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Hydraulic controls on river biota and the consequence for ecosystem processes.

by

Michael Peter Limm

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Integrative Biology

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Dr. Mary E. Power, Chair

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Chair   _____ Date _____

                      _____ Date _____

                      _____ Date _____

University of California, Berkeley

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ABSTRACT

Hydraulic controls on river biota and the consequence for ecosystem processes.

by

Michael Peter Limm

Doctor of Philosophy in Integrative Biology

University of California, Berkeley

Dr. Mary E. Power, Chair

Disturbance by flooding can dramatically disrupt population and community structure in stream ecosystems. My dissertation research focused on two species that are vulnerable to high flow events: the caddisfly *Dicosmoecus gilvipes* and the western pearlshell mussel *Margaritifera falcata*. I investigated their influence on energy and nutrient dynamics in a Northern California coastal river.

In Chapter 1, I examined the impact of the limnephilid caddisfly *Dicosmoecus gilvipes* on periphyton structure and ecosystem processes. *Dicosmoecus* larvae reduced periphyton accrual, chlorophyll *a*, gross primary productivity, and ammonium uptake in experimental channels, and their impact persisted 46 days after the larvae were removed. Given *Dicosmoecus* vulnerability to high flow events, any change in flood timing, frequency, and/or magnitude due to river regulation or climate conditions may significantly alter ecosystem processes in Northern California streams.

In Chapter 2, I investigated whether flood timing would have a differential impact on *Dicosmoecus gilvipes* populations. Specifically, I measured how critical flow thresholds and habitat use varies with larval size. Critical flow velocity and dimensionless flow threshold indices increased with larval size, as did their flow velocity preference. The results suggest early flood events will have a greater impact on *Dicosmoecus* populations than later flood events of a similar magnitude, and during low-flow periods the interaction between *Dicosmoecus* distribution, periphyton composition and productivity, and flow velocity may significantly impact ecosystem processes on smaller scales.

In Chapter 3, I investigated the functional role of cases built by *Dicosmoecus gilvipes*. The larvae collect thin plant material and Douglas-Fir needles and build arrow-shaped lateral extensions on their case. Larvae with lateral extensions experienced fewer revolutions and regained their footing faster in experimental trials than those without. The results suggest lateral extensions provide stability against overturning in fast flow and may improve their ability to forage efficiently in turbulent flow conditions.

In Chapter 4, I manipulated the presence and absence of the mussel

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Margaritifera falcata in stream mesocosms. I measured their impact on organic matter accrual, microbial activity in the sediment, and the growth of larval Pacific lamprey, *Lampetra tridentata*. *Margaritifera* presence increased microbial activity in the sediment and larval lamprey growth. Organic matter accrual was not significantly affected. The results suggest that lamprey larvae benefit from native mussels, and that lamprey populations may decrease with the rapid decline of native freshwater mussels.

In summary, the presence of both *Dicosmoecus gilvipes* and *Margaritifera falcata* had significant affects on ecosystem processes. Knowledge of species impacts on energy and nutrient dynamics and the physical conditions that control species abundance and distribution is essential to predicting both small- and large-scale consequences of an altered hydrograph, whether due to river regulation or climate change.

I dedicate my thesis to

my family

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CHAPTER 1

The impact of a dominant grazer, the caddisfly *Dicosmoecus gilvipes*, on periphyton and ecosystem processes.

Abstract

Disturbance by flooding can dramatically disrupt population and community structure in stream ecosystems. If strongly interacting species are affected, energy and nutrient dynamics may be altered. We examined the impact of the limnephilid caddisfly *Dicosmoecus gilvipes* on periphyton structure and ecosystem processes. *Dicosmoecus* larval presence was manipulated in experimental channels for 21 days, during which periphyton structure and ecosystem processes were monitored. Larvae were then removed from the treatment channels to simulate larval diapause and grazing cessation. Periphyton structure and ecosystem processes were again measured 46 days after removal.

Dicosmoecus larvae reduced periphyton accrual, chlorophyll *a*, gross primary productivity, and ammonium uptake in the experimental channels, and their impact persisted 46 days after the larvae were removed. Given *Dicosmoecus* vulnerability to high flow events, any change in flood timing, frequency, and/or magnitude due to river regulation or climate conditions may impact *Dicosmoecus* populations and alter ecosystem processes in Northern California streams.

Introduction

Grazers are important regulators of productivity and nutrient cycling in aquatic systems (Flint and Goldman 1975, Lehman 1980, Mulholland et al. 1983, Vanni 1996, Wallace and Webster 1996, Vanni 2002). In streams, grazer removal of both biotic (plant, bacteria, fungi) and abiotic (senescent material, sediment) components of periphyton can influence periphyton structure (e.g. Hill and Knight 1987), productivity (e.g. Lamberti 1989), and nutrient uptake (e.g. Mulholland et al. 1983, Mulholland et al. 1994).

These impacts can vary with grazing pressure (Cooper 1973, Porter 1976, Steinman et al. 1987, Steinman 1991, Lamberti et al. 1995). At low grazing pressure, removal of periphyton overgrowth (e.g. Lamberti et al. 1989) and sediment (e.g. Power 1990) can stimulate algal productivity and offset biomass loss. At higher grazing pressure, more rapid periphyton removal will reduce area-specific biomass, productivity and nutrient uptake, even if stimulation of biomass-specific productivity occurs (Cooper 1973, Flint and Goldman 1975, Mulholland et al. 1983, Lamberti et al. 1989, Mulholland et al. 1991). In their review of experimental studies that quantify grazer effects on algal productivity, Feminella and Hawkins (1995) report that when stocked at ambient density, grazers reduced area- and biomass-specific productivity in over 60 percent of the studies.

In the present study, we examined the impact of the limnephilid caddisfly *Dicosmoecus gilvipes* (Hagen) on periphyton structure and ecosystem processes in a

Northern California stream. Distributed across western North America, Japan, and eastern Russia (Wiggins 1977), *Dicosmoecus* larvae grow up to 3 cm long and spend the majority of their active time grazing periphyton (Hart 1981, Li and Gregory 1989). Larval densities can reach up to 200 m^{-2} in California and Oregon streams (Lamberti et al. 1987, Lamberti et al. 1995). When stocked at these and lower densities, they can reduce periphyton accrual and area-specific productivity (Li and Gregory 1989). Their relatively large size and armored case reduce their vulnerability to predators (Wootton et al. 1996, Chapter 2), but their size may also increase their vulnerability to flood events (Wootton et al. 1996, Wright and Li 1998). Variation in larval density has been associated with seasonal variation in precipitation and high flow events (Power 1992, Power et al. 1996).

Our study addressed the following questions. First, if critical flow conditions are reached and *Dicosmoecus* larvae are removed from a stream reach, what impact will that have on periphyton and energy and nutrient dynamics? Second, will their presence or absence influence potential top-down effects of a fish predator, the steelhead trout *Oncorhynchus mykiss* (hereafter referred to as steelhead)? And third, will any impact on periphyton accrual and ecosystem processes persist after *Dicosmoecus* larvae undergo diapause (resting phase prior to pupation) and are no longer grazing?

To address these questions, we manipulated *Dicosmoecus* larvae and steelhead in channels that were placed in the South Fork of the Eel River, Mendocino County, CA.

Methods

Site

Our study was conducted in the South Fork of the Eel River in Mendocino County, California (39°44"N 123°39"W) within the Heath and Marjorie Angelo Coast Range Reserve of the University of California Natural Reserve System. This region has a Mediterranean climate with warm, dry summers and wet, cool winters. Most rainfall occurs between October and April. The drainage area at our study site is approximately 140 km^2. The river habitat consists of shallow runs, riffles, and large pools (1-7 m deep) during summer low flow periods. Vegetation in the watershed is a mixed-evergreen forest dominated primarily by old-growth Douglas fir (*Pseudotsuga menziesii*) and redwood (*Sequoia sempervirens*) trees. The major aquatic food web components consist of producers (primarily diatoms and filamentous green algae), grazing insects (midges, mayflies, caddisflies) and snails, predatory insects (stoneflies, dragonflies, aquatic beetles and hemiptera), fish (stickleback, *Gasterosteus aculeatus*, juvenile steelhead, *Oncorhynchus mykiss*, California roach, *Lavinia symmetricus*), and filter feeders (lamprey larvae, *Lampetra tridentata*, unionid mussels, *Margaritifera falcata* and *Anodonta californiensis*) as reported by Power et al. (1996).

We conducted experiments in a 100 m long run that becomes a slow pool (flow velocities 0-5 cm s^{-1}) under summer base flows. During base flow, the mean depth of the run is 0.4-0.6 m, stream width is 13 m, and mean velocity is 0.02 - 0.04 ms^{-1}. A thin layer (< 1 m) of mixed alluvium covers the bedrock channel. The median grain size (D$_{50}$) of our study site is approximately 50 mm based on pebble counts (Wolman and Union 1954). Sedges (*Carex nudata*) line the riverbank and stream margins.

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Experimental channels

All manipulations were conducted in experimental channels made from 55 gallon polyurethane drums. After removing the top and bottom, each drum was cut in half length-wise. Each half was then connected and sealed end to end to create a channel 1.8 m long. Both ends of the channel were covered with a permeable screen that extended 15 cm above the water level. To minimize the possible complicating effect of manipulating species other than our target species, we used the largest mesh size (6mm) that would prevent *Dicosmoecus* larvae from entering or leaving the channels. The mesh screen was cleared of debris approximately every 2 days.

In late spring the channels were placed into the 100 m reach described above and filled with gravel. We collected 0.05 m^3 of gravel adjacent to each channel and evenly distributed it within the channel. Gravel depth along the centerline of each channel was 10 cm. The channel height was adjusted to a water depth of 15 cm. Area of the channel utilized by the larvae was 0.81 m^2.

After channels had seasoned in the river for thirty days, we randomly assigned experimental channels to one of four treatments: control, *Dicosmoecus*, steelhead, and *Dicosmoecus*+steelhead. Prior to applying the treatments we sampled periphyton ash-free dry mass (AFDM), chlorophyll *a*, algal assemblage, metabolism, and ammonium and phosphorus uptake.

Periphyton sampling

To quantify AFDM, chlorophyll *a*, and algal assemblages, we randomly sampled 6 rocks in each channel. We used two perpendicular measuring tapes to establish a 2-dimensional coordinate system over each channel, and then used a random number generator to select six rocks. If the rock surface at the sampling point was less than 0.036 m x 0.024 m, we randomly selected another rock. To standardize sampling a template with a known area (0.00086 m^2) was placed on the rock surface and periphyton was removed from the area with a wire brush. Scraped material was rinsed into a 50 mL jar and placed into a cooler. In the lab, two subsamples (10 mL for AFDM, 5 mL for chlorophyll *a*) were filtered onto a 1.2 µm pore glass fiber filter (GF/F, Whatman Ltd.). The filter and material used for chlorophyll *a* analysis were immediately wrapped in foil and stored at -20°C. A third subsample was placed in a glass vial and fixed with 4% formalin for analysis of algal assemblage.

AFDM

Each filter plus material was dried at 60°C for 48 hours and weighed. We then ashed the sample in a muffle furnace for 2 hours at 550°C and re-weighed the filter to quantify ash-free dry mass (AFDM).

Chlorophyll a

To quantify chlorophyll *a* we used a modified fluorometric technique as described in EPA Method 440.5 (http://www.epa.gov/nerlcwww/ordmeth.htm#marine). A Turner Designs 10-040R non-acidification kit was used in conjunctions with a TD-700 fluorometer (Turner Designs, Inc.). We extracted chlorophyll *a* by placing samples in 90% acetone and storing in the dark at 4°C for 24 hours. The TD-700 was calibrated prior

to running the samples using the 10-040R kit standard.

Algal assemblage

To quantify algal assemblage we pooled treatment replicates for each sampling period. We agitated each pooled sample thoroughly to mix contents and withdrew 1 mL using a pipette. The 1 mL subsample was placed onto a Palmer cell and analyzed with a compound microscope at 400x. A horizontal and vertical transect was made across each Palmer cell. More than 300 cells were counted for most samples. Cells were identified to genus using Wehr and Sheath (2002). Measurements of cell length and width were used to estimate biovolume (Hillebrand et al. 1999).

Metabolism and nutrient uptake

We measured channel metabolism by creating a water- and airtight chamber. The channel ends were sealed with a rubber gasket and an acrylic sheet. A thin (0.5 mil), clear, transparent polyethylene sheet was placed on the water surface to prevent oxygen exchange across the air-water interface. Water current was maintained in each stream with a 12 volt submerged pump (Rhule, Inc). The pump was adjusted so that the average water speed in each channel was 0.05 ms^{-1}, similar to ambient flow velocity in the surrounding reach.

To quantify periphyton respiration by both autotrophic and heterotrophic components, we prevented light from reaching the channel bed with an opaque 6 mil thick tarp. Dissolved oxygen was measured after the opaque tarp was placed over the channel, and measured again after approximately 45 minutes. We then removed the opaque tarp to expose periphyton to sunlight. After 15-20 minutes, dissolved oxygen was again recorded. Gross primary productivity was calculated as the sum of the net metabolism and respiration measurements. Short time periods were used to minimize nutrient limitation and supersaturation of oxygen (Bott et al. 1997). Temperature in each channel was recorded during the measurements. Channel temperatures were similar and did not vary more than 1.8 °C between initial and final dissolved oxygen measurement.

After we quantified channel metabolism, we removed the channel ends and clear plastic cover to allow flow through the channel. After 24 hours, the channel ends were again sealed and the water pump created flow. We added a concentrated nutrient cocktail to the channels to increase ammonium (NH$_4$-N) and phosphorus (PO$_4$-P) concentrations to roughly 40 µgL^{-1}. (Background concentrations in the South Fork of the Eel River are typically between 10-14 µgL^{-1} for both nutrients during the experimental period.) Water samples were collected from each channel after four minutes (the time required for the channels to be fully mixed based on preliminary tests using rhodamine dye) and every 15 minutes thereafter (4 water samples total from each channel). Water samples were filtered through a 0.7 µm pore glass fiber filter (GF/F, Whatman Ltd.) into a pre-rinsed 60 mL bottle. Sample bottles were placed into a cooler for transport to the laboratory.

In the laboratory, ammonium and phosphorus were analyzed within 24 hours. Ammonium was analyzed using a modified OPA-fluorometric technique (Taylor et al. 2007) from Holmes et al. (1999) with a portable fluorometer (Turner Designs, Inc., Sunnyvale, California, USA). We measured soluble reactive phosphorus (SRP) in each sample by the standard molybdenum blue procedure (American Public Health Association 1994).

Treatments

After initial sampling of periphyton AFDM, chlorophyll *a*, algal assemblage, metabolism, and nutrient uptake was completed, treatments were applied to each channel. Fifty *Dicosmoecus* larvae were added to both the *Dicosmoecus* and *Dicosmoecus*+steelhead channels. Larval density in the experimental channels was within the range of their ambient densities. Two steelhead were added to the steelhead and *Dicosmoecus*+steelhead channels. Steelhead were collected using a backpack electroshocker (LR-24, Smith-Root, Inc.). After lightly anesthetizing the steelhead with MS-222, we measured their length and weight and randomly assigned them to a treatment and channel. Average standard length and weight are reported in Table 1.

Fourteen days after applying treatments, we sampled periphyton AFDM, chlorophyll *a*, algal assemblage, and loose organic and inorganic material on the channel bed. To quantify loose organic and inorganic material, we gently lifted the randomly selected rocks to be scraped and placed them in a shallow container underwater. After placing a lid on the container, we lifted the container out of the water. The water within the container was poured into a large tray and any invertebrates were removed with forceps. The rock was gently rinsed with filtered stream water over the large tray, and all contents of the tray were then transferred into 1 L bottles. The bottles were placed into a cooler and filtered in a laboratory onto 1.2 µm pore glass fiber filter (GF/F, Whatman Ltd.). Organic and inorganic content on the filter was analyzed as described above for AFDM.

Twenty-one days after applying treatments we sampled periphyton AFDM, chlorophyll *a*, algal assemblage, metabolism, and nutrient uptake. We then removed *Dicosmoecus* larvae from all channels to simulate larvae undergoing diapause. Due to low conductivity and the potential disruption of other grazers by excessive electrofishing, the steelhead and *Dicosmoecus*+steelhead treatment channels were destructively sampled to ensure all fish were removed, and these treatments were terminated. Gravel was removed from the channels and nets were used to collect the steelhead, and the number of *Dicosmoecus* in each channel was recorded.

Forty-six days after removing *Dicosmoecus* larvae from the *Dicosmoecus* treatment we sampled periphyton AFDM, chlorophyll *a*, algal assemblage, metabolism, and nutrient uptake in the control and *Dicosmoecus* treatment.

Analysis

During the period when *Dicosmoecus* was present (day 1 to 21) we analyzed treatment effects on periphyton accrual, chlorophyll *a*, GPP, and ammonium and phosphorus uptake with a repeated measures MANOVA design. When differences were significant, we used between subject contrasts to determine which treatments were different. *Dicosmoecus* and control treatment means 46 days after *Dicosmoecus* removal were compared using Student's t-test. Deposited mineral and loose organic matter and were analyzed with an ANOVA design and post hoc pair-wise comparisons were conducted using Tukey's (alpha= 0.05). All analysis was conducted with the statistical program JMP (7.0, SAS Institute Inc., Cary, NC).

Results

We recovered on average 41 (SE 2.8) *Dicosmoecus* larvae from each experimental channel after 21 days (Table 1). Dippers were frequently observed on channel walls and predation by them may be responsible for the missing *Dicosmoecus* larvae. A garter snake (*Thamnophis couchii*) was observed in a channel during the experiment.

One dead steelhead was observed in a steelhead treatment channel one week after applying treatments and replaced with a steelhead of similar size. At the end of the experiment four steelhead were recovered from three steelhead treatment channels and four steelhead were recovered from three *Dicosmoecus*+steelhead treatment channels (Table 1). Missing steelhead either escaped from a channel by jumping over barrier walls or were consumed by predators. Individual fish were not tagged, and therefore steelhead growth rates could not be measured.

Periphyton
AFDM

Periphyton accrual was reduced in channels when *Dicosmoecus* was present ($F_{3,16} = 38.35$, $p < 0.001$, between subject contrasts, Figure 1). After 14 and 21 days, periphyton standing crop was less than half of the abundance in *Dicosmoecus* and *Dicosmoecus*+steelhead treatments. Accrual was similar between *Dicosmoecus* and *Dicosmoecus*+steelhead treatments and greater in the steelhead treatment than in the control (no *Dicosmoecus*, no steelhead) treatment. Forty-six days after larvae were removed, periphyton standing crop in both control and *Dicosmoecus* treatments was reduced, but standing crop in the control treatment was still over 2x higher than in the *Dicosmoecus* treatment ($t_8 = 2.49$, $p = 0.03$).

Chlorophyll a.

Chlorophyll *a* accrual was also reduced when *Dicosmoecus* was present ($F_{3,16} = 11.04$, $p < 0.001$, between subject contrasts, Figure 2). Fourteen and 21 days after larvae were introduced chlorophyll *a* was over 2X higher in control and steelhead treatments. Accrual was similar between *Dicosmoecus* and *Dicosmoecus*+steelhead and similar between control and steelhead treatments. 46 days after larvae were removed chlorophyll *a* was still reduced in the *Dicosmoecus* treatment relative to control ($t_8 = 2.71$, $p = 0.03$).

Settled material

After 14 days the applied treatments had a significant effect on loose organic and loose mineral accrual ($F_{3,16} = 9.14$, $p < 0.001$, $F_{3,16} = 13.58$, $p < 0.001$, Figure 3a). Organic matter accrual was reduced by a factor of 3 in the *Dicosmoecus* and *Dicosmoecus*+steelhead treatments relative to the steelhead treatment (Tukey's test, $\alpha = 0.05$). Loose mineral matter (ash) accrual was reduced by a factor of 9 in the *Dicosmoecus* and *Dicosmoecus*+steelhead treatments relative to steelhead treatment (Tukey's test, $\alpha = 0.05$, Figure 3b).

Algal assemblage and biovolume

Common algal taxa observed on scraped rocks during the experiment include *Acanthidium* sp., *Cocconeis pediculus*, *Cocconeis placentula*, *Epithemia adnata*, *Epithemia sorex*, *Epithemia turgida*, *Fragilaria* sp., *Gomphenema* sp., *Rhoicosphenia* sp., *Navicula* spp., *Melosira* sp., *Rhopalodia* sp., *Synedra* spp., *Cladophora glomerata*, and

various cyanobacteria sp (Figure 4a). Based on pooled treatment periphyton samples, algal cell density appeared similar between treatments at the beginning of the experiment. After 21 days algal cell density was much higher in the control and steelhead treatments, with the highest cell counts for most species in the steelhead treatment. The filamentous diatom *Melosira* made up a significant number of total cells in the control and steelhead treatments and were rare or absent in the *Dicosmoecus* or *Dicosmoecus*+steelhead treatments. Another filamentous diatom, *Fragilaria* sp., was also present in control and steelhead treatments but absent from *Dicosmoecus* treatments. *Cladophora glomerata* filaments were not observed in *Dicosmoecus* or *Dicosmoecus*+steelhead treatments, only in control and steelhead treatments. Forty-six days after larvae were removed algal cell density was higher for all algal species in the control treatment. Similar patterns were observed when algal cell count data was converted to algal biovolume (Figure 4b).

Metabolism

Area-specific GPP was affected by the treatments ($F_{3,16}$ = 7.80, *p* = 0.002, Figure 5a). Based on between-treatment contrasts, area-specific GPP was reduced in the *Dicosmoecus* and *Dicosmoecus* +steelhead treatments relative to control and steelhead treatments. Area-specific GPP was similar between control and steelhead treatment, and similar between the *Dicosmoecus* and *Dicosmoecus* +steelhead treatments. Forty-six days after larvae were removed aerial-specific GPP in the *Dicosmoecus* treatment was similar to the control (t_8 = 1.50, *p* = 0.09).

Biomass-specific GPP was affected by the treatments (($F_{3,16}$ = 7.80, *p* = 0.002, Figure 5b). Biomass-specific GPP in the *Dicosmoecus* and *Dicosmoecus* +steelhead treatments was significantly higher than the control and steelhead treatments. Biomass-specific GPP in the control treatment was significantly higher than in the steelhead treatment. Forty-six days after larvae were removed biomass-specific GPP in the *Dicosmoecus* treatment was still significantly higher than in the control treatment (t_8 = 4.85, *p* < 0.001).

Nutrient uptake
Ammonium

Area-specific ammonium uptake rate by periphyton in the channels was affected by the treatments ($F_{3,16}$ = 19.12, *p* < 0.001, Figure 6a). Area-specific ammonium uptake rate was significantly reduced in both the *Dicosmoecus* and *Dicosmoecus* +steelhead treatments relative to the control and steelhead treatments. Uptake rates were similar between control and steelhead treatments, and similar between the *Dicosmoecus* and *Dicosmoecus* +steelhead treatments. Area-specific ammonium uptake rate was still reduced in the *Dicosmoecus* treatment 46 days after larvae were removed (t_8 = 3.58, *p* = 0.006).

Biomass-specific ammonium uptake rates differed between treatments when *Dicosmoecus* was present ($F_{3,16}$ = 5.64, *p* = 0.008, Figure 6b). Based on between-treatment contrasts, biomass-specific ammonium uptake rates were higher in *Dicosmoecus*, steelhead, and *Dicosmoecus* +steelhead treatments than in the control treatment. Biomass-specific ammonium uptake rate was higher in the *Dicosmoecus* treatment than in the control treatment 46 days after larvae were removed (t_8 = 2.32, *p* = 0.03).

Phosphorus

No difference in area-specific phosphorus uptake rate by periphyton was observed between treatments ($F_{3,16}$ = 1.41, p = 0.28, Figure 7a). Area-specific phosphorus uptake rate was similar between control and *Dicosmoecus* treatments 46 days after larvae were removed (t_8 = 1.16, p = 0.29).

Biomass-specific phosphorus uptake rates were significantly different between treatments when *Dicosmoecus* was present ($F_{3,16}$ = 3.52, p = 0.04, Figure 7b). Biomass-specific phosphorus uptake rates were higher in *Dicosmoecus* and *Dicosmoecus* +steelhead treatments than in the steelhead treatment, and higher in the *Dicosmoecus* +steelhead treatment than the control treatment, according to between subject contrasts. Biomass-specific phosphorus uptake rate was higher in the control treatment than in the *Dicosmoecus* treatment 46 days after larvae were removed (t_8 = 2.1, p = 0.04).

Ammonium:Phosphorus uptake ratio

The ammonium:phosphorus uptake ratio differed between treatments ($F_{3,16}$ = 7.84, p = 0.0019, Figure 8). The ammonium:phosphorus uptake ratio was higher in the control treatment than in the other three treatments. The ammonium:phosphorus uptake ratio was similar between the steelhead, *Dicosmoecus* and *Dicosmoecus* +steelhead treatments. Forty-six days after larvae were removed the ammonium:phosphorus uptake ratio was not significantly different in the control treatment than in the *Dicosmoecus* treatment (t_8 = 0.89, p = 0.2).

Discussion

The absence or removal of an important consumer can influence prey distribution (e.g. Connell 1970), species abundance (e.g. Estes and Palmisano 1974), species interactions and community structure (e.g. Brooks and Dodson 1965, Paine 1966). Our study provides further evidence that *Dicosmoecus gilvipes* is a strong interactor in California channels. The larvae reduced periphyton accrual, structure, productivity, and nutrient uptake, and these effects persisted 46 days after the larvae were removed from experimental channels.

Dicosmoecus *on periphyton*

Experimental channels with *Dicosmoecus* had reduced periphyton accrual after 14 and 21 days and low between-channel variation relative to control channels. Reduced periphyton accrual has been observed at lower (25 m^{-2}, Li and Gregory 1989), higher (200 m^{-2}, Lamberti et al. 1987), and similar (65 m^{-2}, Wootton et al. 1996) densities in California and Oregon channels. Li and Gregory (1989) stocked aquaria at 25 m^{-2} and observed a 50% reduction in periphyton biomass after 48 hours, and only a thin layer of periphyton remained after 72 hours. When Lamberti and others (1995) manipulated *Dicosmoecus* larval density in channels, they observed an inverse relationship between grazer density and periphyton biomass after 32 days. At 50 m^{-2}, they observed 70% less periphyton and chlorophyll *a* accrued than when larval density was 25 m^{-2}. When other grazers were allowed to enter channels, Wootton et al. 1996 observed an 83% reduction in periphyton biomass. We observed a 60% reduction in periphyton standing crop after

14 days and a 55% reduction after 21 days in *Dicosmoecus* treatments relative to control. The results suggest that when at or even below ambient density, periphyton removal rate by *Dicosmoecus* can greatly exceed periphyton regeneration rate.

Grazing and activity by *Dicosmoecus* larvae also altered periphyton structure by reducing the loose top layer of periphyton. Similar results have been observed in previous studies on *Dicosmoecus* (Lamberti et al. 1987, Lamberti et al. 1995), snails (Mulholland et al. 1983, Lamberti et al. 1995), mayflies (Hill and Knight 1987, Lamberti et al. 1995) and predatory stoneflies (Zanetell and Peckarsky 1996). Relative to ungrazed channels, Lamberti and others (1995) observed over 2X more organic material exported from channels when *Dicosmoecus* was present. *Dicosmoecus*-induced resuspension and export of algae and loose organic material may have significant consequences for downstream filter and deposit feeders.

Alteration of periphyton structure by *Dicosmoecus* and selective feeding may have influenced the different algal assemblages we observed. By modifying periphyton structure, grazers can alter the physical conditions important to specific algal species (Hill and Knight 1987). When feeding, *Dicosmoecus* larvae brush, claw, and scrape periphyton off the rock surface with their mandibles and tarsal claws on front and middle legs (Hart 1981, Li and Gregory 1989). This feeding action dislodges loose material on the periphyton surface. In a tributary of the South Fork of the Eel River, feeding and activity by the mayfly *Ameletus validus* disproportionally removed loose and highly motile diatoms found in the loose layer of periphyton (Hill and Knight 1987). The removed diatoms included *Nitzschia* spp., *Surirella spiralis*, *Cymatopleura elliptica*, and *Navicula cyptocephala*. Adnate species including *Gomphonema clevei*, *Achnanthes minutissima*, *Synedra ulna*, *Rhoicosphenia curvata*, *and Epithemia* spp. increased their relative abundance as grazing pressure increased (Hill and Knight 1987). In the marine intertidal, limpets selectively removed the loose filamentous diatoms *Melosira* spp. and *Fragilaria* sp. (Nicotri 1977). In our study, *Dicosmoecus* reduced the algal cell densities and biovolume of both loose and adnate species after 21 days. The filamentous diatoms *Melosira* sp. and *Fragilaria* sp. were observed in the control and steelhead treatments but were absent from *Dicosmoecus* treatment. Only the filamentous diatom *Melosira* was observed in the *Dicosmoecus*+steelhead treatment, where it occurred at a relatively low cell density (100X and 200X less than in control and steelhead treatments, respectively). The filamentous green alga *Cladophora glomerata* was also observed in control and steelhead treatments but absent from *Dicosmoecus* and *Dicosmoecus*+steelhead treatments. *Dicosmoecus* has shown a feeding preference for *Cladophora* filaments in previous studies (Hart 1981, Li and Gregory 1989), but whether their absence was due to selective feeding is unclear, given the reduction in all algal taxa when *Dicosmoecus* was present, including epiphytic diatoms on *Cladophora*.

Dicosmoecus *on ecosystem processes*

Dicosmoecus reduced area-specific productivity in channels. *Dicosmoecus* increased biomass-specific productivity, but grazing pressure at ambient density removed enough periphyton to offset the stimulatory effect. Our finding is in agreement with previous studies where *Dicosmoecus* was the sole grazer (Lamberti et al. 1995), where periphyton renewal rate was calculated relative to *Dicosmoecus* grazing rate (Big Sulphur Creek, Sonoma County, CA, Hart 1981), and of course where reduced periphyton accrual

occurred when *Dicosmoecus* was present (Lamberti et al. 1987, Lamberti et al. 1989, our study). Relative to ungrazed channels, Lamberti et al. (1995) reported a 50% reduction of area-specific productivity when *Dicosmoecus* was the sole grazer at 25 m^{-2}. We observed a lower reduction in area-specific productivity (30%) at 62 m^{-2}, but grazing pressure in our channels was not limited solely to *Dicosmoecus* due to channel ends permeable to grazers small enough to pass through 6mm mesh.

Associated with the *Dicosmoecus*-induced reductions in area-specific primary productivity were lower ammonium uptake rates. Ammonium uptake rate was 400% less in *Dicosmoecus* and *Dicosmoecus*+steelhead treatments relative to the control treatment after 21 days. The disproportionate reduction in ammonium uptake relative to periphyton accrual (54% reduction) and area-specific productivity (30%) suggests the reduced periphyton standing crop and altered periphyton composition were responsible. A two-fold reduction in standing crop (total biovolume) should lower nutrient demand. The removal of senescent algal cells or deposited organic and inorganic matter, however, can affect nutrient demand by increasing the proportion of active cells and increasing light availability. This, coupled with an increased nutrient mass transfer potential to underlying cells due to overstory removal, can increase biomass-specific ammonium uptake rate and offset the effects of reduced standing crop on area-specific ammonium uptake rate. While biomass-specific productivity was higher in *Dicosmoecus* treatments, biomass-specific ammonium uptake rates were reduced relative to the control treatment. The results suggest standing crop removal and biovolume reduction by *Dicosmoecus* was the primary control of ammonium uptake rate.

Taxonomic composition may have also influenced ammonium uptake rates in the *Dicosmoecus* treatments. Periphyton demand for nutrients is influenced by which species are present, their abundance, and their chemical constituents. In our study, *Melosira* sp. dominated algal biovolume in control and steelhead treatments after 21 days, but was absent from *Dicosmoecus* and *Dicosmoecus*+steelhead treatments. *Epithemia* spp. (diatoms with nitrogen-fixing endosymbionts (Round et al. 1990)) made up the majority of the biovolume in *Dicosmoecus* and *Dicosmoecus*+steelhead treatments. If ammonium demand by *Melosira* and *Epithemia* differs, the different species composition may have influenced both area- and biomass-specific ammonium uptake rates.

Phosphorus uptake rate was similar between treatments and was over a magnitude lower than the ammonium uptake rate. The results are consistent with predicted grazer effects in a nutrient-limited system (Newbold 1982). In the nitrogen-limited South Fork of the Eel River (Marks et al. 2000), reduced standing crop and productivity in the *Dicosmoecus* and *Dicosmoecus*+steelhead treatments reduced the total uptake of ammonium, while the lower phosphorus uptake reflected the higher phosphorus availability relative to periphyton demand.

The higher ammonium:phosphorus uptake ratio in control treatments was driven primarily by the higher ammonium uptake. The ratio of available nutrients can impact bottom-up forces in both aquatic and terrestrial ecosystems (Vitousek and Howarth 1991), and the lower ammonium:phosphorus uptake ratio by periphyton where *Dicosmoecus* is present may have significant consequences to species downstream. We did not, however, quantify nitrate uptake. Nitrate concentration (10 µg L^{-1}) is similar to those of ammonium (Power 1992), and may also influence total nitrogen uptake dynamics.

Post-grazer removal

Increased accrual of periphyton has been observed after grazing caddisflies undergo diapause/pupation (e.g. Douglas 1958, Hart and Resh 1980). After we removed *Dicosmoecus* to simulate diapause-induced grazing cessation, however, we did not observe positive responses in periphyton accrual, metabolism, or ammonium uptake. The reduced accrual, metabolism, and ammonium uptake rate observed in the *Dicosmoecus* treatment after 21 days persisted 46 days later despite larval removal. Increased grazing pressure by other invertebrates may have prevented a positive response after *Dicosmoecus* removal, but increased grazing pressure was not observed in control treatments, where periphyton accrual remained similar. The reduced area-specific productivity after 46 days in control treatments suggests that, if anything, grazing pressure was reduced in control treatments. Power (1992) observed mobile grazer densities decline in August and September while the number of sites with *Cladophora* filaments present increased. If grazer pressure did not compensate for *Dicosmoecus* removal or increase in control treatments, the reduced area-specific productivity in both the control and *Dicosmoecus* treatment after 46 days (Pair-wise t-test, $t_4 = 7.13$, $p < 0.001$) suggests the physical conditions for periphyton growth declined or the algal assemblage underwent senescence. Lack of periphyton recovery following larval removal suggests that *Dicosmoecus* impacts on periphyton and ecosystem processes may persist well into fall given certain seasonal conditions.

We did observe a 5X increase in phosphorus uptake rate after 46 days. One possible explanation is greater cell density, biovolume, or activity by nitrogen fixing species (Nausch et al. 2004). *Epithemia* spp. cell density and biovolume increased in *Dicosmoecus* treatments while *Rhopalodia* sp. cell density and biovolume increased in control treatments. Both diatom species have endosymbiotic cyanobacteria. Their increase, and possible increases in nitrogen fixing activity, may account for the increased phosphorus uptake rate.

Steelhead

Adding or removing a top predator can induce a trophic cascade when strong trophic links exist (Paine 1980). Steelhead predation on invertebrate predators and grazers in the South Fork of the Eel River can alter periphyton accrual and community structure (Power 1990, Power 1992, Wootton et al. 1996). In a previous study, similarly sized steelhead at a lower density (1.6 m^{-2} versus 2 m^{-2}) reduced predator abundance (-62%) and algal accrual (-54%), but had no effect on mobile grazer abundance (Wootton et al. 1996). In our study, periphyton accrual and settled organic material was greater in the steelhead treatment than in either the control, *Dicosmoecus*, and *Dicosmoecus*+steelhead treatments, suggesting steelhead suppressed grazer activity either through predation or predator cues (McIntosh et al. 2004). When *Dicosmoecus* was present with steelhead, periphyton accrual was similar to that in the *Dicosmoecus* treatment. This absence of cascading effects dues to steelhead was likely due to the high periphyton removal rates by *Dicosmoecus.* Large and armored *Dicosmoecus* are invulnerable to predation by the small steelhead (Power et al. 1996, Wootton et al. 1996), and any reductions in grazing pressure due to predation on more vulnerable grazers was likely compensated for by *Dicosmoecus* grazing pressure. *Dicosmoecus* grazing pressure

may have also reduced the number and type of grazers present and weakened trophic links between steelhead and periphyton. McAullife (1984) observed fewer mayflies (*Ephemerella doddsi* and *Baetis* spp.) on substrates where the caddisfly *Glossosoma* were abundant and periphyton abundance was reduced. From short-term manipulations he determined that resource exploitation by *Glossosoma* was the only mechanism driving the lower mayfly densities. *Dicosmoecus* have been shown to compete exploitatively in previous studies (Hart 1980, Lamberti et al. 1995) and fewer invertebrate predators and sessile grazers have been observed in the presence of *Dicosmoecus* (Wootton et al. 1996). Unfortunately, potential impacts of other grazers were not evaluated in the current study.

The impacts of *Dicosmoecus* larvae on periphyton and ecosystem processes will likely vary temporally and spatially with seasonal abiotic conditions and larval ontogeny. For example, disturbance by flooding can dramatically reduce larval densities (77%, Wootton et al. 1996, 83%, Wright and Li 1998). Their ability to resist high velocity flows varies with larval size (Chapter 3), and therefore a given magnitude flood occurring earlier in the season may have a different impact on *Dicosmoecus* populations than a later occurring flood. The interaction of biotic (which species and how many) and abiotic (hydrologic conditions, temperature, nutrient concentrations) conditions after a flood can dramatically impact community structure later in the season (e.g. Power 1990, Power 1992, Biggs et al. 2005). This, coupled with abiotic conditions that influence periphyton growth, can ultimately influence seasonal productivity and nutrient cycling in a stream. In our study, the absence of *Dicosmoecus* in July (simulating a late flood occurring in spring), when productivity was the highest in all channels, resulted in higher periphyton accrual, productivity, and nutrient uptake from July and into early September.

Our results suggest that *Dicosmoecus* larvae increase downstream transport of nutrients and organic particles. Their grazing upstream would reduce local demand for a limiting nutrient. By reducing local deposition of organic material, larval presence will likely increase the distance that both energy (carbon) and nutrients will travel downstream (Newbold et al. 1982) before being taken up by ecosystem components. This has important implications given the number of regulated rivers in the Pacific Northwest and potential impacts of climate change on flood timing, frequency and magnitude. How changes in the hydrologic cycle influence ecosystem processes directly by altering the flux of water and materials, and indirectly via the impact on strong interactors like *Dicosmoecus*, has immediate value to ecosystem and resource managers. Future research on earlier larval instars, whose mobility, feeding activity and diet can differ from later instars (Hart and Resh 1980, Li and Gregory 1989), will improve our ability to quantify the total potential impact of a cohort on ecosystem processes.

Acknowledgements

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Tables

Table 1. Summary of Dicosmoecus and steelhead in treatments.

Treatment	Initial *Dicosmoecus* per channel	Recovered *Dicosmoecus* per channel	Initial steelhead length (mm)	Final steelhead length (mm)	Initial steelhead mass (g)	Final steelhead mass (g)
Control	-	-	-	-	-	-
Dicosmoecus	50	40.2 (2.5)	-	-	-	-
Steelhead	-	-	51.0 (1.5)	52.5 (5.6)	1.8 (0.1)	2.2 (0.7)
Dicosmeocus + steelhead	50	41.8 (1.56)	48.7 (0.9)	49.7 (4.6)	1.7 (0.1)	1.89 (0.6)

Values in parenthesis represent standard error of the means (SEM).

Figure Legends

Figure 1. Organic matter (AFDM) accrual in the different treatments over the course of the experiment.

Figure 2. Chlorophyll *a* accrual in the different treatments over the course of the experiment.

Figure 3. Accrual of loose organic (a) and mineral (b) material after 14 days. Letters above columns represent relationship between treatments determined by Tukey's test (α= 0.05). Treatments with a different letter are significantly different.

Figure 4. Algal cell density (a) and biovolume (b) for control (white bar), steelhead (black bar), *Dicosmoecus* (light grey bar), and *Dicosmoecus*+steelhead (dark grey bar).

Figure 5. Area-specific GPP (a) and biomass-specific GPP (b) in the different treatments over the course of the experiment.

Figure 6. Area-specific (a) and biomass-specific (b) ammonium uptake rate in the different treatments over the course of the experiment.

Figure 7. Area-specific phosphorus uptake rate (a) and biomass-specific phosphorus uptake rate (b) in the different treatments over the course of the experiment.

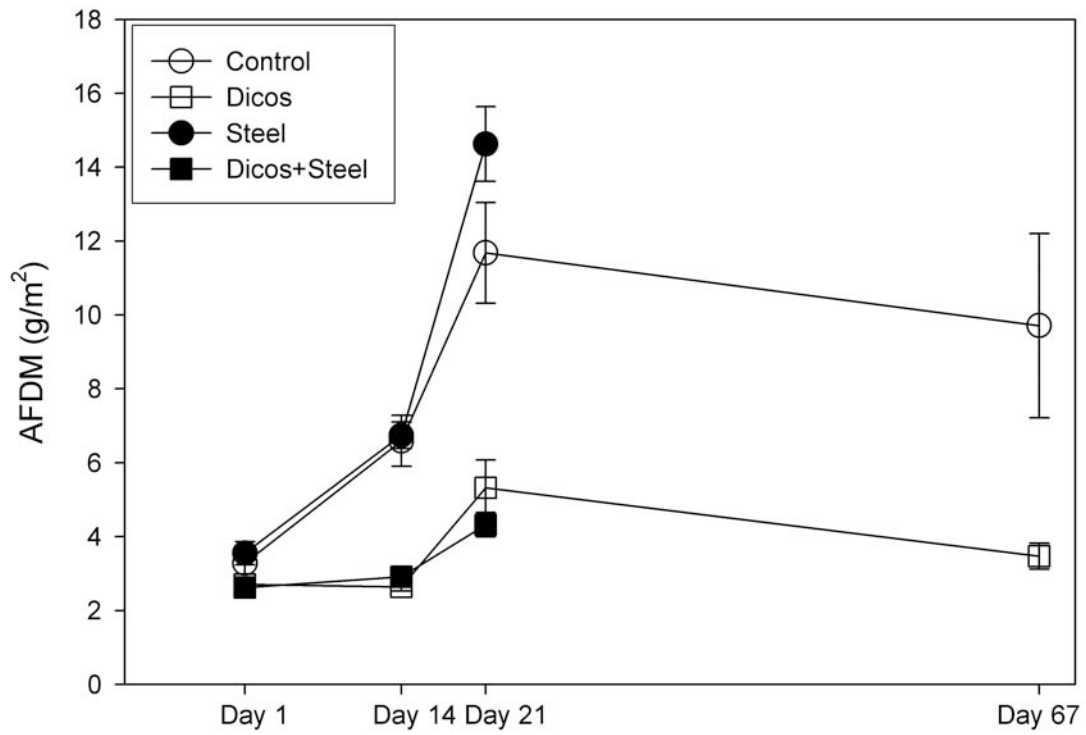**Figure 8.** Ammonium to phosphorus uptake ratio for the different treatments.
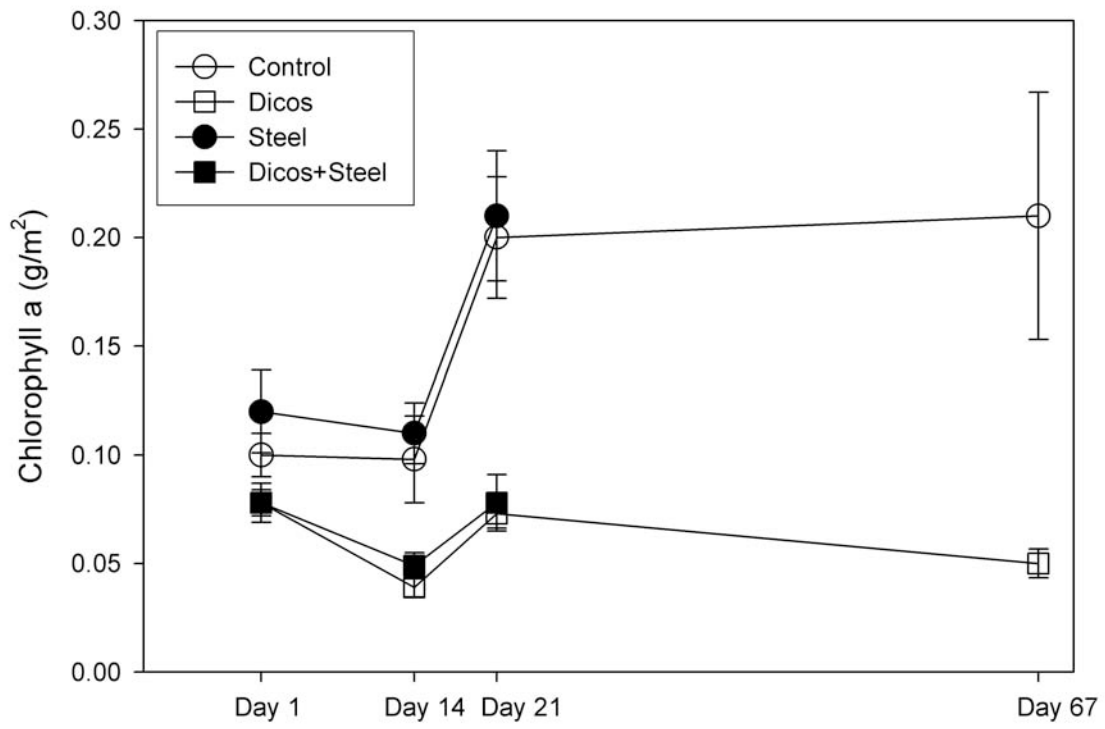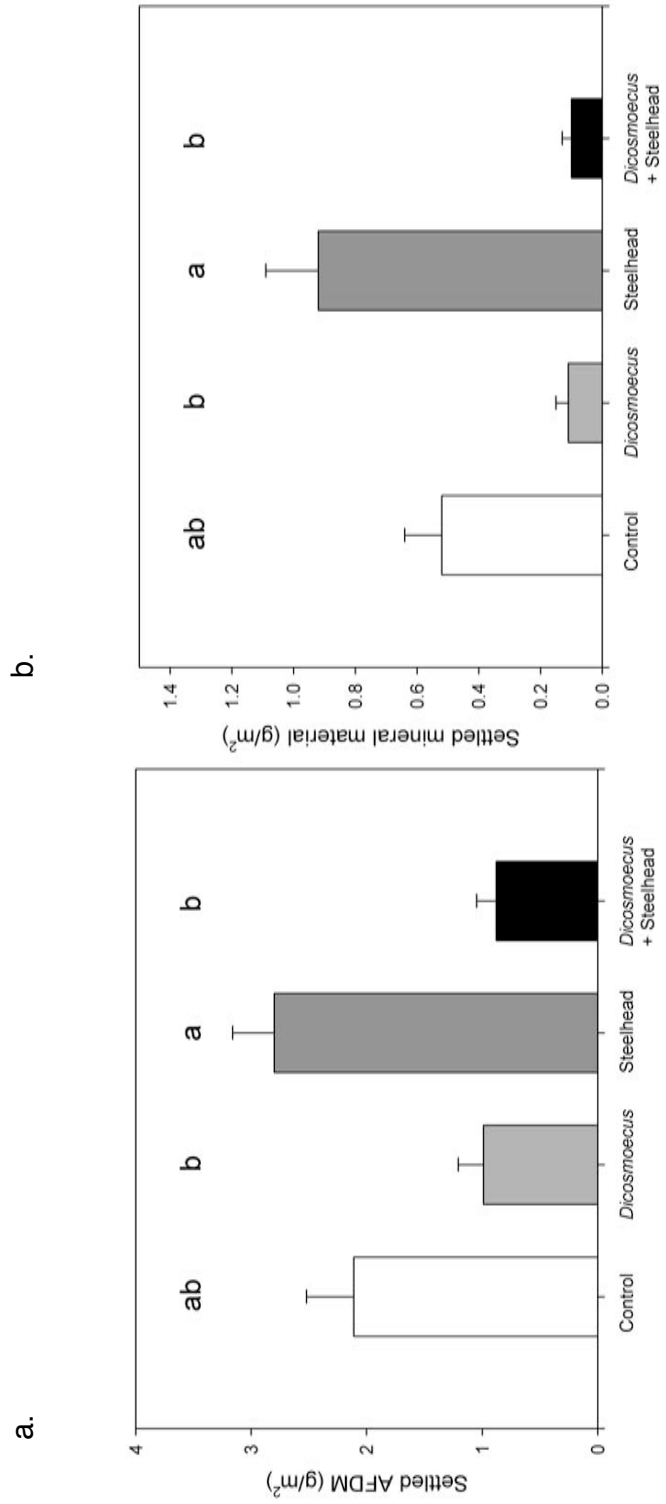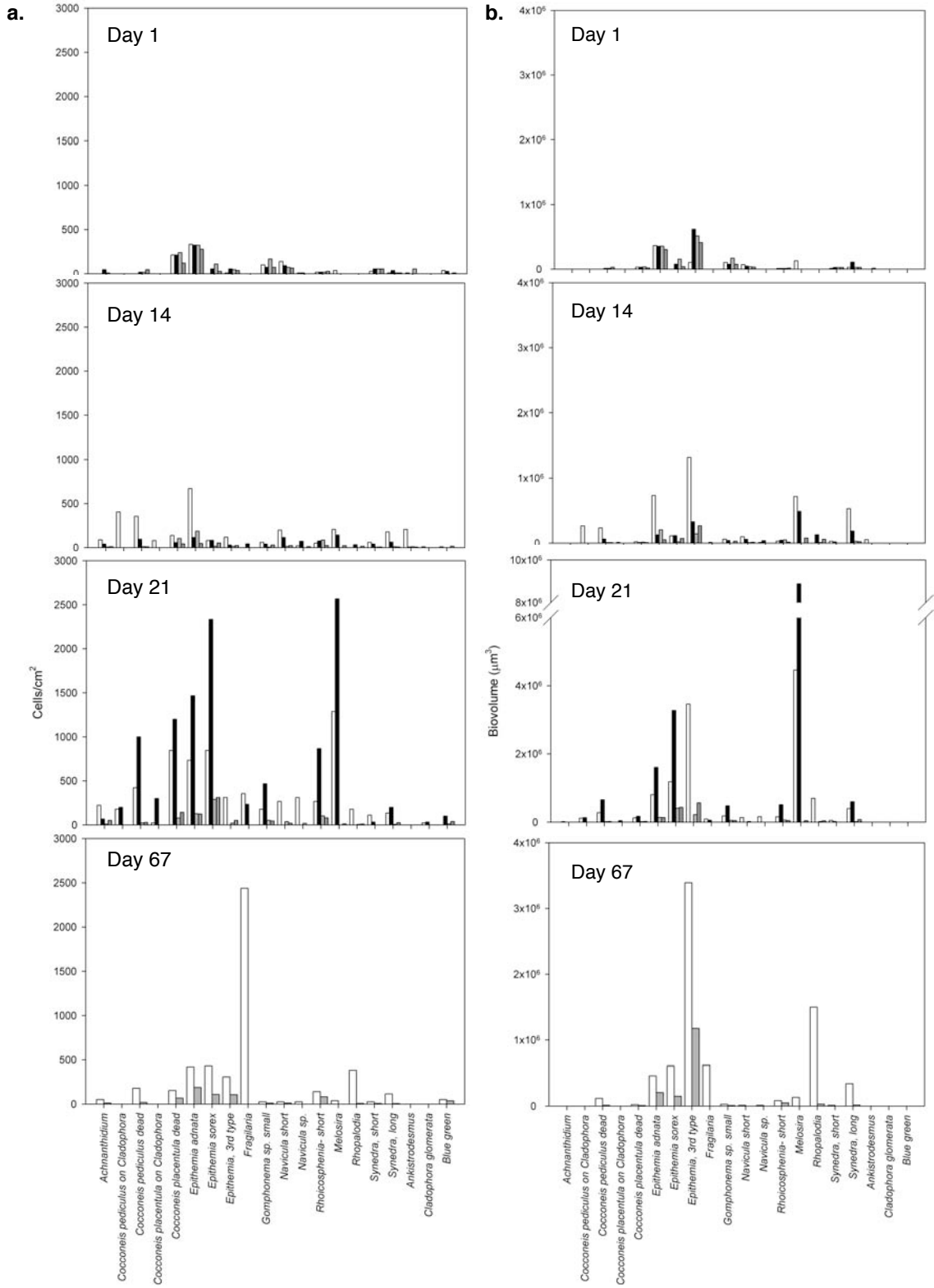
Figure 1

Figure 2

Figure 3

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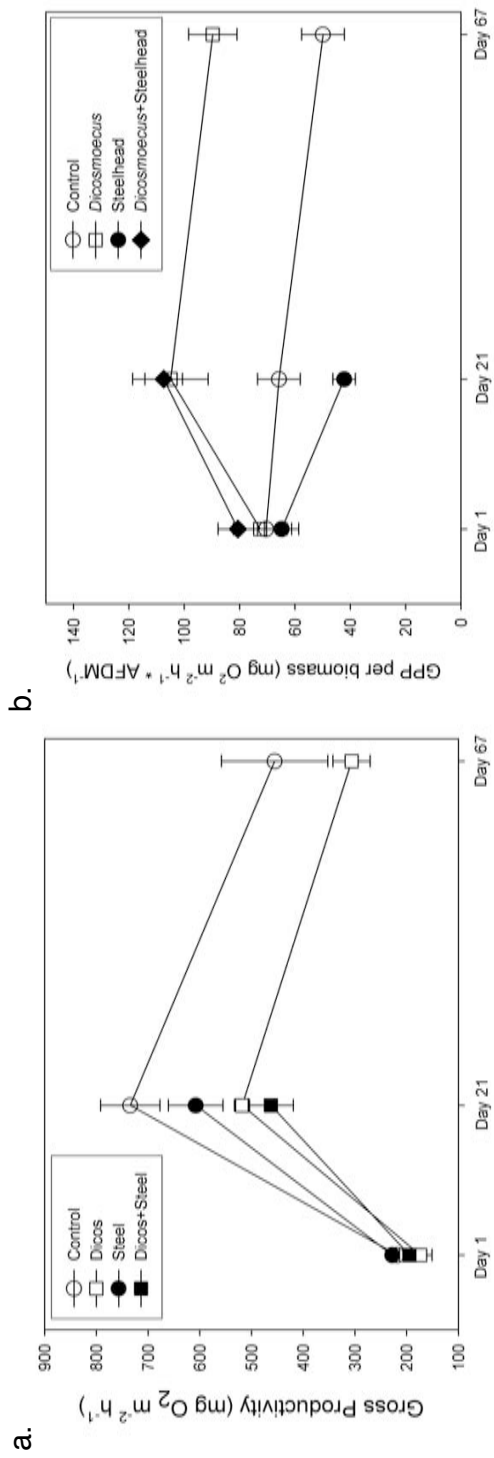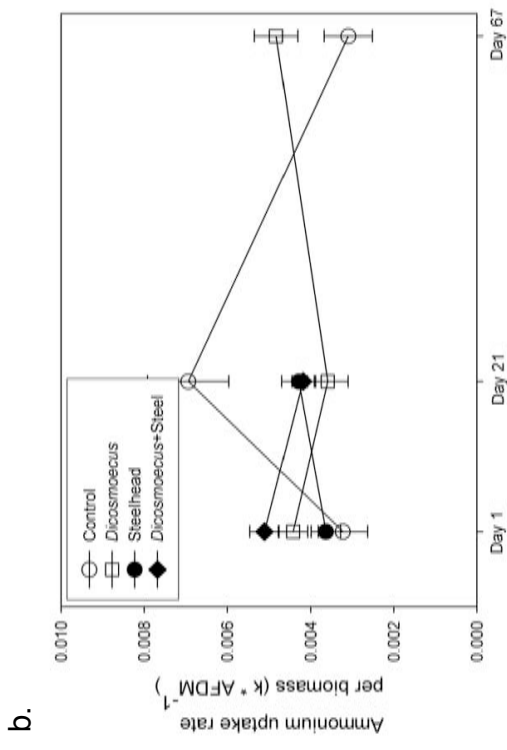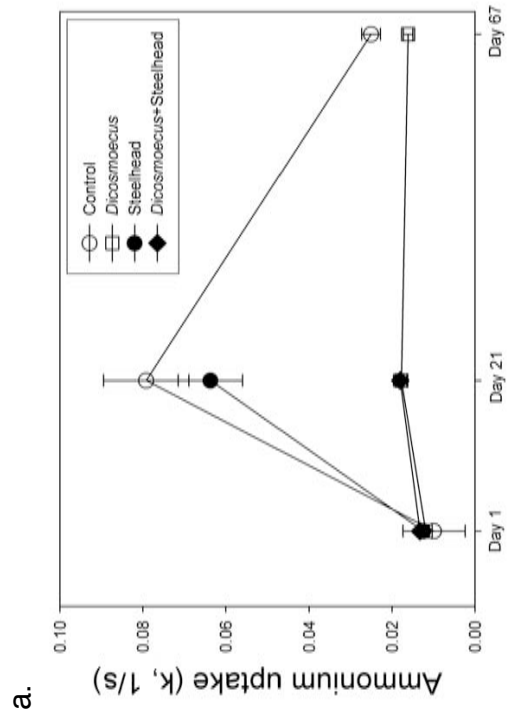
Figure 4

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Figure 6

Figure 7

Figure 8

CHAPTER 2

Ontogenic shift in habitat use and critical flow threshold by the caddisfly *Dicosmoecus gilvipes.*

Abstract

A species vulnerability to disturbance can vary with organism ontogeny. We investigated whether flood timing would have a differential impact on *Dicosmoecus gilvipes* populations. Specifically, we measured whether critical flow thresholds and habitat use vary with *Dicosmoecus* larval size. Critical flow threshold increased with larval size, as did larval flow velocity preference. The results suggest early flood events will have a gr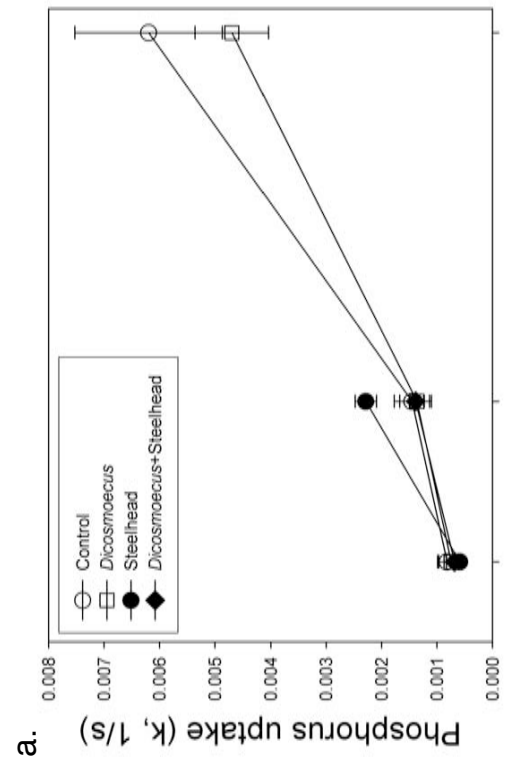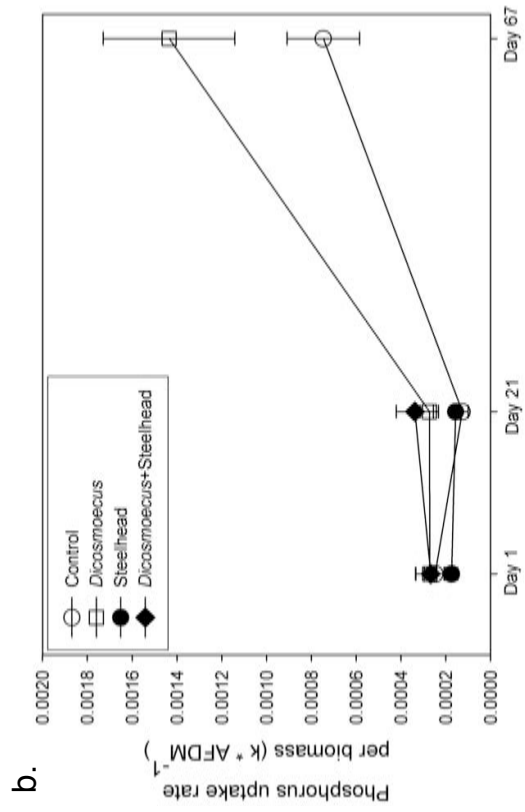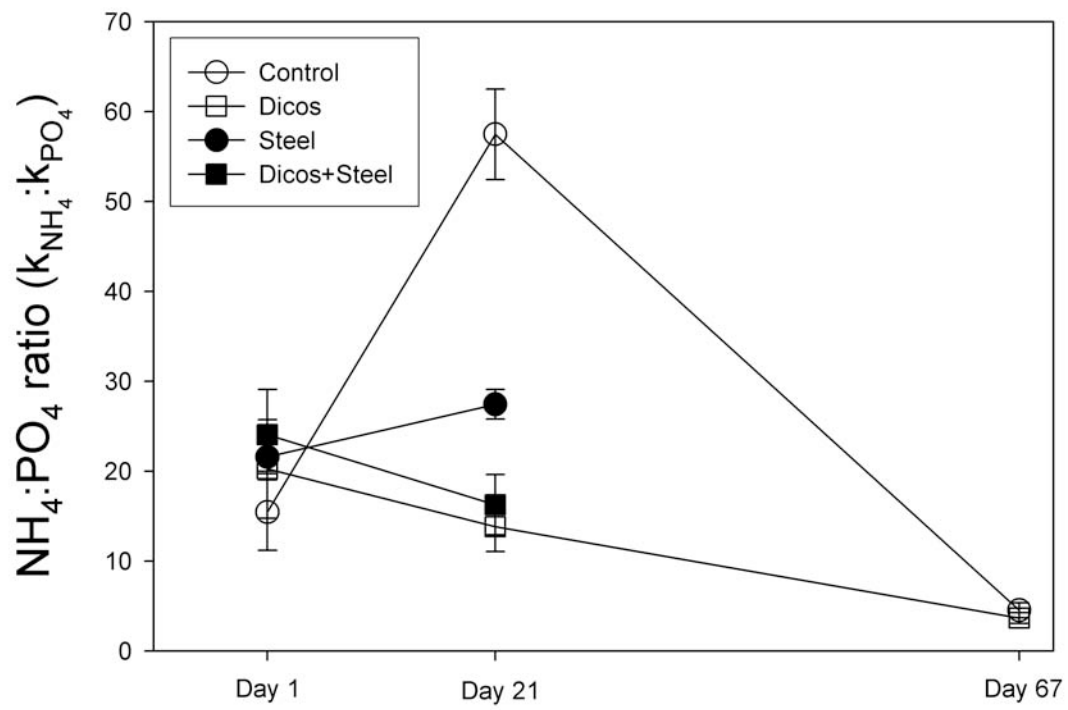eater impact on *Dicosmoecus* populations than later flood events of a similar magnitude, and during low-flow periods the interaction between *Dicosmoecus* distribution, periphyton composition and productivity, and flow velocity may significantly impact ecosystem processes on smaller scales.

Introduction

Disturbance by flooding can dramatically disrupt population and community structure in stream ecosystems (Seegrist and Gard 1972, Fisher et al. 1982, Hemphill and Cooper 1983, Resh et al. 1988, Scrimgeour et al. 1988). Floods can dislodge organisms on the bed surface and amongst the bed sediment if bed materials are mobilized (Power and Stewart 1987, Erman et al. 1988, Biggs 1995). When strongly interacting species are affected, both food web dynamics and ecosystem processes can be altered (Power et al. 1995, Chapter 4), and effects can persist well after the flood event (e.g. Elwood and Waters 1969).

Some benthic organisms have refuge seeking behaviors (e.g. Meffe 1984, Lytle 2002) or life histories (e.g. Lytle 2002, Gray and Fisher 1981) that protect individuals from flood events. Organisms unable to find refuge must rely on strength, swimming ability, weight, and/or contact with the bed surface to withstand the currents. At a critical flow threshold, the hydraulic forces of lift and drag overcome the organism's ability to maintain position through swimming or resistance. Knowledge of this critical flow threshold is crucial to predicting when and where increases in flow will remove an organism. If the threshold varies with organism ontogeny, a flood event occurring early in the season, when the organism is small, may have a different impact than a flood occurring later, when the organism is larger.

The critical flow threshold required to initiate motion of non-living mineral particles and how this threshold varies with particle size has been well studied by geomorphologists (e.g. Shields 1936, Fenton and Abbott 1977, Wiberg and Smith 1987, Buffington and Montgomery 1977). The critical shear stress required to initiate particle movement is a function of the particle weight, particle protrusion, particle exposure, and intergranular friction angle (e.g. Fenton and Abbot 1977, Wiberg and Smith 1987, Kirchner et al. 1990, Johnston and Andrews 1998). Protrusion and exposure influence the lift and drag forces on the particle, while weight and intergranular friction angle resist movement. Other factors controlling critical shear stress, include particle size distribution

(Parker et al 1982, Dietrich et al. 1989), bed surface roughness (Naot 1984), and bed slope (Lamb et al. 2008), all of which influence particle protrusion, exposure, and flow turbulence. For example, on a bed with mixed grain sizes the smaller particles can 'hide' amongst larger ones and reduce their protrusion and exposure to flow. Larger particles, although heavier, protrude more and are more exposed on a mixed bed, and they experience greater lift and drag forces than smaller particles These particle tradeoffs can lead to a bed condition in which all the particles begin motion at the same critical shear, typically scaled by the median grain size of the bed (Parker et al. 1982).

How the critical flow threshold will vary with *living* organisms is less clear. Hydraulic forces should increase proportionally with organism size if morphology does not change significantly with growth. Resistance forces, however, consist of both passive (weight) and active components (e.g. muscle strength, claws, fins, tenacity). The resistance components, and how they scale relative to the hydraulic forces, will determine how the critical flow threshold varies with organism ontogeny. Organisms will likely become stronger as they grow, but how strength increases relative to hydraulic forces exerted on their larger bodies is unknown. Their tenacity vs tendency to drift might also vary due to ontogenic changes in behavior (Hart and Resh 1980). In the current study, we examine how hydraulic and resistance force influence the critical flow threshold for the caddisfly larva (Trichoptera) *Dicosmoecus gilvipes* (Hagen).

Dicosmoecus gilvipes is a strong interactor (*sensu* MacArthur 1972, Paine 1980) in northern California stream ecosystems. The larvae can control algal accrual, reduce local invertebrate densities (Hart 1981, Lamberti and Resh 1983, Wootton et al. 1996), and alter energy and nutrient flowpaths in a stream ecosystem (Power et al. 1995, Limm unpublished). The larvae are also vulnerable to high flows. Wootton et al. (1996) observed a 77% decrease in larval density after an April flood event. Greater larval densities have been observed during years when floods were absent and in rivers with regulated peak flows (Power et al. 1995, Wootton et al. 1996). By quantifying how the critical flow threshold varies for different sized *Dicosmoecus* larva, we can address whether disturbance severity (*sensu* Sousa 1984) for a flood of a given magnitude varies with flood timing. If a single critical flow threshold can characterize a population, it will simplify models used to predict flood impacts on a population. Second, variation in critical flow threshold with organism size may explain ontogenic shifts in habitat use and distribution.

In the current study, we measure the critical flow velocity required to dislodge different sized *Dicosmoecus* larvae from a rock surface. From the empirical data we calculate larval resistance force and two dimensionless numbers, Weber number and Shields stress, to investigate how the critical flow threshold varies with larval size and Reynolds number. In addition, we quantify habitat use by *Dicosmoecus* larvae in a coastal California stream to assess whether critical flow thresholds influence larval distribution.

Methods

Study area

Experiments were conducted in Elder Creek within the Heath and Marjorie Angelo

Coast Range Reserve in Mendocino County, California (39°44"N 123°39"W, Figure 1). Elder Creek drains 17 km^2. The bed substrate consists of a thin layer of cobble and gravel over bedrock. The study area has a Mediterranean climate with wet, cool 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-decidous evergreen forest dominated primarily by old-growth Douglas fir (*Pseudotsuga menziesii*) redwood (*Sequoia sempervirens*) and tanoak (*Lithocarpus densiflorus*). The major aquatic food web components consist of producers (primarily diatoms and filamentous green algae), grazing insects (midges, mayflies, caddisflies), predatory insects (stoneflies, aquatic beetles, naucorid bugs), and predatory vertebrates (Rough skinned newt, *Taricha granulosa,* Pacific giant salamander, *Dicamptodon ensatus*, juvenile steelhead, *Oncorhynchus mykiss*).

In Elder Creek and in the larger Eel River, *Dicosmoecus gilvipes* has a univoltine life cycle. Larvae emerge from eggs during February-March and build cases out of silk and organic materials that include Douglas-Fir needles (Figure 1). As they grow, the larvae increase the mineral content of their cases and by the fifth instar, the case is made entirely of silk and minerals. In April, second instar densities can reach 160 m^{-2}. By mid-July the fifth instar larvae adhere to the underside of rocks and begin diapause. Winged adults emerge in September.

Biometric measurements

To quantify relationships between caddisfly case length, diameter, and frontal projected area, we collected thirty *Dicosmoecus* larvae from Elder creek in May, June, and July 2008. In the laboratory each larva and its case were photographed using two cameras on fixed tripods. To quantify case length and case diameter, we photographed the larva and a calibration scale with a camera was placed 0.5 m directly above. To quantify frontal projected area, we placed the camera 1.5 m in front of a larva with the lens axis directly in line with the larvae. We analyzed the images with ImageJ software (http://rsbweb.nih.gov/ij/index.html).

Critical velocity

We used a water jet to manipulate *in situ* flow velocity and quantify the critical near-bed velocity required to dislodge *Dicosmoecus* larvae. The water jet was generated using a 12 V water pump (Rule-Mate 750, ITT Corporation) connected to a flexible tube with a 0.019 m diameter. At the end of the flexible tube we attached a 1.2 m long x 0.019 m diameter solid tube with an adjustable valve. We calibrated the adjustable valve with a Marsh McBirney Flowmate 2000 flowmeter so that each incremental adjustment increased water velocity 0.05 m/s. The solid tube was angled 120 degrees 0.05 m prior to the nozzle.

We began each trial by locating undisturbed individual larva on large cobble, boulder, or bedrock surfaces and measuring their case length with a ruler and view box. Only larvae on flat, relatively horizontal surfaces were targeted. We then placed the nozzle, with the adjustable valve closed, 0.05 m directly in front of the larva. The solid tube was set parallel to the rock surface to ensure parallel flow with respect to the

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surface. We then opened adjustable valve and increased water jet flow velocity 0.05 m/s every 5 seconds until the larva was dislodged. Once dislodged, the flowmeter sensor was placed at the initial larva location to quantify the water jet flow velocity 0.019 m above the surface, the minimum depth at which the flow sensor can measure velocity. Keeping the flowmeter sensor in place, we then removed the water jet and measured ambient flow velocity at the location.

Resistance force

An organism on the bed surface will be dislodged when drag and lift forces overcome those keeping it in contact with the bed surface. Forces acting on a *Dicosmoecus* larva along the mean flow are: fluid drag force (F_D), lift force (F_L), buoyancy force (F_B), gravity force (F_G), and larval resistance force (F_A) (Wiberg and Smith 1979). Just before the larva gets dislodged, these forces sum to zero (Eq. 1):

$$F_D \cos\alpha + F_L \sin\alpha + F_B \sin\alpha - F_G \sin\alpha - F_C \sin\alpha = 0 \qquad (1)$$

where α is the angle between the rock surface and case axis (Figure 2). To measure α, we photographed thirty larvae (from 4 to 27 mm long) resting on a surface. The camera lens axis was at the height of the surface and α was analyzed using ImageJ software. α averaged 17.4 degrees ($\pm$ 0.5 SEM).

We calculated the larval resistance force F_A by incorporating the following into Eq. 2:

$$F_D = \frac{\rho}{2}\frac{D^2\pi}{4}C_D U_C^2$$

$$F_L = \frac{\rho}{2}\frac{D^2\pi}{4}C_L U_C^2 \qquad (2)$$

$$F_B = \rho\frac{D^2\pi}{4}L_c g$$

$$F_G = \rho_L\frac{D^2\pi}{4}L_c g$$

where ρ is water density, ρ_L is larval density, D is the case diameter, g is the acceleration due to gravity, and U_C is the critical velocity when a larva is dislodged. The following expression was attained (Eq. 3):

$$F_A = \frac{D^2\pi}{8}\left(\rho C_D U_C^2 \cot\alpha + \rho C_L U_C^2 + 2(\rho_L - \rho)L_c g\right) \qquad (3)$$

We used 0.8 for the drag (C_D) and lift (C_L) coefficients, an estimate for a cylinder with the long axis parallel to the flow (Munson et al. 1998), and previously used for the caddisfly *Allogamus auricollis* (Waringer 1989).

Dimensional analysis

Dimensional analysis can provide insight into system properties across multiple spatial and temporal scales, independent of the unit of measurement used to quantify the physical variables involved. A common dimensionless number used in fluid mechanics is the Reynolds number, *Re* (Eq. 4):

$$\text{Re} = \frac{UL}{v} \tag{4}$$

where U denotes the fluid velocity, L is a characteristic length scale, and v is the fluid kinematic viscosity. *Re* describes the ratio of inertial to viscous forces on an element of fluid and is useful for characterizing the flow regime around objects of different lengths. For example, small macroinvertebrates live at lower *Re* than large macroinvertebrates in similar flow conditions (Statzner 1988). At lower *Re* the viscous forces, and therefore friction drag, play a larger role in the fluid environment experienced by the smaller organisms.

We examine two dimensionless numbers for understanding critical flow conditions with respect to *Dicosmoecus* larvae. The Weber number (Eq. 5):

$$We = \frac{\rho U^2 D}{\sigma_A} \tag{5}$$

is a ratio of the inertial force of the moving fluid to the resistance force. In our study, larvae 'resistance' consists of both active (F_A) and passive (F_G, F_B) forces. The active component F_A is a function of larval strength, larval claws, friction between the claws and surface, and behavior (tenacity). Since all of these may scale with larval size we can consider:

$$F_A \approx (\text{characteristic length, attachment coefficient})$$

We used case diameter, D, for the characteristic length. The resistance coefficient is defined as $\sigma_A = F_A / D$. The critical Weber number denotes when the inertial force of the fluid reaches a critical value relative to the larval resistance force, and the larva is dislodged. By plotting Weber number versus morphometric ratio Lc/D, we can evaluate the relationship across different combinations of U, Lc, and D.

From empirical data collected on inorganic particles, motion will occur when a critical shear stress (τ_b) is reached. In dimensionless form, $\tau_b/\rho RDg$ (with R equal to $\frac{\rho_{larvae} - \rho_{water}}{\rho_{water}}$) is termed the Shields stress (τ_c^*). When Shields stress is plotted against Reynolds roughness (U_*D/v), the resulting curve denotes the threshold for initial particle

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motion. We calculated the Shields stress of a living *Dicosmoecus* larva by:

$$\frac{1}{2}\rho\frac{D^2\pi}{4}C_DU_m^2 + \tan\alpha\frac{1}{2}\rho\frac{D^2\pi}{4}C_LU_m^2 = \tan\alpha(\rho R\frac{D^2\pi}{4}L_Cg + D\sigma_A)$$

then,

$$\rho U_m^2(\frac{1}{2}\frac{D^2\pi}{4}C_D + \tan\alpha\frac{1}{2}\frac{D^2\pi}{4}C_L) = \tan\alpha(\rho R\frac{D^2\pi}{4}L_Cg + D\sigma_A) \qquad (6)$$

From Wygnanski (1992), we calculated the fluid function ψ for maximum velocity U_m and shear velocity U_* for a water jet:

$$\psi = \frac{U_m}{U_*} = 3.85\xi^{0.063} \qquad (7)$$

where $\xi = \frac{XJ}{v^2}$, X equals distance from the nozzle (0.05 m), J= U^2b with b equal to the nozzle opening (0.019 m), and v is the kinematic viscosity. For the range of velocities measured in our study ψ averaged 11.8 (±0.03 SEM). Substituting $U_*^2\psi^2$ for U_m in Eq. 6:

$$\rho U_*^2\psi^2(\frac{1}{2}\frac{D^2\pi}{4}C_D + \tan\alpha\frac{1}{2}\frac{D^2\pi}{4}C_L) = \tan\alpha(\rho R\frac{D^2\pi}{4}L_Cg + D\sigma_A)$$

Boundary shear stress $\tau_b = \rho U_*^2$, and our resulting equation for the non-dimensional Shields stress is:

$$\tau_C^* = \tau_b / \rho RDg = \frac{2\tan\alpha}{(C_D + \tan\alpha C_L)\psi^2}(\frac{Lc}{D} + \frac{4\sigma_A}{\rho RD^2\pi g}) \qquad (8)$$

Larval habitat use

To quantify whether flow velocity influences *Dicosmoecus* larval distribution we set up 16 cross-stream transects 5 m apart (longitudinally) in an 80 m long reach of Elder Creek. The reach contained multiple pool-riffle-run complexes. The average wetted width was 6 m and the average depth along the thalweg was 0.36 m. The deepest pool was 0.81 m deep and average slope was 0.024. Along each transect we measured near-bed water velocity (0.019 m above the bed surface), water depth, substrate size, *Dicosmoecus* larval density, and larval case lengths every 0.5 m. At each sampling point along the transect, we recorded the number of *Dicosmoecus* larvae in a 0.031 m^2 area using a view-box and measured the case length of all individual larvae using a ruler. A Marsh McBirney Flowmate 2000 flow meter was used to measure water velocity. We used Pearson product-moment correlations (JMP software) to assess correlations between the physical

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variables in May, June, and July.

To assess instar preference for a specific depth, flow velocity, or substrate size, we Jacobs Selectivity Index D (Jabob 1974):

$$D = (r - p) / (r + p - 2rp)$$

(9)

where r is the proportion of larvae observed in a particular physical condition and p is the proportion of a particular physical condition to total available in the stream. If larvae show exclusive use a particular physical condition, D will equal +1. If larvae show complete avoidance of a particular physical condition, D will equal -1.

On June 12th we sampled periphyton within the experimental reach. In order to sample along a velocity gradient we characterized the pool (depth > 0.25m), run (depth between 0.10-0.24m), and riffle (depth 0-0.09m) habitats in the reach and stratified where random points would be selected. A measuring tape was placed along the reach centerline and a random number generator was used to select six points in each habitat type. At each longitudinal point, a measuring tape was placed across the stream and perpendicular to the current. A random number generator was used to select the rock to be scraped for periphyton. Prior to removing the rock, the depth and near-bed velocity was measured and a curved barrier was placed just upstream of the rock to decrease flow velocity. The rock was then slowly lifted and lightly rinsed with water to remove loose sediment. The loose sediment was collected in a pan and any invertebrates were removed. The sediment and water was placed in a 1 L bottle and stored in a cooler. A template of known area was placed on the rock and periphyton was removed with a wire brush. The periphyton was rinsed into a 50 mL jar. In the lab, both the sediment and periphyton scraping were filtered onto a glass-fiber filter (GFF, Whatman Co.). Each filter was dried at 50°C for 48 hours, weighed, ashed in a muffle furnace for 2 hours at 550°C, and re-weighed to quantify ash-free dry mass (AFDM).

Streambed availability

To assess the total area of the streambed at specific velocities, we imported the transect data in a GIS system (ESRI ArcGIS) as non-georeferenced point locations. Y values started at 0 upstream and incremented + 5 meters for each transect. X values started at stream left, facing downstream and incremented moving right at 0.5 meter intervals. To convert from point to grid, a spline method was adopted. Spline methods estimate values using a mathematical function that minimizes overall surface curvature, resulting in a smooth surface that passes exactly through the input points (Franke 1982, ESRI 2009). The spline grid of near bed velocity was organized into 27 categories from 0 to 48 cm/s at increments of 2, then 50 & 100 cm/s. For each instar, the average critical velocity from the water jet experiment and average ambient velocity from transect data were used to calculate the available streambed area available to larvae. We followed the case diameter criteria calculated by Li and Gregory (1989) to categorize instar.

Results

Critical velocity

We quantified the critical flow velocities for 162 *Dicosmoecus* larvae (Figure 5). Critical flow velocity increased with larval size ($p < 0.001$, Table 1). Average critical flow velocity across all larvae was 0.27 m/s (±0.01, SE). Variation in critical flow velocity for a specific-size instar was high ($R^2 = 0.09$).

Resistance force

Using the biometric measurements (Figures 3 and 4) and Eq. (4), we calculated the larval resistance force. The larval resistance force increased with case diameter ($p < 0.0001$, $R^2 = 0.27$, Figure 6, Table 1). Resistance forces ranged from 0.0002 to 0.02 N. The average resistance force across all instars was 0.006 N (±0.0003, SE).

Dimensional analysis

Weber number
The critical Weber number calculated from water jet removal experiments ranged from 0.29 to 0.52 (Figure 7) with a mean value of 0.34 (±0.003, SE). The critical Weber number increased with larval size (Table 1). Weber number values calculated from ambient flow conditions (Figure 7) were well below critical values, and averaged 0.04 (±0.003, SE).

Shields stress

Shields stress (τ_C^*) values for *Dicosmoecus* larvae were significantly higher than the empirically derived Shields curve that denotes the threshold for motion of inorganic particles (Shields 1936, Parker 2003, Figure 8). Shields stress ranged between 0.17 and 5.22 (Table 1). Critical Reynolds numbers ranged between 23.5 and 220.5. When the larval resistance force was set to zero ($\sigma_A = 0$ in Eq. 8), Shield stress values were nearly 100-fold smaller, and the values were clumped around the Shields curve.
Larval habitat use
We measured physical conditions and *Dicosmoecus* larvae density at 180 positions along the 80 m reach. Total streambed area available to *Dicosmoecus* in May was 530 m^2. Since ninety-seven percent of the second instar size class was observed May we used May physical condition availability for analysis. Habitat use by third and fourth instars was compared to physical condition availability in June and July, respectively. In May, near-bed flow velocity, water depth, and substrate size were not correlated with locations where *Dicosmoecus* larvae were present. In June, substrate size was significantly correlated with near-bed velocity ($p < 0.001$) and depth ($p = 0.001$). In July, only velocity and depth values were correlated ($p = 0.02$).
Assuming our instantaneous measurement of larval presence reflects the physical conditions utilized by the larvae, all instars preferred specific flow velocities (Figure 9, Table 2). Second instar larvae preferred velocities between 0-0.03 m/s while third, fourth, and preferred faster velocities above 0.03 m/s but below 0.19 m/s.
Dicosmoecus larvae were rarely found in water deeper than 0.6 m (Figure 10). Second instar larvae preferred depths from 0 to 0.3 m. Third instar larvae preferred

depths from 0.1 to 0.4 m and under-utilized other depths. Fourth instar larvae showed the largest range of preferred depths, from 0.1 to 0.6 m. Fifth instar larvae preferred depths from 0 to 0.3 m.

Larval preference for a specific substrate size was less clear (Figure 11). All instars under-utilized substrates smaller than 0.05 m. For larger substrate sizes, the difference between proportion utilized by larvae and proportion available was rarely greater than 10%. Fifth instar larvae did show a preference for substrates between 0.15-0.3 m.

As near-bed velocity increased in the reach, periphyton AFDM decreased (Figure 12a). AFDM was nearly ten times greater in the slower velocity pools than in the fast velocity riffles. Loose organic sediment on the rocks also decreased with velocity (Figure 12b), and contributed between 0 to 13 percent of total organic material on the rocks.

Streambed area

Based on the average critical velocity for each instar (Table 1), 14 percent of the experimental reach is unavailable to second instar larvae. Six percent of the reach is unavailable to third and fourth instar larvae while fifth instar larve can access all but three percent.

As the average ambient velocity they were observed in increased up to the fourth instar, so did the streambed area available (Table 2). For fifth instar larvae, the streambed area decreased based on the lower average ambient velocity they were observed in.

Discussion

Critical flow threshold

Flow has long been recognized as an important factor controlling caddisfly distribution and morphology (Rousseau 1921, Webster and Webster 1943). For *Dicosmoecus gilvipes*, critical flow conditions vary with larval size. As the larvae grow, their resistance force increases disproportionately more than the size-induced increase in hydraulic forces, allowing them to withstand higher flow velocities.

We can assess whether passive and/or active resistance force component(s) are responsible for the increased flow resistance with size by graphing the relationship between hydraulic force components and resistance force components (Figure 13). The active component, calculated by subtracting the passive component (larval weight) from total resistance force, increases with respect to hydraulic force at a greater rate than the passive larval weight. A similar pattern between passive and active resistance components was observed in the caddisfly *Allogamus auricollis* (Waringer 1989). Some aspect of the active component- larval strength, their claws, friction between claws and surface, tenacity- is responsible for the increased critical flow threshold with larval size.

The positive relationship between larval size and critical flow threshold was evident in the dimensionless plot of Weber number versus morphometric ratio. Critical Weber number, which relates critical flow conditions to organism length, diameter, and contact coefficient, increased with larvae size. Our results suggest the Weber number may be a useful tool for predicting organism removal when a contact coefficient (σ_A=Fc/characteristic length) can be estimated from empirical data. While the

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relationship between Weber number and morphometric ratio could be criticized for having the same dimensioned parameter (diameter) in both dimensionless parameters, leading to spurious correlation, Parker and others (2003) argue that, "an appropriate dimensionless correlation is more likely to be in accord with the underlying physics than a correlation of parameters of differing dimensions".

When calculating the dimensionless Shields stress for different sized larvae we followed the physics-based approach Wiberg and Smith (1987) used for mineral particles. When we did not include the organism resistance component (F_A), the physical model predictions agreed closely with values along the empirically derived Shields curve. Larval motion was initiated at the same Shields stress as similar sized mineral particles. When the resistance component was included, Shields stress increased roughly 100-fold, further evidence that the active component of resistance dominates their ability to withstand hydraulic forces.

The active component may also explain the variation in Shields stress we observed for a given Reynolds roughness. Individual larva may respond differently to experimental conditions due to variation in their strength, physical condition, and/or tenacity. Our experimental methods may have also influenced the variability. We measured the critical flow velocity 0.019 m above the surface using a time-averaging flow meter. Peak velocities due to periodic sweeps of high momentum fluid were not measured. These turbulent fluctuations around the time-averaged value we measured can significantly elevate shear stresses above mean values. Localized peak velocities can vary greater than 70 percent and play an important role in mobilizing mineral particles (Knighton 1998). In addition, we applied the water jet *in situ*, and background eddy structure may have influenced flow conditions around individual larva.

We used the same coefficient for both lift and drag. Both drag and lift influence particle entrainment and the importance of each can shift with particle size (Stautzner 1988). Drag and lift coefficients may also vary with Reynolds number (Vogel 1996, Full and Koehl 1998). Actual values for the different sized instars should be experimentally derived.

Despite the observed variation, incorporating the resistance force into the Shields stress equation can be useful for forecasting where larvae will persist after a flood. The upper Shields stress threshold for the larvae can be compared to predicted values from hydraulic models. For example, using the HEC-RAS (http://www.hec.usace.army.mil/), a 1D hydraulic model that uses energy conservation to solve for steady, non-uniform flow along an arbitrary channel geometry, we can calculate bed shear stress at a given position in a river during a flood. Bed shear stress can be non-dimensionalized with respect to the caddisfly larvae and plotted with respect to river position (Figure 14). Where the non-dimensionalized Sheilds stress is lower than the larval threshold we would expect the larvae to persist.

We acknowledge that using a 1D hydraulic model has limitations. The models cannot accurately reproduce turbulent eddies and other complex flow patterns found in natural streams. Typically a river is subdivided into rectangular cells for which a uniform depth and velocity are calculated. For the data presented in Figure 14, the Shields stress calculation is for a 100m reach (cell). Smaller scale bed features that influence eddy formation and peak shear stress are not included, nor are possible larval responses to increasing flows. Grain size distribution, pebble clusters, and vegetated banks can alter

the turbulence intensity and velocity gradient near a particle (Helley 1969). As discharge increase larvae may move off the top of rock surfaces to minimize their exposure to the flow, although some caddisflies do remain on top until they are dislodged (Holomuzki and Biggs 2003). While larger larvae cannot move into interstitial spaces under the bed surface, they can reduce their protrusion into the flow by moving between cobbles and boulders. The use of higher dimensional hydraulic models can improve flow characterization both on the top of rock surfaces and between rock locations where larvae may be hiding. This coupled with a 'hiding' function that incorporates larval size-local grain size distribution may improve prediction accuracy for where larvae will persist.

Habitat use

Critical flow thresholds may also influence aquatic organisms pre- and post-flood. Hydraulic conditions can control the mass transfer of materials (e.g. Whitford and Schumacher 1961), species distributions (e.g. Hansen et al. 1991), and predation rates (e.g. Malmqvist and Sackmann 1996). Some aquatic organisms prefer specific hydraulic conditions, including turbulent eddies, transverse flows, and different velocity gradients (Fausch and White 1981, Hayes and Jowett 1994, Riis and Biggs 2007). In the current study, while *Dicosmoecus* larvae were rarely observed near their critical flow threshold (ambient velocity averaged two-thirds the critical velocity), we did observe a size-related flow preference.

Size-related patterns with flow have been reported for other Trichoptera larvae including *Helicopsyche* (Allen 1951) and *Costachorema* (Collier et al. 1995). Larger larvae of both genus are found in faster flow velocities. A similar relationship is observed for the water bug *Aphelocheirus aestivalis* (Statzner 1988) and members of the mayfly genus *Deleatidium* (Jowett et al. 1991, Collier 1994). Proposed reasons for the size-related patterns include size-related current preferences and flow-related differences in growth rate (Hynes 1970, Collier 1994). Size-related current preferences may be due to resource availability. In mesocosm experiments, *Dicosmoecus* larval growth at ambient densities is density dependent (Lamberti et al. 1995) and larval grazing rates can exceed periphyton regrowth rates (Hart 1981). Food demand increases with *Dicosmoecus* larval size (Hart and Resh 1980), and this competition for food may drive them into faster currents. In addition, size-related current preferences may reflect seasonal availability due to changes in discharge. While fifth instar larvae can tolerate faster flow conditions, they were observed at a lower average velocity than third and fourth instar due to lower discharge in July.

In our study reach, periphyton accrual was greater in slower velocity flow. This might suggest food-limited larvae should move into slower habitats. Net periphyton accrual, however, is due to periphyton productivity and its removal by grazers or hydraulic forces. In nutrient limited streams periphyton productivity is positively correlated with flow velocity (Biggs et al. 1988, Hondzo and Wang 2002). Grazers can also alter periphyton physical structure and increase per capita supply of nutrients to algae and microbes, which may further stimulate periphyton growth (McCormick and Stevenson 1991, Mulholland et al. 1991). Grazer removal may have offset the faster periphyton re-growth at higher velocities. Whether periphyton re-growth was fast enough to result in higher food uptake per individual is dependent upon the density of grazers

present, their size and size-specific grazing rates, and periphyton growth rates across the range of velocities and growing conditions (light and nutrients), none of which were quantified in our study.

In addition to food quantity, food type and food quality may influence size-related patterns with flow velocity. In Big Elk Creek (Oregon Coast Range, U.S.A.) *Dicosmoecus* larvae shift their feeding effort from diatoms during their third instar to filamentous algae during the fourth and fifth instars (Li and Gregory 1989). Hart (1981) observed *Dicosmoecus* densities ten times greater on detached clumps of filamentous *Cladophora*. At Big Sulfur Creek, where Hart conducted the study, *Cladophora* is typically found in faster flow conditions inaccessible to *Dicosmoecus*, and the increased density on *Cladophora* may reflect the importance of maximizing food quantity or quality prior to pupation (Anderson and Cummins 1979, Hart and Resh 1980).

The nutritive quality of periphyton may also be affected by velocity. One reason proposed for the positive relationship between periphyton growth and velocity, as mentioned above, is a thinner diffusive boundary layer. As flow velocity increases, reduction or disruption of the diffusive boundary layer by turbulent eddies improves mass transfer of nutrients across the water-periphyton interface and can increase algal nutrient uptake (Whitford and Schumacher 1961). When inorganic N and P availability is increased in lake and streams, periphyton N and P concentrations increase (Hillebrand Kahlert 2001, Stelzer and Lamberti 2001), and therefore *Dicosmoecus* larvae may be tracking higher quality food in faster flow conditions.

Oxygen may also drive size-related current preferences. For organisms that depend on passive diffusion of oxygen across gills or body surface (Hynes 1970), the decrease in surface area to volume ratio with body size can make it difficult to meet oxygen demands. Moving into faster, well-mixed flows can increase the movement of well oxygenated water through their case and past their gills. Large *Dicosmoecus* larvae were observed in both fast and slow flow velocities in our study reach, however, and we did not observe any larvae leaving their case, a possible sign of oxygen stress, in slow flow conditions.

The possible costs influencing size-related current preferences include predation and effort. An invertebrate entrained into the water column is more vulnerable to predation by column feeders (Waters 1972). Known predators on *Dicosmoecus* include harlequin ducks (*Histrionicus histrionicus* L.) (Wright 1997), dippers (*Cinclus mexicanus* Swainson) (Harvey and Marti 1993), and rainbow trout (*Oncorhynchus mykiss*) (Tippets and Moyle 1978). *Dicosmoecus* larvae, which have an armored case, were not consumed by large steelhead trout in our study reach when a case was present (unpublished, Chapter 2). Some predators selectively consume larger-sized organisms (e.g. Allan 1978), and the larvae may be seeking refuge where predators are less effective.

Larval effort when foraging in faster flow conditions may outweigh any benefits. From our critical threshold results, larval resistance force decreases with larval size. As flow velocity and turbulence increase, the frequency at which smaller, weaker larvae get dislodged may negate any potential benefit. In addition, larvae may be more vulnerable when upside-down (Otto 2000), increasing predation risk in fast flow.

Understanding how the active component of larval resistance varies with organism ontogeny can improve our ability to predict the impact of large-scale events, like a flood, on individual organisms at different locations in a river network. For a

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strongly interacting species like *Dicosmoecus*, knowing where it will persist after a given sized flood allows us to generate hypotheses about how food web dynamics and ecosystem processes may affected. This information will also be useful to resource and ecosystem managers when planning flow releases in managed rivers or anticipating altered flood timing or magnitude due to seasonal or long term climate change. Their active component of resistance may also influence distributional patterns during non-flood periods, and their interaction with periphyton composition and productivity in different flow velocities may significantly impact ecosystem processes on smaller scales.

Acknowledgements

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Tables

Table 1. Summary of critical conditions for Dicosmoecus larvae.

Instar	Diameter (m)	$\overline{U}_*$ (m/s)	$\overline{F}_A$ (N)	$\overline{We}$	$\overline{\tau}_c$	Percent streambed area above $\overline{U}_*$
Second	$0.0029 - 0.0038$	0.21 ± 0.03	0.002 ± 0.0007	0.304 ± 0.004	0.96 ± 0.07	0.14
Third	$0.0039 - 0.0049$	0.28 ± 0.01	0.005 ± 0.0003	0.317 ± 0.001	1.05 ± 0.10	0.06
Fourth	$0.0050 - 0.0058$	0.28 ± 0.01	0.006 ± 0.0005	0.354 ± 0.005	1.20 ± 0.31	0.06
Fifth	$0.0059 - 0.0063$	0.32 ± 0.01	0.010 ± 0.001	0.394 ± 0.009	1.25 ± 0.07	0.03

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Table 2. Summary of ambient velocity conditions from transect data.

Instar	Diameter (m)	$\overline{U}$ (m/s)	Min U (m/s)	Max U (m/s)	Percent streambed area available at $\overline{U}$
Second	$0.0029 - 0.0038$	0.021 ± 0.003	0.00	0.11	0.26
Third	$0.0039 - 0.0049$	0.086 ± 0.006	0.01	0.20	0.64
Fourth	$0.0050 - 0.0058$	0.097 ± 0.008	0.01	0.20	0.70
Fifth	$0.0059 - 0.0063$	0.059 ± 0.012	0.02	0.16	0.56

Figure Legends

Figure 1. Drawing of *Dicosmoecus gilvipes* larval instars and their cases. Illustration by Aron Bothman.

Figure 2. Illustration of Dicosmoecus larva (a) and a sketch (b) of the force components influencing removal. Force components keeping the larva attached are the larval resistance force F_A (active) and weight component F_G (passive). Force components influencing removal are the drag component F_D, the lift component F_L, and the buoyant force F_B. Illustration by Aron Bothman.

Figure 3. Relationship between *Dicosmoecus* larval case length and case diameter.

Figure 4. The relationship between the frontal projected area and case diameter.

Figure 5. Plot of critical velocities for *Dicosmoecus* larval instars.

Figure 6. Resistance force versus case diameter for *Dicosmoecus* larval instars.

Figure 7. Weber number versus morphometric ratio. Critical values (open symbols) were calculated from the water jet experiment. Ambient values (closed symbols) were calculated from the ambient flow velocity the larvae were in prior to removal by water jet.

Figure 8. Shield stress (from Equation 8) required to initiate motion of *Dicosmoecus* larvae as a function of Reynolds roughness. Theoretical Shield curve was taken from Parker et al. (2003).

Figure 9. Proportion of larvae and available habitat at different velocities in the experimental reach (a) and Jabobs selectivity index (b). Values equal to +1 represent exclusive use by larvae and values equal to -1 represent complete avoidance.

Figure 10. Proportion of larvae and available habitat at different depths in the experimental reach (a) and Jabobs selectivity index (b). Values equal to +1 represent exclusive use by larvae and values equal to -1 represent complete avoidance.

Figure 11. Proportion of larvae and available habitat at different substrate sizes in the experimental reach (a) and Jabobs selectivity index (b). Values equal to +1 represent exclusive use by larvae and values equal to -1 represent complete avoidance.

Figure 12. Ash-free dry mass (AFDM) of periphyton (a) and loose sediment (b) at different velocities in the experimental reach.

Figure 13. Resistance force components versus hydraulic force components (see Figure 3). Hydraulic force components increase with flow velocity and frontal projected area. The passive resistance component is due to organism weight. Larval strength, claws,

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friction between claws and surface, and tenacity influence the active component. The active component was calculated by subtracting the passive resistance component from the total resistance force.

Figure 14. Plot of Shields stress on bed surface along the South Fork of the Eel river for a 1-year and 5-year flood. In the Hec-RAS model we used cross-sections collected from 1-m resolution LiDAR data (National Center for Airborne Laser Mapping) and two U.S.G.S. gaging stations (Branscomb and Elder). We assumed linear scaling between discharge and drainage area to calculate discharge for the flood events.
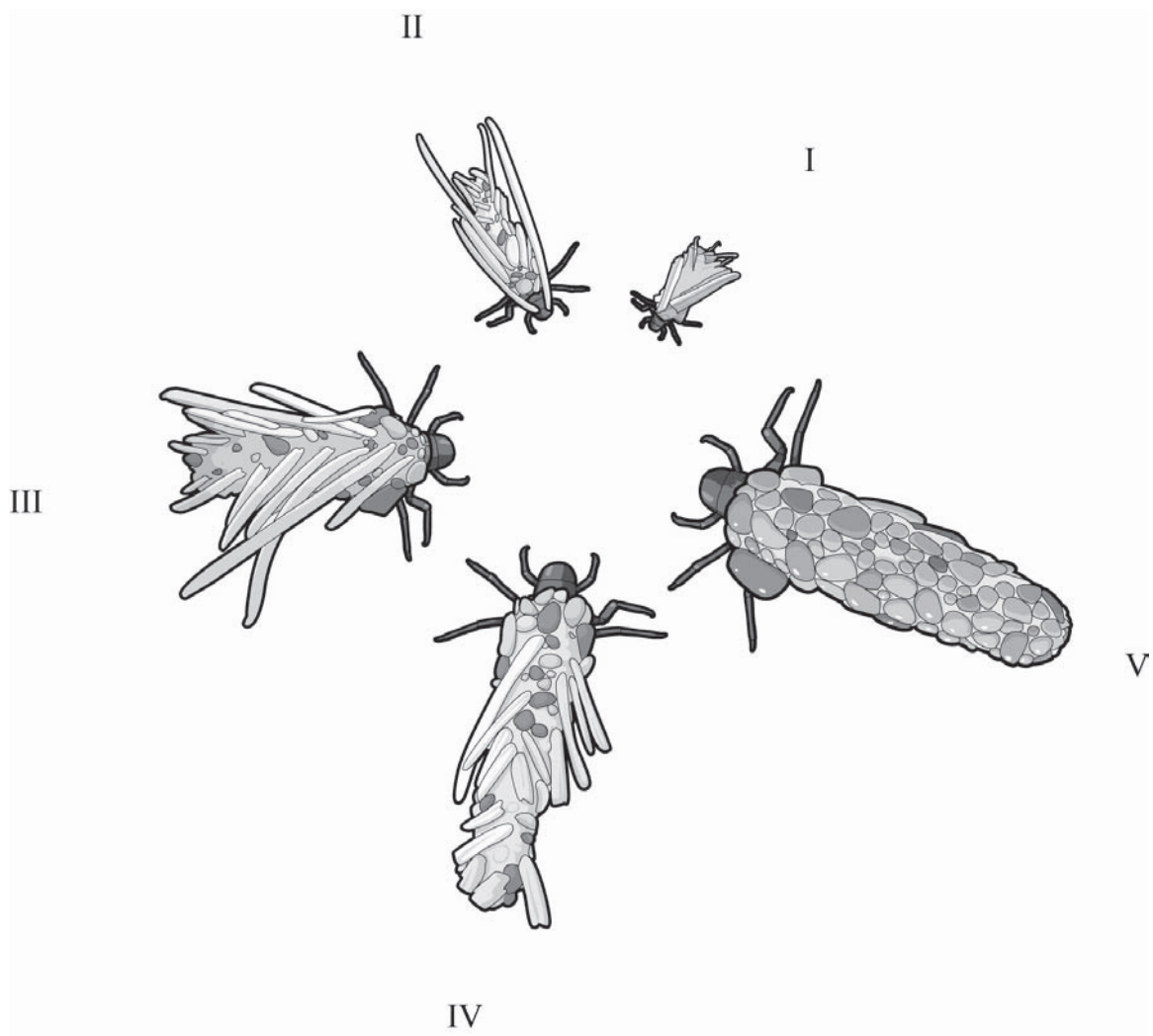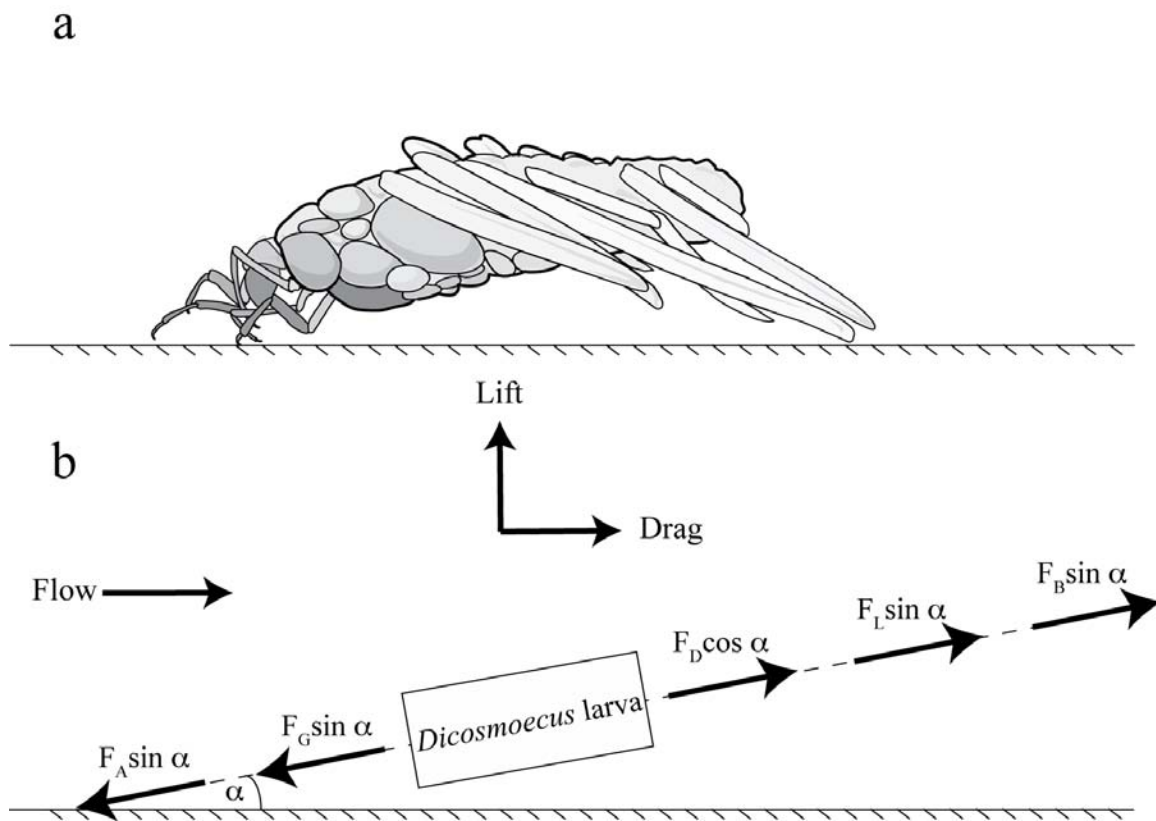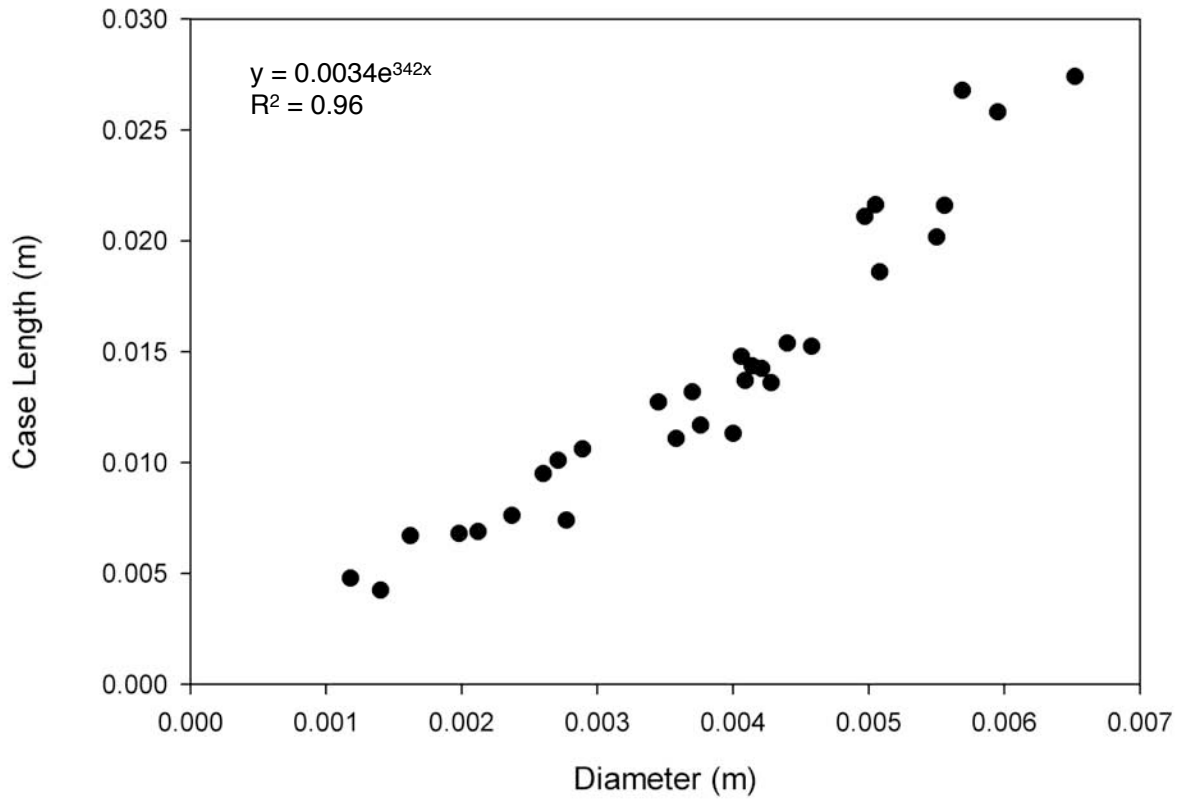
Figure 1.

a

Lift

Drag

b

Flow

$F_B \sin \alpha$

$F_L \sin \alpha$

$F_D \cos \alpha$

Dicosmoecus larva

$F_G \sin \alpha$

$F_A \sin \alpha$

α

Figure 2.

Figure 3.

$y = 0.6497x^{1.8}$
$R^2 = 0.92$
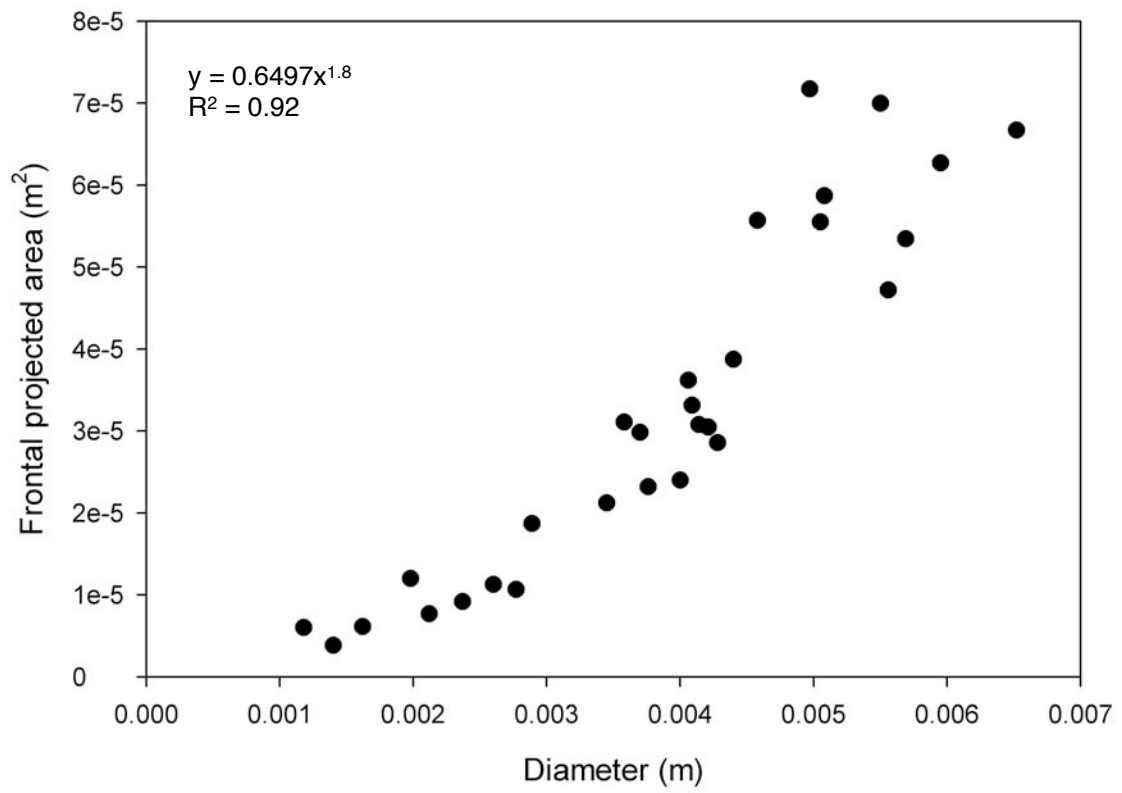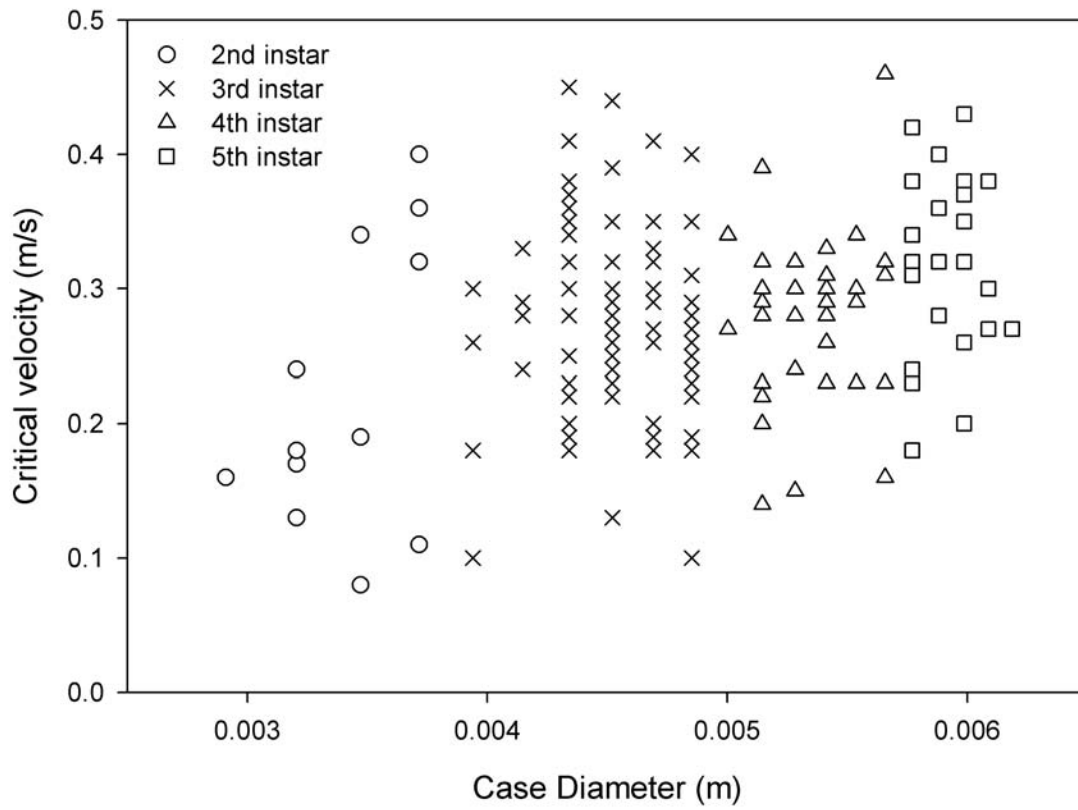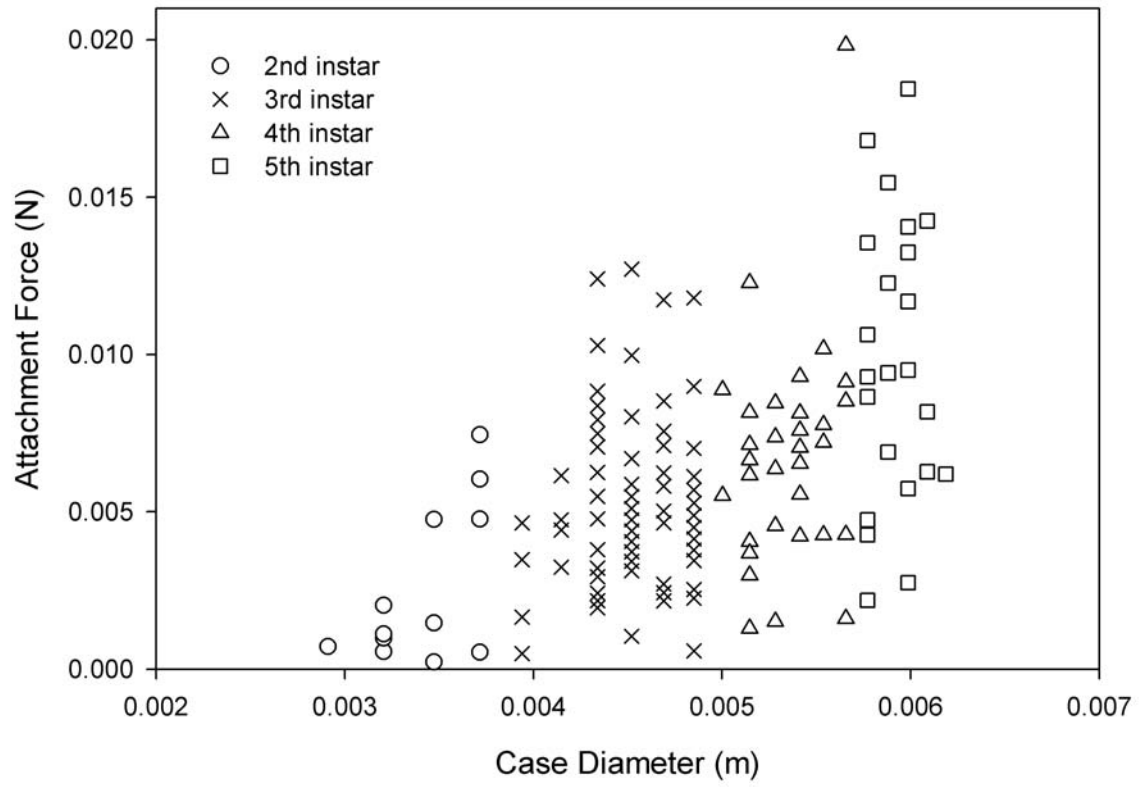
Figure 4.
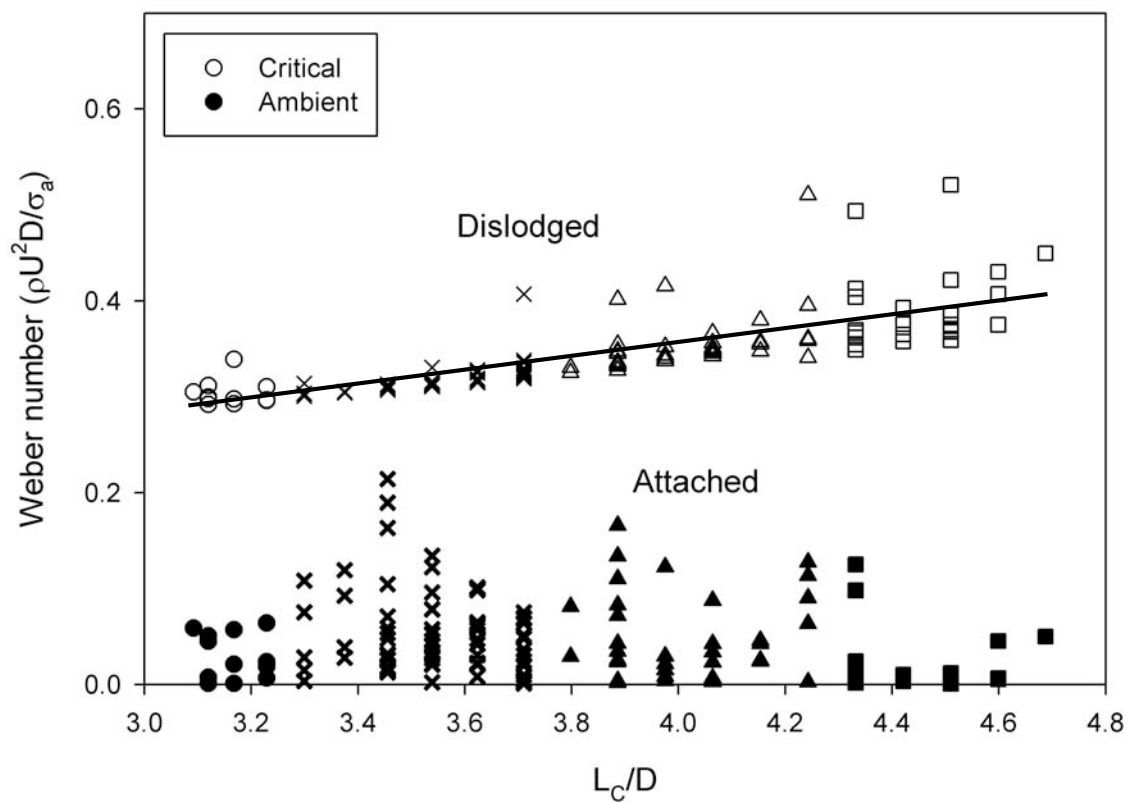
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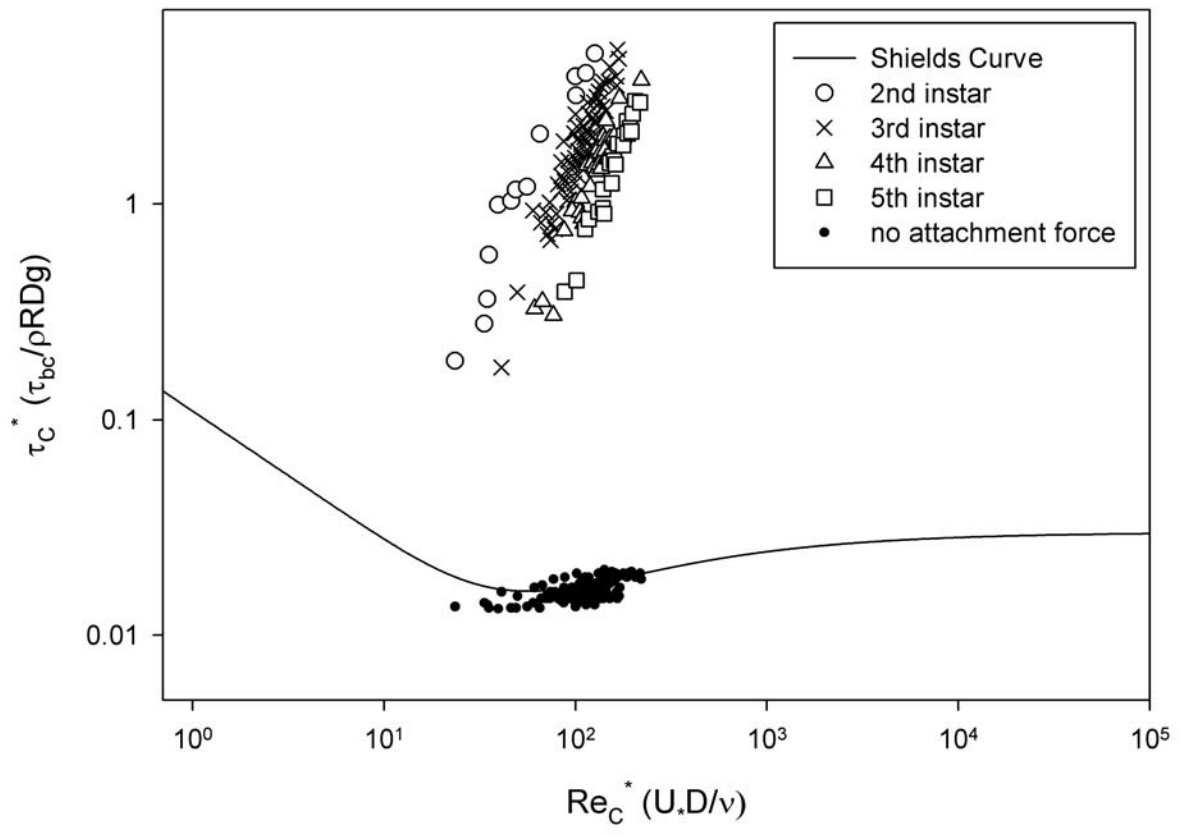
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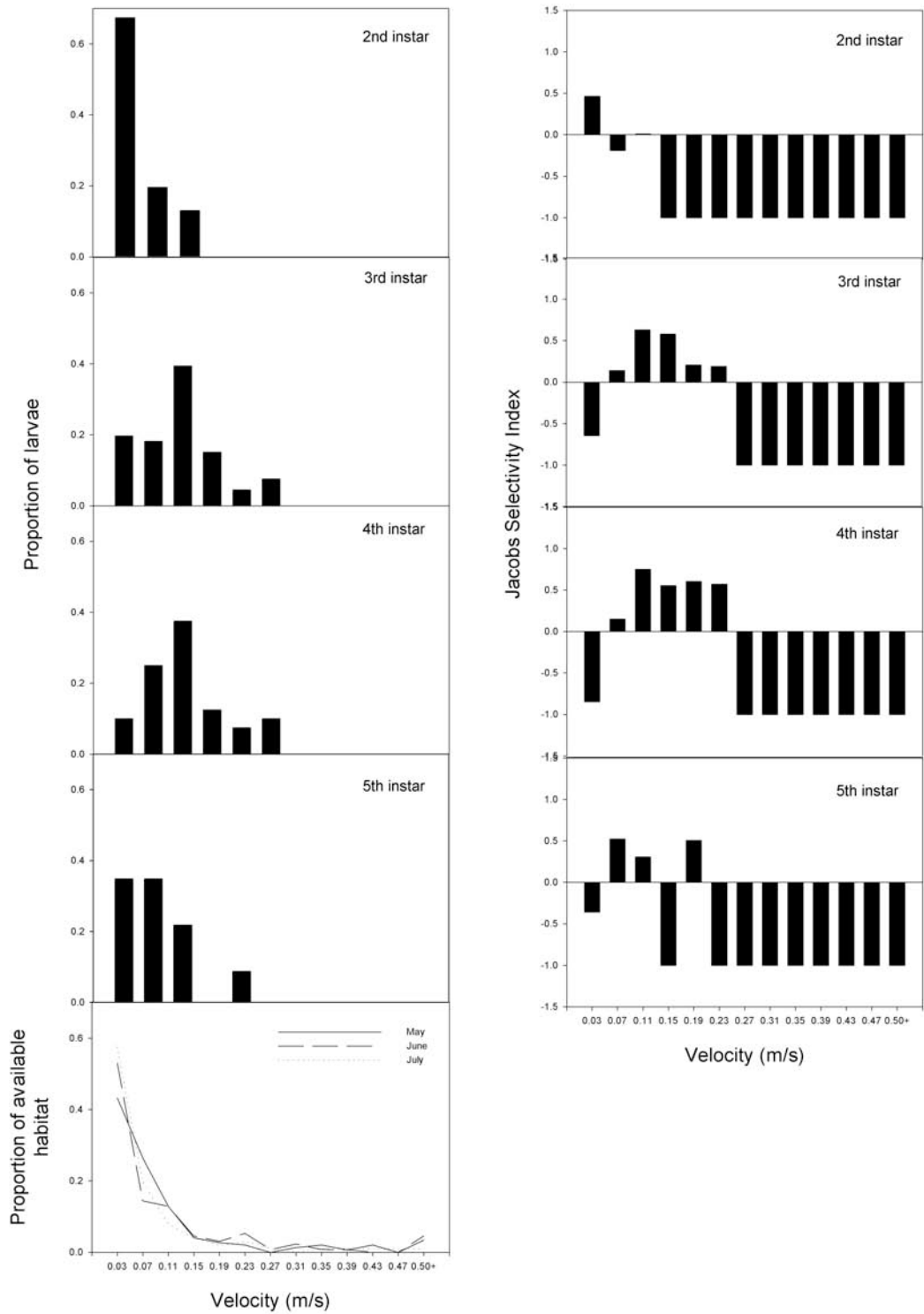
Figure 7.

Figure 8.

Figure 9.
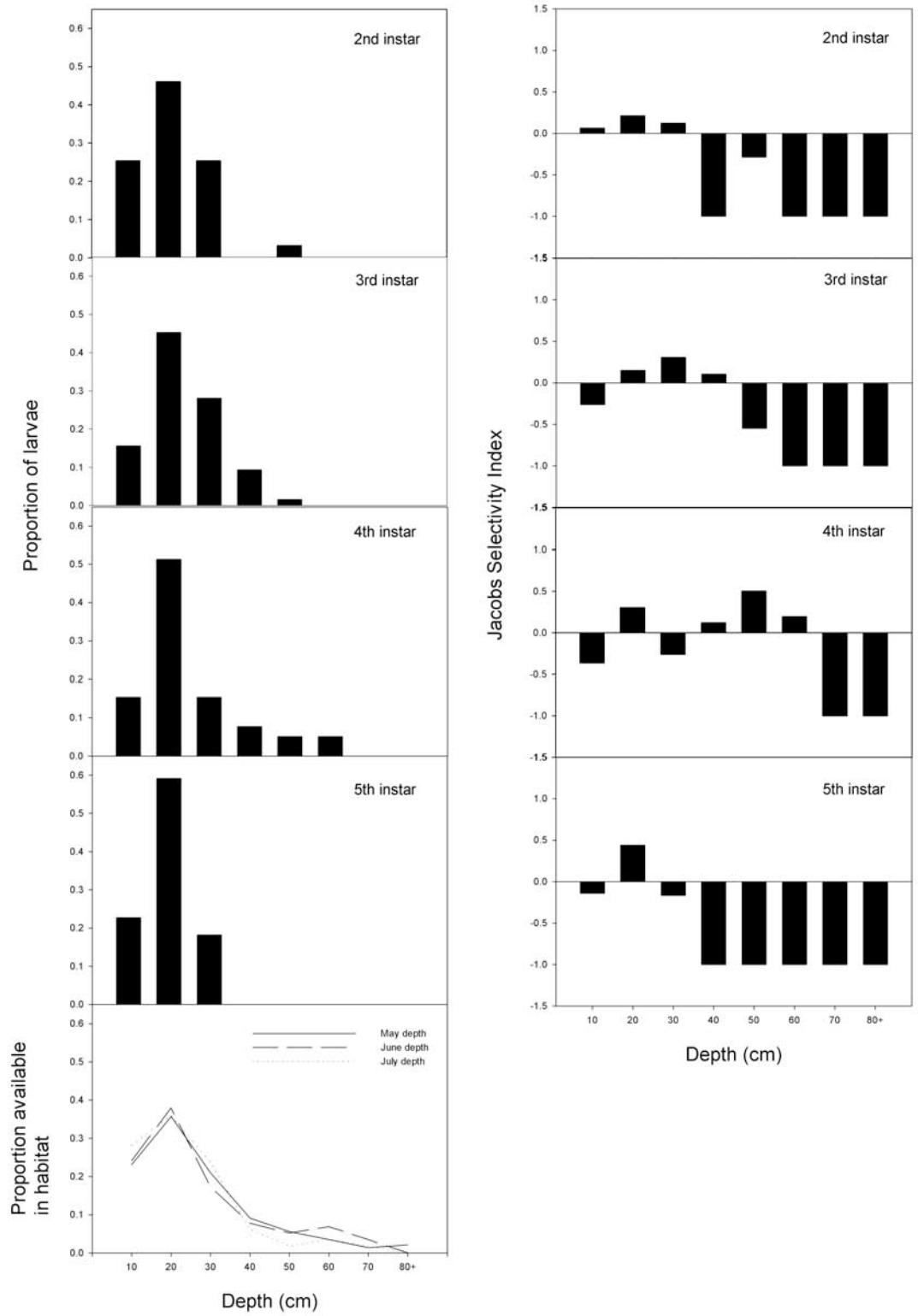
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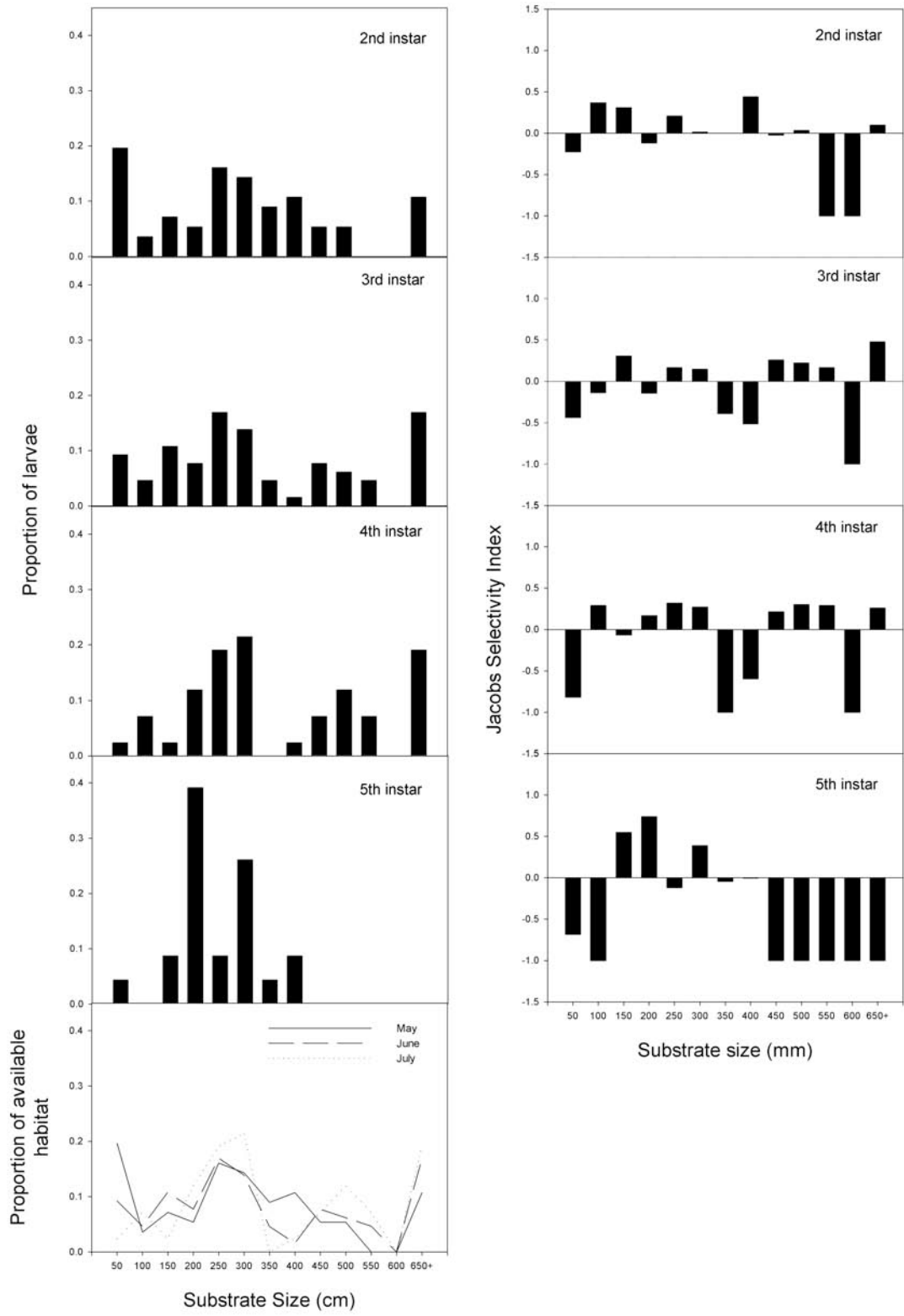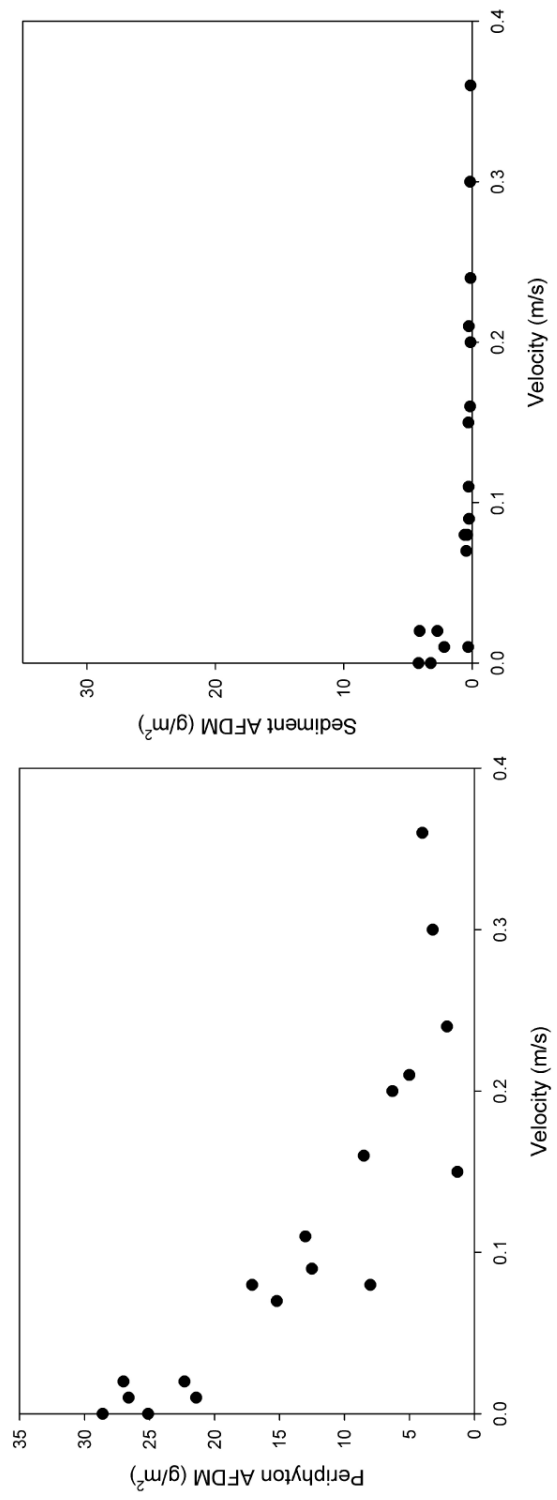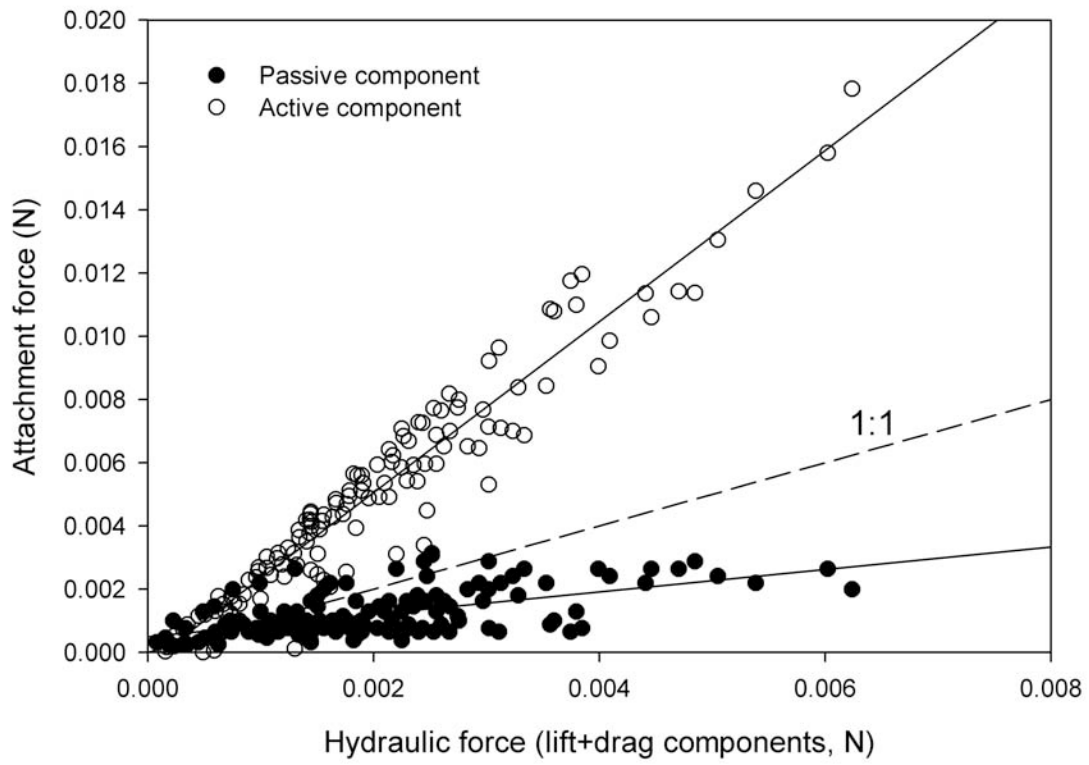
Figure 11.
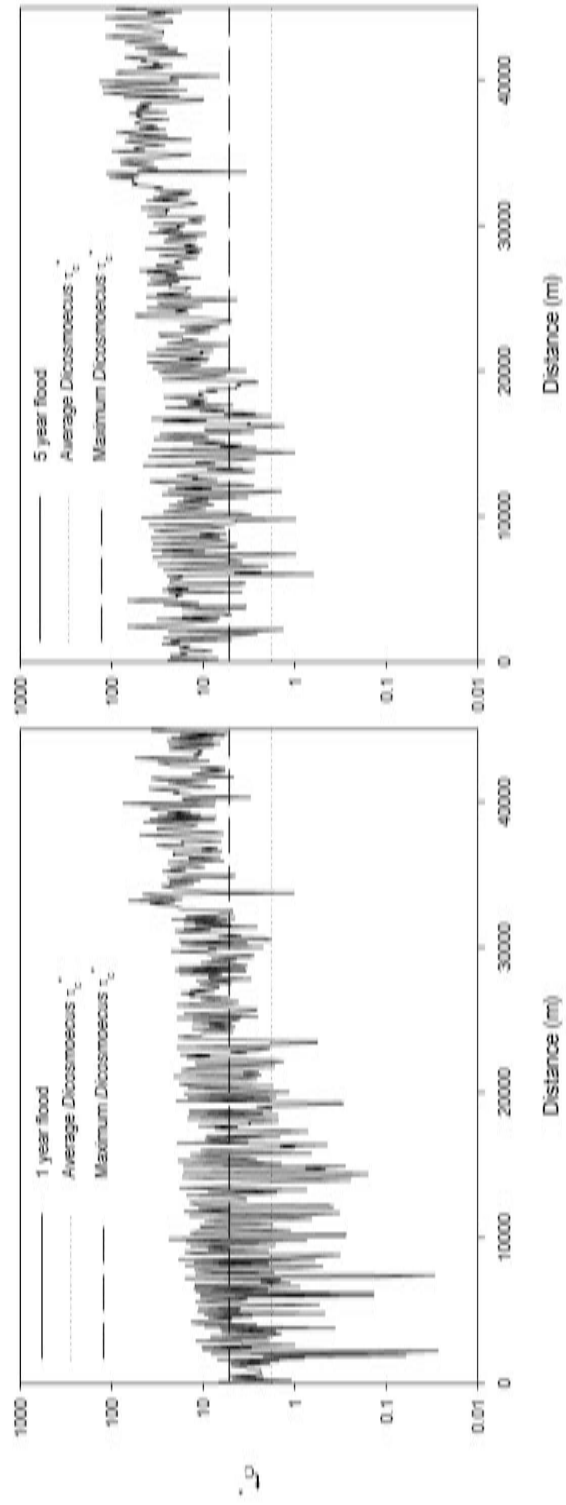
Figure 12.

Figure 13.

Figure 14.

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CHAPTER 3

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

Abstract

The majority of caddisfly larvae build cases using silk and a variety of collected materials. Multiple functions have been suggested for caddisfly cases including protection from predators, resistance to entrainment by high flows, and improved respiration. Our study investigates the functional role of cases built by *Dicosmoecus gilvipes,* a Limnephilid caddisfly. In Mendocino County, CA, the 1st through 4th instar larvae collect thin plant material and Douglas-Fir needles and build arrow-shaped lateral extensions on their case. To test whether the lateral extensions deter predators relative to cases lacking them we manipulated lateral extension presence and exposed the larvae to large steelhead trout. All larvae with a case survived, whether lateral extensions were present or not, while all larvae without a case were consumed. To test whether lateral extensions provide stability against overturning and entrainment we again manipulated lateral extension presence and subjected larvae to turbulent flow conditions. Once dislodged, larvae with lateral extensions experienced fewer revolutions and regained their footing faster than those without. Our results suggest lateral extensions provide stability against overturning in fast flow and may improve their ability to forage efficiently in turbulent flow conditions. Other caddisfly species build lateral extensions on their case, and the extensions may provide a similar function for these taxa.

Introduction

Larvae in 30 of the 45 recognized caddisfly (Trichoptera) families make portable cases out 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 additional extensions. Some caddisfly species will alter both material type and 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 was a case function that probably evolved early in the order's evolution (Wiggins 2004). Case shape, strength, and materials provide structural protection from predators, and some larvae will 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), while others use cases to appear as a non-prey item (Otto and Johansson 1995) or use lateral case extensions to protect themselves from gape-limited predators (Otto 1982).

Some caddisfly species attach large mineral grains to their case sides. The grains are often referred to as ballast stones (e.g. Wiggins 1977), and as the term implies, the additional 'ballast' or weight of these stones may lower their risk 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

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currents constructed heavier cases than those in slower currents. Otto and Johansson (1995), however, found ballast stones in *Silo pallipes cases* had a negligible effect on their current resistance (2-5%). In addition to increasing case inertia, ballast stones may improve stability by altering fluid motion around the case and/or increase the base width (Otto 2000).

Caddisfly cases may enhance larval respiration (Milne 1938, Williams et al. 1987), potentially enabling caddisfly range expansion into slower, less oxygenated environments (Wiggins 1977). Dodds and Hisaw (1924) observed that "many if not all of the case bearing species maintain a constant current of water through the case by undulation of the abdominal lateral fringe, or of the abdomen itself, insuring constant change of water over the respiratory surface...". The unidirectional flow generated may decrease boundary layer development around the gills and steepen the oxygen diffusion gradient. To quantify case effects on respiration, Williams et al. (1987) measured oxygen uptake in 22 species from a variety of habitats, both with and without a case. Their results were mixed: the case conferred a respiratory advantage in some, and had no effect or was a disadvantage to respiration in others. In addition, some lentic species leave their case under low oxygen conditions (Otto 1976), which would further suggest not all caddisfly species gain a respiratory benefit.

Our study investigates the functional role of cases built by *Dicosmoecus gilvipes* (Hagen) larvae. The species occurs in western North America, Japan, and eastern Russia (Wiggins 1977), where they graze periphyton in cool flowing water. In the South Fork of the Eel River watershed (Mendocino, CA), early instars (1-2) construct cases using silk and mostly plant materials. Later instars use a higher proportion of minerals in their case, and during their 5th and final instar, the larvae cut off any remaining plant material at the posterior end, leaving a case made entirely of minerals.

Prior to the 5th instar, *Dicosmoecus* larvae use silk to stick Douglas-fir needles onto the sides of their slightly curved cylindrical case (Figure 1a). The needles are arranged like feathers on the end of an arrow shaft, with the ends swept towards the rear and downwards (Figure 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 two possible functional roles of the lateral case extensions made from Douglas-fir needles. *Hypothesis 1: The lateral extensions on the case provide camouflage and/or protection from a large predator. Hypothesis 2: The lateral extensions increase larval stability in turbulent flows by increasing their effective base width.*

Methods

Site

All experiments were carried out in Elder Creek within the Heath and Marjorie Angelo Coast Range Reserve in Mendocino County, California (39°44"N 123°39"W). The study area has a Mediterranean climate with wet, cool 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-decidous evergreen forest dominated

primarily by old-growth Douglas fir (*Pseudotsuga menziesii*), redwood (*Sequoia sempervirens*), and tanoak (*Lithocarpus densiflorus*). The major aquatic food web components consist of producers (primarily diatoms and filamentous green algae), grazing insects (midges, mayflies, caddisflies), predatory insects (stoneflies, aquatic beetles, naucorid bugs), and omnivorous (California roach, *Lavinia (Hesperoleucas) symmetricus*) and predatory vertebrates (Rough skinned newt, *Taricha granulose,* Pacific giant salamander, *Dicamptodon ensatus*, Threespine stickleback, *Gasterosteus aculeatus,* juvenile steelhead, *Oncorhynchus mykiss*).

Case information

We collected 30 larvae from Elder Creek, Mendocino, CA 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. The center of mass was estimated by finding the longitudinal balance point. After marking the point, the lateral extensions were removed and the change in center of mass height was then measured.

Hypothesis 1. The lateral extensions on the case provide camouflage and/or protection from a large predator.

We conducted feeding trials to investigate whether the lateral extensions on *Dicosmoecus* cases deter predation by steelhead (*Oncorhynchus mykiss*). The trials were conducted in a large clear pool in Elder Creek. The oval-shaped pool was 16 m long, 7 m wide, and 1.8 m deep in the middle. Based on visual observations the pool contained forty to fifty small steelhead (45-60 mm), four medium-large steelhead (90-120 mm), and one large steelhead (160+ mm). *Dicosmoecus* larvae were present upstream and along the bottom of the pool.

Prior to the experiment we collected thirty-six *Dicosmoecus* larvae approximately 30 m upstream from the pool and placed them into a flow-through basket. Case length ranged from 1.8-2.5 cm (3rd and 4th instars). We randomly assigned individual *Dicosmoecus* larvae to one of three treatments: (i) lateral extensions present as constructed by larvae (n=12), (ii) lateral extensions removed from the case (n=12), and (iii) the entire case removed (n=12). The lateral extensions, constructed out of Douglas-fir needles, were clipped off the case sides with small scissors for treatment iii.

We then released individual larvae from the three treatments into the top one-third of the pool. An observer was positioned roughly perpendicular to the point of release and remained stationary for 10 minutes prior to beginning the experiment. The person releasing the *Dicosmoecus* was positioned behind a rock and could not be seen by the fish. Larvae were released approximately 5 minutes apart in the order as randomly assigned. The observer recorded whether the steelhead approached, mouthed, and/or ate the larvae. The size of the steelhead doing the activity was also recorded. To test whether inspection and predation by steelhead differed between treatments we used analysis of variance (ANOVA).

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

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We quantified stability by subjecting thirty-five 3rd and 4th instar *Dicosmoecus* larvae to turbulent bursts in a rocking tank (Figure 2). The rocking tank was 1.0 m long x 0.15 m wide x 0.5 m tall and constructed out of clear 6 mm acrylic. The tank rested in a metal cradle that pivoted midway along the base. A variable speed motor rocked the tank on the middle pivot, creating sweep events along the bottom as the water rushed from one side of the tank to the other. The rocking tank completed a full cycle every 7.5 seconds. Based on video of suspended/saltating particles moving just above the bottom surface, larvae were exposed to peak velocities of 21 cm s^{-1}.

Revolutions before recovery

At the start of each trial we placed a single *Dicosmoecus* into the middle of the tank and turned on the rocking motor. Once a larva was dislodged, we visually recorded the number of revolutions the larva underwent before recovering. We defined recovery as the point at which larvae were upright and either holding their position or walking. Ten separate dislodgement events were recorded on each larva. An average number of revolutions for each larva was calculated from the ten observations. We then removed the lateral extensions from the case, let the individual rest for five minutes in a holding tank, and then repeated the experiment. To assess the possible effect of fatigue and handling on the second trial when lateral extensions were removed, six *Dicosmoecus* underwent two trials where the extensions were present and six *Dicosmoecus* underwent two trials where extensions were removed for both trials. No significant difference (Paired t-test) was observed in the number of revolutions between the first ($t_5 = 0.53$, $p = 0.61$) and second trial ($t_5 = 1.24$, $p = 0.27$). To assess possible differences in revolutions before recovery between treatments we compared the mean revolutions for individual larva with and without fins using a Paired t-test.

Recovery Time

We quantified the recovery time for dislodged larvae by video recording an additional 15 *Dicosmoecus* in the rocking tank, both with and without lateral extensions. The two trials for each individual were conducted as described above. The video was recorded at 30 frames per second and analyzed with the software program Quicktime Pro (Apple Inc., Cupertino, CA). To measure the time required for recovery we counted the number of frames between the dislodgement and recovery. The difference between mean recovery times with and without lateral extensions was calculated. As in the first experiment, we defined recovery as the point when larvae were upright and either holding on or walking. To assess possible differences in recovery time between treatments we compared the mean recovery time for individual larva with and without fins using a Paired t-test.

Results

Case structure

For the 30 2nd-4th instar *Dicosmoecus* larvae we collected, the maximum case width increased with case length (Figure 3). On average, the lateral extensions increased total width by 410%, total length by 36%, and total dry mass (larvae + case) by 22% (Figure 4). Fifty-six percent of case mass was mineral and this proportion increased with case length (Figure 5).

Predation

All *Dicosmoecus* (n=36) released into the pool were visually inspected by at least one steelhead. No preference was seen in the number of inspections between treatments ($F_{31,2}= 0.292$, $p= 0.72$), suggesting the needles did not provide effective camouflage to the larvae. Steelhead did not consume any *Dicosmoecus* with a case (n=24), while every *Dicosmoecus* released without a case (n=12) was consumed. Seven of the twelve *Dicosmoecus* with needle-covered cases were mouthed by at least one steelhead while 8 of the twelve *Dicosmoecus* with needle-removed cases were mouthed. Large (100+ mm) and small steelhead (45-60 mm) mouthed both the needle-covered and needle-removed cased *Dicosmoecus*.

Stability

Dicosmoecus larvae with lateral extensions on their case experienced fewer rotations after getting dislodged ($t_{33}= 14.91$, $p < 0.0001$). On average, those with lateral extensions rotated around their longitudinal axis one-third as many times after getting dislodged as those without.

The fewer rotations by larvae with lateral extensions translated into faster recovery times ($t_{14}= 7.25$, $p < 0.0001$). Based on the thirty video-recorded trials, *Dicosmoecus* regained their footing over three times faster when their cases had lateral extensions.

Discussion

While discussing caddisfly cases Rousseau (1921) states, "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". Results from the current study suggest the cases built by *Dicosmoecus gilvipes* improve their stability and assist their 'resisting the current'. By adding lateral extensions the larvae widen their effective base and increase their resistance to overturning by cross currents.

Both plants and animals can modify their structure and/or behavior to resist overturning. Trees living 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* will 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-fold when moving from air to water, and the wider stance provides stability against

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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 out of mineral particles. The 'shield' consists of wing-like lateral extensions that effectively double the case width. In a laboratory experiment, Christian 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.

From Alexander (1971), we can estimate the drag force (D) needed to overturn larval cases with and without lateral extensions present:

$$D = F_V \frac{MA_S}{MA_O} \qquad\qquad (1)$$

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). For *Dicosmoecus* cases, the lateral extensions increase total mass by 19% and base width (MA_S) by 410% for 2nd to 4th instars. The lateral extensions also elevate the rear of the case, increasing center of mass height (MA_O) 14%. From Eq. (1), the drag force required to overturn a *Dicosmoecus* case with lateral extensions is over four times greater than on a case without. The estimate for *Dicosmoecus* cases is likely conservative since we used the widest point on the cylindrical case for calculating the stabilizing point. The actual moment arm stabilizing the organism is the point where the cylindrical case contacts the surface. We can apply a similar analysis to *Molanna angustata* from Otto's study (2000). *Molanna* cases with lateral extensions were 57% heavier and 200% wider than cases without. If we assume a negligible change in MA_O (the shield curves down towards the bed surface), the drag force required to overturn a 5th instar *Molanna* case is again, over four times greater when lateral extensions are present. For *Molanna* larvae, which are more vulnerable to predation when upside-down (Otto 2000), the benefit of lateral extensions offsets the cost of additional weight and reduced mobility.

Once overturned by hydrodynamic forces, *Dicosmoecus* larvae with lateral extensions regained their footing faster than those without. Faster recovery may improve their ability to move efficiently in turbulent conditions. Using the equation for calculating the drag force on an object, $F_D = \frac{1}{2}\rho C_D A U^2$, the estimated four-fold increase in drag required to overturn a case with lateral extensions translates into a critical velocity 2-fold greater than for a case without (assuming the projected area and drag coefficient do not change). From a velocity survey in a 80m reach (530 m^2) in Elder creek (M. Limm, unpublished data), 1st and 2nd instar larvae inhabit low velocity areas (near-bed velocity ≤ 0.04 m/s), while 3rd, 4th, and 5th instar larvae can forage mid-channel where near-bed velocities exceed 0.2 m s^{-1}. Based on the surveyed reach, if 1st and 2nd instar larvae with lateral extensions can withstand a critical velocity 2-fold greater, 20.3% more streambed area is available to the larvae. For 3rd, 4th, and 5th instars, streambed availability increases by 16.4%. While other factors may influence larval overturning- such as lift, larval strength, texture of rock surfaces, and flow direction- the additional stability provided by their case increases the available streambed area.

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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 to *Dicosmoecus* larvae (Hart 1981, Lamberti et al. 1995), and with phenological changes exploitative competition for periphyton can increase (Li and Gregory 1989). Movement through and access to more turbulent environments may alleviate competition with conspecifics and other grazers. Periphyton productivity, nutrient uptake, and accrual are known to increase with velocity (0.15-0.30 m s^{-1}) (Whitford and Schumacher 1961, Biggs et al. 1998, Hondzo and Wang 2002). Algae growing in faster flowing environments may not only be more productive, but also of higher food quality for grazers than algae in slack water, where algae may become covered with fine deposited sediments, reducing algal growth (Van Nieuwenhuyse and LaPerriere 1986) and organic content (Cline et al. 1982). By building cases that resist overturning and improve recovery time, *Dicosmoecus* larvae can not only forage across more of the bed surface but also in more productive habitats that other grazers are not equipped to access. Their more extensive grazing will reduce algal accrual over a wider area and in more productive habitats. This may have significant impacts on ecosystem processes.

Lateral projections may also reduce *Dicosmoecus* vulnerability to gape-limited predators by increasing their apparent size. Known predators on the larvae include harlequin ducks (*Histrionicus histrionicus* L.) (Wright 2000), dippers (*Cinclus mexicanus* Swainson) (Harvey and Marti 1993), and rainbow trout (*Oncorhynchus mykiss*) (Tippets and Moyle 1978). All of these occur at our study site. In our experiment, however, large steelhead (> 120 mm SL) consumed 3rd and 4th instar *Dicosmoecus* only when larvae were removed from their case. *Dicosmoecus* larvae were exposed to seven predator species in a previous study (Wootton et al. 1996) and no mortality occurred over 24 hours. In the McCloud River (Siskiyou and Shasta Counties, CA) 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, but our results suggest that any case, with or without lateral extensions, can deter large steelhead predation. We did not observe steelhead feeding off the benthos before or during the experiment, and 3rd and 4th instar *Dicosmoecus* were relatively abundant (20-30 per m^2) on the pool bottom. More research concerning predation on *Dicosmoecus* is needed.

Our study does not address whether their case enhances larval respiration. Mechanisms by which cases might influence oxygen transfer to the larvae are unclear. Other members of the Limnephilidae family did not show enhanced respiration when a case was present (Williams et al. 1987). *Dicosmoecus* inhabit cool, well-oxygenated streams, and while it is possible the case may confer a respiratory advantage in late summer, most *Dicosmoecus* undergo diapause by mid-July.

While our results suggest *Dicosmoecus* larvae clearly benefit from building lateral extensions on their case, one possible cost to the larvae, in addition to the effort building the lateral extensions (finding and attaching Douglas-fir needles with silk) and additional weight (21% heavier), may be increased form drag. The lateral extensions do increase the projected frontal area (M. Limm, unpublished data) and therefore increase form drag. The point along the case where flow separation occurs also influences drag. If Douglas-fir needles attached to the posterior case moves the point of flow separation rearward, wake

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region size and the subsequent drag generated may be reduced, as is the case for flow separation mediated by dorsal spines on tuna behind the dorsal fin.

The lateral extensions may also influence both lift and the peak drag force. As fluid slows when flowing over an organism a velocity gradient develops. The velocity gradient generates a lift force on the organism that is directed away from the surface. By reducing effective weight (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 surface. It is possible the change in case orientation relative to a naked case may influence the lift force it experiences.

Lateral extensions may also decrease peak drag forces by increasing directional sensitivity to flow, like fins on a weather vane. From observations, as *Dicosmoecus* larvae move from slow (0-0.05 m s^{-1}) to higher (> 0.15 m s^{-1}) velocity flow, their case will 'weather-vane' and orient into the flow. The larvae will then 'crab walk' perpendicular to the flow until they reach slower flow conditions. By rapidly orienting the case into the flow, for example during peak velocity fluctuation, the lateral needle extensions may reduce the peak drag force that larvae experience.

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

Acknowledgements

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FIGURE LEGENDS

Figure 1. Plan (a) and side (b) view of a 3rd instar *Dicosmoecus* larva. Illustration by Aron Bothman.

Figure 2. Experimental rocking tank used at Elder Creek. Motor was driven by a 12 volt battery.

Figure 3. Relationship between *Dicosmoecus* case length and case width when lateral extensions are present and removed.

Figure 4. Relationship between case mass and case width when lateral extensions are present and removed.

Figure 5. Relationship between *Dicosmoecus* case length and mineral content of the case.

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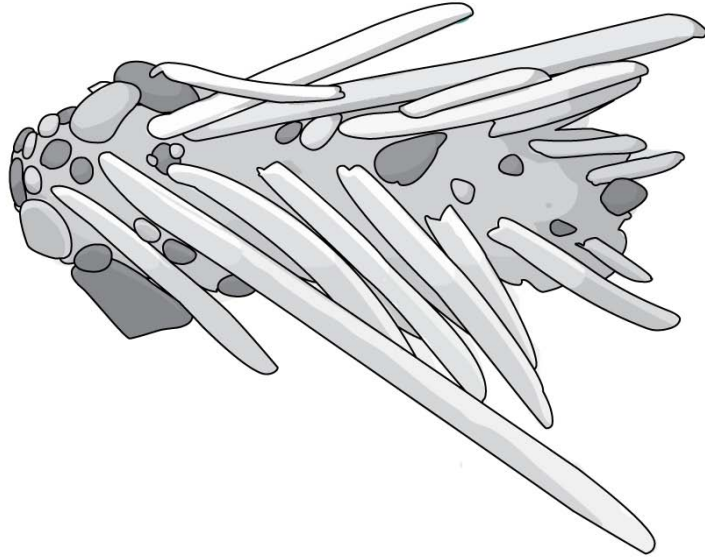
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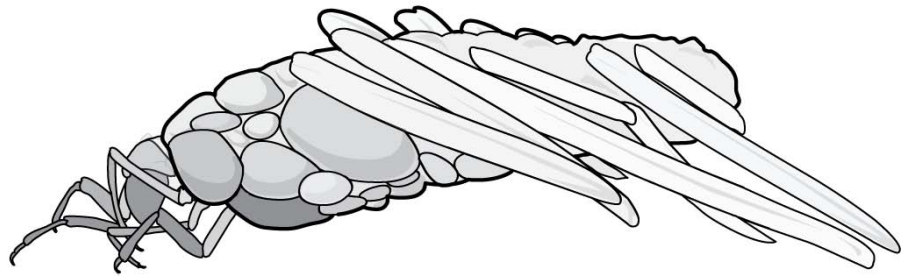
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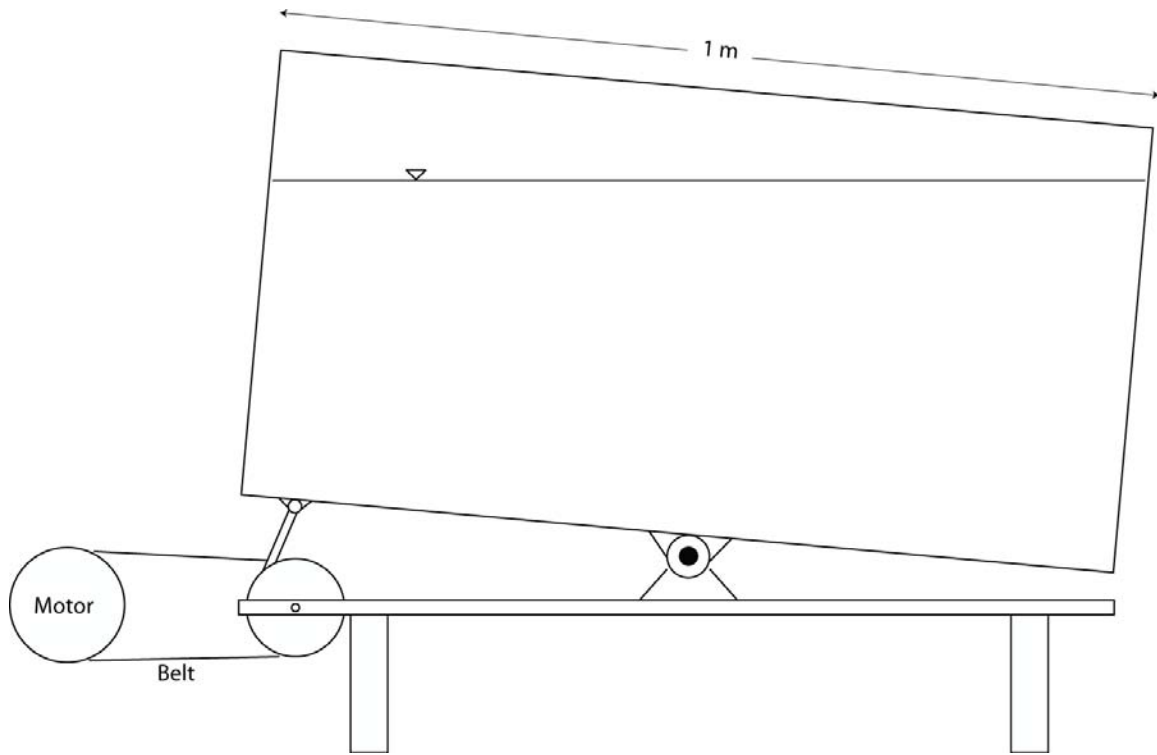
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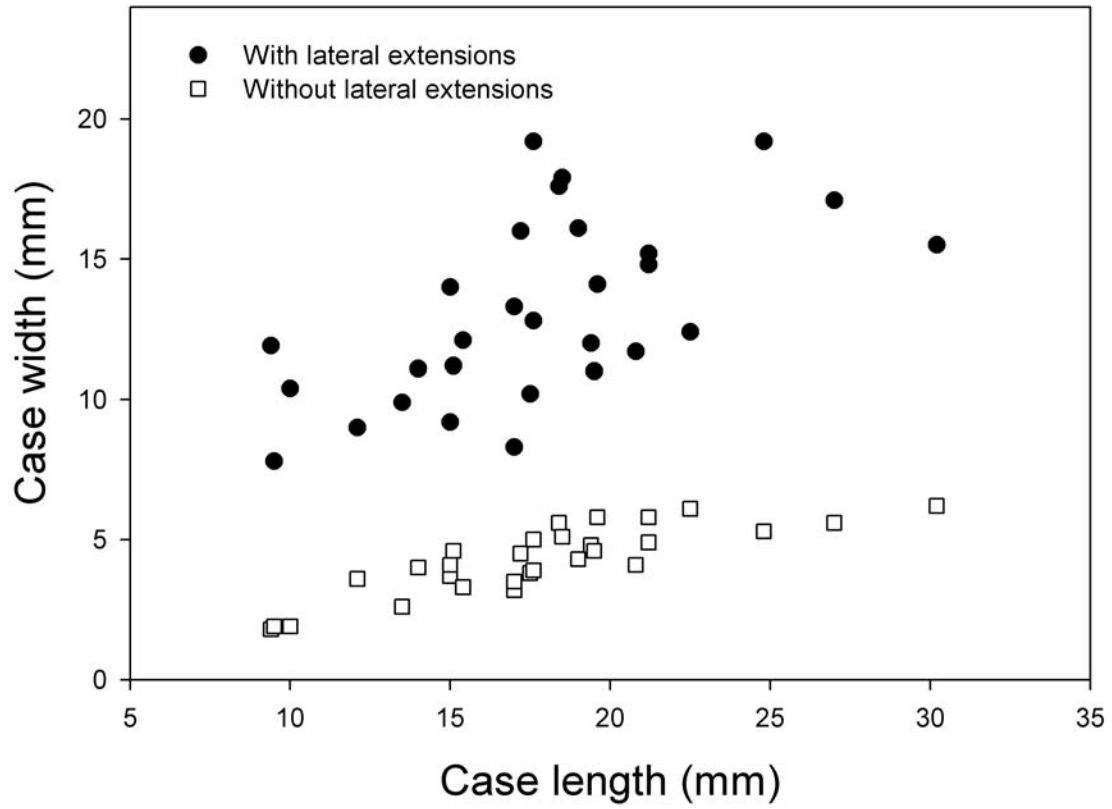
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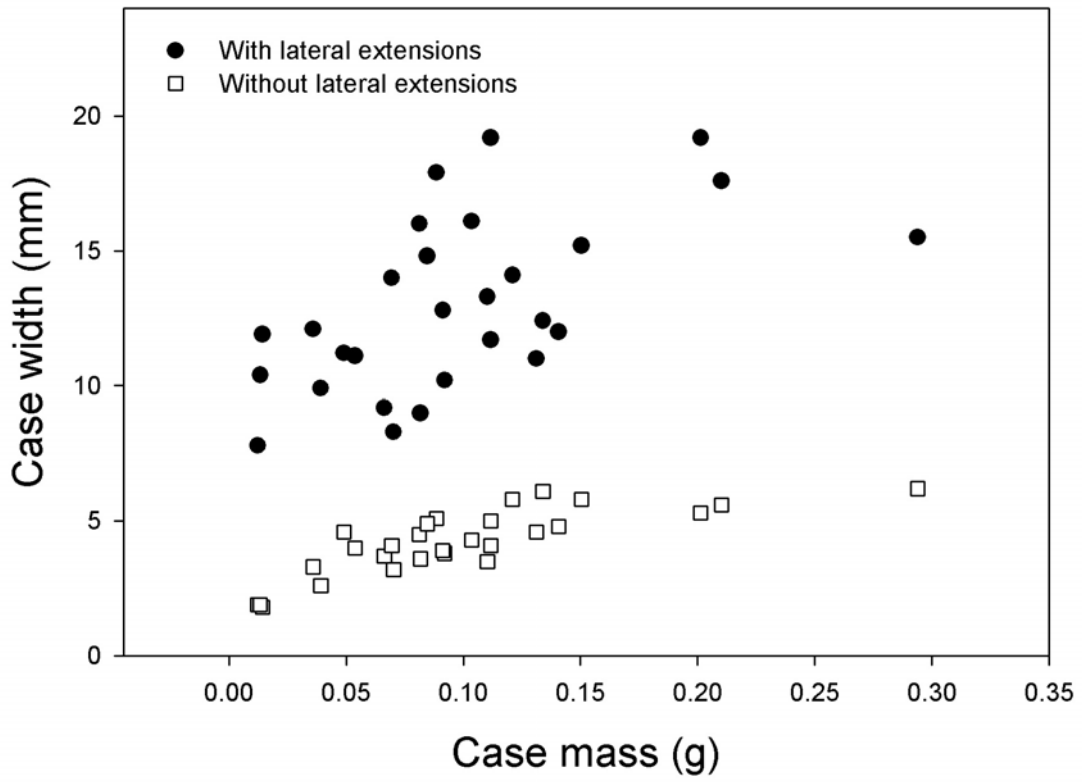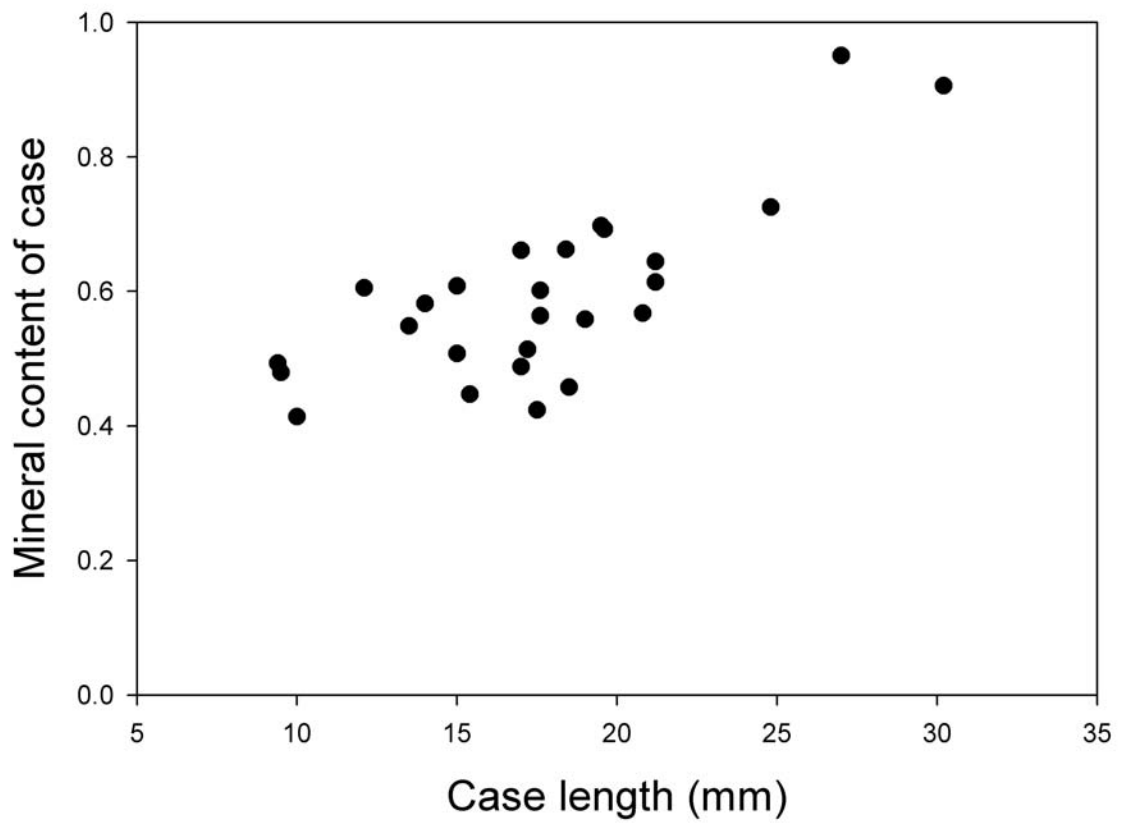
Figure 4.

Figure 5.

CHAPTER 4

Effect of the Western Pearlshell Mussel (*Margaritifera falcata*) on Pacific Lamprey (*Lampetra tridentata*) and Ecosystem Processes

Abstract

Suspension feeders concentrate organic material from the water column and enhance deposition to the surrounding benthos. On the South Fork of the Eel River (Mendocino, California) two suspension feeders, the freshwater mussel *Margaritifera falcata* and Pacific lamprey larvae *Lampetra tridentata*, co-occur in areas with low flow velocities and boundary sheer stresses. We investigated mussel/lamprey larvae interactions, and their impacts on nutrient and organic matter cycling, in flow-through baskets placed where lamprey larvae and mussels naturally occurred. Over the 80-day study, lamprey larvae grew faster in the presence of mussels and in food addition treatments. Our results suggest that lamprey larvae benefit from native mussels, and that lamprey populations and organic matter retention in rivers may both decrease with the rapid decline of native freshwater mussels.

Introduction

Bivalve suspension feeders play important roles in freshwater and marine ecosystems. They filter large volumes of water and seston, and deposit faeces and pseudofaeces locally on the benthos (Newell et al. 1982, Kryger and Rusgard 1988, Norrko et al. 2001, Howard and Cuffey 2006). Bivalves enhance the nutrients available to aquatic plants (Peterson and Heck 1999 Aquilino et al. 2009) and deposit-feeding animals (Howard and Cuffy 2006, Spooner and Vaughn 2006) by increasing the quantity (Graf and Rosenberg 1997, Spooner and Vaughn 2006) and quality (Kautsky and Evans 1987, Peterson and Heck 1999) of deposited material, nutrient cycling rates (Peterson and Heck 1999) and organic matter retention (Wotton and Malmqvist 2001). Since bivalve biomass can exceed that of all other local macroinvertebrates (Negus 1966, Dame 1996) they can dramatically alter ecosystem structure and function (Strayer et al. 1999).

How bivalves affect other suspension feeders is less clear, and may depend on species composition and local physical conditions that control the supply and delivery of food particles such as flow velocity, bed topography, channel geometry, and depth. Bivalve filtration can reduce edible particles in the water column by removing material faster than it is replenished by advective and turbulent processes (Wildish and Peer 1983, Kryger and Riisgard 1988, Strayer et al. 1999). For example, since its introduction to the Hudson River, the invasive zebra mussel, *Dreissena polymorpha*, has reduced phytoplankton biomass by 80-90% (Caraco et al. 1997). On local scales, bivalves frequently form dense aggregations with hundreds (e.g. *Mytilus californianus*, Paine 1974) to thousands (e.g. *Dreissena polymorpha*, Hunter and Bailey 1992) per square meter. Bivalves within these aggregations may exhibit stress and starvation symptoms (Baker and Hornbach 1997) and slower growth (Bertness and Grosholz 1985, Okamura 1986, but see Hanson et al.1988). Experimental research suggests bivalve filtering

depletes food particles in the benthic boundary layer and leads to slower bivalve growth rates (Wildish and Kristmanson 1984).

Given that bivalves can reduce food availability for local suspension feeders, observations of dense larval Pacific lamprey (*Lampetra tridentata*) within Western pearlshell mussel (*Margaritifera falcata* Gould 1850) aggregations in coastal rivers of California (Eel River, Jeanette Howard, unpublished data, and Klamath River, Ron Reed, personal communication) is intriguing. Larval lamprey, also filter feeders, and mussels are both in decline along the Pacific coast of North America due to habitat loss caused by river regulation and pollution (Williams et al. 1993, Renaud 1997, Moser and Close 2003). Both are found along stream margins and in pools where flow-induced boundary shear stresses are reduced (Hardisty 1944, Howard and Cuffey 2003, Torgerson and Close 2004). *Margaritifera* can live 100+ years and aggregations can exceed 80 individuals per square meter (Hastie and Toy 2007). *Lampetra* larvae rear in freshwater for 5-8 years before undergoing metamorphosis and migrating to salt water habitats (Beamish and Northcote 1989, Moyle 2002). Lamprey larvae burrow into sediment and actively pump water and materials into their oral hood, out through their gills, and into surrounding sediment. If larval lamprey feed on suspended material, why are they abundant in dense aggregations of mussels, whose feeding can deplete edible particle concentrations in the water column?

In the summer of 2004, we studied the interaction between *Margaritifera falcata* and *Lampetra tridentata* in the South Fork of the Eel River, a coastal river in Northern California. Our study addressed three questions: 1) Are lamprey food limited? 2) Do mussels influence growth of lamprey larvae (hereafter referred to as lamprey)? 3) Do mussels and lamprey influence organic matter deposition and microbial activity? These questions were investigated with field experiments in which lamprey were reared with and without additional food, and with and without mussels present.

Methods

Site

Our study area along the South Fork of the Eel River in Mendocino County, California (39°44"N 123°39"W, Figure 1) was within the Heath and Marjorie Angelo Coast Range Reserve of the University of California Natural Reserve System. This region has a Mediterranean climate with warm, dry summers and wet, cool winters. Most rainfall occurs between October and April. The drainage area at our study site covers approximately 140 km^2. The river habitat consists of shallow runs, riffles, and large pools (1-7 m deep) during summer low flow periods. Vegetation in the watershed is a mixed-evergreen forest dominated primarily by old-growth Douglas fir (*Pseudotsuga menziesii*) and redwood (*Sequoia sempervirens*) trees. The major aquatic food web components consist of producers (primarily diatoms and filamentous green algae), grazing insects (midges, mayflies, caddisflies) and snails, predatory insects (stoneflies, dragonflies, aquatic beetles and hemiptera), fish (stickleback, *Gasterosteus aculeatus*, juvenile steelhead, *Oncorhynchus mykiss*, California roach, *Lavinia symmetricus*), and filter feeders (lamprey larvae, *Lampetra tridentata*, unionid mussels, *Margaritifera falcata* and *Anodonta californiensis*) (Power et al. 1996).

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We conducted experiments in a 100 m long run that becomes a slow pool (flow velocities 0-5 cm s^{-1}) under summer base flows. *Margaritifera* and larval *Lampetra* are patchily distributed within the study area. During base flow, the mean depth of the run is 0.4-0.6 m, stream width is 13 m, and mean velocity is 0.02 - 0.04 m/s. A thin layer (< 1 m) of mixed alluvium covers the bedrock channel. The median grain size (D_{50}) of our study site is approximately 50 mm based on pebble counts (Wolman and Union 1954). Sedges (*Carex nudata*) line the riverbank and stream margins.

Collection

Lamprey

We sampled lamprey from two large pools in the South Fork of the Eel River using a backpack electrofisher (Smith-Root Inc. LR-24, Vancouver, WA) in mid-July 2004. The two pools were approximately 150 m apart. We used short bursts to stimulate larvae to emerge from the bed, collected them with hand nets, and stored them in a bucket filled with aerated stream water. Mass and length of lightly anesthetized (with MS-222) larvae were measured locally, then individuals were randomly assigned to a treatment and placed into assigned flow-through enclosures. Initial lamprey wet mass and length were similar between treatments ($F_{5,99}$= 0.035, p= 0.99) with a mean wet mass of 1.0 gram (SD = 0.2) and a mean length of 82 mm (SD=5).

Experimental enclosures

We reared lamprey in flow-through enclosures. We used 36 cm tall, 24 cm diameter mesh baskets (mesh size = 4 mm by 2 mm diamond shape, IKEA Inc. Emeryville, CA) with a solid bottom. The enclosures were filled with sediment collected from dry deposits near the study site. All sediment was passed through a 2 mm mesh sieve. We homogenized the < 2 mm fraction and used this to fill the enclosures to a depth of 0.15 m. We lowered enclosures carefully into the stream, and placed rocks around the outside of the base for stability. Depths varied within the study reach, so we arranged enclosures into 5 blocks and assigned each treatment randomly within each individual block.

Mussels

Mussels were haphazardly collected from nearby aggregations and pooled. We measured an individual mussel's length and wet mass (live tissue plus shell) and randomly assigned it to a mussel treatment enclosure. Initial mussel mass and length were similar between treatments ($F_{1, 48}$= 2.51, p= 0.12) with a mean wet mass of 25 g (3.9 g) and a mean length of 68.7 mm ± 3.4 mm SD (these mussels were approximately 15-20 years old, Howard and Cuffey 2006b).

Experiment 1

Food addition on lamprey growth

To determine if lamprey are food limited, we subjected lamprey to four food treatments: three different types of food and an ambient control. Each treatment was replicated five times, with three lamprey randomly assigned to each experimental enclosure. Three lamprey per enclosure are equivalent to 58 individuals m^{-2}, within the range (40-100 individuals m^{-2}) we observed in open sites with fine sediments. The three food addition treatments received aquatic (*Cladophora glomerata* and epiphytes), terrestrial (leaves), or artificial (fish flakes, Nutrifin Inc.) foods. The algae and leaves represent two different detrital sources, while the fish flakes selected to represent a higher quality food in the form of carbon and nitrogen. Each food type was dried and ground to a fine powder prior to addition. *Cladophora* was visually estimated to have 10-30% of its macroalgal surface covered with epiphytes, predominantly the diatoms *Gomphonema* sp. and *Cocconeis* sp. Leaves were collected from the stream and include bay, oak, madrone, maple, and Douglas fir needles. No food was added to the control treatment.

Based on the amount of organic biodeposits (faeces and pseudofaeces) generated per week by five mussels from previous research (Howard and Cuffey 2006b), we added 3 g dry mass of each food type to their respective enclosures once a week. To prevent food from getting swept out of the enclosure by water currents, we used a plastic cylinder with an 0.22 m inner diameter into the enclosure. The bottom of the plastic cylinder rested on the sediment and top was above the water line. After food was added and allowed to settle, we removed the plastic cylinder slowly from the enclosure, and observed very little loss of suspended material in the process. After 80 days we processed the lamprey as described above.

Lamprey element and stable isotopes

To assess whether lamprey larvae were assimilating the supplemented food, we measured the carbon and nitrogen stable isotope ratios of the three supplemented foods and larvae tissue from each experimental enclosure. After 80 days, the lamprey were removed, killed with MS-222, and placed on ice. In the laboratory, we measured larval length and mass and collected a tissue sample from the tail of individual larvae for stable isotope analysis. Food and larval tissue samples were rinsed and stored at -5 °C. In preparation for analysis, samples were freeze-dried (Freezone 12, Labconco Corporation), ground, and placed into tin capsules. We measured carbon and nitrogen content and stable isotopes using a Europa Anca-NT elemental analyzer connected to a Europa Scientific 20-20 stable isotope analyzer. The $\delta^{13}C$ and $\delta^{15}N$ values we report are in reference to Pee Dee Belemnite and atmospheric nitrogen standards, respectively.

Experiment 2

Lamprey growth near mussels

To investigate whether mussels enhance or reduce lamprey growth, we randomly assigned three lamprey to a mussel and control treatments. For the mussel treatment, five mussels were placed into an enclosure. Five mussels per enclosure (area= 520 cm^2) produce a density of 96 individuals m^{-2}, close to ambient densities observed in nearby mussel aggregations (~85 individuals m^{-2}, Howard 2006). No mussels were added to the

control treatment. Each treatment was replicated five times.

Organic Matter and Respiration

To quantify lamprey and mussel impacts on organic matter accrual and respiration in the sediment, we sampled sediment from four treatment enclosures. The treatments were three lamprey, three lamprey with 5 mussels, 5 mussels, and an ambient control with no lamprey or mussels present. We sampled organic matter in the enclosures after 30 days and 80 days. Before sampling organic matter at 30 days, we visually inspected enclosures and counted invertebrates on the surface. We then placed a plastic cylinder within each enclosure to retain re-suspended material. We measured the water depth to calculate the volume from which we were sampling. To re-suspend surface organic matter, we rotated a plastic 20 cm diameter disk 360 degrees every second for ten seconds. A 500 mL sample was immediately collected and filtered through a 47 mm, 1.2 μm glass fiber filter (Whatman GFC) in the laboratory. We dried, weighed, ashed, and re-weighed the filter to quantify AFDM.

After 80 days, we sampled sediment in the enclosures to quantify microbial respiration and AFDM. To compare organic matter and microbial activity between the surface and deeper sediments, we collected the sediment from the top 2 cm and from the bottom 8 cm. We homogenized sediment from each layer and placed a subsample of measured volume into a 500 mL plastic bottle. Each bottle was filled with stream water, sealed, and inverted to mix and dislodge any air bubbles. The bottle was then topped off with water, resealed, and inverted again. We then took the initial dissolved oxygen measurement using a DO probe (YSI meter 550, YSI Inc., Yellow Springs, Ohio, USA). The bottle was then resealed, placed into a dark chamber in the stream, and agitated every 5 minutes. After 30-40 minutes, we measured dissolved oxygen again using the DO probe. Respiration values were standardized by both sediment mass and organic matter present. In the laboratory the sediment was placed into a drying oven at $60\,^{o}$ C for 72 hours. The sediment was weighed and then ashed in a muffle furnace at $550\,^{o}$ C for 4 hours. After removal from the furnace, the sediment was dried again at $60\,^{o}$ C for 72 hours, and weighed.

Analysis

We analyzed the larval growth in Experiment 1 (when reared with and without mussels) with a mixed-model ANOVA design with treatment fixed and block random. In Experiment 2 (when reared with and without the 3 food additions) we analyzed larval lamprey growth with mixed model design with treatment fixed and block random. If treatment was significant we compared means using a Tukey's test (alpha=0.05).

We analyzed data from the 30 and 80 day measures of AFDM, the 80 day measure of respiration, and the 80 day measure of larval lamprey δ^{13}C and δ^{15}N with a mixed model with treatment fixed and block random. We used Tukey's test (alpha=0.05) to compare means if treatments were significantly different. JMP (SAS Institute Inc.) software was used for all analyses.

Results

Experiment 1

Food addition

After 80 days, one lamprey in the *Cladophora* addition treatment and two lamprey in the leaf addition treatments were not found. The two lamprey missing in the leaf addition treatments were from different replicates. All mussels were actively filtering at the end of the experiment.

In the food addition experiment, lamprey grew nearly twice as fast in the leaf and fish-flake treatments as in the control treatment ($F_{3,12}$=2.66, *p*=0.07, Figure 3). Lamprey grew the slowest on ground *Cladophora*, which had a lower carbon content (22% of total) than ground fish flakes and ground leaves (49% and 44% of total, respectively). Lamprey growth was also low in the same block (block 2), but in experiment 2, the effect was not significant.

Lamprey tissue $\delta^{15}N$ in the fish flake treatment was significantly higher than in the other treatments (Table 1), as was the $\delta^{15}N$ of the fish flakes relative to that of the leaves and *Cladophora*, which suggests lamprey were assimilating the nitrogen from the fish flakes. We observed no differences in %C, %N, and $\delta^{13}C$ of lamprey mussel tissue between food addition treatments.

Experiment 2

Lamprey growth near mussels

Over the eighty day period, lamprey grew twice as fast (0.08 mm day^{-1} versus 0.037 mm day^{-1}) when reared with mussels ($F_{1,4}$=71.66, *p* < 0.001, Student's t=2.77, Figure 2). We also observed a significant block effect with lamprey growing significantly more slowly in one block (block 2).

Organic matter and Respiration

Surface organic matter was similar amongst treatments after 30 days ($F_{3,16}$= 2.23, *p*=0.12). After 80 days, organic matter was similar amongst treatments in the top 2 cm ($F_{3,12}$= 0.62, *p*= 0.62) or the bottom 8 cm ($F_{3,16}$= 2.84, *p*= 0.39) of sediment. A block effect was observed after 80 days in the top 2 cm of sediment ($F_{4,12}$= 14.6, *p*< 0.001), with significantly lower organic matter in block 3 (Tukey's, alpha= 0.05).

We observed significant differences in respiration between treatments in the top 2 cm of sediment ($F_{3,16}$= 3.22, *p*= 0.05, Figure 4). Respiration was significantly higher in the mussel+lamprey treatment than in control or lamprey treatments (Tukey's, alpha= 0.05). Respiration was not different between treatments in the bottom 8 cm ($F_{3,16}$= 1.11, *p*= 0.38).

Due to unequal variances we log-transformed Gumaga count data. After 30 days we observed higher numbers of the caddisfly *Gumaga nigricula* in the mussel (mean= 14.8, SE= 2.7), mussel+lamprey (mean= 12.0, SE= 2.6), and lamprey (mean= 9.8, SE= 4.5) enclosures relative to control enclosures that lacked both mussels and lamprey (mean=

5.8, SE= 1.4), but the differences were not significant ($F_{3,16}$= 1.70, p= 0.21).

Discussion

Filter-feeding bivalves concentrate and deposit organic-rich material, excrete nutrients into their surroundings, and mix and stabilize sediment. In coastal habitats, bivalves enhance leaf growth in salt marsh cordgrass *Spartina alterniflora* (Bertness 1984), the seagrass *Thalassia testudinum* (Peterson and Heck 2001) and the seaweed *Porphyra perforata* (Aquilino et al. 2009). In freshwater, Spooner and Vaughn (2006) observed higher periphyton abundance on the shells of two unionid mussel species relative to non-feeding sham mussels. In our study the mussel *Margaritifera falcata* significantly enhanced Pacific lamprey larvae growth and increased respiration in the sediment.

Mussel biodeposits, by increasing the quality and/or quantity of available food, may have fueled faster lamprey growth. In both marine and freshwater systems, mussels increase bulk deposition rates and the organic and nutrient concentration of the deposited material (Kautsky and Evans 1987, Greenwood et al. 2001). In the South Fork of the Eel River, *Margaritifera falcata* aggregations increase both the deposition rate and the percent organic material of deposits relative to background levels (Howard and Cuffey 2006a). Lamprey larvae feed predominantly on organic detritus, which typically accounts for 96-98% of their stomach contents (the remainder includes diatoms and bacteria, Manion 1967, Moore and Beamish 1973, Moore and Potter 1976, Sutton and Bowen 1994, Mundahl et al. 2005). Of the organic detritus ingested, lamprey assimilate > 60 % (Sutton and Bowen 1994, Mundahl et al. 2005). The evidence of faster lamprey growth in both the mussel and food addition treatments suggests lamprey were food limited in the ambient control treatments.

The lamprey δ^{13}C values (ca. -23 °/oo) suggest lamprey feed on a mix of aquatic sources (e.g. riffle and pool derived algae, with relatively depleted and enriched carbon, respectively as shown by Finlay et al. 1999) and/or possibly terrestrial sources. Lamprey tissue values were similar to *Margaritifera* tissue δ^{13}C and δ^{15}N values (-22.9°/oo, 2.6 °/oo, respectively) reported by Howard and Cuffey (2005) during the summer period in the South Fork of the Eel River. Finlay et al. (1999) report summer δ^{13}C values in the South Fork of the Eel River of -17.9 °/oo for epilithic algae in pool habitats, -26.2°/oo for epilithic algae in riffle habitats, and -27.5°/oo for terrestrial detritus. Stable isotope values of control lamprey (δ^{13}C= -23.2°/oo, δ^{15}N= 2.7°/oo) reflect aquatic and terrestrial source contributions to both suspended (seston) and deposited material.

The pathway by which mussel biodeposits and the added food reached lamprey is unclear. Lamprey in the mussel enclosures may have ingested mussel biodeposits settling into their burrow. Lamprey larvae are often described as suspension feeders (Moore and Potter 1976, Moore and Mallatt 1980, Malmqvist and Bronmark 1982) and food has been kept in suspension during previous lamprey growth experiments (Hardisty 1944, Moore and Mallatt 1980). In our food addition experiment, however, lamprey grew faster even though added food was deposited. Lamprey fed on ground fish flakes, which are enriched in ^{15}N, had significantly higher δ^{15}N isotope values than other lamprey. These results, and the presence of sand grains in lamprey stomach contents (Moore and Beamish 1973), suggest lamprey may feed directly off the bed surface and/or filter interstitial water.

Bioturbation in the enclosures may have influenced lamprey feeding and growth. Mussel biodeposits, coupled with animal movement and activity (e.g. water pumping, Van Duren et al. 2006), could have increased food particle re-suspension and flux over lamprey burrows. Mussels are also bioturbators (Dame 1996), and their activity can mix material both in the water column (van Duren et al. 2006) and the sediment (Vaughn and Hagenkamp 2001). In addition to increasing food particle deposition, mussel activity may have increased the food available to lamprey both in the water above their burrows and in interstitial spaces.

The increase in lamprey growth but no difference in organic matter accrual is at face value, paradoxical, but bioturbation may have played a role. We did not observe organic matter accruing at higher rates near mussel aggregations, as seen in previous studies (Norkko et al. 2001, Kryger and Rusgard 1988, Graf and Rosenberg 1997, Grenz et al. 1990, Commito and Boncavage 1989, Peterson and Heck 1999, Spooner and Vaughn 2006). Animal activity can remove fine particles from interstitial spaces (Zanetell and Peckarsky 1996), and the more numerous invertebrates (*Gumaga*, and possibly other invertebrates we did not quantify) in the mussel enclosures may have removed mussel biodeposits by ingesting them, or resuspending and dispersing them out of the enclosures.

In addition to bioturbation, rapid degredation of biodeposits may have offset the higher rate of deposition in mussel enclosures. Respiration rates in sediment from mussel and mussel+lamprey enclosures were higher than in control enclosures. Mussels and other bioturbators are known to mix organic material and oxygen into the sediment and to enhance water flux across the water-sediment boundary (Spooner and Vaughn 2006). This mixing can enhance microbial processing and degradation of organic matter (Dame 1996). Bacteria abundance and exoenzymatic activity increases rapidly after mussel biodeposits settle, and degradation can occur over short time periods (Stuart et al. 1982, Grenz et al. 1990). Stuart et al. (1982) observed a rapid increase in bacterial abundance in deposited mussel faeces and pseudofaeces relative to background levels. Maximum mineralization occurred three days after deposition and gradually declined in their study. Grenz et al. (1990) also observed similar rapid increases in bacteria production on sediments enriched with mussel biodeposits. These studies suggest biodeposits degrade within days.

Lamprey, like mussels, may act as bioturbators. Lamprey increased respiration in the sediment, but only when mussels were present. Their movement and filtering activity may mix and aerate the sediment and increase microbial activity. We did not quantify lamprey movement, but we did observe new lamprey burrows in the enclosures during the experiment. Lamprey also flush the surrounding sediment with water and introduce unassimilated particles during filtering. Lamprey selectively filter and ingest particles smaller than 400 μm (Moore and Mallat 1980), while larger particles are ejected out through the gills and into the surrounding sediment. Sea lamprey and brook lamprey larvae were found to ingest 5 mg AFDM g^{-1} ammocoete day^{-1} in July (Sutton and Bowen 1994). If approximately 60% is assimilated, the remaining 40% is released into the sediment. Three lamprey in each enclosure would add approximately 6 mg of organic material to the enclosure daily and possibly increase microbial activity. In our experiment, however, this increase in organic matter or sediment respiration by lamprey larvae was not detectable when mussels were absent.

Interactions between mussels and lamprey larvae may vary with mussel species (Spooner and Vaughn 2006), season, and environment (substrate, flow conditions). Lamprey larval densities increase with deposited organic matter and chlorophyll *a* (Hardisty 1944, Malmqvist 1980, Potter et al. 1986, Beamish and Jebbink 1994, Beamish and Lowartz 1996), suggesting that they track variation in food availability. Where mussel aggregations enhance these resources, they may facilitate lampreys during their larval rearing stages. Mussel biomass once dominated the benthos of many North American freshwaters (Dame 1996), and their decline throughout the continent (Williams et al. 1993) could have negative consequences for lamprey populations.

Acknowledgements

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TABLES

Table 1. Results of lamprey tissue composition from IRMS analysis.

	% C	± SE	% N	± SE	$d^{13}C$	± SE	$d^{15}N$	± SE
Lamprey	53.6	0.9	11.1	0.4	-23.2	0.2	2.7	0.1
Lamprey with mussels	54.1	0.8	10.7	0.4	-23.2	0.2	2.5	0.1
Lamprey fed cladophora	52.7	1.0	11.4	0.5	-23.7	0.3	2.7	0.1
Lamprey fed leaves	53.2	0.6	11.6	0.3	-23.3	0.2	2.7	0.1
Lamprey fed fish flakes	53.4	1.2	11.2	0.5	-23.5	0.3	3.3*	0.2
Note: * denotes significance at a= 0.01								
Algae	21.6	0.1	2.2	0.0	-21.7	0.08	-0.9	0.02
Leaves	48.7	0.1	0.6	0.01	-27.7	0.03	-0.1	0.14
Fish flakes	43.8	0.3	5.9	0.05	-20.9	0.03	9.9	0.2

FIGURE LEGENDS

Figure 1. Map of the South Fork of the Eel River, Mendocino, CA.

Figure 2. Larval lamprey growth after 80 days with and without mussels in the enclosures. Error bars represent 1 S.E.

Figure 3. Larval lamprey growth after 80 days in control (no food added) and food addition treatments. Error bars represent 1 S.E.

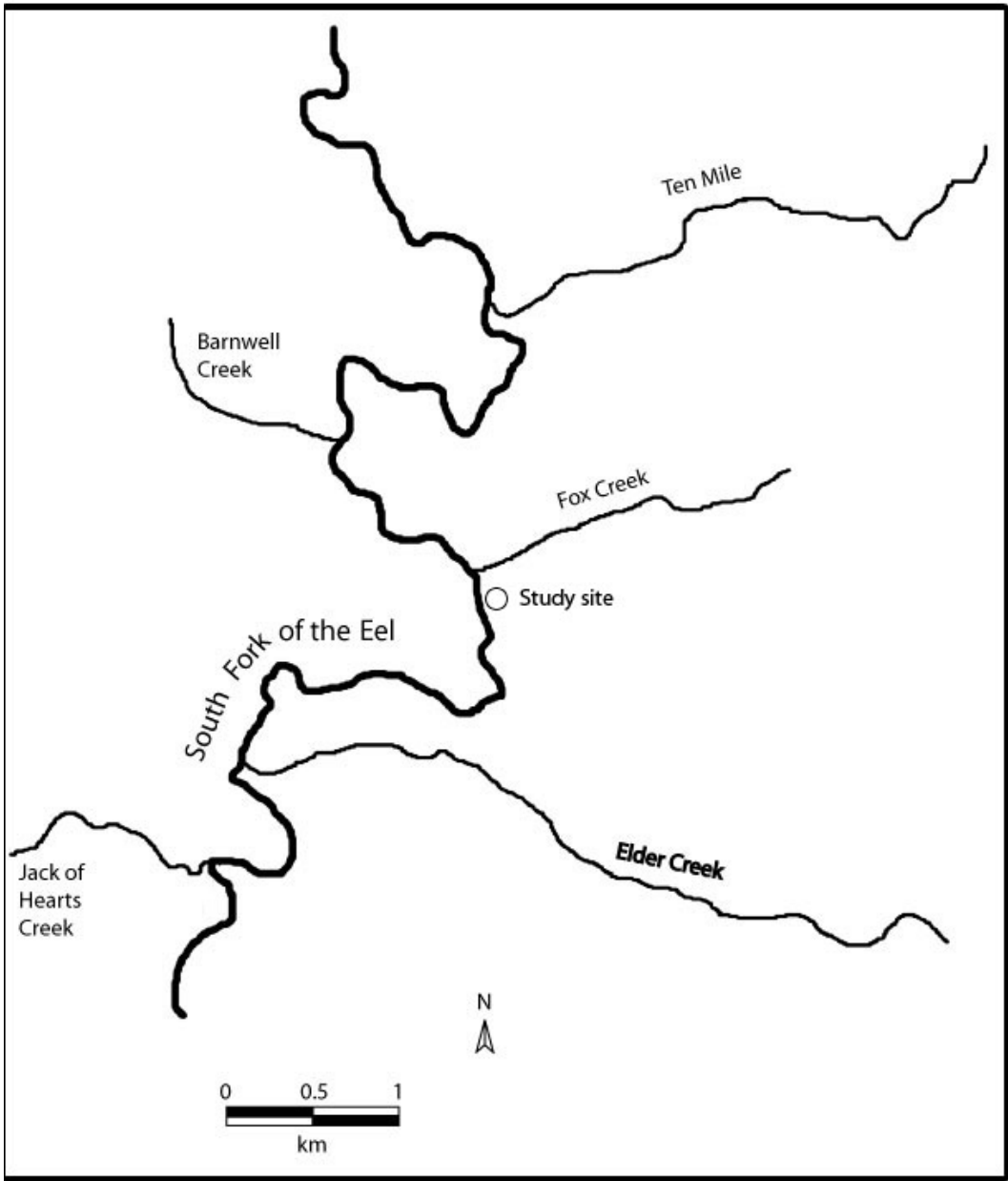**Figure 4.** Respiration measured after 80 days in the top 2 cm and bottom 8 cm of sediment. Error bars represent 1 S.E.
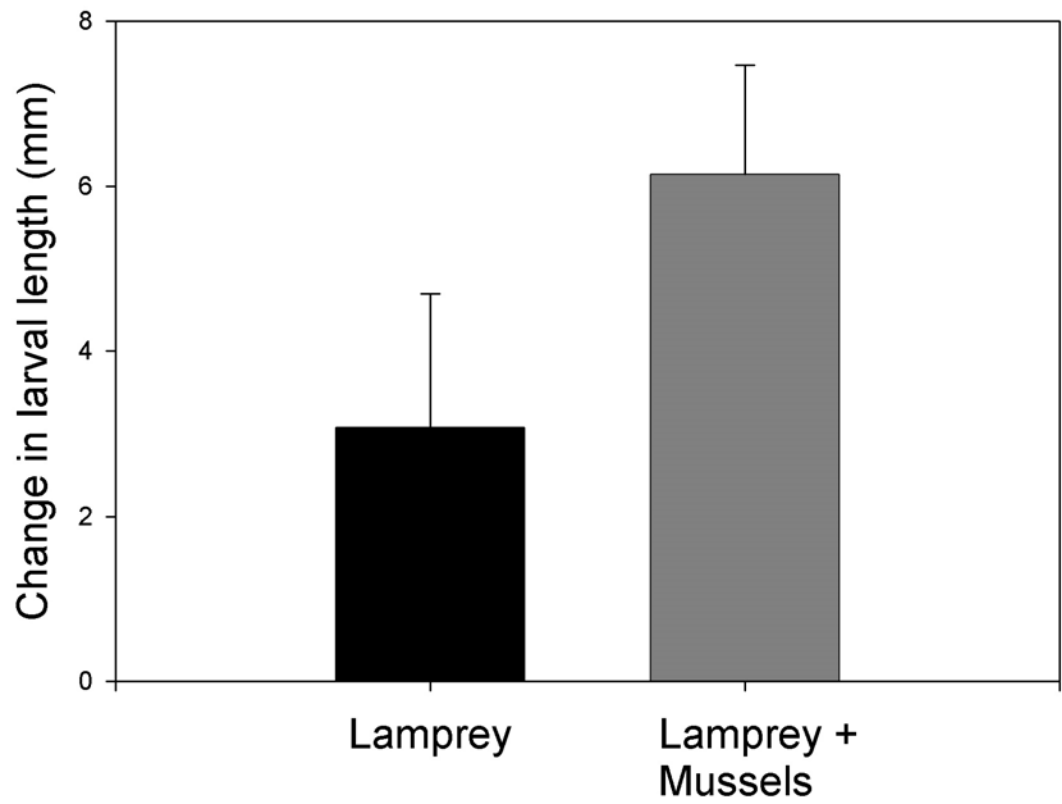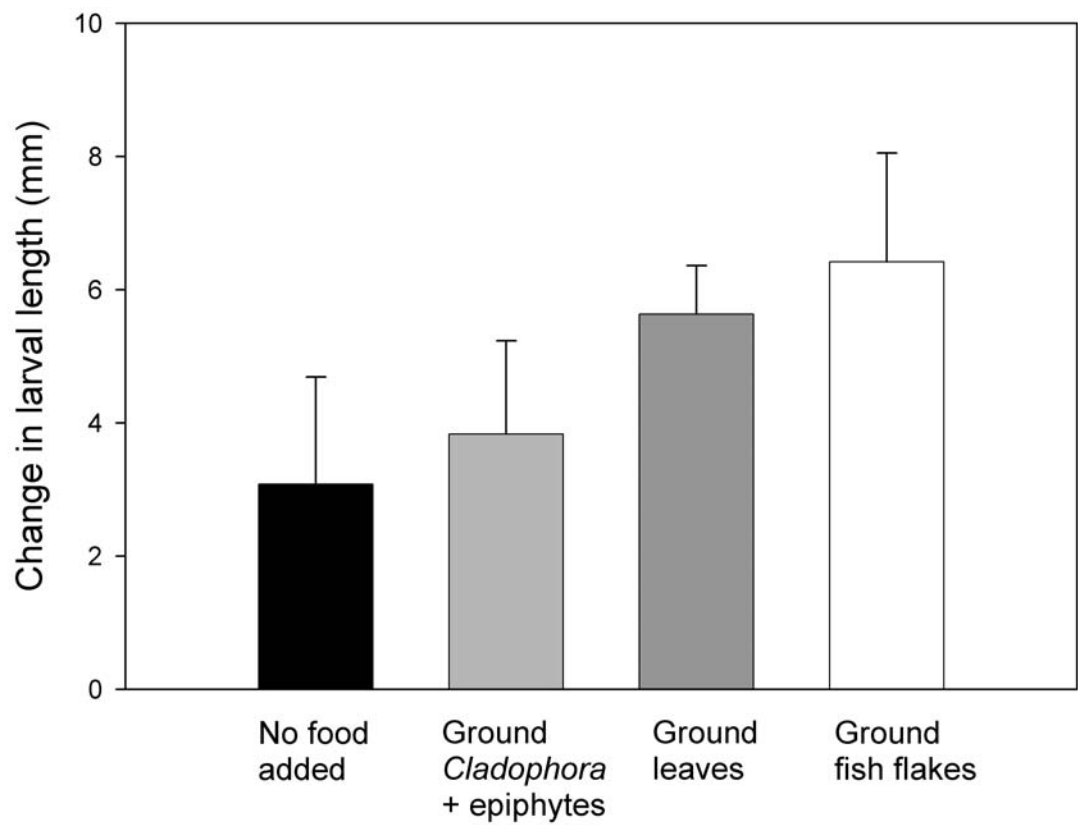
Figure 1.

Figure 2.
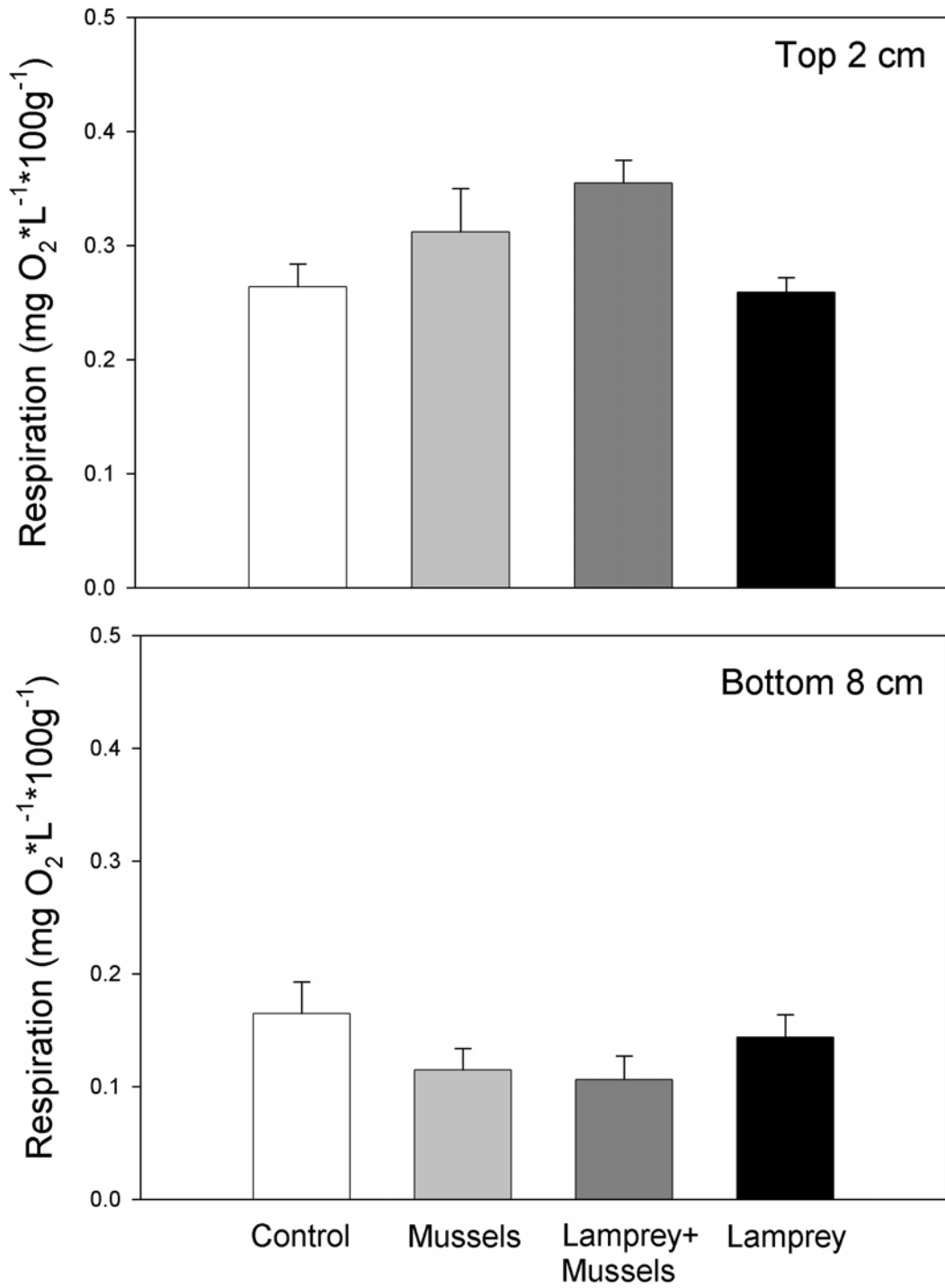
Figure 3.

Figure 4.