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PATTERNS OF ORIENTATION IN UNIONIDS AS A FUNCTION OF RIVERS WITH DIFFERING HYDROLOGICAL VARIABILITY

JOANNE DI MAIO and LYNDA D. CORKUM
Department of Biological Sciences, University of Windsor, Windsor, ON, Canada, N9B 3P4

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ABSTRACT

As unionids can become dislodged with high flows, it may prove beneficial for an individual to minimize its exposure to the flow. This can be accomplished by either burrowing as deep as possible or orienting in a way that effectively reduces the drag exerted on the mussel by the flow. The patterns of orientation were examined in unionids with respect to hydrological variability. The orientation of mussels to flow was measured at four sites along an event river (hydrologically variable) and a stable river (hydrologically stable). Burrowing depth was measured at a reference site in each river. Most individuals in both river types were oriented with their siphons pointing upstream. Mussel orientation differed significantly between the two river types with mussels in the event river orienting more parallel to the flow than those in the stable river. Mussels in the event river were significantly larger than those in the stable river but the size of a mussel did not determine its orientation within a river. Burrowing depth did not differ for mussels between event and stable rivers. The observed differences in orientations among river types are likely a function of differences in the pattern of orientation of the mussel community as a whole, within each drainage. This burrowing behaviour may be an attribute that enhances the adaptations mussels have for remaining burrowed in the sediment.

INTRODUCTION

The ability to remain anchored in the substrate is an important aspect of mussel survival (Stanley, 1981). The mechanism by which bivalves burrow has been examined in detail by several researchers (Trueman, Brand & Davis, 1966; Trueman, 1968; Stanley, 1975). This work has concluded that the bivalved shell and burrowing mechanism are important adaptations for active burrowing. The structures occurring on bivalved shells (shell ornamentations) such as ribs, ridges, knobs, and spines have also been thought to be important in aiding mussel burrowing and in reducing scouring of sediment around individual mussels (Stanley, 1981; Watters, 1994).

As unionids can become dislodged with high flows (Roscoe & Redelings, 1964; Valentine & Stansbery, 1971), it may prove beneficial for an individual mussel to minimize its exposure to high flow. This can be accomplished by either burrowing as deep as possible or orienting in a way that effectively reduces the drag exerted on the mussel by the force of the flow.

The normal position for most species of unionids is with the shell buried with the siphons pointed upstream and angled in a vertical or partly horizontal position (Baker 1928). Tevesz, Cornelius & Fisher (1985) found that the orientation of the unionid, *Lampsilis radiata luteola* (Barnes) (= *L. siliquoidea* Barnes), in an Ohio stream was variable but individuals were commonly found buried two-thirds into the substrate and with their siphons aligned perpendicular to the flow. Monismith, Koseff, Thompson, O'Riordan & Nepf (1990), through research on model bivalve siphons, predicted that bivalves living in unidirectional flow would be oriented with their siphons normal to the flow or with their excurrent siphon downstream of the incurrent one. These strategies were posed as ways of avoiding refiltration of excurrent fluid.

In a previous study, we showed that the hydrological regime of a river was an important factor influencing unionid distribution (Di Maio & Corkum, 1995). In rivers, mussels must be able to withstand and adjust to changes in the flow intensity over periods of time. The present study was designed to examine patterns of orientation in unionids in rivers with differing hydrological regimes. In event rivers, the tractive force is greater and the flow varies over time more than it does in stable rivers (Richards, 1990). Mussels in event rivers may respond by orienting themselves in a way that minimizes the force of the flow on them (i.e., parallel with respect to the direction of flow). In stable rivers, a mussel will not have to endure as high a force of flow. As such, these mussels may not adjust their orientation to the same extent as mussels in event rivers.

METHODS

We limited our study to sampling two rivers. While a more extensive study could have been imagined, a comparison of contrasting rivers is the obvious place to begin exploring a new concept. One event river (Ausable River) and one stable river (Saugeen River) were selected from the rivers examined in Di Maio & Corkum (1995). Both rivers drain into Lake Huron with the Saugeen River draining a larger area (3 960 km^2) than the Ausable River (1 110 km^2). The hydrological variability of the drainage basins corresponds to classifications made by Richards (1990). That flow varies more over time in the event river than the stable river is evident in a plot of discharge for 1991 in the Ausable and Saugeen Rivers (Fig. 1). Each river was selected because the drainage basin was relatively large (so that several sites could be sampled), there was a large mussel community present, and discharge data were available. Although the substrate in the two rivers was not examined in this study, data collected for a previous study (Di Maio & Corkum, 1995) indicates that median substrate particle size between sites on the two rivers does not differ significantly.

Discharge (m^3·s^{-1}) was calculated for a series of depths and the width profile at a site in the Ausable River and Saugeen River using Manning's equation:

$$Q = \frac{AR^{2/3}S_0^{1/2}}{n};$$

where A (m^2) = area, R (m) = hydraulic radius = A/P, P (m) = wetted perimeter, S_0 = slope, and n = Manning's roughness factor (m$^{1/6}$). Tractive force (kg·m^{-2}), a generalized measure of shear stress, was determined using the slope of the channel and the depth (Newbury & Gaboury, 1993):

$$T = 1000DS_0;$$

where 1000 (kg·m^{-3}) = specific weight of water, D (m) = depth. Using daily discharge data for a

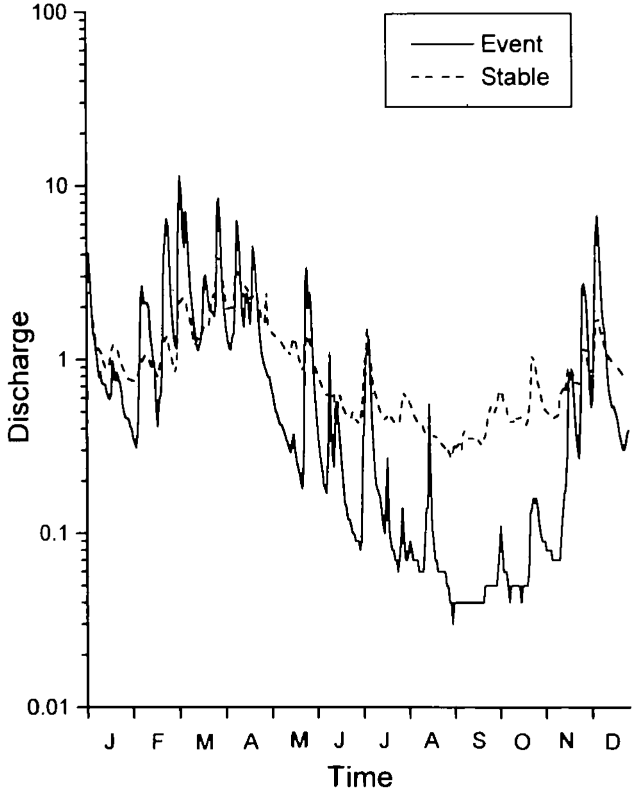

Figure 1. Discharge (expressed as daily discharge over mean yearly discharge) for the Ausable River (Event) and Saugeen River (Stable) in 1991.

gauging station on each river, provided by the Water Survey of Canada, cumulative frequency curves were plotted and predicted values of discharge for 1, 5, 10, 25, and 50 year floods in both rivers were determined. Five years of daily discharge data were used for the Ausable River plot and three years of daily discharge data were used in the Saugeen River plot, based of the available data over these years. As the values of discharge associated with each flood interval were, in most cases, extrapolated from the cumulative frequency curve, maximum and minimum values of discharge were determined for each river. The tractive force of the five flood intervals (Fig. 2) was estimated for each river using the relationship between tractive force and discharge (from Manning's equation). The Ausable River attains values of tractive force that begin at 27.3 kg·m^{-2} for a one year flood and reach between 52.2 and 81.8 kg·m^{-2} for a 50 year flood (Fig. 2). In contrast, tractive force in the Saugeen River ranges from only 7.7 to 8.2 kg·m^{-2} for a one year flood to between 9.3 and 15.5 kg·m^{-2} for a 50 year flood (Fig. 2). It is apparent from these values that mussels in the event (Ausable) river are exposed to higher forces of flow on a regular basis than are mussels in the stable (Saugeen) river. Thus, the Ausable and Saugeen Rivers differ in the shear stress produced by both common and rare hydrological events (Fig. 2) as well as in the variability of discharge occurring over time (Fig. 1).

On June 21–22, 1994, preliminary observations were made on the orientation of mussels in the Ausable and Saugeen Rivers and burrowing depth was examined. At one site in each river, measurements were made of the surface area of a number of mussels (using a technique recommended by Minshall, 1984). When a mussel was located, by feeling the substrate bottom, it was removed, identified to species and wrapped entirely in aluminum foil. To distinguish between the portion of the shell buried and that exposed, the foil was cut where there was a visible difference in colour and/or texture of the periostracum. This technique separated the more weathered, above-surface shell portion from the burrowed portion. The surface area of the foil was measured using the

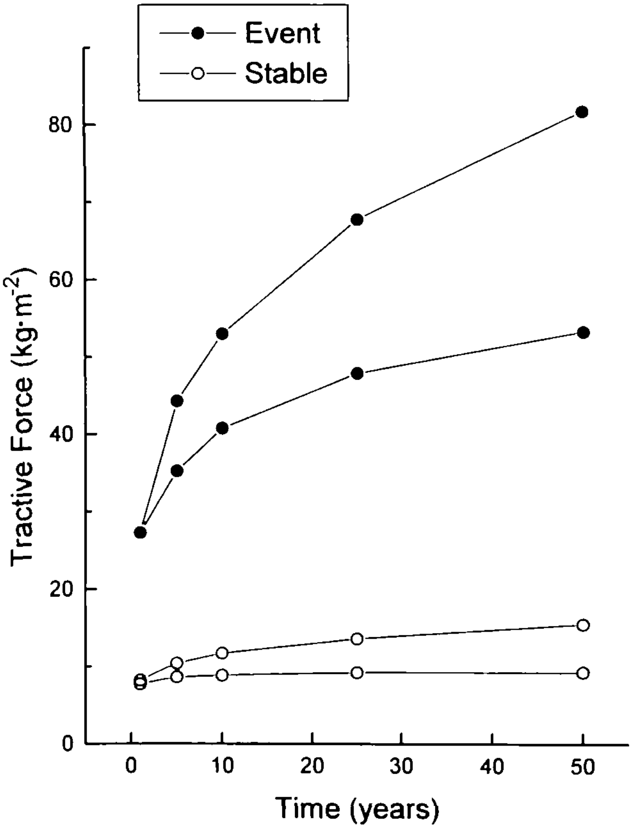

Figure 2. Estimates of maximum and minimum tractive force (kg m^{-2}) associated with five flood intervals in both the Ausable River (Event) and Saugeen River (Stable).

JAVA® Image Analysis software (Jandel Scientific) and the proportion of shell above the sediment surface was calculated.

The orientation study was performed in early September 1994 when water levels could be expected to be at a minimum (based on Water Survey of Canada discharge data). Four sites along the Ausable River were sampled for mussels from Sept. 1–2 and four Saugeen River sites were sampled from Sept. 7–8. A semi-quantitative technique was used to collect mussels whereby, wading through the river, the substrate was searched at each site for 60 minutes by feeling the stream bottom for individuals. Although using quadrats will give a more quantitative answer, the method is much more time consuming and costly to use with timed searches being a better method for detecting rare and uncommon species at a site (Vaughn, 1995; Strayer, Claypool & Sprague, 1995). A site was defined as the area of the river searched in 60 minutes. Balfour & Smock (1995) found that populations of *Elliptio complanata* (Lightfoot) moved almost 3 m in one year, and that this movement was non-directional. Since our sites were at least 6 km apart from each other, movement of individuals between sites would be unlikely. We considered the sites to be independent of each other on a river.

Once a mussel was located, the orientation was noted (see below) before the mussel was removed from the substrate, then the mussel was identified to species. Measurements (to the nearest 0.1 cm) were also made of the length, width, and height of each mussel (see Hinch, Kelly & Green, 1989) using calipers. Voucher specimens were collected of each species at each site and are stored at the Royal Ontario Museum, Center for Biodiversity and Conservation Biology, Toronto, Ontario Canada (ACC # 1996–003).

To quantify the orientation of mussels in the substrate, the relative direction of the umbo with respect to the flow of water was recorded. The direction of water flow was determined by the collector judging its path at the sediment (i.e., mussel location). If this was not possible, due to low flow, the direction of water flow at the water surface was used. We recognize that this is a 'rough' estimate of flow direction, but it was acceptable for our study, since orientation was only measured in general terms, using 30 degree intervals (see below). The umbo was used since it falls along the same plane as the siphons (the long axis of the mussel). Mussel orientation was recorded according to the hourly markings on an analogue watch with the flow arbitrarily assigned as passing from 12:00 to 6:00. Accordingly, each mussel was assigned a position corresponding to any of the 12 positions on the clock, based on the direction of the umbo.

The hourly data were converted to degrees with 0° at the 12:00 position and 180° at the 6:00 position and analyzed using techniques for circular data (Zar, 1984). Raleigh's nonparametric test was used to test directionality of orientation and Watson's nonparametric U^2 test was used to test the differences in the directions of the populations in the two river types.

The size data (length, width, and height) were used to determine if variation existed in the size of mussels at different orientations between the two rivers. To obtain a simple, overall measure of mussel size, the three size variables were log transformed and analyzed using a correlation-based principal components analysis (PCA) (BMDP, Dixon & Brown, 1985). This reduced the size variables into an independent component for which associations with orientation could be more readily determined.

RESULTS

Burrowing depth was compared for mussels found at one site in the event river and stable river. The proportion of shell above the sediment surface was measured for 19 individuals in the Ausable River and 26 individuals in the Saugeen River (Table 1). The number of indi-

Table 1. Mean and standard errors of the proportion (expressed as a percentage) of shell surface area above the substrate for mussels in the Ausable (Event) and Saugeen (Stable) rivers. Numbers of individuals measured for each species are in brackets.

Species	Mean Ausable ± S.E. (n)	Mean Saugeen ± S.E. (n)
A. plicata	44.0 ± 2.48 (10)	–
P. grandis	34.7 ± 12.20 (2)	–
E. dilatata	–	53.8 ± 3.26 (10)
L. siliquoidea	43.8 ± 2.90 (2)	23.3 ± 3.12 (5)
L. costata	36.9 ± 1.86 (5)	38.9 ± 2.83 (10)
A. marginata	–	35.1 (1)
mean ± S.E. for river	41.1 ± 1.88 (19)	41.3 ± 2.74 (26)

viduals collected did not allow for species specific comparisons between river types but overall differences in the mussel community could be examined. There was no significant difference ($t = 0.06$, $df = 43$, $p > 0.05$) in the mean proportion of mussel shell above the substrate in event and stable rivers (Table 1). Except for *Elliptio dilatata* (Rafinesque), it appeared that mussels kept a larger proportion (at least 55%) of their shell burrowed in the substrate than above.

A Chi Square test was used to test the null hypothesis that the distribution among orientations at each site was the same as the average for all sites on that river. The species at each site and among sites were pooled for this analysis due to small sample sizes. The pattern of orientation of mussels across the four sites did not differ significantly within each river ($\chi^2 = 43.13$, $p > 0.05$, $df = 33$ for the Ausable River; $\chi^2 = 32.06$, $p > 0.05$, $df = 33$ for the Saugeen River). Consequently, the data for each of the four sites were pooled giving 162 mussels for the Ausable River and 157 for the Saugeen River. Although some information on site-specific and species-specific differences is lost in pooling the data, a broader interpretation of the patterns observed can be achieved with the pooled set.

The species found in the Ausable were (in order of decreasing abundance) *Amblema plicata* (Say), *Ligumia recta* (Lamarck), *Lasmigona costata* (Rafinesque), *Lampsilis siliquoidea* (Barnes), *Fusconaia flava* (Rafinesque), *Pyganodon grandis* (Say), *Ptychobranchus fasciolaris* (Rafinesque), *Actinonaias ligamentina* (Barnes), *Alasmidonta marginata* Say, *Lampsilis cardium* Rafinesque, and *Strophitus undulatus* (Say). Species found in the Suageen were *Elliptio dilatata*, *A. marginata*, *L. siliquoidea*, *L. costata*, *Lasmigona compressa* (Lea) and *L. cardium*. No one species pattern of orientation differed significantly from the average of the assemblage for each river ($\chi^2 = 73.97$, $p > 0.05$, $df = 110$ for the Ausable River; $\chi^2 = 20.16$, $p > 0.05$, $df = 55$ for the Saugeen River). Therefore, species tend to orient in a similar manner within the same drainage.

Raleigh's test was used to determine if mussel orientation was random in the two rivers. In both cases, orientation was not random ($z = 40.35$, $p < 0.001$ in the Ausable; $z = 6.40$, $p < 0.001$ in the Saugeen). From the relative frequency of the orientations of mussels in the Ausable and Saugeen rivers (Figure 3), it is clear that the majority of individuals in both river types orient with their umbo pointing away from the direction of the flow and their siphons directed upstream. This pattern is more evident in mussels from the Ausable (Fig. 3).

Since mussels are approximately symmetrical, an individual oriented at an equal angle to the right or left of the direction of the flow offers the same surface area to the flow in either position. As such, it could be assumed that, for example, an orientation directed at 60° was the same as an orientation at 300°. Accordingly, the 360° directional data were then converted to a set ranging from 0° to 180° by converting an orientation between 180° and 360° to its mirror value from 0° up to and including 180°. Watson's two-sample U^2 test (Zar, 1984) was performed on this one sided orientation data to determine if mean bearings of mussels in the Ausable River varied from those in the Saugeen River. There was a significant difference ($U^2 = 0.91$; $p < 0.001$) in the directions of mussels between the two river types. Mussels in the Ausable oriented themselves more parallel to the flow than did mussels in the Saugeen.

Although sample sizes are small, comparisons can be made of the orientation of some mussels species across the two drainages. Watson's F test was used to determine whether the average orientation differed for *L. costata* and for *L. siliquoidea* in the Ausable and Saugeen rivers. There was no significant difference in the mean orientation of *L. costata* among the two rivers ($F = 2.92$, $p > 0.05$, $df = 22$) as well as for *L. siliquoidea* ($F = 0.15$, $p > 0.05$, $df = 28$). While this analysis was conducted with only two species, it suggests that individuals of the same species may be orienting in a similar manner across the river types.

Mussel size was analyzed by reducing the three size measures to one representing overall size using PCA. The first principal component (PC1) explained 95% of the variation and was strongly, positively associated with each size variable. Correlations ranged from 97.3% to 98.1%. This component described the size of the mussels with larger individuals having higher loadings on PC1.

To examine the relationship between size and orientation, the orientations in degrees (which were grouping or class variables) were transformed to a linear measure using $\sin^2 \theta$. This changed the seven degree classes (0° to 180°) into six values ranging from 0 to 1. The PCA scores were then compared to the sine squared angle using Analysis of Covariance (ANCOVA) to test for differences in the regression lines

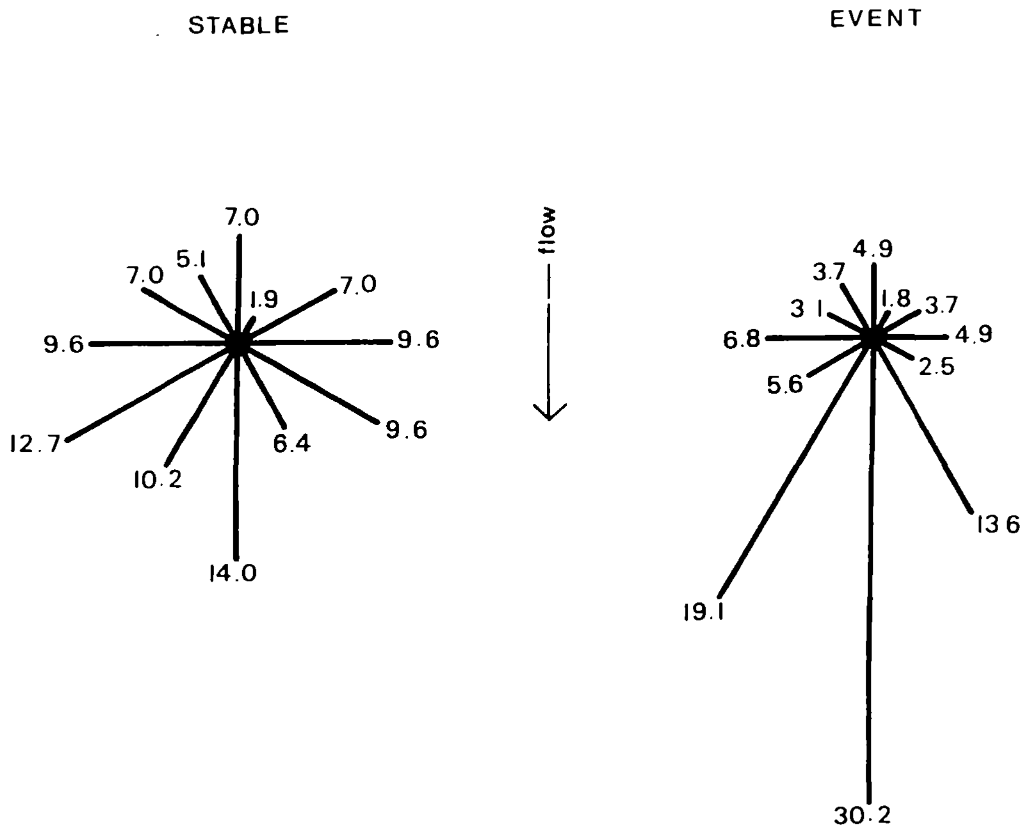

Figure 3. Frequency histograms of relative occurrence of mussels within each orientation for the Ausable River (EVENT) and Saugeen River (STABLE). The arrow represents the direction of flow at which measurements were taken. Values next to bars are percentages.

through these values, and thereby, test for differences in size. If the regression lines differed from zero, then the mussels showed orientations which were a function of mussel size.

The slope of the regression between mean size of mussels and $\mathrm{Sin}^2\ \theta$ was not significantly different from zero for either the Ausable ($p > 0.1$) or Saugeen ($p > 0.1$) rivers (Fig. 4). Therefore, mussel size did not influence orientation within a river. There was, however, a significant difference in the intercepts of the two regression lines ($p < 0.0001$), indicating that mussel size differed between rivers. Mussels in the event river were significantly larger than those in the stable river (Fig. 4). It is not clear how the size of a mussel affects its orientation across the two river types since the size distribution of mussels in the Ausable River and Saugeen River does not overlap.

DISCUSSION

The overall pattern we found for mussels in both rivers was that individuals orient with their siphons pointing upstream (Fig. 3). In comparing orientations of mussels between rivers, mussels oriented more parallel with respect to the flow in the event river than in the stable river (Fig. 3). Within a river, mussels behaved the same (i.e., no one species had an average orientation that differed significantly from that of another species). For the two species examined (*L. costata* and *L. siliquoidea*), we found that individuals of the same species appeared to be orienting in a similar manner across the two rivers. But when the orientations of mussels in the two rivers were compared, average orientation differed. This suggests that the observed differences in orientations between event and

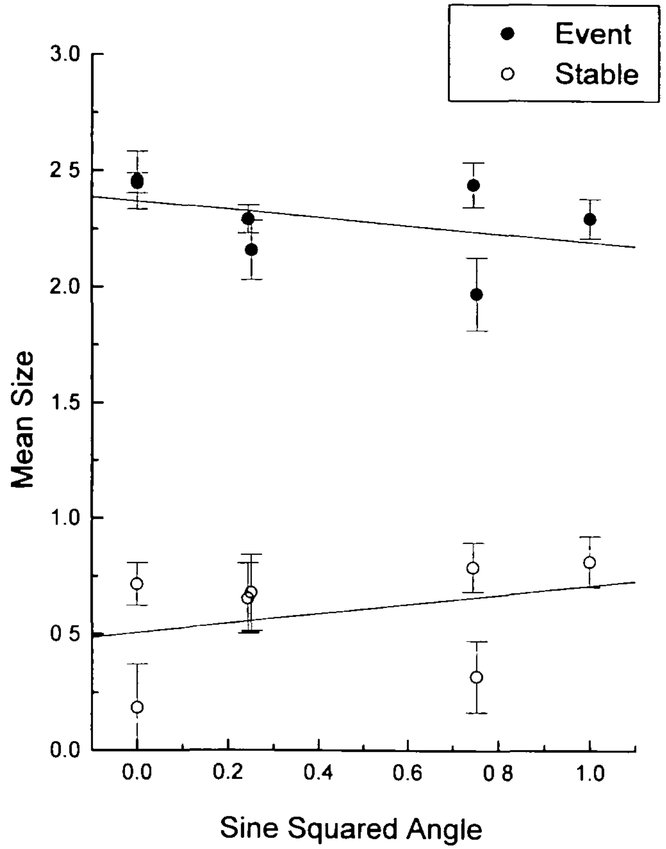

Figure 4. Mean size (± Standard Error) expressed as the scores from PC1 at each of the sine squared angles for the Ausable River (Event) and Saugeen River (Stable). Values on the sine squared angle axis range from 0 (oriented parallel to flow) to 1 (oriented perpendicular to flow).

stable rivers are likely a function of differences in the pattern of orientation of the mussel community as a whole, within each drainage.

There are several factors that influence the orientation of mussels. Mussel dislodgment is often attributed to seasonal floods (Roscoe & Redelings, 1964; Valentine & Stansbery, 1971; Thoms & Berg, 1985). Orientations that are parallel to the flow may reduce the chance of a mussel becoming dislodged. Burrowing depth also becomes important in reducing dislodgment. Thoms & Berg (1985) note that *Margaritifera margaritifera* (Linnaeus) burrows as deep as necessary to avoid being dislodged by the current. Although burrowing depth did not differ for mussels in our two river types, patterns of burrowing may differ with changing flow conditions and merits further study.

There can be filtering benefits derived from specific orientations. The positions of the inhalant and exhalant siphons with respect to the flow can be important in bivalve feeding (Wildish, Kristmanson, Hoar, DeCoste, McCormick & White, 1987; Vincent, Desrosiers & Gratton, 1988; Monismith *et al.* 1990). Unionids likely receive feeding benefits by maintaining their inhalant siphon upstream of the exhalant while oriented with the umbo downstream rather than upstream. The potential for interactions between the siphon flows would be virtually eliminated in this position, preventing recirculation of exhalant fluid.

Shell sculpturing has been identified as being important to unionids in that these ribs, ridges, spines, and knobs help individuals to remain in the substrate (Stanley, 1981; Watters, 1994). Although shell sculpturing and shape was not explored in this study, several species that we encountered have sculptured shells. Watters (1994) suggested that the 'broad ribs' of *Amblema plicata* might function as an anchoring device. Some *Lasmigona* species have dorsal ribbing, like *L. costata*, which is used as an anti-scouring device (Watters, 1994). *Fusconaia* spp. also have anti-scouring devices, in the form of pronounced dorsal ridges (Watters, 1994). We found *A. plicata* and *F. flava* exclusively in the Ausable River, whereas *L. costata* was found in both drainages. Presumably, these shell features, along with orientations with respect to the flow, act together to aid in maintaining a suitable position in the substrate for unionids.

Although direct comparisons cannot be made, the results of this study appear to correspond to those of a study in which *Lampsilis radiata luteola* (= *siliquoidea*) was found most often oriented perpendicular to the flow (Tevesz *et al.*, 1985). In our study, *L. siliquoidea* was found, on average, oriented almost perpendicular to the direction of flow in the Saugeen River, but less so in the Ausable River. Tevesz *et al.* (1985) attribute this orientation to the location of the mussel within the river they studied (i.e., near shore, shallow water habitats). These are areas of the river associated with low-flow velocities.

There was a significant difference in the size of mussels between the two rivers (Fig. 4) with mussels in the Ausable River being larger than those in the Suageen River. It is not known how the size of a mussel affects its susceptibility to dislodgment or its orientation in the two rivers examined. An analogy can be made using adult and juvenile mussels, based on their size. Vincent *et al.* (1988), in examining the orientation of the deep burrowing bivalve, *Mya arenaria* Linnaeus, found that the bivalves they sampled most likely represented older animals with orientations that had enhanced their survival. In another study, Vannote & Minshall (1982) found that, in areas where large block-boulders stabilized the substrate of *Margaritifera falcata* (Gould) beds, mussels in these areas had size distributions highly skewed towards larger, older individuals. Although we did not age our mussels, they appear to be older individuals since many were found producing glochidia. As such, they may represent individuals that survived because of benefits derived from their orientation (e.g., reduced dislodgment, enhanced filtration).

Orientation to flow may vary with season, habitat and among different groups of mussels. Additional work on the ecological significance of burrowing behaviour would be fruitful. It does appear that orientation to flow may be an attribute that enhances the adaptations mussels have for remaining burrowed in the sediment.

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