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Effects of substrate composition, stream-bed stability, and sediment supply on survival and trophic role of a dominant stream grazer

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Introduction

Understanding the effects of disturbance on river environments and their biotic communities has long been a goal of stream ecologists and resource managers (e.g. RESH et al. 1988). Food web structure and energy flow patterns through river communities can be highly altered by changes in geomorphic processes such as the frequency and intensity of scouring floods (POWER 1992), sediment composition and supply, and channel shape and stability (LIGON et al. 1995). Such changes often result from dams and diversions built to store and redistribute water within and between watersheds (DYNESIUS & NILSSON 1994). Sediment movement during high flows is an important mechanism regulating benthic invertebrate populations (HOLOMUZKI & BIGGS 2000). Large, univoltine taxa with relatively blunt body forms are more susceptible to being dislodged or crushed by moving sediment particles, and their populations are slower to recover from scouring floods than small, multivoltine taxa with higher immigration rates (e.g. TOWNSEND & HILDREW 1994). In northern California rivers with regulated flows, bed-scouring winter floods are often reduced or eliminated. As a consequence, functionally important food chains become shorter as large predator-resistant grazers, such as the stone-cased caddisfly *Dicosmoecus gilvipes*, come to dominate the primary consumer trophic level and reduce energy flow to higher trophic levels (POWER et al. 1996, WOOTTON et al. 1996).

Bed scour can also be reduced or eliminated, even at high flows, in incised channels with reduced sediment supplies. Under such conditions, large-bodied, predator-resistant invertebrates could become the dominant primary consumers, even at flows that would normally scour the stream bed and drastically reduce their populations. This study (1) explored the effects of sediment composition on larval *Dicosmoecus* survival during simulated bed scour, (2) compared responses to scouring flows by *Dicosmoecus* populations in bedrock-dominated stream reaches with low sediment supply and reaches with abundant sediment, and (3) compared the effects of *Dicosmoecus* on algal and primary consumer abundances in stable, sediment-starved and scoured stream reaches.

Study sites

Bear Creek is a fourth-order tributary of the middle Rogue River (T37-38S; R1W-1E) and Jenny Creek is a fifth-order tributary of the middle Klamath River (T39-40S; R3E), SW Oregon. This region is characterized by mild, wet winters and hot, dry summers. Discharge peaks occur most commonly between late November and early April. During the wet seasons of 1996 and 1997, both streams experienced scouring floods (one bankful event in 1996, two or more in 1997), but in 1998–2000 neither stream experienced flows sufficient to cause extensive bed scour. Both streams have storage reservoirs within their upper reaches, and numerous small diversion dams and reservoirs along their main channels and major tributaries, which trap large volumes of sediment during high flows. As a result, both streams have extensive sediment-starved, bedrock-dominated reaches that do not scour even at bankful flows. Stable, sediment-starved reaches alternate with sediment-rich reaches downstream of tributaries that experience considerable bed scour during high flows. Bear Creek is shaded by a dense canopy of cottonwood and alder for much of its length, while the main stem of Jenny Creek has an open canopy, resulting in much higher primary production.

Methods

Scouring flows were simulated, and the effect of sediment grain size tested on *Dicosmoecus* mortality in a narrow wooden chamber (1.25 m long × 0.23 m wide × 0.95 m deep) mounted on a central beam which allowed it to be tipped back and forth. A layer of sediment 15 cm deep was added to the chamber and it was filled with stream water to a depth of 50 cm. Up and down 'teeter-totter' motion of the

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chamber produced sediment movement similar to that observed in natural channels during high flows, in which surface particles saltate and skid over stationary deeper layers. When tipping is reversed, surface particles stop briefly, then skid in the reverse direction, similar to changes in direction of particles in natural channels exposed to complex, turbulent flows. Sediment sizes used in the trials were coarse sand (2 mm particle diameter), gravel (24 mm; range 14–32 mm), and a gravel layer with five cobbles placed on the surface (64 mm; range 57–72 mm). In addition, trials were run with no sediments, to simulate turbulent flows in channels lacking mobile sediments. Trials were run during April 1997 and 1998 using third instar *Dicosmoecus* larvae collected from Bear Creek and other local streams, and during June and July 1998 using fifth instar larvae collected from Jenny Creek. Four trials, of 15-min duration, were run for each sediment–instar combination. At the end of a trial, water was removed from the trough using a hand-operated diaphragm pump, sediment was spread evenly on a tarp, and living and dead larvae were removed and counted. Surviving larvae were held in plastic tubs of aerated stream water, and those found dead after 8 h were combined with counts of larvae killed during the trial, to estimate percent mortality. Two-way ANOVA (arcsine transformed data) was used to assess the effects of sediment size and larval instar on percent mortality.

Dicosmoecus populations were censused in late May to mid June, 1996–1999 in Bear Creek and 1996–2000 in Jenny Creek. Visual counts of larvae within a 0.0875-m^2 quadrat were conducted at 0.5- to 1.0-m intervals along cross-stream transects in sediment-starved reaches experiencing little or no bed scour, and in reaches with abundant sediment and bed scour.

In 1997 (flood year), food web structures were compared in sediment-starved and sediment-rich reaches of Jenny Creek, approximately 2 weeks prior to and 2 weeks after *Dicosmoecus* larvae entered prepupation diapause. Relative changes in abundances of common organisms within primary producer and consumer trophic levels would reveal potential impacts of *Dicosmoecus* on energy flow to higher trophic levels (e.g. WOOTON et al. 1996). On 21 July, fifth instar *Dicosmoecus* densities remained high in sediment-starved reaches (144–190/m^2) and were much lower in sediment-rich reaches (10–28/m^2). By 8 August, densities were reduced by 80–90%, and by 21 August no active larvae were present.

On 21 July and 22 August, six algae and six benthic invertebrate samples were collected from reaches with low and high *Dicosmoecus* densities. Algae were scraped from cobble surfaces (n = 6 cobbles from each site; 9.8 cm^2 area scraped per cobble) and collected on glass-fiber filters (Whatman A/E). In the lab, filters were dried and weighed, then ashed (480 °C, 2 h) and re-weighed. Individual cobbles (mean diameter, 69.4 mm: range, 61–79 mm) also served as sampling units for benthic invertebrates. Samples were collected by placing a D-frame dip net (0.33-mm mesh) downstream of a cobble and rolling it into the net. Macroinvertebrates were washed from the cobble surface, retained in the net, and net contents were preserved (80% ethanol). In the laboratory, macroinvertebrates were sorted from sediments and debris under 10× magnification, identified to family or genus, and enumerated. Differences in densities of major groups, before and after *Dicosmoecus* went into diapause, were compared using t-tests.

Results and discussion

Sediment size and instar had significant effects on *Dicosmoecus* survival in simulated bed-scour trials (Fig. 1) (two-way ANOVA, P = 0.0001 substrate; P = 0.044 instar; P = 0.56 substrate × instar interaction). Mortality was highest in trials with cobble-size particles but was very low in no sediment and sand trials. Third instar larvae suffered higher mortality in all sediments. These data show that stream-bed composition probably plays an important role in determining population responses to scouring flows, with the mortality of large-bodied, univoltine taxa, like *Dicosmoecus*, being reduced downstream of dams and diversions that trap gravel–cobble-size sediments.

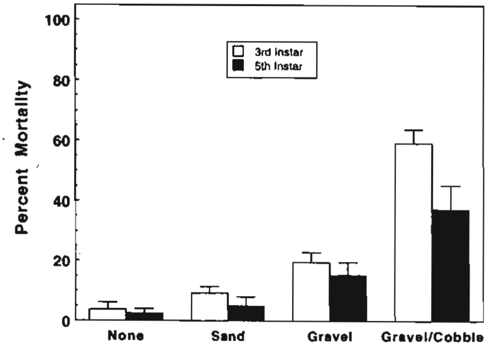

Fig. 1. Effects of sediment composition on percent mortality of third (open bars) and fifth (dark bars) instar *Dicosmoecus gilvipes* larvae during simulated bed scouring flows (values are means ± 1 S.E.; n = 4).

Population censuses revealed that *Dicosmoecus* densities were consistently higher in sediment-starved reaches (Fig. 2). Although densities fluctuated among years, they were similar between years with and without scouring flows (e.g. 1996 and 1997 versus 1998–2000), suggesting that populations were not significantly reduced during floods. *Dicosmoecus* densities in reaches with mobile sediments, in contrast, were lowest in flood years, and increased 2- to 3-fold in years without significant bed scour.

Enhanced survival, resulting in higher *Dicosmoecus* densities in sediment-starved reaches clearly had strong effects on algal standing crops (Fig. 3) and densities of other primary consumers (Fig. 4). Algal abundance increased 8-fold after *Dicosmoecus* went into diapause in high density, sediment-starved reaches ($P < 0.0001$; t-test), but increased by only 20% in scoured reaches with low *Dicosmoecus* densities ($P > 0.05$). Small, mobile primary consumers (mayflies and midges) responded with large density increases ($P < 0.001$ for both), whereas densities of the pleurocerid snail, *Juga silicula* increased by a smaller, but significant ($P < 0.02$) amount. Changes in densities of these groups in low *Dicosmoecus* reaches were not significant ($P > 0.05$ for all comparisons).

Taken together, these results show that differences in sediment composition and supply strongly influence population densities of *Dicosmoecus,* with strong indirect effects on lower trophic levels. The large difference in *Dicosmoecus* densities between the two streams was likely due to differences in productivity, suggesting that the effects of artificial channel stabilization on food web structure and energy flow may be magnified in more productive, sunlit streams. Few studies have examined the effects on stream communities of small dams that do not regulate winter flows. The present results suggest that small dams, by altering sediment supply, may affect food webs in ways qualitatively similar to larger dams that eliminate scouring flows (see POWER 1992, POWER et al. 1996). Since small diversion dams can be much more numerous within a watershed than large irrigation storage or flood control dams, their ecological effects at the watershed scale

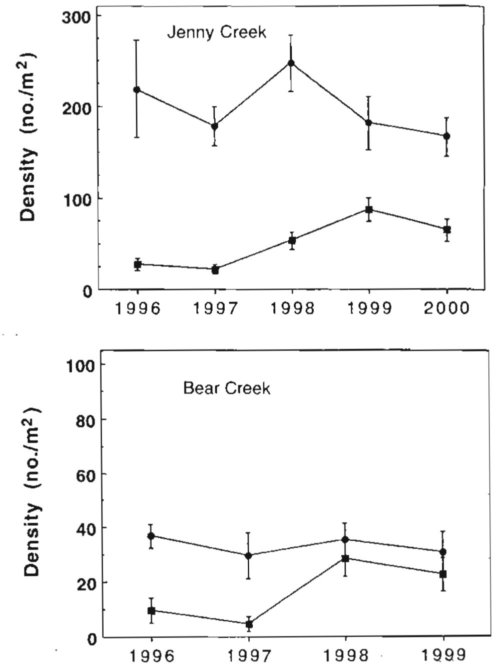

Fig. 2. Spring (late May–mid June) population densities of *D. gilvipes* in sediment-starved stream reaches that did not experience bed scour during high winter flows (circles) and reaches, downstream from tributary junctions, with abundant sediment that experienced extensive bed scour during high flows (squares) (values are means ± 1 S.E.).

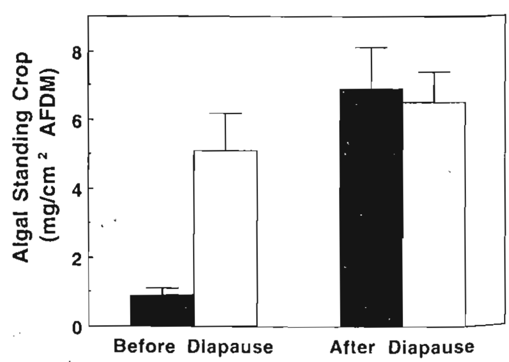

Fig. 3. Algal biomass before and after *Dicosmoecus* larvae went into prepupation diapause, illustrating relative grazing pressures in unscoured stream reaches with high *Dicosmoecus* densities (dark bars) and scoured reaches with low *Dicosmoecus* densities (open bars) (values are means ± 1 S.E.; n = 6).

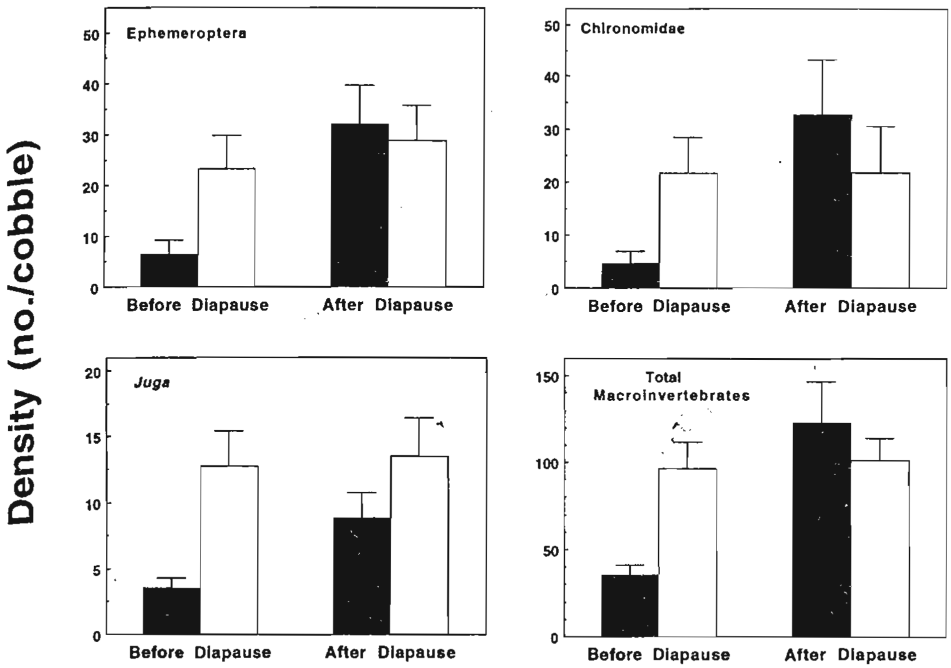

Fig. 4. Densities of common primary consumers and total macroinvertebrates before and after *Dicosmoecus* went into prepupation diapause in unscoured stream reaches with high *Dicosmoecus* densities (dark bars) and scoured reaches with low *Dicosmoecus* densities (open bars) (values are means ± 1 S.E.).

could be extensive.

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