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Digging with a vortex: Flow manipulation facilitates prey capture by a predatory stream mayfly

Abstract—The effect of rapid flow and substrate instability on the distribution of benthic organisms is viewed as negative. Larvae of the mayfly *Pseudiron centralis* McDunnough not only tolerate rapid flows and loosely consolidated shifting sands (typical features of the beds of large lowland rivers), but are unique in their ability to exploit these conditions to facilitate the capture of prey. Unusual posturing allows *Pseudiron* larvae to transform themselves from streamlined forms closely appressed to the sediment surface into bluff objects that project from the surface and cause local disruption of flow. By obstructing the flow in this way, a *Pseudiron* larva creates an energetic vortex whose erosive power is used to excavate pits in the loose sands. Small burrowing and interstitial invertebrates exposed by removal of sand grains in the pits are then attacked and consumed. Using a vortex as a digging tool allows *Pseudiron* larvae to exploit infaunal prey, although they lack morphologically specialized fossorial appendages.

In streams and rivers, many benthic organisms live in habitats (e.g. the upper surfaces of large stones) where they are directly exposed to rapidly flowing water. There are benefits of living in such habitats since respiration and removal of metabolic wastes is facilitated by flow (Hynes 1970; Vogel 1981; Nowell and Jumars 1984), but for many benthic organisms these benefits seem small relative to costs such as the risk of dislodgement or the energy expended to move and maintain position in rapid flows. Thus benthic invertebrates living in habitats exposed to the direct effects of flow are often described as having morphological or behavioral adaptations that allow them to cope or tolerate rapidly flowing water (e.g. Hynes 1970; Vogel 1981; Statzner and Holm 1982).

Among the harshest aquatic habitats in terms of flow environment are the large areas of noncohesive, shifting sands that typically dominate the beds of larger lowland rivers (Hynes 1970; Barton and Smith 1984). Substrate instability and the absence of any refuge from the flow makes these areas extremely difficult, both for surface dwellers and for animals that construct permanent tubes or retreats. Most species associated with these areas live beneath the surface of the sediments, either as burrowers or in the interstices between the grains of sand. One exception is the larva of the heptageniid mayfly *Pseudiron centralis* McDunnough, which frequents the surface of shifting sands in many North American rivers (Edmunds et al. 1976; Pescador 1985).

Pseudiron larvae have various unusual morphological adaptations such as extremely long tarsal claws and maxillary palps (Edmunds et al. 1976; Pescador 1985). It is their behavioral attributes, however, such as their choice of habitats and their predatory habits (almost all other mayflies being herbivores or detritivores), that make them unique. In the Sand River in east-central Alberta, larger *P. centralis* larvae are almost exclusively associated with areas of actively moving sand bedforms in the mainstream channel (Soluk and Clifford 1985) where they are specialist feeders on the chironomid larvae that live in the interstitial environment between the grains of sand (Soluk and Clifford 1984).

Chironomid larvae can occur in great abundance in shifting sands where they feed on diatoms, detritus, and probably each other (Benke et al. 1984; Soluk 1985). By sectioning frozen sediment cores Soluk (1985) found that ~80% of these chironomid larvae live in the first 10 cm below the surface of the sand. Although chiron-

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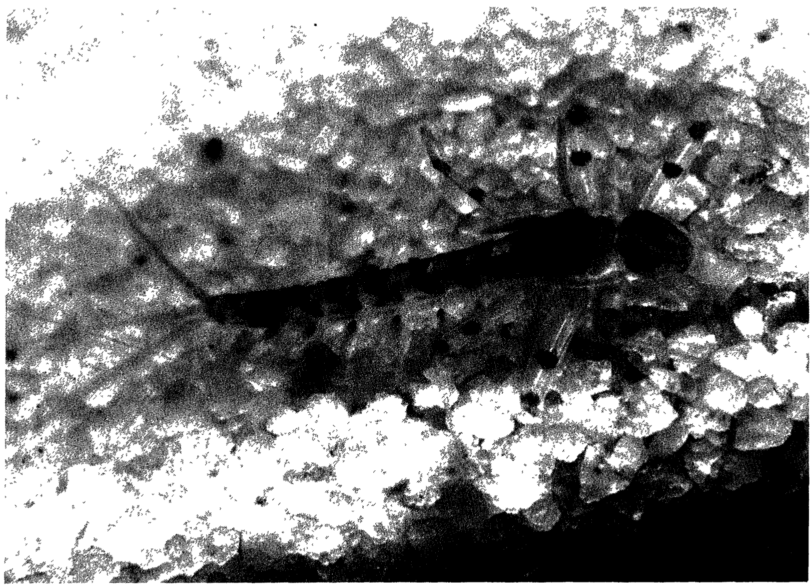


Fig. 1. Larva of *Pseudiron centralis* in typical resting position with tarsal claws anchored into the sand and the body closely appressed to the face of a sand dune. Direction of flow is from right to left. In this position, *Pseudiron* larvae present a flattened streamlined profile that minimizes resistance to the flow. Larva in the photograph is 15.0 mm long.

omid larvae may occur in great abundance beneath shifting sands, they do not frequent the surface of these sediments and if placed upon them, rapidly re-enter (D. A. Soluk pers. obs.). Thus, potential predators of these chironomid larvae must either excavate them from the sediments or wait to capture individuals temporarily exposed as sand is eroded from the upstream side and deposited on the downstream side of a sand dune or ripple.

Given that *Pseudiron* larvae possess no obvious digging appendages, they might appear to be totally dependent on such erosion to expose their prey. Observation of foraging *Pseudiron* larvae suggests, however, that they have an active alternative. In this note we discuss the unique way in which *P. centralis* larvae can manipulate flow in order to increase erosion locally and thus facilitate capture of chironomid larvae.

All *P. centralis* larvae used in the study were collected from the mouth of the Sand River (*see* Soluk and Clifford 1984). Larvae were observed in the laboratory in air-powered recirculating stream tanks (similar to that described by Soluk and Collins 1988) and an artificial stream (elliptical shape; channel width, 11.0 cm; depth, 10.0 cm) powered by a paddle wheel (Ciborowski 1983).

Photographs of feeding behavior were obtained with a 35-mm camera and electronic flash. To enhance visibility we photographed *P. centralis* larvae on white sand of 0.5–2.0-mm grain size, somewhat coarser than typical of natural shifting sands (mostly 0.25–1.00-mm grain size). All other observations were made on sand collected from the bed of the Sand River.

Flow velocities 1 cm or more above the substrate were obtained with a Novonics model 403 (Nixon Instr. Ltd.) propeller-driven current meter. Boundary layers are not uniform over sand bedforms and at any fixed point velocities may vary with time because of bedform migration, so flow in the vicinity of a feeding larva is not easily characterized. One way to avoid this problem of flow characterization over bedforms is to measure flow velocities near enough to the substrate that they reflect flows encountered by the animal. Thus, velocities 2–4 mm above the sand surface and 1–2 cm in front of a larva were measured with a hot-bead thermistor (Vogel 1981) attached to a

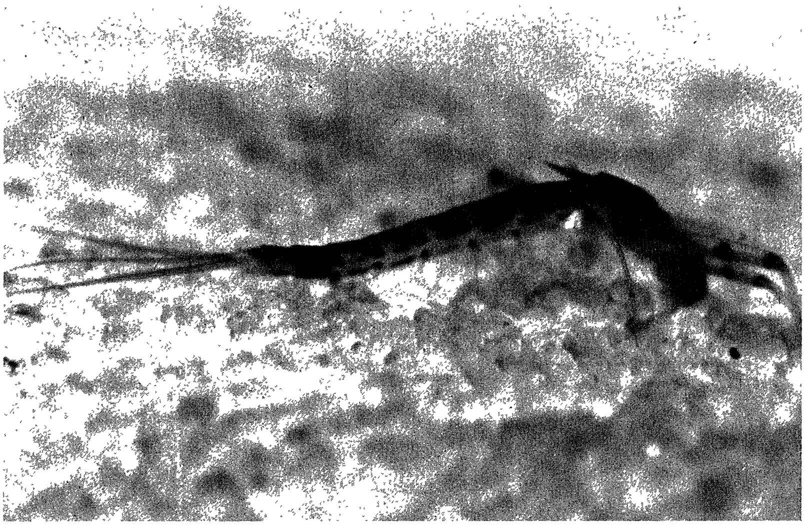


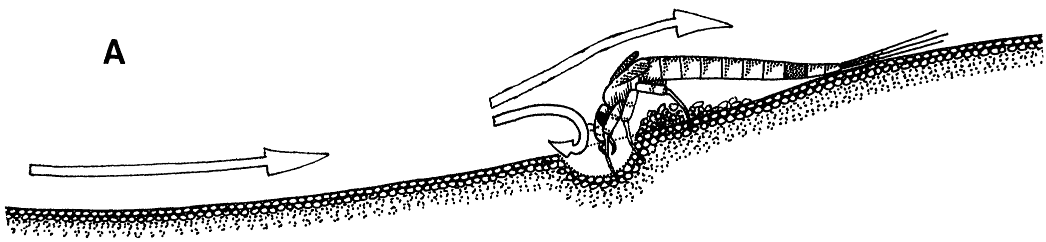
Fig. 2. Larva of *Pseudiron centralis* in typical arched feeding position on the upstream (erosional) face of sand dune. Direction of flow is from right to left and slightly toward the viewer. By assuming this position, a *Pseudiron* larva presents a bluff profile that projects higher into the boundary layer and deflects the flow.

micromanipulator. These measurements were carried out in an air-powered recirculating tank (working section length, 100 cm; width, 63 cm; depth, 6 cm minimum over dunes; water temperature, 17°C).

Observations in both the laboratory and field indicated that *Pseudiron* larvae frequent upstream ("windward") faces of small sand dunes and ripples where they spend much of their time resting flat against the sediment (Fig. 1) or moving about the dune in a crablike manner. Larvae usually faced headfirst into the flow and if the current swept them from the dune they were able to swim rapidly back to the bottom. In laboratory streams larvae were seldom swept from dunes and ripples even when near-bottom flows (2–4 mm above the sand surface) in recirculating flumes were as high as 15 cm s^{-1}. In relatively slow flowing or still water, foraging *P. centralis* larvae would rapidly consume small enchytraeid worms and chironomid larvae placed on the surface of the sand, but they made no apparent attempts to dig in the loose sand.

When current speed was high enough to cause significant movement of sand (0.25–1.00-mm grain size) on the upstream face of the dune (>14 cm s^{-1} 1 cm above upstream side of dunes), *Pseudiron* larvae arched their bodies up into the flow and bent their heads steeply downward (Fig. 2). An immediate consequence was that sand in front of and beneath the head was swept away, leaving a small shallow pit 1–2 mm deep (Fig. 3A). Larvae remained in the arched position (projecting 4–5 mm above the sand surface) while moving slowly backward toward the crest of the small dune, leaving a shallow groove in its upstream face (Fig. 3B). The long maxillary palps of *Pseudiron* larvae (Fig. 4) were thrust into the sediments at the bottom of the pit and appeared to function in detecting and removing chironomid larvae exposed by the sudden removal of the upper layer of sand. When larvae detected a chironomid in the pit they pounced on it, drew it from the sediments and consumed it whole. During this whole foraging process, neither the legs nor the mouthparts of the *Pseudiron* larvae appeared to be engaged in the active removal of sand from the pit.

Given that *Pseudiron* larvae are not using their appendages to move sand, then what is excavating the pit in which the larvae are foraging? We suggest that *Pseudiron* larvae were able to excavate sediments because of the way they interrupt flows within the boundary layer. By assuming an unusual, arched posture, a *Pseudiron* larva transforms itself from a streamlined shape, lying



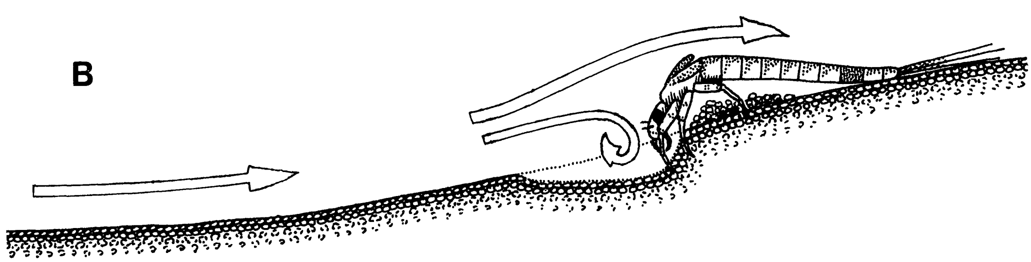


Fig. 3. Diagrammatic representation of feeding behavior of *Pseudiron centralis*. Arrows indicate direction of flow. Larva in arched position creates a solenoidal vortex that spins out laterally on both sides of the head. The vortex rapidly erodes sand from under the mouthparts, forming a pit (A) in which the *Pseudiron* larva probes for the small, interstitial chironomids on which it feeds. Subsequent backward movement of larvae expands the pit (B) temporarily leaving a shallow groove up the face of the dune.

against the surface of the sediments (Fig. 1), into a bluff body (Fig. 2) (Reynolds number, Re, ~150–300 based on larval headwidth) that projects up from the bottom and impedes the flow.

In situations where Re is >10, bluff objects projecting up through boundary flows create a characteristic solenoidal vortex (usually referred to as a horseshoe vortex) that forms on either side of the stagnation point, wraps around the front and sides, and eventually rises up behind the object (*see* Chance and Craig 1986). Flow in this vortex locally increases tractive and lifting forces on the sediments immediately in front of and around the sides of objects projecting into the flow (Nowell and Jumars 1984). In loosely consolidated sediments this increase in shear stress will move material from around that part of the object (usually the base) lowest in the boundary layer. Common examples of the action of this vortex can be seen in the grooves that form in the sand around stones on beaches, or in the way snow is swept from around the bases of telephone poles during a winter storm.

For *Pseudiron* larvae in the arched position, the tractive and lifting forces in the horseshoe vortex lift and displace sand grains from around and beneath the head (Fig. 3A), creating the shallow pit into which larvae thrust their palps. By directing flow into a

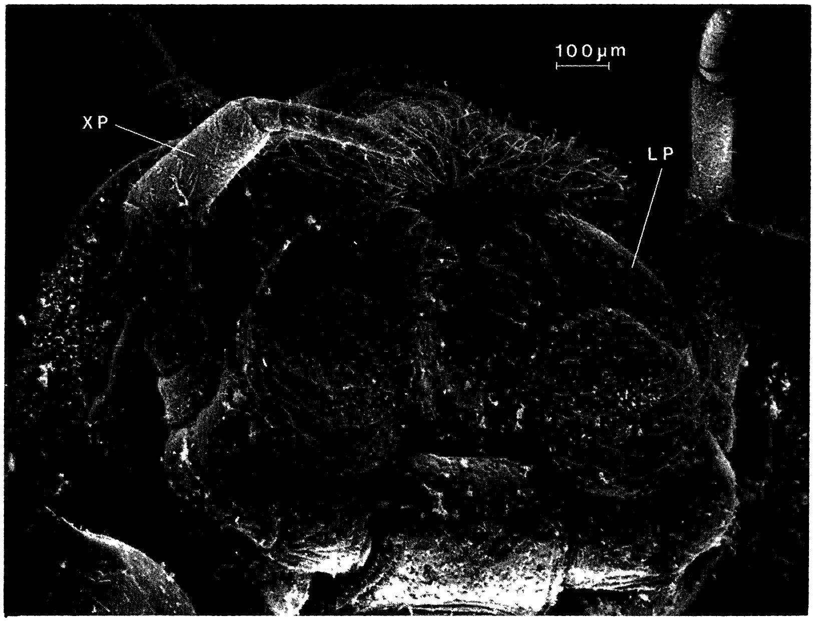


Fig. 4. Scanning electron micrograph of the ventral surface of the head of *Pseudiron centralis.* The long maxillary palps (XP) are used to probe in the sediments and manipulate prey. Labial palps (LP) are also clearly visible.

vortex *Pseudiron* larvae were able to dig rapidly for prey without using their appendages. The unusual ability to manipulate vortices allows *Pseudiron* larvae to exploit the combination of noncohesive, shifting sands and rapid flow near the substrate, two features normally thought to be major factors restricting the ability of benthic organisms to survive in sandy habitats.

The hydraulic processes involved in the feeding behavior of *Pseudiron* larvae can be simulated by using a small (~1 : 1) model of the head and thorax (legs removed) of a large *Pseudiron* larva (headwidth, 2.5 mm). The model was constructed by flattening a small steel rod and then filing it to approximate the shape of the head capsule and thorax of a *Pseudiron* larva. The model was attached to a micromanipulator via a steel rod (1.6-mm diam) soldered onto the model at about the same position and angle that the abdomen of a feeding *Pseudiron* larvae would assume (Figs. 2, 3). The model was then lowered to the upstream face of a small dune so that it was at an angle of between 50 and 60° relative to the dune surface (approximate angle assumed by the head and thorax of a feeding *Pseudiron* larva, Figs. 2, 3) and its performance was recorded on videotape. In a current velocity of 5–7 cm s^{-1} (2–4 mm above the substrate, measured from particle tracks), the model was quite effective in excavating pits 1–2 mm deep and was able to move sand grains >0.5 mm in diameter.

Horseshoe-shaped vortices form in front of any bluff object that projects up through the boundary layer to intercept higher velocity flows above the substrate, and *Pseudiron* larvae are not unique in manipulating vortices. For example, suspension-feeding larvae of black flies (Diptera: Simuliidae) and some marine polychaetes appear to use vortices to resuspend settled material (Carey 1983; Chance and Craig 1986). Larvae of at least one other type of mayfly (*Ametropus neavei*) may enhance its ability to suspension feed by using vortices to concentrate and transport fine particles to its filtering devices (Soluk and Craig 1988). Ours is the first documentation, however, of creation and use of a vortex by a predatory invertebrate. The process of excavation using a vortex seems such a simple and elegant way of exploiting a hydrodynamic phenomenon that it is unlikely to be unique to *Pseudiron* larvae.

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