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Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams

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Summary

1. Riparian trees regulate aquatic ecosystem processes, such as inputs of light, organic matter and nutrients, that can be altered dramatically when these trees are harvested. Riparian buffers (uncut strips of vegetation) are widely used to mitigate the impact of clear-cut logging on aquatic ecosystems but there have been few experimental assessments of their effectiveness.

2. Forests along 13 headwater stream reaches in south-western British Columbia, Canada, were clear-cut in 1998, creating three riparian buffer treatments (30-m buffer, 10-m buffer and clear-cut to the stream edge), or left as uncut controls, each treatment having three or four replicates.

3. We predicted that periphyton biomass and insect consumers would increase as buffer width decreased, because of increased solar flux. We used two complementary studies to test this prediction.

4. In one study, we compared benthic communities before and after logging in all 13 streams; a second study focused on periphyton and insect colonization dynamics over 6-week periods in each of four seasons in four streams, one in each treatment.

5. Photosynthetically active radiation, and mean and maximum water temperature, increased as buffer width narrowed.

6. Periphyton biomass, periphyton inorganic mass and Chironomidae abundance also increased as buffer width narrowed, with the largest differences occurring in the clear-cut and 10-m buffer treatments.

7. Photosynthetically active radiation, water temperature, periphyton biomass and periphyton inorganic mass were significantly greater in the 30-m buffer treatment than in controls during some seasons.

8. *Synthesis and applications.* We have shown that a gradient of riparian buffer widths created a gradient in light and temperature that led to non-linear increases in periphyton biomass and insect abundance. For example, Chironomidae abundance was generally greater in the 10-m and 30-m buffer treatments than in controls, whereas this was not always the case in the clear-cut treatment. This pattern may be due to the high sediment content of the periphyton mat in the clear-cut treatment, which potentially limited the response of some insects to increased food resources. Overall, our results indicate that uncut riparian buffers of 30-m or more on both sides of the stream were needed to limit biotic and abiotic changes associated with clear-cut logging in headwater, forested watersheds.

Key-words: communities, forestry logging, riparian zones, solar radiation, water temperature, watershed.

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Introduction

Riparian zones are among the most diverse and functionally important ecotones on earth (Naiman *et al.* 1998). Riparian vegetation modifies light and temperature regimes, provides food for aquatic and terrestrial consumers and is the source of woody debris to streams (Pollock 1998). The removal of riparian trees along streams or lakes can affect aquatic ecosystem structure and function (Platts & Megahan 1975; Vouri & Joensuu 1996). For example, forest harvest can increase sediment delivery to streams (Chamberlin, Harr & Everest 1991), covering stream substrates (Davies & Nelson 1994) and negatively affecting some stream organisms (Osmundson *et al.* 2002). In small, headwater streams, one of the major microclimatic changes resulting from logging is an increase in solar energy reaching the stream surface (Brosofske *et al.* 1997). Increased solar energy can affect a host of factors such as water temperature (Beschta 1997), primary production (Hill, Ryon & Schilling 1995) and insect abundance (Fuller, Roelofs & Fry 1986). As far as we know, however, there have been no experimental studies linking changes in microclimatic gradients, as a result of different forest management strategies, to process-based studies on stream organisms.

A management practice designed to minimize the impacts of forest harvest on aquatic systems, especially for resources such as water quality and fish habitat, is to leave a strip of trees (riparian buffers or reserves) adjacent to the water body. The required width of this buffer depends on many factors, including the management objective. If the objective is to protect terrestrial or aquatic vertebrates, buffer zones need to be wider than if the objective is to protect water quality (Castelle, Johnson & Conolly 1994). For instance, Semlitsch (1998) recommended a 164-m wide buffer around wetlands for an assemblage of pond-breeding amphibians, whereas a 30-m wide forest buffer may be sufficient to remove excess nitrate from groundwater (Pinay & Dècamps 1988).

Despite the widespread use of riparian buffers as a management tool to maintain a variety of ecological functions (FEMAT 1993), there has been little experimental evaluation of how effective these buffers are. Watershed-scale experiments are critical for evaluating the functional significance of riparian buffers of different widths, but replicated experiments at this scale are logistically difficult (except see Darveau *et al.* 1995). As a result, the effects of riparian buffers on streams is known mostly from short-term (one or two seasons of sampling), post-hoc observational studies (Newbold, Erman & Roby 1980; Murphy *et al.* 1986; Davies & Nelson 1994) and unreplicated experimental watershed studies (Hall, Brown & Lantz 1987; Hartman *et al.* 1987). Therefore, there is a need for replicated experiments to infer causation in different riparian management approaches and to separate site-specific differences from treatment effects.

Small, headwater (first- and second-order channels; Strahler 1957) streams can account for 70–80% of a total watershed area (Leopold, Wolman & Miller 1964; Gomi, Sidle & Richardson 2002) and they supply water, organic matter, sediment and nutrients to downstream fish-bearing channels (Kiffney, Richardson & Feller 2000; Wipfli & Gregovich 2002; Volk, Kiffney & Edmonds 2003). Not only do these channels provide ecological services to the downstream network, such as the sequestration of nitrogen (Peterson *et al.* 2001), but they are also inhabited by fauna not found in other portions of the river network. For example, the tailed frog *Ascaphus truei* Stejneger and the coastal giant salamander *Dicamptodon tenebrous* Good are specifically adapted to the physically demanding conditions of coastal headwater streams of the Pacific northwest. Despite the high density of headwater streams, their importance to downstream channels, unique fauna and their potential importance as fish habitat (Brown & Hartman 1988), they receive little protection in the form of riparian reserves in the Pacific northwest (Young 2000) or elsewhere (Meyer & Wallace 2001).

In 1996, a riparian management experiment was initiated at the University of British Columbia's Malcolm Knapp Research Forest (MKRF), Canada. The purpose was to evaluate the effects of riparian buffer width on headwater streams using a large-scale, replicated experiment. These riparian manipulations included clear-cutting to the stream edge, 10-m and 30-m wide riparian buffers and uncut controls. In this paper, we present data from two concurrent studies that examined the response of periphyton and primary consumers to this riparian gradient. We measured surface-water nutrient concentrations, periphyton biomass and inorganic mass and insect consumer abundance monthly for 1 year before and 1 year after logging in 13 streams. We also present data on surface-water temperature and light regime in all 13 streams after logging. An intensive, short-term colonization study was conducted in the first year after logging, where periphyton biomass, periphyton inorganic mass and insect abundance were measured weekly for 6 weeks, four times a year, in one stream in each treatment.

Abiotic characteristics (e.g. light) that affect stream food webs can change dramatically following clear-cutting of riparian trees (Brosofske *et al.* 1997). Less well known is how riparian buffer width mediates change in these abiotic factors to regulate the distribution and abundance of periphyton and insect consumers, and whether these effects differ by season. With this in mind, the main questions in our study were as follows. How does riparian buffer width affect periphyton biomass, periphyton composition and insect consumer abundance, as mediated by changes in light, nutrients, and water temperature? Was there a buffer width that had no detectable effect on these response variables? Were the effects of logging on stream communities consistent among seasons?
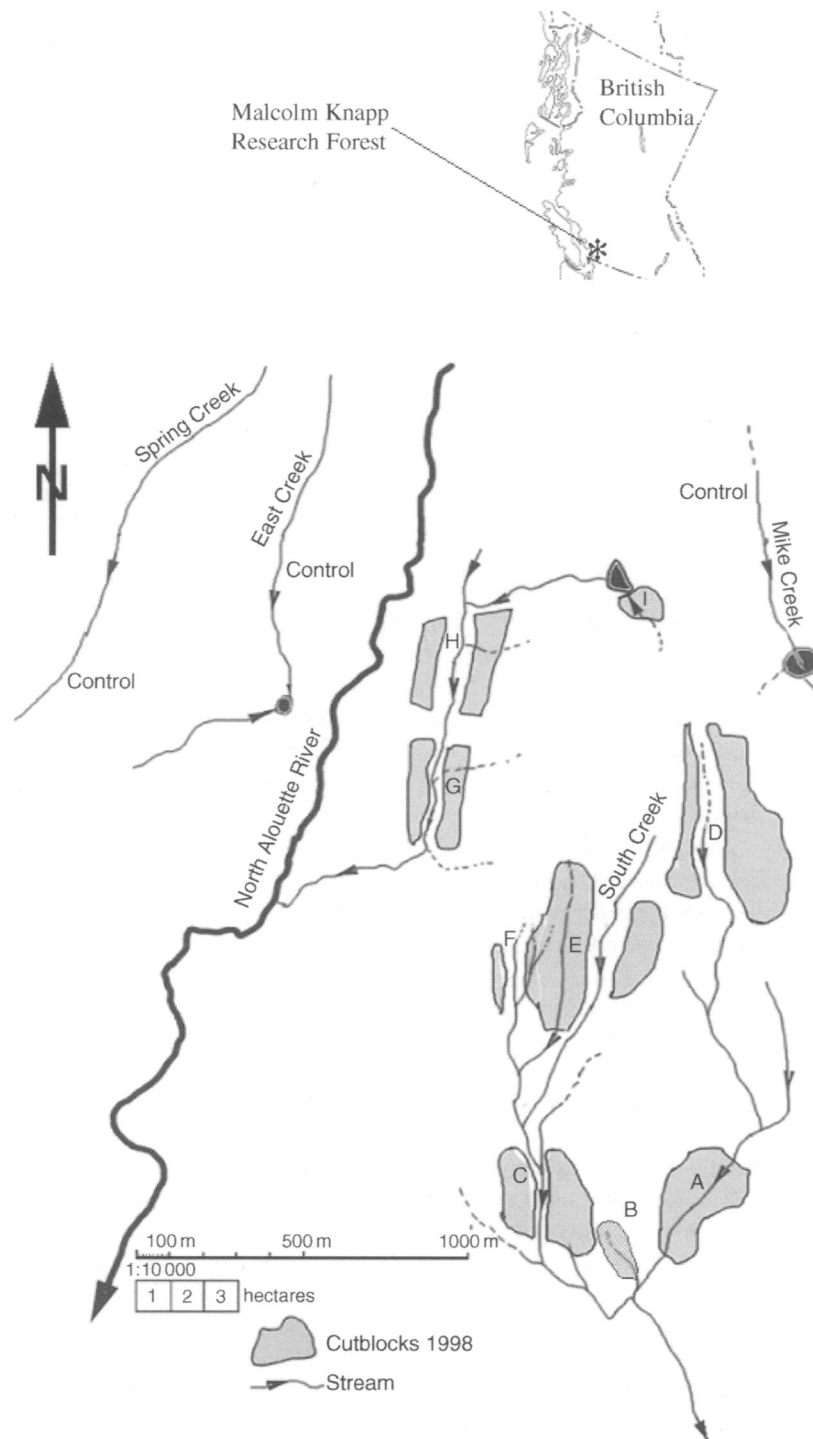
Fig. 1. Map showing the south-eastern portion of the Malcolm Knapp Research Forest, Maple Ridge, British Columbia, Canada. Reach designations and their associated riparian buffer treatments are shown.

Methods

STUDY SITE AND STUDY DESIGN

The experimental watersheds were located in the Coast Range of the Pacific Coastal ecoregion (Naiman & Bilby 1998) about 45 km east of Vancouver, near Maple Ridge, British Columbia, Canada (122°34′W, 49°16′N; Fig. 1). The research forest lies in the coastal western hemlock biogeoclimatic zone, and the conifers western hemlock *Tsuga heterophylla* (Raf.) Sarg., western red cedar *Thuja plicata* Donn and Douglas-fir *Pseudotsuga menziesii* (Mirb.) Franco are the dominant forest tree species (Franklin & Dyrness 1969). Broadleaf riparian species comprise primarily black cottonwood *Populus trichocarpa* Torr. & Gray, red alder *Alnus rubra* Bong., vine maple *Acer circinatum* Pursh and salmonberry *Rubus spectabilis* Pursh. Understorey vegetation is sparse and is dominated by ferns and salal *Gaultheria shallon* Pursh. The forest was logged in the early 1900s

Table 1. Physical characteristics and riparian treatments (buffer width) for experimental stream reaches at the Malcolm Knapp Research Forest, Maple Ridge, British Columbia, Canada. Reach G is about 300-m downstream of H, A is approximately 1 km downstream of reach D, and C is approximately 500-m downstream of E, F and South Creek, so physical characteristic and treatments represents values for these subwatersheds

Stream	Riparian buffer width (m)	Watershed area (ha)	Summer base flow discharge ($l\,s^{-1}$)	Elevation range (m)	Stream gradient (%)	Total area of watershed logged (%)	Stream length logged (m)
East Creek*	Control	44	2·0	295–555	4	0	0
Mike Creek	Control	25	0·6	240–310	8	0	0
Spring Creek	Control	35	3·2	135–500	4	0	0
H*	30 m	55	0·6	205–320	3	22	300
South Creek	30 m	19	0·3	175–320	10	20	400
D	30 m	43	0·03	180–335	8	22	450
C*	10 m	89	0·9	110–285	4	21	335
F	10 m	12	0·07	170–285	14	24	340
G	10 m	84	0·6	190–325	4	23	265
A*	Clear-cut	63	0·6	110–225	6	21	325
B	Clear-cut	14	0·08	110–265	10	24	250
I	Clear-cut	13	0·2	255–320	6	21	215
E	Clear-cut	12	0·1	170–320	12	53	650

*Streams that were part of the colonization study.

and burned in 1931, so comprises mostly dense stands [550–650 trees ha^{-1}, average diameter at breast height (d.b.h.) 40 cm; average stand height 45 m] of second growth, fire-initiated forest approximately 70 years old. Small patches of upland forest at streams A and C were logged in 1994, and approximately 75-m of stream length was affected; these sites had an approximately 30–40-m wide buffer before additional logging occurred in 1998.

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. Elevations of experimental watersheds ranged from 110 to 555 m. The streams drained thin, glacial till underlain by igneous bedrock (Feller & Kimmins 1979) and had a southerly aspect, except stream I, which drained north (for physical features of streams and riparian treatments see Table 1). Channel reaches were composed primarily of pool–riffle and step–pool sequences (Montgomery & Buffington 1998). Substrata consisted primarily of gravel and cobbles with a few boulders in riffles, and sand, gravel and organic detritus in pools. Thirteen first- and second-order reaches in the south-eastern section of the MKRF were studied from November 1997 to October 1999. Three of the 13 reaches were downstream of other test sites. Specifically, reach G was approximately 300 m downstream of reach H, reach A is approximately 1 km downstream of reach D and reach C is approximately 500-m downstream of reaches on South Creek (SCK), E and F. Water flowing out of logged reaches flowed through fully forested sections before entering another logged reach. Although these sites were downstream of one another, we suggest that distances were long enough to minimize the effects of upstream logging on downstream reaches, except for possibly sediment, organic

matter or insects transported during large storms, based on the following evidence. Reaches G and A were downstream of a 30-m buffer treatment, and this treatment had characteristics most similar to unlogged controls (see the Results, Replicated, whole-watershed experiment). Some studies have shown that the effects of clear-cut logging dissipate over relatively short distances. Annual sediment loads increased 123–269% in logged tributaries of the Caspar Creek watershed, but these increases were not detected at downstream mainstem stations except during storms (Lewis *et al.* 2001). In this study, some of the mainstem stations were less than 500 m downstream from tributary stations. Water flowing through clear-cuts can cool as it passes through forested stream reaches due to inflowing cooler water. Observed rates of cooling have varied from 1·2 °C in 130 m, 4 °C in 200 m and 5·5 °C in about 60–120 m (McGurk 1989; Keith *et al.* 1998; Story, Moore & Macdonald 2003). There is also evidence to suggest that distances travelled by insects entering the drift is minimal, with mean drift distances ranging from 3 to 20 m at moderate stream velocities (30–60 cm s^{-1}). In addition, nutrient uptake lengths in streams are relatively short (2–89 m for PO_4 and 5–271 m for NH_4; Hall, Bernhardt & Likens 2002), suggesting that nutrient enhancement from cutting would not travel far downstream. Based on these results, we suggest that the impacts of upstream logging on downstream reaches were minimal, except possibly during large storm events.

Due to logistical considerations, we could not fully randomize treatments among replicate streams. East Creek (EC) was chosen as a control because it is a long-term monitoring site and Mike Creek (MC) flows into a provincial park. Stream A and C were not randomly assigned because both had fish, and we wanted at least one planned replicate in each treatment to have fish (EC, A, C, G and H, for treatments see Table 1).

Clear-cut logging of upland areas occurred primarily during autumn and winter 1998. From 215 to 650 m of stream length were affected in each of the logged watersheds (Table 1). There was no logging within riparian buffers. Our study reaches were approximately 100 m long and were within areas affected by logging.

REPLICATED, WHOLE-ECOSYSTEM MANIPULATIONS

Pre-logging data for periphyton biomass were collected from the 13 reaches between November 1997 to October 1998, and post-logging data from November 1998 to October 1999. Although most of the logging occurred between September and November 1998, some streams (D, E, I and SCK) were logged earlier due to logistical constraints, so fewer than 12 months of data were collected for these streams.

Six unglazed ceramic tiles (112 cm^2 each) were randomly distributed between pools ($n = 3$) and riffles ($n = 3$) along a 100-m reach. These tiles were sampled and returned to the stream monthly (see Periphyton sampling and analysis) to measure periphyton biomass. Periphyton is a complex mixture of bacteria, algae and detritus embedded in a polysaccharide matrix (Lock *et al.* 1984), and is consumed by a variety of stream invertebrates (Merritt & Cummins 1996). Tiles were used instead of natural rock because of their reproducibility, and the large number of samples that had to be collected and processed to ensure high statistical power. Lamberti & Resh (1985) showed that tiles supported algal and primary consumer communities similar to those found on natural inorganic substrata.

Pre-logging counts of invertebrate primary consumers on tiles were made from May 1998 to November 1998. These data were compared with counts collected during the same months after logging in 1999. Invertebrates observed on tiles included mayflies (Ephemeroptera: Baetidae and Heptageniidae), caddisflies (Trichoptera: *Glossosoma* and *Neophylax*), blackflies (Simuliidae), stoneflies (Plecoptera: Nemouridae) and chironomids (Chironomidae: predominantly Orthocladiinae). Based on the composition of this tile community, these insects primarily consumed periphyton either as collector-gatherers (e.g. Baetidae) or as scrapers (e.g. Glossosomatidae; Merritt & Cummins 1996). We focused on the response of Chironomidae and Ephemeroptera (primarily Baetidae) because the abundances of other taxa were relatively low in both studies.

Because mayflies were sensitive to observer and tile movement, when possible mayflies were counted while the tile was in water. After this count, the tile was slowly lifted from the stream, and the remaining consumers were identified and counted. The same methods for counting invertebrates on tiles were used among streams and between studies (see Colonization study). Although some insects were probably lost when the tile was removed from the water, each tile was treated in a similar manner. Thus any bias introduced by our

approach was similar across replicates, treatments and studies.

A control site (EC) and SCK had V-notch weirs where instantaneous water level was recorded and converted to mean daily discharge. Stream discharge at other sites was measured once to twice monthly using the velocity area method (Gore 1996). To test the accuracy of this method, discharge at EC was calculated using the velocity-area technique and compared with data from the V-notch weir, and there was a strong relationship between the two methods $\{r^2 = 0.9, n = 15, P = 0.0001$, velocity-area discharge [L s^{-1}] = 0.002 + 1.15(weir discharge [L s^{-1}]), P. M. Kiffney, unpublished data}. Water samples were collected monthly and analysed for nitrate-nitrogen (NO_3-N) (Armstrong, Stearns & Strickland 1967) and soluble reactive phosphorus (PO_4-P) (Murphy & Riley 1962). Stream water was filtered through a glass fibre filter (Gelman Type A/E) and the filtrate frozen until analysis. Stream temperature was measured at hourly intervals with Onset temperature loggers (Onset®, Pocasset, MA). In 1997 before logging, some temperature loggers were lost during a large storm or malfunctioned, so we do not have complete pre-logging temperature data at all sites for all months. From June to November 1999, photosynthetically active radiation (PAR) was measured at each stream once or twice a month using a LiCor light meter and quantum sensor (Model LI–250; LiCor, Lincoln, NB). Six to nine measurements at each stream were taken directly above the water surface at random locations within each study reach. These measurements were taken between 10:00 and 14:00 h under a range of conditions (e.g. rain, partly cloudy, clear sky). Because we did not have regular access to a light meter before logging, only one day of pretreatment measurements ($n = 6$ per stream) of PAR was taken (Kiffney, Richardson & Bull 2000). We did not compare these data to post-treatment data because pre-logging measurements were taken using a different model PAR sensor under one type of environmental condition (a clear, sunny day in April 1998; Kiffney, Richardson & Bull 2000).

COLONIZATION STUDY

One experimental watershed from each treatment was selected for the colonization study, including a control (EC), a 30-m buffer (stream H), a 10-m buffer (stream C) and a clear-cut (stream A). Streams were selected based on similar physical attributes (width, discharge, gradient and substrata) and food web structure (similar invertebrate communities and resident populations of *Oncorhynchus clarki clarki* Richardson, coastal cutthroat trout). Headwater streams of coastal British Columbia are subjected to frequent flood events at all times of the year due to abundant rainfall, but especially during the rainy season (October through April). High flows can scour algae and invertebrates from substrata (Grimm & Fisher 1989), potentially limiting

our ability to detect differences in biological attributes among treatments with monthly sampling. Therefore, the objective of this study was to measure colonization patterns of algae and insect consumers weekly over a 6-week period during winter, spring, summer and autumn at one stream within each buffer treatment. We predicted the intensive nature of this study would allow us to identify differences among sites with different buffer widths, especially during the rainy season.

Six periphyton templates were placed in each stream to collect periphyton biomass and count insect consumers for 6-week colonization studies during winter (26 January–10 March 1999), spring (6 April–18 May), summer (15 June–27 July) and autumn (23 September–4 November). Each periphyton template consisted of six unglazed, ceramic tiles (total of 36 tiles per stream; upper surface of each tile = 25 cm^2) secured to wire screens with cable ties; screens were attached to the stream bottom using metal rods. Six templates were randomly distributed between riffles ($n = 3$) and pools ($n = 3$) within each study reach. This distribution of templates between habitat types was similar to the monthly monitoring study. One tile was randomly selected from each template weekly, and sampled with the same methods (i.e. periphyton and insects) described previously (see Replicated, whole-ecosystem manipulations).

PERIPHYTON SAMPLING AND ANALYSIS

Periphyton was removed from the upper surface of tiles by scraping with a razor blade, scrubbing with a toothbrush and rinsing into a small collecting bucket using distilled water. The sample (*c.* 30 ml) was poured into an opaque vial and frozen. Thawed periphyton suspensions were diluted to a volume of 50 ml. Two subsamples of 25 ml each were withdrawn from each suspension to determine ash-free dry mass (AFDM) and chlorophyll *a* (Colonization study only). The AFDM subsamples were filtered onto pre-combusted and pre-weighed glass fibre filters (Gelman Type A/E; 1·0 μm nominal pore size), dried at 70 °C for 24 h and weighed. The filters were then ashed for 2 h at 550 °C and weighed. Chlorophyll *a* subsamples were filtered through glass fibre filters (Gelman Type A/E) in a darkened room and chlorophyll extracted with 25 ml of 99·7% acetone (OmniSolv, EM SCIENCE, Oldsmar, Florida, USA) for 24 h. Chlorophyll *a* was analysed using a fluorometer (Model 10-005R; Turner Designs, Mt View, CA). To determine periphyton community composition, three samples from each stream were collected by scrubbing a known area of a tile on 18 May 1999 at the end of the spring accrual study. This material was preserved in 10% Lugol's solution, and algae were identified using a Zeiss inverted microscope. For each site, the relative abundances of major algal orders (Cyanophyceae, Chlorophyceae, Chrysophyceae and Bacillariophyceae) and dominant species were determined.

STATISTICAL ANALYSIS

Because response variables were measured on the same experimental units over time ($n = 13$ streams), we used repeated-measures analysis of covariance (ANCOVA, PROC MIXED; Littell *et al.* 1996) to determine the effects of buffer width on post-logging values of nutrients, periphyton AFDM and inorganic mass, and Chironomidae and Ephemeroptera abundance. The covariates were baseline values for these variables measured before treatments were applied. Previous research has shown that abiotic and biotic attributes of streams in the research forest show strong seasonal dynamics due to pronounced differences in stream flow, water temperature and solar flux (Kiffney, Richardson, & Feller 2000; P. M. Kiffney, unpublished data). Because of these strong seasonal patterns, we pooled post-logging data across months within seasons (autumn = September–November; winter = December–February; spring = March–May; summer = June–August) and replicates, and used season as the repeated data. We first tested the appropriateness of using ANCOVA (i.e. parallelism of regression lines); these tests showed no significant interactions, so interaction terms were dropped from the model. The model indicated significant seasonal differences for all response measures, so if the mixed model also indicated significant treatment effects we analysed for differences among treatments within each season using the least-square means multiple comparison procedure. Because some temperature probes were lost during high flow events before logging in 1997 and we had limited PAR data from before logging, a univariate *F*-test was used to test for treatment differences on post-logging data for these response variables. If the ANOVA indicated significant treatment effects, it was followed by the Ryan–Einot–Gabriel–Welsch multiple comparison procedure.

To determine which variables (nutrients, PAR, stream power, water temperature, presence of fish) explained most among-stream variation in periphyton and insect consumers in the long-term experiment, we used stepwise multiple regression and the forward selection procedure. If the partial *r*-square of the predictor variable was greater than 10%, it was included in the model. Stream power (ω, Watts) was calculated using the following formula: $\omega = \rho g Q h$ where ρ is the density of water (kg m^{-3}), g is the acceleration due to gravity (m s^{-2}), Q is the flow of water (m^3 s^{-1}) and h is the slope of the channel (metres). Because the regression analysis did not develop a model for Ephemeroptera abundance, we used the *r*-square (Akaike's information criterion) to determine the most parsimonious model explaining variability in mayflies. We then used simple linear regression to derive parameter estimates and their statistical significance for this model. In these regression analyses, stream was the experimental unit and values for each measure were after logging means, pooled across months.

In the colonization study, ANCOVA was used to test for differences among sites within each season for

periphyton AFDM and chlorophyll *a*, periphyton inorganic mass, and chironomid and mayfly abundance. Sample date was treated as the covariate. In this analysis, the weekly value for each response measure at each stream was the sample unit, and we conducted separate ANCOVAs for each season. If the date by stream interaction was not significant but there were significant stream differences, means for the different response variables were compared using the least-square means procedure. Summer data for chironomid and mayfly abundance were used in these analyses, as abundances were low during other seasons. We acknowledge that samples collected through time may be autocorrelated and that we have only one stream per treatment; hence, inferences from this component of the study should be made with caution. We suggest, however, that data from this study combined with the before–after experiment provide strong inference for identifying riparian treatment effects.

To test for the effects of periphyton inorganic mass accumulating on tiles on the presence of invertebrates, we conducted logistic regression. In this analysis, we used summer data from the short-term colonization study and from the whole-ecosystem, replicated experiment.

Analysis of residuals for each model indicated that some response measures did not exhibit homogeneous variances, so these responses were transformed using natural logarithms [$\ln(x + 1)$] prior to analysis.

Results

REPLICATED, WHOLE-WATERSHED EXPERIMENT

Physical and chemical characteristics

Overall, the ecological effects of riparian buffer width were greatest in clear-cut and 10-m buffer treatments; however, we also observed significant differences in response variables in the 30-m buffer treatment. One of most pronounced differences among treatments was solar input, as the amount of light reaching the stream surface increased as buffer width narrowed (Fig. 2). Mean solar flux in the clear-cut treatment was 58 times greater and 16 times greater in the 10-m treatment compared with controls. Light flux was also five times greater in the 30-m buffer treatment compared with controls. Water temperature varied seasonally; mean water temperature in controls ranged from a low of about 4 °C in winter to a high of 12 °C in summer. Decreasing buffer width was also related to increased mean water temperature in winter ($F_{3,9}$, $P = 0.0002$), spring ($P = 0.04$) and summer ($P = 0.01$; Fig. 3a), and maximum water temperature in spring ($P = 0.03$) and summer ($P = 0.0003$; Fig. 3b). For example, maximum water temperature in summer was 4.8 °C higher in the clear-cut treatment, 3 °C higher in the 10-m treatment and 1.6 °C higher in the 30-m treatment compared with controls.
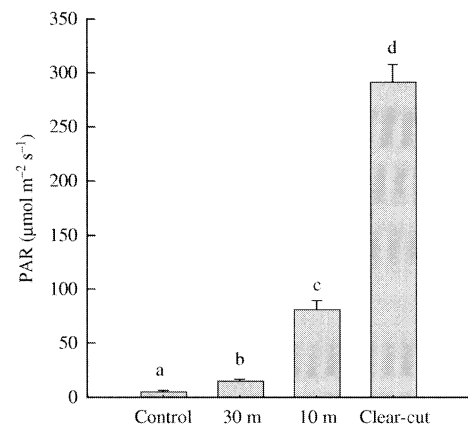
Fig. 2. Mean (1 SD) annual PAR (400–700 nm) measured in each treatment the first year after logging. Means with the same letter were not statistically different based on the within-season comparison.

Dissolved NO_3-N concentrations in water were significantly higher in controls compared with other treatments before logging ($F_{1,8}$, $P = 0.01$), but there were no statistical differences among treatments after logging (Fig. 4). Dissolved NO_3-N ($F_{3,27}$, $P = 0.006$) and PO_4-P ($P < 0.0001$) concentrations were significantly different among seasons after logging, with NO_3-N concentration highest in autumn and PO_4-P highest in winter.

Biological characteristics

The repeated-measures ANCOVA showed no differences among treatments before logging or any significant interaction terms, whereas after logging periphyton biomass, periphyton inorganic mass and insect consumer abundance increased with decreasing riparian buffer width. Periphyton AFDM differed among treatments ($F_{3,8}$, $P = 0.02$) and seasons ($F_{3,36}$, $P < 0.0001$; Fig. 5a), with lower biomass levels in winter compared with other seasons. In autumn, periphyton AFDM at logged sites was significantly greater than controls ($P = 0.008$); periphyton biomass was twofold higher in the 30-m treatment compared with controls. In spring ($F_{3,9}$, $P < 0.05$) and summer ($P = 0.08$), periphyton biomass in the clear-cut treatment was greater than all other treatments. During summer, periphyton AFDM in the clear-cut treatment was six times higher than controls and three times higher than the 30-m treatment.

Periphyton inorganic mass also increased as buffer widths narrowed ($F_{3,8}$, $P = 0.02$) and was lower in winter than other seasons ($F_{3,27}$, $P < 0.0001$; Fig. 5b). Periphyton inorganic mass on tiles in the 30-m treatment was approximately four times greater and about nine times greater in the clear-cut and 10-m treatments compared with controls during autumn ($F_{3,9}$, $P = 0.004$). In spring, periphyton inorganic mass was three times greater in the 10-m buffer treatment and 18 times greater in the clear-cut treatment compared with controls ($P = 0.01$).
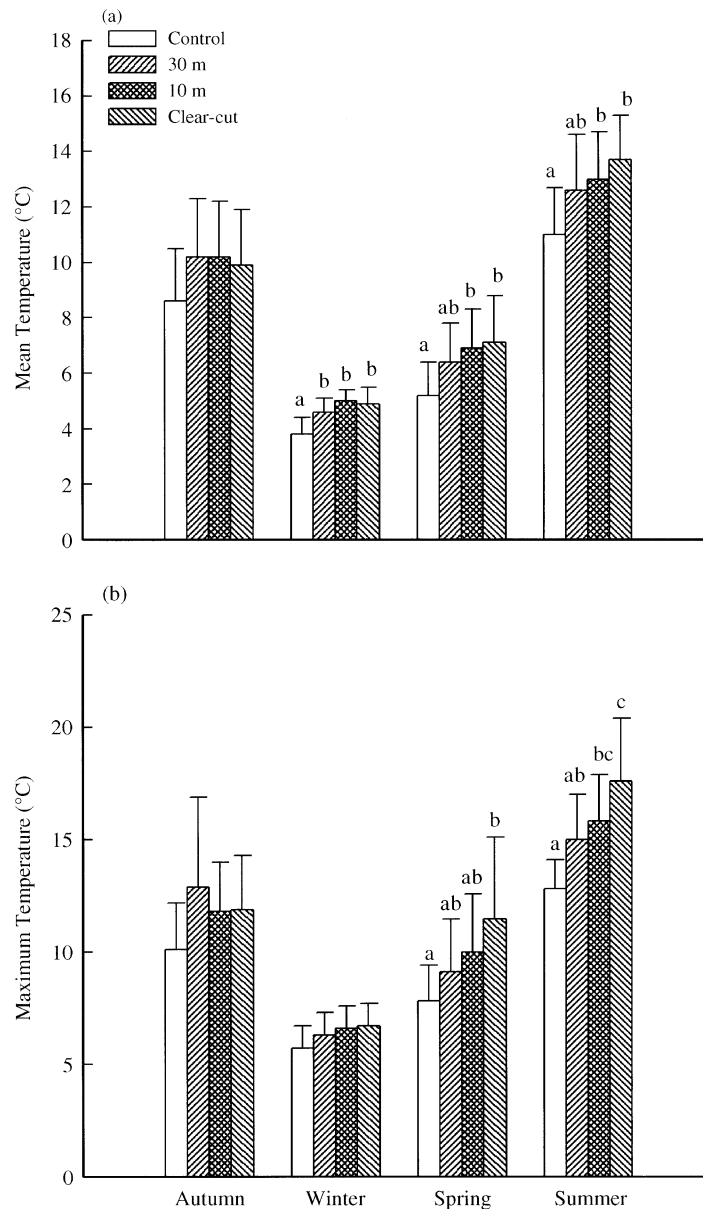
Fig. 3. Mean (1 SD) (a) daily and (b) maximum daily water temperature in each riparian treatment in each season the first year after logging. Means with the same letter were not statistically different based on the within-season comparison.

Chironomidae abundance was higher in summer and autumn than in spring ($F_{2,23}$, $P < 0.0002$), and generally increased with decreasing buffer width ($F_{3,9}$, $P < 0.004$; Fig. 6a). Chironomid abundance was about twofold higher in logged sites compared with controls during all seasons, except spring when abundances in the 30-m treatment and controls were similar. The number of chironomid larvae in spring was threefold greater in the 10-m treatment compared with controls ($F_{3,9}$, $P = 0.08$). Mayfly abundance also increased as buffer width narrowed, but there were no statistical differences among treatments (Fig. 6b).

Multiple, linear regression showed that variation in light level among streams was important in structuring stream communities. Variability in periphyton AFDM was significantly related (+ = positive slope, − = negative slope) to PAR (+), mayfly abundance (−) and

stream power (−) (Table 2). These predictor variables explained 77% of the variability in periphyton AFDM. More than 86% of the variability in chlorophyll *a* biomass was predicted by PAR (+), mayfly abundance (−), dissolved phosphorus concentrations (−) and stream power (−). Based on partial r^2 values, PAR was the most important predictor variable for periphyton AFDM ($r^2 = 0.55$) and chlorophyll *a* ($r^2 = 0.32$), whereas mayfly abundance was the second most important variable ($r^2 = c.\ 0.24$) explaining periphyton biomass. Maximum water temperature was the only variable selected, and accounted for 66% of the variation in Chironomidae abundance. Mayfly abundance was also associated with PAR (+) and periphyton inorganic mass (−): these two variables saccounted for 55% of the variation in the number of mayflies per tile.
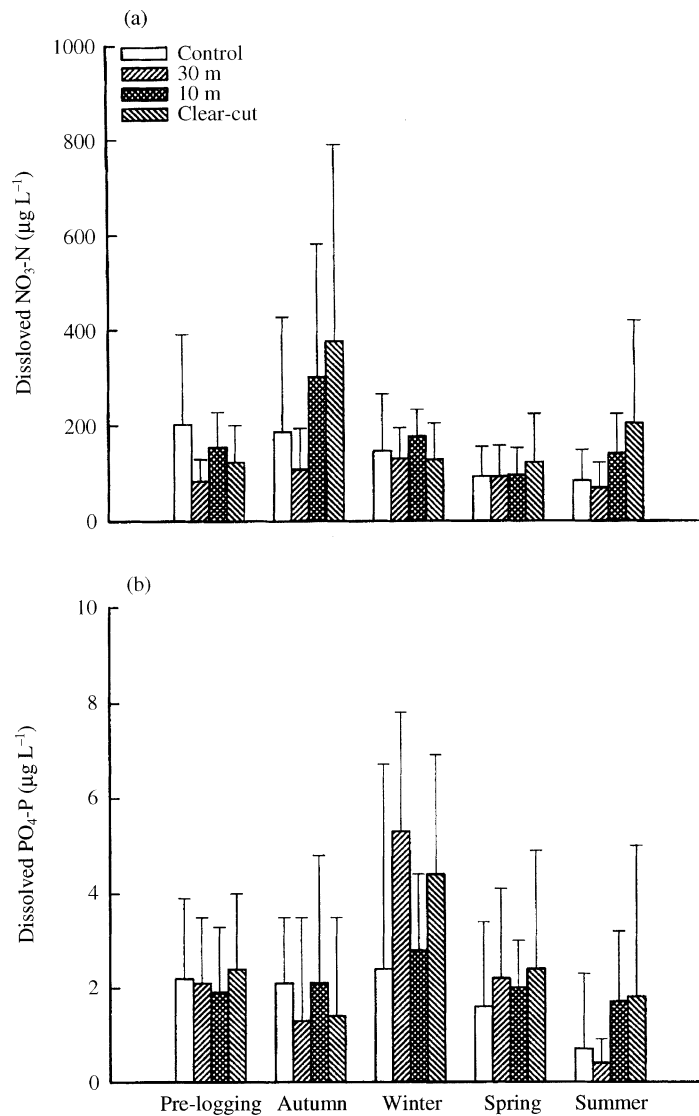
(a)

(b)

Fig. 4. Mean (1 SD) (a) dissolved NO_3-N and (b) PO_4-P in each riparian treatment before logging and in each season the first year after logging. Means with the same letter were not statistically different based on the within-season comparison.

SHORT-TERM COLONIZATION STUDIES

Similar to the replicated experiment, periphyton biomass and inorganic mass, chlorophyll *a* biomass and insect consumer abundance increased with decreasing buffer width. However, results from this intensive study showed that there were differences in periphyton biomass among streams even during winter. Moreover, these data support the observation revealed in the long-term, replicated study that there were statistical differences in food web attributes between the 30-m buffer treatment and controls. Chlorophyll *a* biomass in winter was significantly different among streams: chlorophyll *a* biomass in the 30-m, 10-m, and clear-cut streams was two, three and four times greater, respectively, than in controls (Fig. 7 and Table 3). Periphyton AFDM and chlorophyll *a* in autumn, and Chironomidae abundance in summer, were significantly greater in the 30-m stream compared with controls (Table 3). For example, summer Chironomidae abundance was four times greater in the 30-m buffer stream than the control stream.

We also observed qualitative differences in algal community composition in relation to riparian buffer width (Fig. 8). Diatoms (Baccillariophyceae) dominated the tile community (relative abundance of 99%) in the low-light environment of the control and 30-m buffer streams, with trace amounts of the filamentous green algae *Draparnaldia plumosa* Vauch. and blue-green algae *Oscillatoria* sp. and *Lyngbya* sp. A filamentous chrysophyte *Hydrurus foetidus* Kirschner and *D. plumosa* were more abundant in the high-light environments of the clear-cut and 10-m buffer sites. Filamentous algae made up 20% of the periphyton community at the 10-m buffer site and 45% at the clear-cut site.

Using summer data from the short-term colonization study, mayflies were less likely to colonize tiles with high loads of periphyton inorganic mass. Logistic regression showed that mayflies were significantly dependent upon this covariate {logit(probability of mayfly on tile) = 1·8
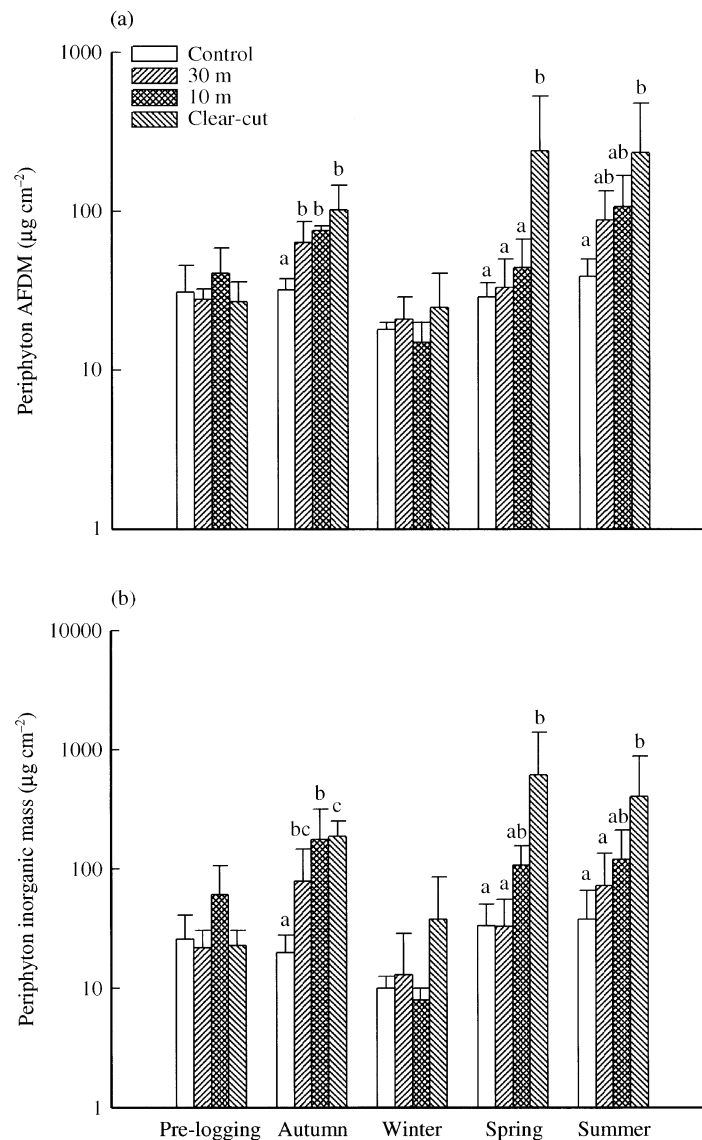
Fig. 5. Mean (a) periphyton AFDM ($\mu g\ cm^{-2}$) and (b) periphyton inorganic mass ($\mu g\ cm^{-2}$) in each riparian treatment before logging and in each season the first year after logging. Note the log-scale for the y-axis. Means with the same letter were not statistically different based on the within-season comparison.

+ -0.93(log[periphyton inorganic mass]), $P = 0.003$, $n = 41$}, whereas chironomids were not affected by periphyton inorganic matter. Mayflies showed a similar response to periphyton inorganic mass when examining data from all 13 streams in August {logit(probability of mayfly on tile) = $0.8 + -0.4$(log[periphyton inorganic mass]), $P = 0.04$, $n = 78$}.

Discussion

This study is unique because we examined the effects of a replicated, experimentally created gradient of riparian buffer width on a variety of abiotic and biotic response variables across all seasons. This approach allowed us to develop potential causal links between changes in PAR and water temperature resulting from riparian manipulations with changes in biological communities. Our experimental manipulation of riparian forests showed that these headwater streams were highly sensitive to forest harvest. We found that mean and maximum water temperature, PAR, periphyton AFDM, chlorophyll *a*, periphyton inorganic mass and chironomid abundance increased as buffer width narrowed. The greatest differences were observed at the clear-cut and 10-m buffer treatments; however, our results also showed that abiotic and biotic attributes were even higher in the 30-m buffer treatment compared with controls during some seasons.

After logging, water temperature and PAR reaching the stream increased as buffer width narrowed. Increased solar flux as riparian buffer width narrowed was a direct result of removal of riparian vegetation, because solar flux is a function of tree height and over-storey canopy cover (Lee 1978). Our observations suggest that additional light penetration comes through the sides of the buffer (Brosofske *et al.* 1997). Brosofske *et al.* (1997) also observed a significant relationship between light level and buffer width along small
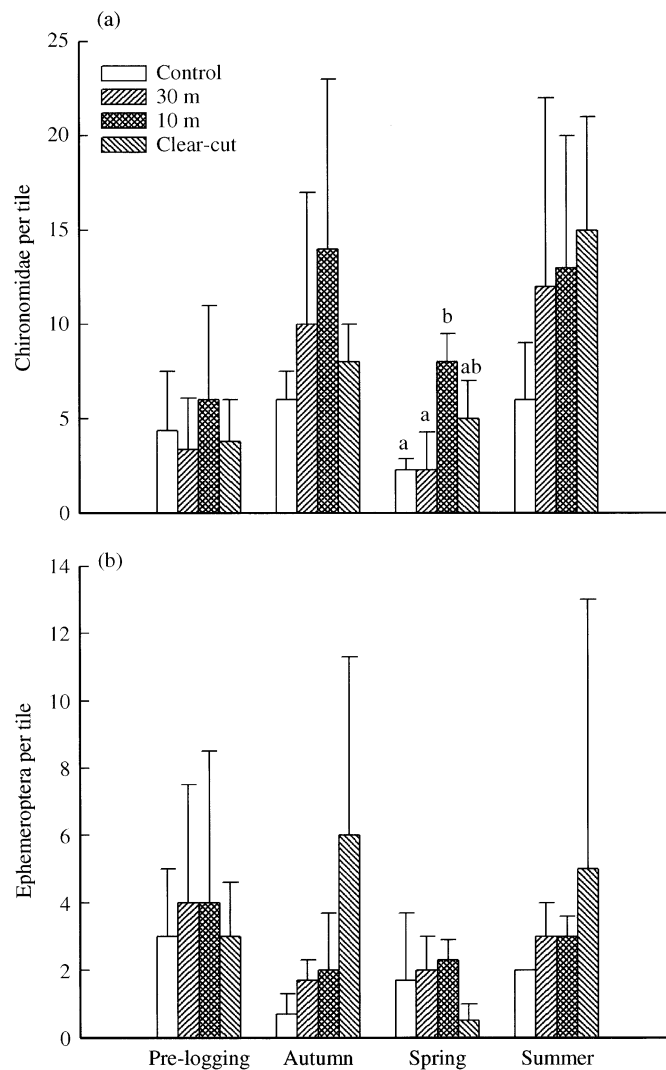
Fig. 6. Mean (a) Chironomidae and (b) Ephemeroptera per tile in each riparian treatment before logging and in each season the first year after logging. Means with the same letter were not statistically different based on the within-season comparison.

Table 2. Best models predicting periphyton biomass and insect consumer abundance in experimental reaches ($n = 13$ streams) using the stepwise and r-square (Akaike's information criterion, used for Ephemeroptera only) selection procedures. Candidate independent variables for periphyton AFDM and chlorophyll a biomass ($\mu g\ cm^{-2}$) included PAR ($\mu mol\ m^{-2}\ s^{-1}$); mean and maximum water temperature (°C); dissolved NO_3-N and PO_4-P ($\mu g\ l^{-1}$); stream power (Watts m^{-1}); Chironomidae and Ephemeroptera abundance (number tile^{-1}); and presence of fish. Candidate independent variables for Chironomidae and Ephemeroptera abundance were the same as for periphyton except for periphyton AFDM and inorganic mass, and chlorophyll a. All variables, except for periphyton inorganic mass and PAR for the model predicting mayfly abundance, were transformed using natural logarithms prior to analysis (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$)

| Dependent variable	Parameter	Estimate (1 SE)	F-statistic	Model r^2
Periphyton AFDM	Intercept	3·46 (0·3)	169·8***	
	PAR	0·42 (0·1)	44·5**	0·77
	Ephemeroptera	−0·43 (0·14)	9·4**	
Chlorophyll a	Intercept	3·39 (0·3)	135·5***	0·86
	PAR	0·3 (0·05)	39·6***	
	Ephemeroptera	−0·38 (0·1)	15·5**	
	Stream power	−0·000004 (0·000001)	7·3*	
	Dissolved PO_4-P	−0·4 (0·1)	8·9*	
Chironomidae	Intercept	−1·15 (0·7)	2·6	0·66
	Maximum water temperature	0·3 (0·07)	21·2***	
Ephemeroptera†	Intercept	2·12 (1·1)	2·0	0·55
	PAR	0·03 (0·01)	3·2*	
	Periphyton inorganic mass	−0·01	−2·7*	

†Parameter estimates derived from simple linear regression.
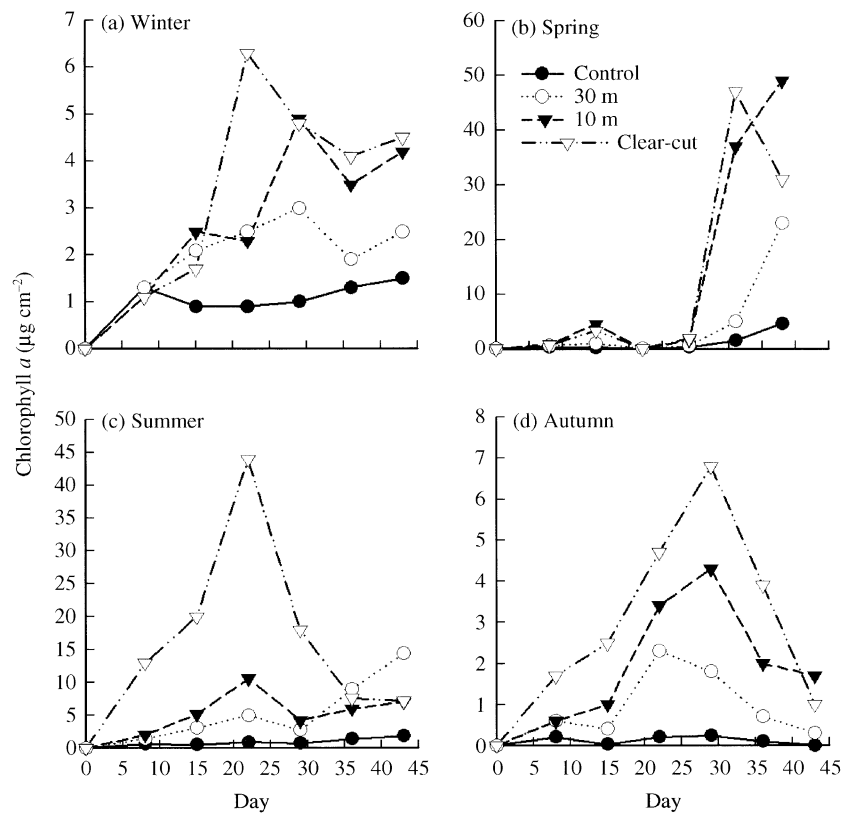
Fig. 7. Mean periphyton chlorophyll *a* (µg cm^{-2}) on each sample date averaged across templates (*n* = 6) during (a) winter (26 January–10 March 1999), (b) spring (6 April–18 May), (c) summer (15 June–27 July) and (d) autumn (23 September–4 November). Templates were placed in a control (East Creek), a 30-m buffer (stream H), a 10-m buffer (stream C) and a clear-cut (stream A). Standard errors are omitted for clarity.

Table 3. Mean (± 1 SD) and *F*-statistics for analysis of covariance, with day as a covariate for biotic response measures after logging within each season (winter, 26 January–10 March; spring, 6 April–18 May; summer, 15 June–27 July; and autumn, 23 September–4 November) for the short-term colonization study. Primary consumer data from summer only are presented because abundances were low during other seasons. The treatment × day (test of equal slopes model) was significant for chlorophyll *a* in summer; therefore, we did not compare differences among treatments in summer. Means followed by the same letter were not statistically significant at a *P* < 0·05 based on least-square means procedure (***P < 0·001, **P < 0·01)

|	Control	30-m	10-m	Clear-cut	Treatment $F_{3,16}$	Day $F_{1,16}$
Autumn						
Periphyton AFDM (µg cm^{-2})	25 (12)[a]	48 (27)[b]	50 (25)[b]	65 (38)[b]	5·0**	25·0***
Chlorophyll *a* (µg cm^{-2})	0·1 (0·1)[a]	1 (0·8)[b]	2 (1)[bc]	4 (2)[c]	13·0***	0·2
Periphyton inorganic mass (µg cm^{-2})	15 (10)[a]	66 (51)[a]	86 (64)[b]	100 (66)[b]	9·5**	43***
Winter						
Periphyton AFDM (µg cm^{-2})	24 (11)[a]	26 (13)[a]	43 (24)[b]	29 (15)[a]	3·0**	16·7***
Chlorophyll *a* (µg cm^{-2})	1 (0)[a]	2 (1)[b]	3 (1)[bc]	4 (2)[c]	9·5**	11·7**
Periphyton inorganic mass (µg cm^{-2})	20 (11)[a]	27 (20)[a]	82 (65)[b]	29 (23)[a]	4·8**	3·6
Spring						
AFDM (µg cm^{-2})	32 (18)[a]	40 (21)[a]	121 (90)[b]	122 (119)[b]	4·2**	11·6**
Chlorophyll *a* (µg cm^{-2})	2 (2)[a]	6 (10)[a]	19 (23)[b]	17 (21)[b]	4·2**	31·8***
Periphyton inorganic mass (µg cm^{-2})	17 (13)[a]	36 (20)[a]	220 (192)[b]	150 (142)[b]	5·0**	40·8***
Summer						
AFDM (µg cm^{-2})	32 (16)[a]	41 (24)[a]	47 (32)[a]	138 (70)[b]	15·0***	13***
Chlorophyll *a* (µg cm^{-2})	1 (0·5)	6 (5)	6 (3)	19 (13)	14·4***	4·0**
Periphyton inorganic mass (µg cm^{-2})	16 (12)[a]	40 (31)[a]	88 (105)[a]	361 (300)[b]	4·2**	13·9***
Chironomidae per tile	1 (0·6)[a]	4 (3)[b]	7 (6)[b]	4 (3)[b]	4·3**	22·2***
Ephemeroptera per tile	0	1 (1)	3 (4)	4 (7)	2·8	8·5**
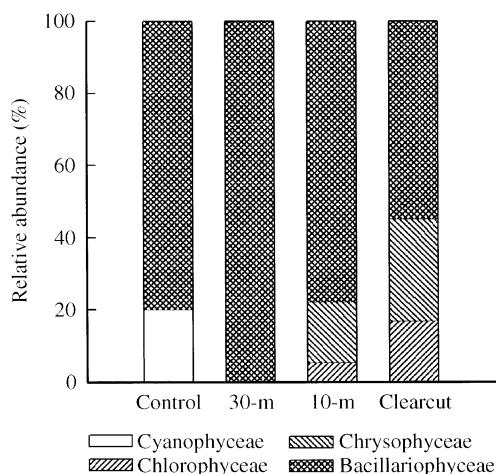
Fig. 8. Relative abundance of the dominant algal orders at the control, 30-m riparian buffer, 10-m buffer and clear-cut streams used in the short-term colonization study in May 1999, the first spring after logging.

streams of western Washington. Changes in water temperature were probably a result of increased solar radiation, as direct-beam solar radiation is the main driver influencing water temperature (Beschta *et al.* 1987; Beschta 1997). Support for this relationship was provided by the strong correlation between water temperature and PAR ($r = 0.92$, $n = 13$). Other studies have also shown a strong relationship between riparian vegetation cover and water temperature (Holtby 1988). Skelly, Freidenburg & Kiesecker (2002) observed that mean water temperature in open-canopied ponds was 5 °C warmer than close-canopied ponds. Vegetation in the riparian zone helps regulate the microclimate of aquatic–riparian ecosystems, and increased solar energy input can lead to higher maximum water temperature, especially in small streams (Sullivan *et al.* 1990). Small streams may be particularly sensitive to removal of riparian vegetation and therefore at increased risk from temperature problems relative to large streams, because small streams have low flow rates and high width-to-depth ratios (Welch, Jacoby & May 1998).

In our study, differences among treatments for water temperature and PAR are based on the assumption that these variables were similar among treatments before logging. We assert that this assumption is valid for our study for the following reasons. First, solar flux has been measured in upstream, forested sections of streams that are part of our riparian experiment, and these values were similar to those measured in controls (P. M. Kiffney, unpublished data). Secondly, elevation, aspect, forest age and composition, geology and geographical location were similar among streams, with the major difference being the riparian buffer treatment left along the water's edge. Thirdly, buffers were experimentally manipulated, and there were at least three replicates within each treatment. Because of these considerations, we suggest that after logging differences in PAR and water temperature can be attributed to riparian buffer width.

Although the actual manipulation of riparian buffer width constituted a disturbance, we suggest impacts associated with these activities were minimal and transient compared with changes in microclimate created by the gradient in riparian buffer width (see the Results, Replicated, whole-watershed experiment). First, to minimize any direct impact on stream habitat, trees were felled away from the stream, which prevents impacts on stream habitat. Secondly, logging equipment (e.g. skidders) was never driven through our stream reaches in the process of removing cut logs. Thirdly, no new roads were built to access watersheds for logging; road construction during logging can have a major impact on stream habitat (Ziemer 1981). These actions therefore minimized any direct impacts of forest removal on our study reaches.

We observed biological gradients that mirrored microclimatic gradients, which were related to buffer width. Periphyton biomass increased as light levels and water temperature increased and buffer width narrowed. We found similar patterns in two large-scale (215–650-m long reaches) and long-term (1–2 years) experimental studies, whereas most of the research examining controls on periphyton communities has been conducted at relatively small spatial and short temporal scales (Hillebrand 2002) and primarily under summer, base flow conditions (Feminella & Hawkins 1995). Periphyton biomass was higher in studies comparing clear-cut with unlogged streams (Gregory 1980; Lowe, Golladay & Webster 1986; Kiffney & Bull 2000; but see Shortreed & Stockner 1983) and in open vs. closed canopy reaches within a stream (Hill & Knight 1988; Feminella, Power & Resh 1989). In general, stream periphyton increases as a non-linear function of light due to increases in photosynthetic rate (Hill 1996). Consumers (Hill, Ryon & Schilling 1995), trophic structure (Wootton & Power 1993) and nutrients (Hillebrand 2002) can also be important in controlling algal accrual. We did not manipulate consumer abundance or nutrients, but our data strongly support the hypothesis that light was the primary constraint on accrual of periphyton biomass. Specifically, our analyses showed that PAR was the single best predictor variable for periphyton biomass.

Not only did periphyton biomass increase, so did the abundance of common primary consumers. Although our ability to detect statistical differences among treatments for insects was low compared with other measures, the consistent trends among seasons and between studies suggest that these animals were responding to changes in light and water temperature, mediated by riparian buffer width. For example, summer chironomid abundance was approximately 100–150% higher in the clear-cut, 10-m and 30-m buffer treatments compared with controls in the replicated experiment, and 300–600% higher during the summer colonization study. Mayflies showed similar patterns. Consumer abundance may have been limited by food resources, as periphyton biomass increased with increased light level

associated with narrow buffers. The abundance or bio-mass of primary consumers has been shown to increase (Quinn *et al.* 1997) as light levels increase, possibly due to increased primary production (Hill, Ryon & Schilling 1995). Others have found that primary consumers did not increase along a light gradient in experimental channels, because predators cropped surplus secondary production (Wootton & Power 1993).

Water temperature can also constrain insect populations (Rempel & Carter 1986) and we found that chironomid abundance was positively related to maximum water temperature. Water temperature has complex effects on life cycles of stream biota (Hogg & Williams 1996). For example, water temperature influences the rate at which eggs develop and juveniles grow, which, in turn, determines voltinism, rates of growth and productivity (Allan 1995). The strong relationship between water temperature and Chironomidae abundance, however, was confounded by the correlation between water temperature and PAR. One of the difficulties with large-scale experiments such as this one is that multiple factors (e.g. light and water temperature) change in response to the manipulation. We addressed this issue with a small-scale channel study (P.M. Kiffney, J.S. Richardson & J.P. Bull, unpublished data). Results from this study showed that chironomids and other primary consumers were indirectly constrained by light level, probably mediated through increased primary production because water temperature was held constant.

Although periphyton and consumer abundance increased as buffer width narrowed, so did periphyton inorganic mass. Forest harvest can influence both upland erosional processes and the way that streams process sediment in channels (Chamberlin, Harr & Everest 1991). We propose an additional mechanism that may help explain the increased sediment levels in periphyton. High light environments primarily support filamentous algal growth forms, while low light environments primarily support diatoms (Hansmann & Phinney 1973; Duncan & Blinn 1989; Wellnitz, Radar & Ward 1996). We observed similar qualitative differences in algal community composition during spring in the four streams of the colonization study (Fig. 8). We hypothesize that filamentous growth forms at the clear-cut and 10-m streams were more efficient at trapping suspended sediment from the water column than the diatom-dominated biofilm of the control and 30-m sites. Evidence for this can be found in the ratio of organic mass to inorganic mass averaged across seasons: a ratio less than one indicates a periphyton community dominated by organic matter, whereas a ratio greater than one indicates a community dominated by inorganic matter. The ratio was less than one in the control and 30-m treatments but increased to 1·7–1·9 in the 10-m and clear-cut treatments. Suren & Jowett (2001) showed that the periphyton mat in untreated stream channels contained less fine sediment and more organic material than channels where fine sediment

was added. It is possible that the increase in periphyton inorganic mass was a result of increasing algal biomass. In other words, increases in periphyton inorganic mass may reflect an increase in ash content due to greater algal biomass. We suggest that this was not the case in our study, because algal communities dominated by diatoms will have a higher ash content due to the presence of silica in their cell walls than other algal forms (Nalewajko 1966). The relative abundance of diatoms was higher at control and 30-m buffer sites, while the high light sites were dominated by filamentous algae and diatoms were rare. Therefore, we conclude that the high inorganic content of periphyton in the clear-cut and narrow buffer sites was due to deposition of fine sediment on the stream bottom.

We also speculate that algal growth form and higher periphyton inorganic content accounted for some of the non-linear responses of consumers to riparian buffer width. For example, there was a trend for mayfly and chironomid abundance in spring to be lower in the clear-cut treatment than in the 10-m treatment. Kiffney & Bull (2000) found that insect abundance on tiles was negatively correlated with periphyton inorganic mass on the same tiles, and periphyton inorganic mass was higher in logged streams compared with controls. Results from the long-term replicated and short-term colonization studies provided additional evidence to suggest that some invertebrates (i.e. mayflies) are negatively correlated with periphyton inorganic mass. Stream invertebrates are negatively affected by sediment deposited on the streambed (Suren & Jowett 2001; Zweig & Rabeni 2001) and high suspended sediment loads (Shaw & Richardson 2001). Insect drift was more than double from stream channels treated with fine sediment compared with untreated channels (Suren & Jowett 2001). Large amounts of inorganic sediment in the periphyton mat and the filamentous nature of the algal community may inhibit attachment by some grazers (Kiffney & Bull 2000) or it may decrease the nutritional quality of periphyton (Hawkins & Sedell 1981). Increased sediment delivery to streams due to forest harvest also has negative consequences for fish (Scrivener & Brownlee 1989; Osmundson *et al.* 2002) and amphibians (Corn & Bury 1989).

MANAGEMENT ISSUES AND APPLICATIONS

The most surprising results from our study were significant changes in some abiotic and biotic attributes at the widest buffer (30 m), which points out how sensitive these headwater streams are to forest harvest. Forest clearing has been shown to affect a wide variety of taxa, such as bryophytes (Hylander, Jonsson & Nilsson 2002), terrestrial (Watt, Stork & Nigel 2002; Hamer *et al.* 2003) and aquatic invertebrates (Newbold, Erman & Roby 1980), salamanders (Vesely & McComb 2002), fish (Murphy *et al.* 1986; Rowe, Smith, Quinn & Boothroyd 2002), birds (Pearson & Manuwal 2001; Williams *et al.* 2001) and mammals (Law & Chidel 2002; Cockle &

Richardson 2003). Some of these studies specifically addressed the relationship between buffer width and biotic abundance and diversity, with most finding that wide buffers (> 30 m) minimized the ecological effects of clear-cut logging on aquatic and terrestrial ecosystems. Results from our replicated, watershed-scale experiment support this conclusion. Other factors besides riparian buffers are important in maintaining ecosystem structure and function when harvesting trees. These include environmental heterogeneity (Hamer *et al.* 2003), successional trajectories of regenerated forest (Summerville & Crist 2002), corridors between watersheds (Law & Chidel 2002) and partial harvest techniques (Sullivan & Sullivan 2001).

It is important to note that we observed these differences by logging a relatively small proportion of the watershed (*c.* 20–25% of total area logged). Although we observed higher dissolved nitrate concentrations in water as the buffer width narrowed, these differences were not statistically significant. If more of the watershed was logged, we may have observed larger differences in nitrate levels (Likens *et al.* 1970). Lewis *et al.* (2001) found that the average increase in annual storm runoff was higher when more of the watershed was logged. We also emphasize that this portion of the study was concerned with elements of the aquatic food web, and other components of the ecosystem such as fish, mammals and amphibians must be considered when determining the most appropriate strategy for managing forested landscapes. These issues will be addressed in future papers.

Acknowledgements

References

Allan, J.D. (1995) *Stream Ecology: Structure and Function of Running Waters.* Chapman & Hall, New York, NY.

Armstrong, F.A.J., Stearns, C.R. & Strickland, J.D.H. (1967) The measurement of upwelling and subsequent biological processes by means of the Technicon Autoanalyzer and associated equipment. *Deep-Sea Research,* **14**, 381–389.

Beschta, R.L. (1997) Riparian shade and stream temperature: an alternative perspective. *Rangelands,* **19**, 25–28.

Beschta, R.L., Bilby, R.E., Brown, G.W., Holtby, L.B. & Hofstra, T.D. (1987) Stream temperature and aquatic habitat: fisheries and forestry interactions. *Streamside Management: Forestry and Fishery Interactions* (eds E.O. Salo &

T.W. Cundy), pp. 191–232. Institute of Forest Resources, University of Washington, Seattle, WA.

Brosofske, K.D., Chen, J., Naiman, R.J. & Franklin, J.F. (1997) Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. *Ecological Applications,* **7**, 1188–1200.

Brown, T.G. & Hartman, G.F. (1988) Contributions of seasonally flooded lands and minor tributaries to the production of coho salmon in Carnation Creek, British Columbia. *Transactions of the American Fisheries Society,* **117**, 546–551.

Castelle, A.J., Johnson, A.W. & Conolly, C. (1994) Wetland and stream buffer size requirements – a review. *Journal of Environmental Quality,* **23**, 878–882.

Chamberlin, T.W., Harr, R.D. & Everest, F.H. (1991) Timber harvesting, silviculture, and watershed processes. *American Fisheries Society Special Publication,* **19**, 181–206.

Cockle, K.L. & Richardson, J.S. (2003) Do riparian buffer strips mitigate the impacts of clearcutting on small mammals? *Biological Conservation,* **113**, 133–140.

Corn, P.S. & Bury, R.B. (1989) Logging in western Oregon: responses of headwater habitats and stream amphibians. *Forest Ecology and Management,* **29**, 39–57.

Darveau, M., Beauchesne, P., Bélanger, L., Huot, J. & Larue, P. (1995) Riparian forest strips as habitat for forest birds in boreal forest. *Journal of Wildlife Management,* **59**, 67–78.

Davies, P.E. & Nelson, M. (1994) Relationship between riparian buffer widths and the effects of logging on stream habitat, invertebrate community composition, and fish abundance. *Australian Journal of Marine and Freshwater Research,* **45**, 1289–1305.

Duncan, S.W. & Blinn, D.W. (1989) Importance of physical variables on the seasonal dynamics of epilithic algae in a highly shaded canyon stream. *Journal of Phycology,* **25**, 455–461.

Feller, M.C. (1977) Nutrient movement through western hemlock – western red cedar ecosystems in southwestern British Columbia. *Ecology,* **58**, 1269–1283.

Feller, M.C. & Kimmins, J.P. (1979) Chemical characteristics of small streams near Haney in southwestern British Columbia. *Water Resources Research,* **15**, 247–258.

FEMAT (1993) Aquatic ecosystem assessment. *Forest Ecosystem Management: An Ecological, Economic, and Social Assessment.* Report of the Forest Ecosystem Management Assessment Team. USDA Forest Service, Washington, DC.

Feminella, J.W. & Hawkins, C.P. (1995) Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. *Journal of the North American Benthological Society,* **14**, 465–509.

Feminella, J.W., Power, M.E. & Resh, V.H. (1989) Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. *Freshwater Biology,* **22**, 445–457.

Franklin, J.F. & Dyrness, C.T. (1969) *Vegetation of Oregon and Washington.* PNW-80. United States Department of Agriculture, Forest Service, Portland, OR.

Fuller, R.L., Roelofs, J.L. & Fry, T.F. (1986) The importance of algae to stream invertebrates. *Journal of the North American Benthological Society,* **5**, 290–296.

Gomi, T., Sidle, R.C. & Richardson, J.S. (2002) Headwater and network systems: understanding processes and downstream linkages of headwater systems. *Biosciences,* **52**, 905–916.

Gore, J.A. (1996) Discharge measurements and streamflow analysis. *Methods in Stream Ecology* (eds F.R. Hauer & G.A. Lamberti), pp. 53–74. Academic Press, San Diego, CA.

Gregory, S.V. (1980) *Effects of light, nutrients, and grazing on periphyton communities in streams.* PhD Thesis. Oregon State University, Corvallis, OR.

Grimm, N.B. & Fisher, S.G. (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.

Hall, R.O., Bernhardt, E.S. & Likens, G.E. (2002) Relating nutrient uptake with transient storage in forested mountain streams. *Limnology and Oceanography*, **47**, 255–265.

Hall, J.D., Brown, G.W. & Lantz, R.L. (1987) The Alsea watershed study: a retrospective. *Streamside Management: Forestry and Fishery Interactions* (eds E.O. Salo & T.W. Cundy), pp. 399–416. Institute of Forest Resources, University of Washington, Seattle, WA.

Hamer, K.C., Hill, J.K., Benedick, S., Mustaffa, N., Sherratt, T.N., Maryati, M. & Chey, V.K. (2003) Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology*, **40**, 150–162.

Hansmann, E.W. & Phinney, H.K. (1973) Effects of logging on periphyton in coastal streams of Oregon. *Ecology*, **54**, 194–199.

Hartman, G., Scrivener, J.C., Holtby, L.B. & Powell, L. (1987) Some effects of different streamside treatments on physical conditions and fish population processes in Carnation Creek, a Coastal Rain Forest stream in British Columbia. *Streamside Management: Forestry and Fishery Interactions* (eds E.O. Salo & T.W. Cundy), pp. 330–373. Institute of Forest Resources, University of Washington, Seattle, WA.

Hawkins, C.P. & Sedell, J.R. (1981) Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. *Ecology*, **62**, 387–397.

Hill, W.R. (1996) Effects of light. *Methods in Stream Ecology* (eds F.R. Hauer & G.A. Lamberti), pp. 123–148. Academic Press, San Diego, CA.

Hill, W.R. & Knight, A.W. (1988) Nutrient and light limitation of algae in two northern California streams. *Journal of Phycology*, **24**, 125–132.

Hill, W.R., Ryon, M.G. & Schilling, E.M. (1995) Light limitation in a stream ecosystem: responses by primary producers and consumers. *Ecology*, **76**, 1297–1309.

Hillebrand, H. (2002) Top-down versus bottom-up control of autotrophic biomass: a meta-analysis on experiments with periphyton. *Journal of the North American Benthological Society*, **21**, 349–369.

Hogg, I.D. & Williams, D.D. (1996) Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. *Ecology*, **77**, 395–407.

Holtby, L.B. (1988) Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 502–515.

Hylander, K., Jonsson, B.G. & Nilsson, C. (2002) Evaluating buffer strips along boreal streams using bryophytes as indicators. *Ecological Applications*, **12**, 797–806.

Keith, R.M., Bjornn, T.C., Meehan, W.R., Hetrick, N.J. & Brusven, M.A. (1998) Response of juvenile salmonids to riparian and instream cover modifications in small streams flowing through second-growth forests of southeast Alaska. *Transactions of the American Fisheries Society*, **127**, 889–907.

Kiffney, P.M. & Bull, J.P. (2000) Factors controlling periphyton accrual during summer in headwater streams of southwestern British Columbia, Canada. *Journal of Freshwater Ecology*, **15**, 339–353.

Kiffney, P.M., Richardson, J.S. & Feller, M.C. (2000) Fluvial and epilithic organic matter dynamics in headwater streams of southwestern British Columbia, Canada. *Archives für Hydrobiologie*, **149**, 109–129.

Lamberti, G.A. & Resh, V.H. (1985) Comparability of introduced tiles and natural substrates for sampling lotic bacteria, algae and macroinvertebrates. *Freshwater Biology*, **15**, 21–30.

Law, B. & Chidel, M. (2002) Tracks and riparian zones facilitate the use of Australian regrowth forest by insectivorous bats. *Journal of Applied Ecology*, **39**, 605–617.

Lee, R. (1978) *Forest Microclimatology*. Columbia University Press, New York, NY.

Leopold, L.B., Wolman, M.G. & Miller, J.P. (1964) *Fluvial Processes in Geomorphology*. Dover Publications, New York, NY.

Lewis, J., Mori, S.R., Keppeler, E.T. & Ziemer, R.R. (2001) Impacts of logging on storm peak flows, flow volumes and suspended sediment loads in Caspar Creek, California. *Land Use and Watersheds: Human Influence on Hydrology and Geomorphology in Urban and Forest Areas* (eds M.S. Wigmosta & S.J. Burges), pp. 85–125. Water Science Application 2. American Geophysical Union, Washington, DC.

Likens, G.E., Bormann, F.H., Johnson, N.M., Fisher, D.W. & Pierce, R.S. (1970) Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed ecosystem. *Ecological Monographs*, **40**, 23–47.

Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS® for Mixed Models*. SAS Institute, Cary, NC.

Lock, M.A., Wallace, R.R., Costerton, J.W., Ventullo, R.M. & Charlton, S.E. (1984) River epilithon: toward a structural-functional model. *Oikos*, **42**, 10–22.

Lowe, R.L., Golladay, S.W. & Webster, J.R. (1986) Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. *Journal of the North American Benthological Society*, **5**, 221–229.

McGurk, B.J. (1989) Predicting stream temperature after riparian vegetation removal. *Proceedings of the California Riparian Systems Conference* (ed. D. Abell), pp. 157–164. Technical Report PSW-110. USDA Forest Service, Davis, CA.

Merritt, R.W. & Cummins, K.W. (1996) *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt, Dubuque, IA.

Meyer, J.L. & Wallace, J.B. (2001) Lost linkages and lotic ecology: rediscovering small streams. *Ecology: Achievement and Challenge* (eds M.C. Press, N. Huntly & S. Levin), pp. 295–317. Blackwell Science, Oxford, UK.

Montgomery, D.R. & Buffington, J.M. (1998) Channel processes, classification, and response. *River Ecology and Management* (eds R.J. Naiman & R.E. Bilby), pp. 13–42. Springer-Verlag, New York, NY.

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

Murphy, M.L., Heifetz, J., Johnson, S.W., Koski, K.V. & Thedinga, J.F. (1986) Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1521–1533.

Naiman, R.J. & Bilby, R.E. (1998) River ecology and management in the Pacific Coastal Ecoregion. *River Ecology and Management* (eds R.J. Naiman & R.E. Bilby), pp. 1–12. Springer-Verlag, New York, NY.

Naiman, R.J., Fetherston, K.L., McKay, S.J. & Chen, J. (1998) Riparian forests. *River Ecology and Management* (eds R.J. Naiman & R.E. Bilby), pp. 289–323. Springer-Verlag, New York, NY.

Nalewajko, C. (1966) Dry weight, ash, and volume data for some freshwater planktonic aglae. *Journal of the Fisheries Research Board of Canada*, **23**, 1285–1288.

Newbold, J.D., Erman, D.C. & Roby, K.B. (1980) Effects of logging on macroinvertebrates in streams with and without buffer strips. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 1076–1085.

Osmundson, D.B., Ryel, R.J., Lamarra, V.L. & Pitlick, P. (2002) Flow-sediment-biota relations: implications for river regulation on native fish abundance. *Ecological Applications*, **12**, 1719–1739.

Pearson, S.F. & Manuwal, D.A. (2001) Breeding bird response to riparian buffer width in managed Pacific Northwest Douglas-fir forests. *Ecological Applications*, **11**, 840–853.

Peterson, B.J., Wollheim, W.H., Mulholland, P.J., Webster, J.R., Meyer, J.L., Tank, J.L., Martí, E., Bowden, W.B., Valett, H.M., Hershey, A.E., McDowell, W.H., Dodds, W.K., Hamilton, S.K., Gregory, S. & Morrall, D.D. (2001) Control of nitrogen export from watersheds by headwater streams. *Science*, **292**, 86–90.

Pinay, G. & Dècamps, H. (1988) The role of riparian woods in regulating nitrogen fluxes between the alluvial and surface water: a conceptual model. *Regulated Rivers: Research and Management*, **2**, 507–516.

Platts, W.S. & Megahan, W.F. (1975) Time trends in riverbed sediment composition in salmon and steelhead spawning areas: South Fork Salmon River, Idaho. *Transactions of the North American Wildlife Natural Resource Conference*, **40**, 229–239.

Pollock, M.M. (1998) Biodiversity. *River Ecology and Management* (eds R.J. Naiman & R.E. Bilby), pp. 423–454. Springer-Verlag, New York, NY.

Quinn, J.M., Cooper, A.B., Stroud, M.J. & Burrell, G.P. (1997) Shade effects on stream periphyton and invertebrates: an experiment in streamside channels. *New Zealand Journal of Marine and Freshwater Research*, **31**, 665–683.

Rempel, R.S. & Carter, J.C.H. (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.

Rowe, D.K., Smith, J., Quinn, J. & Boothroyd, I. (2002) Effects of logging with and without riparian strips on fish species abundance, mean size, and the structure of native fish assemblages in Coromandel, New Zealand, streams. *New Zealand Journal of Marine and Freshwater Research*, **36**, 67–79.

Scrivener, J.C. & Brownlee, M.J. (1989) Effects of forest harvesting on spawning gravel and incubation of chum (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) in Carnation Creek, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 681–696.

Semlitsch, R.D. (1998) Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conservation Biology*, **12**, 1113–1119.

Shaw, E.A. & Richardson, J.S. (2001) Direct and indirect effects of sediment pulse duration on stream invertebrate assemblages and rainbow trout (*Oncorhynchus mykiss*) growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 2213–2221.

Shortreed, K.S. & Stockner, J.G. (1983) Periphyton biomass and species composition in a coastal rainforest stream in British Columbia: effects of environmental change caused by logging. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 1887–1895.

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

Story, A., Moore, R.D. & McDonald, J.S. (2003) Stream temperature in two shaded reaches below cutblocks and logging roads: downstream cooling linked to subsurface hydrology. *Canadian Technical Reports on Fisheries and Aquatic Sciences*, in press.

Strahler, A.N. (1957) Quantitative analysis of watershed geomorphology. *Transactions of the American Geophysical Union*, **38**, 913–920.

Sullivan, K., Tooley, J., Doughty, T., Caldwell, J. & Knudsen, P. (1990) *Evaluation of Prediction Models and Characterization of Stream Temperature Regimes in Washington.* TFW-Wq3-90-006. Washington State Department of Natural Resources, Olympia, WA.

Sullivan, T.P. & Sullivan, D.S. (2001) Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. *Journal of Applied Ecology*, **38**, 1234–1252.

Summerville, K.S. & Crist, T.O. (2002) Effects of timber harvest on forest Lepidoptera: community, guild, and species responses. *Ecological Applications*, **12**, 820–835.

Suren, A.M. & Jowett, I.G. (2002) Effects of deposited sediment on invertebrate drift: an experimental study. *New Zealand Journal of Marine and Freshwater Research*, **35**, 725–737.

Vesely, D.G. & McComb, W.C. (2002) Salamander abundance and amphibian species richness in riparian buffer strips in the Oregon Coast Range. *Forest Science*, **48**, 291–297.

Volk, C.J., Kiffney, P.M. & Edmonds, R.L. (2003) Role of riparian red alder (*Alnus rubra*) in the nutrient dynamics of coastal streams of the Olympic Peninsula, WA, USA. *American Fisheries Society Special Publication*, **34**, 213–228.

Vouri, K. & Joensuu, I. (1996) Impact of forest drainage on the macroinvertebrates of a small boreal headwater stream: do buffer zones protect lotic biodiversity? *Biological Conservation*, **77**, 87–95.

Watt, A.D., Stork, N.E. & Bolton, B. (2002) The diversity and abundance of ants in relation to forest disturbance and plantation establishment in southern Cameroon. *Journal of Applied Ecology*, **39**, 18–30.

Welch, E.B., Jacoby, J.M. & May, C.W. (1998) Stream quality. *River Ecology and Management: Lessons from the Pacific Coastal Ecoregion* (eds R.J. Naiman & R.E. Bilby), pp. 69–96. Springer-Verlag, New York, NY.

Wellnitz, T.A., Rader, R.B. & Ward, J.V. (1996) Light and a grazing mayfly shape periphyton in a Rocky Mountain stream. *Journal of the North American Benthological Society*, **15**, 496–507.

Williams, M.R., Abbott, I., Liddeow, G.L., Vellios, C., Wheeler, I.B. & Mellican, A.E. (2001) Recovery of bird populations after clearfelling of tall open eucalypti forest in Western Australia. *Journal of Applied Ecology*, **38**, 910–920.

Wipfli, M.S. & Gregovich, D.P. (2002) Invertebrate and detritus export from fishless headwater streams in southeast Alaska: implications for upland forest management and downstream fish-bearing habitats. *Freshwater Biology*, **47**, 957–970.

Wootton, J.T. & Power, M.E. (1993) Productivity, consumers, and the structure of a river food chain. *Proceedings of the National Academy of Sciences*, **90**, 1384–1387.

Young, K.A. (2000) Riparian zone protection in the Pacific northwest: who's cutting what? *Environmental Management*, **26**, 131–144.

Ziemer, R.R. (1981) Stormflow responses to roadbuilding and partial cutting in small streams of northern California. *Water Resources Research*, **17**, 907–917.

Zweig, L.D. & Rabeni, C.F. (2001) Biomonitoring for deposited sediment using benthic invertebrates: a test on four Missouri streams. *Journal of the North American Benthological Society*, **20**, 643–657.