Seasonal and temporal variation in the effects of forest thinning on headwater stream benthic organisms in coastal British Columbia

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Abstract

Removal of riparian trees can alter aquatic ecosystem structure and function by influencing factors such as light availability, sediment input, and stream temperature. Contemporary forest practices such as variable retention harvest are used to mitigate the effects of clear-cut forest harvest on stream communities, but few studies have examined the effects of these techniques on aquatic ecosystems. We examined the effects of variable retention harvest on light, temperature, biofilm biomass and macroinvertebrate consumers in three coastal headwater streams in British Columbia, Canada and compared them to three nearby reference streams with unlogged riparian stands. Variable retention harvest increased light and stream temperature variability. Harvested catchments had higher stream biofilm biomass in all seasons except winter and higher invertebrate abundance in summer. Variable retention harvest altered invertebrate community composition, largely driven by increasing Chironomidae abundance and decreasing Simuliidae abundance. In conclusion, we found that variable retention harvest modified stream benthic communities, but responses varied seasonally and among taxa. This is one of few studies to investigate the impacts of variable retention harvest on multiple trophic levels over multiple seasons and years. Understanding the cascading effects of forest harvest over multi-year time scales is important for management decisions.

Keywords: timber harvest; variable retention; riparian zones; headwater streams; watershed; biofilm

1. Introduction

Riparian zones are important ecotones that provide a number of ecosystem services. Riparian vegetation stabilizes banks and limits sediment inputs, provides nutrients and energy to aquatic and terrestrial organisms, supplies large wood to streams that dissipates energy and provides habitat, and regulates microclimate and water temperature (Naiman and Décamps, 1997). Therefore, the removal of riparian trees can profoundly modify the structure and function of aquatic ecosystems (Vuori and Joensuu, 1996; Sabater et al., 2000; Studinski et al., 2012). For example, clear-cutting riparian forests alters the size, location, and decomposition rate of woody debris in streams (Bilby and Ward, 1991). This change can alter stream morphology and nutrient input, affecting fish and other aquatic species (Fetherston et al., 1995).

One of the most significant impacts of removing riparian forests via logging is the change in solar energy reaching the stream surface (Kiffney et al., 2004; Kaylor et al., 2017). The increase in light has a multifold effect, causing an increase in water temperature and primary productivity, which in turn can increase the biomass and abundance of higher trophic levels (Kiffney et al., 2004; Danehy et al., 2007). For example, riparian logging has been shown to affect the community structure of aquatic invertebrates (Murphy and Hall, 1981; Richardson and Danehy, 2007). In small headwater streams, aquatic invertebrates are ubiquitous and play a central role in the functioning of stream and adjacent riparian ecosystems (Wallace and Webster, 1996). Changes in invertebrate abundance and community composition can affect streams by decreasing food availability for higher trophic levels and altering ecosystem functions such as nutrient retention or litter decomposition (Suter and Cormier, 2014).

Headwater streams compose the upper portion of a watershed and can make up 70-80% of network stream length (Leopold et al., 1964). Headwater streams are extremely important to downstream reaches, providing cool water, sediment, nutrients, and organic matter to larger fish-bearing rivers (Macdonald and Coe, 2007; Wipfli et al., 2007). Due to their small size, they are more vulnerable than larger river sections to environmental perturbations such as changes in forest cover and sediment inputs from logging or other human impacts (Benda et al., 2005; Richardson et al., 2005). However, headwater streams are often overlooked compared to larger downstream sections because of the difficulty of accessing and managing large and complex stream networks (Gomi et al., 2002; Benda et al., 2005).

The use of vegetated riparian buffers has become standard practice for protecting water quality and stream biota with the goal of mitigating anthropogenic disturbance to stream ecosystems (Richardson et al., 2012). Buffer strips are shown to be effective at reducing the impacts of clear-cutting on streams (Kiffney et al., 2003). However, the lack of disturbance in these carefully managed buffers can create a habitat that is simplified to a degree that is unnatural in the system (Swanson et al., 2011). More active management techniques such as variable retention harvest are gaining traction as a way to minimize logging effects while maintaining and promoting biodiversity within the cut site. Variable retention harvest is a relatively new silviculture method designed to maintain structural diversity (such as snags, coarse woody debris, and herb and shrub layers) and forest influence (i.e. the biophysical effects of the forest on surrounding land) in a majority of the harvest site (Mitchell and Beese, 2002). The variable retention method was first developed in the Pacific Northwestern United States, and it is used as a harvesting and forest management technique by governmental organizations such as the United States Forest Service and the Bureau of Land Management (Franklin and Donato, 2020). It has also been adopted in northern Europe and British Columbia, Canada: in British Columbia about 29% of coastal public lands were harvested using the variable retention system between 2006 and 2017 (Beese et al., 2019; Gustafsson et al., 2020). Variable retention harvest creates “life-boating” habitat that maintains tree diversity in the cut site and allows some species to persist after harvest, resulting in better maintenance of biodiversity compared to clear-cut forests (Beese et al., 2019). However, little is known regarding the effects of this contemporary land management practice on streams.

Studies on the effects of variable retention harvest have shown that increased forest cover helps mitigate the effects of increased light on stream temperature, but this effect was highly dependent on thinning intensity, stream morphology, and depth (Macdonald et al., 2003; Guenther et al. 2014; Roon et al., 2021). Previous studies on commercial riparian thinning showed little difference in biofilm or macroinvertebrate assemblages between unlogged and thinned treatments, suggesting that selective cutting has less of an effect on streams when compared to clear cutting or other harvesting strategies (Danehy et al., 2007; Wilkerson et al., 2009). These studies show some potential for variable retention and other selective cutting methods in mitigating the impacts of clearcutting. However, there is a need for more studies that examine how the complex relationships between light, temperature, streamflow, biofilm accumulation, and insect consumer abundance are altered by these harvesting methods.

The purpose of this study was to investigate the impacts of riparian forest harvest using the variable retention method in headwater streams in British Columbia, Canada. We investigated logging impacts on abiotic and biotic factors at several trophic levels in multiple seasons and years to understand the cascading effects of logging and subsequent forest recovery on headwater stream ecosystems. Our main research questions were as follows. What is the extent to which increases in light from variable retention harvest increase water temperature, biofilm biomass, and insect consumer abundance and biomass? How will these changes vary seasonally and over time due to forest regrowth? How does the composition of insect consumer taxa change with increased light availability? We predicted that increases in light due to reduced forest cover would increase water temperature and periphyton AFDM, which would in turn increase benthic invertebrate abundance and diversity of primary consumers because of increased food. We expected the effects of harvest to be most pronounced in the summer because of the combination of increased light and temperature and decreased streamflow, resulting in more accumulation of biofilm and survival of insects. We predicted that these effects would be largest immediately after harvest and then become less pronounced over time due to the growth of riparian grasses and shrubs in the forest understory. We compared three streams with riparian forests that were thinned using the variable retention method with three fully-forested reference streams. We measured water temperature and biofilm biomass before and after logging and streamflow and insect consumer abundance after logging. This study provides a more comprehensive look into the multi-trophic, seasonal, and longer term effects of variable retention forest harvest, which is important for management decisions.

2. Materials and Methods

2.1 Study Site

The experimental watersheds were located in the Malcolm Knapp Research Forest (MKRF) near Maple Ridge, British Columbia, Canada, approximately 60 km east of Vancouver (Table 1). The research forest lies within the Coastal Western Hemlock biogeoclimatic zone (Feller, 1977). The dominant tree species are Western Redcedar (*Thuja plicata*), Western Hemlock (*Tsuga heterophylla*), and Douglas-fir (*Pseudotsuga menziesii*). Black cottonwood (*Populus trichocarpa*), paper birch (*Betula papyrifera*), red alder (*Alnus rubra*), vine maple

(*Acer circinatum*), and salmonberry (*Rubus spectabilis*) comprise most of the broadleaf riparian species. The forests in the experimental watershed have been greatly affected by humans and natural disturbances, including logging in the early 1900s and large fires in 1925 and 1931. The forest consists of naturally regenerated ~85 year old stands (Kiffney et al., 2003).

Climate in the study area is described as marine warm temperate rainy (Feller 1977. Between 1945 and 2007, average annual total precipitation (64 % falling as rain) measured at the research forest headquarters was 2879 mm, with a low of ~1700 mm in the 2002–2003 water year (1 Oct. – 30 Sept.) and a maximum of almost 3900 mm in 1996–1997. The elevation of the experimental watershed ranges from 135-610 m. These small (~ 0.5–1.5 m wetted width), generally steep headwater streams drain glacial soil underlain by igneous bedrock; all have a southerly aspect and are tributary to the Fraser River (Feller and Kimmins, 1979). Channel reaches consist mostly of step-pools, pools, and riffles. Stream substrates were a mix gravel and cobbles with some boulders in riffles and step-pools, with sand, gravel, and organic detritus dominant in pools and wetlands. East, Mirror, and Mike creeks also have small populations of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*).

Stream	Treatment	Watershed area (ha)	Thinned area (ha)	Watershed logged (% area)	Summer base flow discharge (1 m^3/s)	Elevation range (m)	Stream gradient (%)	Stream length logged (m)
East Creek	Reference	44.0	0	0	0.018	295-455	4	0
Mike Creek	Reference	25	0	0	0.005	240-310	8	0
Spring Creek	Reference	35	0	0	0.0097	135-500	4	0
Mirror Creek	Thinned	26.3	7.8	14.8	0.0035	250-320	5	137
Griffith Creek	Thinned	27.3	6.8	12.5	0.0049	370-525	13	283
Sidle Creek	Thinned	38.1	4.4	5.8	0.0031	405-610	19	233

Table 1. Physical characteristics of experimental reaches at Malcolm Knapp Research Forest in Maple Ridge, British Columbia, Canada. 50% of the basal area was removed in each thinned section.

2.2 Experimental Design

Three streams were selected for each of the two treatments. Due to logistical considerations, the selection of these streams was not completely random. East Creek, Mike Creek, and Spring Creek were chosen as reference treatments where the riparian forest remained unlogged. East Creek was chosen as a reference site because it is a long-term monitoring site, while Mike and Spring creeks were reference streams for a related study (e.g., Kiffney et al. 2003). Mirror Creek, Sidle Creek, and Griffith Creek were harvested using the variable retention method, where 50% of the basal area was removed within the cut block. This treatment involved dispersed retention of single-spaced trees. Logging in Griffith Creek began in September 2004 and was completed in November of 2004. Logging in Sidle and Mirror creeks began in late 2004 and was completed in early 2005.

2.2.1. Abiotic data collection

We measured photosynthetically active radiation (PAR as $\mu mol \cdot m^{-2} \cdot s^{-1}$) at each stream during each sample event using a hand-held LiCor light meter and quantum sensor (Model LI 250; LiCor, Lincoln, NB). Several PAR measurements were taken directly above the water surface at each tile locations between 10:00 and 14:00 h under a range of weather conditions (e.g. cloudy, partly cloudy, and sunny). Stream temperature was measured hourly with Onset temperature loggers (Onset®, Pocasset, MA). East Creek, one of the reference sites and Griffith Creek, the variable retention site, had v-notch weirs where instantaneous water level was recorded and converted to mean daily discharge (L/s). Because we only had discharge data from East Creek through 2007 and Griffith Creek streamflow data from 2006 onward, we performed a linear regression of discharge of the two streams and used the equation to predict discharge in East Creek for the last year of the study. East Creek and Griffith Creek had a strong linear relationship ($R^2 = 0.93$, $P < 0.001$).

2.2.2. Biotic data collection

Biofilm is a complex mixture of algae, bacteria, and detritus that accumulates on submerged substrates in freshwater ecosystems. We sampled biofilm using six unglazed ceramic tiles (112 cm^3 each) placed in each stream and randomly distributed between pools (n = 3) and riffles (n = 3). Tiles were used instead of natural substrata to increase reproducibility and consistency within and between streams. A previous study found that unglazed tiles support algal and invertebrate communities similar to natural substrates (Lamberti and Resh, 1985). Tiles were secured to wire screens using cable tiles and attached to the stream bottom using metal rods. We measured biofilm accumulation and insect abundance on tiles every 3-4 months from June 2004 to April 2008. Due to logistical constraints, we were not able to sample all seasons in all years of the study (Table 2).

	Pre-harvest	**Pre-harvest**	**Harvest**	**Post-harvest**	**Post-harvest**	**Post-harvest**
Measurement	2002-2003	2003-2004	2004-2005	2005-2006	2006-2007	2007-2008
PAR	None	None	Spring, Summer	Fall, Winter, Spring	Spring	None
Temperature	Daily	Daily	Daily	Daily	Daily Until 03/29/07	None
AFDM	Fall, Winter, Spring	Summer	Fall, Winter, Spring, Summer	Fall, Spring	Winter, Spring, Summer	Winter, Spring
Invertebrates	None	None	Winter, Spring, Summer	Fall, Spring	Winter, Spring, Summer	Winter, Spring

Table 2. Seasons in each water when measurements were taken over the course of the study. Water year in the Northern hemisphere is 1 Oct to 30 Sept.

To quantify invertebrate abundance and biomass, we counted, measured, and identified invertebrates on each tile using a hand-held 10× magnifying lens (Baush & Lomb). We observed a range of invertebrate taxa including mayflies (Ephemeroptera: Baetidae and Heptageniidae), caddisflies (Trichoptera: *Glossosoma* and *Neophylax*), blackflies (Simuliidae), stoneflies (Plecoptera: Nemouridae), and chironomids (Diptera: Chironomidae). These insects primarily feed on biofilm as collector-gatherers or scrapers (Merritt and Cummins, 1996). Although invertebrates were likely lost when the tiles were removed, each tile was treated in the same manner, therefore minimizing bias. Each individual was measured to the nearest millimeter and the length of each invertebrate was converted to biomass using equations from Benke et al. (1999). Insect taxa richness was measured as the number of different taxa observed on the tile.

After counting insects, we removed biofilm from the top surface of tiles by scraping with a razor blade, scrubbing with a toothbrush, and rinsing into a collection vessel using distilled water. The sample was then poured into a vial and frozen. In the laboratory, thawed samples were filtered onto pre-combusted and pre-weighed glass fiber filters (Gelman type A/E) then dried at 70º C overnight and weighed. Filters were ashed for 2–4 h at 550º C and weighed again to calculate the ash-free dry mass (AFDM).

2.3 Statistical Analyses

To evaluate how thinning influenced stream temperature regimes, we used several descriptors detailed in Benjamin et al. (2016) and Steel et al. (2017). These temperature metrics were chosen to highlight different components of thermal regimes, magnitude and variability, each of which have different ecological consequences (Steel et al., 2017). We used average weekly average temperature (AWAT), maximum weekly average temperature (MWAT), and the maximum weekly maximum temperature (MWMT) as measures of magnitude, and daily temperature range as a measure of variability.

We conducted a before-after control-impact (BACI) analysis to evaluate the effects of variable retention harvest on each stream temperature metric (AWAT, MWAT, MWMT, and daily range) and biofilm AFDM using linear mixed effects models in the `nlme` package in R (Pinheiro et al., 2021). Our fixed effects were season, before/after logging (BA), and logging treatment. We included a random intercept by stream to account for variation between streams. A significant BA and treatment interaction indicates a significant BACI effect. When models did not meet the assumption of independent residuals, we fit autoregressive moving average (ARMA) correlation structures to account for temporal autocorrelation in stream temperature. Daily range and biofilm AFDM were log transformed to meet the assumption of normality. We used the `emmeans` package to calculate pairwise temperature comparisons within each season (Lenth, 2021). We also used linear mixed effects models on each stream temperature metric and biofilm AFDM to test whether there was evidence of a decrease in the treatment effect over time as riparian plants establish and grow, potentially thriving as more light reaches the surface. We used treatment, water year, and season as fixed effects with a random intercept by stream. Only post-logging data was used for this analysis.

We used a linear mixed model with treatment, season, and their interaction as fixed effects, stream as a random effect, and log transformed biofilm AFDM as the response to determine whether there were differences in biofilm AFDM between treatments in certain seasons. This model was performed only on post-harvest data. This was done in addition to the BACI analysis to determine how increases in biofilm AFDM in treatment streams compared to natural variation between streams. To determine the relative importance of abiotic variables in explaining variation in biofilm AFDM, we fit a linear model with log transformed AFDM as the response, PAR, streamflow, and daily average stream temperature as the predictors and used the forward selection procedure. We also tried maximum daily temperature in the model and found no difference in the variance explained. We used Spearman's correlation test to explore the relationships between PAR, stream temperature, streamflow, biofilm AFDM, and invertebrate abundance and biomass. We used a Spearman's test because it is based on ranked data and does not have the assumption of normality.

We did not collect pre-logging data for PAR and invertebrate abundance and biomass so we could not perform a BACI analysis on these variables. Additionally, PAR and invertebrate abundance and biomass deviated significantly from normality and could not be transformed to meet parametric assumptions. We tested for differences between treatments using non-parametric permutation tests. In addition to testing overall differences between treatments across all seasons and years, we tested for differences between treatments within each season. We also used randomized permutations to test for differences between treatments within each water year (1 October – 30 September) to evaluate the effects of logging over time and to see whether recovery of riparian vegetation had any effect on these responses.

Randomized permutation tests create the null distribution by reshuffling data, assigning datapoints randomly to treatments, and calculating the test statistic for each random reshuffling (Good, 2013). In our experiment, the test statistic of interest was the difference in mean values of each tile between variable retention and reference streams. We repeated the randomizations 10,000 times, calculated the mean difference between groups for each randomization, and then compared those randomized test statistics to our observed difference. The *P*-value was obtained by calculating how many times our observed difference was larger than the randomized difference and dividing it by the number of permutations (10,000).

Macroinvertebrates were identified at various taxonomic levels, so we divided them into five groups: mayflies, caddisflies, stoneflies, blackflies, and chironomids. We used Analysis of Similarities (ANOSIM) in the R ‘vegan’ package to test for differences in tile invertebrate community composition between logging treatments (Oksanen et al., 2019). We created a matrix of the abundances of each taxonomic group per tile and sampling date and analyzed whether there were more similarities within or among treatment groups. To see which taxonomic groups were driving differences in community composition, we used randomized permutations to test for differences in the response of each group to the logging treatment.

3. Results

3.1. Physical Characteristics

The most pronounced effect of variable retention harvest was the 10-fold higher amount of light, as photosynthetically active radiation, reaching the variable retention streams ($P < 0.001$). PAR was 11 times higher in variable retention streams in winter, spring, and summer ($P < 0.001$) and 8 times higher in variable retention streams in fall ($P < 0.001$; Fig. 1). Moreover, PAR was higher in variable retention streams in all and years measured (2004-2005, 2005-2006, and 2006-2007; $P < 0.001$). Average weekly temperature (AWAT), average weekly maximum temperature (MWAT), and maximum weekly temperature (MWMT) varied seasonally, while daily temperature range did not. AWAT in the summer was 1.7 °C warmer than fall ($P < 0.001$), 2.11 °C warmer than winter ($P < 0.001$) and 0.92 °C warmer in spring ($P = 0.1$). MWMT in summer was 1.5 °C warmer than fall ($P < 0.01$) and 1.9 °C warmer than winter ($P < 0.01$). Daily temperature range had a significant treatment and BA interaction, indicating an effect of logging on stream temperature variability (Fig. 2d). Pairwise contrasts show that daily temperature range was higher in all seasons in treatment streams ($P < 0.01$). The statistical model indicated AWAT, MWAT, and MWMT did not differ between treatments and there was no treatment and BA interaction or treatment, BA, and season interaction. However, two of the streams, Griffith Creek and Mirror Creek, had clear increases in all temperature metrics in the summer season after logging (Fig. 2). When Sidle Creek was removed, AWAT was 1.1 °C higher, MWAT was 1.7 °C higher, and MWMT was 2.8 °C in Griffith and Mirror Creek in the summer compared to reference. The insignificant model results indicate that the observed increases in summer water temperature are comparable to between-stream and interannual variation. Additionally, stream temperature did not differ by year and there was no treatment by year interaction for any of the stream temperature metrics, indicating that there was no effect of vegetation recovery on stream temperature over the course of the study.

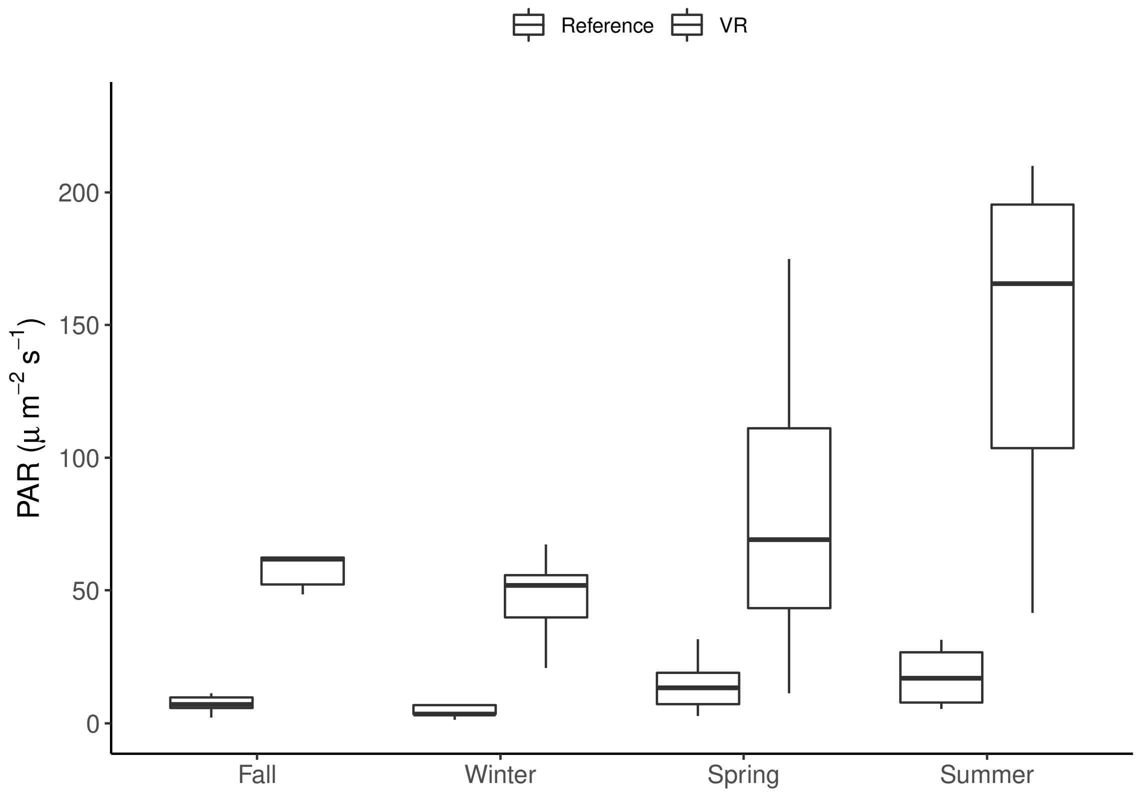

Figure 1. Photosynthetically active radiation (PAR) and timber harvest treatment by season. Includes values from all post-harvest years.

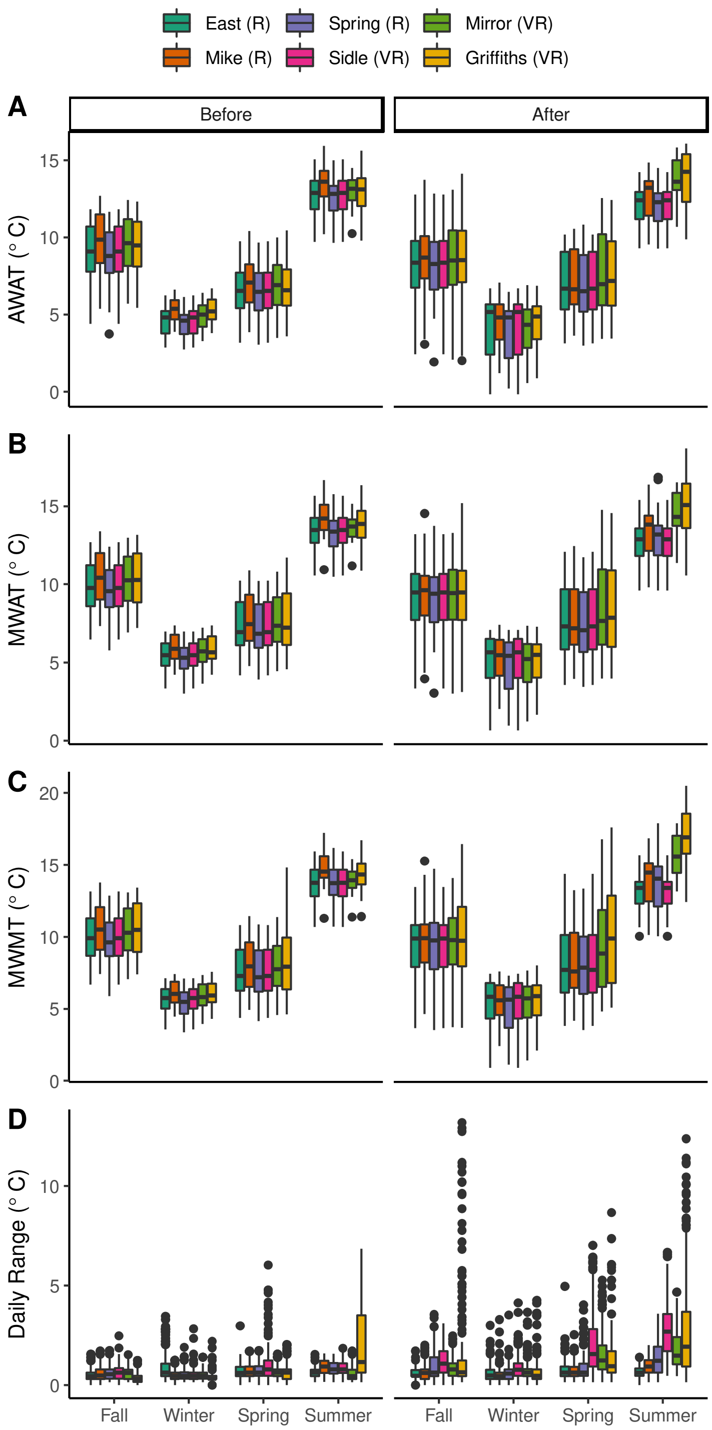

Figure 2. Seasonal patterns of A) Average weekly temperature, B) Average weekly average temperature, C) Maximum weekly temperature, and D) Daily temperature range for each stream. Treatments are indicated next to streams in the legend (R is reference and VR is variable retention).

3.2 Biological Characteristics

On average, variable retention streams had three times higher biofilm AFDM than reference streams. AFDM differed between seasons ($P < 0.001$) and the interaction of BA and treatment was marginally non-significant ($P = 0.09$). However, post-hoc pairwise contrasts based on the BACI model indicate that thinned streams had significantly higher biofilm after logging ($P < 0.01$), while control streams did not (Fig. 3). The model comparing treatments using only post-harvest data found no treatment effect in any season, suggesting that post-logging increases in biofilm were comparable to the natural variation in biofilm biomass between streams. Biofilm AFDM differed between years ($P < 0.001$), but there was no treatment and year interaction, indicating that there was no effect of riparian plant recovery on biofilm biomass over time. The multiple regression multiple showed that PAR, streamflow, and stream temperature were important in explaining variation in biofilm biomass, explaining almost 50 % of total model variation ($R^2 = 0.49$, $F_{3,149} = 49.47$, $P < 0.001$). PAR, average daily temperature, and streamflow all had a positive effect on biofilm AFDM. PAR explained the most variation in biofilm AFDM ($R^2 = 0.40$, $P < 0.001$), followed by average daily stream temperature ($R^2 = 0.21$, $P < 0.001$), then streamflow ($R^2 = 0.03$, $P = 0.04$).

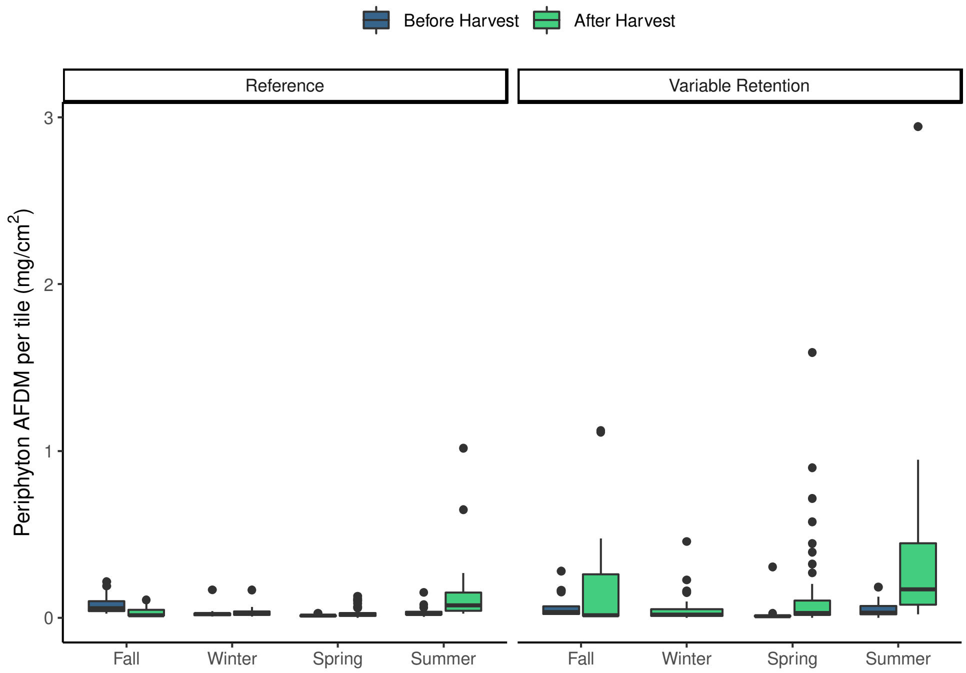

Figure 3. Seasonal differences in biofilm AFDM on each tile in streams before and after logging.

Invertebrate abundance and biomass did not differ between treatments when pooled across seasons, but responses varied seasonally. Mean invertebrate abundance in variable retention streams was approximately three times higher in the summer ($P < 0.001$), while there were no differences in other seasons (Fig. 4a). Differences in abundance between treatments also varied by water year. Abundance was slightly higher in reference streams in the 2006-2007 water year ($P = 0.02$), but there were no treatment differences in other years (2004-2005, 2005-2006, and 2007-2008). There were no differences in average invertebrate biomass or total biomass between treatments in any seasons or years (Fig. 4b). Taxa richness also showed no response to logging when averaged over seasons and years but did show a response in some seasons and years. When data were pooled across years, mean taxa richness was 22.5 times higher in variable retention streams in the fall ($P < 0.001$). However, sample size was small in fall, and we only observed one taxon in the reference streams (Fig. 5), so this difference was only slightly over one species per tile (1.25 in variable retention streams compared to 0.06 in reference streams). Taxa richness was significantly lower in harvested streams in the 2004-2005 water year (P = 0.01) and was higher in harvested streams in the three subsequent years (2005-2006, 2006-2007, and 2007-2008), but high variability limits our inference regarding these differences (P = 0.11; P = 0.056; P = 0.11).

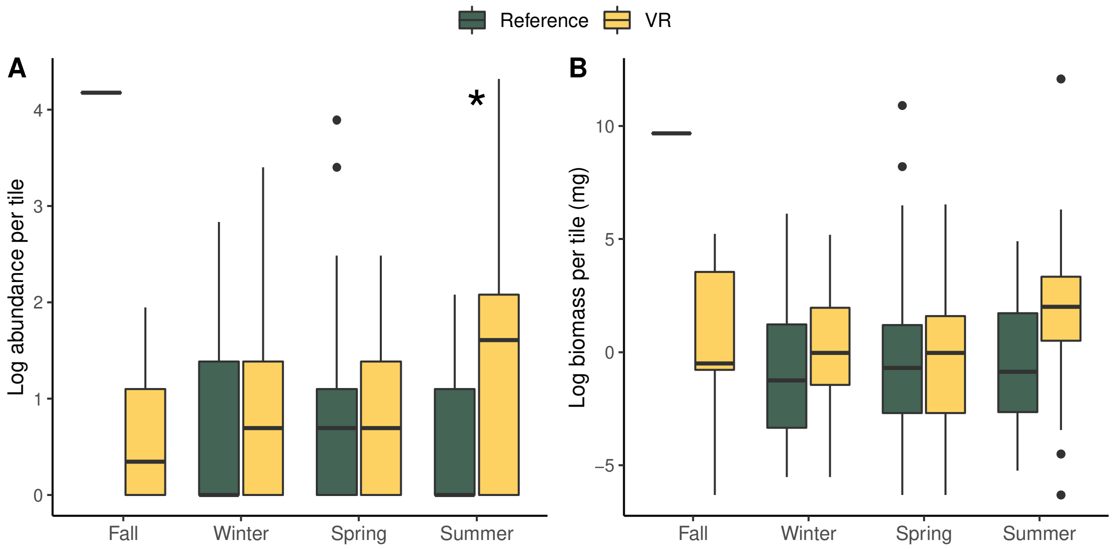

Figure 4. Seasonal differences in A) Invertebrate abundance and B) Invertebrate biomass in reference and variable retention (VR) streams. Data include all years post-logging. Stars indicate significant within-season differences between treatments.

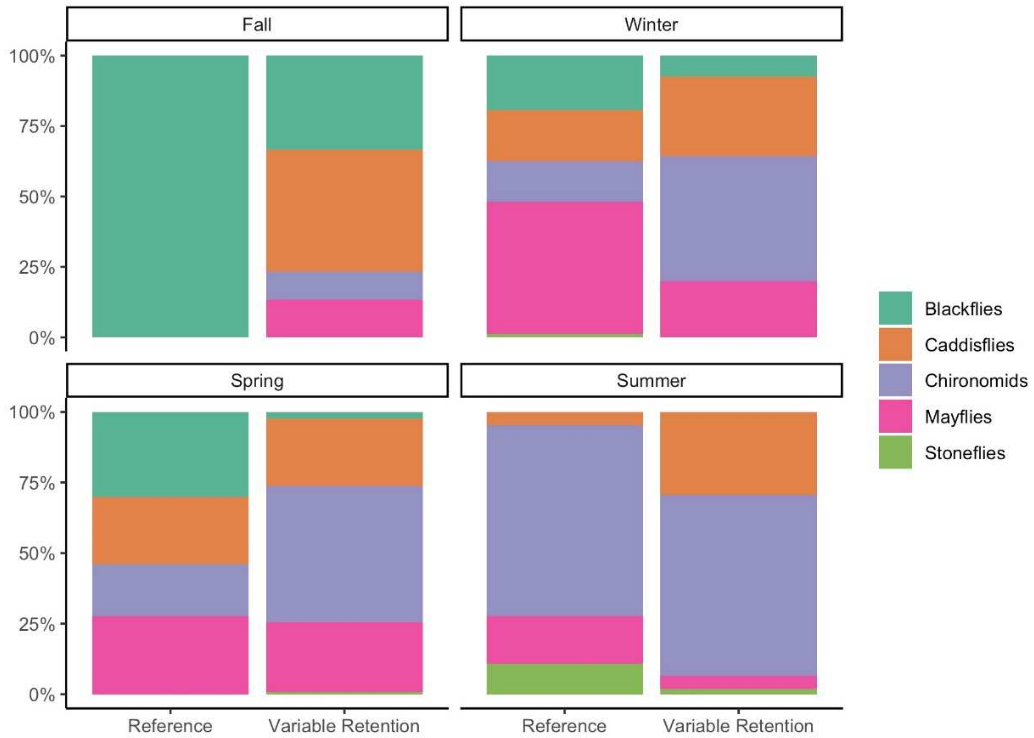

Figure 5. Seasonal percent composition of invertebrate taxa in variable retention and reference streams.

The results of our ANOSIM showed that invertebrate tile community composition in variable retention streams was different relative to the reference treatment ($R = 0.31$, $P = 0.001$; Fig. 6). Our analyses of individual taxa suggest that the shift in community composition was largely driven by changes in chironomid and blackfly abundance in harvested streams. In terms of taxon-level responses, Chironomid abundance ($P < 0.001$), total biomass ($P < 0.001$), and average biomass ($P < 0.001$) were higher in variable retention streams compared to reference streams (Fig. 6a). Correlation analysis showed that chironomid abundance was positively correlated with PAR ($\rho = 0.23$, $P < 0.001$) and biofilm AFDM ($\rho = 0.16$, $P < 0.001$) as well as mean ($\rho = 0.07$, $P = 0.04$) and maximum ($\rho = 0.09$, $P < 0.01$) daily stream temperature. There was no difference in mayfly abundance between treatments, but mayfly total biomass ($P < 0.001$; Fig. 6b) and average biomass ($P < 0.001$) were higher in variable retention streams. There was a five-fold but marginally non-significant decrease in the abundance of blackflies in the thinned treatment (P = 0.1; Fig. 5).

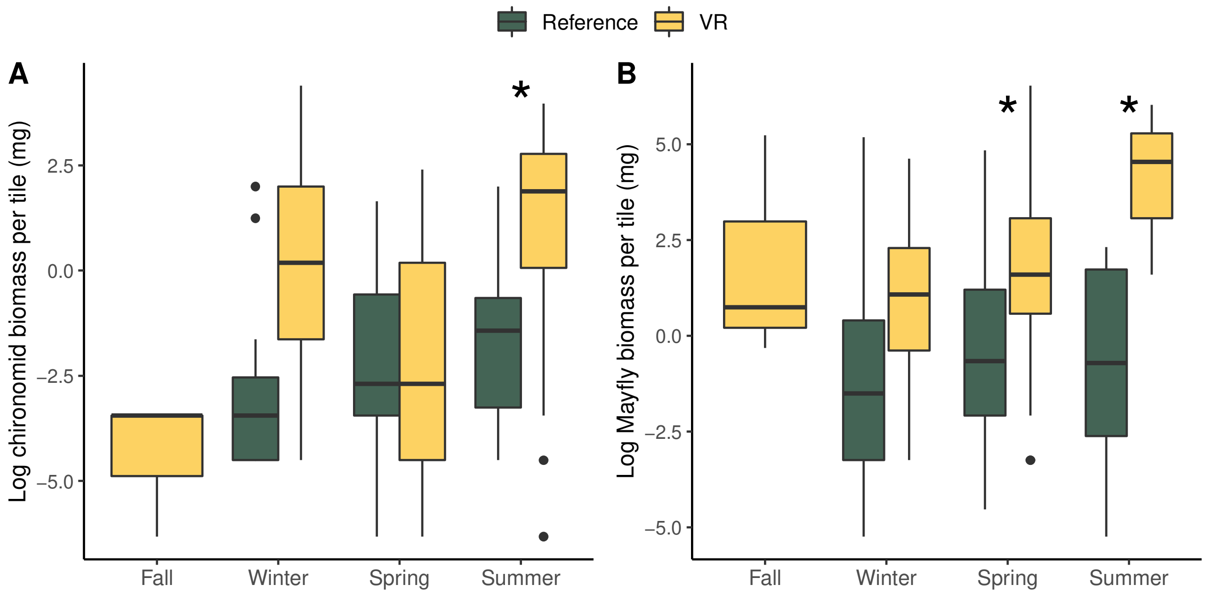

Figure 6. Seasonal differences in A) Chironomid biomass B) Mayfly biomass in reference and variable retention (VR) streams. Data include all years post-logging. Stars indicate significant within-season differences between treatments.

PAR was positively correlated with all of the daily stream temperature metrics, and most strongly correlated with MWMT. PAR had a weak positive relationship with biofilm AFDM and invertebrate abundance. Streamflow had a weak but significant positive correlation with invertebrate biomass. Stream temperature was positively correlated with biofilm AFDM, with maximum daily temperature and daily range having the strongest relationship with AFDM. There was a positive relationship between temperature range and invertebrate biomass and a weak relationship between biofilm AFDM and invertebrate abundance and biomass (Fig. 7).

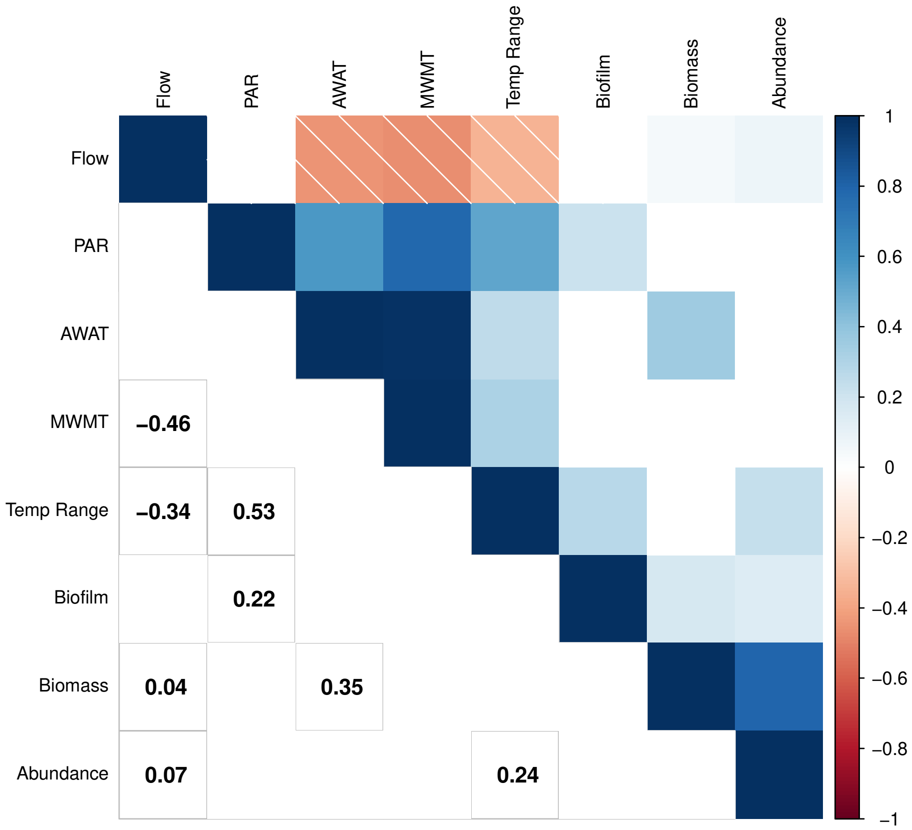

Fig. 7. Plot of correlations between streamflow, PAR, average weekly average temperature (AWAT), maximum weekly maximum temperature (MWAT), temperature range, biofilm AFDM, invertebrate biomass, and invertebrate abundance. The bottom diagonal contains Spearman's correlation coefficients. Non-significant correlations are left blank.

4. Discussion

This is one of few experimental studies examining the effects of riparian thinning on stream communities (but see Danehy et al., 2007; Wilkerson et al., 2010). To our knowledge, it is the only study to examine these effects seasonally and over multiple years. As predicted, variable retention harvest increased the amount of light reaching the stream. However, the effects of increased light on stream temperature and higher trophic levels were season, and potentially site-specific, and often comparable to the between stream and year variability. This suggests that variable retention harvest is a method that leads to smaller changes in the stream environment and associated benthic communities compared to clear-cutting (Kiffney et al. 2003).

4.1 Abiotic Variables

The ten-fold increase in light was the direct result of the removal of riparian vegetation, as solar flux reaching the stream surface is largely influenced by stream width, tree height, and canopy density (Lhotka and Loewenstein, 2006). Compared to the Kiffney et al. (2003) study on the effects of riparian buffer treatments, the relative increase in PAR reaching the variable retention streams was smaller than clear-cut (58x) and the 10 m (16x) buffer treatment, but larger than the 30 m buffer treatment (5x). This is likely because variable retention harvest involves cutting trees closer to the stream edge. The increase in biofilm AFDM after logging suggests that the light increase in variable retention streams had an effect on primary productivity. Primary productivity is primarily limited by light in small heavily shaded forested streams (Richardson and Danehy, 2007; Hill and Fanta, 2008). However, there was a relatively weak correlation between PAR and biofilm AFDM, especially compared to results of previous studies on riparian logging (Kiffney et al., 2003), potentially due to a smaller treatment effect in variable retention streams compared to clear-cut or buffered or reduction of biofilm accrual by stream invertebrate consumers.

The effect of variable retention harvest on stream temperature was minimal and seasonally dependent. The most pronounced effect of harvest on stream thermal regimes was an increase in stream temperature variability, which may be due to a reduction in the ability of this habitat to regulate the microclimate (Moore et al., 2005). Increases in stream temperature variability due to riparian thinning have been observed in other studies (e.g. Roon et al., 2021) and can have biological consequences such as changing the emergence time of fish and other organisms (Steel et al., 2012). The lack of significant BACI results for other metrics suggest the temperature increases we observed in some streams and seasons (see Fig. 2) are comparable to the temperature variation between streams. A previous study on one of the same treatment streams, Griffith Creek, found an increase in temperature compared to reference streams (Guenther et al., 2014). In our study, Griffith Creek was the variable retention site with the largest change in stream temperature magnitude and variability followed by Mirror Creek, with no change in Sidle Creek (Fig. 2). One possibility explaining this discrepancy in responses may be due to the steepness of Sidle Creek relative to the other two streams, which may limit the influence of solar heating on stream water. These among-site differences in the temperature response to thinning suggests that the effects of variable retention harvest is dependent on local conditions and highly variable between streams within the same treatment. These site-specific effects of thinning on stream temperature regimes have been observed previously (Roon et al., 2021), suggesting that evaluating the best forest management strategy must be done on a case by case basis. However, variable retention harvest seems to have less of an impact on stream temperature than buffer systems, as Kiffney et al. (2003) observed an 3 °C and 1.6 °C increase in 10 m and 30 m buffer treatments, respectively, compared to reference streams.

Although two of the variable retention streams had a 1.1 °C increase in average temperature in the summer, none of the observed temperature increases were significant due to high variation in responses between streams. This suggests that variable retention harvest has a smaller effect stream temperature regimes than the buffer method.

In agreement with a variety of studies in larger streams, our results suggest that streamflow is important in structuring headwater stream communities. Streamflow was negatively associated with both water temperature and biofilm AFDM. Because we were not able to measure streamflow in all streams and used data from one stream as a proxy for the others, this association could be stronger than our study detected. However, we do not think streamflow confounded our results for the following reasons. First, these sites were close in proximity and the climate and precipitation did not differ between them. Second, the stream gradients were higher in treatment streams, which would cause faster flows and thus greater scour and decrease, not increase, the biofilm biomass in those streams. Because of these reasons, we believe the differences in biofilm AFDM are attributable to the effects of the logging treatment.

4.2 Biotic Variables

Our data did not support the prediction that biofilm AFDM or stream temperature would decrease over time due to the recovery of riparian plant assemblage. This is likely because the time frame of our study was not long enough to observe the effects of forest recovery on stream benthic communities. Because both temperature and biofilm AFDM are related to PAR, and PAR is largely determined by canopy cover (Kaylor et al. 2017), the growth of underbrush that likely occurred in the short term was not enough to reduce the amount of light reaching the stream. However, we were unable to determine whether PAR decreased over time because of limited sampling in the final years of the study. A previous study on the long-term effects of clear-cut logging on streams found that it took 16 years for stream macroinvertebrates to fully recover (Stone and Wallace, 1998). Future studies should explore whether the rate of stream recovery is faster in forests harvested with the variable retention method than forests that are clear-cut or buffered (Warren et al., 2016; Kaylor et al., 2017).

Stream biofilm increased after logging in all seasons, most likely due to an increase in PAR reaching the stream. Results from previous studies on the effects of riparian thinning on biofilm or periphyton (the autotrophic component of biofilm; Suberkropp, 1998) biomass have been mixed. One study found that streams with thinned riparian reserves had higher periphyton AFDM than streams with clear cut and buffer treatments (Danehy et al., 2007) while another study found no difference in periphyton between thinned and reference streams (Wilkerson et al., 2010). The relative increase that we observed is similar to the AFDM increase in streams with 30 m buffer treatments in Kiffney et al. (2003). In the summer season, variable retention streams had twice the biofilm AFDM than control streams, while Kiffney et al. (2003) observed a 6-fold increase in periphyton AFDM in clear-cut streams and a 3-fold increase in streams with a 30 m buffer. However, there was high variation in AFDM between sites in our study.

Variation in the response of biofilm to logging may be caused by site and seasonal variation in light, temperature, and geomorphology; limitation by consumers; differences in nutrient availability; or variation in thinning intensity (Hillebrand, 2002; Roon et al., 2021). Important site characteristics that may influence how logging influences stream light flux are gradient, channel confinement, substrate composition, and aspect. For example, light flux to high gradient, confined streams may be less affected by riparian thinning because of topographic shading. Studies on the effects of riparian buffer systems have found that biofilm increases with decreasing buffer widths and is strongly influenced by light (Kiffney et al., 2003; Wilkerson et al., 2010). However, we speculate local site attributes can have a large influence on the relative change in headwater stream light conditions associated with forest harvest.

We observed a seasonal increase in invertebrate abundance, which was positively correlated with both stream temperature and biofilm (Fig. 6). Stream temperature increases can accelerate invertebrate growth and development, which may increase productivity (Patrick et al. 2019). Additionally, previous studies have shown that stream invertebrates and vertebrates that consume biofilm are often limited by food resources (Towns 1981, Feminella and Hawkins, 1995; Quinn et al., 1997), so increased primary productivity would be expected to increase the abundance of consumers that feed on stream biofilm. We did not measure the impact of logging on other invertebrate functional feeding groups, but previous studies have shown that shredder abundance decreases with forest loss due to reductions in leaf litter input, while other groups (gathering-collectors, filtering-collectors, and predators) do not experience changes in percent composition (Moraes et al., 2014; Brand and Miserendino, 2015).

The difference in invertebrate abundance and community composition between the reference and variable retention treatment was largely driven by an increase in the absolute and relative abundance of chironomids. Chironomids are the most widely distributed and abundant invertebrate in freshwater systems (Pinder, 1986) and they are often used as a proxy to monitor water quality due to the sensitivity of some taxa to environmental change (Rosenberg, 1992; Brooks and Birks, 2004; Engels et al., 2020). Chironomids are also key sources of energy for a variety of species ranging from fish to ducks to songbirds (e.g., Einarsson et al., 2004). The increase in chironomid abundance and biomass in response to logging has been observed in several studies (Kiffney et al., 2003; Nislow and Lowe, 2006; Martel et al., 2007). Chironomids have life-history strategies that are advantageous to colonizing disturbed habitats, such as strong dispersal, rapid juvenile development, short generation times, and synchronized emergence (Verberk et al. 2008). Additionally, they are generalists and can live off of a variety of food sources (Gurtz and Wallace, 1984). Chironomid abundance was positively correlated with biofilm AFDM, suggesting that chironomids were responding to increased food resources. Chironomid abundance was also positively correlated with PAR and stream temperature. It is difficult to disentangle the effects of these environmental variables, but previous studies suggest that light is more important than stream temperature in structuring invertebrate communities (Kiffney et al. 2004).

We also observed a five-fold reduction in blackfly abundance in harvested streams. Although blackfly abundance was highly variable between sampling events and streams, this effect was consistent across seasons (Fig. 5). Blackflies play a key role in stream ecosystems as filterers of suspended organic matter, making nutrients available for other aquatic invertebrate species that feed on them (Ciadamidaro et al., 2016). Variable retention harvest was also associated with an increased mayfly biomass. Previous studies have attributed increases in mayfly biomass after logging to increased food availability (Wallace and Gurtz, 1986) or increased stream temperature (Imholt et al., 2010). Increased stream temperature has also been associated with accelerated emergence time, which could impact adult fecundity (Harper and Peckarsky, 2006). However, we did not find an association between mayfly biomass and temperature or biofilm AFDM.

Changes to macroinvertebrate communities can alter ecosystem function in headwater streams (Cao et al., 2018). Macroinvertebrates provide a number of ecosystem services, including providing food for fish and other vertebrates, retaining nutrients for the stream and surrounding forest, and helping maintain healthy amounts of organic matter (Suter and Cormier, 2014). The dominance of chironomids and reduction of the relative abundance of other species could alter nutrient transport and ecosystem function in harvested streams (Cao et al., 2018). Additionally, increases in mayfly biomass and earlier emergence time could have far-reaching effects, such as increased predation and reduced fitness (Harper and Peckarsky, 2006).

Average taxonomic richness in variable retention streams was 22.5 times higher than reference streams in fall. Some studies have observed increases in macroinvertebrate species richness due to logging, likely because of increased primary productivity and water temperature (Stone and Wallace, 1998), while others have observed decreases (Newbold et al., 1980). However, we had a small sample size in the fall and only observed one invertebrate taxa in reference streams, so it is unclear whether this differences is ecologically important. It is also important to note several limitations to our measure of taxa richness. First, our taxonomic resolution was coarse (family to order-level), second, our tile method largely selects for biofilm consumers and does not capture the diversity of other functional feeding groups, and third, we were unable to use a diversity index due to the large number of tiles with zero or only one individual. Therefore, this measure does not take into account the relative abundance of each taxonomic group, only the number of unique taxonomic units.

Previous studies on the effects of riparian thinning have found no differences in macroinvertebrate assemblages or abundances between reference and thinned streams (Danehy et al., 2007; Wilkerson et al., 2010). These studies had higher stand retention (60%-70%) and only sampled at one point in the year (late spring-early summer), both possible reasons why they obtained different results. Additionally, in the Danehy et al. (2007) study, there was no logging within 15 meters of the stream edge. Kreutzweiser et al. (2005) found that low-intensity selective logging (29% removed) had no detectable effect on insect communities in streams, while medium intensity logging (42% removed) increased invertebrate abundance. However, these changes were similar in magnitude to interannual changes in the reference site over the course of the five-year study. Studies on the effects of riparian buffers have found that invertebrate abundance increases with decreasing buffer width, and a 30 m buffer is necessary to prevent significant changes in macroinvertebrate communities (Kiffney et al., 2003; Sweeney and Newbold, 2014).

An important caveat of our invertebrate results is because we did not have pre-logging data for our invertebrate measures, we are unable to distinguish between differences due to logging and underlying site variation. It is possible that observed differences are due to stream-level variation in insect abundance, diversity, and/or community composition rather than the effects of logging. However, because we performed BACI analyses on biofilm and stream temperature, which are positively correlated with invertebrate measures, we believe it is likely that these differences are attributable to logging impacts.

4.3 Management Implications

Our results suggest that variable retention harvest has a smaller effect on streams than clear-cut harvesting. Studies have shown that clear-cut harvest results in large alterations in light, temperature, primary productivity, and insect consumer abundance and diversity (Kiffney et al. 2003; Danehy et al. 2007; Wilkerson et al. 2010). Previous studies have found that 30 m buffer sites can prevent the effects of timber harvest on streams (Kiffney et al., 2003; Sweeney and Newbold, 2014). Comparing our results with previous studies on buffer width suggests that variable retention harvest causes larger changes to stream abiotic and biotic factors than the 30 m buffer treatment. This makes sense considering that variable retention harvest involves cutting trees closer to the stream edge. However, the effects of harvest were highly variable across seasons and sites, with the largest effect in summer when there is low streamflow and high light levels and temperature. Important considerations for determining the best logging practice include species composition and demographics, the size of the area harvested, location and size of sensitive areas like wetlands, the magnitude of the impact on downstream reaches, and the speed of regrowth and recovery. Variable retention harvest may be the most effective approach for limiting changes to streams and forests while preserving biodiversity and promoting regeneration in regions that regularly undergo natural disturbance (Martínez-Pastur et al. 2020).

Riparian ecosystems often undergo natural disturbances such as landslides, windthrow or wildfires that create light gaps fueling stream productivity and promoting forest regeneration, habitat heterogeneity, and species diversity and abundance (Kiffney et al., 2004; Kreutzweiser et al., 2012; Warren et al. 2016). In the absence of natural disturbance (e.g. in a carefully managed riparian buffer), habitats can become homogenized (Swanson et al., 2011). An alternative approach to riparian forest management is finding a logging method that mimics natural disturbance, but also maintains economic viability in the long term (Kreutzweiser et al., 2012). The variable retention logging method results in many of the characteristics that promote diversity in habitats recovering from natural disturbance, such as increased spatial heterogeneity and light availability (Swanson et al., 2011; Beese et al., 2019; Franklin and Donato, 2020). Additionally, structural retention results in higher carbon storage and sequestration compared to clear cut forests (Nunery and Keeton, 2010). Future assessments of the impacts of various logging practices on riparian systems should consider not only how they compare to alternative management practices or unharvested reserves, but also how they compare to natural disturbance events in that system and how they influence climate resiliency (Dymond et al. 2015).

5. Conclusion

Our study demonstrated that variable retention logging had the largest effects on PAR and biofilm AFDM, which were consistently higher in harvested streams year-round. Stream temperature and invertebrate abundance and richness only responded to the effects of logging during specific seasons. Additionally, the invertebrate response to logging was taxa-specific, with only mayflies, chironomids, and blackflies showing changes in abundance and biomass.

Based on the results of previous studies, variable retention harvest can have a smaller effect on stream communities than clear-cut harvest and 10 m buffers and a similar effect to the use of 30 m buffer strips (Kiffney et al. 2003, Danehy et al., 2007). However, more direct comparisons of the effects of buffer systems and variable retention harvest on stream dynamics over time are needed.

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Authorship contributions

P. Kiffney: Designed the study and helped collect data. Kiffney advised on data analysis and contributed to writing and editing the manuscript.

J. Griffith: Conducted data analysis and led manuscript preparation.

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