DiMaio
Corkum
1995

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Referee's Confidential Recommendation

Review should be sent to Associate Editor before 20 Mar 95

MS # 95-017 MS Copy # 2 Referee # 2

Author(s) Di Maio and Corkum

Title The orientation of unionids in rivers as a function of the hydrological variability.

Overall assessment:

- ☐ Acceptable
- ☒ Does not merit publication
- ☐ Acceptable after moderate revision
- ☐ Publishable, but not in *J-NABS*
  Suggested journal(s) ______
- ☐ Acceptable after major revision

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Signature Richard J. Neves Date 3/1/95

This manuscript by DiMaio and Corkum is well written, describing a somewhat simplistic study of burrowing depth and orientation of unionids in rivers. Although the data have been exhaustively analyzed (some would say overanalyzed) to reach certain conclusions, at issue is whether the paper meets the JNABS expectation of making "a substantial contribution to benthological science." I provide the following comments that need to be addressed by the authors to clarify the rigor of the study and the "new science" they feel is contained in this manuscript.

1. The Abstract is somewhat mundane with statements of common knowledge to mussel biologists.
2. Freshwater mussel do not have siphons; they have incurrent and excurrent apertures.
3. The authors exhibit a lack of experience with bivalves by not citing most of the pertinent studies describing the interaction of hydraulics, functional morphology of shells, and substratum type and stability. Their reliance on Vogel (1981) and admittance (p. 11) that "perhaps the effect of flow on an object protruding from an erodible substrate differs from what can be predicted from existing theory based on other objects found in the flow "reflect their naiveté. Stanley (1970, 1975, etc.), Watters (1994) and many others provide a wealth of knowledge and analyses of shell shape, sculpture, anchoring, and anti-scouring functions. A review of this literature by the authors should convince them of the naive nature of their study.
4. I am troubled by the small sample size (19 and 26 mussels), only 1 site sampled in the burrowing depth experiment, and the lumping of all species as a community statistic. Because of differences in species composition between the 2 sites, sculpturing and density differences among species, and the role of shape in buried stability (Watters 1994), it is unacceptable to treat all species together. This approach violates common knowledge of form and function in burrowing of mollusks.
5. I am also troubled by the manner of the sampling technique in the entire study. Mussels were located by feeling the substratum in all sampling conducted. Was the stream waded or snorkeled? This method of qualitative sampling is undoubtedly biased, leading to the collection of mussels that protrude from the substratum more than mussels that are burrowed further into the substratum. Hence, the tendency is to collect large specimens of certain species noted to be more epibenthic than subsurface in occurrence and to assume that results pertain to the entire population of a species and to all species. Analysis of burrowing depth and orientation by this sampling scheme is fraught with species and size biases that are glossed over in the study. Could this be why there was no statistical difference in the proportion of mussel shell above the substrate in both rivers? Quadrant sampling would have been a much better unbiased approach to answering questions of depth and orientation.
6. What is the reference for the aluminum foil technique to measure surface area, and what is the degree of accuracy and precision? My personal experience with this foil technique for measuring rounded surfaces is that it is inaccurate and imprecise.
7. Define 'event river,' 'stable river,' and 'tractive force.'
8. Substratum composition and compaction are of major importance in the ability of mussels to withstand flow velocities and flood events, and yet they are not mentioned at all in this study. Is the reader to assume that substratum was identical in both rivers? This isn't likely in 2 rivers with vastly different tractive forces and the sorting of sediments that occurs under different flows.

9. How exactly was the relative direction of the umbo determined in situ before the mussel was removed.

10. The Ausable River had 11 species whereas the Saugeen River had 6 species. Comparing the orientation of readily "feelable" mussels of different species in 2 rivers and attempting to relate this only to hydrologic variability is speculative at best. The final statement in Results, "however there is strong evidence to suggest that there is a preferred streamlined orientation by mussels in the more hydrologically variable river," is pure speculation based on a problematic sampling design and oversight of other important molluscan and substratum traits. The authors allude to this by admitting that other factors may be responsible for the orientation observed (p. 13).

11. Most of the Discussion is speculation with no clear statements interpreting their results. In essence, the Discussion identifies the inadequacy of the study to achieve its objective; namely, patterns of burrowing and orientation in unionids as a function of rivers with differing hydrological variability.

12. Replace Figure 1 with a brief narrative of river locations in Methods and reference DiMaio and Corkum (in press). Delete Figure 3 and reference one of numerous studies that show shell dimensions. Assign values to the vectors in Figure 4 rather than including a legend. Figure 5 is obtuse and difficult to interpret. Isn't there a more straightforward way to show that mussel sizes differed between rivers?

13. I regret that the authors did not make use of important descriptive literature on bivalves before initiating their study. The oversimplification of factors affecting burrowing and orientation is unfortunate. Applying results from "feelable" mussels to the population of each species and to all species (as inferred in manuscript) is not credible to malacologists who have sampled these species in a wide array of rivers throughout their range. The functional morphology of shells of infaunal bivalves is critical literature to the interpretation of field observations (e.g. Stanley, Ortmann, Watters, etc.) as described here.

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21 February 1995

Dr. Richard J. Neves
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Dear Dr. Neves:

Thank you for agreeing to review the enclosed manuscript "The orientation of unionids in rivers as a function of the hydrological variability" by Di Maio and Corkum (MS#95-017). I am sending it to you for review because of your expertise in the subject matter it contains. Please review the enclosed manuscript by **Mar. 20th**. If you will not be able to complete the review by that date, return the manuscript immediately to me at the address above.

I have enclosed three forms. One provides information on the editorial standards and expectations of J-NABS. Please use the other two forms for your assessment and detailed review. If you are using a word processor, feel free to attach your comments to the form rather than struggling to fit your printout onto the form itself. Note that you are requested NOT to express an opinion on the acceptability of the manuscript in your review; confine such remarks to the Confidential Recommendation form.

The success of JNABS depends on our receiving high-quality, timely reviews. Thank you for your time and effort. Please let me know if you have any questions.

Sincerely,

Ted Georgian

Ted Georgian
Associate Editor

enclosures

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3. Publishable papers should make a substantial contribution to the broad field of benthological science. The research and/or hypotheses examined should be solid and worthwhile. Preliminary or pilot studies are usually inappropriate for *J-NABS*.

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5. Referees should make a confidential recommendation (on the form provided) to the Associate Editor concerning publication. Any comments on acceptance or rejection should be made on this form ONLY.

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COPY #2

Running Head: Unionid orientation and flow variability

The orientation of unionids in rivers as a function of the hydrological variability

Joanne Di Maio and Lynda D. Corkum
Department of Biological Sciences, University of Windsor, Windsor, Ontario, Canada N9B 3P4

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 burrowing and 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 and a stable river. 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 (U^2=0.904; p<0.001) between the two river types with event mussels orienting more parallel to the flow than those in the stable river. Mussels in the event river were significantly (F=378.8; p<0.0001) 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. It is not clear how the size of a mussel affects its orientation across the two river types, but there is strong evidence to suggest that there is a preferred streamlined orientation by mussels in the more hydrologically variable river. This burrowing behaviour may enhance the streamlined nature of the unionids and lessen the force of the flow on them.

Key Words: orientation, Unionidae, flow, burrowing, mussels

Introduction

Flow has long been considered to be an important factor influencing the distribution of aquatic organisms (Hynes 1970). Research has focused on both the physical and biological effects on individuals within different flow environments.

Rivers are good systems in which to examine the influence of flow on benthic organisms for several reasons. The direction of flow in a river can be easily assessed and not expected to vary. The benthic organisms in rivers can be readily sampled and identified with relative ease. Also, variability exists in flow regimes within and among rivers over time. As such, rivers can be grouped according to their flow variability (Richards 1990) and comparisons made of the aquatic invertebrate communities among rivers (Di Maio and Corkum in press, Robinson et al. 1993).

If an organism protrudes above the streambed, it must be able to withstand the force of the flow (Nowell and Jumars 1984). The total drag on an organism is an important aspect of the force of the flow. At high and moderate Reynold's numbers (i.e., flow turbulence), an object in the flow can reduce the effect of high drag by streamlining its shape (Vogel 1981).

Unionids are burrowing freshwater mussels capable of maintaining a relatively large surface area projected into the flow. They also possess a distinctly streamlined shape (similar to an airfoil in cross section), as do many bivalves. As unionids can become dislodged with high flows (Roscoe and Redelings 1964, Valentine and Stansbery 1971), it ~~may prove~~ beneficial for an individual mussel 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. Even though unionids are morphologically streamlined, their burrowing behaviour may enhance this attribute.

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). More detailed research on the orientation patterns of unionids is lacking, with few examples describing preferred orientation. Tevesz et al. (1985) found that the orientation of the unionid, Lampsilis radiata luteola, in an Ohio stream was variable, but individuals were commonly found buried two-thirds into the substrate and with their siphons aligned normal (i.e., perpendicular) to the flow.

Within the superfamily Unionacea, Thoms and Berg (1985) examined the burrowing behaviour of Margaritifera margaritifera and found that the preferred orientation of this running-water bivalve was with its inhalant opening pointing upstream and with its shell buried to about one-half of its length.

Outside of the freshwater bivalves, additional examples of bivalve orientation to flow can be found. Caddy (1968) examined the behaviour of the epifaunal scallop, Placopecten magellanicus, in Northumberland Strait, Gulf of St. Lawrence. A preferred direction of orientation was found, but it was not clear if this was related to the direction of tidal flow.

Monismith et al. (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 and Corkum in press). Within hydrologically variable rivers, mussels must be able to withstand and adjust to changes in the flow intensity over periods of time. This study was designed to examine patterns of burrowing and orientation in unionids as a function of rivers with differing hydrological variability. 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., more streamlined with respect to the 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

One event river (Ausable River) and one stable river (Saugeen River) were selected from the rivers examined in Di Maio and Corkum (in press) (Fig. 1). The hydrological variability of the drainage basins corresponds to classifications made by Richards (1990). Each river was selected because the drainage basin was relatively large

Fig. 1

what was drainage area?

(so that several sites could be sampled), there was a large mussel community present, and discharge data were available.

Discharge ($m^3 \cdot s^{-1}$) 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:

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

where A (m^2) = area, R (m) = hydraulic radius = A/P, P (m) = wetted perimeter, S_o = slope, and n = Manning's roughness factor ($m^{1/6}$). Tractive force ($kg \cdot m^{-2}$) was determined using the slope of the channel and the depth:

$$\tau = 1000DS_o \quad ;$$

where 1000 ($kg \cdot m^{-3}$) = specific weight of water, D (m) = depth. Using daily discharge data for gauging stations 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. 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 $kg \cdot m^{-2}$ for a one year flood and reach between 52.2 and 81.8 $kg \cdot m^{-2}$ for a 50 year flood (Fig. 2). In contrast, tractive force in the Saugeen River ranges

Fig. 2

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.

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. When a clam 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 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 (Fig. 1). The substrate was searched at each site for 60 minutes by feeling the stream bottom for individuals. 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 (Fig. 3) using calipers. Voucher specimens were collected of each species at each site and are stored at the Department of Biological Sciences, University of Windsor.

To quantify the orientation of mussels in the substrate, the relative direction of the umbo (i.e., the beak-like prominence situated anterior to the hinge line) with respect to the flow of water was recorded. 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 and 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 individuals 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*, it appeared that mussels kept a larger proportion (at least 55%) of their shell burrowed in the substrate than above.

The abundance of mussels within each orientation at the four sites along a river was compared (using Chi Square) to test for differences among the sites. The orientation samples collected at the four sites within each river were independent ($\chi^2=25.45$, $p>0.05$, $df=18$ for the Ausable River; $\chi^2=20.96$, $p>0.05$, $df=18$ for the Saugeen River) and so they were pooled giving 162 observations for the Ausable River and 157 for the Saugeen River. Although some information on site 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*, *Ligumia recta*, *Lasmigona costata*, *Lampsilis radiata*, *Fusconaia flava*, *Pyganodon grandis*, *Ptychobranchus fasciolaris*, *Actinonaias carinata*, *Alasmidonta marginata*, *Lampsilis ventricosa*, and *Strophitus undulatus*. Species found in the Saugeen were *Elliptio dilatata*, *A. marginata*, *L. radiata*, *L. costata*, *Lasmigona compressa*, and *L. ventricosa*. There were no significant differences (X^2=73.97, p>0.05, df=110 for the Ausable River; X^2=20.16, p>0.05, df=55 for the Saugeen River) in the pattern of species found within each orientation. No one species showed a preference for a specific orientation.

Raleigh's test was used to determine if mussel orientation was random in the two rivers. In both cases, orientation was not random (z=38.96, 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 (Fig. 4), it is clear that the majority of individuals in both river types orient themselves with the umbo pointing away from the direction of the flow and the siphons directed upstream. This pattern is more evident in mussels from the Ausable (Fig. 4).

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 it's 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=0.904; 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.

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 (Table 2). 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 $\mathrm{Sin}^2\ \theta$. 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 through these values, and thereby, test for differences in size. If the regression lines differed from zero, then the mussels showed preferred orientations based on their size.

The slope of the regression between mean size of mussels and

$Sin^2\ \theta$ was not significantly different from zero for either the Ausable ($p>0.1$) or Saugeen ($p>0.1$) Rivers (Fig. 5). 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. 5). 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. However, there is strong evidence to suggest that there is a preferred streamlined orientation by mussels in the more hydrologically variable river.

Discussion

Significant differences in the patterns of orientation of unionids were observed between the two river types (Fig. 4). Mussels were more streamlined with respect to the flow in the event river than in the stable river. This behaviour is attributed to the hydrological variability of the river with mussels in the event river reducing the forces exerted on them by the current.

The manner in which the force of the flow is operating on individual mussels is unknown. According to Vogel (1981), an object in the flow experiences the least amount of drag when shaped as an airfoil, but if the airfoil is reversed in the flow, the drag can be much greater. Regardless, the drag on an airfoil in either of these two positions is much less than what would be experienced by a sphere (Vogel 1981). The reversed airfoil reflects the orientation that mussels are found in most frequently in our study (i.e., a teardrop shape with respect to the flow). Flow dynamics seem to suggest that mussels are experiencing a greater drag in this orientation, however, this may not be the case. Perhaps the effect of flow on an object protruding from an erodible substrate differs from what can be predicted from existing theory based on other objects found in the flow (S. Vogel, Duke University, pers. comm.). As this area of research is essentially unexplored, definitive explanations for the patterns observed cannot be provided.

The results of this study appear to differ from those of a study in which L. radiata luteola was found most often oriented normal to the flow (Tevesz et al. 1985). However, this mussel occurred in areas of the river associated with low-flow velocities (i.e., near shore, shallow water habitats). As such, the mussel might not be expected to be found streamlined since its locality reflects more stable conditions.

Other factors may be responsible for the orientations observed in this study. The positions of the inhalant and exhalant siphons with respect to the flow can be important in bivalve feeding (Wildish et al. 1987, Vincent et al. 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.

Conceivably, there could be a trade off made by mussels between optimal feeding and minimization of drag, depending on their orientation.

Mussel dislodgment is often attributed to seasonal floods (Roscoe and Redelings 1964, Valentine and Stansbery 1971, Thoms and 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 and Berg (1985) note that M. margaritifera 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.

Not only can burrowing depths vary with changing flows, but orientation may as well. There are presumably seasonal differences in the orientation of mussels that are related to spring and autumn flood events. In this study, mussels were sampled at low flows in late summer. If orientations change seasonally, then perhaps mussels in the stable river would be found more streamlined to the flow at times when flood flows occur.

There was a significant difference in the size of mussels between the two rivers (Fig. 5) with mussels in the Ausable River being larger than those in the Saugeen River. It is not known how the size of a mussel affects its susceptibility to dislodgment or its orientation. 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, found that the bivalves they sampled most likely represented older animals with orientations that had enhanced their survival. 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 who have survived as a function of benefits derived from their orientation (e.g., reduced dislodgment, enhanced filtration).

Differences in the distributions of adult and juvenile unionids in the substrate may reflect attempts to minimize dislodgment. Amyot and Downing (1991) showed that juveniles are often found to be endobenthic. Perhaps juveniles can reduce the effect of flow on them by remaining in the substrate.

Additional research is needed to further clarify the patterns observed in this study. Specific studies should be conducted to examine the patterns of flow around unionids at the substrate to identify the extent to which drag affects orientation. Experiments also could be conducted at flood conditions to examine the relationship between orientation and dislodgment or size and dislodgment. One also could determine the influence of one orientation over another on the feeding of unionids (e.g., Wildish et al. 1987). We found mussels at every measured orientation and it would be of interest to identify any trade offs a mussel may make in selecting an orientation.

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TABLE 1. Mean and standard errors of the proportion of shell surface area above the substrate for mussels in the Ausable and Saugeen rivers. Numbers of individuals measured for each species are in brackets.

SPECIES	MEAN EVENT ± S.E. (n)	MEAN STABLE ± 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. radiata	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 type	41.1±1.88 (19)	41.3±2.74 (26)

TABLE 2. Correlations of the size measures (length, width, and height) with the first principal component and the variations explained by each component from PCA.

Factor	Size Measure	Correlation Between Size Measure & Factor	Proportion of Variation Explained
	Width	0.981	
PC1	Height	0.976	0.95
	Length	0.973	

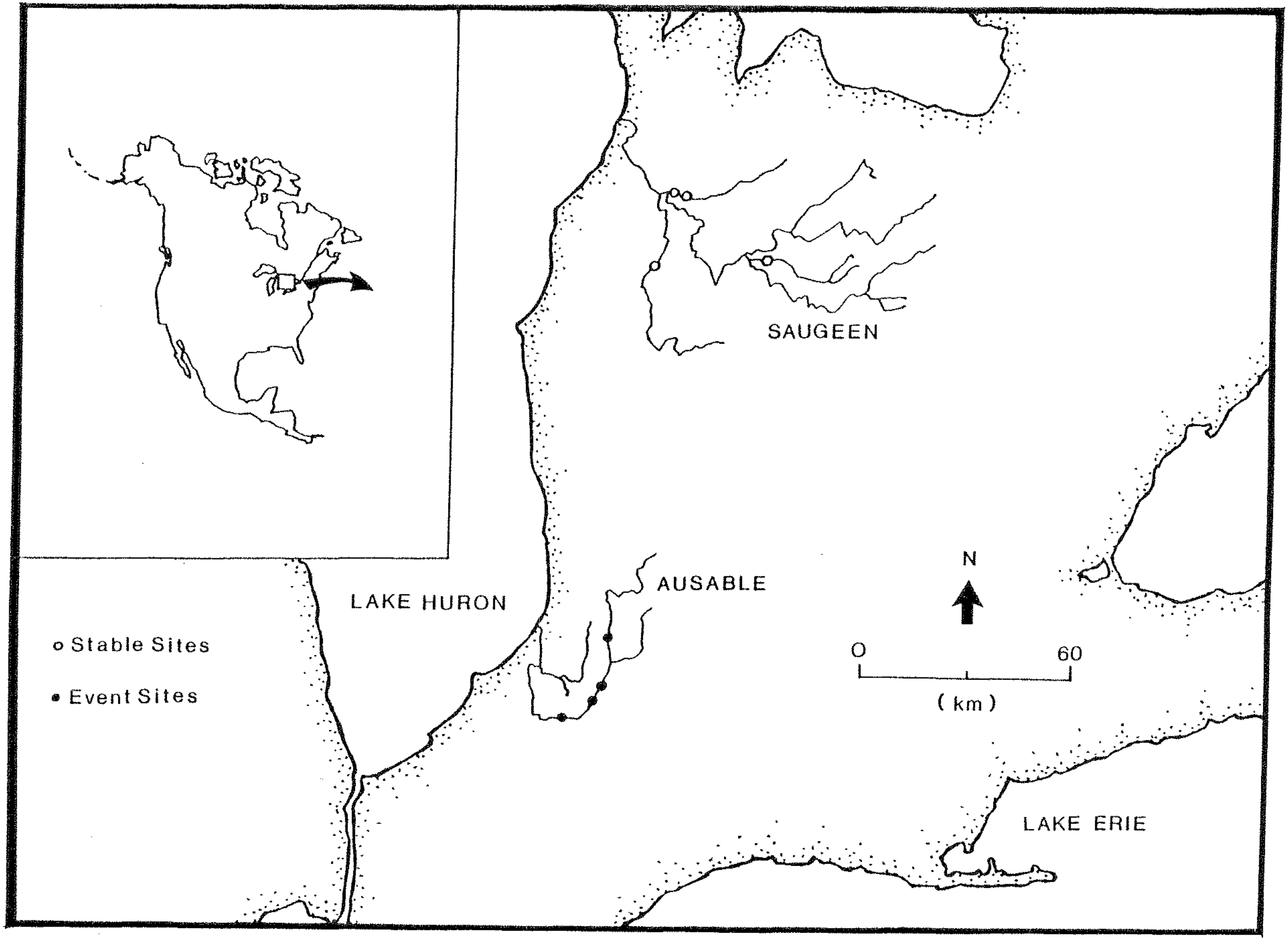
Fig. 1. Map of the study area indicating the four sites sampled for orientation in the Ausable River (Event) and Saugeen River (Stable).

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

Fig. 3. Schematic showing the three size measurements taken on each mussel.

Fig. 4. Frequency histograms of relative occurrence of mussels within each orientation for the Ausable River (EVENT) and Saugeen River (STABLE). Arrow represents the direction of flow at which measurements were taken.

Fig. 5. 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 $Sin^2\ \theta$ axis represent more streamlined to least streamlined orientations, moving from left to right on the axis.



SAUGEEN
AUSABLE
LAKE HURON
LAKE ERIE
N
0
60
(km)
Stable Sites
Event Sites

Fig. 1
[illegible] & Corkum

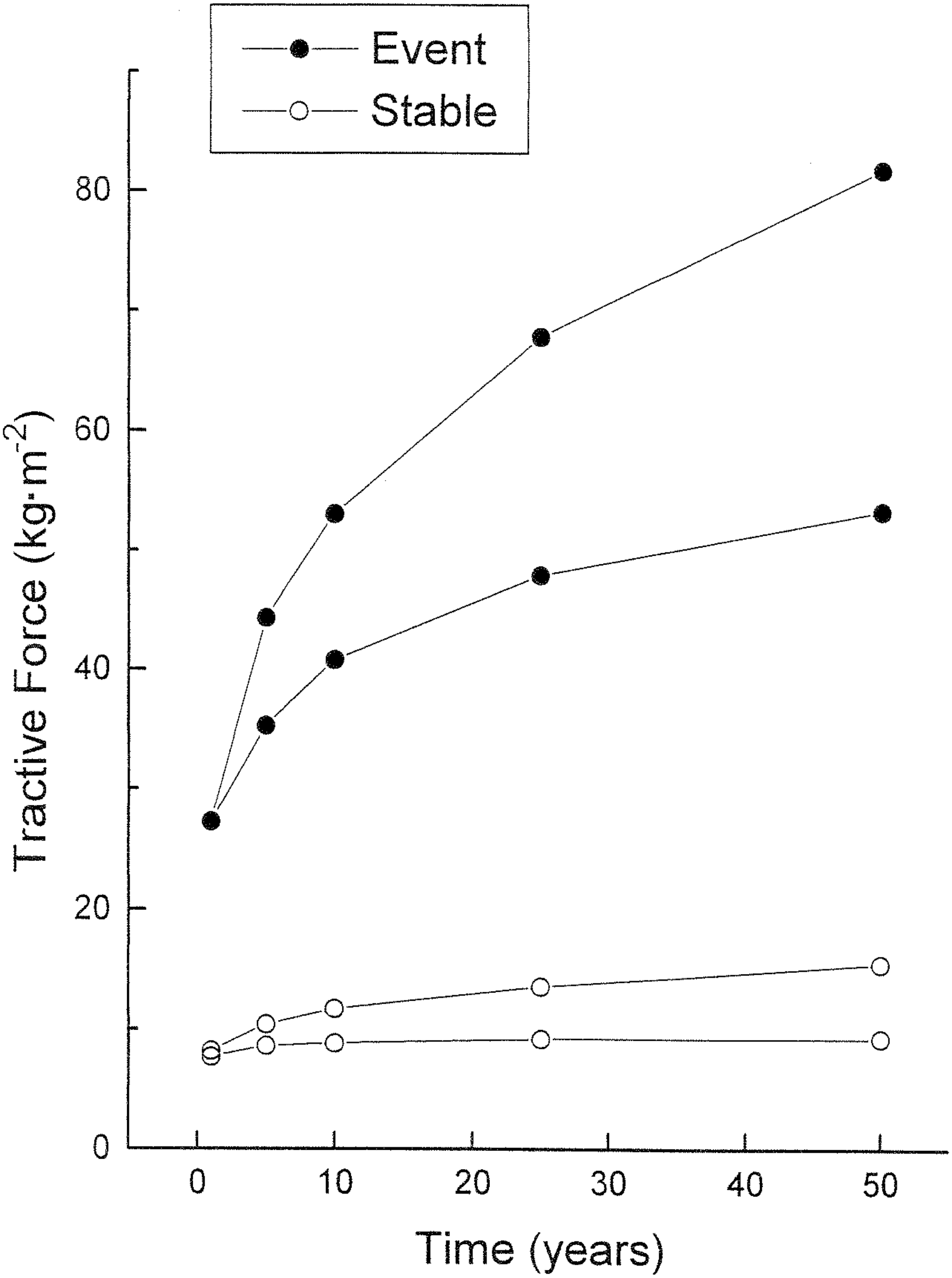

Event
Stable
Tractive Force (kg·m-2)
0
20
40
60
80
0
10
20
30
40
50
Time (years)

Fig. 2

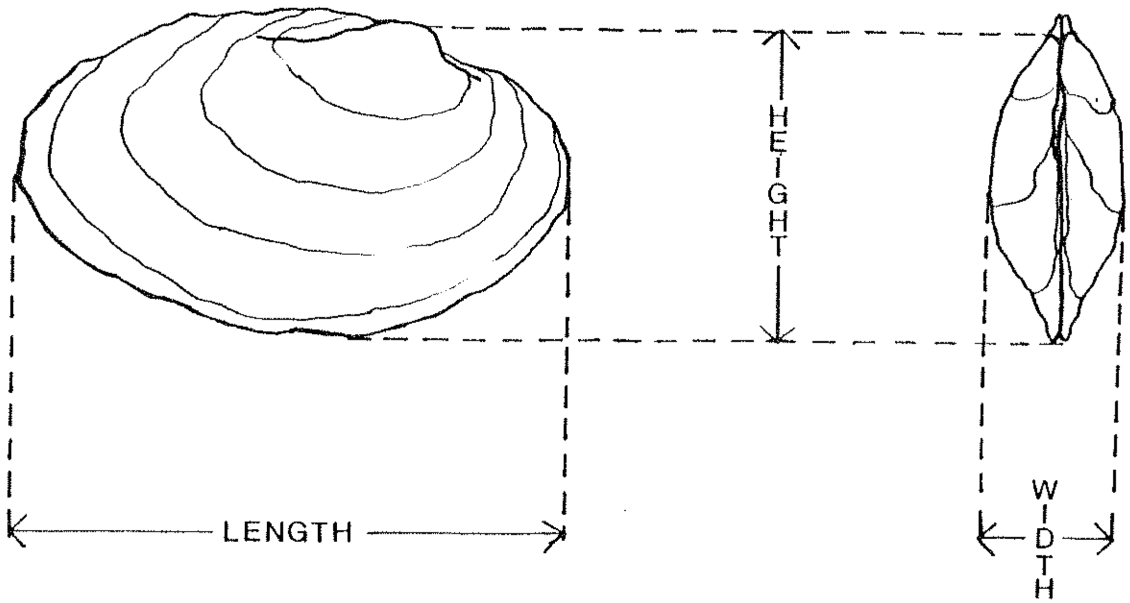


Fig. 3
D.R. ... & Corkum

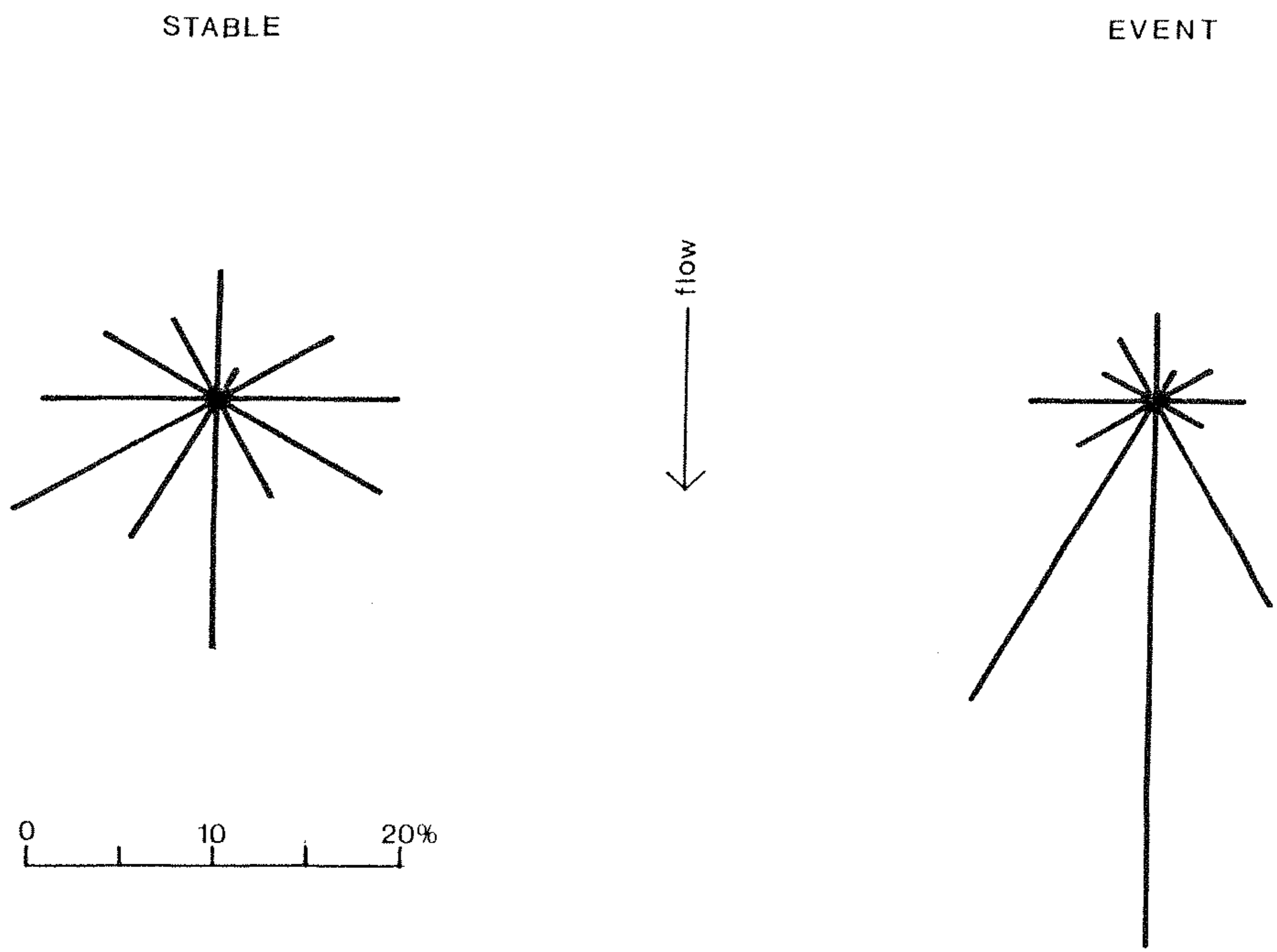


Fig. 4

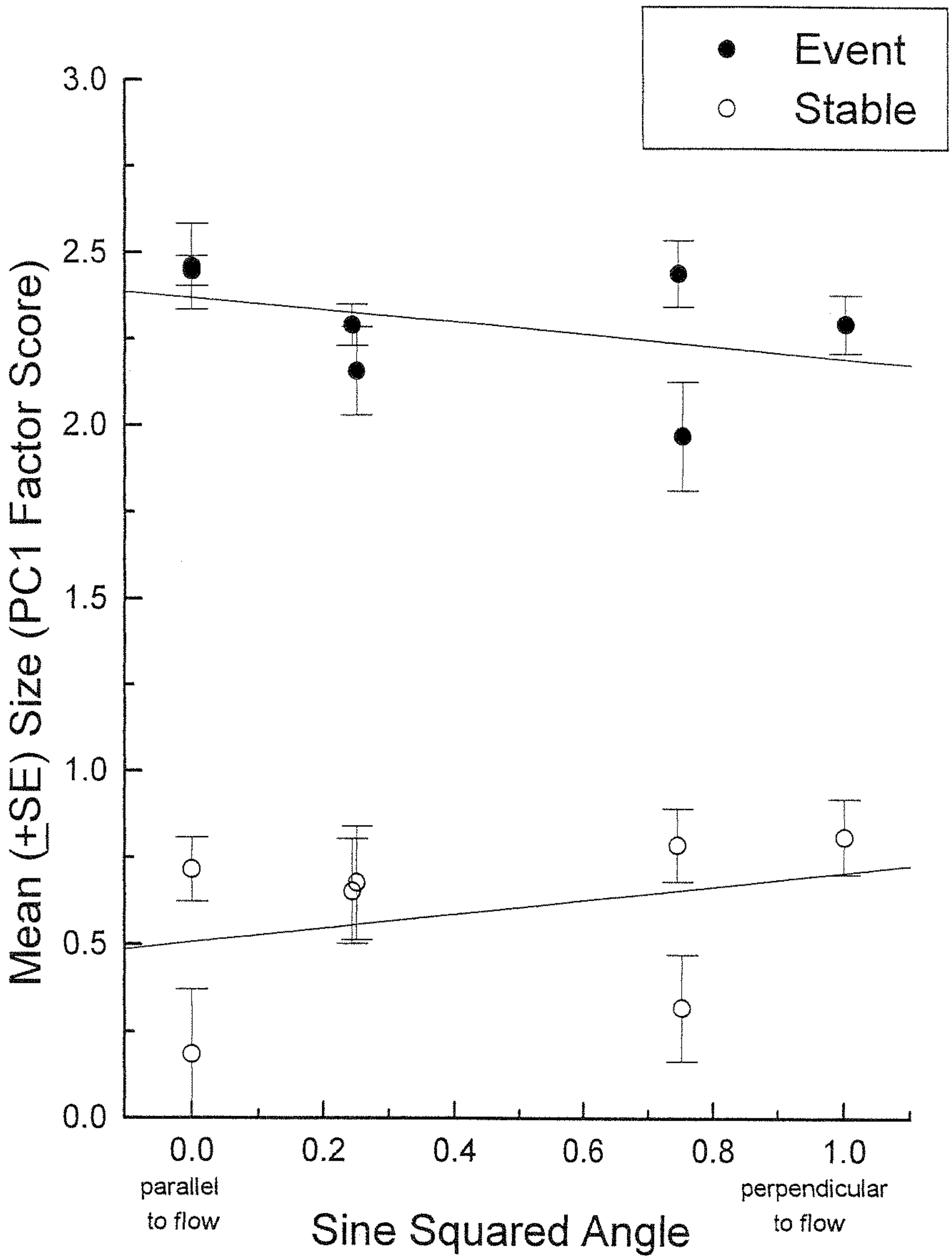

Event
Stable
Mean (±SE) Size (PC1 Factor Score)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0.0
0.2
0.4
0.6
0.8
1.0
parallel to flow
perpendicular to flow
Sine Squared Angle

Fig.5