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PRIMARY RESEARCH PAPER

# Does ambient substrate composition influence consumer diversity effects on algal removal?

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**Abstract** Benthic substrates constitute an important habitat template for aquatic communities and may affect the contributions of benthic organisms to ecological processes. To test the effects of ambient substrate composition on the process of algae accrual and removal, we conducted an experiment to examine how substrate type influenced consumer richness effects. We hypothesized that algal removal from focal substrates (ceramic tiles) would be influenced by the surrounding ambient substrate through its effect on nutrient cycling and subsequent algal growth. We manipulated consumer richness in mesocosms at one or three species while holding consumer biomass constant. Aquatic consumers were an amphipod, a snail, and a water boatman, and ambient substrates were either sand or gravel. After 21 days, ambient substrate influenced epilithic algal accrual on tiles, affected physio-chemical parameters within mesocosms, and modified consumer behavior. Chlorophyll *a* was approximately 2× greater on control tiles surrounded by sand, and FPOM and turbidity were greater on sand than gravel when consumers were present. Substrate modified consumer behavior such that consumers congregated around focal substrates in sand, but dispersed around them in gravel. Consumers also had substrate-specific influences on epilithic chlorophyll, causing a decrease in sand and an increase in gravel. Algal assemblages on focal tiles were dominated by diatoms, and their composition responded to consumer richness and identity, but not substrate. Our data suggest that direct effects (e.g., consumptive removal of epilithon from focal tiles) were more pronounced in sand, whereas indirect effects (e.g., bioturbation and enhanced mixing) promoted algal accrual in gravel. These results show that algae production on exposed surfaces may change as underlying substrate composition changes, and that substrate type can alter consumer diversity effects on algal removal.

**Keywords** Algal removal · Benthic consumers · Substrate composition · Context dependency

## Introduction

Aquatic ecosystems worldwide are being endangered by widespread habitat modification (Dudgeon et al., 2006; Poff et al., 2007). Alterations of natural flows,

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increased nutrient loading, and other modifications to aquatic habitats have received well-deserved attention as important challenges to preserving aquatic communities (Dudgeon et al., 2006). Less noticed have been alterations to benthic landscapes, despite the fact that stream and lake beds constitute a crucial habitat template for aquatic communities (Poff & Ward, 1990). Bed substrates provide the surfaces on which benthic species interactions are played out, and substrate properties influence species' contributions to ecosystem processes. For example, substrate composition can influence epilithic metabolism (Romani & Sabater, 2001; Cardinale et al., 2002; Romani et al., 2004), substrate texture can modify periphyton removal by grazers (Dudley & D'Antonio, 1991; Gawne & Lake, 1995; Downes et al., 2000), and substrate complexity can influence consumer responses to predators (Holomuzki & Hoyle, 1990; Power, 1992). Benthic substrates are also subject to anthropogenic modification at multiple scales. Substrate particle size, for instance, can be influenced locally by dam construction (Ward & Stanford, 1995), regionally by land use practices (e.g., deforestation; Oago & Odada, 2007), and globally by climate change (e.g., via altered precipitation and runoff; Chaplot, 2007).

In addition to direct effects, substrates may influence aquatic processes and species interactions indirectly. Benthic algae growing on surfaces may be influenced by the nutrient cycling within the surrounding bed material (Romani et al., 2004, Gainswin et al., 2006), and ambient substrates may impinge on grazer movement (Hoffman et al., 2006, Lancaster et al., 2006) and provide refuge from predators (Peckarsky, 1991, Franken et al., 2006). Just as aquatic consumers and their predators have important, indirect influences on benthic processes (Power, 1990, McIntosh & Townsend, 1996), so might the physical composition of benthic landscapes.

Here we describe a mesocosm experiment that examines the influence of ambient substrate composition on the relationship between consumer richness and an ecosystem process. We used sand or gravel as ambient substrate, ceramic tiles as focal substrate, and measured algal removal as our ecosystem process. Our three algal consumer species—an amphipod, a snail, and a water boatman—co-occur in nature and have functionally distinct feeding structures. We predicted that greater consumer richness would lead to more algae being removed from focal substrates due to complementarity between these consumers (Loreau & Hector, 2001), but expected that removal would be modified by the surrounding substrate. Specifically, we hypothesized that algal growth would be lower in gravel than sand because gravel has less surface area for microbial colonization and nutrient cycling would be lower. Therefore, consumption being equal between substrate treatments, proportionally more algae would be removed from focal substrates surrounded by gravel.

## Methods

### Experimental design

The experiment was set up as a 2 × 5 factorial design with 2 ambient substrate treatments (sand or gravel) and 5 consumer treatments (3 one-species consumer treatments, 1 combined consumer treatment, and 1 consumer control), each with six replicates (=60 mesocosms). Consumer biomass was held constant across consumer treatments.

The mesocosms were designed to mimic isolated or semi-isolated stream margin pools in which all consumers were found. These pools are typically small (<10 l), shallow, and have negligible current, making 3.8 l (28 × 15 × 11 cm), clear plastic aquariums reasonable surrogates for these habitats. Each aquarium was filled with 2.5 l of dechlorinated tap water and placed in a greenhouse to receive natural light and photoperiod. Aquarium bottoms were lined with 3 cm (750 $cm^3$) of washed gravel or sand, which had particle sizes (mean ± SE) of 5.58 ± 2.57 and 0.43 ± 0.26 mm, respectively. Substrates were mined from naturally occurring deposits rather than being manufactured by crushing, so surfaces were smooth and similar between substrate types. Unglazed, ceramic tiles (4.8 × 4.8 cm) served as focal substrate, and five were placed on top of the ambient substrate in each mesocosm. Prior to placement, tiles were inoculated with epilithic algae for 7 days in Little Niagara Creek, a tributary to the Chippewa River (Eau Claire Co., WI, USA). Before adding consumers, an additional 16 days was allowed for algal growth.

## Invertebrate consumers

We chose the snail *Physa* sp., the amphipod *Gammarus pseudolimneaus*, and the boatman *Hesperocorixa* sp. for this experiment because these consumers co-occur in the Chippewa River (Eau Claire County, WI, USA), have functionally distinct mouthparts, and feed on algae. Snails possess a scraping radula, amphipods have collecting/gathering mouthparts, and water boatmen use a proboscis for sucking up fine particulate food (McIntosh & Townsend, 1996; Thorp & Covich, 2001). Water boatmen and snails were harvested from the Chippewa River and amphipods were taken from Taylor Creek (Eau Claire Co., WI, USA), a nearby tributary. Samples of boatmen ($n = 61$), amphipods ($n = 20$), and snails ($n = 10$, with shells removed) were dried and weighed to determine dry mass per individual. This information was used to calculate the number of individuals needed to attain equivalent consumer biomass across treatments. Single species treatments received three snails, nine amphipods, or 39 boatmen; three species treatments received one snail, three amphipods, and 13 boatmen. These densities approximated natural abundances within the constraints of the experimental design. For example, 20 boatmen per mesocosm would match mean natural boatmen density in the Chippewa River (Wellnitz, unpub. data); however, because snail density could not be made <1 individual per mesocosm, boatmen numbers were increased to achieve equivalent biomass in the single species treatment. Nevertheless, experimental densities for all consumers were within the range of variation found in the natural habitat.

## Data collection

The experiment lasted 21 days from 12 November to 2 December 2006. During this time mesocosms were checked daily, dead invertebrates were replaced, and water was added as needed to maintain constant volume. Greenhouse temperatures were set to a 12-h, day/night cycle of 15.6° and 11.7°C. Algae abundance appeared to asymptote after 2 weeks, so the experiment was terminated after 3 weeks.

### *Algal sampling and analysis*

Epilithic chlorophyll *a* and taxonomic composition were sampled from focal substrates after 21 days. One tile from each mesocosm was randomly selected for each epilithic metric. Periphyton was removed from the entire tile surface using a toothbrush and wash bottle. The resulting slurry was filtered through glass fiber filters (Gelman A/E) for chlorophyll *a* or preserved in 2% formalin to determine taxonomic composition. Chlorophyll *a* was extracted from filters using 90% hot, buffered ethanol following procedures in Biggs & Kilroy (2000). An Opti-sciences GFC-1 fluorometer was used to quantify chlorophyll *a*. Epilithic algal taxonomic composition was determined by extracting sub-samples from slurries and drying on a glass cover slip for identification and enumeration of cells. Diatoms comprised the dominant algae (>90%) and were identified to the genus level and enumerated by making 10 transects across each cover slip.

In addition to epilithic algae, we observed filamentous algae growing in the water column and measured suspended chlorophyll *a* as well. We sampled suspended algae by withdrawing 200 ml of water from each mesocosm, and chlorophyll *a* was determined following the procedures described above.

### *Physio-chemical sampling and analysis*

Biological oxygen demand (BOD), fine particulate organic matter (FPOM), and nitrate/ammonium ($NO_3/NO_4^+$) were measured to assess nutrient cycling and organic matter breakdown in mesocosms. Turbidity was measured to quantify suspended material in the water column. These parameters were all recorded at the end of the experiment.

Biological oxygen demand was measured by adding 100 ml of substrate and 200 ml of water from each mesocosm to BOD bottles (300 ml). Dissolved oxygen (ppm) was measured with a YSI 200- BOD probe before and after incubating BOD bottles in darkness for 8 h. Final dissolved oxygen was subtracted from initial values to determine BOD. FPOM was extracted by rinsing 100 ml of substrate from each mesocosm three times with tap water, and then filtering through a glass fiber filter (Gelman A/E). Filters were dried, weighed, and ashed at 400°C for 4 h to volatilize organic material, and then weighed again to determine ash-free dry mass (AFDM). Water column turbidity was measured in Formazin Turbidity Units (FTU) using a Hach DR/890D colorimeter, and $NO_3/NO_4^+$ was quantified with a Hach$^{TM}$ test kit.

### Statistical analyses

Differences among treatment means for epilithic and suspended algae parameters, and physio-chemical metrics (i.e., BOD, FPOM, and turbidity), were determined using analysis of variance (ANOVA) and means were compared using Tukey's HSD post-hoc tests. To compare the algal assemblages in the different consumer treatments we used Non-Metric Multi-Dimensional Scaling (NMDS) employing Euclidean distance. This non-parametric ordination technique provided a visual representation of dissimilarity distances among the algal assemblages from each consumer treatment. Multivariate analysis of variance (MANOVA) was used on NMDS scores to determine differences in algal community composition. Wilks' $\lambda$ determined the overall significance of the model and Tukey's post-hoc tests were used to compare NMDS score means. Prior to conducting Tukey's tests, normality and homoscedasticity of the data were checked using QQ and residual plots to assure that parametric assumptions were met. Analyses were performed using JMP 8 statistical software (for ANOVA) and the R Project for Statistical Computing (for NMDS and MANOVA).

## Results

Substrate influenced consumer distribution and behavior. Observations indicated that the three consumer species spent more time on or around tiles in sand than gravel. Amphipods typically sought refuge under tiles in sand, but would burrow in gravel, and consequently, occupied more of the bottom area in gravel treatments. Water boatman frequently used tiles and gravel particles for anchoring, but rarely sand. Likewise, snails preferred tiles and gravel to sand when foraging.

Consumers, ambient substrate, and the interaction between these factors influenced epilithic algal biomass on focal tiles. Chlorophyll *a* was lower on control tiles surrounded by gravel (ANOVA, $F_{2,54} = 11.82$, $P < 0.0001$; Tukey's HSD, $P < 0.05$); however, this difference between substrates was absent in the presence of consumers (Fig. 1A). Examination of individual consumer effects showed similar reductions of focal tile algae by all consumers with the exception of water boatmen (Fig. 1B). Boatmen treatments in gravel had about a third more epiphytic algae compared to other consumer treatments (ANOVA, $F_{4,50} = 10.06$, $P < 0.001$; Tukey's HSD, $P < 0.05$).

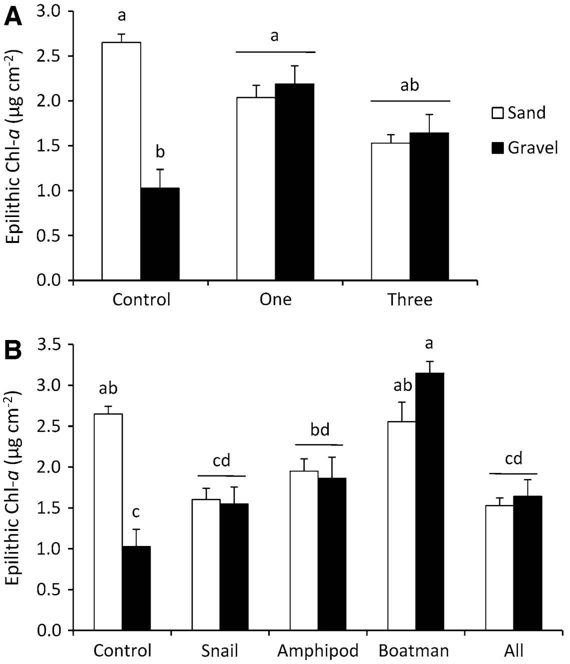

**Fig. 1** Epilithic chlorophyll *a* taken from focal tiles after 21 days. Data are for **A** consumer richness and **B** individual consumer treatments. *Bars* represent means ± 1 SE and similar *letters* indicate means that are not different

Consumers also reduced suspended algae in mesocosms, but there was no interaction with substrate (Fig. 2). The one and three species treatments had a third as much suspended chlorophyll *a* as did controls (Fig. 2A; ANOVA, $F_{2,54} = 13.46$, $P < 0.0001$; Tukey's HSD, $P < 0.05$) and did not differ from one another. Analyzing individual consumer effects showed that the amphipod and combined consumer treatments had the least suspended algae (Fig. 2B; ANOVA, $F_{4,50} = 50.64$, $P < 0.0001$; Tukey's HSD, $P < 0.05$).

We examined chlorophyll *a* on tiles in consumer treatments as a proportion of the chlorophyll *a* on control tiles (Fig. 3). This allowed us to examine substrate-specific effects of richness treatments relative to controls. Two patterns were evident: First, focal tiles in consumer treatments having gravel had more algae relative to controls than treatments with sand (ANOVA, $F_{1,46} = 9.60$, $P = 0.003$; Tukey's HSD, $P < 0.05$). Second, substrate modified consumer richness effects such that the proportion of

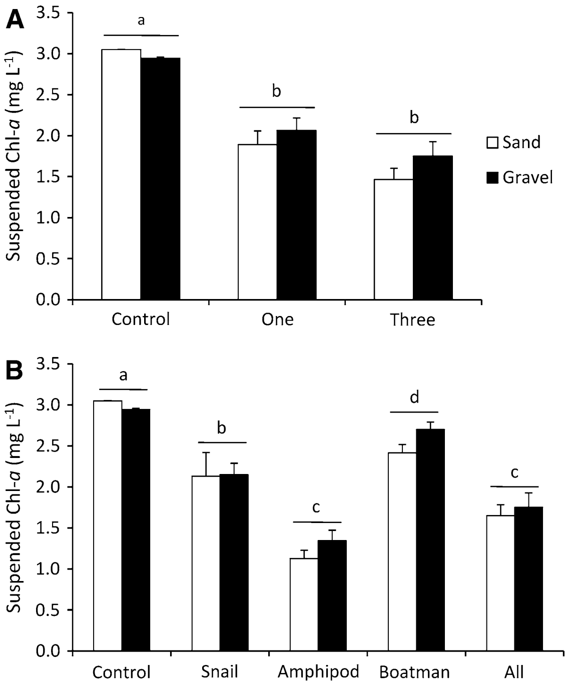

**Fig. 2** The effect of consumers on suspended chlorophyll *a* after 21 days. Substrate effects were not detected so only consumer effects are shown. Data are for **A** consumer richness and **B** individual consumer treatments. Bars represent means ± 1 SE and similar *letters* indicate means that are not different

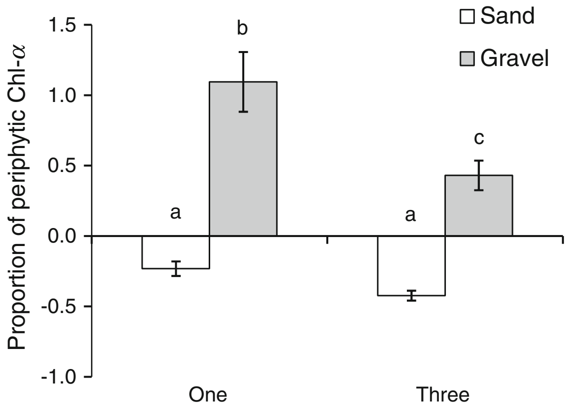

**Fig. 3** Epilithic chlorophyll *a* on focal tiles in consumer treatments as a proportion of the chlorophyll *a* in consumer controls. *Positive values* indicate and increase in chlorophyll *a* relative to controls, *negative values* indicate a decrease

chlorophyll *a* on tiles was different between the species richness treatments for gravel, but was not different for sand (Tukey's HSD, $P < 0.05$).

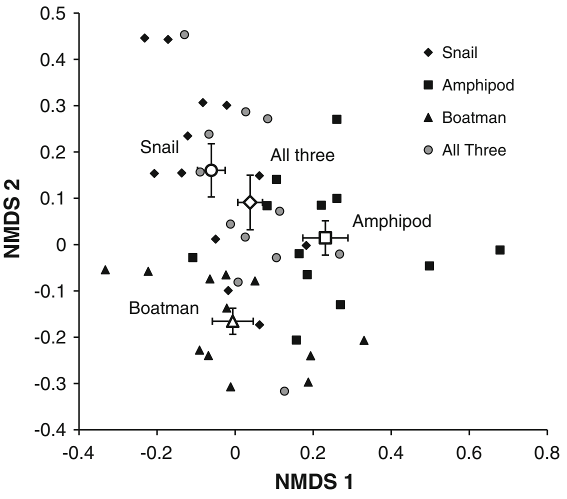

**Fig. 4** Mean NMDS point values for algal community compositions from mesocosms having one or three species after 21 days. *Error bars* represent ± 1 SE, and only the snail and the combined species treatments (i.e., "all three") did not differ

Algal community structure on focal tiles was influenced by consumers. Diatom assemblages grazed by boatmen, amphipods, and snails each contained different proportions of diatom genera, while assemblages grazed by all three were intermediate in composition (Fig. 4). Assemblages grazed by boatmen and amphipods were significantly different from the three species treatment (Wilks' $\lambda$, $F_{3,40} = 8.95$, $P < 0.0001$, Tukey's HSD test, $P < 0.05$), whereas assemblages grazed by snails did not differ. Across treatments, the six most common diatom genera in order of percent abundance were: *Navicula* (40%) *Planothidium* (14%), *Fragillaria* (11%), *Placoneis* (6%), *Nitzchia* (4%), and *Synedra* (3%). *Navicula* spp. always dominated, but the rankings of other diatom genera differed among treatments. After *Navicula*, the three most abundant genera for the snail treatment were *Planothidium, Placoneis*, *Fragillaria*; for amphipods the rankings were, *Planothidium*, *Fragillaria*, *Placoneis*; for boatmen, *Fragillaria*, *Planothidium*, *Synedra*.

In addition to affecting algal abundance and community structure, substrate and consumer type influenced physio-chemical parameters within mesocosms. Metrics for FPOM and turbidity, for example, were on average more than twice as great in

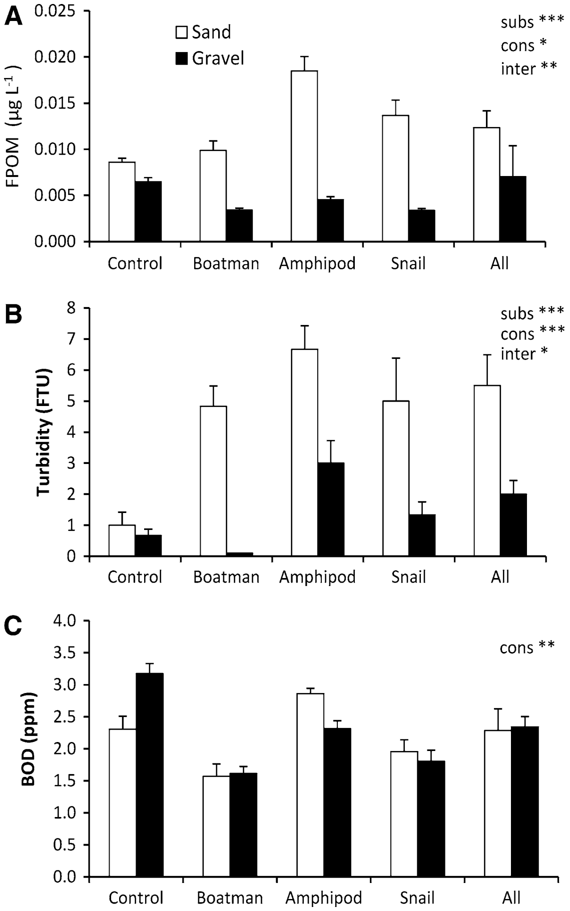

**Fig. 5** The effect of ambient substrate and consumer treatments on **A** water turbidity, **B** FPOM, and **C** BOD relative to consumer-free controls at the end of the experiment. Values are means ± 1 SE and *lines over bars* indicate means that are not different. Treatment effects are indicated in legend for substrate (subs), consumers (cons), and the interaction (inter) between these factors. Significance levels are * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$

mesocosms containing sand than gravel (Fig. 5A, B). Also similar was the influence of consumers on FPOM and turbidity. For each of these parameters, amphipods were associated with the highest values and water boatman the lowest ($\mathrm{ANOVA}_{\mathrm{FPOM}}$, $F_{4,50} = 3.35$, $P = 0.02$; $\mathrm{ANOVA}_{\mathrm{turbidity}}$, $F_{4,50} = 6.05$, $P = 0.0005$; Tukey's HSD, $P < 0.05$). BOD was influenced only by consumer treatments, but no clear pattern emerged except that water boatmen had the lowest values (Fig. 5C; ANOVA, $F_{4,50} = 10.34$, $P < 0.0001$; Tukey's HSD, $P < 0.05$). Measurements of $NO_3/NH_4^+$ did not differ among treatments.

## Discussion

Results from this study show that the substrate surrounding benthic surfaces can influence algal accrual and removal. Consumers reduced mesocosm algae, and richness effects occurred, but only through the interaction with substrate. Two factors appeared to be responsible for this interaction: first, different amounts of epilithon accumulated on focal tiles surrounded by sand versus gravel; and second, consumers behaved differently on the two substrates.

Consumer-free control tiles surrounded by sand had more than twice as much epilithic algae as those surrounded by gravel. These data support our hypothesis that substrate type influenced algal production; however, the exact mechanism by which this occurred is unclear. We reasoned that nutrient cycling would be lower in gravel mesocosms because gravel has less surface area for microbial colonization than sand, but neither BOD nor $NO_3/NH_4^+$ differed between substrates. Nevertheless, substrate type did affect physio-chemistry in terms of FPOM and turbidity, both of which were greater in sand. This difference may be explained by the manner in which FPOM accumulated on sand versus gravel.

Fine particulate organic matter settled on sand as a fine flocculent layer that was easily disturbed, subject to resuspension by consumers, and readily contributed to water column turbidity. By contrast, FPOM in gravel infiltrated between particles and became entrapped interstitially so that its resuspension required more vigorous bioturbation by consumers. Bioturbation mobilizes interstitial FPOM (Covich et al., 2004), and it is noteworthy that turbidity in gravel was greatest in the presence of amphipods, the one consumer that commonly burrows and interacts energetically with the substratum (Starry et al., 1998, Franken et al., 2006).

Consumer behavior was distinctive among the three species in our study, but each exhibited substrate-specific behaviors that resulted in individuals congregating near tiles in sand and dispersing away from them in gravel. Amphipods, for example, tended to burrow in gravel and utilize the whole bottom area, but in sand they sought refuge beneath tiles and this constrained their distribution. Similarly, water boatmen made widespread use of gravel bottoms because the larger particles offered better anchoring opportunities than did sand. Boatmen have a plastron that traps air to serve as a physical gill, and this makes them positively buoyant (Merritt & Cummins, 1996). When not actively swimming, water boatmen must cling to benthic substrates to remain submerged. In mesocosms containing sand, tile edges presented superior anchoring sites to the sand bottom, and consequently, boatmen frequently occurred on tiles. Snails also exhibited a preference for gravel over sand surfaces, probably because their radula are less effective at removing epilithon from fine sediments than hard surfaces (Broekhuizen et al., 2001). Owing to these substrate-specific behaviors, sand concentrated consumers near tiles where consumptive and non-consumptive removal of epilithon was probably greater, whereas gravel dispersed consumers around tiles, likely diminishing their removal of tile epilithon.

Substrate-specific behavior helps explain why consumers had contrary effects on tile epilithon in sand and gravel. In sand, direct effects decreased epilithon; in gravel, indirect effects (e.g., bioturbation and water mixing) increased epilithic production (Mermillod-Blondin et al., 2004, Caliman et al., 2007). This pattern is most clearly seen by examining tile epilithon in consumer treatments as a proportion of controls (i.e., Fig. 3). The proportion of algae on focal tiles shows the substrate × consumer richness interaction in which tile epilithon was lower in the three species + gravel treatment, but did not differ between richness treatments in sand. Complementarity among consumers may partially account for this interaction (Loreau & Hector, 2001), and the diatom composition data support to this hypothesis. Amphipods, water boatmen, and snails each created unique algal assemblages, but combined consumer treatment was intermediate to all three (i.e., Fig. 4), suggesting that each species contributed to shaping the assemblage in the high richness treatment. Complementarity effects may have been more pronounced in gravel because consumers caused algae to nearly double relative to controls, whereas consumers in sand caused algae to decrease by about half that much.

Regardless of the underlying cause of the substrate × consumer interaction, our results demonstrate that the relationship between consumer richness and algal removal in mesocosms was context-dependent. Given that benthic landscapes constitute an important habitat template for aquatic communities (Ward, 1992), such interactions may be common, perhaps more so than is generally appreciated. Other studies have shown that algal accrual and removal can be influenced by consumer diversity (Duffy et al., 2003; Lohrer et al., 2004), and that environment gradients can modify consumer effects (Wellnitz & Poff, 2006; Vaughn et al., 2007), but few have examined the indirect effects of substrate composition on aquatic processes (but see Cardinale et al., 2002). Our results suggest algae production on exposed surfaces may change as underlying substrate composition changes, and that substrate type can indirectly alter consumer diversity effects on algal removal.

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## References

Biggs, B. J. F. & C. Kilroy, 2000. Stream Periphyton Monitoring Manual. NIWA, Christchurch.

Broekhuizen, N., S. Parkyn & D. Miller, 2001. Fine sediment effects on feeding and growth in the invertebrate grazers *Potamopyrgus antipodarum* (Gastropoda, Hydrobiidae) and *Deleatidium* sp. (Ephemeroptera, Leptophlebiidae). Hydrobiologia 457: 125–132.

Caliman, A., J. F. Leal, F. A. Esteves, L. S. Carneiro, R. L. Bozelli & V. F. Farjalla, 2007. Functional bioturbator diversity enhances benthic-pelagic processes and properties in experimental microcosms. Journal of the North American Benthological Society 26: 450–459.

Cardinale, B. J., M. A. Palmer, C. M. Swan, S. Brooks & N. L. Poff, 2002. The influence of substrate heterogeneity on biofilm metabolism in a stream ecosystem. Ecology 83: 412–422.

Chaplot, V., 2007. Water and soil resources response to rising levels of atmospheric $CO_2$ concentration and to changes in precipitation and air temperature. Journal of Hydrology 337: 159–171.

Covich, A. P., M. C. Austen, F. Barlocher, E. Chauvet, B. J. Cardinale, C. L. Biles, P. Inchausti, O. Dangles, M. Solan, M. O. Gessner, B. Statzner & B. Moss, 2004. The role of biodiversity in the functioning of freshwater and marine benthic ecosystems. Bioscience 54: 767–775.

Downes, B. J., P. S. Lake, E. S. G. Schreiber & A. Glaister, 2000. Habitat structure, resources and diversity: the separate effects of surface roughness and macroalgae on stream invertebrates. Oecologia 123: 569–581.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Leveque, R. J. Naiman, A. H. Prieur-Richard, D. Soto, M. L. J. Stiassny & C. A. Sullivan, 2006.

Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81: 163–182.

Dudley, T. L. & C. M. D'Antonio, 1991. The effects of substrate texture, grazing, and disturbance on macroalgal establishment in streams. Ecology 72: 297–309.

Duffy, J. E., J. P. Richardson & E. A. Canuel, 2003. Grazer diversity effects on ecosystem functioning in seagrass beds. Ecology Letters 6: 637–645.

Franken, R. J. M., S. Batten, J. A. J. Beijer, J. J. P. Gardeniers, M. Scheffer & E. Peeters, 2006. Effects of interstitial refugia and current velocity on growth of the amphipod *Gammarus pulex* Linnaeus. Journal of the North American Benthological Society 25: 656–663.

Gainswin, B. E., W. A. House, B. S. C. Leadbeater & P. D. Armitage, 2006. Kinetics of phosphorus release from a natural mixed grain-size sediment with associated algal biofilms. Science of the Total Environment 360: 127–141.

Gawne, B. & P. S. Lake, 1995. Effects of microspatial complexity on a herbivore epilithon interaction in an Australian upland stream. Freshwater Biology 33: 557–565.

Hoffman, A. L., J. D. Olden, J. B. Monroe, N. L. Poff, T. Wellnitz & J. A. Wiens, 2006. Current velocity and habitat patchiness shape stream herbivore movement. Oikos 115: 358–368.

Holomuzki, J. R. & J. D. Hoyle, 1990. Effect of predatory fish presence on habitat use and diel movement of the stream amphipod, *Gammarus minus*. Freshwater Biology 24: 509–517.

Lancaster, J., T. Buffin-Belanger, I. Reid & S. Rice, 2006. Flow- and substratum-mediated movement by a stream insect. Freshwater Biology 51: 1053–1069.

Lohrer, A. M., S. F. Thrush & M. M. Gibbs, 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. Nature 431: 1092–1095.

Loreau, M. & A. Hector, 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412: 72–76.

McIntosh, A. R. & C. R. Townsend, 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish induced changes to grazer behaviour? Oecologia 108: 174–181.

Mermillod-Blondin, F., M. Gerino, S. Sauvage & M. C. de Chatelliers, 2004. Influence of nontrophic interactions between benthic invertebrates on river sediment processes: a microcosm study. Canadian Journal of Fisheries and Aquatic Sciences 61: 1817–1831.

Merritt, R. W. & K. W. Cummins, 1996. An Introduction to the Aquatic Insects of North America, 3rd ed. Kendal/Hunt Publishing Co., Dubuque, Iowa.

Oago, D. O. & E. O. Odada, 2007. Sediment impacts in Africa's transboundary lake/river basins: case study of the east African great lakes. Aquatic Ecosystem Health & Management 10: 23–32.

Peckarsky, B. L., 1991. Habitat selection by stream-dwelling predatory stoneflies. Canadian Journal of Fisheries and Aquatic Sciences 48: 1069–1076.

Poff, N. L., J. D. Olden, D. M. Merritt & D. M. Pepin, 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proceedings of the National Academy of Sciences of the United States of America 104: 5732–5737.

Poff, N. L. & J. V. Ward, 1990. Physical habitat template of lotic systems – recovery in the context of historical pattern of spatiotemporal heterogeneity. Environmental Management 14: 629–645.

Power, M. E., 1990. Effects of fish in river food webs. Science 250: 811–814.

Power, M. E., 1992. Habitat heterogeneity and the functional-significance of fish in river food webs. Ecology 73: 1675–1688.

Romani, A. M. & S. Sabater, 2001. Structure and activity of rock and sand biofilms in a Mediterranean stream. Ecology 82: 3232–3245.

Romani, A. M., A. Giorgi, V. Acuna & S. Sabater, 2004. The influence of substratum type and nutrient supply on biofilm organic matter utilization in streams. Limnology and Oceanography 49: 1713–1721.

Starry, O., J. Wazenbock & D. L. Danielopol, 1998. Tendency of the amphipod *Gammarus roeseli* Gervais to colonize coarse sediment habitats under fish predation pressure. International Review of Hydrobiology 83: 371–380.

Thorp, J. H. & A. P. Covich (eds), 2001. Ecology and Classification of North American Freshwater Invertebrates. Academic Press, San Diego.

Vaughn, C. C., D. E. Spooner & H. S. Galbraith, 2007. Context-dependent species identity effects within a functional group of filter-feeding bivalves. Ecology 88: 1654–1662.

Ward, J. V., 1992. Aquatic Insect Ecology. John Wiley & Sons, Inc., New York.

Ward, J. V. & J. A. Stanford, 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. Regulated Rivers: Research & Management 11: 105–119.

Wellnitz, T. & N. L. Poff, 2006. Herbivory, current velocity and algal regrowth: how does periphyton grow when the grazers have gone? Freshwater Biology 51: 2114–2123.