The caddisfly *Dicosmoecus gilvipes*: making a case for a functional role

Michael P. Limm[1] AND Mary E. Power[2]

3060 Valley Life Science Building, University of California, Berkeley, Berkeley, California 94720 USA

Abstract. Most caddisfly larvae build cases of silk and a variety of collected materials. Multiple functions, including protection from predators, resistance to entrainment by high flows, and improved respiration, have been suggested for caddisfly cases. We investigated the functional role of cases built by *Dicosmoecus gilvipes,* a limnephilid caddisfly. In this species, the 1st- through 4th-instar larvae build cases with plant material and attach Douglas-fir needles as lateral extensions that resemble vanes on an arrow. We tested whether the lateral extensions and entire case deterred predators by manipulating lateral extensions and case presence for larvae exposed to large steelhead trout. No larva with a case (with or without lateral extensions) was consumed during the experiment, whereas all larvae without a case were consumed. We tested whether lateral extensions provided stability against overturning and entrainment by manipulating presence of lateral extensions and subjecting larvae to turbulent flow conditions. Once dislodged, larvae with lateral extensions experienced fewer revolutions and regained their footing faster than those without extensions. Our results suggest lateral extensions provide stability against overturning in fast flow and may improve the ability of larvae to forage efficiently in turbulent flow conditions. Other caddisfly species build lateral extensions on their case, and the extensions may provide similar benefits for these taxa.

Key words: Trichoptera, case, *Dicosmoecus*, function, stability, predation, camouflage, drag.

Larvae in 30 of the 45 recognized caddisfly (Trichoptera) families make portable cases of silk and collected materials including plant fragments, colonies of algae and cyanobacteria, and mineral particles (sand to small gravel; Wiggins 2004). Case architecture varies from a straight cylindrical tube to more elaborate shapes with extensions. Some caddisfly species alter both type of material and case architecture during ontogeny (Otto and Svensson 1980). The variation in case structure among species and over ontogeny raises interesting questions about the relationships of form to function in caddisfly cases.

Protection from predators is a case function that probably evolved early in the history of the order (Wiggins 2004). Case shape, strength, and materials provide structural protection from predators, and some larvae modify these characteristics in response to predation risk (Nislow and Molles 1993, Boyero et al. 2006). Some larvae camouflage themselves with case materials similar to those on the bed surface (Otto and Svensson 1980), whereas others use cases to

appear as a nonprey item (Otto and Johansson 1995) or use lateral case extensions as protection from predators (Otto 1982, Johansson and Johansson 1992).

Some caddisfly species attach large mineral grains to the sides of their cases. The grains are often referred to as ballast stones (e.g., Wiggins 1977), and the additional ballast or mass of these stones may lower the risk to larvae of entrainment in fast currents. Webster and Webster (1943) examined whether ballast was important to *Goera calcarata* by rearing them in different flow environments. *Goera* larvae reared in faster currents constructed heavier cases than those in slower currents. However, Otto and Johansson (1995) found that ballast stones in *Silo pallipes* cases had a negligible effect on their current resistance. In addition to increasing case inertia, ballast stones may improve stability by altering fluid motion around the case or by increasing the base width (Otto 2000).

We investigated the functional role of cases built by *Dicosmoecus gilvipes* (Hagen) larvae. The species occurs in western North America, Japan, and eastern Russia (Wiggins 1977). Larvae feed on periphyton in cool flowing water. Early instars (1–2) construct cases of silk and mostly plant materials. Later instars use a

[1] E-mail addresses: miglimm@gmail.com

[2] E-mail addresses: mepower@berkeley.edu

higher proportion of minerals in their cases, and during their 5th and final instar, the larvae remove any remaining plant material at the posterior end of the case so that it is made entirely of minerals.

Prior to the 5th instar, *Dicosmoecus* larvae use silk to attach Douglas-fir needles as lateral extensions that resemble vanes on an arrow (Fig. 1A). The needles are swept toward the rear and downward (Fig. 1B). Given the significant energetic costs of searching for needles and manufacturing silk to attach them (Otto 1974, 1975, Stevens et al. 1999), we would expect that this case-building behavior confers some selective advantage. We investigated 2 possible functional roles of the lateral case extensions: 1) lateral extensions provide camouflage or protection from a large predator, and 2) lateral extensions increase larval stability in turbulent flows by increasing the effective base width of the case.

Methods

Site

All experiments were done in Elder Creek within the Heath and Marjorie Angelo Coast Range Reserve in Mendocino County, California (lat 39°44″N, long 123°39″W). The study area has a Mediterranean climate with cool, wet winters and warm, dry summers. The habitat consists of shallow runs, riffles, and pools during summer low-flow periods. Vegetation in the watershed is a mixed-deciduous–evergreen forest dominated primarily by old-growth Douglas fir (*Pseudotsuga menziesii*), redwood (*Sequoia sempervirens*), and tanoak (*Lithocarpus densiflorus*). The major aquatic foodweb components consist of producers (primarily diatoms and filamentous green algae), grazing insects (midges, mayflies, and caddisflies), predatory insects (stoneflies, aquatic beetles, and naucorid bugs), and omnivorous (California roach, *Lavinia [Hesperoleucas] symmetricus*) and predatory vertebrates (rough skinned newt, *Taricha granulose*; Pacific giant salamander, *Dicamptodon ensatus*; three-spine stickleback, *Gasterosteus aculeatus*; and juvenile steelhead, *Oncorhynchus mykiss*).

Case information

We collected 30 larvae from Elder Creek, Mendocino, California, and quantified larval dry mass, case mass, lateral extension mass, case width with lateral extensions present and removed, and organic and mineral content of the case. To quantify organic and mineral content, we dried cases for 48 h at 60°C. Cases were then weighed, combusted at 550°C, and reweighed.
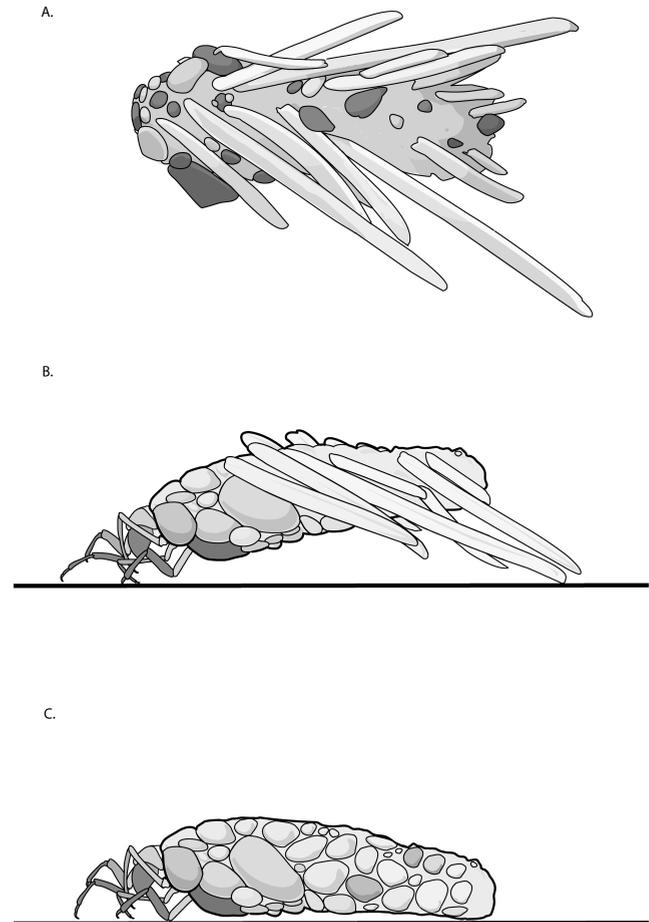

Fig. 1. Plan (A) and side (B) view of a 3rd-instar *Dicosmoecus* larva in a case with lateral extensions and side (C) view showing the change in case orientation and center of mass when lateral extensions are removed. Illustration by Aron Bothman.

Lateral extensions elevate the posterior end of the case and the center of mass of the organism and may influence resistance to drag force. We quantified how lateral extensions changed center of mass height by placing each larva and case on a thin metal bar to determine its balance point. We measured the distance from the case opening to the balance point with a ruler. We assumed a uniform case + larvae density to estimate center of mass along a vertical transect at the balance point. We then photographed the larvae from the side with and without lateral extensions. We put the larva on a flat surface, 2 m from a camera placed to the side of the larva. The lens axis was at the same height as the larvae. We analyzed images (ImageJ, version 1.43i, http://rsbweb.nih.gov/ij/) to calculate center of mass for larvae with and without lateral extensions.
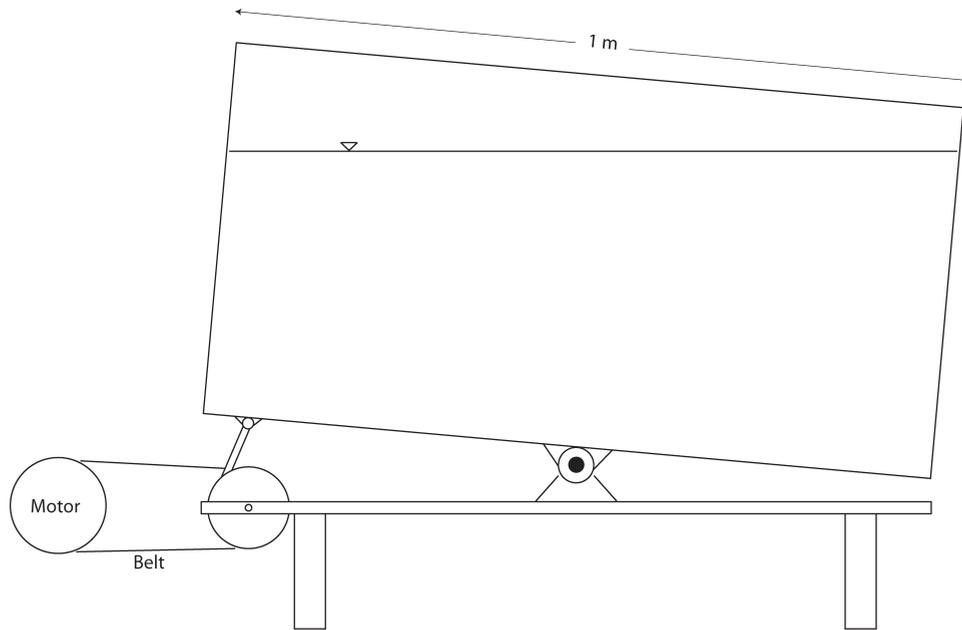
FIG. 2.   Experimental rocking tank used at Elder Creek. The motor was driven by a 12-v battery.

Hypothesis 1. The lateral extensions on the case provide camouflage or protection from large predators

We conducted feeding trials in a large, clear pool in Elder Creek to investigate whether the lateral extensions on *Dicosmoecus* cases deterred predation by steelhead. The oval pool was 16 m long, 7 m wide, and 1.8 m deep in the middle. Based on visual observations, the pool contained 40 to 50 small steelhead (45–60 mm, total length), 4 medium-large steelhead (90–120 mm, total length), and 1 large steelhead (160+ mm, total length). *Dicosmoecus* larvae were present upstream and along the bottom of the pool.

Before the experiment, we collected 36 *Dicosmoecus* larvae at a location ~30 m upstream from the pool and placed them in a flow-through basket. Case length ranged from 1.8 to 2.5 cm (3rd and 4th instars). We randomly assigned individual *Dicosmoecus* larvae to 1 of 3 treatments: 1) lateral extensions present as constructed by larvae ($n = 12$), 2) lateral extensions removed from the case with small scissors ($n = 12$), and 3) the entire case removed ($n = 12$).

We then released individual larvae into the fast flow (50–75 cm/s) at the head of the pool. We have collected *Dicosmoecus* larvae in drift nets in Elder Creek and the South Fork of the Eel river, and they drift onto experimental surfaces that are inaccessible to crawling grazers (MPL, unpublished data). An observer was positioned cross-stream from the point of release and remained stationary for 10 min prior to beginning the experiment. The person releasing the *Dicosmoecus* was positioned behind a large boulder at the head of the pool to reduce visibility to steelhead. Larvae were released ~5 min apart in a randomly assigned order. The observer recorded whether the steelhead approached, mouthed, or ate each larva and recorded the size class of the steelhead. We used analysis of covariance (ANCOVA) with release order and case size as covariates to test whether inspection and predation by steelhead differed among treatments.

Hypothesis 2. The lateral extensions increase larval stability in turbulent flows by increasing the effective base width of the case

We quantified stability by subjecting thirty-five 3rd- and 4th-instar *Dicosmoecus* larvae to turbulent bursts in a rocking tank (1.0 m long × 0.15 m wide × 0.5 m tall, constructed of clear, 6-mm acrylic; Fig. 2). The tank rested in a metal cradle that pivoted midway along the base. A variable-speed motor rocked the tank on the pivot. The movement created flow as the water rushed from one side of the tank to the other. The rocking tank completed a full cycle every 7.5 s. Based on a video recording of suspended/saltating particles moving just above the bottom surface, we estimated that larvae were exposed to peak velocities of 21 cm/s.

Revolutions before recovery.—At the beginning of each trial, we placed a single *Dicosmoecus* in the middle of the tank and turned on the rocking motor. Once a larva was dislodged, we counted (visually)
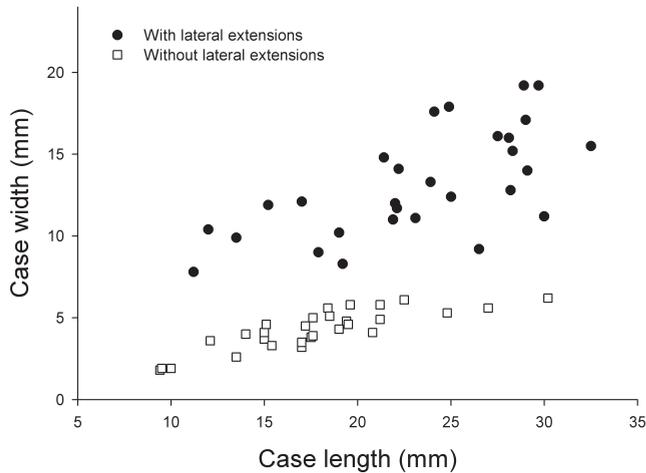
Fig. 3. Relationship between *Dicosmoecus* total length and case width when lateral extensions are present and removed. $n = 30$, some values overlap.

Fig. 4. Relationship between case width and case mass when lateral extensions are present and removed. $n = 30$, some values overlap.

and recorded the number of revolutions the larva underwent before recovering. We defined recovery as the moment at which the larva was upright and either holding its position or walking. We recorded 10 separate dislodgement events for each larva and calculated the mean number of revolutions for each larva. We then removed the lateral extensions from the case, allowed the larva to rest for 5 min in a holding tank, and conducted a 2nd trial with the same larva. We calculated the difference in mean number of revolutions with and without lateral extensions for each larva and used a paired *t*-test to assess the effect of lateral extensions on number of revolutions. To assess the possible effect of fatigue and handling on the 2nd set of observations, we conducted 6 pairs of trials in which extensions were present for both trials and 6 pairs of trials in which extensions were removed for both trials. The number of revolutions did not differ between pairs when lateral extensions were present (paired *t*-test, $t_5 = 0.53$, $p = 0.61$) or absent ($t_5 = 1.24$, $p = 0.27$) in both trials.

Recovery time.—We quantified recovery time for dislodged larvae by video-recording an additional 15 pairs of trials (*Dicosmoecus* larvae with and without lateral extensions) conducted as described above. The video was recorded at 30 frames/s and was analyzed with Quicktime Pro (version 7.0; Apple Inc., Cupertino, California). We measured the time required for recovery by counting the number of frames between the moments of dislodgement and recovery. As in the first experiment, we defined recovery as the moment when the larva was upright and either holding its position or walking. We calculated the difference in
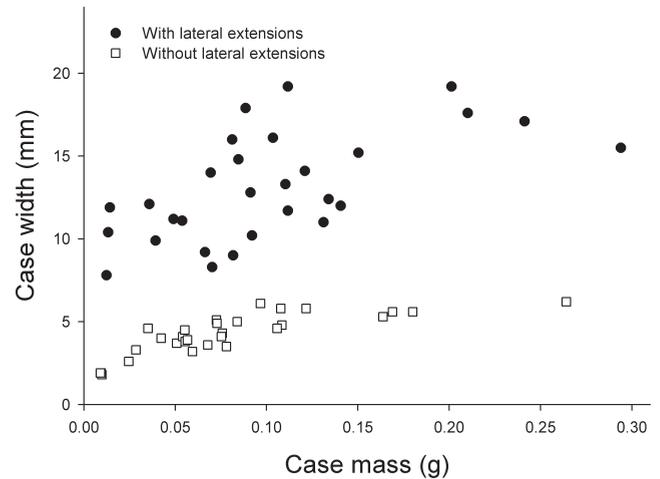
mean recovery time with and without lateral extensions for each larva and used a paired *t*-test to assess the effect of lateral extensions on recovery time.

Results

Case structure

Maximum case width was positively related to case length for the thirty 2nd- to 4th-instar *Dicosmoecus* larvae we collected (Fig. 3). On average, the lateral extensions increased total width by 410%, total length by 36%, and case mass by 24% (Figs 3, 4). On average, 56% of case mass was mineral, and this proportion increased with case length (Fig. 5). Lateral extensions elevated center of mass by 14%.

Predation

Steelhead did not consume any *Dicosmoecus* with a case ($n = 24$), whereas every *Dicosmoecus* released without a case ($n = 12$) was consumed. All *Dicosmoecus* ($n = 36$) released into the pool were visually inspected by ≥ 1 steelhead. No preference was seen in the number of inspections between treatments ($F_{2, 22} = 0.83$, $p = 0.45$), a result suggesting that needles did not provide effective camouflage to drifting larvae. Release order ($F_{1,22} = 0.30$, $p = 0.59$) and case length ($F_{1,22} = 0.63$, $p = 0.44$) did not affect consumption. Seven of the 12 *Dicosmoecus* with needle-covered cases were mouthed by ≥ 1 steelhead, whereas 8 of the 12 *Dicosmoecus* with needle-removed cases were mouthed. The number of times a larvae was mouthed did not differ between the 2 case treatments ($t_{14} = 0.49$,
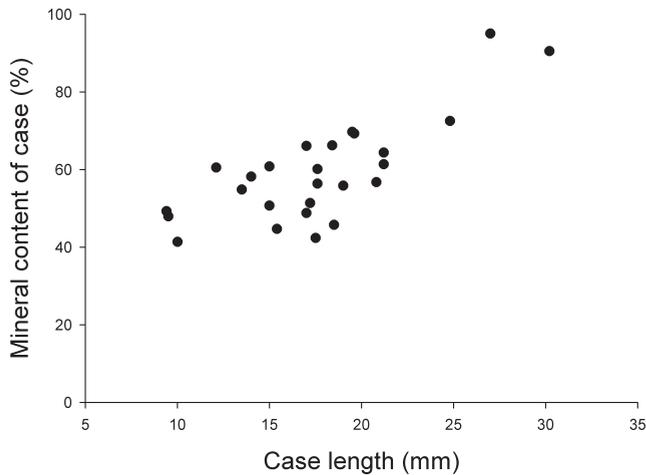
FIG. 5. Relationship between the mineral content of a *Dicosmoecus* case and its length. n = 30, some values overlap.

$p = 0.62$). Large (>90 mm) and small (45–60 mm) steelhead mouthed both needle-covered and needle-removed cased *Dicosmoecus*.

Stability

Dicosmoecus larvae with lateral extensions underwent fewer rotations than larvae without lateral extensions before recovering from dislodgement (t_{33} = 14.91, $p < 0.0001$). On average, dislodged larvae without lateral extensions rotated around their longitudinal axis 3× more than dislodged larvae with lateral extensions (with extensions = 1.0 ± 0.06 rotations [SE], without extensions = 3.3 ± 0.2 rotations).

Larvae with lateral extensions recovered from dislodgement faster than larvae without extensions (t_{14} = 7.25, $p < 0.0001$). *Dicosmoecus* regained their footing ≥3× faster with than without lateral extensions (with extensions = 1.3 ± 0.1 s, without extensions = 4.2 ± 0.4 s).

Discussion

While discussing caddisfly cases Rousseau (1921, p. 375) stated, ''in the absence of current, the cases do not in general offer such adaptations as those which we find in the larvae living in moving water. These last can resist the current, the eddies, and avoid being dragged about by them.'' Our results suggest that cases built by *Dicosmoecus gilvipes* improve their stability and assist them in 'resisting the current.' Lateral extensions widen their effective base and increase their resistance to being overturned by cross currents.

Plants and animals can modify their structure or behavior to resist overturning. Trees in weak or shallow tropical soils grow wider buttresses than those in more stable soils (Richards 1952). Where wind is persistent, the tropical trees *Tachigalia versicolor* and *Pterocarpus officinalis* improve their anchorage (Crook et al. 1997) by growing wider buttresses on the windward side (Warren et al. 1988, Lewis 1988). Amphibious organisms like the marine rock crab *Grapsus tenuicrustatus* and freshwater crayfish *Procambarus clarkii* adopt a wider stance when walking under water than on land (Martinez et al. 1998, Grote 1981). Fluid-dynamic forces increase roughly 800× when moving from air to water, and the wider stance provides stability against the greater forces (Martinez et al. 1998).

Caddisfly larvae contend with fluid-dynamic forces in both lotic and lentic environments, and *Dicosmoecus gilvipes* is not the only caddisfly species that modifies its case with lateral extensions. Members in the Glossosomatidae, Thremmatidae, and Molannidae families build shield-shaped cases of mineral particles. The shield consists of wing-like lateral extensions that effectively double the case width. In a laboratory experiment, Otto (2000) manipulated the lateral extensions on *Molanna angustata* cases and subjected them to simulated waves. Larvae with lateral extensions showed greater resistance to overturning than those without.

The drag force (D) needed to overturn larval cases with and without lateral extensions present can be calculated as

$$D = F_V \frac{MA_S}{MA_O} \qquad [1]$$

where F_V is the net force directed vertically on an organism, MA_S is the moment arm stabilizing the organism (the distance from the center of mass to the stabilizing point), and MA_O is the moment arm overturning the organism (center of mass height above the surface) (Alexander 1971). If we incorporate the effect of lateral extensions on total mass (F_V increases 22%), base width (MA_S increases 410%), and center of mass height (MA_O increases 14%) in Eq. 1, the average drag force required to overturn a *Dicosmoecus* case with lateral extensions is >4× greater than the force needed to overturn a case without lateral extensions. This estimate probably is conservative because we used the widest point on the cylindrical case to calculate the stabilizing point when lateral extensions were absent. The actual moment arm stabilizing the lateral extension-free case occurs where the cylindrical case contacts the streambed

surface. We can apply a similar analysis to *Molanna angusta* (Otto 2000). *Molanna* cases with lateral extensions were 57% heavier and 200% wider than cases without extensions. If we assume a negligible change in MA_O (the shield curves down toward the streambed surface), the drag force required to overturn a 5th-instar *Molanna* case is >4× greater when lateral extensions are present than when they are absent. For *Molanna* larvae, which are more vulnerable to predation when upside-down (Otto 2000), the benefit of lateral extensions offsets the cost of additional mass and reduced mobility.

Once overturned by hydrodynamic forces, *Dicosmoecus* larvae with lateral extensions regained their footing faster than those without lateral extensions. Faster recovery may improve their ability to move efficiently in turbulent conditions. The drag force on an object can be calculated as

$$F_D = \frac{1}{2} \rho C_D A U^2 \qquad [2]$$

where ρ is the fluid density, C_D is the drag coefficient, A is the projected area, and U is the fluid velocity past the object. The estimated 4× increase in drag required to overturn a case with lateral extensions translates into a critical velocity 2× greater for a case with lateral extensions than for a case without lateral extensions (assuming the projected area and drag coefficient do not change). From a velocity survey in a 80-m reach (530 m^2) in Elder Creek (Limm 2009), 1st- and 2nd-instar larvae inhabit low-velocity areas (near-bed velocity ≤ 0.04 m/s), whereas 3rd-, 4th-, and 5th-instar larvae can forage mid-channel where near-bed velocities are > 0.2 m/s. Based on the surveyed reach, if 1st- and 2nd-instar larvae can withstand a critical velocity 2× greater with than without lateral extensions, then 20.3% more streambed area is available to the larvae with lateral extensions. For 3rd, 4th, and 5th instars, streambed availability is 16.4% greater when lateral extensions are present than when they are not. Other factors, such as lift, larval strength, texture of rock surfaces, and flow direction, may influence larval overturning, but the additional stability provided by their case increases the streambed area available to these larvae.

We hypothesize that access to faster flow conditions and more streambed area may reduce competition with other grazers and increase food availability. Previous studies suggest periphyton is a limiting resource for *Dicosmoecus* larvae (Hart 1981, Lamberti et al. 1995), and exploitative competition for periphyton can increase with phenological changes in grazers (Li and Gregory 1989), particularly during periods of seasonal contraction of river habitat (Power 1983). Periphyton productivity, nutrient uptake, and accrual increase with velocity over moderate velocity ranges (0.15–0.30 m/s) (Whitford and Schumacher 1961, Biggs et al. 1998, Hondzo and Wang 2002). Algae growing in faster-flowing environments may be more productive and of higher food quality for grazers than algae in slack water where silt deposition may reduce algal growth (Van Nieuwenhuyse and LaPerriere 1986), C:N, or organic content (Cline et al. 1982). Cases that resist overturning and improve recovery time enable *Dicosmoecus* larvae to forage across more of the bed surface and in more productive habitats than other grazers can use. This ability could affect larval growth and adult reproductive fitness. In addition, their more extensive grazing would reduce algal accrual over a wider area and in more productive habitats, thereby increasing the already large effect of *Dicosmoecus* larvae on ecosystem processes (Limm 2009).

After dislodgement, displacement distance may influence the energetic cost to a larva of returning to its original position. Larval width controls displacement distance per revolution. In our study, 3rd- and 4th-instar larvae with lateral extensions were 2.9× wider than larvae without lateral extensions, and they revolved around their longitudinal axis 3.3× less. This result suggests that distance traveled with and without lateral extensions should be similar. However, the longitudinal axis of revolving larvae with lateral extensions does not maintain the same orientation to the flow as the longitudinal axis of revolving larvae without lateral extensions. Seen from planar view (Fig. 1A), lateral extensions increase rear case width but do not increase front case width. When dislodged by flow from the side (perpendicular to the longitudinal axis), the rear of the case is displaced farther than the front of the case, and total distance traveled is less than that calculated using rear case width alone. In addition, after rotation around 1 side of their triangular shape, the longitudinal axis of rotating larvae with lateral extensions will be oriented more parallel to the flow direction, reducing projected area and drag.

Known predators on *Dicosmoecus* larvae include harlequin ducks (*Histrionicus histrionicus* L.) (Wright et al. 2000), dippers (*Cinclus mexicanus* Swainson) (Harvey and Marti 1993), and rainbow trout (*Oncorhynchus mykiss*) (Tippets and Moyle 1978). All of these predators occur at our study site. In our experiment, large steelhead (>120 mm total length) consumed 3rd- and 4th-instar *Dicosmoecus* only when larvae were removed from their case. In a study during which *Dicosmoecus* larvae with cases were

exposed to 7 predator species, no mortality occurred over 24 h (Wootton et al. 1996). In the McCloud River (Siskiyou and Shasta Counties, California), Tippets and Moyle (1978) observed large adult trout selectively picking "stone-cased" 5th-instar *Dicosmoecus* larvae off the bottom. Fifth-instar *Dicosmoecus* larvae, which have an all-mineral case and lack lateral extensions, may be more vulnerable to predation than earlier-instar larvae, but our results suggest that any case, with or without lateral extensions, can deter large steelhead predation. We did not observe steelhead feeding on the benthos before or during the experiment, and 3rd- and 4th-instar *Dicosmoecus* were relatively abundant (20–30 larvae/m^2) on the pool bottom. More research concerning predation on *Dicosmoecus* is needed.

Our results suggest that *Dicosmoecus* larvae benefit from building lateral extensions on their cases. Costs to the larvae include the effort required to find and attach Douglas-fir needles with silk and the additional mass added by lateral extensions (22% heavier). Another potential cost may be increased form drag. The lateral extensions increase the projected frontal area of the case, and therefore, increase form drag. The point along the case at which flow separation occurs also influences drag. If Douglas-fir needles move the point of flow separation rearward, wake region size and the subsequent drag generated may be reduced, as is the case for flow separation mediated by dorsal spines behind the dorsal fin on tuna (Vogel 1996).

The lateral extensions also may influence lift and peak drag force. A velocity gradient develops as flow over an organism slows. The velocity gradient generates a lift force that pulls the organism away from the surface. By reducing effective mass (Fv in Eq. 1), lift reduces the drag required to overturn the organism. Sticks attached to the case of *Anabolia nervosa* Curtis reduced the flow velocity above the larvae and the resultant lift force (Statzner and Holm 1982). On *Dicosmoecus* cases, the Douglas-fir needles extend both laterally and vertically and elevate the rear of the case off the streambed surface. It is possible the change in case orientation relative to a naked case may influence the lift force it experiences.

Lateral extensions also could decrease peak drag forces by increasing directional sensitivity to flow in a manner similar to that of fins on a weather vane. As *Dicosmoecus* larvae move from slow (0–0.05 m/s) to higher (>0.15 m/s) velocity flow, their cases 'weather-vane' and orient into the flow (MPL, personal observation). The larvae then 'crab walk' perpendicular to flow until they reach slower flow conditions. By rapidly orienting the case into the flow, e.g., during peak velocity fluctuation, the lateral needle extensions may reduce the peak drag force that larvae experience.

Hydraulic controls on aquatic invertebrate micro-distributions (Rousseau 1921, Hynes 1970) and caddisfly case adaptations to flow conditions (Dodds and Hisaw 1925) have long been recognized. Stabilization in fast flow may not be the sole function of lateral extensions on *Dicosmoecus* cases, but their presence on the cases of other caddisfly species that inhabit faster flowing water suggests that stabilization may be a function of this trait in other taxa as well.

Literature Cited

ALEXANDER, R. I. 1971. Size and shape. Edward Arnold Limited, London, UK.

BIGGS, B. J. F., D. G. GORING, AND V. I. NIKORA. 1998. Subsidy and stress responses of stream periphyton to gradients in water velocity as a function of community growth form. Journal of Phycology 34:598–607.

BOYERO, L., P. RINCÓN, AND J. BOSCH. 2006. Case selection by a limnephilid caddisfly [*Potamophylax latipennis* (Curtis)] in response to different predators. Behavioral Ecology and Sociobiology 59:364–372.

CLINE, L., R. SHORT, AND J. WARD. 1982. The influence of highway construction on the macroinvertebrates and epilithic algae of a high mountain stream. Hydrobiologia 96:149–152.

CROOK, M. J., A. R. ENNOS, AND J. R. BANKS. 1997. The function of buttress roots: a comparative study of the anchorage systems of buttressed (*Aglaia* and *Nephelium ramboutan* species) and non-buttressed (*Mallotus wrayi*) tropical trees. Journal of Experimental Botany 48:1703–1716.

DODDS, G. A., AND F. L. HISAW. 1925. Ecological studies on aquatic insects. III. Adaptations of caddisfly larvae to swift streams. Ecology 6:123–137.

GROTE, J. R. 1981. The effect of load on locomotion in crayfish. Journal of Experimental Biology 92:277–288.

HART, D. D. 1981. Foraging and resource patchiness: field experiments with a grazing stream insect. Oikos 37:46–52.

HARVEY, B. C., AND C. D. MARTI. 1993. The impact of dipper, *Cinclus mexicanus*, predation on stream benthos. Oikos 68:431–436.

Hondzo, M., and H. Wang. 2002. Effects of turbulence on growth and metabolism of periphyton in a laboratory flume. Water Resources Research 38:1–9.

Hynes, H. B. N. 1970. The ecology of running waters. University Press, Liverpool, UK.

Johansson, A., and F. Johansson. 1992. Effects of two different caddisfly case structures on predation by a dragonfly larva. Aquatic Insects 14:73–84.

Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, J. L. Li, A. D. Steinman, and C. D. McIntire. 1995. Influence of grazer type and abundance on plant-herbivore interactions in streams. Hydrobiologia 306:179–188.

Lewis, A. R. 1988. Buttress arrangement in *Pterocarpus officinalis* (Fabaceae): effects of crown asymmetry and wind. Biotropica 20:280–285.

Li, J. L., and S. V. Gregory. 1989. Behavioral changes in the herbivorous caddisfly *Dicosmoecus gilvipes* (Limnephilidae). Journal of the North American Benthological Society 8:250–259.

Limm, M. P. 2009. Ontogenic shift in habitat use and critical flow threshold by the caddisfly *Dicosmoecus gilvipes*. PhD Thesis, University of California, Berkeley, California.

Martinez, M. M., R. J. Full, and M. A. R. Koehl. 1998. Underwater punting by an intertidal crab: a novel gait revealed by the kinematics of pedestrian locomotion in air versus water. Journal of Experimental Biology 201:2609–2623.

Nislow, K. H., and M. C. Molles. 1993. The influence of larval case design on vulnerability of *Limnephilus frijole* (Trichoptera) to predation. Freshwater Biology 29:411–417.

Otto, C. 1974. Growth and energetics in a larval population of *Potamophylax cingulatus* (Steph) (Trichoptera) in a South Swedish stream. Journal of Animal Ecology 43:339–361.

Otto, C. 1975. Energetic relationships of larval population of *Potamophylax cingulatus* (Trichoptera) in a South Swedish stream. Oikos 26:159–169.

Otto, C. 1982. Habitat, size and distribution of Scandinavian limnephilid caddisflies. Oikos 38:355–360.

Otto, C. 2000. Cost and benefit from shield cases in caddis larvae. Hydrobiologia 436:35–40.

Otto, C., and A. Johansson. 1995. Why do some caddis larvae in running waters construct heavy, bulky cases? Animal Behaviour 49:473–478.

Otto, C., and B. S. Svensson. 1980. The significance of case material selection for the survival of caddis larvae. Journal of Animal Ecology 49:855–865.

Power, M. E. 1983. Grazing responses of tropical freshwater fishes to different scales of variation in their food. Environmental Biology of Fishes 9:103–115.

Richards, P. W. 1952. The tropical rain forest. Cambridge University Press, Cambridge, UK.

Rousseau, E. 1921. Les larves et nymphs aquatiques des Insecta d'Europe. Lebége et Cie, Bruxelles, Belgium.

Statzner, B., and T. F. Holm. 1982. Morphological adaptations of benthic invertebrates to stream flow—an old question studied by means of a new technique (laser doppler anemometry). Oecologia (Berlin) 53:290–292.

Stevens, D. J., M. H. Hansell, J. A. Freel, and P. Monaghan. 1999. Developmental trade-offs in caddis flies: increased investment in larval defence alters adult resource allocation. Proceedings of the Royal Society of London Series B: Biological Sciences 266:1049–1054.

Tippets, W. E., and P. B. Moyle. 1978. Epibenthic feeding by rainbow trout (*Salmo gairdneri*) in the McCloud River, California. Journal of Animal Ecology 47:549–559.

Van Nieuwenhuyse, E. E., and J. D. Laperriere. 1986. Effects of placer gold mining on primary production in subarctic atreams of Alaska. Water Resources Bulletin 22:91–99.

Vogel, S. 1996. Life in moving fluids: the physical biology of flow. Princeton University Press, Princeton, New Jersey.

Warren, S. D., H. L. Black, D. A. Eastmond, and W. H. Whaley. 1988. Structural function of buttresses of *Tachigalia versicolor*. Ecology 69:532–536.

Webster, D. W., and P. C. Webster. 1943. Influence of water current on case weight in larvae of the caddisfly, *Goera calcarata* Banks. Canadian Entomologist 75:105–108.

Whitford, L., and G. Schumacher. 1961. Effect of current on mineral uptake and respiration by a fresh-water alga. Limnology and Oceanography 6:423–425.

Wiggins, G. B. 1977. Larvae of the North American caddisfly genera (Trichoptera). University of Toronto Press, Toronto, Ontario.

Wiggins, G. B. 2004. Caddisflies: the underwater architects. University of Toronto Press, Toronto, Ontario.

Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of disturbance on river food webs. Science 273:1558–1561.

Wright, K. K., H. Bruner, J. L. Li, R. Jarvis, and S. Dowlan. 2000. The distribution, phenology, and prey of Harlequin Ducks, *Histrionicus histrionicus*, in a Cascade stream. Canadian Field-Naturalist 114:187–195.