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ARTICLE

Canopy closure after four decades of postlogging riparian forest regeneration reduces cutthroat trout biomass in headwater streams through bottom-up pathways

Matthew J. Kaylor and Dana R. Warren

Abstract: Recovery from timber harvest is widespread across North America, but few studies have evaluated long-term stream responses to riparian harvest. We revisited five stream reach pairs where in 1976, periphyton chlorophyll *a*, predatory invertebrate biomass, and cutthroat trout (*Oncorhynchus clarkii clarkii*) biomass were elevated in reaches where canopies were more open following timber harvest. After four decades of riparian regeneration, mean canopy openness, chlorophyll *a*, predatory invertebrate biomass, and cutthroat trout biomass declined in harvested reaches relative to paired old-growth reference reaches. In one reach pair, the harvested reach remained more open than the control reach. In accordance with the hypothesis that light exerts strong controls on predator biomass via bottom-up processes in these forested headwaters, trout biomass was also greater in the harvested reach in this pair in 2014. Changes in large wood and pool area over this time interval do not account for chlorophyll *a*, predatory invertebrate biomass, or cutthroat trout biomass responses. These results provide empirical support for conceptual models relating changes in riparian canopy cover to primary production and bottom-up controls on consumer populations.

Résumé : Si le rétablissement à la suite de la coupe de bois est répandu en Amérique du Nord, peu d'études ont évalué les réactions à long terme des cours d'eau à la coupe en zone riveraine. Nous revisitons cinq paires de tronçons de cours d'eau où, en 1976, la chlorophylle *a* dans le périphyton, la biomasse d'invertébrés prédateurs et la biomasse de truites fardées (*Oncorhynchus clarkii clarkii*) étaient élevées dans les tronçons où la canopée était plus ouverte à la suite de la coupe de bois. Après quatre décennies de régénération des rives, l'ouverture moyenne de la canopée, la chlorophylle *a*, la biomasse d'invertébrés prédateurs et la biomasse de truites fardées ont diminué dans les tronçons ayant fait l'objet d'une coupe par rapport aux tronçons intacts jumelés de référence. Dans une paire de tronçons, le tronçon ayant fait l'objet d'une coupe demeurait plus ouvert que le tronçon témoin. Conformément à l'hypothèse voulant que la lumière exerce une forte influence sur la biomasse de prédateurs par l'entremise de processus ascendants dans ces cours d'eau forestiers d'amont, la biomasse de truites était également plus grande en 2014 dans le tronçon de cette paire ayant fait l'objet d'une coupe. Des modifications de la superficie des peuplements de gros arbres et des fosses durant cet intervalle n'expliquent pas les changements de la chlorophylle *a*, de la biomasse d'invertébrés prédateurs ou de la biomasse de truites fardées. Ces résultats fournissent un soutien empirique aux modèles conceptuels qui relient les changements de la couverture de la canopée riveraine à la production primaire et à des contrôles ascendants sur les populations de consommateurs. [Traduit par la Rédaction]

Introduction

The removal or loss of streamside (riparian) forests have clear acute impacts on associated aquatic environments, particularly headwater streams where interaction between aquatic and terrestrial environments are maximized. Stream responses to riparian harvest have been relatively well studied for the initial years following canopy removal (<10 years), but few studies have evaluated long-term recovery from this disturbance or its effects on stream biota. Conceptual models based on results from comparative studies evaluating stream abiotic and biotic differences between stream reaches of contrasting forest type (e.g., clear-cut, second-growth, old-growth) have been developed to suggest likely trajectories of change in stream biota and stream ecosystem processes over the decadal time scales associated with riparian forest stand development (Sedell and Swanson 1984; Gregory et al. 1987; Mellina and Hinch 2009; Warren et al. 2016). These conceptual trajectories portray increases in primary production, with subsequent bottom-up driven increases in invertebrate production and top consumer (usually salmonids) biomass shortly after riparian canopy removal. Then, following canopy closure that reduces light availability, these conceptual models suggest decreasing primary production with associated declines in consumer biomass. Throughout North America, recovery from 20th century timber harvest is a widespread process that affects riparian zones as well as the upland forest (Pan et al. 2011; Kaylor et al. 2017). Evaluating both short-term and long-term impacts of riparian forest removal and recovery provides a more complete understanding of the impacts of riparian forest harvest on adjacent stream ecosystems.

Removing riparian forests can impact stream habitat, physiochemical conditions of a stream, and the productivity and food web structure of streams (Bilby and Ward 1991; Bilby and Bisson 1992; Wootton 2012). The removal of streamside vegetation reduces allochthonous carbon subsidies (e.g., litter and terrestrial invertebrate inputs), and without any compensatory increases in

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autochthonous carbon, a reduction in detrital and terrestrial invertebrate inputs can lead to decreased abundances and growth of secondary consumers and predators (Wallace 1997; Nakano et al. 1999; Wallace et al. 1999). But riparian timber harvest also reduces stream shading, which may lead to increases in primary production and autochthonous carbon availability (e.g., stream benthic algal communities) by alleviating light limitation (Bilby and Bisson 1992; Ambrose et al. 2004; Wilzbach et al. 2005). When an increase in autotrophy compensates for loss of litter inputs following riparian canopy loss, the abundances and biomass of food-limited invertebrates and fish can increase (Noel et al. 1986; Bilby and Bisson 1992; Wootton 2012). Decreased shading can also lead to increases in stream temperature (Beschta et al. 1987; Moore et al. 2006; Groom et al. 2011), and this can be a concern in systems dominated by cold-water salmonid fishes. Historical timber harvest operations in the riparian zone and upland forest can also negatively impact the stream shortly after logging by increasing sediment inputs (Kreutzweiser and Capell 2001; Croke and Hairsine 2006), decreasing stream habitat complexity (Murphy et al. 1986; Ralph et al. 1994; Sweeney et al. 2004), and creating chemically stressful stream conditions (e.g., pH; Baldigo et al. 2005).

Short-term stream responses to timber harvest have been well studied, particularly the response of salmonid species in the Pacific Northwest region of North America (Hall and Lantz 1969; Murphy and Hall 1981; Bilby and Bisson 1992). However, results from this work have been equivocal, with substantial variation in the magnitude and directionality of fish population responses (reviewed in Mellina and Hinch 2009). The extent of habitat modification (loss) associated with riparian forest management, particularly the removal of large wood from streams and loss of pool habitat, appears to be a key determinant of whether salmonid populations respond positively or negatively on short time scales (Mellina and Hinch 2009). When habitat is not severely degraded, alleviation of light limitation can lead to gains in primary production, thereby enhancing invertebrate production and ultimately top consumer (fish) biomass and growth due to greater prey availability (Murphy and Hall 1981; Bilby and Bisson 1992). Whether initial population responses to harvest are positive (increased biomass) or negative (decreased biomass), few studies have empirically evaluated long-term responses on the decadal time scales riparian forests take to regenerate (Bisson et al. 2008).

One of the earliest and most widely cited studies evaluating the influences of riparian harvest on fish populations is Murphy and Hall (1981), which documented greater summertime periphyton stocks, predatory invertebrate biomass, and coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) biomass in stream reaches adjacent to small patch clear-cuts (4–20 ha) relative to upstream reference reaches. This result was observed despite removal of large wood and reduced pool area in harvested reaches. Given an increase in trout biomass concurrent with reduced large wood and percent pool area in harvested reaches, Murphy and Hall (1981) concluded that changes in trout biomass were likely attributed to greater primary production leading to increased invertebrate prey availability. These findings, along with other Pacific Northwest studies (e.g., Aho 1976; Gregory 1980; Murphy et al. 1981; Hawkins et al. 1983), were used to help develop early conceptual models of the temporal responses of resident salmonids following riparian harvest (Sedell and Swanson 1984; Gregory et al. 1987). These models suggest that fish biomass will be elevated for 10–20 years after harvest, but that biomass will return to preharvest conditions within 40 years. The potential for biomass levels to fall below preharvest conditions are included if or when second-growth forests had lower light levels than preharvest conditions. Updates of this conceptual framework also ascribe high importance to stream light as a potential driver of long-term trends in salmonid abundance in headwater streams (Mellina and Hinch 2009), but acknowledge the potential for substantial variation in long-term stand development trajectories that may affect changes in canopy cover (Warren et al. 2016). To date, empirical support for the long-term trends is limited, especially on streams where the initial responses to harvest have been quantified.

In this study, we revisited five of the six fish-bearing stream reach pairs originally surveyed by Murphy and Hall (1981) to determine how stream conditions, benthic biofilms, invertebrate predators, and ultimately resident coastal cutthroat trout have responded to nearly four decades of riparian forest regeneration. Using the upstream reference reaches identified by Murphy (1979), which were bordered by old-growth riparian forests, this design is similar to a before–after, control–impact (BACI) study with riparian regeneration as the treatment. We hypothesized that canopy closure associated with stand regeneration would correspond with declines in chlorophyll *a* (hereinafter chl *a*) standing stocks, predatory invertebrate biomass, and cutthroat trout biomass. These long-term responses have important implications for stream function across North America where riparian forest recovery is an ongoing and widespread process (Richardson et al. 2012).

Methods

Study system

The five streams evaluated in this study are located within the H.J. Andrews Experimental Forest (hereinafter HJA) and the surrounding Willamette National Forest in the western Cascade Mountains of Oregon (Fig. 1). This region is characterized by a Mediterranean climate of wet winters and dry, warm summers. Stream reaches ranged in elevation from 630 to 940 m and were relatively high gradient (4%–10%; Table 1) with boulder-dominated substrates. Before forest management began in the HJA in the 1950s and 1960s, the area was dominated by a mix of old-growth (dominant trees >400 years of age) and mature (100–150 years old) forests. Today, the HJA remains dominated by late-succession – old-growth forests, but patches of younger forest occur regularly in the system, reflecting the legacy of past experimental forest management. This patchy forest management within the larger basin created areas where a single stream could have some sections that were heavily impacted by logging and others that were largely unaffected. In this study, we assessed stand regeneration effects on established reach pairs that utilized this patchy management history. Each reach pair in a stream consisted of a stream reach bordered by old-growth riparian forest (hereinafter referred to as old-growth reaches) and a reach bordered by previously harvested and currently regenerating riparian forest (hereinafter referred to as previously harvested reaches). Streamside harvesting of the relatively small patch clear-cuts (4–20 ha) evaluated in this study occurred between 1953 and 1971 (Table 1). Harvesting occurred on both stream banks in Mack Creek and Cook Creek, but only on one stream bank at cutblock MR404 on McRae Creek and cutblocks LO701 and LO703 on Lookout Creek. In all cases trees were removed to the stream edge with no buffers, and wood was removed from streams during harvest operations, in accordance with standard forest management practices at that time. Stands were planted with Douglas-fir (*Pseudotsuga menziesii*) within 5 years of harvest in the management areas, with the exception of Mack Creek, which was allowed to naturally regenerate. Following harvest or disturbance, red alder (*Alnus rubra*) commonly occupies riparian zones in this region (Summers 1982; Van Pelt et al. 2006; Villarin et al. 2009) and was a dominant canopy species over the stream along the previously harvested reaches of LO701, Cook, and MR404. Very few alder were present at LO703, where dense vine maple (*Acer circinatum*) was instead the dominant hardwood species directly adjacent to the stream. Forests adjacent to old-growth, reference reaches were dominated by Douglas-fir, western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja*

Fig. 1. Blue River drainage, a tributary of the McKenzie River, and sampling sites. Filled circles indicate upstream old-growth, reference reaches, and open circles indicate previously harvested reaches of each reach pair.

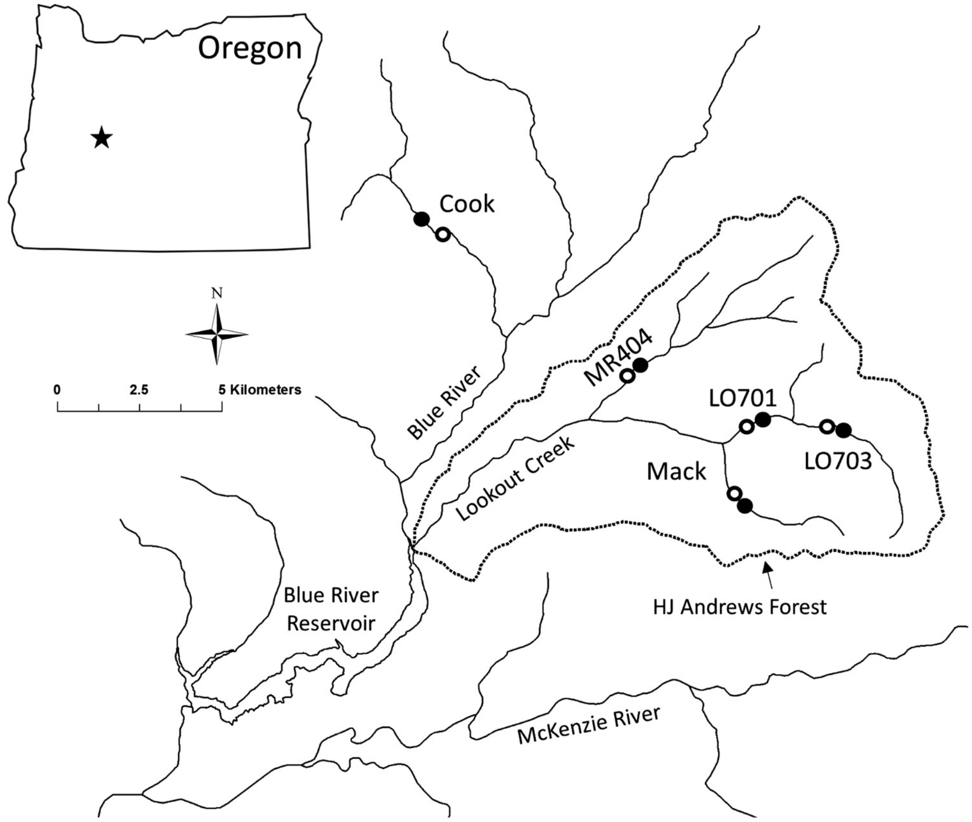


Table 1. Physical attributes of stream reach pairs in summer 2014.

Site	Riparian type	Harvest year	Area harvested (ha)	Bank-full width (m)	Canopy openness (%)	Gradient (%)	Wood volume (m³·100 m⁻²)	Pool area (%)	Elevation (m)	Temp. (°C)
LO703	OG	—	—	7.8	34.0	6.4	2.0	16.8	940	9.1
	PH	1960	7	7.4	53.8	6.4	0.7	15.4	900	9.3
Mack	OG	—	—	9.8	23.9	9.5	6.0	27.0	800	12.4
	PH	1965	4	9.3	32.2	9.9	1.5	21.4	750	12.7
LO701	OG	—	—	9.9	20.2	7.1	2.7	40.2	810	9.9
	PH	1959	12	9.0	10.5	6.0	0.9	42.4	750	10.3
Cook	OG	—	—	10.5	23.8	4.6	6.6	17.5	700	13.8
	PH	1971	7	8.6	4.8	4.0	0.6	21.2	650	13.9
MR404	OG	—	—	10.4	29.0	7.6	6.8	41.0	660	13.7
	PH	1953	20	8.6	32.7	4.0	0.3	19.2	630	13.6

Note: OG = bordered by old-growth riparian forest; PH = bordered by previously harvested riparian forest on at least one stream bank. Temperature is the mean daily mean temperature for a 2-week period in August 2014.

plicata). In these reaches, alder was present but provided notably less direct over-stream canopy cover.

Detailed explanations of where previous reach pair study sites were established are provided in the appendix of the thesis of Murphy (1979), and we were therefore able to identify the locations of both impacted and reference reaches used in the initial surveys. In the initial study (Murphy and Hall 1981), six fish-bearing paired reaches were surveyed. We could no longer access one of these streams due to road closures. The reaches surveyed in Murphy and Hall (1981) were 30– 50 m in length except for Mack Creek, which had a study reach 200 m in length. We increased reach lengths in the 2014 study to a minimum of 10 times bank-full width (range 90–200 m; Table 1) to encompass a wider variety of habitats and account for more spatial variability in fish abundance and biomass. However, lengthening the reaches slightly altered current assessment relative to the initial study. To evaluate whether the use of longer reaches affected the outcome of the stand-regeneration analysis relative to the previous surveys at these sites, we subdivided each individual reach into two sections: (*i*) a 30–40 m reach that corresponded directly to the reach surveyed in Murphy and Hall (1981) and (*ii*) the additional stream section (ranging from 50 to 70 m). Results from the shorter (30–40 m) reaches were similar to results from the entire reach that included the shorter reaches. More specifically, the ratios between the harvested reach and the old-growth reach in each reach pair were similar between the shorter reaches and the full reaches, and in every case, the ratio did not affect which reach had greater trout biomass (i.e., if the ratio was greater than 1 for the longer reach, it was also greater than 1 for the shorter survey). Because longer reaches encompass more habitat units and align more with contemporary survey methods, we present results from the full survey reaches in this manuscript. The distances between the downstream impacted sites and the upstream reference sites in reach pairs within a stream ranged from 135 to 325 m.

Resident coastal cutthroat trout were the dominant fish species at all sites, with sculpin (*Cottus* spp.) present in just one site (MR404). Coastal giant salamanders (*Dicamptodon tenebrosus*) were present at all surveyed reaches and were a substantial component of total vertebrate biomass (>50% in some streams).

Field sampling

We collected data on a suite of abiotic and biotic variables that matched those assessed by Murphy and Hall (1981) to evaluate reach-pair changes over time. All of the initial surveys were conducted in summer during the low-flow period between July and September of 1976, with the exception of Mack Creek fish surveys, which occurred during the summer of 1975. Hereinafter, we refer to the sampling by Murphy and Hall (1981) as "1976 surveys". In the summer of 2014, sampling also occurred during summer low-flow conditions. Physical habitat variables included canopy cover, bank-full width, wetted width, pool area, large wood abundance and volume, mean daily mean temperature, and stream gradient. Canopy cover was quantified in this study using a spherical densitometer with measurements taken in each cardinal direction ($n = 4$) at 11 locations in each reach. Murphy and Hall (1981) visually assessed canopy openness, and while there is potential for these methods to yield different estimates, all analyses are based on a comparison of changes in the differences within reach pairs (old-growth versus harvested) during each sampling period. Thus, methodology is internally consistent within the two periods, and we focus on the change in ratios between reference and regenerated sites over time (rather than comparing the change in reference over time with the change in regenerated sites over time). Bank-full and wetted widths were measured at regularly spaced intervals, and reach area (for subsequent percent pool area and per unit area standardization of invertebrate and fish assessments) were calculated as reach length multiplied by mean wetted width. We followed the methods of Murphy and Hall (1981) in identifying and characterizing pools, which were identified during summer low-flow conditions as slow-velocity habitat units with minimal turbulence. Pool area was calculated using the length and width of each pool, and percent pool area was calculated as the total pool area divided by total wetted reach area. We counted all large wood pieces — dead wood greater than 10 cm in diameter and 1 m in length — within the bank-full channel. For each piece of large wood, we measured the total length within the stream channel and the diameter of the log at both ends. The mean of the two diameter measurements was used with length of wood in the bank-full channel to calculate wood volume. Total channel area (mean bank-full width multiplied by reach length) was used to calculate large wood volume per unit area. Temperature loggers (HOBO Pro v2; Onset Computer Corporation, Bourne, Massachusetts) were deployed for a 2-week period during midsummer to evaluate relative temperature among streams and differences between paired reaches. Owing to a limitation in the number of sensors, temperature data were collected during the same time period (8–24 August) for all streams except Cook Creek, where temperature sensors were deployed from 20 July to 3 August. Temperature data were not collected in Murphy and Hall (1981), and therefore it was not possible to assess long-term changes in temperature.

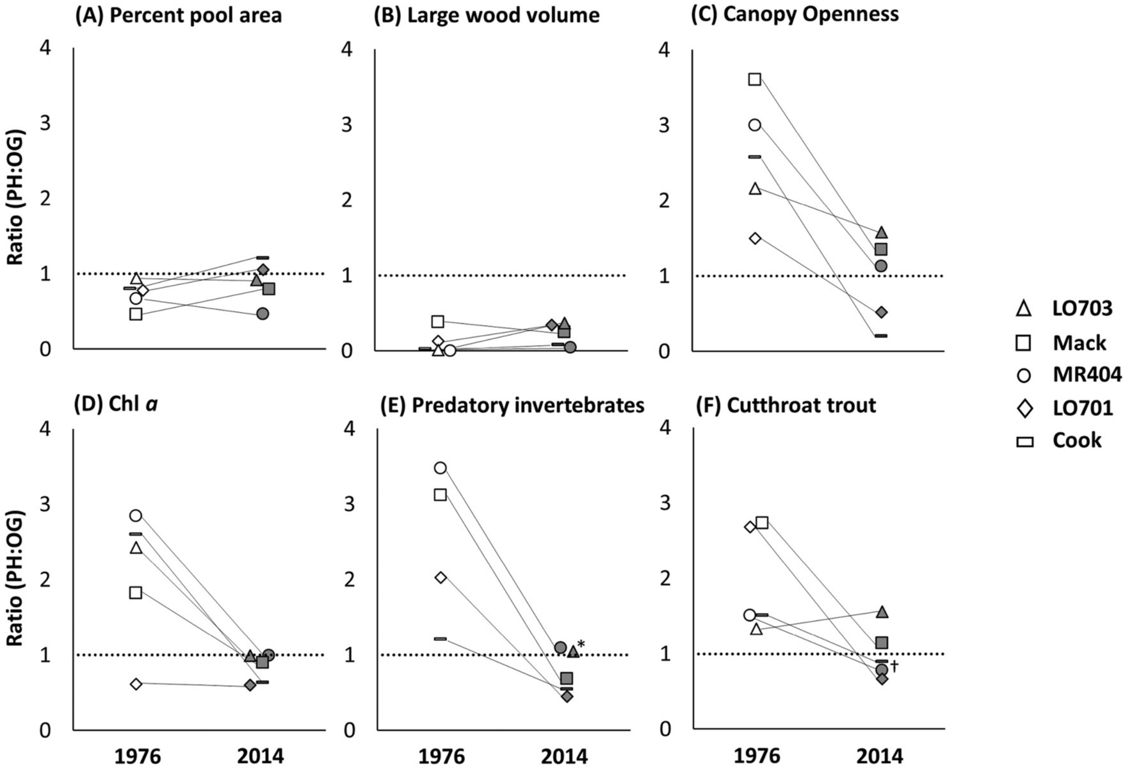
Periphyton chl *a* accrual was quantified in the current study on 15 cm × 15 cm ceramic tiles (225 cm^2) deployed in July and incubated for 6 weeks in riffle sections of the stream ($n = 10$ per reach). Ten tiles were placed in the stream thalweg at regular intervals along each study reach. Tiles were scraped using a wire brush in the field, and slurries containing periphyton and stream water for each tile were placed in a cooler and brought back to the lab. Samples were vacuum-filtered using Whatman 47 mm GF/F glass fiber filters, and filters were frozen for 24–48 h prior to extraction of chl *a* with 15 mL of 90% acetone. Samples were stored in the dark for 2–4 h, brought to room temperature, and shaken twice prior to measurements. Chl *a* concentrations were assessed using fluorometric methods and phaeophytin correction outlined in EPA method 445.0 (Arar and Collins 1997); however, samples were not centrifuged prior to analysis (Turner Designs Chlorophyll Application Guide, p. 4). Chl *a* accrual on tiles was also quantified by Murphy and Hall (1981), but they deployed two ceramic tiles for approximately 4 weeks and analyzed chl *a* concentration using methods outlined in Wetzel and Westlake (1969). We increased sample sizes in this study to provide a more rigorous quantification of differences in periphyton accrual on tiles between reaches in a pair that accounts for potential variability in local periphyton standing stocks.

Predatory invertebrates were quantified in the original study by Murphy and Hall (1981), and we therefore evaluated predatory invertebrate biomass in 2014 to evaluate this response over time. Between August and September of 1976, Murphy and Hall (1981) collected three benthic samples from riffle habitats and pooled these into a single sample for each study reach. The 2014 macroinvertebrate sampling was conducted during low flow in late July, and both reaches of a reach pair were always sampled on the same day. In each sampling event, six surber samples (363 μm, 0.0625 m^2) were collected from riffle habitats at regular intervals along each reach. Substrate within the surber sample quadrate was disturbed to a depth of 10 cm for approximately 30 s. Samples were stored in 90% alcohol until processing. In the laboratory, the contents of each of the six surber samples from each reach were combined into a single pooled sample. This pooled sample was then subsampled using a plankton splitter until a minimum of 500 individuals were picked from the subsample. Murphy and Hall (1981) picked predatory invertebrates from their samples in the field, which clearly biases the final sample composition toward large-bodied individuals. We therefore conducted a 60 s visual search of the remaining sample (less the subsample) to collect large-bodied individuals and more effectively match the initial study. Invertebrates were identified to family or genus (Merritt et al. 2008) and individually measured using an ocular micrometer mounted on a dissecting microscope. Invertebrate length was converted to biomass using length–mass relationships from published studies (Sample et al. 1993; Sabo et al. 2002) and personal data (M. Wipfli, unpublished data). Subsample abundance and biomass was extrapolated (subsample abundance or biomass divided by subsample proportion multiplied by surber sample area) and combined with the 60 s sample to estimate total abundance and total biomass for each stream reach.

In 2014, fish were collected using a backpack electroshocker (Smith-Root model LR-20B). Block nets were set at the upper and lower ends of each reach to prevent movement and close the system for the duration of the surveys (nets were left in place for the duration of the mark–recapture period). Fish were anesthetized using AQUI-S 20E (AQUI-S, Lower Hutt, New Zealand), weighed, and measured (total length). For mark–recapture surveys, fish were marked with a small caudal clip. Fish were released and each reach was resurveyed after approximately 24 h. Mark–recapture population estimates were used in four streams (Cook, MR404, LO701, LO703), and abundance was estimated using the Lincoln–Peterson mark–recapture model, modified by Chapman (1951). Mark–recapture reach-scale biomass was estimated by multiplying abundance estimates by mean mass. Juvenile (0+) and adult (1+) cutthroat trout were analyzed separately. In 1976 surveys, mark–recapture methods were used at Cook Creek, MR404, and LO703, but multiple pass depletion methods were used at LO701.

In both 1976 and 2014, multiple pass depletion methods were used to estimate population abundance in Mack Creek. The long-term research project provided the 2014 electrosurvey data used in this study (S.V. Gregory, Oregon State University, Department of Fisheries and Wildlife, 104 Nash Hall, Corvallis, OR 07331, USA,

Fig. 2. Ratios of previously harvested to old-growth values for percent pool area (A; %), large wood volume (B; $m^3 \cdot 100\ m^{-2}$), canopy openness (C; %), chl *a* (D; $\mu g \cdot cm^{-2}$), predatory invertebrate biomass (E; $g \cdot m^{-2}$), and cutthroat trout biomass (F; $g \cdot m^{-2}$) in five reach pairs in 1976 (open shapes) and in 2014 (filled shapes) after four decades of riparian regeneration.



* No macroinvertebrate sampling in 1976.

† For MR404, the ratio in 2014 is 1.13 when sculpin are included.

unpublished data). However, abiotic and other biotic variables were collected as part of this study, and thus, population estimates, which use reach area, may differ from those of S.V. Gregory.

Salamanders were also sampled during both the 1976 and 2014 survey events. Unfortunately, sparse data from the 1976 surveys (see Murphy 1979, his appendix G) limit our ability to rigorously assess differences in salamander biomass within reach pairs over time (e.g., numbers were too low to provide a robust population estimate in most streams). We therefore only quantitatively evaluate salamander biomass in 2014 and compare estimates of biomass in the harvested and old-growth reach of each reach pair with the other variables collected in this study in 2014. Salamanders were surveyed using the same methods as cutthroat trout. However, salamanders were marked with a visual elastomer tag (Northwest Marine Technology, Shaw Island, Washington) for mark–recapture surveys.

Statistical analysis

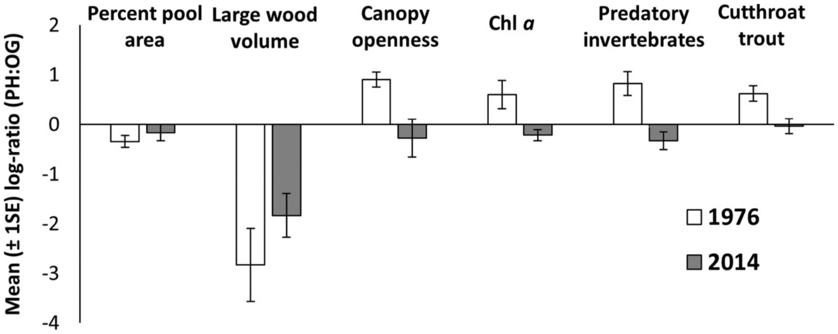
Our comparisons of 2014 results with those of Murphy and Hall (1981) are similar in design to a BACI study. This design has been commonly used to assess the short-term impacts of riparian harvest (and other large-scale perturbations) on an ecosystem using a control or reference reach and a treatment reach with data collected before and after a treatment (Stewart-Oaten et al. 1986). In this study, the Murphy and Hall (1981) data represent our pretreatment condition. Each reach pair ($n = 5$) consisted of an old-growth, reference reach and a previously harvested, treatment reach. The treatment, or "impact" in this case, is nearly four decades of recovery from riparian harvesting.

Methodology was consistent within sampling years but differed slightly between 1976 and 2014 for some metrics (e.g., chl *a*). We therefore focus on assessing changes in the ratios between reaches within each pair (previously harvested : old-growth) in 2014 relative to the 1976 surveys. We compare the ratios of response variables between previously harvested and old-growth reaches within years (1976 and 2014), and we evaluate the mean change in the ratios of each response variable between previously harvested and old-growth reaches before (1976) and after (2014) riparian forest stand regeneration. To statistically evaluate potential differences in response metrics within years, we conduct one-sample *t* tests of the natural-log-transformed ratios (previously harvested : old-growth) within each year. A mean of 0 in this analysis would indicate no difference in the response variable between paired previously harvested and old-growth reaches during that period (1976 or 2014). Because ratios are more easily interpreted, we provide back-transformed estimates of the mean ratio (previously harvested : old-growth), associated 95% confidence intervals, *t* statistics, and *p* values. To evaluate whether the mean ratios for previously harvested and old-growth reaches differed between sampling periods (1976 versus 2014), we conduct paired *t* tests of the difference in log-ratios from 1976 to 2014.

Results

In 1976, Murphy and Hall (1981) compared stream sections bordered by recent patch clear-cuts with paired old-growth reference sections on the same stream. During these initial surveys, percent pool area and large wood volume were lower in the harvested reach compared with the old-growth reach for all five reach pairs (Figs. 2A and 2B, respectively). In contrast, canopy openness, periphyton chl *a* (with one exception), predatory invertebrate biomass, and cutthroat trout biomass were greater in the harvested

Fig. 3. Mean (±1 SE) log-ratios (previously harvested : old-growth) of five reach pairs for the suite of abiotic and biotic variables in 1976 (open bars) and in 2014 (filled bars) after nearly four decades of riparian regeneration. A value of zero indicates no difference between reaches within a reach pair.



reach of each reach pair (Figs. 2C–2F). After nearly four decades of riparian regeneration, the ratios (previously harvested : old-growth) of percent pool area and large wood volume largely persisted, while the ratios of canopy openness, chl *a*, predatory invertebrate biomass, and cutthroat trout biomass decreased, indicating a relative decline of the latter metrics in previously harvested reaches relative to paired old-growth reaches (Fig. 3).

In 1976, percent pool area in harvested reaches averaged 0.71 times (95% CI: 0.50–1.00; back-transformed from log-ratio estimates) that of associated upstream old-growth reaches (one-sample *t* test of natural log-ratios; $T_{[4]} = -2.79$; $p = 0.049$). In 2014, percent pool area was still lower in previously harvested reaches and averaged 0.85 times (95% CI: 0.54–1.33) that of old-growth reaches, although these differences were no longer statistically significant ($T_{[4]} = -1.02$, $p = 0.363$). In 1976, large wood, which had been removed during harvesting operations, was substantially lower in the harvested reach of each pair and averaged only 6% (95% CI: 1%–81%) of wood volume in old-growth reaches ($T_{[3]} = -3.44$; $p = 0.041$). Large wood volume in one previously harvested reach was reported as zero (versus $0.9\ \mathrm{m}^3\cdot 100\ \mathrm{m}^{-2}$ in the paired old-growth reach), and therefore the ratio of this reach pair could not be evaluated. Four decades later, large wood volume was still substantially lower in previously harvested reaches, averaging 16% (95% CI: 5%–54%) of wood volume in paired old-growth reaches ($T_{[4]} = -4.17$; $p = 0.014$). In contrast with percent pool area and large wood volume, changes in the ratio of canopy cover between paired previously harvested and old-growth reaches changed substantially over the four-decade time interval. In 1976, canopy openness was on average 2.46 times (95% CI: 1.62–3.72) greater in the harvested reach compared with paired old-growth reaches ($T_{[4]} = 6.02$; $p = 0.004$). However, in 2014, canopy openness in previously harvested reaches was on average 0.76 times (95% CI: 0.26–2.20) the canopy openness in paired old-growth reaches ($T_{[4]} = -0.72$; $p = 0.510$).

Mean ratios of chl *a*, predatory invertebrate biomass, and cutthroat trout biomass between previously harvested reaches and paired old-growth reaches generally reflected canopy openness results from 1976 and 2014. In 1976, chl *a* was on average 1.86 times (95% CI: 1.21–2.86) greater in the harvested reach of each pair ($T_{[4]} = 2.15$; $p = 0.098$) relative to the old-growth reach. In 2014, chl *a* in previously harvested reaches was on average 0.81 times (95% CI: 0.59–1.09) that of paired old-growth reaches ($T_{[4]} = -1.96$; $p = 0.121$). Predatory invertebrate biomass was quantified in four reach pairs in 1976 but was not collected in LO703. Predatory invertebrate biomass was on average 2.27 times (95% CI: 1.06–4.87) greater in previously harvested reaches compared with paired old-growth reaches during this initial survey period ($T_{[3]} = 3.41$; $p = 0.042$). In 2014, predatory invertebrate biomass was quantified at all five reach pairs, and predatory invertebrate biomass in previously harvested reaches averaged 0.72 times (95% CI: 0.44–1.17) the biomass of paired old-growth reaches ($T_{[4]} = -1.88$; $p = 0.134$). Lastly, in 1976, cutthroat trout biomass was on average 1.86 times (95% CI: 1.21–2.85) greater in previously harvested reaches compared with paired old-growth reaches ($T_{[4]} = 4.00$; $p = 0.016$). Four decades later, cutthroat trout biomass in previously harvested reaches was on average 0.96 times (95% CI: 0.64–1.45) that of paired old-growth reaches ($T_{[4]} = -0.26$; $p = 0.809$).

Differences in ratios of paired previously harvested and old-growth reaches between 1976 and 2014 were evaluated using log-ratios (Fig. 3). The mean difference in log-ratios of percent pool area (paired *t* test of natural-log-ratios; 95% CI: −0.62–0.28; $T_{[4]} = -1.07$; $p = 0.344$) and large wood volume (95% CI: −4.01–1.33; $T_{[3]} = -1.60$; $p = 0.209$) were not significantly different between 1976 and 2014. However, the mean difference of log-ratios between 1976 and 2014 were significantly different for canopy openness (95% CI: 0.15–2.20; $T_{[4]} = 3.19$; $p = 0.033$), chl *a* (95% CI: 0.18–1.46; $T_{[4]} = 3.47$; $p = 0.023$), and predatory invertebrate biomass (95% CI: 0.70–1.78; $T_{[3]} = 7.28$; $p = 0.005$). While the mean log-ratio of cutthroat trout biomass was substantially lower in 2014 compared with 1976, the mean difference in log-ratios was not significant at $\alpha = 0.05$ (95% CI: −0.04–1.36; $T_{[4]} = 2.62$; $p = 0.059$).

Although on average across the five reach pairs, forest regeneration resulted in a decline in canopy openness, chl *a*, predatory invertebrate biomass, and ultimately cutthroat trout biomass, this result was not universal. In 2014, canopy openness was still substantially greater in the previously harvested reach of LO703 relative to the old-growth reach (54% versus 34%) despite four decades of stand regeneration. While the canopy did not close over this time interval as we expected, the lack of canopy closure at this site was fortuitous in that it allowed us to more explicitly evaluate the role of light regulating bottom-up controls on stream biota. In 1976, canopy openness, chl *a*, and cutthroat trout biomass in LO703 were greater in the harvested reach (predatory invertebrates were not collected at this site during initial surveys). In 2014, contrary to expectations, mean chl *a* and predatory invertebrate biomass were relatively similar between the previously harvested and old-growth reaches. However, consistent with expectations, cutthroat trout biomass remained greater in the previously harvested reach relative to the more shaded old-growth reach (8.01 versus $5.13\ \mathrm{g}\cdot\mathrm{m}^{-2}$).

We were not able to rigorously compare estimates of salamander biomass between 1976 and 2014. However, results from 2014 alone are consistent with those observed for cutthroat trout biomass (Appendix A, Fig. A1). Estimates of salamander biomass were similar between the harvested reach and the old-growth reach for MR404, Mack Creek, and LO701. In Cook Creek, where estimates of canopy openness and cutthroat trout biomass were lower in the harvested reach, salamander biomass was just over half the estimated biomass in the old-growth reach (4.41 versus $8.1\ \mathrm{g}\cdot\mathrm{m}^{-2}$). In LO703, estimated salamander biomass was substantially greater in the harvested reach compared with the old-growth reach (14.95 versus $9.82\ \mathrm{g}\cdot\mathrm{m}^{-2}$), a result that is also consistent with canopy openness and trout biomass.

Discussion

After nearly four decades of riparian regeneration, mean canopy openness, chlorophyll *a*, predatory invertebrate biomass, and cutthroat trout biomass declined in harvested reaches relative to paired old-growth reference reaches, which provides empirical data supporting conceptual models of stream abiotic and biotic responses to riparian stand regeneration over time in forested ecosystems. In the sites evaluated in this study, mean chl *a*, predatory invertebrate biomass, and cutthroat trout biomass were initially greater in harvested reaches where canopies were more open relative to paired, old-growth reaches 5–23 years after riparian harvest occurred (Murphy and Hall 1981). These results were observed despite the removal of large wood and lower percent pool area in harvested reaches compared with paired old-growth reaches. In 2014, large wood volume was still substantially lower in previously harvested reaches but percent pool area was similar between paired previously harvested and old-growth reaches. Consistent with the hypothesis that stream light availability can be an important bottom-up driver of the biomass of periphyton and biota in headwater streams, declines in canopy openness in previously harvested reaches relative to paired old-growth reaches over this time interval were accompanied by similar declines in periphyton chl *a*, predatory invertebrate biomass, and cutthroat trout biomass in four of five streams. Overall results from four of the five sites were consistent with trajectories of change portrayed in conceptual models where bottom-up processes strongly influence top predator biomass (usually salmonids), with increases in predator biomass shortly after riparian forest harvest and declines in the biomass of stream predators following stand regeneration when canopies close back over the stream (Sedell and Swanson 1984; Gregory et al. 1987; Mellina and Hinch 2009; Warren et al. 2016).

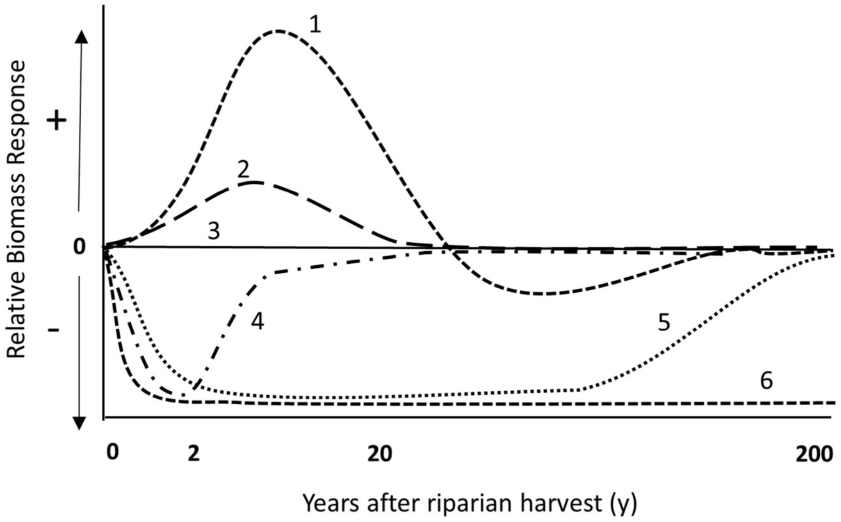
In contrast with our expectations, trout biomass remained substantially greater in the previously harvested reach relative to the reference, old-growth reach at site LO703. While the trend at this site did not fit the classic hypothesized trajectory of biomass over time (e.g., reduced biomass), this result ultimately provides support for the importance of light as a driver of trout biomass in these forested headwater streams. The LO703 site experienced little change in canopy cover from 1976 to 2014, with greater canopy openness in the previously harvested reach during both survey periods. Therefore, the absence of a relative decline in trout biomass following stand regeneration from 1976 to 2014 is consistent with the hypothesized mechanism of changes in canopy cover exerting controls on consumers through bottom-up processes. However, in 2014, chl *a* and the biomass of predatory invertebrates were similar between reaches within this pair despite differences in canopy cover. We speculate that the similarity in chl *a* may be attributed to greater grazing pressure in the previously harvested reach because total invertebrate biomass (not just predatory invertebrates) was approximately 40% greater in the previously harvested reach in 2014 compared with the old-growth reach (Kaylor and Warren 2017), and other studies have found that the effects of changing light on periphyton standing stocks can be missed when macroinvertebrate consumption is high (Kiffney et al. 2004). Additionally, salamander biomass at this site was 1.5 times greater in the previously harvested reach in 2014. The previously harvested reach of LO703 was the only previously harvested reach in which vine maple (rather than alder) dominated the riparian tree community. The results from this reach pair therefore also highlight the importance of considering multiple riparian development trajectories when assessing and projecting forest recovery influences on streams and the biota therein (Warren et al. 2016).

While changes in light over time appear to be the dominant driver of the trout biomass in our study streams, variables not quantified in this study may have also influenced trout biomass over time. Nutrient inputs to streams, particularly nitrogen, often increase in response to riparian harvest (Feller 2005; Kreutzweiser et al. 2008), and increased nutrient inputs have been linked to increased predator production through bottom-up pathways (Johnston et al. 1990; Deegan and Peterson 1992; Peterson et al. 1993; Cross et al. 2006). However, stream nutrient responses to riparian harvest typically depend on the amount of the basin harvested (Tiedemann et al. 1988; Feller 2005), and the size of harvest units in this study were small (<20 ha) within a surrounding basin of unharvested forest. Similarly, temperature may have increased following riparian harvest, which could have altered stream productivity and fish growth rates. In the 1970s, temperature was only monitored at one of the five sites (Mack Creek), and mean weekly temperatures did not exceed 1.0 °C greater in the harvested reach compared with the upstream reference reach (Aho 1976). Given the small sizes of the harvest units and the cool background temperatures of the streams in this study, we do not invoke temperature changes as a major driver of the response in predatory invertebrate or trout biomass. Lastly, because fish are visual feeders, changes in light may have led to changes in fish biomass by altering fish feeding efficiency (Wilzbach and Hall 1985). While decreasing light could lead to reduced feeding efficiency, we do not believe that it was a dominant driver of the responses observed here because it would not account for the changes in chl *a* or predatory invertebrates that we observed.

A limited number of studies have empirically evaluated resident fish responses to timber harvest on the same streams over time scales greater than 10 years (Bisson et al. 2008). These studies reveal the potential for drastically different short- and long-term trajectories from those observed in this study. In the Alsea Watershed study located in the Oregon Coast Range, clear-cut harvesting of the entire 71 ha Needle Branch watershed resulted in a short-term reduction in resident cutthroat trout biomass and abundance (Hall and Lantz 1969). After 25–30 years post-harvest, cutthroat trout biomass had not recovered and remained below preharvest levels (Gregory et al. 2008). Short-term effects of increased temperature, longer-term effects of habitat degradation, and interactions with other salmonid species were identified as possible explanations of continued suppression (Gregory et al. 2008). In East Creek, British Columbia, cutthroat biomass was lower relative to a reference reach following clear-cut harvesting and stream wood removal (Young et al. 1999). Temperatures exceeded 30 °C shortly after harvesting, which likely resulted in high short-term mortality. Approximately a decade later, temperature in the harvested reach had substantially decreased, pool area had increased, and trout abundance was similar to that of the reference reach. Pool area increased again over the next decade, and trout abundance in the previously impacted reach was nearly double that of the reference reach. While this initially appears to contrast with hypothesized trajectories associated with stand recovery and canopy closure, both riparian thinning and habitat restoration occurred in this stream between the second and third sampling events, which confound interpretation of habitat changes alone as the mechanism driving long-term recovery trends (Young et al. 1999).

Our current study along with the two earlier long-term studies and studies quantifying responses over shorter time frames highlight the potential for fish recovery to progress along multiple alternative trajectories that are affected directly and indirectly by trajectories of change in the riparian forest (Hall and Lantz 1969; Young et al. 1999; Gregory et al. 2008; Mellina and Hinch 2009). Long-term recovery from forest management is also a result of how stream habitat and food webs are initially affected by management. In the short term, resident salmonid biomass may substantially decrease when increases in temperature exceed thermal limits or when habitat, particularly loss of pools, is substantially degraded (reviewed in Mellina and Hinch 2009). Populations may recover relatively quickly (<10 years) as temperature recovers or when restoration efforts can enhance the recovery of key habitat

Fig. 4. A suite of potential long-term responses of a resident trout population to riparian timber harvest: (1) Changes in canopy cover drive primary and secondary production; (2) Smaller changes in canopy cover such as those from thinning with a riparian buffer promote smaller magnitude and shorter duration changes in primary and secondary production; (3) Harvesting results in minimal changes in habitat and production; (4) Short-term negative response (e.g., temperature) that quickly recovers; (5) Long-term negative response associated with habitat degradation from the loss of large wood; (6) Alternative steady state in which both habitat and populations do not recover on these time scales (e.g., historical splash dams scouring stream substrate to bedrock). See Appendix B for more detailed explanations of trajectories.



elements such as pool structure (Young et al. 1999). However, natural recovery of pool-forming large wood operates on decadal and centennial time scales (Benda et al. 2003; Gregory et al. 2003; Warren et al. 2009), and it is likely that fish populations affected by the loss of large wood structure will remained suppressed for a long period of time (Connolly and Hall 1999). In high-gradient, boulder-dominated systems where large rocks are functioning as key pool-forming agents during summer, changes or differences in large wood volume may be more likely to yield equivocal results since habitat is not limiting (Warren and Kraft 2003). In these systems, changes in light availability and primary production are likely to be the dominant drivers of consumer biomass over time. To illustrate how trajectories of change over time for resident salmonids following riparian harvest can vary depending on the type, degree impact, and trajectories of recovery in the riparian forest, we suggest six dominant alternative trajectories a resident trout population may follow after riparian harvest (Fig. 4). The set of six alternative trajectories is not exhaustive but demonstrates the complexity of potential resident salmonid responses based on food web and habitat impacts associated with riparian harvest. Greater detail on each trajectory is provided in Appendix B.

In light-limited systems that exhibit trajectories similar to those observed in this study (Fig. 4, trajectory 1), the timing of canopy closure and duration of a closed canopy will ultimately influence long-term responses to timber harvest and subsequent regeneration. If canopies close quickly (<20 years) and are followed by a long period (>50 years) of low light associated with stands in the mid-seral stages of stand development, harvesting may result in a net reduction in benthic biofilms, aquatic macroinvertebrates, and total trout biomass over decadal time scales, even if an initial increase in biomass was observed in the years shortly after canopy removal. In Douglas-fir dominated regions of the Pacific Northwest, canopy closure over headwater streams typically occurs within 30 years after riparian harvest, and canopies remain more closed than preharvest, old-growth conditions from 30 to 100 years (Kaylor et al. 2017). This has important implications considering riparian harvest has been advocated as a potential tool for increasing fish productivity in Pacific Northwest streams (Newton and Ice 2016) with relatively little consideration of long-term responses and alternative trajectories.

Broadly, this study highlights that changes in stream light availability over time, whether associated with forest recovery or in response to other riparian forest changes, can influence consumers through bottom-up pathways in forested headwater streams. Riparian forest recovery from historical harvest is a widespread process that affects light availability in forested streams across North America (Keeton et al. 2007; Kaylor et al. 2017). Results from this study provide support for the hypothesis that decreasing light availability associated with canopy closure is likely to be accompanied by reductions in consumer biomass in light-limited streams (when habitat degradation has been minimal). However, many forest recovery trajectories exist, and these stand development processes will interact with stream conditions and the physiological constraints of stream biota to allow for multiple trajectories of change over time. Understanding long-term responses of stream habitat, productivity, and consumer populations to riparian harvest and recovery will improve our ability to contextualize and project ongoing changes to stream ecosystem function and stream biota in the future.

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Appendices A and B appear on the following pages.

Appendix A

Table A1. Salamander (*Dicamptodon tenebrosus*) biomass and canopy openness in previously harvested and old-growth reaches in 2014.

Site	Riparian type	Salamander biomass (g·m^{-2})	Canopy openness (%)
LO703	OG	9.82 (5.79–13.96)	34.0
	PH	14.95 (7.41–22.48)	53.8
Mack	OG	6.91 (6.22–7.59)	23.9
	PH	7.95 (7.06–8.84)	32.2
LO701	OG	10.58 (1.46–19.70)	20.2
	PH	12.86 (3.95–21.78)	10.5
Cook	OG	8.09 (5.14–11.05)	23.8
	PH	4.41 (2.81–6.02)	4.8
MR404	OG	5.87 (2.04–9.71)	29.0
	PH	6.69 (3.55–9.83)	32.7

Note: OG = bordered by old-growth riparian forest; PH = bordered by previously harvested riparian forest on at least one stream bank. Salamander biomass includes 95% confidence intervals on population estimates in parentheses.

Table A2. Description of reach locations.

Site	Riparian type	Description
LO703	OG	Upstream end 10 m downstream of cold creek; downstream end 70 m upstream of L703 cut break.
	PH	Upstream end 90 m downstream of L703 cut break; downstream end 5 m upstream of channel braid.
Mack	OG	Contact S.V. Gregory for reach information.
	PH	Contact S.V. Gregory for reach information.
LO701	OG	Downstream end 75 m upstream of L701 cut break.
	PH	Upstream end 175 m downstream of L701 cut break.
Cook	OG	Downstream end ~200 m upstream of cut break.
	PH	Upstream end ~100 m downstream of cut break.
MR404	OG	Downstream end ~80 m upstream of L404 cut break.
	PH	Upstream end ~110 m downstream of L404 cut break.

Note: OG = bordered by old-growth riparian forest; PH = bordered by previously harvested riparian forest on at least one stream bank.

Fig. A1. Percent pool area, large wood volume, and canopy openness in 1976 (left) and 2014 (right). Unshaded bars represent reaches within harvested riparian forest, and shaded bars are within the upstream old-growth reference. 2014 canopy openness is shown with 95% confidence intervals of the estimated mean.

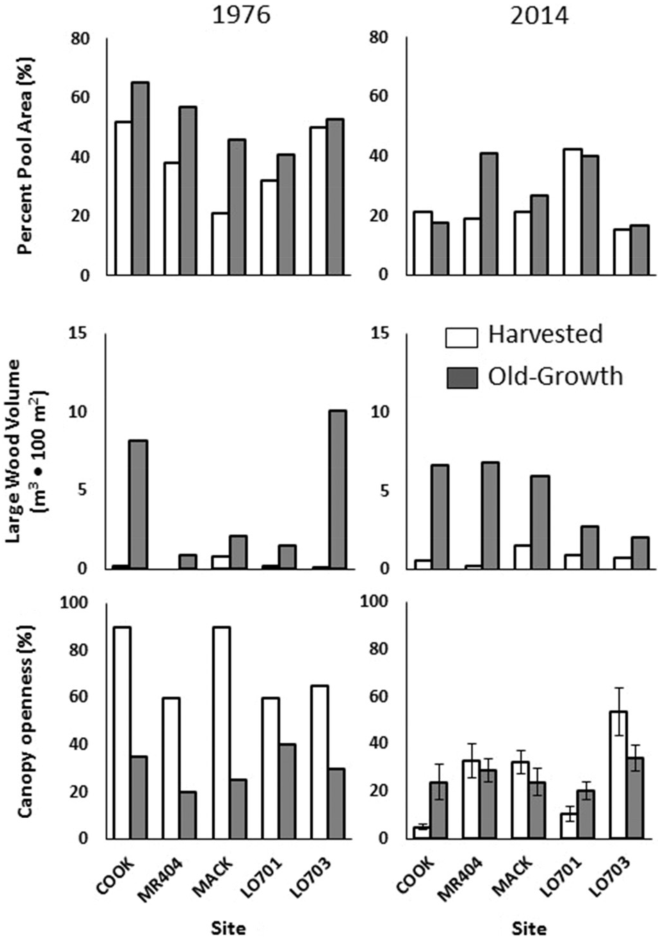
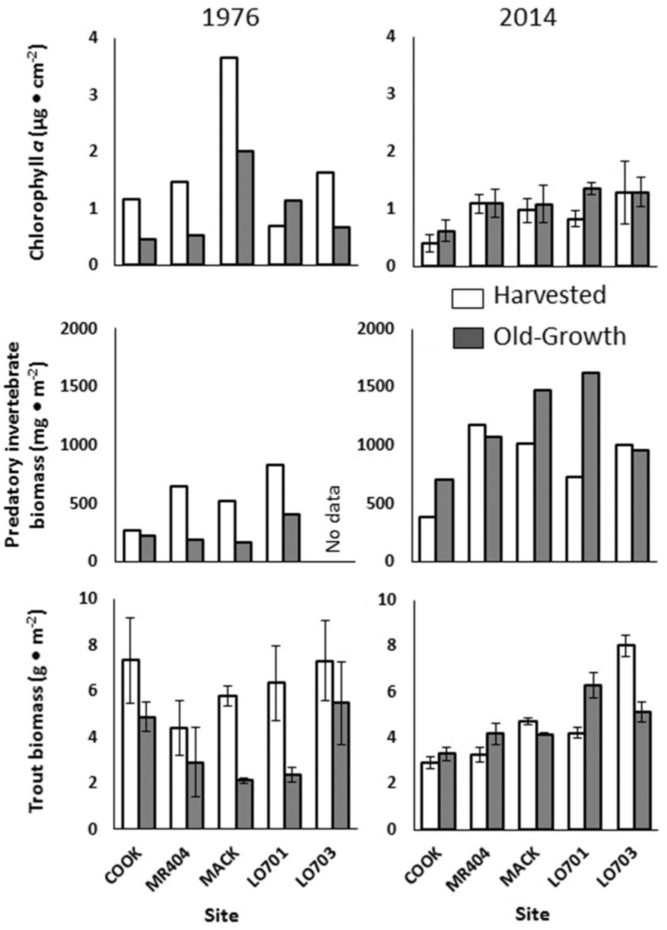


Fig. A2. Chlorophyll *a*, predatory invertebrate biomass, and trout biomass in 1976 (left) and 2014 (right). Unshaded bars represent reaches within harvested riparian forest, and shaded bars are within the upstream old-growth reference. Error bars for chl *a*, and trout biomass are 95% confidence intervals.



Appendix B. Explanations of alternative trajectories of resident salmonid populations

Scenario 1: a short-term positive response (increased biomass) to harvesting associated with greater light and primary production. In this scenario, habitat is minimally effected, temperature increases are minimal or temperature remains relatively low, primary producers are light-limited (at least for part of the year), and invertebrates and resident salmonids are food-limited. Biomass decreases as canopies close and biomass eventually reaches levels below reference conditions because canopy openness (and understory light) is at a minimum in regenerated, second-growth forests (Donato et al. 2012; Kaylor et al. 2017). As stands age and canopy gaps form, biomass slightly increases back to reference (old-growth) levels. This is based on results from this study (Fig. 2), previous studies that document positive resident salmonid responses to harvest (Aho 1976; Murphy and Hall 1981; Hawkins et al. 1983; Bilby and Bisson 1992; Wootton 2012), and previous conceptual diagrams predicting this trend (Sedell and Swanson 1984; Gregory et al. 1987; Mellina and Hinch 2009).

Scenario 2: a short-term positive response that is smaller in magnitude and shorter in duration than that of Scenario 1. This could reflect the effect of increased light associated with harvesting outside of riparian buffers (Kiffney et al. 2003). Because changes in light are relatively small compared with historical clear-cutting, the potential effect size is smaller. Increased stream light may be shorter in duration due to regrowth outside the riparian buffer or to increased branch and understory shrub growth within riparian buffers due to increased light. The same conditions apply as in Scenario 1 — minimal habitat effects and light limitation of primary production.

Scenario 3: the resident salmonid response to harvest is minimal with no clear directionality or long-term population trend (interannual variation excluded). Relatively small, short-term responses were observed in Deer Creek in the Alsea Watershed in which only partial harvest occurred (Gregory et al. 2008) and in a section of East Creek (section B), British Columbia, where clear-cut harvesting occurred but large wood and logging debris were left in the stream (Young et al. 1999). Conditions leading to this scenario may include streams where primary production is limited by other factors (e.g., nutrients), increases in light and primary production are too small to result in an observable invertebrate response, or increased primary production is accumulated by inedible herbivores, which prevents energy flow to higher trophic levels (Power and Dietrich 2002; Power et al. 2013). There are numerous examples of light limitation within heavily forested streams (Gregory 1980; Bilby and Bisson 1992; Ambrose et al. 2004; Warren et al. 2017), but in nutrient-poor, oligotrophic streams, limitation of primary production may only occur at very low light levels. For example, Warren et al. (2017) found that in a stream with low summer nutrient concentrations (~5 $\mu g \cdot L^{-1}$), the light threshold at which limitation switched from light to nutrient limitation was estimated at just 8% of full-sun values.

Scenario 4: there is a short-term negative response (decreased biomass) but a relatively quick recovery. In this scenario, short-term negative responses could be attributed to temperatures exceeding thermal maximums but then recovering as shrubs and trees shade the stream, excess sedimentation that is reduced after vegetative regrowth, altered habitat conditions that are modified by habitat improvement projects, or a combination of these (potentially East Creek, section A; Young et al. 1999). In these streams, major changes to structural habitat (large wood, pools, pool complexity) remain minimally affected. When temperatures or sedimentation rates reduce to preharvest levels or substantially reduce, resident salmonid biomass may return to preharvest levels if light has minimal influence on stream production. Alternatively, but not shown, resident salmonids may increase to levels greater than preharvest if increased light promotes increased primary production after temperatures or sedimentation rates are restored.

Scenario 5: there is a negative response that is sustained over the long term with slow recovery in the absence of management actions. Negative responses are attributed to habitat degradation associated with loss of large wood and pool habitat. Wood inputs to streams, especially large diameter wood, are extremely low following riparian removal and recover slowly as riparian stands develop (Gregory et al. 2003). Full recovery in this scenario could take centuries and would be a high priority for habitat enhancement projects such as large wood addition. In these systems, resident salmonid populations are more strongly habitat-limited, and increased prey availability, if any, is outweighed by the effects of habitat degradation.

Scenario 6: harvesting operations, loss of wood, and intensified debris flows may result in the loss of stream substrates that would take centuries or millenniums to recover. In this "state change", habitat may remain highly degraded and show little sign of recovery over the time frame portrayed in Fig. 4. Scour and the loss of substrates associated with historical splash dams may result in this trajectory. As with Scenario 5, these streams would be high priorities for habitat enhancement projects.

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