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Mechanics and Ecological Role of Swimming Behavior in the Caddisfly Larvae *Triaenodes tardus*

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Abstract Caddisfly larvae are typically restricted to benthic microhabitats due to the presence of mobile tubular cases constructed out of mineral or organic material. Members of one family (Leptoceridae) use setae on extended metathoracic legs to swim. We describe the swimming behavior of a North American caddisfly, *Triaenodes tardus*, and experimentally evaluate two hypotheses proposed to explain this behavior. *Triaenodes* swam 1.47 cm/s, while carrying almost twice their mass in the case material. The larvae employ a stereotypic sequence of motions that likely reduce resistance during the upstroke and increases forward momentum during the downstroke. When placed on substrates of different sizes, larvae swam more on fine sediments but did not elevate off the sediment. After larvae were provided with living or artificial vegetation, the number of swimming bouts decreased compared to a pre-treatment observation period. These results indicate swimming likely does not function to facilitate movement off fine sediments, but rather, helps larvae locate and move between aquatic macrophytes which are the primary habitat of this, and other, swimming species.

Keywords Trichoptera · leptoceridae · *Triaenodes* · swimming · substrate · macrophyte

Selection is expected to favor morphological, physiological, or behavioral modifications that increase an organism's chance of surviving and reproducing in a particular environment (Darwin 1859). Such modifications may include mechanisms to tolerate abiotic environmental conditions (eg. Cloudsly-Thompson 1956; Lillywhite 1970), escape, avoid, or deter predation (eg. Brodie 1983), or increase

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ability to procure resources such as food or mates (eg. Darwin 1871; Grant et al. 1976). These "adaptations" are likely to fit an organism to its environment by reducing the costs and increasing the benefits associated with operating in a particular ecological context. Nevertheless, evolution can only operate in the framework of previous adaptive change and providing a perfect fit between the organism and the environment is unlikely (Freeman and Herron 2007).

For most organisms, locomotion, and corresponding physiology and morphology, is critically important to most daily activities, and is likely to have been molded by natural selection to facilitate survival of the species (Bennett 1989). For example, the fast-start of fishes can facilitate prey capture (Domenici and Blake 1997; Blake 2004), and can be crucial to surviving predatory encounters (O'Steen et al. 2002). However, locomotion is constrained by past selective pressures and evolutionary change (Carrier 1987). For the larvae of the caddisflies (Trichoptera) the primary feature that led to their diversification, the presence of a protective case (Wiggins 2004), is also likely to severely limit locomotory potential (Dodds and Hisaw 1925).

The majority of the caddisfly life cycle consists of an aquatic larval stage where energy and growth are acquired to facilitate reproduction (Wiggins 1996). The larvae of many species occupy the benthic regions of aquatic environments where they primarily consume dead organic material (Betten 1934; Mackay and Wiggins 1979). Using silk, caddisfly larvae (Integripalpia) construct portable shelters out of plant or mineral material that function in defense (Johansson 1991; Otto and Svensson 1980; Wissinger et al. 2006) and also facilitate respiration (Williams et al. 1987). This "mobile home" generally restricts locomotion, and many caddisflies could be characterized as slow and ungainly organisms. Larvae typically move by crawling on the substrate, and even the few case-less predatory species continue to utilize this form of locomotion. Despite the locomotory restrictions imbued by the case, members of one family have overcome the problems associated with limited motility.

The Leptoceridae have extremely elongated posterior legs (metathoracic legs) and some have extensive concentrations of setae on the femur, tibia and tarsus (Tindall 1964). These setae, known as "swimming hairs", enable the larvae to swim via rapid forward and backward movements of these legs (Betten 1934; Tindall 1964). Although larvae might be expected to discard the case to ease swimming, the case is retained and carried with them during swimming bouts. *Triaenodes* is commonly found in the roots or vegetation of lentic and lotic macrophytes (McGaha 1952; Glover 1996). In these habitats fine-grained or shifting sediments are common and swimming has been hypothesized to help these caddisflies move efficiently on these substrates (Haddock 1977). Alternatively, because the larvae are herbivorous, swimming may function in movement and dispersal among aquatic vegetation in search of food or shelter (Mackay and Wiggins 1979; Wiggins 1996; Glover 1996).

Swimming behavior has been reported in several Leptocerid species and the presence of swimming hairs is an important diagnostic characteristic for the group. However, limited information exists about the physical properties and function of the behavior. Tindall (1964) provides the only known detailed study of the swimming behavior by a caddisfly, *Triaenodes bicolor*. However, it is unknown if the mechanics of swimming are similar in other species. Moreover, many authors have hypothesized about the ecological role of swimming in caddisflies, but experimental

evidence is lacking. In this study, we describe the mechanics of swimming behavior in the North American caddisfly *Triaenodes tardus* and experimentally evaluate the two hypotheses (avoiding fine sediments vs. dispersal among vegetation) proposed to explain the function of this behavior. *Triaenodes* are typically herbivorous, and we hypothesize these caddisflies utilize swimming behavior to move between aquatic vegetation for food and shelter.

Methods

Experimental Animals

All larval caddisflies (*Triaenodes tardus*) used in this study were collected from a shallow pond near Preston, Idaho, USA, during August 2010. Animals were caught using a combination of dip-net and seine sampling techniques, and were placed in 739 ml plastic holding containers with pond water and vegetation, for transportation to Utah State University. All larval caddisflies were kept in a communal 38 l glass tank with vegetation (*Myriophyllum spicatum*) from the natural pond habitat, course sand, and approximately 15.0 l of filtered tap water. The tank was located in an environmentally controlled room kept at 17–18°C, with a photoperiod of 12 h light : 12 h dark. The total weight, case length, case weight, and body weight of 10 representative animals were recorded (Table 1).

Experiment 1: Physical Characterization of Swimming Stroke

The swimming behavior of larval caddisflies (*Triaenodes tardus*) was characterized by taking a series of macro digital photographs of animals swimming in a narrow glass tank, using a Nikon™ D70 digital camera with a 150 mm lens set at a shutter speed of approximately 1/800 s at F-stop 14. From these photographs, line drawings of the relative position of the swimming legs in each physical stage of the swimming stroke were illustrated.

To determine the speed with which caddisflies complete a single swim stroke (one upward and downward cycle of the limbs), swimming behavior was video-recorded using a Canon™ Vixia HFS10 digital video camera with a 58 mm 0.45× macro lens, imported into a personal computer, and slowed down 5× with iMovie™ digital video editing software (24 frames per second). A representative sample of 10 distinct

Table 1 Morphological measurements of larval caddisflies used in behavioral trials

Morphological Measurements	Min	Max	Mean ± SE
Total case length (cm)	0.96	2.40	1.44±0.14
Total mass (larva + case) (mg)	12.18	40.26	22.17±2.50
Larva mass (mg)	3.73	10.25	6.39±0.68
Case mass (mg)	7.10	20.11	12.18±1.42
Case : Caddisfly mass Ratio	1.26	2.80	1.95±0.17

swimming bouts lasting 10 s were recorded from three caddisflies. These video segments were watched at this decreased speed by an observer who counted the number of swimming strokes made by the animal. This value was then divided by ten to determine the average number of swim strokes completed by each caddisfly per second.

The physical aspects of caddisfly swimming (e.g. distance swam, time swam, average velocity) were determined by placing an individual caddisfly larva at the beginning of a rectangular plexiglass raceway trough (63 cm×2 cm×3 cm deep) filled with 200 ml of filtered and conditioned tap water, and allowed to swim down the length of the trough. For each swimming bout, the start and end location of the caddisfly was noted by an observer using a cm ruler placed directly underneath the trough. The time to complete each swimming bout was recorded with a digital stopwatch by a second observer. Measurements for the first three swimming bouts each caddisfly made were recorded. This experimental regime was repeated for a total of 10 animals. At the end of the experiment, the experimental animals were blotted dry, and the total weight, case weight, larva weight, and case length were recorded for each caddisfly. All experimental animals were preserved for identification. We calculated the mean distance, time and velocity of the three swimming bouts performed by each caddisfly (Table 2).

Experiment 2: Swimming Performance on Different Substrates

To determine what effect substrate had on swimming propensity and performance, swimming behavior of larval caddisflies was recorded on one of three different substrate types: fine sand (Mean diameter ± SE=0.47±0.06 mm), medium pebbles (2.91±0.27 mm), or coarse gravel (11.78±1.31 mm). Ten grains from each substrate type were measured with an ocular micrometer. The test chamber consisted of a 3.8 l glass jar (24 cm tall×15 cm diameter) filled with 3.5 cm of a randomly chosen substrate (fine, medium, or coarse) and 2.0 l of filtered tap water. A caddisfly was haphazardly selected from the communal holding tank using forceps and dropped into the glass jar. Lightly grasping caddisfly larvae around their case simulates a predation event, and caddisflies enter and remain in the case for several seconds after

Table 2 Summary of physical measurements of larval caddisfly swimming performed in experiment 1 and the maximum time and distance swam in one swimming bout (recorded from data from all experiments). App = Approximate

Physical Measurement	Min	Max	Mean ± SE
Distance swam (cm)	2.20	18.20	6.39±0.72
Time spent swimming (s)	1.45	330.00	4.62±0.59
Velocity (cm/s)	0.59	2.11	1.47±0.06
Leg beats per second	1.65	2.20	1.93±0.06
Maximum time spent swimming (s)	–	335	–
App. Maximum Distance Swam (cm)[a]	–	492.5	–

[a] Maximum distance calculated based on maximum time recorded and average caddisfly swimming velocity

release (Gall and Brodie 2009). This technique ensured that caddisflies would remain in their case and not begin swimming until reaching the substrate at the bottom of the jar. Behavioral trials began when the entire caddisfly case first touched the substrate, and continued for 20 min. After a trial began we recorded latency to swim (swim = repeated cycles of swim strokes with the metathoracic swimming legs), time spent swimming (both touching and elevated off the substrate), and the number of swimming bouts. At the end of each trial, the case length was measured; no caddisfly was tested more than once.

We compared the latency to swim, time spent swimming, number of swimming bouts, and proportion of swimming bouts off the substrate (versus swimming bouts in which the caddisfly did not lift off the substrate) for caddisflies positioned on fine, medium, and course substrates using one-way ANOVA followed by Holm-Sidak multiple comparisons in Sigmaplot 11.0 (Systat Software, Inc., Chicago, IL, USA). Latency to swim, time spent swimming, and number of swimming bouts were square-root transformed to meet assumptions of normality and homoscedasticity.

Experiment 3: Propensity of Swimming Behavior in Response to Presence of Plant

We exposed caddisfly larvae to living and silk plants to determine the effect habitat structure has on swimming behavior. Behavioral trials were conducted in 3.8 l glass jars (24 cm tall×15 cm diameter). Each jar was filled with 3.5 cm of medium pebble substrate and 3.0 l of filtered conditioned water. Caddisflies were exposed to one of three plant treatments: glass rod (control), artificial plant (silk), or live plant (*Myriophyllum spicatum*). Three holes (1 cm) were cut into the lid of the jar. The holes were spaced 7.5 cm apart forming a triangle. A 22 cm glass stir rod was inserted into each hole and glued in place forming a vertical structure that could be inserted into the glass jar during the trial, exposing caddisflies to the appropriate treatment. For the live plant treatment, a 20 cm long segment of live *Myriophyllum spicatum* was attached to each rod using 3 plastic zip ties. Likewise, in the artificial plant treatment, a 20.0 cm long segment of an artificial plant composed of wire and silk, which closely resembled *M. spicatum* in leaf size and structure, was attached to each glass rod using zip ties. Three zip ties were also attached to each glass rod in the glass rod treatment.

Prior to testing, a treatment was randomly selected and a caddisfly larva was removed from the holding tank and dropped into the experimental jar. After the initiation of the trial (see experiment 2), we recorded the behavior of the caddisfly (time spent swimming, number of swimming bouts, time crawling on the substrate, and time resting on the substrate) in an 8 min pre-treatment observation period. After this 8 min pre-treatment period, the plant (live or artificial) or glass rod treatment was introduced to the jar, and the behavior of the caddisfly was recorded for a second 8 min post-treatment period. During the post-treatment observation we recorded the following behaviors: time spent swimming, number of swimming bouts, time crawling on the treatment, time crawling on the substrate, time resting on the treatment and time resting on the substrate. At the end of this second 8 min period, the total length of each caddisfly was measured. The glass rods were removed from the jar and the jar, substrate and treatment were thoroughly rinsed with filtered tap water before the next trial commenced. Each treatment was

replicated 9 times, and individual caddisflies were tested only once. Several caddisflies pupated between the second and third experiment, therefore, we tested 12 caddisflies used in experiment two (substrate experiment) in experiment three (plant experiment). Four days separated experiment two and experiment three, and caddisflies were never retested within an experiment.

We calculated the change in time spent swimming and change in the number of swimming bouts by subtracting pre-treatment activity from post-treatment activity. Change in time swimming did not meet the assumption of normality so a nonparametric Kruskal-Wallis test was performed. The change in the number of swimming bouts met assumptions for parametric statistics and was analyzed using a one-way ANOVA followed by Holm-Sidak multiple comparisons. To evaluate whether caddisflies initially swim to located food resources or shelter, we compared the time caddisflies spent in the live plants versus artificial plants with a Mann-Whitney U-test. Sigmaplot 11.0 (Systat Software, Inc., Chicago, IL, USA) was used for all analyses.

Results

Experiment 1: Physical Characterization of Stroke Behavior

Larval *Triaenodes tardus* swim in the water column through a series of stereotypic upstroke and downstroke movements of the metathoracic legs (Fig. 1). These movements are enhanced through the use of two rows (V-shape) of downward facing setae (Fig. 2c), which fold inwards during the upstroke, minimizing resistance (Figs. 1, 2b), and open during the downstroke, providing maximum forward momentum. The metathoracic tibia and tarsus fold inward during the upstroke (Fig. 1 #4), further reducing drag and minimizing the time required to complete an upstroke. The number of complete swimming strokes (up and down; Fig. 1) averages 1.93 per second (n=10; SE=0.056). Cases from the larvae used to record swimming mechanics weighed on average 1.95 (n=10; SE=0.17) times the mass of the organism (Table 1). In the experimental raceway, caddisflies swam an average of 4.62 s (n=10; SE=0.59) and traveled 6.39 cm (n=10; SE=0.72), yielding an average velocity of 1.47 cm/s (n=10; SE=0.06; Table 2). The maximum swimming velocity achieved by any caddisfly during the experiment was 2.11 cm/s.

Experiment 2: Swimming Performance on Different Substrates

There were significant differences between the three substrate treatments for latency to swim (F=10.20, P<0.001, Fig. 3a), time spent swimming (F=3.63, P=0.040, Fig. 3b), number of swim bouts (F=7.495, P=0.003, Fig. 3c), and proportion swim bouts that occurred off the substrate (F=4.12, P=0.028, Fig. 3d). Caddisflies exposed to fine or medium grained substrates initiated swimming sooner, spent more time swimming, and swam more often than caddisflies exposed to a coarse gravel substrate (Fig. 3a–c). Despite spending the most time swimming (Fig. 3b), caddisflies exposed to the fine substrate spent less of that time swimming in the

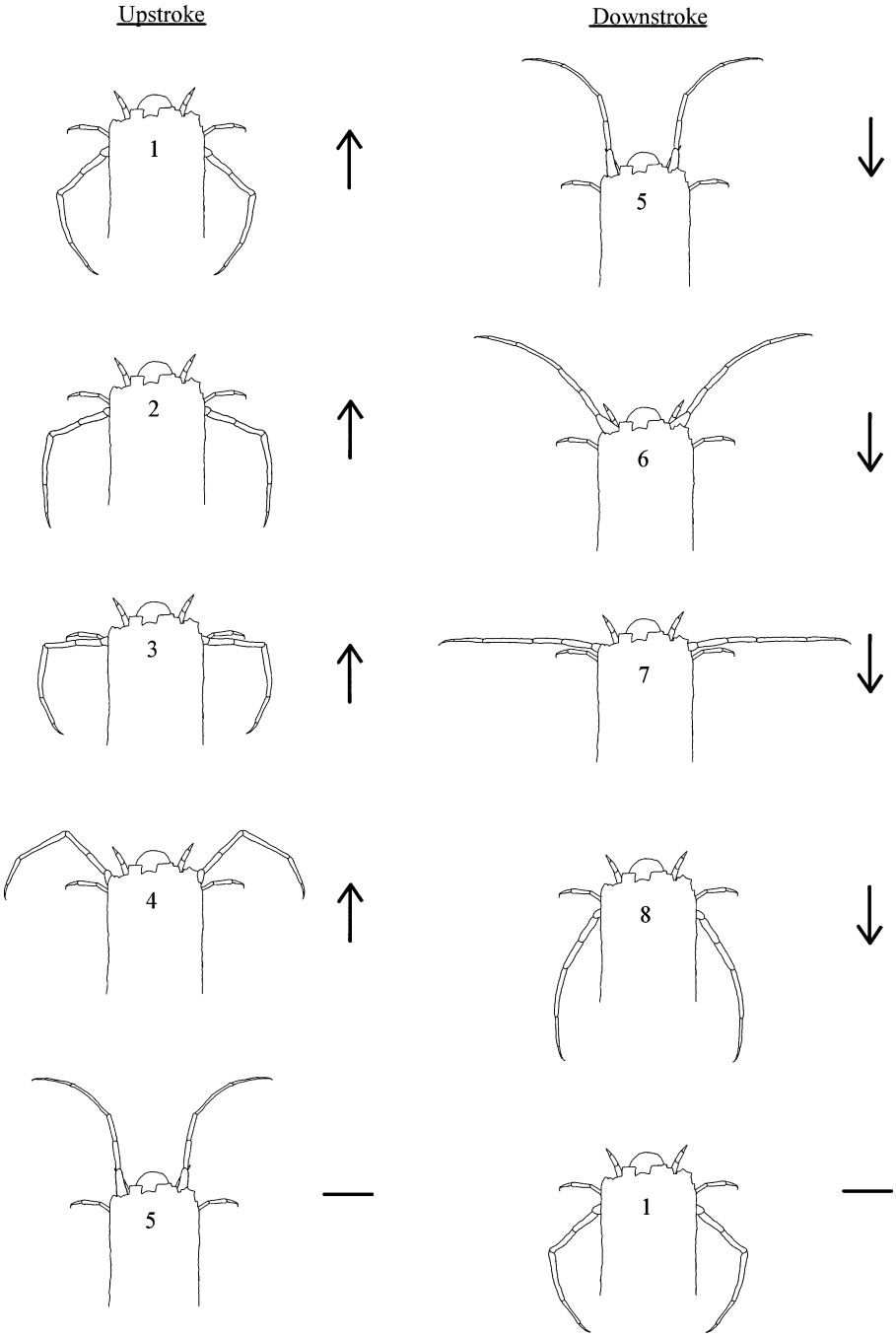

Fig. 1 Line drawings showing characteristic upstroke and downstroke positioning of the metathoracic swimming legs of larval *Triaenodes tardus* during a swimming bout. Numbers indicate order of leg position during swimming stroke, and arrows indicate direction of leg movement. Line drawings by B.F. McIvor

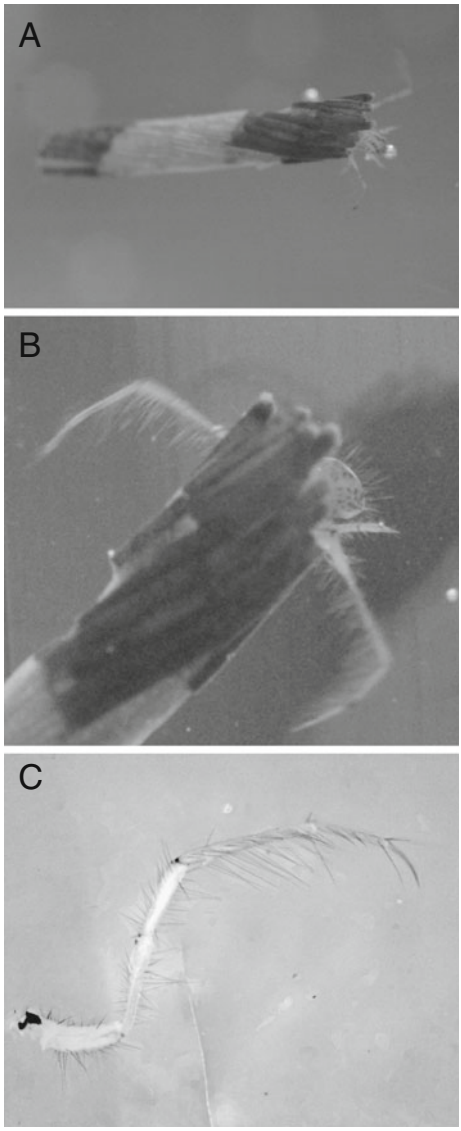

Fig. 2 Swimming behavior of the larval caddisfly (*Triaenodes tardus*). **a**. swimming over substrate. **b**. metathoracic swimming legs in characteristic upstroke action. **c**. detail of metathoracic swimming leg showing rows of setae

water column, and most of their time swimming on the substrate compared to caddisflies on medium and course substrates (Fig. 3d).

Experiment 3: Propensity of Swimming Behavior in Response to Presence of Plants

Caddisflies exposed to living and artificial plants after the 8 min pre-treatment period reduced the number of swimming bouts compared to caddisflies in the glass-rod control treatment (F=4.09, P=0.030, Fig. 4). Caddisflies also reduced the total time spent swimming when provided with artificial or live plants, however this response variable is not significant (H=2.27, P=0.321, Fig. 4). The reduction in swimming

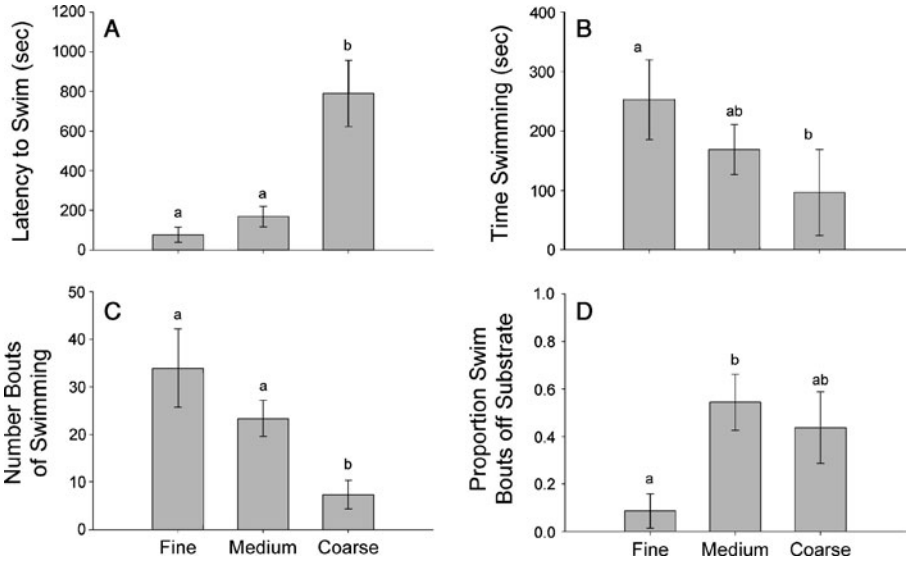

Fig. 3 **a** Latency to swim (mean ± SE), **b** total time spent swimming (mean ± 1 SE), **c** number of swimming bouts (mean ± 1 SE), and **d** proportion of swimming bouts that were elevated off the substrate (mean ± SE) for larval *Triaenodes tardus* exposed to fine sand (fine), medium pebbles (medium), or coarse gravel (coarse). Different letters above bars indicate significant differences between treatments (one-way ANOVA, Holm-Sidak post-hoc test, all $P<0.015$)

following plant introductions was associated with the detection, via swimming, of the plants (Fig. 5). After brushing into a plant, a larva would rotate in the direction of the stimulus and grasp the plant. After grasping the plant, larvae often remained inactive or crawled about the plant. In some cases, larvae that crawled to the end of a leaf would swim to a higher leaf or to a completely new plant. Caddisflies spent a

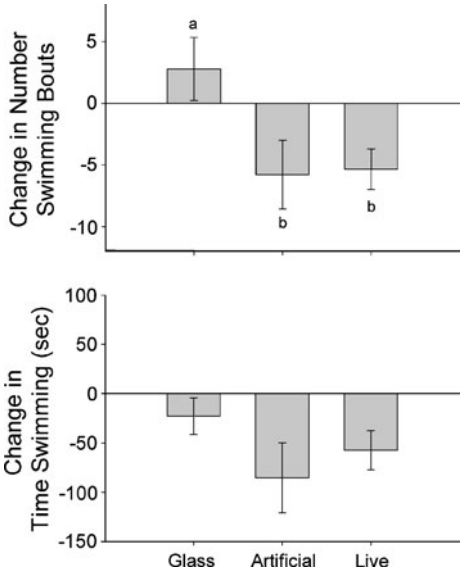

Fig. 4 The mean (± SE) change in behavioral responses of caddisfly larvae (*Triaenodes tardus*) after exposure to three different structural treatments: glass rod control (glass rod), artificial plants, or live plants. (Top) The change in number of swimming bouts. Different letters above bars indicate significant differences between treatments (one-way ANOVA, Holm-Sidak post-hoc test, all $P<0.025$). (Bottom) The change in the time spent swimming. Kruskal-Wallis ANOVA, $P=0.321$)

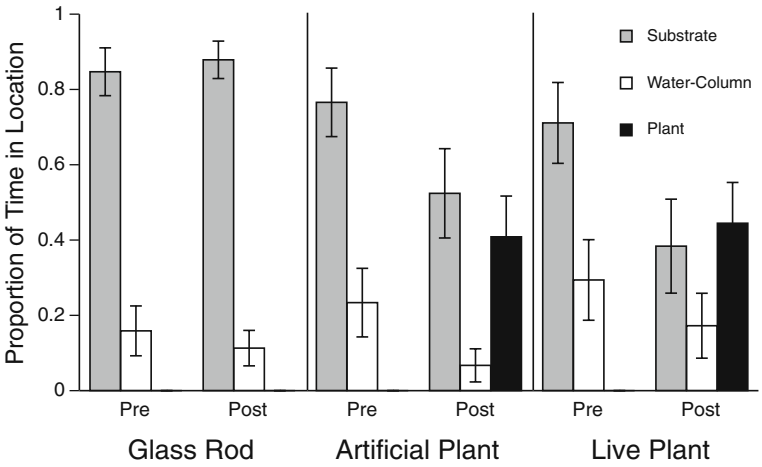

Fig. 5 Proportion (mean ± SE) of time caddisflies spent on the substrate (gray bar), swimming in the water column (white bar), or on the plant (black bar) before and after the introduction of glass rods, artificial plants, or living plants

similar amount of time resting and crawling on the artificial plant compared to the live plant (Mann-Whitney: T=69.5, P=0.846).

Discussion

Triaenodes larvae possess several adaptations that increase efficiency and reduce resistance (during the upward phase) of each swimming stroke. The setae on the swimming leg form a downward facing V-shape that opens during the downstroke (Tindall 1964; this study, Fig. 2), providing maximum forward momentum. During the upstroke, these setae fold inward, minimizing resistance. In addition, the metathoracic tibia folds inward during the upstroke (Tindall 1964; Fig. 1) further reducing drag and minimizing the time and energy required to complete an upstroke. The long and tapered design of the case acts as a rudder, stabilizing the larvae during swimming, and the slight projection on the dorsal surface of the case immediately above the head provide lift (Tindall 1964). Each of these adaptations helps *Triaenodes tardus* achieve an average swimming velocity of 1.47 cm/s, very similar to 1.7 cm/s recorded by Tindall (1964) for *Triaenodes bicolor*. Moreover, caddisflies in this study carry almost twice their mass in case material while swimming; the buoyancy of the case material also may affect the energy required to move the case. Additional observations recorded during experimentation found that some larvae were capable of swimming for almost 6 min without rest, equivalent to a linear distance of five meters. *Triaenodes tardus* in this study achieved a similar velocity as the European caddisfly *T. bicolor,* yet completed 1.93 strokes per second whereas *T. bicolor* required 13 strokes per second.

Swimming in larval Trichoptera has been hypothesized to serve several functions including facilitating movement off shifting or fine-grained substrates (Haddock 1977). *Triaenodes* larvae are often associated with aquatic macrophytes in lentic

habitats (Glover 1996). The substrate in lentic habitats typically consists of very fine sediments and swimming may facilitate movement off or around the substrate. The results of experiment two indicate that swimming likely does not facilitate movement off fluctuating or fine substrates. Although caddisflies exposed to fine sand spent the most time swimming, the majority of those swimming bouts were not elevated off the substrate. Caddisflies readily swam off the substrate when provided with medium and course substrates. A relatively solid substrate, similar to that found in the medium and course substrate treatments, may be necessary for caddisflies to launch themselves into the water column. Swimming therefore does not likely provide a selective advantage on shifting or fine sediments.

Swimming has also been hypothesized to aid caddisflies in movement between aquatic vegetation (Glover 1996), and Wiggins (1996) believed it functioned in dispersal to new food resources. *Triaenodes* are herbivorous and, unlike many other Trichoptera, do not typically consume benthic detritus (Berg 1949; McGaha 1952). Many *Triaenodes* species associate and feed on the leaves of macrophytes in the water column (Glover 1996), and this is where *T. tardus* was collected for this study. In experiment three, caddisflies reduced activity after the introduction of plants (artificial or live). This experiment suggests swimming facilitates detection of a plant and movement within and between aquatic plants, as many researchers have suggested (Mackay and Wiggins 1979; Wiggins 1996; Glover 1996). Interestingly, the time some larvae were capable of swimming during our observations indicates swimming behavior can result in long distance movements (5+ meters) and may indeed aid in dispersal within a pond, potentially supporting Wiggins' (1996) hypothesis of dispersal within pond habitats.

Surprisingly, the presence of living or artificial plants did not affect the time spent on the plants, indicating shelter and not food, may be the most important immediate factor influencing the propensity to swim. In aquatic communities many predators such as fishes and some invertebrates utilize visual cues to locate and capture prey (Oakley and Polka 1967; Jamieson and Scudder 1979; Abrahams and Kattenfeld 1997). The shuddered motions of caddisfly swimming would likely be a strong visual stimulus to these predators, and indeed, *Triaenodes* are less abundant in lakes containing predatory fish (Brett 1989). Swimming to attain shelter, followed by crawling on the plant to locate food, likely provides the greatest reduction in predation risk.

Swimming in Leptoceridae has been hypothesized to function in location and movement between aquatic macrophytes. Despite correlational evidence implicating herbivory and habitat as the likely purpose of swimming (Glover 1996), empirical evidence for the role of swimming in the life cycle of Leptocerid larvae has been lacking. Our study indicates North American *Triaenodes* are indeed excellent swimmers, and that swimming functions to locate and move between aquatic vegetation in search of shelter and food.

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