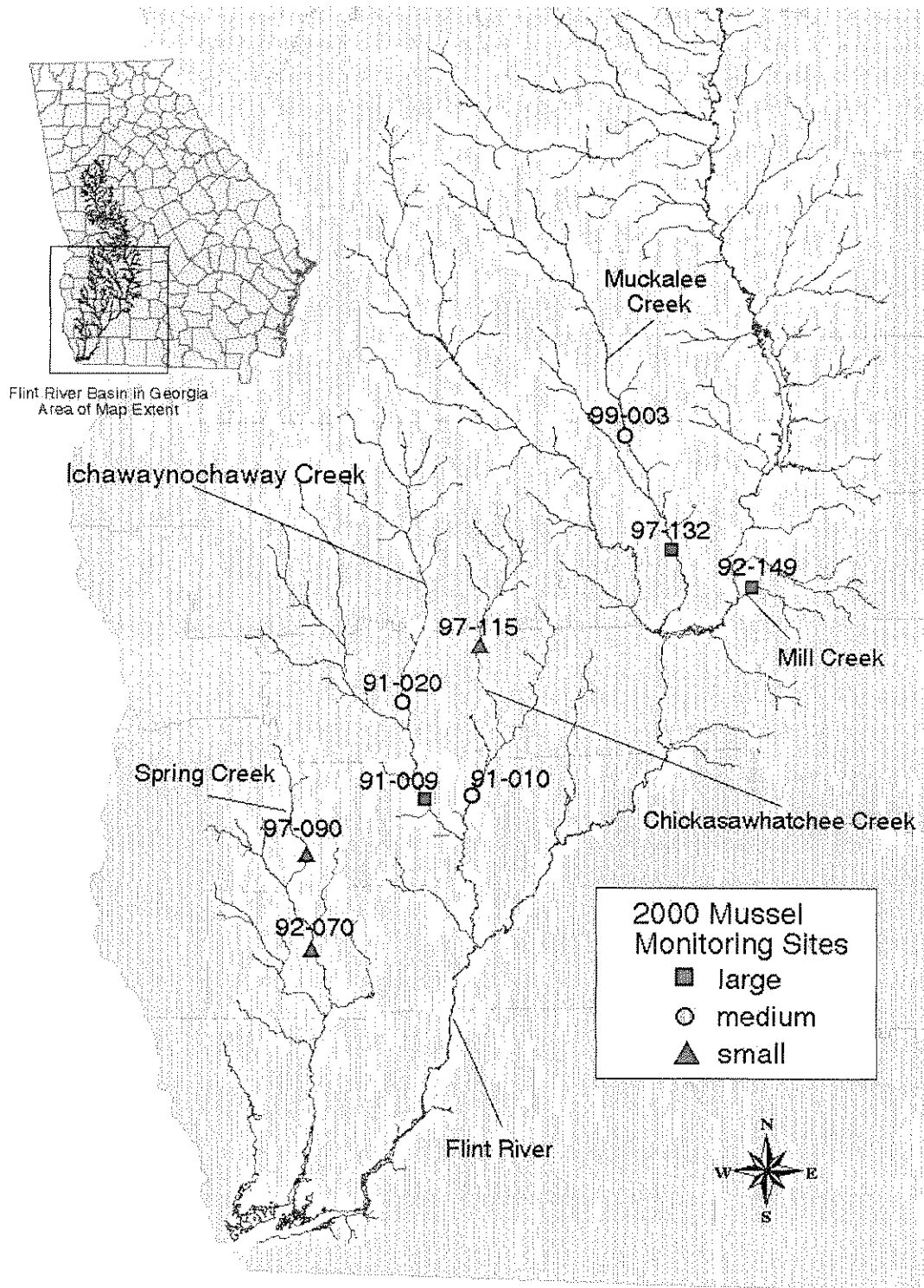


Figure 2. Scatterplot of bottom velocity and dissolved oxygen conditions. (Equation: $y = a - b / (1 + c * x)^{1/d}$; $r^2 = 0.75$; $p < 0.0001$)

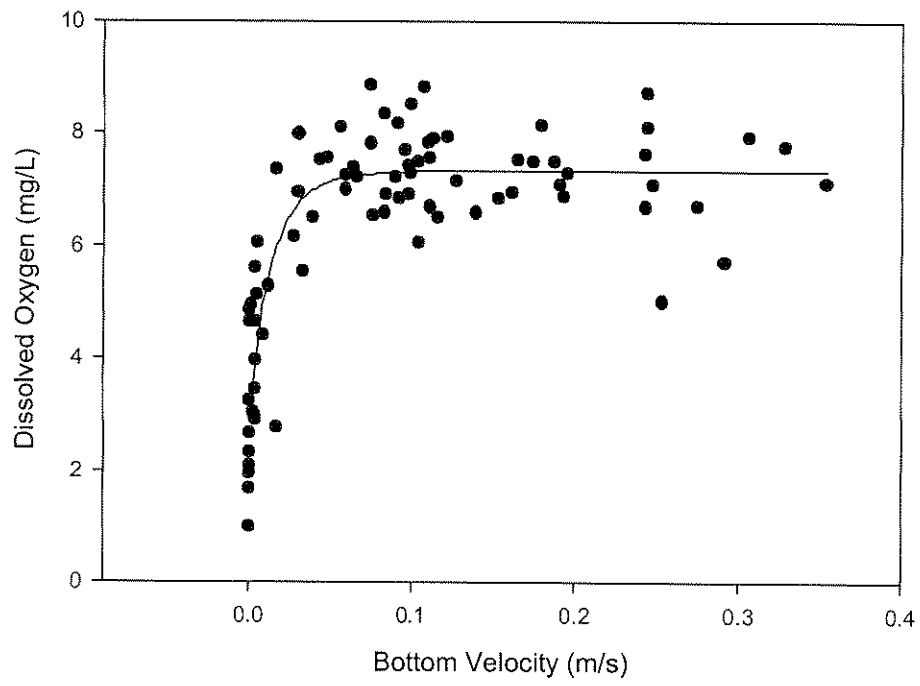


Figure 3. Scatterplot of water depth and weekly unionid mortality at all survey sites.

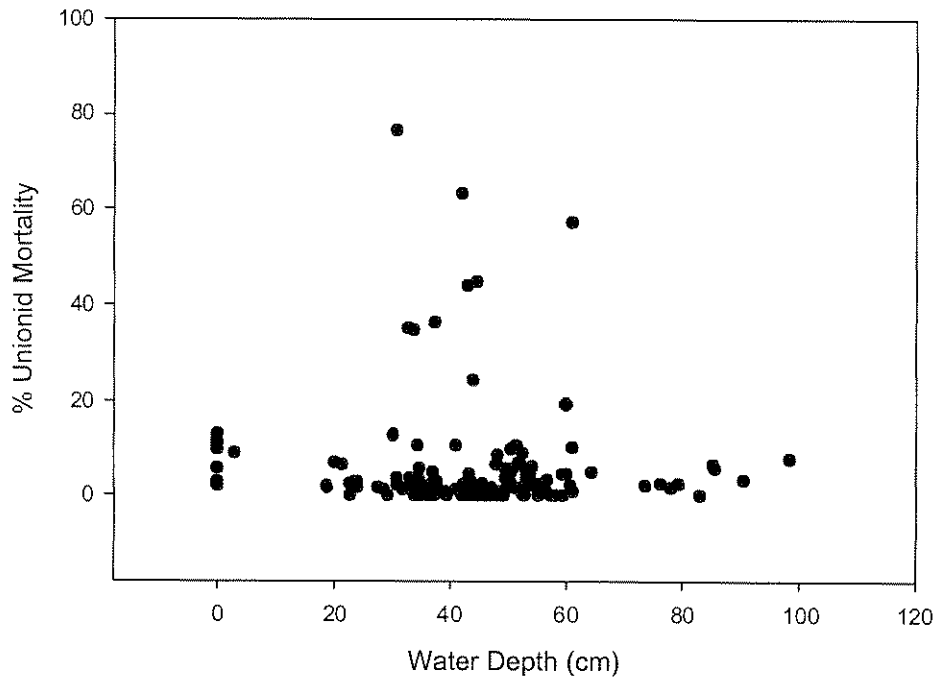


Figure 4. Scatterplot of water temperature and weekly unionid mortality at all survey sites.

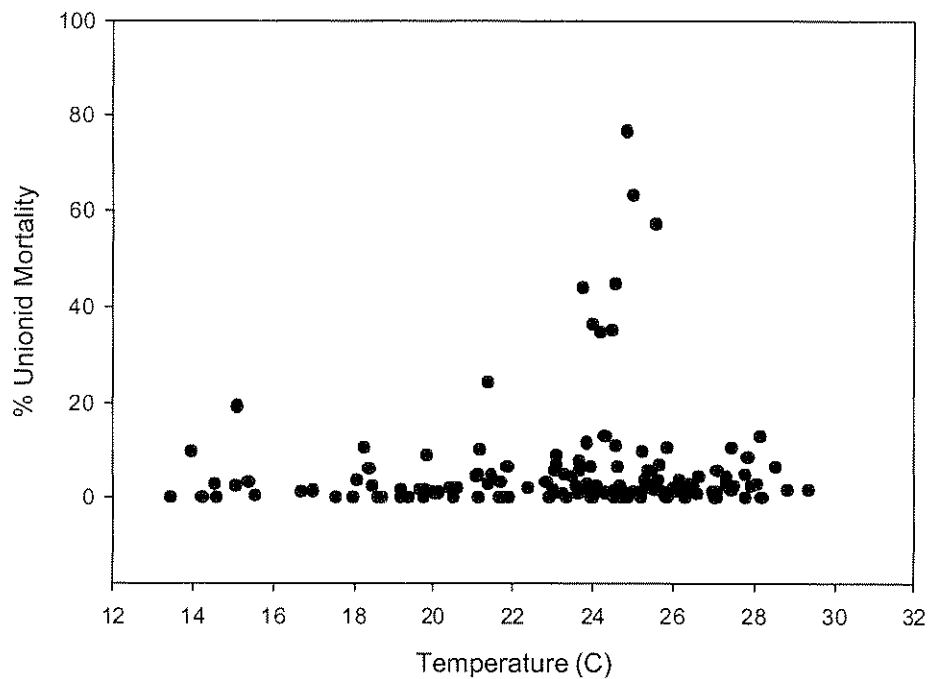


Figure 6. Scatterplot of dissolved oxygen and weekly unionid mortality at all sites.

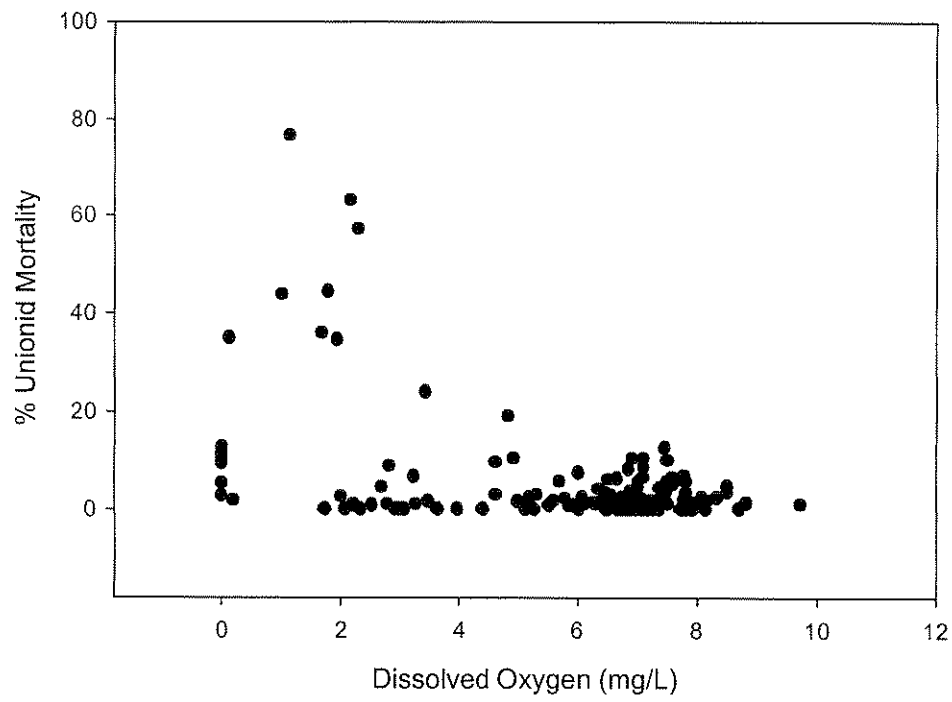


Figure 7. Average weekly mortality rates among mussel assemblage type when dissolved oxygen levels were above or below 5 mg/L. Error bars represent 1 standard error. All difference significant ($p < 0.10$).

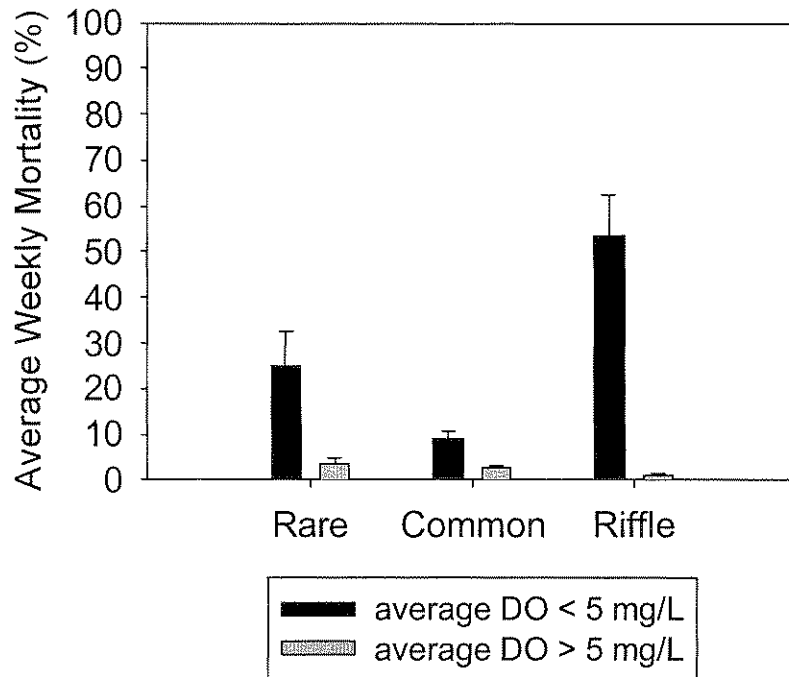
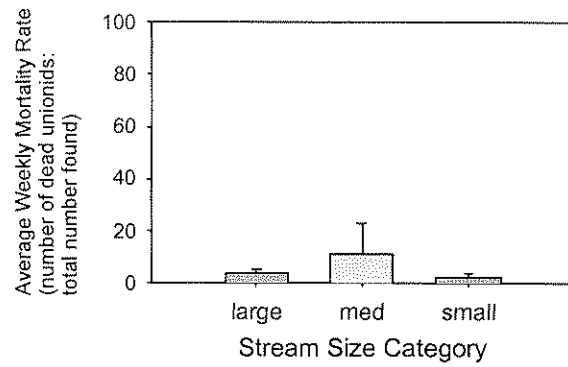


Figure 8. Average habitat conditions and unionid mortality at sites within each stream size class. Bars represent one standard error. N=3 within each category.

Average Mortality



Cumulative Unionid Mortality (non-injured shells only)

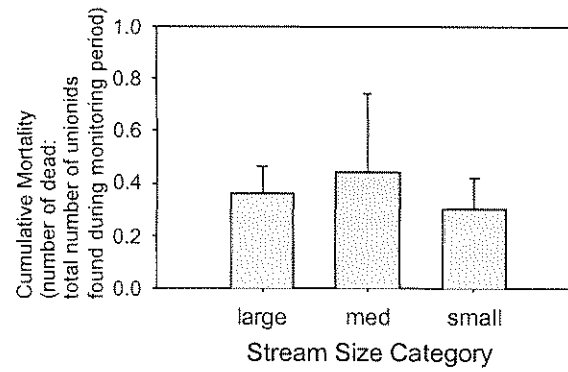
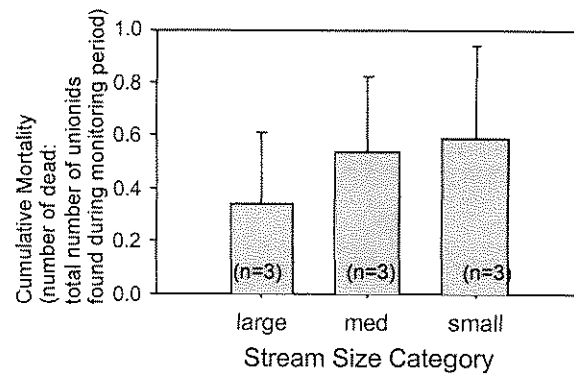
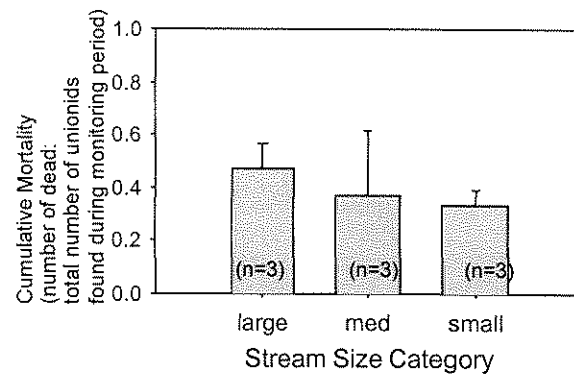


Figure 9. Mussel assemblage type cumulative mortality in each flow sensitivity category. Bars represent one standard error. Differences between groups not statistically significant.

Cumulative Rare Species Mortality



Cumulative Common Species Mortality



Cumulative Riffle Species Mortality

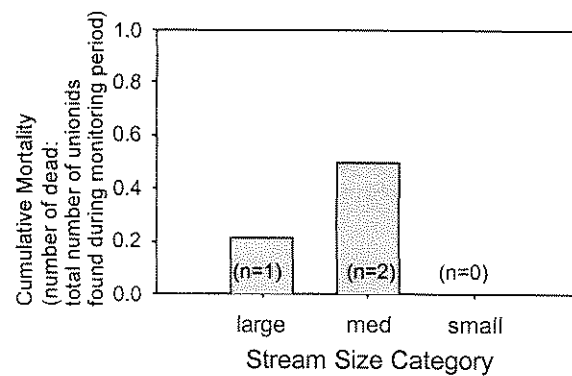
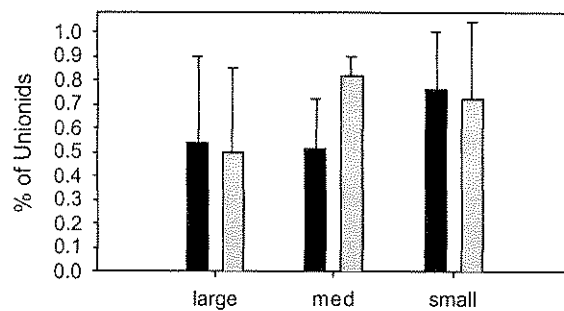
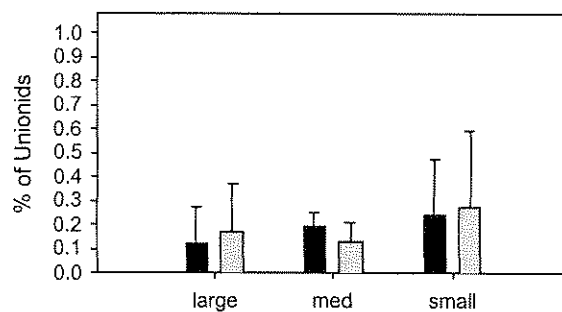


Figure 10. Relative abundance of species in each assemblage type at start and end of survey period. Bars represent one standard error. Differences between groups not statistically significant. N=3 for all categories.

Common Species Relative Abundance



Rare Species Relative Abundance



Riffle Species Relative Abundance

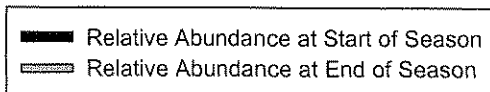
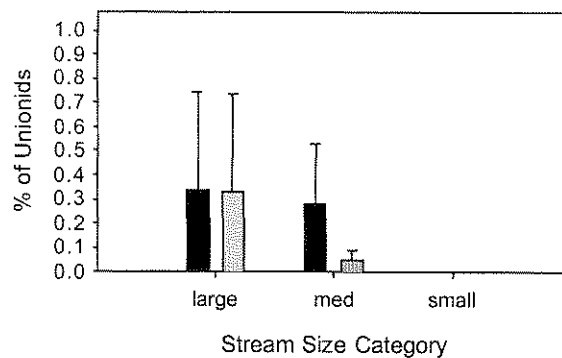
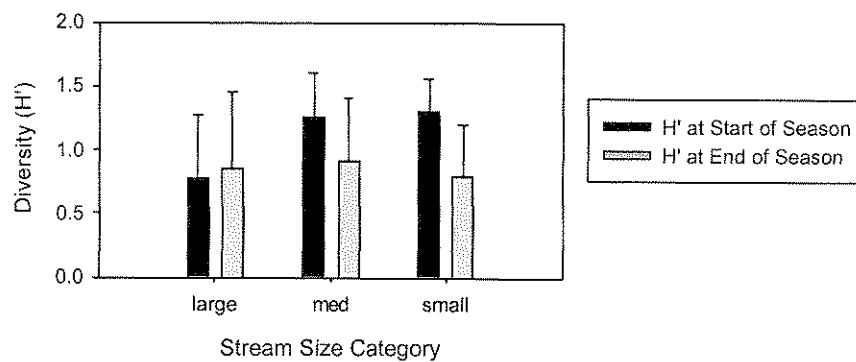
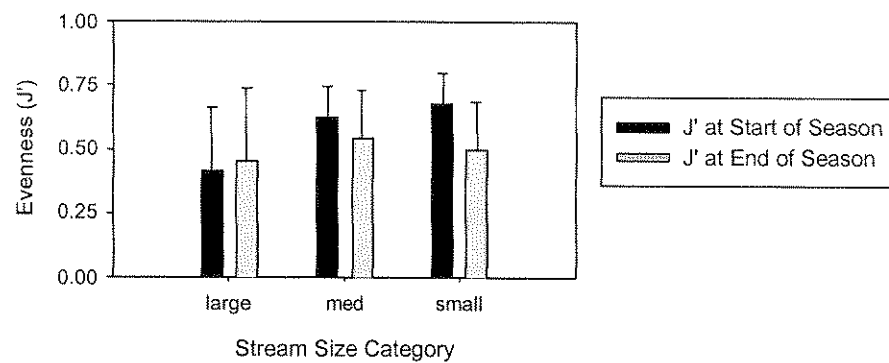


Figure 11. Average Diversity, Evenness and Richness at start and end of survey period across flow sensitivity categories. Differences between groups not statistically significant. N=3 for all categories.

Shannon-Wiener Diversity



Evenness



Species Richness

