Establishing Light as a Causal Mechanism Structuring Stream Communities in Response to Experimental Manipulation of Riparian Buffer Width

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Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width

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Abstract. Previous studies on the effects of logging on streams have suggested that light and water temperature were important variables structuring stream communities but, in many cases, these effects were confounded. We observed pronounced gradients in the flux of solar energy and water temperature in an earlier large-scale experiment in which we manipulated the width of riparian buffers along headwater streams. Associated with these abiotic changes were increases in periphyton biomass and primary consumer abundance. We present results from a study in streamside channels that was designed to isolate the effects of light on stream communities, while holding water temperature constant. Light treatments in the channel experiment simulated inputs of solar radiation created during the prior watershed-scale experiment. Results from the present study suggested that consumers limited periphyton biomass early in the study; however, a rainstorm midway through the experiment reduced periphyton biomass and insect consumer abundance. Following this disturbance, chlorophyll *a* biomass was 2 to 4 times higher in the full sunlight treatment compared to the 2 lowest light treatments. At the end of the study, primary consumer abundance, biomass, survival, and growth rate were positively related to light and periphyton resources. Therefore, we inferred biotic control of periphyton during the early part of the channel study, whereas light appeared to control periphyton at the end of the study. Results from the large-scale and channel experiments suggested that light was the primary constraint on periphyton biomass accrual. Moreover, both experiments, especially the channel study, showed that light indirectly influenced consumer performance as mediated by increased primary production.

Key words: communities, consumers, light, primary producers, riparian buffers, scale, streams, tadpoles.

Human activities, such as logging, can fundamentally alter the supply of limiting resources, such as light, to aquatic systems (Brosofske et al. 1997, Hill et al. 2001, Schindler and Scheuerell 2002), which can affect the structure and function of these systems. It has been proposed that increased solar flux resulting from forest harvest is responsible for increased primary production in streams and rivers, which leads to increased invertebrate and vertebrate production (Murphy 1998). Determining mechanisms driving biological patterns in large-scale observational and experimental studies, however, is limited by the fact that a number of environmental factors change in response to forest harvest. For example, both water temperature and light input can change with removal of riparian trees, and both these factors can profoundly affect stream communities (Hill et al. 1995, Rempel and Carter 1986).

A common management strategy for minimizing impacts of forest harvest on aquatic ecosystems is to leave a buffer strip of uncut vegetation along the waterbody. Brosofske et al. (1997) showed that logging practices that affect the width of riparian reserves along streams also alter the amount of light reaching the stream surface. Although functional relationships have been developed for physical processes such as energy flux and buffer width, how changes in light resulting from riparian management affect community organization re-

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mains untested. Thus, there is a need to develop links between microclimatic parameters that change in response to forest management and process-based research on organisms. We suggest that it is essential to develop these links experimentally, given that leaving a riparian buffer along a waterbody is a primary tool for mitigating the impacts of development on aquatic ecosystems (FEMAT 1993, Castelle et al. 1994).

Furthermore, how different components of the food web respond to light remains unclear. Algal and predator biomass were positively correlated with light, whereas herbivore biomass was not, presumably because of consumption of excess herbivore production by predators (Wootton and Power 1993, but see Nisbet et al. 1997 for an alternative interpretation of these data). Primary production and snail growth rate were significantly higher in small enclosures in unshaded sections of a small Tennessee stream compared to shaded sections (Hill et al. 1995), whereas periphyton biomass was unchanged. It was shown that consumption by snails limited the accrual of algal biomass. In contrast to the previous study, solar flux was correlated with algal biomass in pools of a northern California stream, but the abundance of only 1 of 3 caddisfly species was positively associated with light (Feminella et al. 1989).

What may account for these differences? The empirical studies described above were relatively short term, and ranged in size from small in situ enclosures (Hill et al. 1995) to observational studies along relatively long stream reaches (Feminella et al. 1989). Therefore, temporal scale and size of the study unit may be reasons for these differences (Peckarsky et al. 1997, Weins 2001). If experiments are too short, absence of longer-term processes and indirect effects can magnify the strength of direct interactions (Leibold et al. 1997, Sarnelle 1997). Moreover, size of the experimental or study arena can affect physical conditions or constrain the movement and behavior of organisms (Frost et al. 2001). Therefore, we may gain further insight into the effects of light or other limiting resources on stream communities by experimental and observational studies at multiple scales.

We manipulated riparian buffer width (unlogged controls, 30-m buffer, 10-m buffer, and clearcut) in a replicated large-scale experiment along headwater streams to examine the efficacy of riparian buffers in maintaining stream structure and function. We hypothesized that abiotic and biotic features of streams with wide buffers (30 m) would be more similar to unlogged control streams than streams with no or narrow buffers. To test our hypothesis, we monitored the response of a suite of abiotic and biotic variables for 1 y before and after logging (Kiffney et al. 2003). In brief, that study showed that light level, water temperature, periphyton biomass, and abundance and biomass of 2 insect herbivores, Chironomidae (Diptera) and Baetidae (Ephemeroptera), increased as riparian buffer width narrowed. Both water temperature and light can affect primary and secondary productivity, but our field experiment showed that light was relatively more important than temperature in explaining variation in periphyton biomass (Kiffney et al. 2003). To test whether light limited benthic communities in these forested streams, we isolated the influence of light on periphyton and primary consumers from water temperature by conducting a 2nd experiment in 12 streamside experimental channels. We predicted that periphyton biomass and insect consumer abundance would increase as a function of light level.

Methods

Study site

The research was conducted at University of British Columbia's Malcolm Knapp Research Forest (MKRF) located 45 km east of Vancouver, BC, near Maple Ridge (lat 122°34′W, long 49°16′N) (Fig. 1). The research forest lies in the coastal western hemlock biogeoclimatic zone, and western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Douglas-fir (*Pseudotsuga menziesii*) are the dominant forest tree species (Franklin and Dyrness 1969). The study area has a marine, temperate climate with wet cool winters and dry summers. More than 70% of the total annual precipitation (mean = 2200 mm) falls between October and March (Feller 1977), primarily as rain. Average mean air temperature ranges from a low of 2°C in January to a high of 16°C in July (Kiffney et al. 2002). Additional details of the study site are presented in earlier papers (Kiffney et al. 2000, 2003, Kiffney and Bull 2001, Kiffney and Richardson 2001).

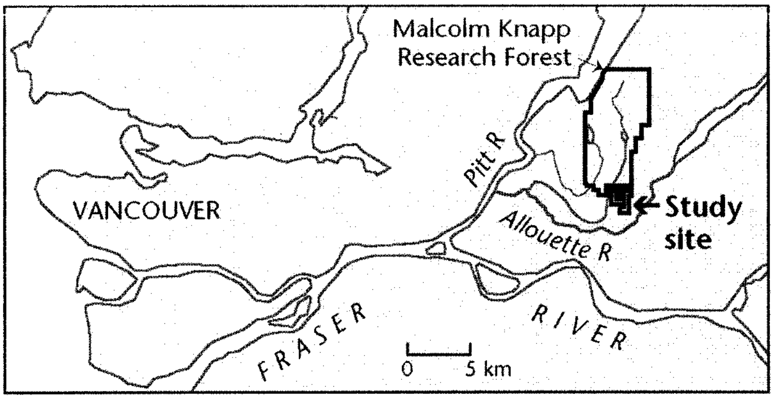

FIG. 1. Location of Malcolm Knapp Research Forest where riparian buffer and channel experiments were conducted.

Our research focused on the response of stream biota that relies mostly on periphyton as a food resource. Periphyton-based food webs in perennial streams of the research forest consist of a primary consumer guild (defined as organisms that feed primarily on periphyton as scrapers or collector-gatherers) that includes tailed frog larvae (*Ascaphus truei*) and insects (Chironomidae, Ephemeroptera, and Trichoptera), and invertebrate (Plecoptera, Odonata, Megaloptera, and Trichoptera) and vertebrate predators (cutthroat trout, *Oncorhynchus clarki clarki*) that eat these consumers. Similar food webs are found in streams that dry for a few months during summer, except they lack fish.

Experimental channels

The experiment was conducted in 12 artificial stream channels (each 15 m long × 0.25 m wide × 0.10 m deep) located on an unshaded floodplain adjacent to Mayfly Creek from 1 September 1999 to 12 October 1999. Mayfly Creek is a permanent stream located within the research forest and ~5 km north of the watersheds that were part of the riparian, buffer-width experiment. Temperature, hydrologic regimes, and surface water nutrient chemistry were similar between experimental channels and the experimental watersheds because of their close proximity (Richardson 1991, Kiffney and Richardson 2001). Moreover, riparian and upland forests in the Mayfly Creek watershed were of similar composition and age to the experimental watersheds.

Channels were constructed from cinder blocks that were placed on top of a plywood frame and lined with impermeable plastic. The plastic sheet was covered by natural substrata (sand, gravel, pebble, cobble, and organic detritus). Water, algae, organic matter and insects were funneled from an intake pipe in Mayfly Creek ~100 m upstream of the channels. These materials were passed through two settling boxes and a final headbox before entering channels via plastic pipes, with gang valves controlling water flow. Habitat within channels was an alternating sequence of runs and riffles. Average slope of the channels was 3%, and water flow was ~1.0 L/s during the study and did not differ among treatments (ANOVA, $p > 0.05$).

Shade cloth of different thickness was draped over channels to create 4 light regimes, except for the ambient light treatment, which was exposed to full sunlight. Treatments included the following: low (2.2% ambient photosynthetically active radiation [PAR]: ~11 μmol m^{-2} s^{-1}); medium (10% ambient PAR: ~53 μmol m^{-2} s^{-1}); high (22% ambient PAR: ~106 μmol m^{-2} s^{-1}); and full sunlight (100% ambient PAR: ~506 μmol m^{-2} s^{-1}). These treatments corresponded to light levels measured in riparian buffer treatments in the following manner: low = unlogged controls, medium = 30-m buffer width, high = 10-m buffer width, and full sunlight = clearcut treatment. Thus, the experiment consisted of a completely randomized, 1-way design in which light was experimentally varied at 4 light levels, each replicated 3 times.

Food webs in channels were similar to those in natural streams, with the dominant insects on tiles consisting of Chironomidae and Baetidae. Fish (cutthroat trout) were excluded from channels for the following reasons: 1) we wanted to test the response of relatively simple food webs to light without the confounding effect of top-down processes; and 2) we did not have enough experimental units to replicate this factorial design.

Channels were colonized for ~40 d by drifting algae, detritus, and insects that entered the channel water supply from Mayfly Creek. Shade cloth was draped over the channels on day 30 of this colonization period. Immigration of tadpoles into channels was restricted by a net (250 μm) placed over pipes that entered each channel from the headbox. Material captured in these nets was placed in the appropriate channel, whereas tadpoles were returned to Mayfly Creek. Forty-eight tadpoles, all within a similar age class (age 1) were collected from Mayfly Creek and added to each channel at a density of 1.3/m^2 (4 per channel). This density is within the range found in streams of western Washington (0.58–4.4/m^2: Hawkins et al. 1988, Lamberti et al. 1992) and southwestern British Columbia (0.1–1.7/m^2: Rosenfeld 1997, JSR, unpublished data).

Tadpoles were not censused to determine densities in streams of the research forest because of logistical constraints. *Ascaphus* tadpoles were included as part of our food web, however, because they are common to streams in the research forest as well as headwater streams throughout the Pacific Northwest; are a US federal species of concern and a species of concern in British Columbia (Richardson and Neill 1999), Washington, Oregon, and California (http://www.pacificbio.org/ESIN/ReptilesAmphibians/TailedFrog/TailedFrogpg.html); and are thought to be sensitive to forest management (Dupuis and Steventon 1999). Tadpoles were wet weighed to the nearest 0.01 mg at the beginning and end of the study, and were measured (snout–vent length) to the nearest 1 mm (mean length = 14.3 cm, mean wet mass = 0.80 g). There were no initial differences among treatments in tadpole size, periphyton biomass, or insect abundance on tiles (ANOVA, $p > 0.1$). Day 0 of the experiment represented the day tadpoles were added to channels.

Sampling protocol

Discharge was measured at the downstream end of each channel weekly using a bucket and stopwatch. Water temperature was measured once to twice weekly between 1000 and 1400 h at the downstream end of each channel using a hand-held thermometer. This approach was adequate for characterizing the temperature regime among treatments for a number of reasons. First, channels received water from the same stream via a headbox; therefore, water temperature entering each channel was the same. Second, water traveled through channels at a relatively fast rate (~30–40 cm/s, 1.0 L/s) and channels were short (15 m long), limiting any warming by the sun in open or lightly shaded channels or cooling in heavily shaded channels. Water samples for nutrient analysis also were collected at the end of each channel on days 0 and 15. Water samples were analyzed for dissolved NO_3+NO_2-N (Armstrong et al. 1967) and soluble reactive P (SRP) (Murphy and Riley 1962) with detection limits of 0.5 and 1.0 μg/L, respectively. Light, as instantaneous PAR, was measured 3 times during the study at the water surface of each channel using a light meter and quantum sensor between 1000 and 1400 hours at 6 to 9 randomly selected locations.

Unglazed ceramic tiles (n = 13 per channel, upper surface area = 25 cm^2) were used to count insect consumers and to measure periphyton biomass. Methods used to sample tiles for periphyton biomass and insect consumers were the same as in the riparian buffer experiment (Kiffney et al. 2003). Tiles were sampled for periphyton and insect consumers 6 times (days 10, 17, 24, 30, 38, and 43) during the channel experiment. Ephemeroptera (primarily Baetidae) were counted before removing tiles from the water, tiles were slowly removed from the water, and remaining consumers were identified, counted, and total body length was measured (±0.5 mm). Chironomids (primarily Orthocladiinae) and ephemeropterans were identified to family (Merritt and Cummins 1996). Tiles were then processed for periphyton biomass (see below). Published length–mass equations based on total body length for Baetidae and Orthocladiinae were used to determine insect biomass on tiles (Benke et al. 1999).

One tile per channel (n = 3 per treatment) was randomly collected for periphyton biomass

TABLE 1. Mean (±1 SE) instantaneous irradiance, dissolved $NO_3 + NO_2 - N$, $PO_4 - P$, water temperature, and discharge in each light treatment ($n = 3$ per treatment) during the 43-d experiment. PAR = photosynthetically active radiation.

Treatment ambient PAR (%)	Irradiance (μmol m^{-2} s^{-1})	$NO_3 + NO_2 - N$ (μg/L)	$PO_4 - P$ (μg/L)	Temperature (°C)	Discharge (L/S)
2.2	11 (1.2)	44 (5)	12 (1)	11 (0.01)	1 (0.1)
10	53 (7)	40 (7)	12 (1)	11 (0.01)	1 (0.1)
22	106 (11)	44 (5)	12 (0.3)	11 (0.01)	1 (0.1)
100	506 (10)	48 (1)	12 (1)	11 (0.01)	1 (0.04)

for each sampling date, except for the last, when 3 tiles were randomly selected from each channel. Periphyton was scraped from the upper surface of tiles and rinsed into a small collecting bucket. The sample was diluted to a volume of 50 mL; 2 subsamples of ~25 mL were withdrawn from each suspension to determine ash-free dry mass (AFDM) and chlorophyll *a*. Subsamples for AFDM were filtered onto precombusted and preweighed glass fiber filters (Gelman Type A/E), dried at 70°C for 24 h, and weighed after cooling. The filters were then ashed for 2 h at 550°C and weighed after cooling. Chlorophyll *a* subsamples (25 mL) were filtered and extracted with 25 mL of 90% acetone (OmniSolv, EM SCIENCE) for 24 h, and analyzed using a fluorometer (Model 10–005R, Turner Designs, Mt. View, California).

Statistical analysis

Periphyton biomass and insect counts were repeatedly measured from the same experimental unit (stream channel, $n = 12$), so a mixed model repeated-measures ANOVA was used to determine treatment ($n = 4$ with 3 replicates or channels per treatment) effects on response measures. In this model, stream channel was the random factor and time was the fixed factor. A mixed model was used because it has several covariance structures (e.g., autoregressive [order 1], compound symmetry) that allows for valid estimation of the covariance structure, which is not possible with general linear models. In addition, subjects with missing data are completely discarded in multivariate methods of repeated measures resulting in low power (Littell et al. 1996); some chlorophyll *a* and periphyton AFDM samples were missing in our experiment because of processing error. Littell et al. (1996) provide a thorough description of mixed models. This analysis tested the effects of light (4 levels) and sampling date (6 dates), and whether the effects of light varied with time for each response measured (periphyton AFDM, chlorophyll *a,* and chironomid and baetid abundance). ANOVA also was used for the last day of the experiment (day 43) to test the overall treatment effect on tadpole relative growth rate and survival, Chironomidae and Baetidae abundance and biomass, and periphyton biomass. Correlation analysis was used to examine the relationship between periphyton biomass, insect consumer abundance and biomass, and tadpole relative growth rate, survival, and density.

Some tadpoles were dead or were not recovered on day 43 of the experiment (mean survival ranged from 41–100% per treatment). Only live animals were used to calculate relative growth rate. No animals were collected from one of the low light (2.2% PAR) channels, so no growth rate could be determined for this channel. Data were $\ln(x+1)$ transformed in some cases to eliminate correlation between means and variances.

Results

Only light was influenced by our treatment; all other abiotic factors were consistent across treatments (Table 1). High stream flows likely occurred on days 23 and 36 through 38 as a result of rainstorms. Discharge at East Creek, a nearby stream where flow is measured continuously, was ~4× greater on day 23 and 15× greater on day 38 compared to baseflow (1.5 L/s). Flow also likely increased in the experimental channels but not to the same magnitude; measurements were not taken during these events.

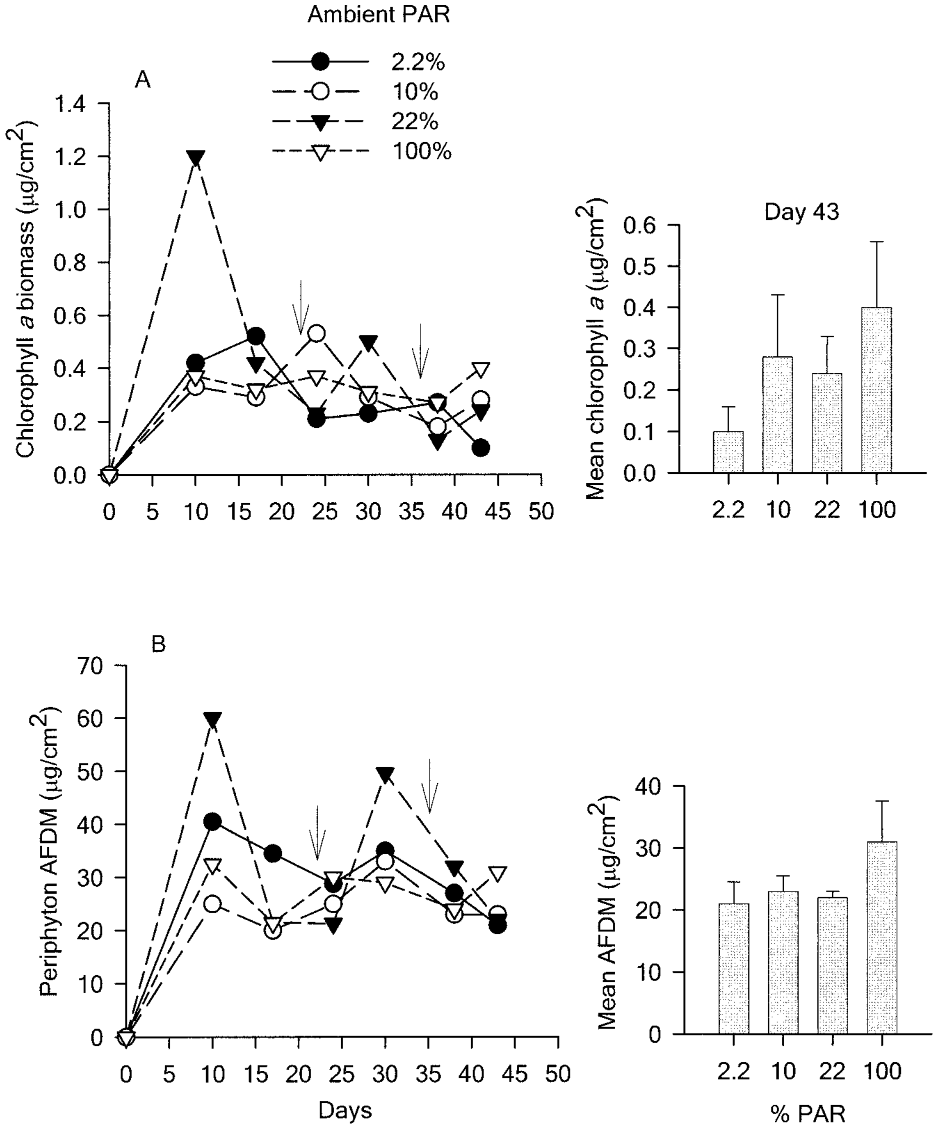

FIG. 2. Mean periphyton chlorophyll *a* (A) and ash-free dry mass (AFDM) (B) in the 4 different light treatments. SD bars were omitted because of high variance and complex temporal patterns. Arrows designate approximate timing of high-discharge events. Bar graphs represent mean (+1 SD) periphyton chlorophyll *a* and AFDM on day 43 in each treatment (n = 3 replicates/treatment).

The influence of light on periphyton was not as marked as in the riparian experiment, and was potentially modified by disturbance and consumption by stream herbivores. Based on the repeated measures ANOVA, there were marginally significant treatment effects on chlorophyll *a* ($F_{3,8}$ = 3.6, p = 0.06, Fig. 2A) and periphyton AFDM ($F_{3,8}$ = 3.9, p = 0.05, Fig. 2B), and both periphyton measures varied significantly over time (chlorophyll *a*: $F_{4,29}$ = 6.7, p = 0.005; AFDM: $F_{5,39}$ = 7.0, $p < 0.0001$). Interpretation of main effects, however, was problematic because significant treatment × day interactions were observed for both chlorophyll *a* ($F_{12,29}$ = 6.7, $p < 0.0001$) and periphyton AFDM ($F_{15,39}$ = 2.5, p = 0.001).

Treatment effects on periphyton biomass differed by day, accounting for the significant interaction terms. On day 10, chlorophyll *a* was about ~3-fold greater in the 22% PAR treatment compared to other treatments, whereas chlorophyll *a* on day 43 was 4× higher in the 100% PAR or full sunlight treatment compared to the lowest light treatment. Periphyton AFDM was 60% higher in the 2.2% PAR treatment on day 17 compared to the other light treatments. This decline in periphyton AFDM with increasing light level may be partially explained by the marginally significant negative correlation between Chironomidae biomass and periphyton AFDM on day 17 ($r = -0.55$, $p = 0.07$). In contrast, periphyton chlorophyll *a* and ADFM on day 43 were 4× and 1.5× higher in the 100% PAR treatment compared to the lowest light treatment (Fig. 2A, B inserts).

The light gradient produced a significant effect on chironomids ($F_{3,8} = 15.5$, $p < 0.001$, Fig. 3A), even though abundance was variable over the experiment ($F_{5,40} = 18.3$, $p < 0.0001$). On day 17, chironomid abundance increased as a function of light and was ~3.8× higher in the 22% PAR treatment and 4.6× higher in the 100% PAR treatment compared to the lowest light treatment. On day 43, chironomid abundance (Fig. 4A) and biomass (Fig. 4B) increased as light levels increased and reached a threshold at 22% PAR: chironomid abundance was 11× greater in the 2 highest light treatments compared to the lowest light treatment. Baetid abundance showed no relationship with light (Figs 3B and 4C), but biomass in the 100% PAR treatment on day 43 was ~13× higher than the 10% PAR treatment and 4× higher than the 2.2% PAR treatment (Fig. 4D, $p = 0.04$). The storm event on day 36 reduced insect consumer abundance on tiles to practically 0, thereby contributing to the significant time effect for both baetids and chironomids (Fig. 3A, B).

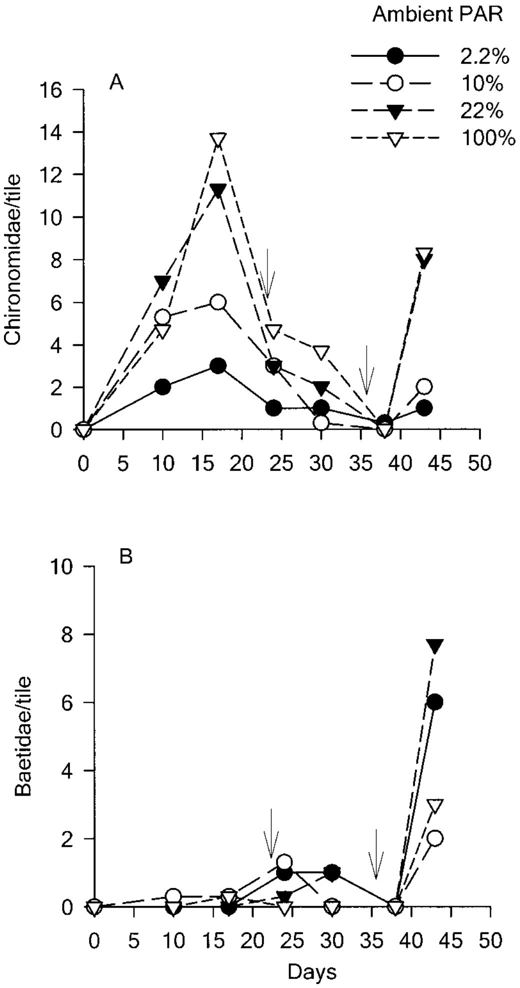

FIG. 3. Mean Chironomidae (A) and Baetidae (B) abundance per tile in the 4 different light treatments. SD bars were omitted because of high variance and complex temporal patterns. Arrows designate approximate timing of high-discharge events.

Variation in light level had strong effects on tadpole growth and survival. Tadpoles lost mass in the 2 lowest light treatments, whereas relative growth rate was 7× greater in the 100% PAR treatment compared to the 22% PAR treatment (Fig. 5A). The proportion of tadpoles surviving was ~40% in the low light treatment compared to 100% in full sunlight, although there were no statistical differences among treatments because of high variability (Fig. 5B). Light level, however, was strongly related to the proportion of tadpoles surviving at the end of the study ($R^2 = 0.96$, $p = 0.02$, $n = 4$, proportion tadpoles surviving = 0.34 + log[0.15] × [% PAR]).

Correlation analysis of data collected on day 43 suggested that consumers were indirectly limited by light mediated by food resources. Baetid biomass and tadpole growth and survival were positively related to chlorophyll *a* biomass (Fig. 6A–C).

Discussion

Results from the large-scale riparian buffer manipulations suggested a tight coupling be-

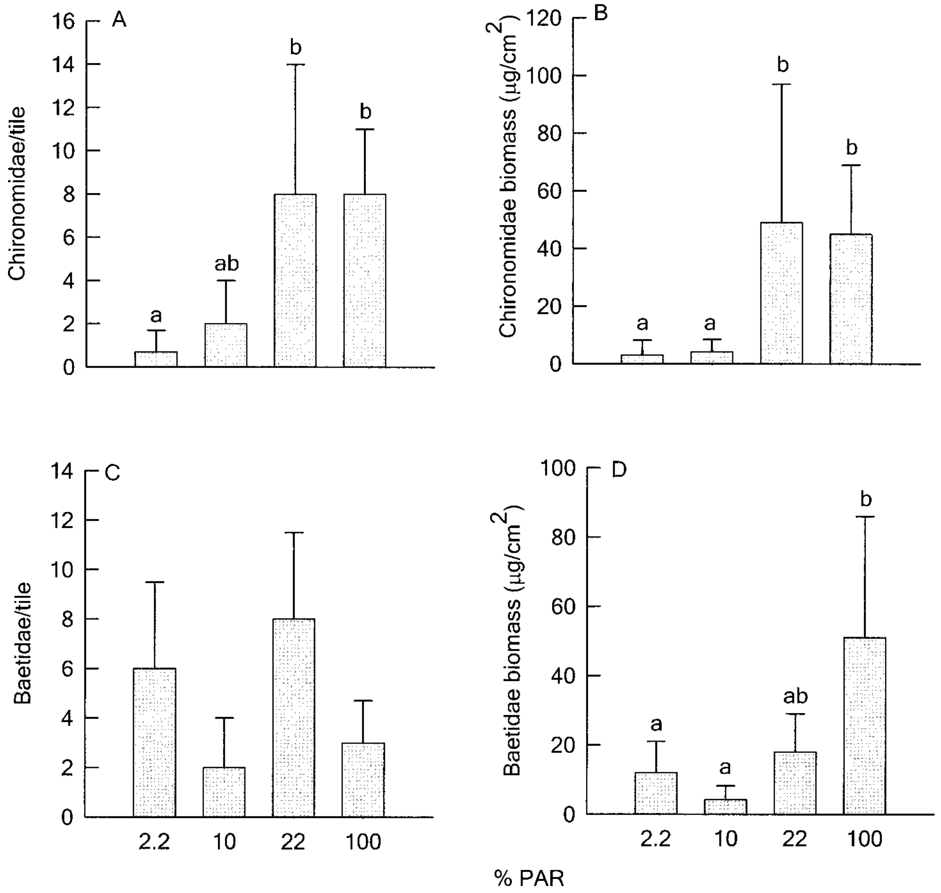

FIG. 4. Mean (+1 SD) Chironomidae abundance (A), Chironomidae biomass (B), Baetidae abundance (C), and Baetidae biomass (D) in the 4 different light treatments on day 43. Means with the same letter were not significantly different at $p < 0.05$ based on the least-square means procedure.

tween limiting resources, primary producers, and consumers (Kiffney et al. 2003). However, both light and water temperature changed in response to logging; therefore, interpreting causal links for biological patterns was problematic. We conducted a 2nd experiment in small stream channels to address this issue. The response of primary producers in the small-scale channel experiment was complex and suggested that resources (light) and consumers (insects and tadpoles) constrained periphyton biomass. Effects of light on consumers in the channels were marked and similar to what we observed in the field. We hypothesize that light indirectly affected primary consumers by increasing primary production. We suggest these effects were independent of water temperature, which was held constant. Results from both experiments provide strong evidence that biotic communities in these headwater streams responded to a gradient of riparian buffer width mediated by changes in light regime. Ideally, we would manipulate light, temperature, and herbivore density or identity in a factorial design to determine factors important in structuring these headwater stream food webs.

Periphyton response

The large-scale, long-term field experiment showed that periphyton chlorophyll *a* and AFDM were positively associated with light (Kiffney et al. 2003). Photosynthesis responds quantitatively to changes in light, so variation in light quantity and quality accounts for much of the variation in population growth and com-

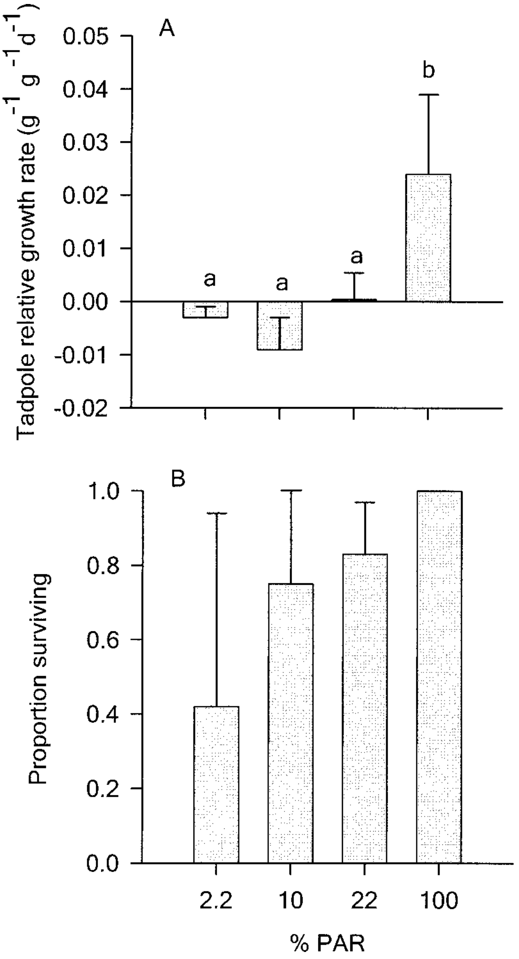

FIG. 5. Mean (+1 SD) tadpole relative growth rate (A) and proportion surviving to the end of the experiment (B) in the 4 different light treatments on day 43. Means with the same letter were not significantly different at $p < 0.05$ based on the least-square means procedure.

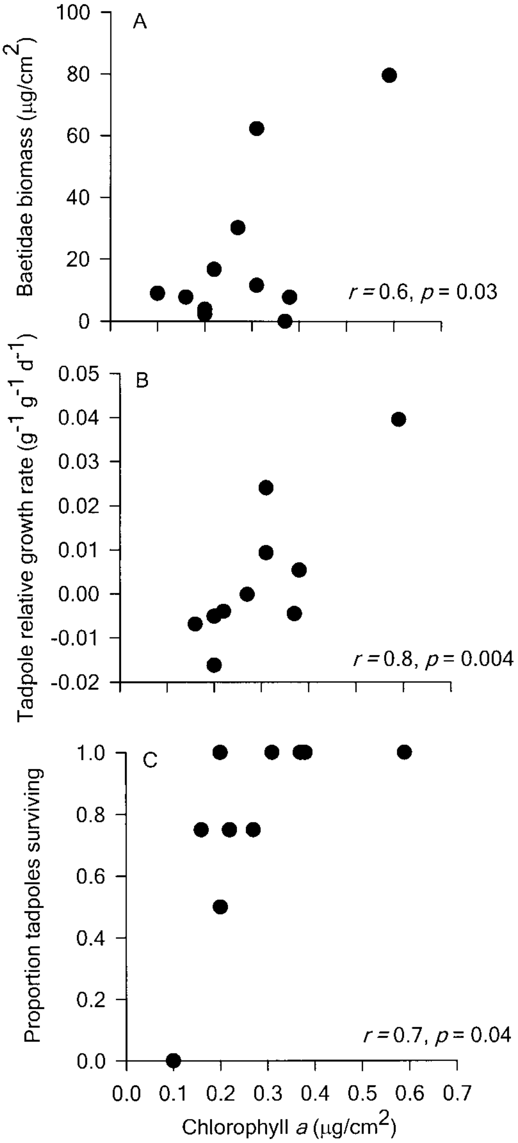

FIG. 6. Scatterplots and Pearson's correlation coefficients (r) showing patterns in chlorophyll *a* biomass vs Baetidae biomass (A), tadpole relative growth rate (B), and proportion of tadpoles surviving (C).

munity structure of benthic algae (Hill 1996). Similar relationships between canopy cover and periphyton biomass have been observed in other small, shaded streams (Feminella et al. 1989, Grether et al. 2001). Hill et al. (1995), however, observed no change in periphyton biomass in small stream enclosures, whereas primary production was positively associated with light in a small Tennessee stream. Hill et al. (1995) hypothesized that consumers limited accrual of periphyton biomass.

The periphyton community in our small-scale, channel study also responded to a light gradient that simulated light levels in natural streams, but there was some evidence of consumer control. On day 17, periphyton biomass was lowest in the high light treatment, which also had the highest densities of chironomids. This result suggests that consumers limited periphyton biomass. Support for this hypothesis is provided by the marginally significant, negative correlation between chironomid biomass and periphyton AFDM on day 17. Consumer control of periphyton, however, was not apparent at the end of the study, because periphyton AFDM and chlorophyll *a* biomass were significantly higher in the treatment receiving the most light compared to other treatments.

One reason for this apparent shift in the relative importance of abiotic vs biotic constraint of periphyton biomass may be flow disturbance (Power et al. 1988, Grimm and Fisher 1989). Flow disturbance is one of the most important drivers of community patterns in lotic ecosystems (Holomuzki and Biggs 2000), and it is thought that the importance of biotic interactions increases during periods of flow stability (Power et al. 1985). Early in our study, flows were constant and consumer abundance increased as a function of light, and reached a density where it potentially limited periphyton biomass. The large rain event on day 36 led to increased flows in the channels, resulting in an almost complete removal of insect consumers. This event temporarily relaxed grazing pressure on primary producers, allowing plant biomass to increase in response to light. Another possibility is that the productive capacity of the periphyton mat at the end of the study was greater than the consumptive capacity of the herbivore population, accounting for the high autotrophic biomass on day 43 (Lamberti et al. 1989).

An alternative explanation for the low periphyton biomass levels in the high light environment was photoinhibition of primary producers (Boston and Hill 1991). Hill et al. (1995) found that C uptake by periphyton communities from shaded sites was inhibited at a solar flux of 500 μmol m^{-2} s^{-1}. Mean instantaneous solar flux in our 100% PAR treatment was 506 μmol m^{-2} s^{-1}, which was high enough to potentially inhibit photosynthesis. Therefore, shade-adapted forms that were inhibited by full sunlight early in the study may have dominated algae colonizing from Mayfly Creek, which has a mature canopy of riparian vegetation shading the stream. Towards the end of the study, growth forms that could tolerate high light levels may have replaced these shade-adapted forms.

Consumer response

Chironomid and baetid consumers in the field experiment increased as riparian buffer width narrowed. Because water temperature and light increased as buffer width narrowed and both were related to consumer responses (Kiffney et al. 2003), we could not causally link changes in these abiotic factors with biological responses. Our small-scale channel experiment clearly demonstrated that chironomid abundance and biomass, baetid biomass, and tadpole growth and survival were positively related to light. These responses were probably mediated through increased primary production because water temperature was held constant. Support for this hypothesis is seen in the positive relations between chlorophyll *a* biomass and consumer performance. Grether et al. (2001) showed that algal availability for guppies (*Poecilia reticulata*) increased with decreasing canopy cover, and guppy growth rate was positively associated with algal availability.

Our results also showed that survival and growth rate of tailed frog tadpoles was compromised at light levels measured in unlogged control streams of the research forest. Skelly et al. (2002) found that populations of some pond amphibians in the northeastern United States were constrained by canopy closure. These authors suggested that afforestation in the northeastern US might have an overriding impact on the distribution and abundance of pond amphibians. Our findings, in conjunction with those of Skelly et al. (2002), suggest that the low-light environments of 2nd-growth forests may be detrimental to stream and pond amphibians.

Forest structure and composition in much of the MKRF and the Pacific Northwest, in general, is a legacy of clearcut logging. Tree density (conifer + hardwood) in naturally regenerated, young (~70-y-old), 2nd-growth patches in the research forest is high (550–650 trees/ha) and streams are narrow (range from 0.5–4 m wide during summer base flow), resulting in low amounts of light (mean annual instantaneous PAR = 5 μmol m^{-2} s^{-1}) reaching the water surface. In contrast, tree density in patches of remaining old growth in the MKRF (trees >300 y old) is ~100 trees/ha (P. Lawson, MKRF). In general, old-growth forests of the Pacific Northwest are more open relative to these 2nd-growth forests because of blowdown, tree mortality, and other natural disturbances. Light levels measured at the stream surface in West Twin Creek, Olympic National Park, Washington, which drains an old-growth forest, are ~10-fold higher than light flux in East Creek, a stream draining an unlogged 2nd-growth stand in the MKRF (PMK, unpublished data). Other studies have observed similar patterns in tree density and stand age in northern California and southeastern Oregon coastal forests (Bingham and Sawyer 1992), and Douglas-fir forests in Washington and Oregon (Spies and Franklin 1991). Because canopy density is the major driver affecting inputs of solar energy in small forested streams (Beschta 1997), we speculate that food webs in streams draining young forests (~40−100 y) with a high density of conifers may be more constrained by light compared to food webs draining mature (>200 y) or thinned coniferous forests, or riparian forests dominated by deciduous, broadleaf vegetation, such as red alder (*Alnus rubra*) (Volk et al. 2003).

Evidence for this constraint was suggested in our channel study, where abundance and biomass of stream insects, and growth and survival of tailed frog tadpoles was significantly lower in the 2.2% PAR than other light treatments; 2.2% PAR represented light levels observed in our unlogged control streams. We note, however, that light limitation of the stream food web in the 2.2% PAR treatment was not consistent across days or response measures. Nevertheless, these data, combined with results from the large-scale experiment, showed that stream food webs in 2nd-growth, unmanaged stands of the MKRF were strongly light limited (Kiffney et al. 2003).

Differences between large-scale and stream channel experiments

Evidence from both studies supports the hypothesis that periphyton-based food webs in these streams responded to riparian buffer width mediated by changes in solar energy. However, results from the small-scale channel experiment differed somewhat from those in the large-scale field experiment. One reason for these discrepancies may be attributed to differences in size and characteristics of experimental units. Experimental units in the channel study (15 m long, 0.25 m wide, and 0.1 m deep) were much smaller than the reaches in the field (300 m long, 1–5 m wide, and 0.1–1 m deep) (Kiffney et al. 2003). The importance of various processes on ecological properties can change as a function of experimental and observational scale (Peckarsky et al. 1997, Englund et al. 2001). We used open (i.e., open to organism immigration and emigration except for tailed frogs and cutthroat trout) experimental channels that were relatively large compared to other studies that examined the effects of light (Rosemond 1993, Wootton and Power 1993, Hill et al. 1995, Bourassa and Cattaneo 2000), nutrients (Rosemond et al. 1993, Bourassa and Cattaneo 2000), or trophic structure (Wootton and Power 1993) on stream communities. Nevertheless, channel size and complexity may have been different enough from the field experiment to provide results suggestive of consumer-driven limitation of periphyton biomass.

Reducing the size of the experimental arena leads to a reduction in spatial heterogeneity, such as loss of woody debris and off-channel habitat. Experiments in these small, less physically diverse habitats may accentuate the importance of biotic interactions such as predation (Sarnelle 1997). For example, *Daphnia* in enclosures exaggerated grazing effects on chlorophyll *a* along a gradient of P loadings compared to a whole-lake experiment (Pace 2001). If herbivory or other biotic interactions are magnified in small, less-complex experimental arenas, then effort should be made to determine whether such processes are also important structuring communities in natural ecosystems.

A 2nd potential mechanism, related to scale, is that differences in the composition of the periphyton community in the natural and artificial streams affected consumption rate, and thereby periphyton biomass. Specifically, algal growth form in the field experiment shifted from one dominated by prostrate forms in the low-light environments of the control and 30-m-wide buffer stream to filamentous forms in the 10-m-wide buffer and clearcut streams (Kiffney et al. 2003). In addition, the % of the periphyton mat that was fine sediment increased from 38% in the unlogged control to ~65% in the 10-m- wide buffer and clearcut streams. These 2 factors may have limited the impact of consumers on periphyton biomass in the high-light environments of the clearcut and 10-m buffer streams of the field study (Kiffney et al. 2003). Based on visual observations, we speculate that prostrate forms also dominated the periphyton mat in all treatments in the mesocosm experiment, and there was no measurable difference in the relative proportion of periphyton inorganic material among treatments. These observations suggest that the edibility of periphyton was relatively similar among treatments in experimental channels. In a review of lake ecosystems, most experimental data showed asymmetric responses by plants and herbivores to increased nutrients, whereas correlational studies showed roughly proportional increases in both (Leibold et al. 1997). These authors suggested that experimental studies were too short to account for compositional change in plant communities that occurs in natural lakes along a productivity gradient. Hence, it is possible that the duration of our channel experiment was too short to allow for compositional change in the algal community that was observed in the field experiment.

In conclusion, the results of both our studies showed that forested headwater streams are sensitive to removal of riparian vegetation primarily because of changes in light regime. Results from the large-scale field experiment showed significant differences among all treatments in light regime, even between the control and the widest buffer (30-m-wide), which led to corresponding changes in abiotic and biotic attributes of treatment streams (Kiffney et al. 2003). Results from the small-scale channel study also showed that chironomid abundance on day 17 was higher in the 10% ambient PAR treatment, which simulated light levels measured in our 30-m buffer, compared to controls.

We recommend that experiments evaluating the effects of forest management or other human impacts on natural systems be conducted at multiple scales (Peterson et al. 1993, Lodge et al. 1997). Results from large-scale experiments have high external validity and can be directly extrapolated to other systems, whereas small-scale experiments have high internal validity because confounding factors are controlled (Naeem 2001). Our large-scale study showed how forest management led to gradients in abiotic and biotic variables; however, because of the complex nature of these responses we could not determine mechanistic links. The small-scale study revealed that, by creating a gradient of light energy similar to that in the field experiment, we produced biological patterns that were similar to those observed in the field. The channel study also provided results that suggested biotic processes might be important in structuring these headwater stream communities. Additional experiments, especially in the field, may clarify the nature and importance of these biotic interactions.

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Literature Cited

ARMSTRONG, F. A. J., C. R. STEARNS, AND J. D. H. STRICKLAND. 1967. The measurement of upwelling and subsequent biological processes by means of the Technicon Autoanalyzer and associated equipment. Deep-Sea Research 14:381–389.

BENKE, A. C., A. D. HURYN, L. A. SMOCK, AND J. B. WALLACE. 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18:308–343.

BESCHTA, R. L. 1997. Riparian shade and stream temperature: an alternative perspective. Rangelands 19:25–28.

BINGHAM, B., AND J. SAWYER. 1992. Canopy structure and tree condition of young, mature, and old-growth Douglas-fir/hardwood forests. Pages 141–149 *in* H. M. Kerner (editor). Proceedings of the Symposium on Biodiversity of Northwestern California. Report No. 29. University of California Wildlands Resource Center, Berkeley, California.

BOSTON, H. L., AND W. R. HILL. 1991. Photosynthesis-light relations of stream periphyton communities. Limnology and Oceanography 36:644–656.

BOURASSA, N., AND A. CATTANEO. 2000. Response of a lake outlet community to light and nutrient manipulation: effects on periphyton and invertebrate biomass and composition. Freshwater Biology 44: 629–639.

BROSOFSKE, K. D., J. CHEN, R. J. NAIMAN, AND J. F. FRANKLIN. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. Ecological Applications 7: 1188–1200.

CASTELLE, A. J., A. W. JOHNSON, AND C. CONOLLY. 1994. Wetland and stream buffer size requirements—A review. Journal of Environmental Quality 23:878–882.

DUPUIS, L., AND D. STEVENTON. 1999. Riparian management and the tailed frog in northern coastal forests. Forest Ecology and Management 124:35–43.

ENGLUND, G., S. D. COOPER, AND O. SARNELLE. 2001. Application of a model of scale dependence to quantify scale domains in open predation experiments. Oikos 92:510–514.

FELLER, M. C. 1977. Nutrient movement through western hemlock—western red cedar ecosystems in southwestern British Columbia. Ecology 58:1269–1283.

FEMAT (FOREST ECOSYSTEM MANAGEMENT ASSESSMENT TEAM). 1993. Aquatic ecosystem assessment. Pages V1–V95 *in* Forest ecosystem management: an ecological, economic, and social assessment. Report of the Forest Ecosystem Management Assessment Team. Forest Service, US Department of Agriculture,Washington, DC.

FEMINELLA, J. W., M. E. POWER, AND V. H. RESH. 1989. Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. Freshwater Biology 22:445–457.

FRANKLIN, J. F., AND C. T. DYRNESS. 1969. Vegetation of Oregon and Washington. PNW-80. Forest Service, US Department of Agriculture, Portland, Oregon.

FROST, T. M., R. E. ULANOWICZ, S. C. BLUMENSHINE, T. F. H. ALLEN, F. TAUB, AND J. H. RODGERS. 2001. Scaling issues in experimental ecology: freshwater ecosystems. Pages 253–280 *in* R. H. Gardner, W. M. Kemp, V. S. Kennedy, and J. E. Peterson (editors). Scaling relations in experimental ecology. Columbia University Press, New York.

GRETHER, G. F., D. F. MILLIE, M. J. BRYANT, D. N. REZNICK, AND W. MAYEA. 2001. Rain forest canopy cover, resource availability, and life history evolution in guppies. Ecology 82:1546–1559.

GRIMM, N. B., AND S. G. FISHER. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. Journal of the North American Benthological Society 8:293–307.

HAWKINS, C. P., L. J. GOTTSCHALK, AND S. S. BROWN. 1988. Densities and habitat of tailed frog tadpoles in small streams near Mt. St. Helens following the 1980 eruption. Journal of the North American Benthological Society 7:246–252.

HILL, W. R. 1996. Effects of light. Pages 123–148 *in* F. R. Hauer and G. A. Lamberti (editors). Methods in stream ecology. Academic Press, San Diego, California.

HILL, W. R., P. J. MULHOLLAND, AND E. R. MARZOLF. 2001. Stream ecosystem responses to forest leaf emergence in spring. Ecology 82:2306–2319.

HILL, W. R., M. G. RYON, AND E. M. SCHILLING. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. Ecology 76:1297–1309.

HOLOMUZKI, J. R., AND B. J. F. BIGGS. 2000. Taxon-specific responses to high-flow disturbance in streams: implications for population persistence. Journal of the North American Benthological Society 19:670–679.

KIFFNEY, P. M., AND J. P. BULL. 2001. Factors controlling periphyton accrual during summer in headwater streams of southwestern British Columbia, Canada. Journal of Freshwater Ecology 15:339–351.

KIFFNEY, P. M., J. P. BULL, AND M. C. FELLER. 2002. Climatic and hydrologic variability in a coastal watershed of southwestern British Columbia. Journal of the American Water Resources Association 38:1437–1451.

KIFFNEY, P. M., AND J. S. RICHARDSON. 2001. Interactions among nutrients, periphyton, and invertebrate and vertebrate (*Ascaphus truei*) grazers in experimental channels. Copeia 2001:422–429.

KIFFNEY, P. M., J. S. RICHARDSON, AND J. P. BULL. 2003. Responses of periphyton and insect consumers to experimental manipulation of riparian buffer width along headwater streams in forested landscapes. Journal of Applied Ecology 40:1060–1076.

KIFFNEY, P. M., J. S. RICHARDSON, AND M. C. FELLER. 2000. Fluvial and epilithic organic matter dynamics in headwater streams of southwestern British Columbia, Canada. Archiv für Hydrobiologie 149:109–129.

LAMBERTI, G. A., S. V. GREGORY, L. R. ASHKENAS, A. D. STEINMAN, AND C. D. MCINTIRE. 1989. Productive capacity of periphyton as a determinant of plant-animal interactions in streams. Ecology 70: 1840–1856.

LAMBERTI, G. A., S. V. GREGORY, C. P. HAWKINS, R. C. WILDMAN, L. R. ASHKENAS, AND D. M. DENICOLA. 1992. Plant-herbivore interactions in streams near Mt. St. Helens. Freshwater Biology 27:237–247.

LEIBOLD, M. A., J. M. CHASE, J. B. SHURIN, AND A. L. DOWNING. 1997. Species turnover and the regulation of trophic structure. Annual Review of Ecology and Systematics 28:467–494.

LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, AND R. D. WOLFINGER. 1996. SAS® system for mixed models. 1st edition. SAS Institute Inc., Cary, North Carolina.

Lodge, D. M., S. C. Blumenshine, and Y. Vadeboncoeur. 1997. Insights and applications of large-scale, long-term ecological observations and experiments. Pages 202–235 *in* W. J. Resetarits and J. Bernardo (editors). Experimental ecology: issues and perspectives. Oxford University Press, New York.

Merritt, R. W., and K. W. Cummins (editors). 1996. An introduction to the aquatic insects of North America. 3rd edition. Kendall/Hunt, Dubuque, Iowa.

Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta 27:31–36.

Murphy, M. 1998. Primary production. Pages 144–168 *in* R. J. Naiman and R. E. Bilby (editors). River ecology and management. Springer-Verlag, New York.

Naeem, S. 2001. Experimental validity and ecological scale as criteria for evaluating research programs. Pages 223–252 *in* R. H. Gardner, W. M. Kemp, V. S. Kennedy, and J. E. Peterson (editors). Scaling relations in experimental ecology. Columbia University Press, New York.

Nisbet, R. M., S. Diehl, W. G. Wilson, S. D. Cooper, D. D. Donalson, and K. Kratz. 1997. Primary productivity gradients and short-term population dynamics in open systems. Ecological Monographs 67:535–553.

Pace, M. L. 2001. Getting it right and wrong: extrapolations across experimental scales. Pages 157–178 *in* R. H. Gardner, W. M. Kemp, V. S. Kennedy, and J. E. Petersen (editors). Scaling relations in experimental ecology. Columbia University Press, New York.

Peckarsky, B. L., S. D. Cooper, and A. W. McIntosh. 1997. Extrapolating from individual behavior: implications for interactions between stream organisms. Journal of the North American Benthological Society 16:375–390.

Peterson, B. J., L. Deegan, J. Helfrich, J. E. Hobbie, M. Hullar, B. Moller, T. E. Ford, A. Hershey, A. Hiltner, G. Kipphut, M. A. Lock, D. M. Fiebeg, V. McKinley, M. C. Miller, J. R. Vestal, R. Ventullo, and G. Volk. 1993. Biological responses of a tundra river to fertilization. Ecology 74:653–672.

Power, M. E., W. J. Matthews, and A. J. Stewart. 1985. Grazing minnows, piscivorous bass and stream algae: dynamics of a strong interaction. Ecology 66:1448–1456.

Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Matthews, P. B Moyle, B. Statzner, and I. R. Wais De Badgen. 1988. Biotic and abiotic controls in river and stream communities. Journal of the North American Benthological Society 7:456–479.

Rempel, R. S., and J. C. H. Carter. 1986. An experimental study on the effect of elevated temperature on the heterotrophic and autotrophic food resources of aquatic insects in a forested stream. Canadian Journal of Zoology 64:2457–2466.

Richardson, J. S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. Ecology 72:873–887.

Richardson, J. S., and W. E. Neill. 1999. Headwater amphibians and forestry in British Columbia: Pacific giant salamanders and tailed frogs. Northwest Science 72:122–123.

Rosemond, A. D. 1993. Interactions among irradiance, nutrients, and herbivores constrain a stream algal community. Oecologia (Berlin) 94:585–594.

Rosemond, A. D., P. J. Mulholland, and J. W. Elwood. 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. Ecology 74:1264–1280.

Rosenfeld, J. S. 1997. The effect of large macroinvertebrate herbivores on sessile epibenthos in a mountain stream. Hydrobiologia 344:75–79.

Sarnelle, O. 1997. *Daphnia* effects on microzooplankton: comparisons of enclosure and whole-lake ecosystems. Ecology 78:913–928.

Schindler, D. E., and M. D. Scheuerell. 2002. Habitat coupling in lake ecosystems. Oikos 98:177–189.

Skelly, D. K., L. K. Freidenburg, and J. M. Kiesecker. 2002. Forest canopy and the performance of larval amphibians. Ecology 83:983–992.

Spies, T. A., and J. F. Franklin 1991. The structure and function of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 91–109 *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff (editors). Wildlife and vegetation of unmanaged Douglas-fir forests. General Technical Report PNW-GTR-285. Pacific Northwest Research Station, Forest Service, US Department of Agriculture, Portland, Oregon.

Volk, C. J., P. M. Kiffney, and R. L. Edmonds. 2003. Role of riparian red alder in the nutrient dynamics of the Olympic peninsula, Washington, USA. Pages 213–228 *in* J. G. Stockner (editor). Nutrients in salmonid ecosystems: sustaining production and biodiversity. Symposium 34. American Fisheries Society, Bethesda, Maryland.

Weins, J. A. 2001. Understanding the problem of scale in experimental ecology. Pages 61–89 *in* R. H. Gardner, W. M. Kemp, V. S. Kennedy, and J. E. Peterson (editors). Scaling relations in experimental ecology. Columbia University Press, New York.

Wootton, J. T., and M. E. Power. 1993. Productivity, consumers, and the structure of a river food chain. Proceedings of the National Academy of Sciences of the United States of America 90:1384–1387.

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