

The Effects of Disturbance Time Interval on Algal Biomass in a Small Idaho Stream

Abstract

An experiment was designed to test the potential effect that disturbance frequency may have on benthic algal accumulation in a stream ecosystem. The stream was divided into segments. After measuring algal biomass in each segment, the stream substrate was left undisturbed, or physically disturbed once or twice per month. The highest levels of algal biomass were found in the segments that had the short between-disturbance intervals. Intervals may have been short enough to allow r-selected algal species to re-colonize, flourish and maximize biomass potential. Possible explanations for these results may be an increase in nutrient availability by the removal of senescent or competitor algal cells and the change to a disturbance-resistant community, or a release from invertebrate grazing as disturbance frequency increased.

Introduction

Disturbance is an important factor in structuring terrestrial and aquatic communities (Krohne 2001). In freshwater streams, disturbance in the form of increased flows or scouring events can have direct, negative effects on benthic organisms. With streambed scouring, aquatic macroinvertebrates can be displaced from preferred habitat, swept out of the stream segment, or crushed by moving bedload (Resh et al. 1988).

Although disturbance may be detrimental for some organisms, it can be a positive circumstance for others. For example, long periods between disturbance events may reduce biodiversity, while shorter between-disturbance intervals may increase it (Connell 1978, Sousa 1979). Like trophic cascades, disturbance may indirectly benefit one group because it negatively impacts another (Koetsier 1993). For example, plant communities may benefit from periodically harsh abiotic factors if these factors keep herbivore numbers low. Small streams lend themselves particularly well to the study of disturbance on community structure. Streams have relatively simple trophic structure and clearly defined boundaries, which allow for tightly controlled experimental manipulations (Koetsier and McArthur 2000).

The intent of this study was to examine how a stream's benthic community would organize under periodic disturbance events (substrate scouring) occurring at different time intervals. Specifically,

I was interested in how scouring might alter primary producers, a basal energy source for arid stream ecosystems. To do this, I controlled for the timing and between-disturbance interval of each scouring event.

Methods

Study Site

The study site was located on the south fork (SF) of Thorn Creek. SF Thorn Creek is a perennial, spring-fed, 2nd-ordered stream originating in the southern, forested mountains of the Idaho Batholith Ecoregion (N. 43° 44' 053" latitude, W. 115° 50' 899" longitude; elevation: 1351 msl). Terrestrial vegetation in the drainage basin consists of Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and mountain sagebrush (*Artemisia tridentata*). Chokecherry (*Prunus* spp.), willow (*Salix* spp.), and stinging nettle (*Urtica dioica*) are the dominant riparian plants found along the stream's corridor. Specifically, the study site encompassed a 300-m section of the stream. Within the section, 76% of the substrate had a range in particle diameter between 31–129 mm, while 18% was less than 2.6 mm in diameter. The average wetted channel width during the time of the study was 2.6 m (1 SD = 0.4; n = 20) with an average thalweg current velocity of 2.6 m/s (1 SD = 0.1; n = 20). Though contained within the Boise National Forest, the catchment of SF Thorn Creek is relatively free of human impact (e.g., logging, mining, grazing).

¹E-mail: pkoet@boisestate.edu

Sampling Design

I randomly selected three study segments on SF Thorn Creek in which to conduct the disturbance experiment. Each segment was 60 m long and was separated from the others by a minimum of 40 m. I chose a 40-m interval (or farther) between segments because I anticipated that macroinvertebrates, disturbed by my manipulations, may drift and settle out in the downstream segments. In most streams, macroinvertebrates tend to drift, during a single period, 5-20 m (Elliott 1971, Townsend and Hildrew 1976, Allan 1995). Therefore, I used a 40-m distance to prevent increased herbivory due to upstream manipulations.

Each segment was sub-divided into three, 20-m experimental zones. In the upstream-most zone, the stream's substrate was left undisturbed (0x). The middle zone was the moderately disturbed treatment (1x), in which the benthic substrate was disturbed once each month. The downstream-most zone was the frequently disturbed zone (2x) in which I disturbed the substrate twice each month (Figure 1). My experiment began on June 4, 2003

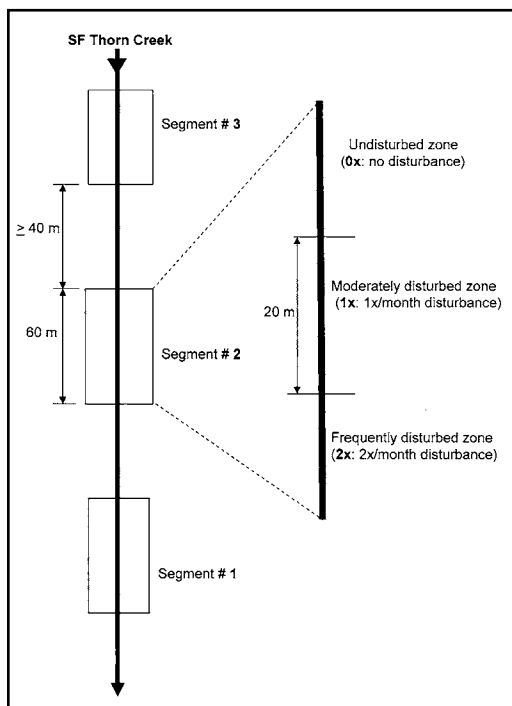


Figure 1. Schematic drawing of the experimental design showing the relative size and position of the stream segments, and the treatment zones within each segment.

and concluded on August 22, 2003. I chose this time period because abiotic disturbances (i.e., flooding, scouring) usually don't occur in SF Thorn Creek during the summer. Subsequently, the only disturbances my sections encountered were ones that I artificially produced. Twice each month, for three months, I collected algal samples, measured water chemistry and stream discharge, and disturbed experimental sections as scheduled.

Each period, before the disturbance of treatment zones, I sampled benthic algal biomass and measured some of the stream's physical variables. First, I measured algal biomass by taking slurry samples from six cobbles in each section. To collect the slurry sample, I used a small plastic tube (4 cm long; 2 cm diameter) fitted with a neoprene gasket at one end, which provided a water-tight seal when placed on the cobble. Filling the tube with 5 ml of water, I used a small brush to gently scrub the area of the stone enclosed by the tube. The resulting slurry was drawn out with a syringe (for a detailed description, see Robinson and Rushforth 1987). These samples were placed on ice for transport to the laboratory. In the laboratory, algal biomass was estimated by measuring the absorbance of Chlorophyll-a from the slurry samples. Following the methods of Holm-Hansen (1978) and Hansson (1988), each sample was vacuum filtered through a Whatman GF/F glass filter (pore size: 0.45 μm). Chlorophyll-a was extracted by immersing the filters in 10 ml of absolute methanol and then refrigerating the sample at 4°C for 3 hr. After centrifuging, chlorophyll-a concentrations were measured with a spectrophotometer; these values were corrected for phaeophytin.

Second, I recorded water chemistry parameters (water temperature, dissolved oxygen, specific conductance: Figure 2) *in situ*, and measured stream discharge downstream of Segment 1. Discharge was estimated by dividing the cross-section of the stream's channel into 20 cells. In each cell, a single flow measurement was made at 6/10 depth below the water's surface. Discharge was calculated by summing the volume of water flowing through the area of each individual cell per unit time (Gordon et al. 2004).

After benthic algal samples and physical measurements were taken, I manually disturbed the 1x- or 2x- treatment zones. In each zone (according to the treatment protocol), material on the streambed (cobbles, pebbles, sand, and silt)

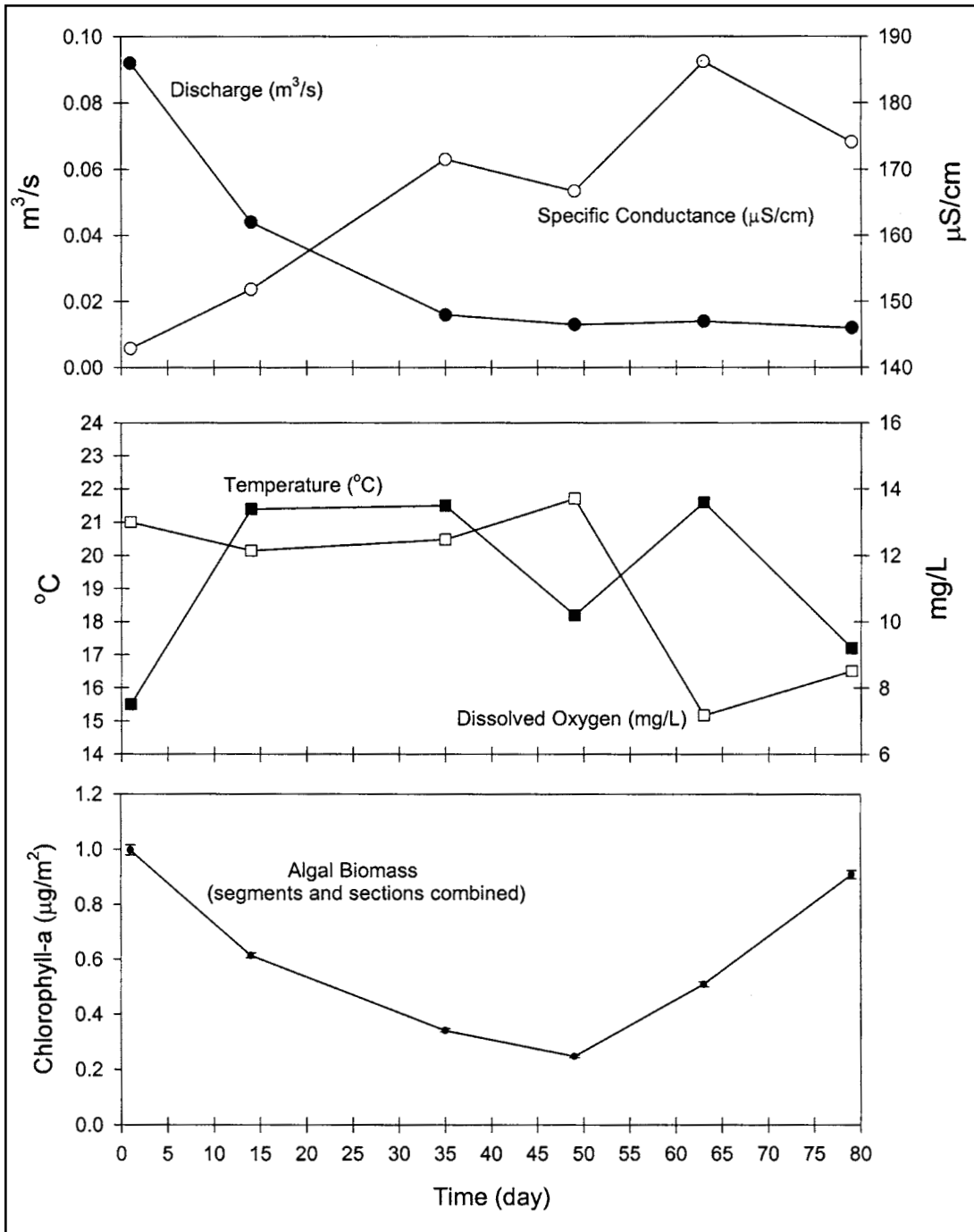


Figure 2. Water chemistry, stream discharge, and mean algal biomass (± 1 SE, $n = 54$) of SF Thorn Creek measured from June 4 (Day 0) to August 22 (Day 79), 2003.

was rigorously moved, rolled, and scrubbed using iron rakes, pry bars, and brooms. Each treatment zone was disturbed for a minimum of 15 minutes before moving upstream to the next. Following the protocol, 1x zones were disturbed three times and 2x zones disturbed six times, throughout the duration of the study.

The experiment was designed such that Spearman rank correlations and three-way analyses of variance (ANOVA) were used for data analysis. In all of the analyses, the dependent variable was algal biomass (as measured by Chlorophyll-a). Independent factors were time (days from the start of the experiment), segments (1: downstream; 2: middle; 3: upstream), and treatments (0x, 1x, 2x; each with six replicates per treatment).

Results

Algal biomass varied through time over the course of this study ($F_{5,270} = 15.89$; $P < 0.01$; Table 1), and was negatively correlated with both water temperature ($r^2 = 0.51$) and the stream's specific conductance ($r^2 = 0.63$) (Figure 2). Chlorophyll-a measurements were highest prior to the start of the experiment (Day 0: mean = $0.997 \mu\text{g}/\text{cm}^2$), dropped to their lowest value on Day 49 (mean = $0.247 \mu\text{g}/\text{cm}^2$), then increased throughout the remainder of the study, ending with a mean of $0.908 \mu\text{g}/\text{cm}^2$ on Day 79 (August 22, 2003). Algal biomass did not differ between segments ($P = 0.08$), but was significantly affected by disturbance frequency ($F_{2,270} = 3.47$; $P = 0.03$). Unexpectedly, Chlorophyll-a was lowest in the undisturbed (0x), but highest in the frequently disturbed (2x) zones (Figure 3a). When mean algal biomass was examined at the

different disturbance levels within each segment ($F_{4,270} = 2.97$; $P = 0.02$), I found that in both Segments 1 and 2 the same general pattern of lowest values in the 0x and highest values in 2x were evident. However, in Segment 3 (upstream-most segment), the biomass pattern was reversed (Figure 3b). Though light levels were not measured in any of the sections, Segment 3 was perpetually in the shade of several large ponderosa pines located in the riparian corridor.

Discussion

In this study, I was surprised to find that algal biomass was negatively related to the time interval between substrate disturbance events. Resh et al. (1988) suggested that in most situations, streams that are more frequently disturbed should show lower algal standing crop than less frequently disturbed streams. Other studies show that with an increase in flooding/scouring events, comes a decrease in algal biomass (Biggs et al. 1999a, 1999b, Zimmermann and Death 2002). Intuitively, in highly disturbed streams' algal biomass would be low due to the actual scouring of the substrate and, once bedload material was overturned, the lack of sunlight for algal photosynthesis. However, this was not the case in the present study. In my experiments, algal biomass accumulation was positively related to the frequency of disturbance. This result contradicts those reported by Robinson and Rushforth (1987), one of the few published stream studies that altered algal biomass by experimentally manipulating disturbance frequency. In their experiments, algal biomass increased when benthic substrate was disturbed every 3-9 d, but remain constant when the substrate disturbance interval was longer than 9 d (regardless of riparian canopy cover). Conversely, in nine New Zealand streams that underwent 46 distinct spate events over a 13-month period, Biggs and Close (1989) found increases in Chlorophyll-a (algal biomass) only 39% of the time.

Two alternative hypotheses can be advanced to explain my findings. First, disturbance may facilitate the sloughing off of dead and dying algal cells, and favor a more disturbance-resistant algal assemblage. Some studies found that, after scouring events, growth rates of benthic algae are negatively related to the algal biomass prior to the event (see Peterson 1996 for a review). The mechanism behind this may involve renewed access

TABLE 1. Results of the 3-way analysis of variance for time, stream segment, and disturbance interval (0x, 1x, or 2x per month) on benthic algal biomass in the south fork of Thorn Creek during the summer.

Source	df	MS	F-ratio	P
Time	5	4.89	15.89	0.00
Segment	2	0.77	2.49	0.08
Disturb. Interval	2	1.07	3.47	0.03
Time x Segment	10	0.67	2.16	0.02
Time x Disturb.	10	0.47	1.53	0.13
Segment x Disturb.	4	0.91	2.97	0.02
Time x Segment x Disturb.	20	0.45	1.46	0.09
Error	270	0.31		

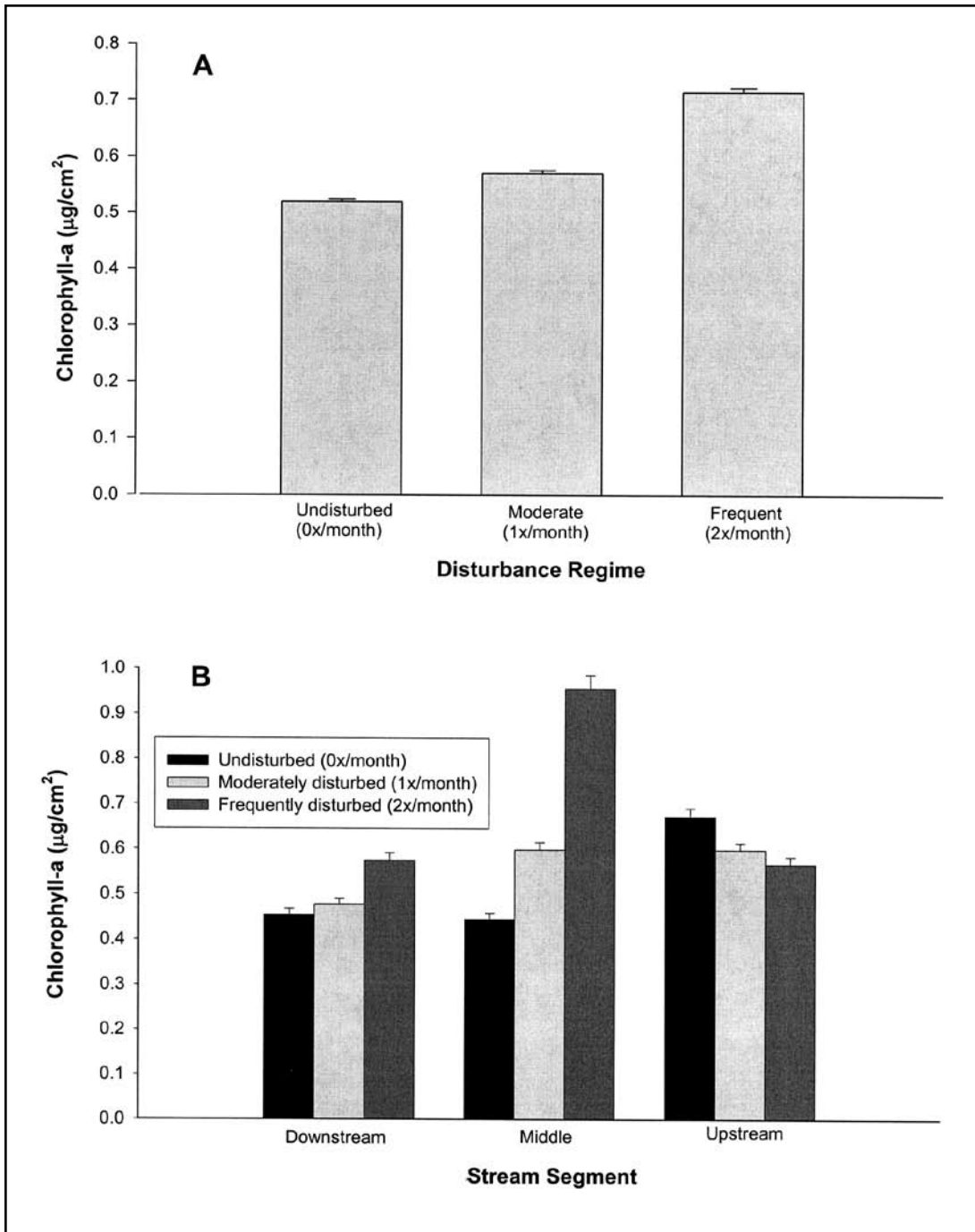


Figure 3. Mean algal biomass (+ 1 SE) in: (A) different disturbance regimes ($n = 108$) and, (B) the treatment zones within each stream segment ($n = 15$) of SF Thorn Creek during the summer experiment.

to resources by active algal cells. The removal of senescent cells allows more metabolically active cells access to space, sunlight, and nutrients. This would allow for an overall increase in algal biomass. Biggs (1996) noted that decay and loss of algal cells occurred in moderately fast current velocities. He reasoned that because dying cells could not maintain adequate contact with the substrate, they drifted away in the current. Once gone, space on the substrate opened up for more metabolically active cells or disturbance-resistant taxa. In addition, a frequently disturbed environment would favor tightly adherent, adnate algal forms. After a scour event, these species would remain and rapidly colonize the empty substrate without competitors. As disturbance frequency increases, the algal community would be composed solely of these resistant diatoms (Peterson 1996).

A second hypothesis is that disturbance may indirectly increase algal biomass by decreasing grazing invertebrates. Research conducted in streams indicates that macroinvertebrate diversity and biomass is negatively related to disturbance frequency (Death and Winterbourn 1995, McCabe and Gotelli 2000). In these studies, invertebrate diversity decreased (and with it, a drop in herbivore numbers) as the interval between disturbance events grew shorter. Further, in enclosures with predators, grazing insects decreased while algal biomass increased (Koetsier 1989, 2005). Benthic stream algae, having faster turnover rates than invertebrates (Minshall 1978), may not be as adversely affected by my disturbance regime as were the macroinvertebrate herbivores. Consequently, algal biomass, released from grazing pressure, would increase.

Although most previous work on algal responses to disturbance deals with species richness and diversity, biomass accumulations may be more important from a management viewpoint,

especially in eutrophic systems (Lowe and Pan 1996). The results presented here fit within the framework of disturbance theory. By periodically disturbing the streambed, tightly-adhered, r-selected algae (lacking competitors or grazers) may be able to quickly re-colonize the substrate and flourish. A harsh environment, one with 'perpetual' disturbance (i.e., waves crashing on shore), may minimize algal biomass potential. However, an environment with periodic disturbance (i.e., storm events) could result in greater-than-expected algal biomass accumulations.

Whether disturbance affects benthic algae directly (opening up space) or indirectly (via the invertebrate assemblage), more study is needed to distinguish between the two hypotheses.

Whichever hypothesis accepted, it is clear that disturbance plays a defining role in small stream structure and function. Localized, small-scale disturbances, may affect biotic patterns within a stream segment. If these effects are additive, disturbance may alter algal biomass and productivity thus, dictate secondary production and the number of trophic levels throughout the stream's food web (Fretwell 1977, Oskanen et al. 1981). Biotic patterns that are evident in lotic ecosystems may ultimately be traced back to small-scale disturbances.

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Literature Cited

- Allan, J.D. 1995. Stream ecology: structure and function of running waters. Chapman & Hall Publishing, New York. 388pp.
- Biggs, B. J. 1996. Patterns in benthic algae of streams. Pages 31-56 *In* R.J. Stevenson, M.L. Bothwell, and R.L. Lowe (editors), Algal ecology: freshwater benthic ecosystems. Academic Press, San Diego, Calif.
- Biggs, B. J., and M. E. Close. 1989. Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology* 22:209-231.
- Biggs, B. J., R. A. Smith, and M. J. Duncan. 1999a. Velocity and sediment disturbance of periphyton in headwater streams: biomass and metabolism. *Journal of the North American Benthological Society* 18:222-241.
- Biggs, B. J., N. C. Tuchman, R. L. Lowe, and R. J. Stevenson. 1999b. Resource stress alters hydrological disturbance effects in a stream periphyton community. *Oikos* 85:95-108.
- Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460-490 *In* M.L. Cody and J. Diamond (editors), *Ecology and evolution of*

- communities. Belknap of Harvard University Press, Cambridge, Mass.
- Death, R. G., and M. J. Winterbourn. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology* 76:1446-1460.
- Elliott, J.M. 1971. The distance traveled by drifting invertebrates in a Lake District stream. *Oecologia* 6:191-220.
- Fretwell, S. D. 1977. The regulation of plant communities by food chains exploiting them. *Perspectives in biology and medicine* 20:169-185.
- Gordon, N.D., T.A. McMahon, B.L. Finlayson, C.J. Gippel, and R.J. Nathan. 2004. *Stream hydrology: an introduction for ecologists* (2nd ed.), Wiley and Sons Ltd, West Sussex, England.
- Hansson, L. A. 1988. Chlorophyll-a determination of periphyton on sediments: identification of problems and recommendation of methods. *Freshwater Biology* 20:347-352.
- Holm-Hanson, O. 1978. Chlorophyll-a determination: improvements in methodology. *Oikos* 30:438-447.
- Koetsier, P. 1989. The effects of fish predation and algal biomass on insect community structure in an Idaho stream. *Journal of Freshwater Ecology* 5:187-196.
- Koetsier, P. 1993. Direct and indirect effects of predator type on the structure and function of a lotic benthic community. Unpubl. Ph.D. dissertation, Dept. of Biol. Sci., Idaho State University, Pocatello, Idaho.
- Koetsier, P. 2005. Response of a stream diatom community to top predator manipulations. *Aquatic Sciences* 67:517-527.
- Koetsier, P. and J.V. McArthur. 2000. Organic matter retention by macrophyte beds in 2 southeastern USA, low-gradient, headwater streams. *Journal of the North American Benthological Society* 19:633-647
- Krohne, D.T. 2001. *General ecology* (2nd ed.), Brooks/Cole Publ. Co., Pacific Grove, CA.
- Lowe, R.L., and Y. Pan. 1996. Benthic algal communities as biological indicators. Pages 705-740 *In* R.J. Stevenson, M.L. Bothwell, and R.L. Lowe (editors), *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego, Calif.
- McCabe, D. J., and N. J. Gotelli. 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. *Oecologia* 124:270-279.
- Minshall, G. W. 1978. Autotrophy in stream ecosystems. *Bioscience* 28:767-771.
- Oskanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118:240-262.
- Peterson, C. G. 1996. Response of benthic algal communities to natural physical disturbance. Pages 375-402 *In* R.J. Stevenson, M.L. Bothwell, and R.L. Lowe (editors), *Algal ecology: freshwater benthic ecosystems*. Academic Press, San Diego, Calif.
- Resh, V.H., A.V. Brown, A.P. Covich, M.E. Gurtz, H.W. Li, G.W. Minshall, S.R. Reice, A.L. Sheldon, J.B. Wallace, and R. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:433-455.
- Robinson, C. T., and S. R. Rushforth. 1987. Effects of physical disturbance and canopy cover on attached diatom community structure in an Idaho stream. *Hydrobiologia* 154:49-59.
- Sousa, W. P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* 49:227-254.
- Townsend, C.R., and A.G. Hildrew. 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. *Journal of Animal Ecology* 45:759-772.
- Zimmermann, E. M., and R. G. Death. 2002. Effects of substrate stability and canopy cover on stream invertebrate communities. *New Zealand Journal of Marine and Freshwater Research* 36:537-545.

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