Influences of riparian logging and in-stream large wood removal on pool habitat and salmonid density and biomass: a meta-analysis

Eric Mellina and Scott G. Hinch

Abstract: We conducted a meta-analysis using data from 37 studies to assess whether the effects of streamside clear-cut logging on large wood (LW), pool size and number, and summertime salmonid density and standing crop biomass were influenced by stream size and gradient, time since logging was last conducted (1–100 years), and removal of in-stream LW. Age-specific (age 0 (fry) and age 1+ (juveniles)) and species-specific (coho salmon (*Oncorhynchus kisutch*), cutthroat trout (*Oncorhynchus clarki*), and steelhead and rainbow trout (*Oncorhynchus mykiss*)) comparisons were also made. The majority of studies reported negative postlogging responses for LW and pool habitat but positive responses for salmonid density and biomass, with the greatest reductions in all variables generally associated with a thorough removal of in-stream LW. The magnitude of postlogging responses was largely independent of stream size, gradient, and time since logging last occurred. In terms of density and biomass, juveniles were more negatively affected by logging than fry. Of the surveyed species, steelhead trout appeared to be most resilient to riparian logging. Within the time frame covered by the analyses, streams whose riparian zones have been logged may be able to sustain salmonid populations (and even exceed preharvest levels) as long as rigorous removal of LW is not undertaken.

Résumé : Nous avons réalisé une méta-analyse à partir des données de 37 études pour évaluer si les effets d'une coupe à blanc le long d'un cours d'eau sur les grosses pièces de bois, le nombre et la dimension des fosses, la densité et les stocks de salmonidés durant l'été étaient influencés par la dimension et le gradient du cours d'eau, le temps écoulé depuis la dernière coupe (1–100 ans) et le retrait des grosses pièces de bois dans le cours d'eau. Des comparaisons spécifiques à l'âge (alevin et un ans et plus) et à l'espèce (saumon coho (*Oncorhynchus kisutch*), truite fardée (*Oncorhynchus clarki*) et truite arc-en-ciel (*Oncorhynchus mykiss*)) ont également été faites. La majorité des études ont rapporté des réactions négatives après une coupe dans le cas des grosses pièces de bois et des fosses mais des réactions positives dans le cas de la densité et de la biomasse des salmonidés. Les plus fortes réductions de toutes les variables étaient généralement associées au retrait complet des grosses pièces de bois dans les cours d'eau. L'ampleur des réactions après la coupe était largement indépendante de la dimension du cours d'eau, du gradient et du temps écoulé depuis la dernière coupe. La densité et la biomasse des jeunes salmonidés étaient plus négativement influencées par la coupe que celles des alevins. Parmi les espèces inventoriées, la truite arc-en-ciel semblait la plus résiliente à la coupe en zone riveraine. Durant la période de temps couverte par les analyses, les cours d'eau dont la zone riveraine a été coupée peuvent être capables de soutenir les populations de salmonidés (et même de surpasser les niveaux antérieurs à la coupe) à condition de ne pas procéder au retrait systématique des grosses pièces de bois.

[Traduit par la Rédaction]

Introduction

Riparian zones help maintain the ecological integrity of small streams by providing shade, large organic debris, cover for stream-dwelling fish, and energy in the form of allochthonous organic matter and riparian arthropods, as well as by stabilizing stream banks and intercepting sediments (Gregory et al. 1987; Sullivan et al. 1987; Murphy and Meehan 1991). Clear-cut logging practices that remove streamside timber can have subsequent complex spatial and temporal effects on the physical and biological components of small-stream ecosystems (Fig. 1). For example, solar energy and nutrient inputs generally increase in the years immediately following logging, and typically elevate stream temperatures and primary productivity (Beschta et al. 1987; Feller 2005; Moore et al. 2005). Provided summer temperatures remain sublethal, these changes can temporarily increase the densities and biomass of benthic macroinvertebrates (Beschta et al. 1987; Anderson 1992) and consequently those of resident fish (Hicks et al. 1991; Bilby and Bisson 1992).

Concomitant with these energy-related effects, short-term postlogging changes to in-stream habitat have also been reported (Gregory et al. 1987). For example, hillside slope erosion and landslides during or shortly after logging operations can input large amounts of sediment and debris to
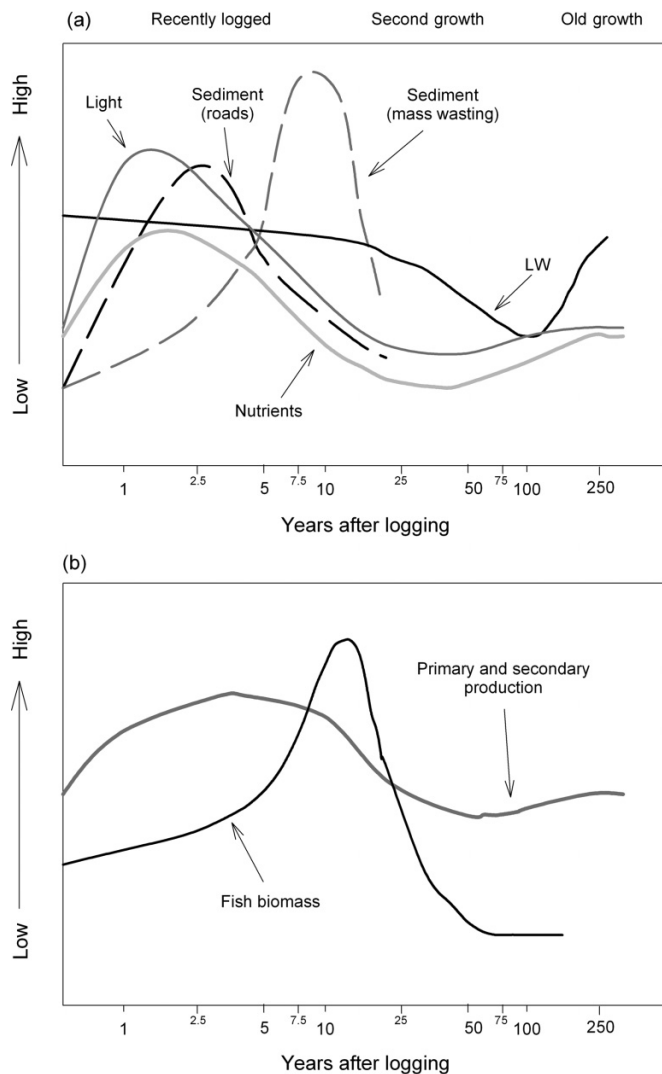
E. Mellina.[1] Department of Forest Sciences, The University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada.
S.G. Hinch. Department of Forest Sciences, The University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada; Institute for Resources, Environment and Sustainability, The University of British Columbia, 2206 East Mall, Vancouver, BC V6T 1Z3, Canada.

[1]Corresponding author (e-mail: mellina@interchange.ubc.ca).

Fig. 1. Predicted temporal trends in short- and long-term postlogging responses of select stream abiotic (*a*) and biotic (*b*) variables. In streams where large wood (LW) influences pool habitat formation, the abundance of pools would be expected to follow a trajectory similar to that of LW. The trends assume that no riparian buffers were maintained and that stream cleaning did not take place. A general descriptor of forest types is presented above *a*. Note that time since logging is on a logarithmic scale. Adapted from Sedell and Swanson (1984), Gregory et al. (1987), Murphy and Koski (1989), Hartman and Scrivener (1990), Bragg (2000), Feller (2005), Gomi et al. (2005), and Moore et al. (2005).

or promoting scour (Sedell and Luchessa 1982; Bisson et al. 1987; Bilby and Ward 1989), and its deliberate removal can lead to further short-term reductions in fish habitat through stream channelization (Hicks et al. 1991). The practice of deliberately removing in-stream LW (hereinafter referred to as stream cleaning) was relatively common in the Pacific Northwest of North America prior to the 1980s and was carried out to enhance navigation, log transportation, fish passage, and water quality, but there was no consideration of the detrimental consequences for stream habitat (Bryant 1983; Sedell and Luchessa 1982; Sedell and Swanson 1984). These changes to the physical habitat can, in turn, lead to reductions in fish abundance and biomass through decreased survival of various life-history stages or through reductions in stream carrying capacity (Lestelle and Cederholm 1984; Scrivener and Brownlee 1989). Shifts may also occur in the composition of age-classes or species in favor of those that are able to utilize riffle habitats that may become more prevalent following logging (e.g., salmonid fry, steelhead and rainbow trout (*Oncorhynchus mykiss*)) at the expense of those that are more dependent on pools (e.g., juvenile salmonids, coho salmon (*Oncorhynchus kisutch*) and cutthroat trout (*Oncorhynchus clarki*); Gregory et al. 1987; Bisson et al. 1988; Roni 2002; Hicks and Hall 2003).

In contrast to these relatively short-term effects, a different suite of impacts may become more prevalent over longer periods of time (Fig. 1; Scrivener and Brown 1992; Hall et al. 2004). For example, 5–10 years after logging, regeneration of streamside deciduous vegetation can stabilize soils and reduce suspended sediment loadings, but the consequent closure of the riparian canopy may mitigate any energy-related benefits resulting from earlier increases in exposure to solar radiation (Gregory et al. 1987; Murphy and Meehan 1991; Scrivener and Brown 1992). Furthermore, the removal of streamside timber can lead to a loss of future LW recruitment and, with the degradation of existing LW, to a subsequent longer term reduction in stream-bank stability, retention of organic matter, the quantity and quality of fish habitat, and fish density and biomass (Gregory et al. 1987; Andrus et al. 1988; Fausch and Northcote 1992). Such changes to in-stream habitat and biota generally take longer to fully manifest themselves, as in-stream LW abundance can decline and remain low for 50–100 years following logging and take over 250 years to recover to preharvest levels in Pacific Northwest forests (Murphy and Koski 1989; Beechie et al. 2000). However, because pool habitat formation in higher gradient streams (e.g., >8%–10%; Anonymous 1996) is often influenced more by boulders than by LW, these stream types may be less susceptible to postlogging reductions in this habitat feature (Murphy and Hall 1981; Sullivan et al. 1987; Ralph et al. 1994).

Previous studies have reported a diversity of stream abiotic and biotic responses to streamside logging practices, with some studies reporting negative postlogging effects, others positive effects, and still others no effect (e.g., see reviews in Gregory et al. 1987; Hicks et al. 1991). For example, with respect to salmonid density, Murphy et al. (1986) reported a 100% increase 1–12 years after logging, whereas Young et al. (1999) reported a 80% reduction 2 years after logging and Mellina et al. (2005) found no difference

streams, as road networks are typically still in use and the surrounding slopes are not yet stabilized by vegetative regrowth (Slaney et al. 1977; Chamberlin et al. 1991; Gomi et al. 2005). Debris torrents and mass wasting (the rapid downstream movement of large amounts of soil, rock, and organic debris; Swanston 1991) can also reduce physical habitat by eroding banks, removing large organic debris or large wood (LW), and creating shallower and wider stream channels (Chamberlin et al. 1991; Hogan and Bird 1998; Benda et al. 2005). In addition to impounding sediment and organic matter and dissipating hydrologic energy, in-stream LW influences pool habitat formation by impounding water

Table 1. Habitat variables, salmonid species, and age range of recent cutblocks and second-growth forests obtained from the studies included in the meta-analysis.

	Region	Habitat variable	Salmonid species	Age of logging? (years)
Burns 1972 (C±*)	California	Pool size	Coho salmon, steelhead and cutthroat trout	1–2; —
Narver 1972 (S±*)	British Columbia	Pool size	Coho salmon, steelhead trout	3; —
Moring and Lantz 1974 (C*Ω)	Washington	—	Coho salmon, cutthroat trout	1–2; —
Moring and Lantz 1975 (B*Ω)	Oregon	—	Coho salmon, cutthroat trout	3–4; —
Chapman and Knudsen 1980 (S±*ΦΩ)	Washington	—	Coho salmon, steelhead and cutthroat trout	5; —
Murphy and Hall 1981 (S*Ω)	Oregon	LW volume; pool size	Cutthroat trout	5–17; 12–35
Murphy et al. 1981 (S±Ω)	Oregon	—	Cutthroat and rainbow trout	5–10; 30–40
Bryant 1982 (BΦ)	Alaska	LW no. and volume	—	2; —
Toews and Moore 1982 (C±*)	British Columbia	LW no. and volume	Coho salmon	2; —
Bryant 1983 (S)	Alaska	LW volume	—	11; —
Bilby 1984 (S)	Washington	Pool no.	—	1; —
Bisson and Sedell 1984 (S±*)	Washington	LW no.; pool no. and size	Coho salmon, steelhead and cutthroat trout	1–11; —
Grette 1985 (S±*Ω)	Washington	LW volume	Coho salmon, steelhead and cutthroat trout	10–13; 20–62
Dolloff 1986 (S±*Φ)	Alaska	—	Coho salmon, Dolly Varden char	1; —
Elliott 1986 (B±*Φ)	Alaska	—	Dolly Varden char	1–5; —
Grant et al. 1986 (SΩ)	Nova Scotia, New Brunswick	—	Atlantic salmon, brown trout, brook char	(1–11; -)
Hogan 1986 (S)	British Columbia	LW no. and volume; pool no. and size	—	2–22; 22
House and Boehne1986 (S±*Φ)	Oregon	LW no. and volume; pool no. and size	Coho salmon, steelhead trout	—; 18
Johnson et al. 1986 (S±*)	Alaska	LW no.; pool no.	Steelhead and cutthroat trout	4; —
Lisle (1986) (S)	Alaska	Pool no. and size	—	2–11; —
Murphy et al. 1986 (S±*)	Alaska	LW volume; pool size	Coho salmon, steelhead and cutthroat trout, Dolly Varden char	1–12; —
Tripp and Poulin 1986 (S)	British Columbia	LW volume; pool size	—	1–15; 16–46
House and Boehne 1987 (S±*Φ)	Oregon	Pool no.	Coho salmon, steelhead and cutthroat trout	—; 10–30
Bilby and Ward 1991 (S)	Washington	LW no. and volume; pool no. and size	—	1–5; 40–60
Fausch and Northcote 1992 (S±*Φ)	British Columbia	LW no. and volume; pool size	Coho salmon, cutthroat trout	—; 40–100
Tripp and Poulin 1992 (S±*)	British Columbia	LW no.; pool size	Coho salmon, steelhead trout, Dolly Varden char	—; 0–46
Flebbe and Dolloff 1995 (S)	North Carolina	LW no.; pool no. and size	Rainbow and brown trout, brook char	—; 80
Connolly and Hall 1999 (S±*Ω)	Oregon	LW no.; pool no.	Cutthroat trout	—; 20–60
Young et al. 1999 (S±*)	British Columbia	LW no. and volume; pool no.	Cutthroat trout	2; —
Johnston 2001 (S)	British Columbia	LW no.; pool no. and size	—	2–22; —
Warren and Kraft 2003 (BΦ)	New York State	—	Brook char	1; —
Fuchs et al. 2003 (S)	British Columbia	LW no.	—	1–5; 20–25
Hicks and Hall 2003 (S±*Ω)	Oregon	LW no.; pool no.	Coho salmon, steelhead and cutthroat trout	—; 24
Dahlstrom and Nilsson 2004 (S)	Sweden	LW no. and volume; pool size	—	—; 50–100
McCleary et al. 2004 (S)	Alberta	Pool size	—	1–3; 17–20
Mellina et al. 2005 ?(S±*)	British Columbia	Pool no. and size	Rainbow trout	1–10; 25–28
De Groot et al. 2007 (B±*)	British Columbia	LW no.; pool no. and size	Cutthroat trout	3; —

Note: The letters C, S, and B in parentheses beside the author names denote studies that used case study (before–after), comparative survey (post-treatment), and before–after - control–impact (BACI) designs, respectively. Stream cleaning refers to the postlogging removal of large wood (LW). ± denotes studies that yielded age-specific data; * denotes studies that yielded species-specific data; Φ denotes studies in which comparisons were made between streams that were cleaned and those that were not cleaned of LW; and Ω denotes studies in which stream bank-full width was estimated from linear regression equations (see Materials and methods). Age-specific data for rainbow trout collected as part of the study by Mellina et al. (2005) are unpublished. The age range of logging is given for recently logged streams followed by second-growth streams.

between old-growth streams and those logged 25–30 years previously. This diversity led us to conduct a meta-analysis of data from published studies in an attempt to assess whether general patterns are evident in stream habitat and fish responses to riparian logging practices, and to determine whether certain stream types are more susceptible than others to the removal of streamside timber. Our goal was to examine whether the impacts of logging on select stream abiotic variables (number and volume of in-stream LW, as well as number and size of pools) and biotic variables (salmonid density and standing-crop biomass) were influenced by commonly reported stream attributes, including stream size and gradient, time since logging last occurred, and whether or not in-stream LW was removed. We compared the magnitude of postlogging responses in small high-gradient versus larger low-gradient streams, in recently logged streams versus those surrounded by second-growth forests, and in cleaned versus noncleaned streams. Similar comparisons were made using age-specific (fry versus juveniles) and species-specific salmonid data to investigate how streamside timber harvesting practices affect specific age-classes and species. We made the following predictions: (*i*) in the short term (<10–15 years after timber harvesting) the amount of LW and the number and size of pools in streams will be unaffected by streamside logging, but salmonid density and standing-crop biomass will increase relative to streams with nonharvested riparian zones; (*ii*) in the longer term (15–100 years after logging), the number and volume of LW and pools in streams, as well as salmonid density and standing-crop biomass, will decrease relative to streams with nonharvested riparian zones; (*iii*) the number and volume of pools, together with salmonid density and biomass, will show greater postlogging reductions in large low-gradient streams than in smaller high-gradient streams; (*iv*) logged streams in which LW was removed (through either deliberate cleaning or debris torrents) will show greater reductions in the amount and volume of LW, the number and size of pools, and salmonid density and biomass, relative to streams in which LW was left in place; and (*v*) the density and biomass of salmonid fry (age 0) will be greater than those of juveniles (age 1+) in logged versus forested streams, as will the density and biomass of steelhead trout compared with those of coho salmon and cutthroat trout.

Materials and methods

Literature-search criteria

We searched for articles in the primary literature that examined the effects of clear-cut logging on streams and salmonid populations, using the Biosciences Information Service (BIOSIS) and the keywords fish–forestry, logging, salmonid, large organic debris, and stream habitat. Peer-reviewed journals that we examined spanned the years 1969–2007 and included *Canadian Journal of Fisheries and Aquatic Sciences*, *Canadian Journal of Forest Research*, *Transactions of the American Fisheries Society*, *Journal of Forestry*, and *North American Journal of Fisheries Management*. Reference sections of the studies uncovered by this search, as well as those of compendia (e.g., Salo and Cundy 1987; Meehan 1991; Northcote and Hartman 2004*a*) and nonrefereed, secondary literature

(e.g., technical reports, conference and symposium proceedings), were subsequently explored for additional studies. To be considered for inclusion in our survey, a study had to include data on the impacts of streamside logging on any of the following six main response variables: LW number and volume, pool number and size, and salmonid density and biomass (the latter two being separated into age- and species-specific subdivisions when possible). It was also necessary for logging-related impacts to be reported relative to a reference category (typically, old-growth forests) to allow us to calculate the magnitude of postlogging responses (see Data analyses below).

LW data were restricted to in-stream woody debris ≥10 cm in diameter and ≥1 m in length (Murphy et al. 1986; Murphy and Koski 1989; Hassan et al. 2005). Habitat responses were limited to the number and size of pools because this habitat feature has the advantage of being biologically and energetically important to salmonids (as areas for feeding, rearing, and refuge; Murphy et al. 1986; Rosenfeld and Boss 2001) and can be measured independently of discharge (Lisle 1987). Pool size includes area, volume, and depth but does not distinguish between pool types (e.g., plunge, dammed, and lateral-scour pools; Bisson et al. 1987). For our analyses a study had to either report the following additional data or allow us to infer them through cross-referencing studies conducted in the same general areas and during the same general period: (*i*) time elapsed since the area was last logged (hereinafter "age of logging"); (*ii*) whether in-stream LW was removed during or following logging (either deliberately or via debris torrents); and (*iii*) stream bank-full width and gradient. Studies were restricted to those conducted between late-spring and early-autumn months (April–October), which represents the period of most intense study in the fish–forestry literature. Studies were also restricted to non-anadromous species or the freshwater stages of anadromous species, thereby avoiding the potentially complex interactions between logging and the migratory and estuarine phases of anadromous species (e.g., alterations in the timing of seaward migrations of juvenile salmon; Holtby 1988). Salmonids in our data set were two species of salmon (coho and Atlantic (*Salmo salar*)), three species of trout (brown (*Salmo trutta*), cutthroat, and steelhead), and two species of char (Dolly Varden (*Salvelinus malma*) and brook char (*Salvelinus fontinalis*)).

The resultant data set comprised 37 studies, of which 27 were from the primary and 10 from the secondary literature (Table 1). The majority of studies (29) were conducted in the Pacific Northwest region of North America (coastal regions of Alaska, Oregon, Washington, California, and British Columbia), with additional studies from the east coast of Canada (Nova Scotia and New Brunswick), north-central and southeastern British Columbia, southern Alberta, North Carolina, New York State, and Sweden. In all studies the logging treatments consisted of clear-cutting to both stream banks, but in eight studies the comparisons were not between streams in logged and old-growth areas but between streams that were cleaned and not cleaned of LW (see Table 1), and in these cases the reference categories were the noncleaned streams. These studies were retained in our final data set because they contained the required data, enabling us to maximize our sample sizes and providing an independ-

ent measure of the effect of stream cleaning. Of the 37 studies, 29 used a comparative survey design (also called post-treatment design; Hicks et al. 1991) whereby separate reference and treatment streams or reaches were monitored concurrently but without obtaining prelogging data for the treatment streams (Table 1). Three studies used a case-study (before–after) design whereby the same streams were monitored both before and after logging but without the use of independent reference streams, and five used a before–after - control–impact (BACI) design involving the concurrent monitoring of treatment and independent reference streams (Table 1).

Data analyses

Magnitude of postlogging responses

To circumvent the problem of comparing data reported in different units (e.g., salmonid biomass in the literature was reported in grams per metre, grams per square metre, and kilograms per hectare), we first converted all data into a measure representing the magnitude of postlogging responses (for simplicity, hereinafter "response"). For a given variable, the response (in percent) from the 29 studies using a comparative survey design is defined as the difference between the reference category and the logged category, and was calculated as [(mean value for logged streams – mean value for reference streams) / mean value for reference streams] × 100. A negative difference indicates a decrease (detrimental response) relative to the reference category, with larger negative numbers denoting more detrimental responses. Conversely, a positive difference indicates an increase (positive response) relative to the reference category. For the three studies using a case-study design, prelogging data were used for the reference category. For the five studies using a BACI design, the response was calculated as [(mean observed value for logged streams – mean expected value for logged streams) / mean expected value for logged streams] × 100, where the mean expected value for logged streams was determined on the basis of the temporal trends in the control stream (see the sample calculation in Appendix A). This calculation was used for the BACI designs to retain consistency among the various study designs. In all analyses the responses for each variable were transformed using a Box–Cox transformation (Krebs 1999) to meet the assumptions required for parametric statistical tests. For each variable's data set the minimum value + 1 was first added to each datum to render all responses >0, thereby allowing transformations to be calculated. However, for clarity all figures were constructed using the original, untransformed data.

Of the 29 comparative survey (post-treatment) studies, 13 involved comparisons between individual treatment and control stream pairs, and the postlogging response calculated for each pair was used as the sampling unit (n; "case") in the analyses. The remaining 16 post-treatment studies involved comparisons between multiple control and treatment streams with no separation into stream pairs, and in these instances mean values for the treatment and control groups were used to calculate postlogging responses. For the eight studies using before–after or BACI designs, the response calculated for each stream was used as the sampling unit in the analy-

ses. Data extraction was further conducted in such a way as to maximize the amount of information that could be gained. For example, the studies by Tripp and Poulin (1986) and Grette (1985) provided sufficient detail to allow streams to be grouped into 10 m bank-full width and 10-year age-of-logging increments, respectively. This allowed us to make maximum use of stream-level variation in the variables as well as to maximize the sample sizes of the resultant data sets.

Stream size and gradient

We evaluated the influence of stream size (bank-full width) and gradient on postlogging responses, given their importance in helping determine channel morphology (Murphy and Hall 1981; Andrus et al. 1988; Bilby and Ward 1991). Values for these two characteristics were taken only for the logged streams within each study (the sizes and gradients of control streams being omitted), as it was the logged streams for which effects were being assessed. Associations among each variable's postlogging response and stream size and gradient were examined using linear regression, with bank-full width and gradient requiring $\log_{10}$ transformations to satisfy the assumptions of the analyses (Kleinbaum et al. 1988). In three studies (see Table 1), stream gradients were not provided and a value of 2% was assigned, based on the reported pool–riffle morphologies of the study reaches (Murphy and Hall 1981; Anonymous 1996). Furthermore, in nine studies (see Table 1), estimates of discharge or drainage area were provided in lieu of stream size, and in these cases stream size was determined on the basis of the following linear regressions developed using bank-full width and discharge data presented in Burns (1972), Narver (1972); Fuchs et al. (2003); McCleary et al. (2004), and Mellina et al. (2005) and bank-full width and drainage-area data from Bilby and Ward (1991):

[1] $$\log_{10}(\text{bank-full width}) = 0.86 \\ + 0.23 \log_{10}(\text{discharge}) \\ R^2 = 0.50, \ n = 38, \ P < 0.001$$

[2] $$\log_{10}(\text{bank-full width}) = 0.59 \\ + 0.32 \log_{10}(\text{drainage area}) \\ R^2 = 0.68, \ n = 70, \ P < 0.001$$

where bank-full width, discharge, and drainage area are expressed in metres, cubic metres per second, and square kilometres, respectively.

Age of logging and removal of LW

Linear regression analysis was used to examine associations between postlogging responses and time since logging occurred, with age of logging requiring a Box–Cox transformation for each of the six main variables. In those studies comparing cleaned and noncleaned streams, age of logging was taken to be the time elapsed since cleaning occurred (i.e., the treatment effect was stream cleaning). Age of logging was further treated as a categorical variable and grouped into old-growth (reference), recently logged (a mean of approximately 5 years since logging; range 1– 12 years), and second-growth (a mean of approximately

33 years since logging; range 16.5–80 years) categories (Table 1). The upper age limit for recently logged streams was based on Grette (1985), House and Boehne (1986), and Hartman and Scrivener (1990), who all reported that the shading provided by the riparian canopy returned to prelogging levels within 15 years of logging. Most energy-related benefits arising from an increase in solar radiation reaching a stream would thus be expected to have been neutralized after this period of time.

Data for the six main response variables were also grouped according to whether or not streams were cleaned of LW, with cleaned streams further separated into whether cleaning was selective or thorough. Selective cleaning involved the removal of small or unstable pieces of LW as part of careful postharvest cleaning efforts (e.g., Dolloff 1986; Elliott 1986; Lisle 1986), whereas thorough cleaning involved the indiscriminate removal of LW (including large, stable pieces; House and Boehne 1987; Fausch and Northcote 1992; Young et al. 1999). Three studies (Hogan 1986; Tripp and Poulin 1986, 1992) included streams that were mass wasted and subjected to debris torrents, and this was considered a form of thorough stream cleaning in the analyses (Bisson et al. 1987; Sullivan et al. 1987).

Two-way analysis of variance (ANOVA) was used to simultaneously test for differences in each variable's postlogging responses among the age-of-logging and stream-cleaning categories. For these analyses, stream cleaning had two levels without regard for whether the cleaning was selective or thorough, as a paucity of data in some categories did not allow for separation into three levels. Instead, separate one-way ANOVAs were used to test whether the extent of cleaning (selective or thorough) influenced each variable's postlogging responses. All tests were considered statistically significant at alpha = 0.05. Given that two separate ANOVAs were conducted for each variable, a Bonferroni correction was applied to the overall alpha level, bringing the level of significance for the above tests to alpha = 0.03. However, because of the high degree of conservatism of Bonferroni corrections, we indicate significance at both alpha = 0.05 and alpha = 0.03, allowing readers to define for themselves which levels are most ecologically meaningful (e.g., see Cabin and Mitchell 2000).

Age- and species-specific comparisons

Of the 37 studies in our survey, 19 allowed us to extract data to assess the impacts of logging on the density and biomass of fry and juvenile salmonids (Table 1). The density and biomass data sets were treated separately for each age-class, and after conversion to postlogging responses, the same suite of transformations and linear regression analyses described above were carried out. However, because of a lack of data in some categories, we could not conduct the two-way ANOVAs, and separate one-way ANOVAs (with a Bonferroni correction) were performed instead, using age of logging (two levels) and stream cleaning (three levels) as factors.

Lastly, to examine the effects of streamside logging on species-specific salmonid density and biomass, data were extracted for coho salmon and cutthroat and steelhead trout from 18 of the 37 studies (Table 1). Steelhead trout includes both anadromous (steelhead) and non-anadromous (rainbow) forms because they have similar freshwater life-history

Table 2. Average postlogging responses (%; mean ± 1 standard error) of the four abiotic and two biotic variables grouped according to age of logging and whether or not the streams were cleaned of large wood (LW).

Variable	No. of positive responses	No. of negative responses	Recently logged		Second growth		Stream cleaning		
			Noncleaned	Cleaned	Noncleaned	Cleaned	None	Selective	Thorough
LW number	8 (4)	24 (9)	−11.9 (13.0)	0.9 (22.9)	−4.7 (35.1)	−49.9 (12.0)	−8.4 (17.4)	10.5 (23.2)	−43.2 (16.4)
LW volume	8 (1)	31 (19)	26.0 (47.7)	−50.3 (11.3)	−30.7 (11.0)	−71.5 (7.3)	−6.8 (21.3)	−44.5 (14.0)	−67.9 (7.6)
Pool no.	9 (3)	20 (10)	−7.1 (11.2)	−13.2 (22.4)	4.4 (20.4)	−50.2 (4.4)	−2.1 (10.6)	2.6 (19.1)	−49.0 (10.9)
Pool size	16 (6)	35 (24)	−9.6 (9.6)	−15.6 (8.5)	7.6 (11.7)	−27.4 (8.5)	−3.0 (7.5)	−25.2 (13.3)	−17.0 (6.4)
Salmonid density	32 (11)	25 (15)	34.0 (16.2)	63.2 (58.0)	124.2 (41.2)	−28.2 (20.1)	63.1 (18.5)	91.1 (71.9)	−32.9 (15.5)
Salmonid biomass	30 (17)	22 (14)	26.5 (20.6)	37.5 (21.9)	60.3 (41.0)	−19.4 (13.2)	33.0 (18.2)	42.9 (22.2)	−23.9 (13.3)

Note: Stream cleaning is subdivided into selective and thorough. The overall number of cases with positive or negative responses is also given; values in parentheses indicate the number of cases in which stream cleaning was undertaken.

Fig. 2. Relations between postlogging responses and stream bank-full width, gradient, and age of logging for large wood (LW) number and volume and pool number and size. Data are grouped into those for recently logged streams that were not cleaned (□), recently logged cleaned streams (■), second-growth streams that were not cleaned (○), and second-growth cleaned streams (●); * denotes a stream that was mass wasted; † denotes a study in which comparisons were made between streams that were cleaned and not cleaned. Probability (*P*) values are included for linear regressions conducted on the entire transformed data set, with R^2 values for regressions that are significant at $P \leq 0.05$ (see Materials and methods for details). Arrows link symbols to specific data points, and a logarithmic scale for the age-of-logging graphs was used to increase clarity. The dotted line shows the line of zero effect.
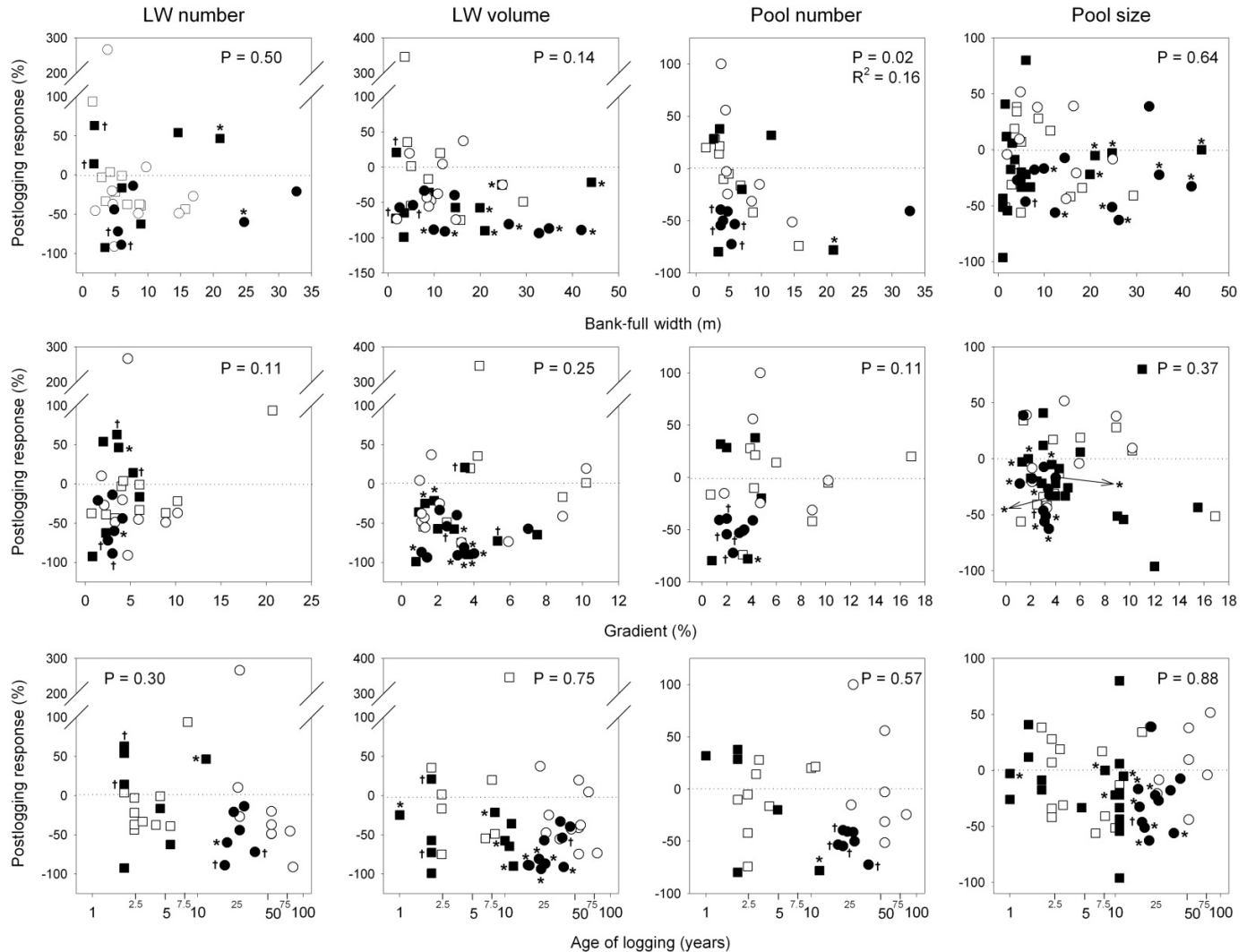
phases. We treated the density and biomass data sets separately for each species and used the procedures and analyses described above for the age-specific data, except that only two levels of stream cleaning (cleaned and noncleaned) were possible in the ANOVAs.

Results

LW number and volume and pool number and size

Postlogging responses of the four abiotic variables were negative in the majority of cases, with 56% of these involving stream cleaning (Table 2 and Fig. 2). Where positive responses were observed, in most cases postlogging cleaning of LW did not occur (Table 2). The responses of LW number and volume, as well as pool size, appeared to be largely independent of stream size and gradient (linear regression probability (*P*) values >0.11), the exception being a weak

($R^2 = 0.16$, $P = 0.02$) negative relation between stream bank-full width and the postlogging responses of pool number (Fig. 2). No significant relations were found between age of logging and the responses of any of the four abiotic variables ($P > 0.30$; Fig. 2).
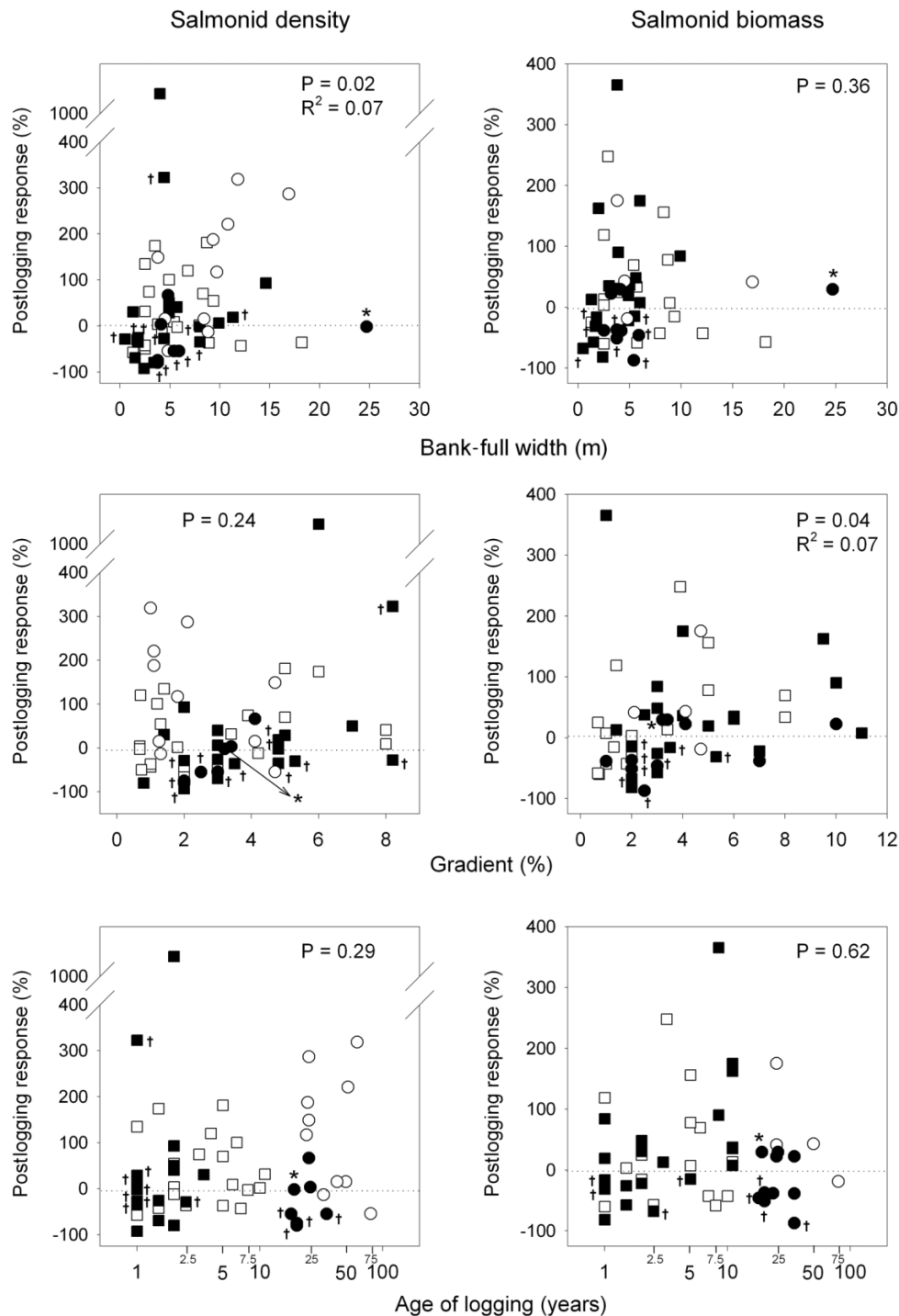
Significantly greater negative responses were found in cleaned versus noncleaned streams for LW volume (two-way ANOVA, $P = 0.001$) as well as for number and size of pools ($P = 0.05$ in both cases; Table 2 and Fig. 3). In contrast, the age of logging factor and the interaction terms (age of logging × stream cleaning) were nonsignificant in the analyses ($P > 0.11$ and $P > 0.18$, respectively; Fig. 3). Furthermore, mean postlogging responses were generally negative (12 of 16 times) when the combination of stream cleaning and age of logging categories was considered, the exceptions being recently logged cleaned and noncleaned streams for LW number and volume, respectively, and

Fig. 3. Effect of streamside logging on large wood (LW) number and volume and pool number and size. In the left-hand panels, variables are grouped according to age of logging (○, a recently logged stream; ●, a second-growth stream) and whether or not the streams were cleaned of LW. Significant differences ($P \le 0.05$) in either category are indicated in each panel. In the right-hand panels, stream cleaning was subdivided into selective and thorough; values with a different letter are significantly different at $P \le 0.05$ (*) or $P \le 0.03$ (**). Error bars represent the standard error; the samples size (*n*) is provided for each category. Note that axis scales are not consistent.
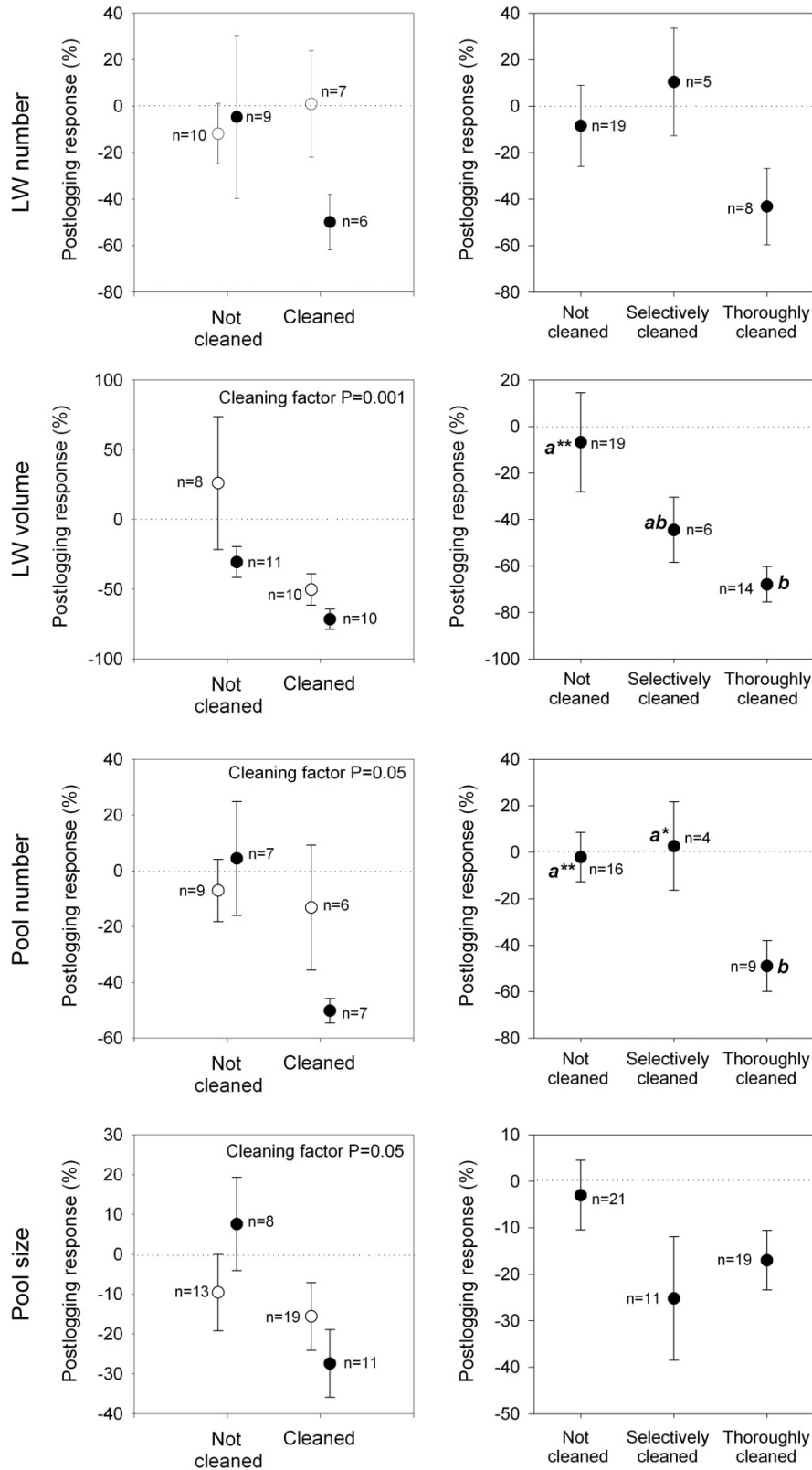
Fig. 4. Relations between postlogging responses and stream bank-full width, gradient, and age of logging for salmonid density and biomass. Data represent the freshwater life-history stages of all reported salmonid species (see the text for a list of species). For a description of axes and explanation of symbols see Fig. 2.


second-growth, noncleaned streams for pool number and size (Table 2 and Fig. 3). When cleaning was further separated into selective and thorough, significantly greater negative responses were observed in thoroughly cleaned streams than in noncleaned streams for LW volume (one-way ANOVA, $P = 0.001$) and pool number ($P = 0.009$; Table 2 and Fig. 3). For the latter response variable, significantly more negative responses ($P = 0.05$) were also found

in thoroughly cleaned streams than in those in which the cleaning was selective (Fig. 3). Thoroughly cleaned streams also generally had the most negative abiotic postlogging responses of all cleaning categories (Table 2).

Salmonid density and biomass

In contrast to the four abiotic variables, postlogging responses were positive in a small majority of cases for sal-

Fig. 5. Effect of streamside logging on salmonid density and biomass according to age of logging and stream cleaning categories. For an explanation of symbols and categories see Fig. 3.
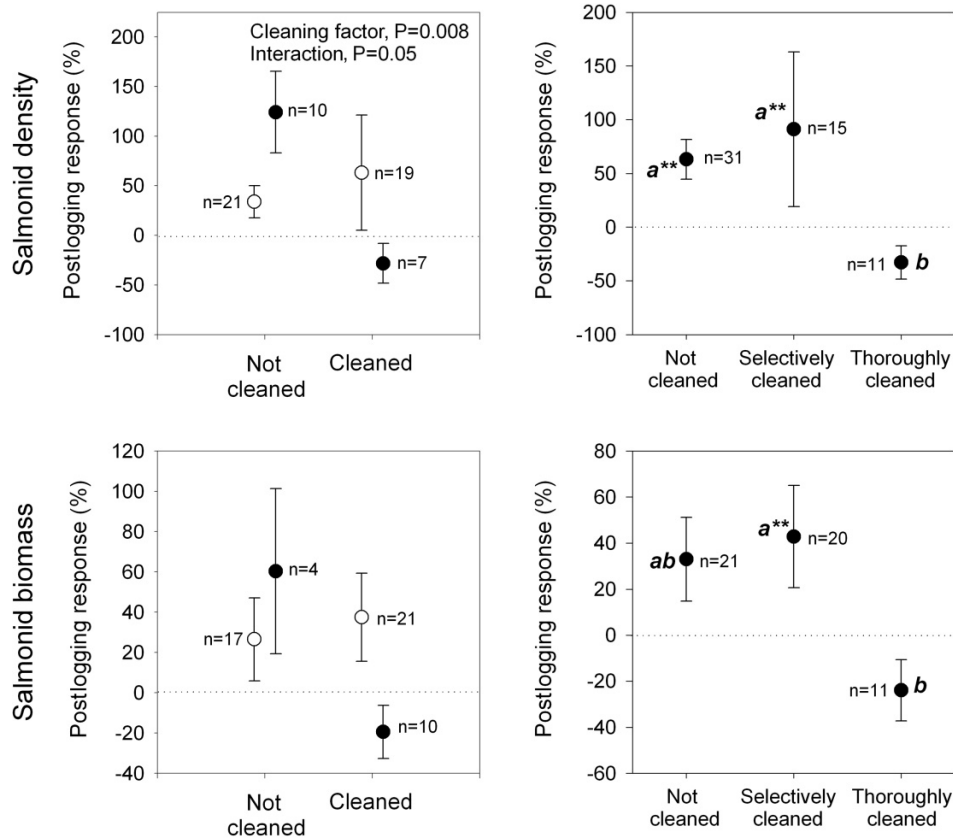
monid density and biomass, with cleaning of LW reported in 45% of these cases (Table 2 and Fig. 4). Furthermore, stream cleaning was reported in 59% of cases where negative responses were observed for these two variables (Table 2). There were weak positive relations between the postlogging responses of salmonid density and stream bankfull width ($P = 0.02$, $R^2 = 0.07$) as well as between salmonid biomass responses and stream gradient ($P = 0.04$, $R^2 = 0.07$), but none with age of logging ($P > 0.29$; Fig. 4).

Stream cleaning resulted in significantly more negative postlogging responses for salmonid density (two-way ANOVA, $P = 0.008$), with age of logging being nonsignificant ($P = 0.99$; Table 2 and Fig. 5). However, in this case the interaction term was marginally significant ($P = 0.05$). No significant differences were found between age of logging ($P = 0.73$) and stream cleaning ($P = 0.14$) for salmonid biomass responses, nor was the interaction term significant ($P = 0.09$; Fig. 5). Moreover, mean postlogging responses for salmonid density and biomass were generally positive when the combination of stream cleaning and age of logging is considered, the exception being second-growth cleaned streams (Table 2 and Fig. 5). Significantly more negative responses were observed in thoroughly cleaned streams than in noncleaned and selectively cleaned streams for salmonid density (one-way ANOVA, $P < 0.02$), and than in selectively cleaned streams for biomass ($P = 0.03$; Fig. 5). As with the abiotic response variables, thoroughly cleaned streams also had the most negative postlogging responses for density and biomass of all cleaning categories (Table 2).

Fry and juvenile age-classes

Postlogging responses were positive in a small majority of cases for fry density and biomass, with cleaning of LW reported in 45% of these (Table 3 and Fig. 6). Of those cases where negative responses were observed, 81% involved stream cleaning (Table 3). In contrast, slightly more than half of the juvenile density and biomass responses were negative, with the majority of these (73%) involving stream cleaning (Table 3 and Fig. 6). Of the cases in which positive juvenile responses were observed, 40% involved stream cleaning. No significant relations were found between fry and juvenile postlogging responses and stream bank-full width and gradient ($P > 0.06$), with the exception of fry density and bankfull width, where a weak ($P = 0.03$, $R^2 = 0.17$) positive relation was found (Fig. 6). Furthermore, no significant relations were found between age of logging and the density and biomass responses of either fry or juveniles ($P > 0.22$; Fig. 6).

With age of logging as a categorical variable, significant differences were only found for fry biomass, with a more negative response in second-growth than in recently logged streams (one-way ANOVA, $P = 0.03$; Table 3 and Fig. 7). Fry biomass in second-growth streams was also the only instance in the age-specific data sets in which a negative mean postlogging response (–4%) was calculated (Table 3). When the influence of stream cleaning on fry and juvenile densities was considered, significantly more negative responses ($P \leq 0.02$) were found in streams that were thoroughly cleaned of LW than in noncleaned streams (Table 3 and Fig. 7). A significantly more negative response ($P = 0.03$)

Table 3. Mean postlogging responses (%; mean ± 1 standard error) for the density and biomass of salmonid fry (age 0) and juveniles (age 1+) according to age of logging and whether or not the streams were cleaned of large wood (LW).

| Variable | No. of positive responses | No. of negative responses | Age of logging | | Stream cleaning | | |
			Recently logged	Second growth	None	Selective	Thorough
Fry density	12 (3)	10 (8)	27.2 (19.1)	83.7 (48.0)	135.7 (42.2)	−5.7 (28.7)	−29.5 (19.4)
Fry biomass	10 (7)	6 (5)	118.9 (62.9)	−4.1 (31.8)	62.0 (33.8)	134.6 (111.3)	18.1 (23.8)
Juvenile density	15 (4)	15 (10)	5.2 (20.2)	26.9 (16.2)	51.4 (16.9)	−35.9 (6.1)	−15.4 (20.0)
Juvenile biomass	10 (6)	11 (9)	44.4 (48.2)	8.8 (21.5)	71.3 (51.1)	30.5 (51.1)	−18.7 (19.1)

Note: The overall number of cases with positive or negative responses is also given; values in parentheses indicate the number of cases in which stream cleaning was undertaken.

Fig. 6. Relations between postlogging responses and stream bank-full width, gradient, and age of logging for the density and biomass of salmonid fry (age 0) and juveniles (age 1+). For an explanation of symbols see Fig. 2.
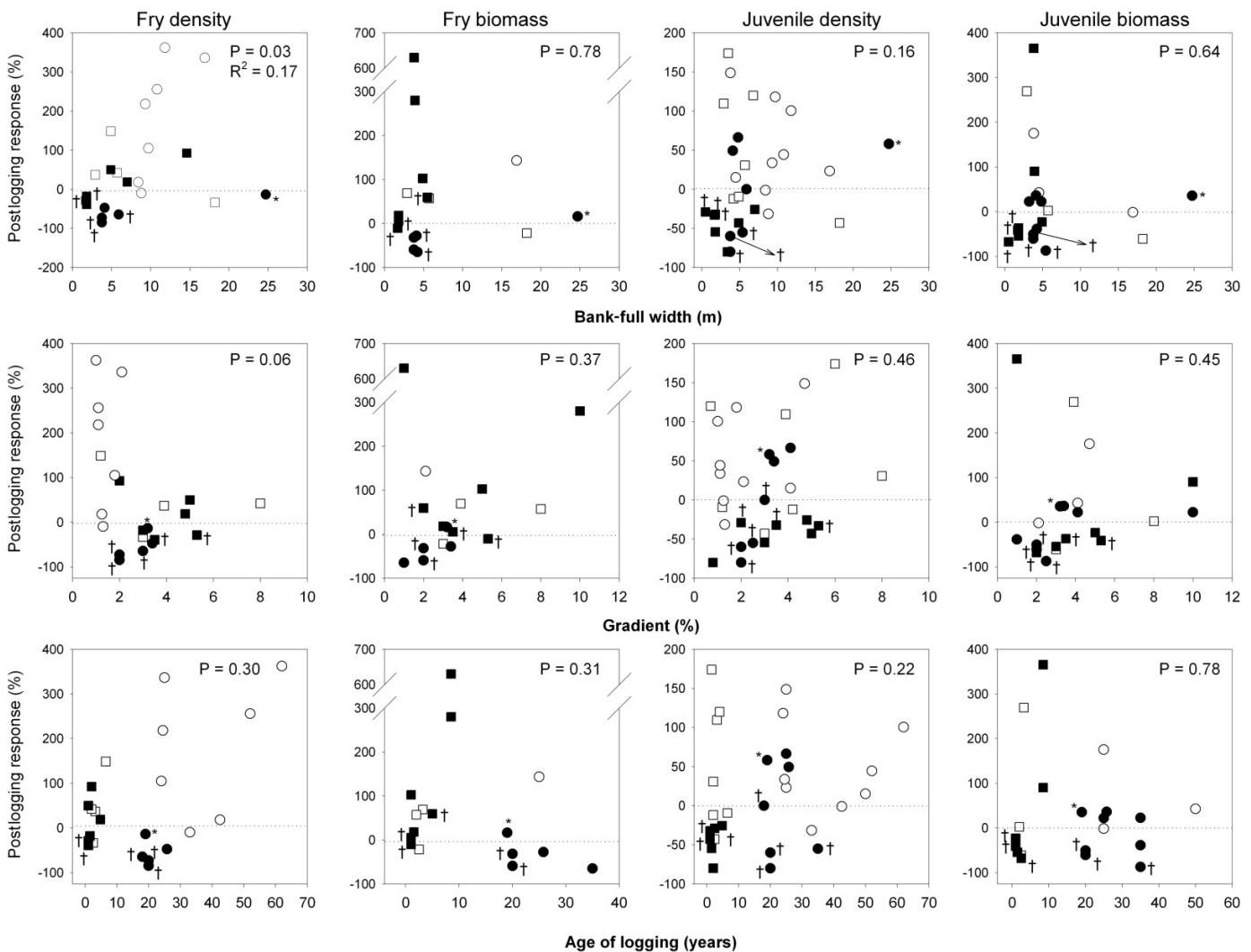

was also found for juvenile density in selectively cleaned streams than in noncleaned streams (Fig. 7). Mean postlogging responses for both age-classes were positive in all noncleaned streams, whereas they were negative in cleaned (whether selectively or thoroughly) streams for fry and juvenile densities and in thoroughly cleaned streams for juvenile biomass (Table 3 and Fig. 7). For all age of logging and

stream cleaning categories, mean postlogging responses were generally more positive for fry than for their juvenile counterparts (Table 3 and Fig. 7).

Species-specific density and biomass

Postlogging responses were negative in a small majority of cases for coho salmon density and biomass, with postlog-

Fig. 7. Effect of streamside logging on the density and biomass of salmonid fry (age 0) and juveniles (age 1+) according to age of logging (top row) and whether or not stream cleaning of large wood (LW) took place (bottom row). Values with a different letter are significantly different at $P \le 0.05$ (*) or $P \le 0.03$ (**). Error bars represent the standard error; the sample size (n) is provided for each category. The dotted line shows the line of zero effect. Note that axis scales are not consistent.
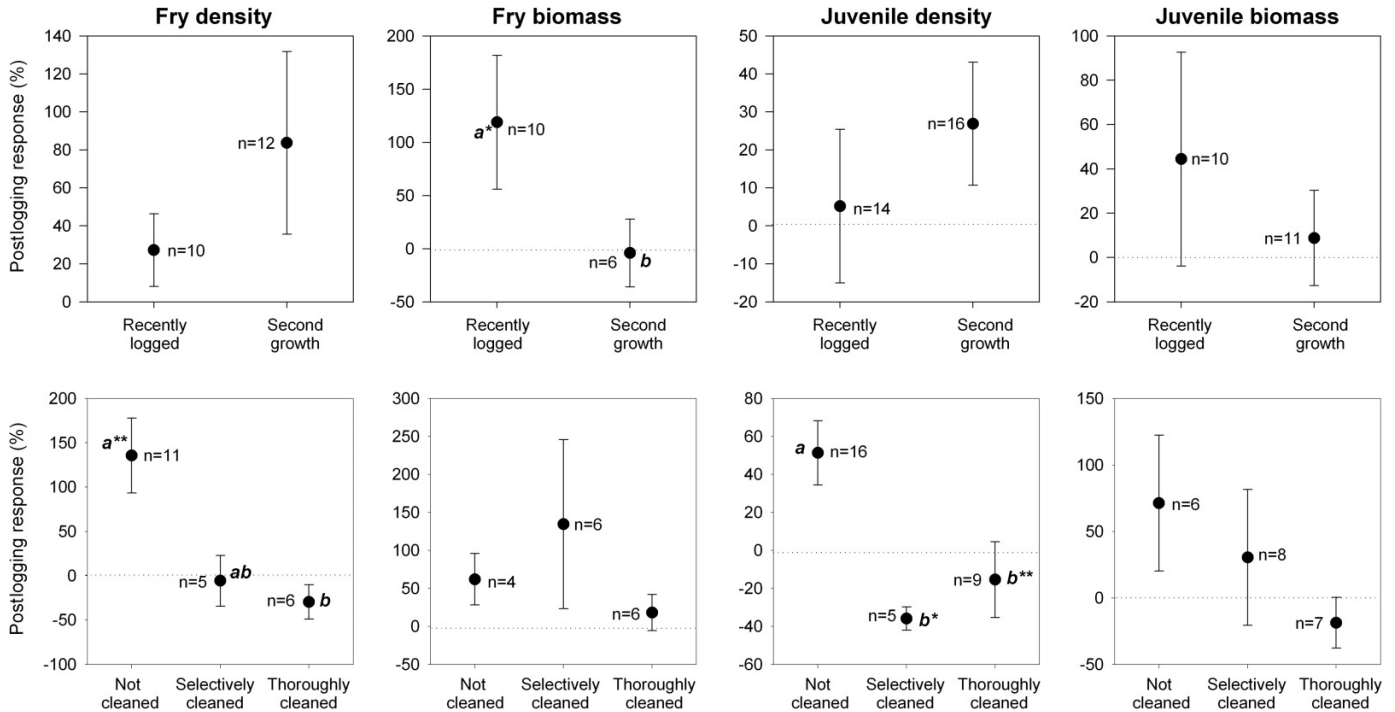
ging cleaning of LW being reported in 83% of these (Table 4 and Figs. 8a and 8b). Of the remaining cases reporting positive responses, stream cleaning was conducted in only 29%. The results for cutthroat trout were more variable, with a small majority of cases reporting negative responses for density (of which 38% involved stream cleaning) and the reverse trend being observed for biomass (with 78% of these involving cleaning; Table 4 and Fig. 8). In contrast, postlogging responses were positive in a majority of cases for steelhead trout density and biomass, with stream cleaning reported in 31% of these. Of the cases in which negative responses were reported for this species, 67% involved stream cleaning (Table 4 and Figs. 8a and 8b). Coho salmon density responses were weakly positively related to stream bank-full width ($P = 0.03$, $R^2 = 0.16$) but negatively related to stream gradient ($P = 0.007$, $R^2 = 0.24$; Fig. 8a). In contrast, no significant relations were found between any of the remaining species-specific density or biomass responses and stream bank-full width or gradient ($P > 0.13$) or age of logging ($P > 0.06$; Fig. 8).

There were also no significant differences in postlogging responses for density or biomass between recently logged and second-growth streams for any of the three species we examined (one-way ANOVAs, $P > 0.06$; Table 4 and Fig. 9). Although no consistent patterns were observed across these categories, steelhead trout was the only species for which mean density and biomass responses were positive regardless of age of logging (Table 4 and Fig. 9). When the influence of stream cleaning was considered, the general trend was for more negative postlogging responses in cleaned than in noncleaned streams for all species-specific comparisons of density and biomass, although significant

differences were only found for coho salmon density ($P = 0.001$) and biomass ($P = 0.05$) and steelhead trout density ($P = 0.04$; Table 4 and Fig. 9). Overall responses for steelhead trout were generally greater (more positive) than those of the other two species for all stream cleaning and age of logging categories.

Discussion

Our predictions relating to time since logging were largely unsupported by the data, given that this factor did not appear to strongly influence LW, pool habitat, or salmonid density and biomass (whether total or broken down into age- and species-specific categories) postlogging responses, even accounting for stream cleaning. We had expected salmonids in recently logged streams to benefit from short-term, energy-related effects and for populations in second-growth streams to be negatively affected by longer term reductions in LW and pool habitat (Sedell and Swanson 1984; Hicks et al. 1991; Scrivener and Brown 1992). This pattern was only exhibited by the fry biomass data, and it may be that not enough time had elapsed in the studies that we surveyed for the expected longer term impacts to fully manifest themselves (Murphy and Koski 1989; Scrivener and Brown 1992; Bragg 2000). For example, although the mean time since logging last occurred for the second-growth streams in our survey was approximately 33 years, the streams monitored by Fausch and Northcote (1992) and Flebbe and Dolloff (1995) exhibited some of the longest elapsed times since logging occurred (40–100 years), and they were also among those showing the greatest postlogging reductions in LW, pool habitat, and salmonid density and biomass. Therefore,

Table 4. Average postlogging responses (%; mean ± 1 standard error) for the density and biomass of coho salmon and cutthroat and steelhead trout according to age of logging and whether or not the streams were cleaned of large wood (LW).

	No. of positive responses	No. of negative responses	Age of logging		Stream cleaning	
			Recently logged	Second growth	None	Cleaned
Coho salmon density	10 (2)	15 (11)	9.0 (23.8)	94.7 (49.6)	135.5 (42.2)	−28.6 (19.1)
Coho salmon biomass	7 (3)	9 (9)	−3.2 (18.1)	−0.6 (26.4)	48.3 (27.0)	−19.3 (14.5)
Cutthroat trout density	7 (1)	8 (3)	−23.8 (34.2)	38.1 (26.8)	25.7 (26.6)	−35.9 (34.9)
Cutthroat trout biomass	9 (7)	5 (4)	38.1 (27.0)	22.2 (45.0)	62.9 (60.1)	24.1 (25.0)
Steelhead trout density	11 (3)	4 (2)	48.1 (19.6)	30.6 (24.0)	60.4 (18.1)	−4.5 (17.2)
Steelhead trout biomass	5 (2)	2 (2)	62.2 (66.1)	86.7 (33.2)	132.5 (58.1)	27.9 (41.9)

Note: Steelhead trout data include rainbow trout. The overall number of cases with positive or negative responses is also given; values in parentheses indicate the number of cases in which stream cleaning was undertaken.

although responses did not differ substantially between recently logged and second-growth streams, over a longer time frame, second-growth streams may show more pronounced declines in both abiotic and biotic variables.

In contrast, negative postlogging responses for LW and pool number and size were most strongly influenced by stream cleaning, particularly when the cleaning was thorough. Given that deliberate removal of LW is a key factor in postlogging declines in the quality and quantity of pool habitat (Hicks et al. 1991; Fausch and Northcote 1992), it was expected that this practice would have a dominant and negative influence on the abiotic variables. However, several studies reported postlogging increases in LW despite stream cleaning, and this may have been due to trqansportation of LW into the study reaches from upstream areas, as well as to the practice of placing pieces of LW along stream banks, where they could subsequently have been re-entrained during periods of high flow (Bisson et al. 1987; Toews and Moore 1982). That selectively cleaned streams showed postlogging responses for pool size (and juvenile density) that were approximately the same as those in thoroughly cleaned streams may have stemmed from the intentional or unintentional removal of large, stable pieces of LW during cleaning operations. For example, legislation introduced in the mid-1970s in Oregon and Washington made it a legal requirement for forestry companies to remove postlogging debris (primarily smaller pieces of slash; Sedell and Luchessa 1982; House and Boehne 1987) from streams, but in some cases even stable pieces of LW were removed, partly to offset the high costs associated with cleaning operations (Bilby and Ward 1989; Peter A. Bisson, United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, 3625 93rd Avenue SW, Olympia, WA 98512–9193, USA, personal communication, February 2008).

Some studies in which postlogging reductions in LW were observed also reported positive responses for the size and number and size of pools (including streams where cleaning took place), a discrepancy that may be related to the different mechanisms involved in the formation of this habitat feature. For example, smaller high-gradient streams rely less on LW for pool formation because of the availability of other habitat-forming structures, such as boulders and even small trees and logging debris (Bilby and Ward 1991; Berg et al. 1998; Warren and Kraft 2003; Kreutzweiser et al. 2005). Larger low-gradient streams (e.g., <25 m bank-full width and <8% gradient; Anonymous 1996) may therefore be most susceptible to postlogging reductions in pool number and size, and this was partially supported by our analyses of pool number, where a negative relation was found between postlogging responses and stream size.

As with the pool habitat and LW data, postlogging responses for salmonid density and biomass were most strongly influenced by whether or not the streams were cleaned of LW, with noncleaned streams generally showing positive responses and cleaned streams showing negative responses (particularly when the cleaning was thorough). This too was expected, given that in addition to enhancing pool formation and retaining organic matter, LW provides cover that is required by most stream-dwelling salmonids and that can increase fish abundance and biomass (Dolloff 1986; Bjornn and Reiser 1991; Murphy and Meehan 1991). However, for salmonid density, our results suggested that the effect of stream cleaning was moderated by the age of logging (specifically, that cleaning resulted in more negative responses in second-growth streams but not in recently logged streams). Furthermore, there was a general disagreement in qualitative trends between the abiotic and biotic variables, given that postlogging responses were largely positive for salmonid density and biomass, but largely negative for LW and pool habitat. How were streams able to support postlogging salmonid densities and biomasses that, on average, exceeded levels found in forested streams when LW and pool number and size largely declined? Part of this discrepancy may lie in the possibility either that LW is critical in creating refugia for fish only during periods of high flow (Solazzi et al. 2000; Roni and Quinn 2001), that different species have different habitat preferences (Gregory et al. 1987; Hicks and Hall 2003), or that salmonids may be able to use habitat and cover provided by elements other than LW and pools (such as undercut stream embankments, overhanging vegetation, and boulders; Lestelle and Cederholm 1984). The latter speculation is supported by our regression analyses, which suggested that the most beneficial postlogging effects were observed in large (for salmonid density, including fry) high-gradient (for biomass) streams, given that steeper as well as very large streams would be less reliant on LW for pool formation (Sullivan et al. 1987; Bilby and Ward 1991; Anonymous 1996). Therefore, despite postlogging reductions in pool number and size and any concomitant changes in carrying capacity, sufficient habitat may have remained in most of the surveyed streams (especially those that were not cleaned or only selectively cleaned) to support

Fig. 8. Relations between postlogging responses and stream bank-full width, gradient, and age of logging for species-specific salmonid density (*a*) and biomass (*b*). Steelhead trout data include rainbow trout. For an explanation of symbols see Fig. 2.
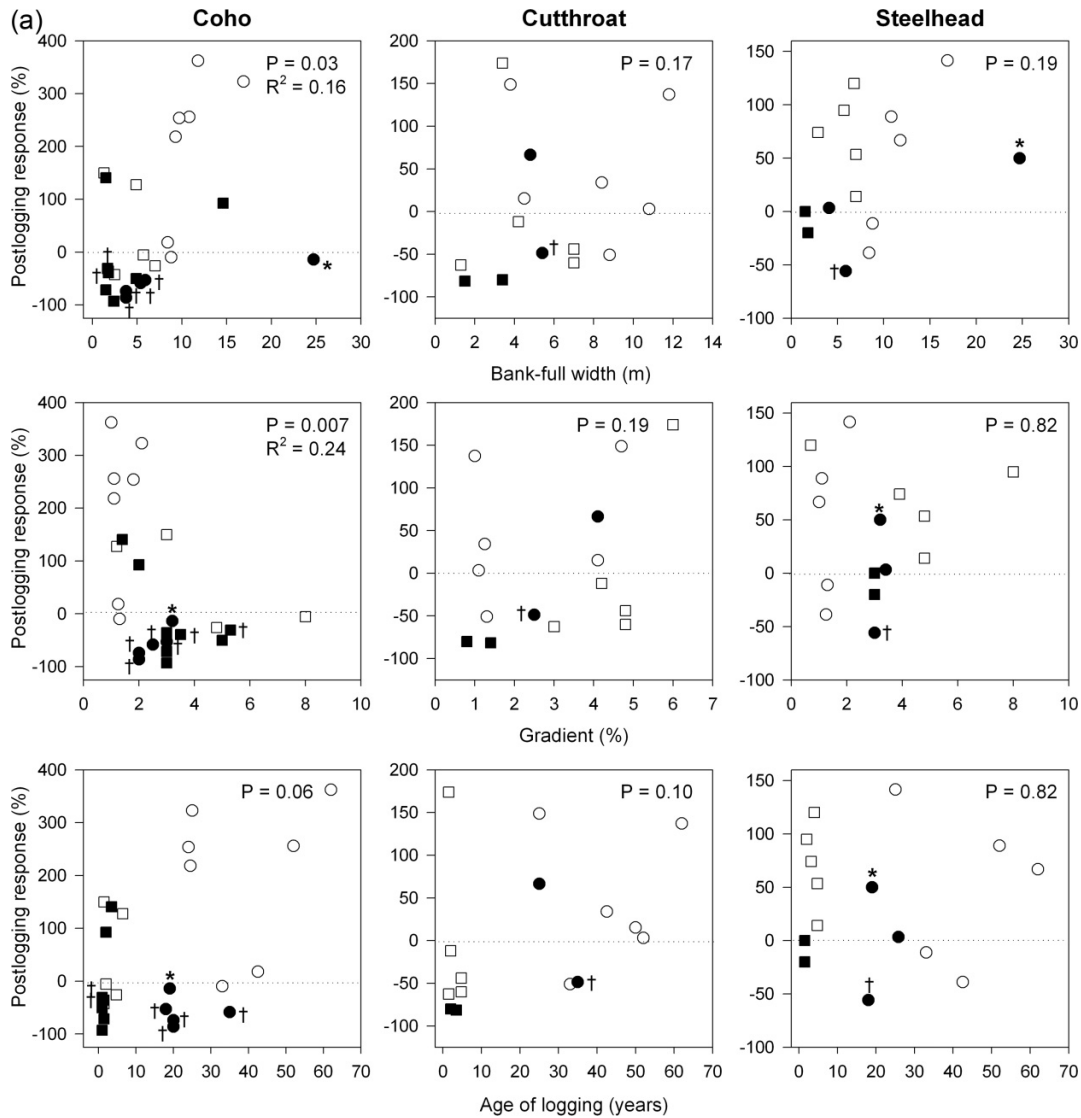

and even exceed prelogging salmonid population levels, with thorough cleaning reducing that capacity below prelogging levels.

The link between stream cleaning and the postlogging temporal responses of salmonid density and biomass suggested by our analyses may also warrant a modification of the hypothesis proposed by Sedell and Swanson (1984) that a short-term increase in salmonid biomass is followed by a longer term decline relative to prelogging levels (e.g., see Fig. 1*b*). Our results support this scenario only when considering streams that were cleaned, which showed the expected short-term increase in biomass in recently logged streams followed by a longer term decline in second-growth streams (e.g., see Fig. 7). In contrast, noncleaned streams showed increases in biomass in both recently logged and second-growth streams (patterns that were largely mirrored by the density data), and the hypothesized longer term decline proposed by Sedell and Swanson (1984) may therefore only be apparent in cleaned streams. The effects of stream cleaning were further demonstrated by Lestelle and Cederholm

(1984), who examined the short-term (1 year) effects of removing 70% of LW from a small low-gradient coastal stream in the absence of logging, and reported responses that were similar in magnitude to those resulting from our analyses (–10% to –50% for LW volume and pool number and size, and 30%–67% for salmonid density and biomass). This suggests that thorough cleaning of LW, even without logging, is a principal contributor to short-term reductions in pool habitat, thereby potentially setting the stage for longer term detrimental effects in the future.

The age-specific postlogging responses may also help explain the patterns in overall salmonid density and biomass, as these suggested that juveniles are more negatively affected by streamside logging than fry. This may be related to the seasonal factors that generally impose limits on the production of stream-dwelling fish. For example, during the summer, food resources may be most important in determining salmonid abundance in streams, whereas in winter it is habitat availability that typically constitutes a bottleneck and limits survival (Wilzbach 1985; Johnson et al. 1986;

Fig. 8. *(Concluded.)*
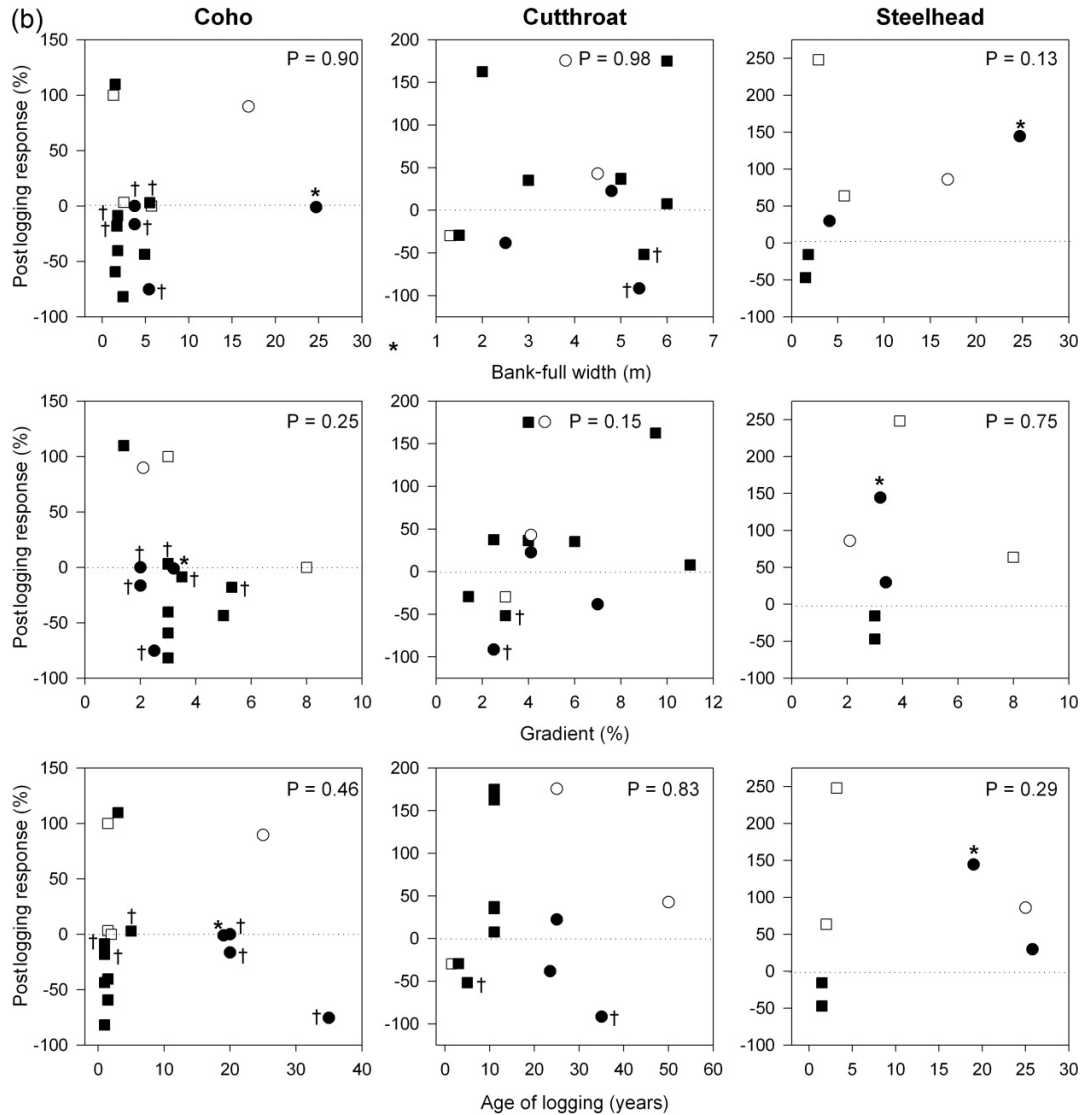
Murphy et al. 1986; Murphy and Meehan 1991). Given that our literature survey focused on studies conducted during the summer months, fry may have taken advantage of potential increases in postlogging food resources (resulting from reductions in canopy cover and increased primary and secondary production) during their first summer, thereby enhancing their growth and survival. In contrast, during the winter, reductions in critical overwintering habitat (such as pools with cover; Heifetz et al. 1986; Reeves et al. 1991) may have largely counterbalanced any energy-related benefits gained during the previous summer, leading to increased mortality and subsequent reductions in juvenile density and biomass (Johnson et al. 1986; Hartman et al. 1996). Furthermore, the greatest reductions in juvenile density and biomass would be expected in cleaned streams, because LW and the associated habitat, cover, and the protection from high velocities it provides become particularly important during winter (Dolloff 1986; Elliott 1986; Hicks et al. 1991). This pattern was generally supported by our analyses, given that postlogging responses of juvenile density were significantly lower in selectively and thoroughly cleaned

streams than in noncleaned streams, and that the response for juvenile biomass was, on average, negative for thoroughly cleaned streams but positive for fry. Salmonid fry may also be able to use lateral habitats (e.g., backwaters and side channels) more effectively than juveniles and therefore not be as influenced by the loss of pool habitat or by changes in LW (Moore and Gregory 1988). The age-specific analyses therefore help reinforce the conclusion reached in individual studies that streamside logging may favor salmonid fry at the expense of juveniles (e.g., Chapman and Knudsen 1980; Dolloff 1986, Johnson et al. 1986; Murphy et al. 1986; Hicks and Hall 2003). However, it should be noted that juvenile postlogging responses in our analyses were, on average, still positive in noncleaned streams and in both age of logging categories, suggesting that sufficient cover and habitat remain in the absence of cleaning to allow for over-winter survival.

The species-specific results suggested that coho salmon and cutthroat trout were more susceptible to the effects of streamside logging than steelhead and rainbow trout, as average postlogging responses for the latter species were

Fig. 9. Effect of streamside logging on species-specific salmonid density (●) and biomass (○) according to age of logging (left-hand panels) and whether or not stream cleaning of large wood (LW) took place (right-hand panels). Steelhead trout data include rainbow trout. Significant differences at $P \leq 0.05$ (*) and $P \leq 0.03$ (**) are indicated. Error bars represent the standard error; the samples size (n) is provided for each category. The dotted line shows the line of zero effect. Note that axis scales are not consistent.
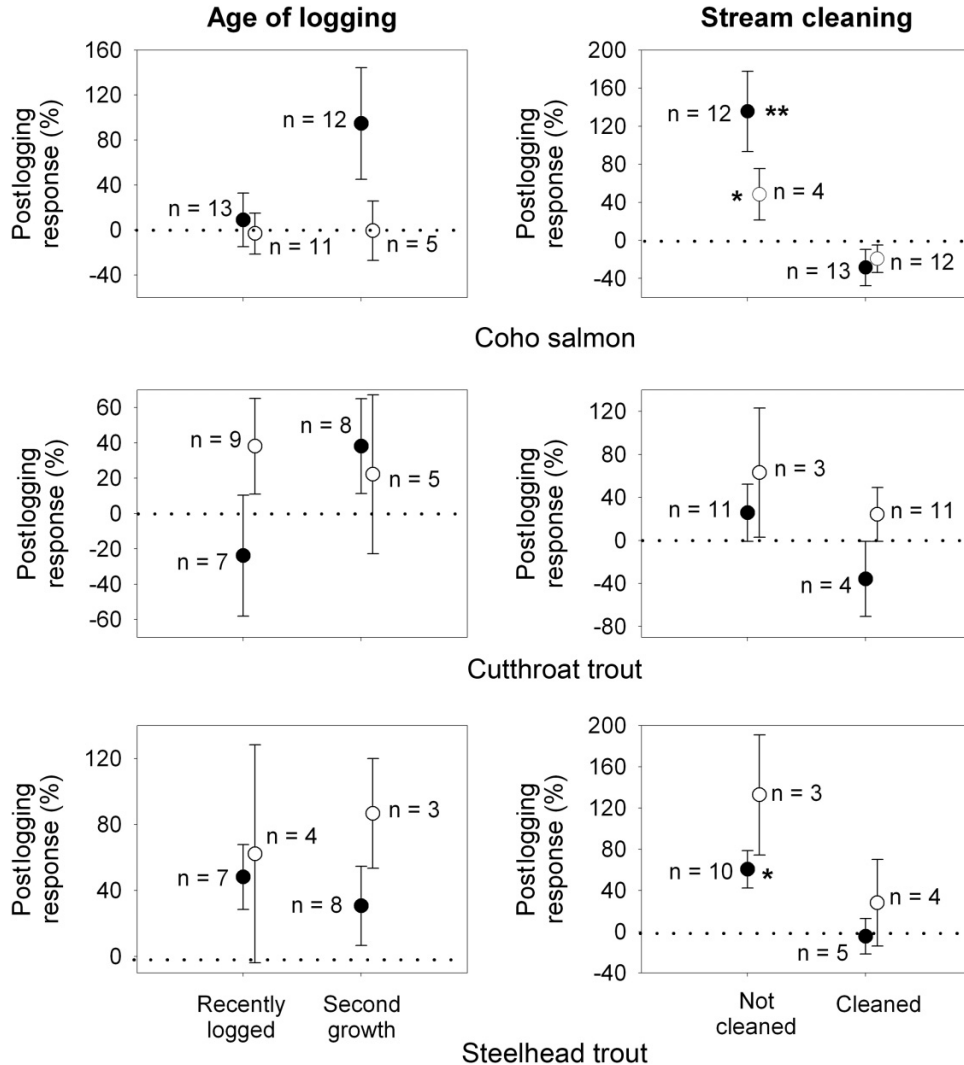
generally more positive than those for the other two species. Given that stream-dwelling coho salmon in particular appear to require pools and cover for their survival (Dolloff 1986; House and Boehne 1986; Solazzi et al. 2000; Roni 2002), this species was expected to be most sensitive to streamside logging and any associated reductions in LW and pool habitat. This was generally supported by our regression analyses, as coho salmon was the only species in which positive postlogging responses were associated with large streams (i.e., those in which the influence of LW on pool formation is expected to be diminished), and by the significant reductions in both density and biomass in cleaned compared with noncleaned streams. In contrast, the proposed resilience of steelhead and rainbow trout may reflect their wide range of behavioral plasticity and environmental tolerances. For example, their thermal tolerance is among the widest in the salmonids (0–29 °C; Jobling 1981), and often allows them to out-compete closely related species for food and habitat resources (Gibson 1981). Furthermore, although all the salmonid species included in our survey use pools during the summer and winter months (e.g., Bustard and Narver 1975; Roni 2002), steelhead and rainbow trout are able to thrive in other habitats such as riffles, making them potentially well suited to withstand the effects of logging (Sullivan et al. 1987; Bjornn and Reiser 1991). The timing of this species' spawning activities may also influence its postlogging responses. For example, for salmonids that spawn in streams, the short-term increases in stream temperature that often accompany logging can accelerate egg development and lead to earlier emergence of fry from stream gravels (Bisson and Sedell 1984; Thedinga et al. 1989; Hartman et al. 1996). For spring-spawning species like steelhead trout, this would lengthen the period in summer during which fry can grow and accumulate energy reserves, thereby conferring a size advantage and increasing the likelihood of over-winter survival (Slaney et al. 1977; Quinn and Peterson 1996). This is supported by our analyses which showed that steelhead trout had the highest postlogging density and biomass responses for recently logged streams (where the effects of increased temperatures and food levels are expected to be most pro-

nounced). Alternatively, accelerated egg development might be detrimental for autumn-spawning species like coho salmon because it would lead to earlier, possibly untimely emergence when environmental conditions are unsuitable (Macdonald et al. 1998). Therefore, the combination of wide thermal tolerances, aggression, the ability to use a variety of habitats, and a life-history strategy of spring spawning may make this species more resilient than other salmonids to the impacts typically associated with streamside logging.

Certain shortcomings inherent in our survey need to be addressed. For example, we only included studies that were conducted during the spring to autumn months, and the effects of logging during the winter season remain relatively poorly understood. In addition, our survey focused only on the freshwater life-history stages of stream-resident salmonids without examining the migratory or estuarine phases of anadromous species, and did not consider the potential effects of logging on specific physical (e.g., suspended-sediment dynamics, substrate characteristics, stream flow and temperature, dissolved oxygen) or biological (e.g., salmonid movement patterns and reproduction, the presence or absence of competitors and predators, and invertebrate production) aspects of stream ecosystems. Making predictions about species-specific responses to logging may be rendered more difficult by the potential for interactions within sympatric populations, and postlogging salmonid density and biomass responses may consequently depend to some extent on the composition of fish communities (Sullivan et al. 1987). Also, various biases are inherent in meta-analyses, including publication and English-language biases (i.e., studies with significant results are more likely to get published in the primary literature, particularly English-language journals) and inclusion bias (the criteria for inclusion are influenced by knowledge of the results; Egger and Smith 1998). Our literature-search methodology likely helped minimize these biases, given that we included several studies which reported nonsignificant results (e.g., Bilby and Ward 1991; Fausch and Northcote 1992; Mellina et al. 2005; De Groot et al. 2007) and that 27% of the studies were from the secondary literature.

We also found a paucity of studies from interior regions during our literature search, and the fact that the majority of studies in our survey were carried out in coastal areas may have influenced the magnitude of postlogging effects (Hicks et al. 1991; Mellina et al. 2005). Much of the future timber supply in the Northern Hemisphere is expected to come from boreal and sub-boreal forests in temperate, interior regions (Bryant et al. 1997), and differences in climate, topography, soils, forest cover, and logging methods raise the question of whether results obtained from coastal fish–forestry studies are applicable to interior regions (Slaney et al. 1977; Scrivener and Brown 1992). For example, the more moderate slopes of hillsides in interior regions, combined with their drier soils, make them less prone to erosion and landslides, which may help mitigate losses of LW due to debris torrents (Carlson et al. 1990). However, because streamside logging often results in a loss of future LW recruitment regardless of region, reductions in stream habitat in interior areas may ultimately be similar to those seen in coastal regions but may take longer to manifest themselves, in part

because LW decay is slower in colder, drier climates (Scrivener and Brown 1992; Bilby et al. 1999).

Conclusions and management implications

In conclusion, the majority of surveyed studies reported negative postlogging responses for LW and pool habitat but positive ones for salmonid density and biomass, with the most detrimental effects generally being seen in streams that were thoroughly cleaned of LW. Our results suggest that over the time frame during which the studies were conducted (1–100 years), streams whose riparian areas were logged may be able to sustain salmonid populations and even exceed preharvest levels as long as rigorous removal of in-stream LW is avoided. The results also indicated that the abiotic and biotic postlogging responses were not strongly influenced by stream size or gradient, nor did they appear to be influenced by the amount of time that had elapsed since logging last occurred. The data therefore largely refuted our expectation that the greatest postlogging declines in stream habitat and salmonid density and biomass would be seen in second-growth streams, but further suggested that not enough time had elapsed for impacts to fully manifest themselves. The second-growth streams in our survey that were cleaned had some of the most negative responses of all abiotic and biotic variables, and conditions in these streams may mimic or portend the expected longer term declines in habitat quality and quantity. The age-specific results suggested that salmonid fry may benefit from short-term postlogging increases in food resources, only for these to be subsequently outweighed by a loss of critical over-wintering habitat, leading to greater mortality of juveniles. Lastly, there was some evidence that steelhead and rainbow trout, possibly by virtue of a combination of behavioural plasticity, spring spawning activities, and a wide range of thermal tolerances, may be more resilient to the impacts associated with streamside logging practices than coho salmon and cutthroat trout.

Our meta-analysis therefore suggests that the most detrimental postlogging effects are wrought by thorough stream cleaning, and we ponder whether it was this practice that was primarily responsible for the adverse impacts that characterized many early fish–forestry studies and helped raise awareness about riparian logging in general and the importance of LW in particular. However, we know of no North American jurisdiction where stream cleaning is still sanctioned, so the relevance of our results naturally comes into question. Although many countries have codes that regulate forestry practices or promote sound ones, there are jurisdictions worldwide where compliance is voluntary (e.g., parts of North America) or enforcement is difficult (e.g., China, Russia, and Central America; Moore and Bull 2004; Northcote and Hartman 2004b). Our results may therefore help guide streamside-management strategies by highlighting those factors that are most important for maintaining healthy stream ecosystems (e.g., the critical role played by LW in pool formation and its links to the creation of the complex habitat required to support salmonid populations, versus the relatively minor influence of stream size and gradient on the magnitude of postlogging responses). Even so, stream cleaning of LW is clearly not the only consideration for maintain-

ing the integrity of small streams, as other logging-related activities undoubtedly contribute to negative effects. Alternative streamside logging practices to those carried out in our surveyed studies, including keeping logging machinery away from stream banks, retaining deciduous vegetation and noncommercial trees within riparian zones for the provision of shade and future sources of LW, abstaining from conducting in-stream work, and using bridges as crossing structures, have been shown to substantially reduce detrimental postlogging impacts, at least in the short term (<10 years; e.g., Mellina et al. 2002; Herunter et al. 2004; De Groot et al. 2007). However, the longer term (>100 years) trends in our response variables remain largely unknown, as there is a recognized dearth of long-term information from second-growth streams (particularly those that were not cleaned; Connolly and Hall 1999), and continued monitoring of streams for which data already exist is therefore encouraged to assess whether expected declines in salmonid density and biomass eventually manifest themselves.

Acknowledgements

References

Anderson, N.H. 1992. Influence of disturbance on insect communities in Pacific Northwest streams. Hydrobiologia, **248**: 79–92. doi:10.1007/BF00008887.

Andrus, C.W., Long, B.A., and Froehlich, H.A. 1988. Woody debris and its contribution to pool formation in a coastal stream 50 years after logging. Can. J. Fish. Aquat. Sci. **45**: 2080–2086.

Anonymous. 1996. Channel assessment procedure guidebook [online]. Forest Practices Code of British Columbia.British Columbia Ministry of Forests and British Columbia Ministry of Environment, Victoria, B.C. Available from http://www.for.gov.bc.ca/tasb/legsregs/fpc/FPCGUIDE/CHANNEL/CHAN-TOC.HTM [accessed 15 April 2008].

Beechie, T.J., Pess, G., Kennard, P., Bilby, R.E., and Bolton, S. 2000. Modeling recovery rates and pathways for woody debris recruitment in northwestern Washington streams. N. Am. J. Fish. Manage. **20**: 436–452. doi:10.1577/1548-8675(2000) 020<0436:MRRAPF>2.3.CO;2.

Benda, L., Hassan, M.A., Church, M., and May, C.L. 2005. Geomorphology of steepland headwaters: the transition from hillslopes to channels. J. Am. Water Resour. Assoc. **41**: 835–851.

Berg, N., Carlson, A., and Azuma, D. 1998. Function and dynamics of woody debris in stream reaches in the central Sierra Nevada, California. Can. J. Fish. Aquat. Sci. **55**: 1807–1820. doi:10.1139/cjfas-55-8-1807.

Beschta, R.L., Bilby, R.E., Brown, G.W., Holtby, L.B., and Hofstra, T.D. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. *In* Streamside management: forestry and fishery interactions. *Edited by* E.O. Salo and T.W. Cundy. College of Forest Resources, University of Washington, Seattle, Wash. pp. 191–232.

Bilby, R.E. 1984. Removal of woody debris may affect stream channel stability. J. For. **82**: 609–613.

Bilby, R.E., and Bisson, P.A. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Can. J. Fish. Aquat. Sci. **49**: 540–551. doi:10.1139/f92-064.

Bilby, R.E., and Ward, J.W. 1989. Changes in characteristics and function of woody debris with increasing size of streams in western Washington. Trans. Am. Fish. Soc. **118**: 368–378. doi:10.1577/1548-8659(1989)118<0368:CICAFO>2.3.CO;2.

Bilby, R.E., and Ward, J.W. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. Can. J. Fish. Aquat. Sci. **48**: 2499–2508. doi:10.1139/f91-291.

Bilby, R.E., Heffner, J.T., Fransen, B.R., and Ward, J.W. 1999. Effects of immersion in water on deterioration of wood from five species of trees used for habitat enhancement projects. N. Am. J. Fish. Manage. **19**: 687–695. doi:10.1577/1548-8675(1999) 019<0687:EOIIWO>2.0.CO;2.

Bisson, P.A., and Sedell, J.R. 1984. Salmonid populations in streams in clearcut vs. old-growth forests of western Washington. *In* Proceedings of the Symposium on Fish and Wildlife Relationships in Old-growth Forests, Juneau, Alaska, 12–15 April 1982. *Edited by* W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley. American Institute of Fishery Research Biologists, Asheville, N.C. pp. 121–129.

Bisson, P.A., Bilby, R.E., Bryant, M.D., Dolloff, C.A., Grette, G.B., House, R.A., Murphy, M.L., Koski, K.V., and Sedell, J.R. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. *In* Streamside management: forestry and fishery interactions. *Edited by* E.O. Salo and T.W. Cundy. College of Forest Resources, University of Washington, Seattle, Wash. pp. 143–190.

Bisson, P.A., Sullivan, K., and Nielsen, J.L. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Trans. Am. Fish. Soc. **117**: 262–273. doi:10.1577/1548-8659(1988)117<0262:CHHUAB>2.3.CO;2.

Bjornn, T.C., and Reiser, D.W. 1991. Habitat requirements of salmonids in streams. Am. Fish. Soc. Spec. Publ. 19. pp. 83–138.

Bragg, D.C. 2000. Simulating catastrophic and individualistic large woody debris recruitment for a small riparian system. Ecology, **81**: 1383–1394.

Bryant, M.D. 1982. Organic debris in salmonid habitat in southeast Alaska: measurement and effects. *In* Proceedings of a Symposium on Acquisition and Utilization of Aquatic Habitat Inventory Information, Portland, Oregon, 28–30 October 1981. *Edited by* Neil B. Armantrout. Western Division of the American Fisheries Society, Bethesda, Md. pp. 259–265.

Bryant, M.D. 1983. The role and management of woody debris in west coast salmonid nursery streams. N. Am. J. Fish. Manage. **3**: 322–330. doi:10.1577/1548-8659(1983)3<322:TRAMOW>2.0.CO;2.

Bryant, D., Nielsen, D., and Tangley, L. 1997. Last frontier forests: ecosystems and economies on the edge. WRI Publications, Baltimore, Md.

Burns, J.W. 1972. Some effects of logging and associated road construction on northern California streams. Trans. Am. Fish. Soc. **101**: 1–17. doi:10.1577/1548-8659(1972)101<1:SEOLAA>2.0.CO;2.

Bustard, D.R., and Narver, D.W. 1975. Preferences of juvenile coho salmon (*Oncorhynchus kisutch*) and cutthroat trout (*Salmo*

clarki) relative to simulated alteration of winter habitat. J. Fish. Res. Board Can. **32**: 681–687.

Cabin, R.J., and Mitchell, R.J. 2000. To Bonferroni or not to Bonferroni: when and how are the questions. Bull. Ecol. Soc. Am. **81**: 246–248.

Carlson, J.Y., Andrus, C.W., and Froehlich, H.A. 1990. Woody debris, channel features, and macroinvertebrates of streams with logged and undisturbed riparian timber in northeastern Oregon. Can. J. Fish. Aquat. Sci. **47**: 1103–1111. doi:10.1139/f90-127.

Chamberlin, T.W., Harr, R.D., and Everest, F.H. 1991. Timber harvesting, silviculture, and watershed processes. Am. Fish. Soc. Spec. Publ. 19. 181–205.

Chapman, D.W., and Knudsen, E. 1980. Channelization and livestock impacts on salmonid habitat and biomass in western Washington. Trans. Am. Fish. Soc. **109**: 357–363. doi:10.1577/1548-8659(1980)109<357:CALIOS>2.0.CO;2.

Connolly, P.J., and Hall, J.D. 1999. Biomass of coastal cutthroat trout in unharvested and previously clear-cut basins in the central coast range of Oregon. Trans. Am. Fish. Soc. **128**: 890–899. doi:10.1577/1548-8659(1999)128<0890:BOCCTI>2.0.CO;2.

Dahlstrom, N., and Nilsson, C. 2004. Influence of woody debris on channel structure in old growth and managed forest streams in central Sweden. Environ. Manage. **33**: 376–384. doi:10.1007/s00267-003-3042-2. PMID:15031768.

De Groot, J.D., Hinch, S.G., and Richardson, J.S. 2007. Effects of logging second-growth forests on headwater populations of coastal cutthroat trout: a 6-year, multi-stream, before-and-after field experiment. Trans. Am. Fish. Soc. **136**: 211–226. doi:10.1577/T04-232.1.

Dolloff, C.A. 1986. Effects of stream cleaning on juvenile coho salmon and Dolly Varden in southeast Alaska. Trans. Am. Fish. Soc. **115**: 743–755. doi:10.1577/1548-8659(1986)115<743:EOSCOJ>2.0.CO;2.

Egger, M., and Smith, D.G. 1998. Meta-analysis — bias in location and selection of studies. Br. Med. J. **316**: 61–66. PMID:9451274.

Elliott, S.T. 1986. Reduction of a Dolly Varden population and macrobenthos after removal of logging debris. Trans. Am. Fish. Soc. **115**: 392–400. doi:10.1577/1548-8659(1986)115<392:ROADVP>2.0.CO;2.

Fausch, K.D., and Northcote, T.G. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Can. J. Fish. Aquat. Sci. **49**: 682–693. doi:10.1139/f92-077.

Feller, M.C. 2005. Forest harvesting and streamwater inorganic chemistry in western North America: a review. J. Am. Water Resour. Assoc. **41**: 785–811.

Flebbe, P.A., and Dolloff, C.A. 1995. Trout use of woody debris and habitat in Appalachian wilderness streams of North Carolina. N. Am. J. Fish. Manage. **15**: 579–590. doi:10.1577/1548-8675(1995)015<0579:TUOWDA>2.3.CO;2.

Fuchs, S.A., Hinch, S.G., and Mellina, E. 2003. Effects of streamside logging on stream macroinvertebrate communities and habitat in the sub-boreal forests of British Columbia, Canada. Can. J. For. Res. **33**: 1408–1415. doi:10.1139/x03-070.

Gibson, R.J. 1981. Behavioural interactions between coho salmon (*Oncorhynchus kisutch*), Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*), and steelhead trout (*Salmo gairdneri*) at the juvenile fluviatile stages. Can. Tech. Rep. Fish. Aquat. Sci. No. 1029.

Gomi, T., Moore, R.D., and Hassan, M.A. 2005. Suspended sediment dynamics in small forest streams of the Pacific northwest. J. Am. Water Resour. Assoc. **41**: 877–898.

Grant, J.W.A., Englert, J., and Bietz, B.F. 1986. Application of a method for assessing the impact of watershed practices: effects

of logging on salmonid standing crops. N. Am. J. Fish. Manage. **6**: 24–31. doi:10.1577/1548-8659(1986)6<24:AOAMFA>2.0.CO;2.

Gregory, S.V., Lamberti, G.A., Erman, D.C., Koski, K.V., Murphy, M.L., and Sedell, J.R. 1987. Influence of forest practices on aquatic production. *In* Streamside management: forestry and fishery interactions. *Edited by* E.O. Salo and T.W. Cundy. College of Forest Resources, University of Washington, Seattle, Wash. pp. 233–256.

Grette, G.B. 1985. The role of large organic debris in juvenile salmonid rearing habitat in small streams. M.S. thesis, University of Washington, Seattle, Wash.

Hall, J.D., Cederholm, M.L., Murphy, M.L., and Koski, K.V. 2004. Fish–forestry interactions in Oregon, Washington and Alaska, USA. *In* Fishes and forestry. *Edited by* T.G. Northcote and G.F. Hartman. Blackwell Publishing, Ames, Iowa. pp. 365–388.

Hartman, G.F., andScrivener, J.C. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia [Canada]. Can. Bull. Fish. Aquat. Sci. No. 223.

Hartman, G.F., Scrivener, J.C., and Miles, M.J. 1996. Impacts of logging in Carnation Creek, a high-energy coastal stream in British Columbia, and their implication for restoring fish habitat. Can. J. Fish. Aquat. Sci. **53**: 237–251. doi:10.1139/cjfas-53-S1-237.

Hassan, M.A., Hogan, D.L., Bird, S.A., May, C.L., Gomi, T., and Campbell, D. 2005. Spatial and temporal dynamics of wood in headwater streams of the Pacific northwest. J. Am. Water Resour. Assoc. **41**: 899–919.

Heifetz, J., Murphy, M.L., and Koski, K.V. 1986. Effects of logging on winter habitat of juvenile salmonids in Alaska streams. N. Am. J. Fish. Manage. **6**: 52–58. doi:10.1577/1548-8659(1986)6<52:EOLOWH>2.0.CO;2.

Herunter, H.E., Macdonald, J.S., and MacIsaac, E.A. 2004. Effectiveness of variable-retention riparian buffers for maintaining thermal regimes, water chemistry, and benthic invertebrate communities of small headwater streams in central British Columbia. *In* Proceedings of the Forest–Land–Fish Conference II — Ecosystem Stewardship through Collaboration, Edmonton, Alberta, 26–28 April 2004. *Edited by* G.J. Scrimgeour, G. Eisler, B. McCulloch, U. Silins, and M. Monita. pp. 105–113.

Hicks, B.J., and Hall, J.D. 2003. Rock type and channel gradient structure salmonid populations in the Oregon Coast Range. Trans. Am. Fish. Soc. **132**: 468–482. doi:10.1577/1548-8659(2003)132<0468:RTACGS>2.0.CO;2.

Hicks, B.J., Hall, J.D., Bisson, P.A., and Sedell, J.R. 1991. Responses of salmonids to habitat changes. Am. Fish. Soc. Spec. Publ. 19. 483–518.

Hogan, D.L. 1986. Channel morphology of unlogged, logged, and debris torrented streams in the Queen Charlotte Islands. Land Management Rep. No. 49, Research Branch, British Columbia Ministry of Forests, Victoria, B.C.

Hogan, D., and Bird, S. 1998. Forest management and channel morphology in small coastal watersheds: results from Carnation Creek and the Queen Charlotte Islands. *In* Proceedings of the Forest–Land–Fish Conference: Land Management Practices Affecting Aquatic Ecosystems, Calgary, Alberta, 1–4 May 1996. *Edited by* M.K. Brewin and D.M.A. Monita. Can. For. Serv. North. For. Res. Cent. Inf. Rep. NOR-X-356. pp. 209–226.

Holtby, L.B. 1988. Effects of logging on stream temperatures in carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **45**: 502–515. doi:10.1139/f88-060.

House, R.A., and Boehne, P.L. 1986. Effects of instream structures on salmonid habitat and populations in Tobe Creek, Oregon. N.

Am. J. Fish. Manage. **6**: 38–46. doi:10.1577/1548-8659(1986) 6<38:EOISOS>2.0.CO;2.

House, R.A., and Boehne, P.L. 1987. The effect of stream cleaning on salmonid habitat and populations in a coastal Oregon drainage. West. J. Appl. For. **2**: 84–87.

Jobling, M. 1981. Temperature tolerance and the final preferendum — rapid methods for the assessment of optimum growth temperatures. J. Fish Biol. **19**: 439–455. doi:10.1111/j.1095-8649.1981.tb05847.x.

Johnson, S.W., Heifetz, J., and Koski, K.V. 1986. Effects of logging on the abundance and seasonal distribution of juvenile steelhead in some southeastern Alaska streams. N. Am. J. Fish. Manage. **6**: 532–537. doi:10.1577/1548-8659(1986)6<532:EOLOTA>2.0. CO;2.

Johnston, N.T. 2001. Synoptic surveys of the effects of riparian management regulations along S5 and S6 streams on downstream fish habitat. Fisheries Project Rep. No. RD 92, British Columbia Ministry of Water, Land, and Air Protection, British Columbia Fisheries Branch, Vancouver, B.C.

Kleinbaum, D.G., Kupper, L.L., and Muller, K.E. 1988. Applied regression analyses and other multivariate methods. PWS–Kent Publishing Co., Boston, Mass.

Krebs, C.J. 1999. Ecological methodology. 2nd ed. Addison Wesley Longman, Inc., Menlo Park, Calif.

Kreutzweiser, D.P., Good, K.P., and Sutton, T.M. 2005. Large woody debris characteristics and contributions to pool formation in forest streams of the Boreal Shield. Can. J. For. Res. **35**: 1213–1223. doi:10.1139/x05-053.

Lestelle, L.C., and Cederholm, C.J. 1984. Short-term effects of organic debris removal on resident cutthroat trout. *In* Proceedings of the Symposium on Fish and Wildlife Relationships in Old-growth Forests, Juneau, Alaska, 12–15 April 1982. *Edited by* W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley. American Institute of Fishery Research Biologists, Asheville, N.C. pp. 131–140.

Lisle, T.E. 1986. Effects of woody debris on anadromous salmonid habitat, Prince of Wales Island, southeast Alaska. N. Am. J. Fish. Manage. **6**: 538–550. doi:10.1577/1548-8659(1986) 6<538:EOWDOA>2.0.CO;2.

Lisle, T.E. 1987. Using residual depths to monitor pool depths independently of discharge. U.S. For. Serv. Res. Note PSW-394.

Macdonald, J.S., Scrivener, J.C., Patterson, D.A., and Dixon-Warren, A. 1998. Temperatures in aquatic habitats: the impacts of forest harvesting and the biological consequences to sockeye salmon incubation habitats in the interior of BC. *In* Proceedings of the Forest–Land–Fish Conference: Land Management Practices Affecting Aquatic Ecosystems, Calgary, Alberta, 1–4 May 1996. *Edited by* M.K. Brewin and D.M.A. Monita. Can. For. Serv. North. For. Res. Cent. Inf. Rep. NOR-X-356. pp. 313–324.

McCleary, R., Shelburne, C., and Bambrick, C. 2004. Long-term effects of riparian harvest on fish habitat in three Rocky Mountain Foothills watersheds. *In* Proceedings of the Forest–Land–Fish Conference II — Ecosystem Stewardship through Collaboration, Edmonton, Alberta, 26–28 April 2004. *Edited by* G.J. Scrimgeour, G. Eisler, B. McCulloch, U. Silins, and M. Monita. pp. 189–198.

Meehan, W.R. 1991. Influences of forest and rangeland management on salmonid fishes and their habitats. Am. Fish. Soc. Spec. Publ. 19.

Mellina, E., Moore, R.D., Hinch, S.G., Macdonald, J.S., and Pearson, G. 2002. Stream temperature responses to clear-cut logging in British Columbia: the moderating influences of groundwater and headwater lakes. Can. J. Fish. Aquat. Sci. **59**: 1886–1900. doi:10.1139/f02-158.

Mellina, E., Hinch, S.G., Donaldson, E.M., and Pearson, G. 2005. Stream habitat and rainbow trout (*Oncorhynchus mykiss*) physiological stress responses to streamside clear-cut logging in British Columbia. Can. J. For. Res. **35**: 541–556. doi:10.1139/x04-202.

Moore, K., and Bull, G. 2004. Guidelines, codes and legislation. *In* Fishes and forestry. *Edited by* T.G. Northcote and G.F. Hartman. Blackwell Publishing, Ames, Iowa. pp. 707–728.

Moore, K.M.S., and Gregory, S.V. 1988. Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in Cascade Mountain streams. Can. J. Fish. Aquat. Sci. **45**: 1921–1930. doi:10.1139/f88-224.

Moore, R.D., Spittlehouse, D.L., and Story, A. 2005. Riparian microclimate and stream temperature response to forest harvesting: a review. J. Am. Water Resour. Assoc. **41**: 813–834.

Moring, J.R., and Lantz, R.L. 1974. Immediate effects of logging on the freshwater environment of salmonids. Ore. Wildl. Comm. Rep. AFS-58.

Moring, J.R., and Lantz, R.L. 1975. The Alsea watershed study: effects of harvesting on the aquatic resources of three headwater streams of the Alsea River, Oregon. Part 1. Biological responses. Fisheries Research Rep. No. 9, Oregon Department of Fish and Wildlife, Corvallis, Ore.

Murphy, M.L., and Hall, J.D. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Can. J. Fish. Aquat. Sci. **38**: 137–145. doi:10.1139/f81-018.

Murphy, M.L., and Koski, K.V. 1989. Input and depletion of woody debris in Alaska streams and implications for streamside management. N. Am. J. Fish. Manage. **9**: 427–436. doi:10.1577/1548-8675(1989)009<0427:IADOWD>2.3.CO;2.

Murphy, M.L., and Meehan, W.R. 1991. Stream ecosystems. Am. Fish. Soc. Spec. Publ. 19. 17–46.

Murphy, M.L., Hawkins, C.P., and Anderson, N.H. 1981. Effects of canopy modification and accumulated sediment on stream communities. Trans. Am. Fish. Soc. **110**: 469–478. doi:10.1577/1548-8659(1981)110<469:EOCMAA>2.0.CO;2.

Murphy, M.L., Heifetz, J., Johnson, S.W., Koski, K.V., and Thedinga, J.F. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. Can. J. Fish. Aquat. Sci. **43**: 1521–1533. doi:10.1139/f86-190.

Narver, D.W. 1972. A survey of some possible effects of logging on two eastern Vancouver Island streams.. Fish. Res. Board Can. Tech. Rep. 323.

Northcote, T.G., and Hartman, G.F. (*Editors*). 2004*a*. Fishes and forestry. Blackwell Publishing, Ames, Iowa.

Northcote, T.G., and Hartman, G.F. 2004*b*. Towards a new fish–forestry interaction in the world's watersheds. *In* Fishes and forestry. *Edited by* T.G. Northcote and G.F. Hartman. Blackwell Publishing, Ames, Iowa. pp. 759–782.

Quinn, T.P., and Peterson, N.P. 1996. The influence of habitat complexity and fish size on over winter survival and growth of individually marked coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Can. J. Fish. Aquat. Sci. **53**: 1555–1564. doi:10.1139/cjfas-53-7-1555.

Ralph, S.C., Poole, G.C., Conquest, L.L., and Naiman, R.J. 1994. Stream channel morphology and woody debris in logged and unharvested basins of western Washington. Can. J. Fish. Aquat. Sci. **51**: 37–51. doi:10.1139/f94-006.

Reeves, G.H., Hall, J.D., Roelofs, T.D., Hickman, T.L., and Barker, C.O. 1991. Rehabilitating and modifying stream habitats. Am. Fish. Soc. Spec. Publ. 19. 519–557.

Roni, P. 2002. Habitat use by fishes and Pacific giant salamanders in small western Oregon and Washington streams. Trans. Am.

Fish. Soc. **131**: 743–761. doi:10.1577/1548-8659(2002) 131<0743:HUBFAP>2.0.CO;2.

Roni, P., and Quinn, T.P. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in western Oregon and Washington streams. Can. J. Fish. Aquat. Sci. **58**: 282–292. doi:10.1139/cjfas-58-2-282.

Rosenfeld, J.S., and Boss, S. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Can. J. Fish. Aquat. Sci. **58**: 585–593. doi:10.1139/cjfas-58-3-585.

Salo, E.O., and Cundy, T.W. (*Editors*). 1987. Streamside management: forestry and fishery interactions. College of Forest Resources, University of Washington, Seattle, Wash.

Scrivener, J.C., and Brown, T.G. 1992. Impact and complexity of forest practices on streams and their salmonid fishes in British Columbia. *In* Proceedings of the Symposium on Development of the Atlantic Salmon in Quebec: Rules for Success. Federation quebecoise pour le Saumon Atlantique, Sainte-Foy, Que.

Scrivener, J.C., and Brownlee, M.J. 1989. Effects of forest harvesting on spawning gravel and incubation survival of chum (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) in Carnation Creek, British Columbia. Can. J. Fish. Aquat. Sci. **46**: 681–696.

Sedell, J.R., and Luchessa, K.J. 1982. Using the historical record as an aid to salmonid habitat enhancement. *In* Proceedings of a Symposium on Acquisition and Utilization of Aquatic Habitat Inventory Information, Portland, Oregon, 28–30 October 1981. *Edited by* Neil B. Armantrout. Western Division of the American Fisheries Society, Bethesda, Md. pp. 210–223.

Sedell, J.R., and Swanson, F.J. 1984. Ecological characteristics of streams in old-growth forests of the Pacific Northwest. *In* Proceedings of the Symposium on Fish and Wildlife Relationships in Old-growth Forests, Juneau, Alaska, 12–15 April 1982. *Edited by* W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley. American Institute of Fishery Research Biologists, Asheville, N.C. pp. 9–16.

Slaney, P.A., Halsey, T.G., and Smith, H.A. 1977. Some effects of forest harvesting on salmonid rearing habitat in two streams in the central interior of British Columbia. Fisheries Management Rep. No. 71, Fish and Wildlife Branch, British Columbia Ministry of Environment, Victoria, B.C.

Solazzi, M.F., Nickelson, T.E., Johnson, S.L., and Rodgers, J.D. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Can. J. Fish. Aquat. Sci. **57**: 906–914. doi:10.1139/cjfas-57-5-906.

Sullivan, K., Lisle, T.E., Dollof, C.A., Grant, G.E., and Reid, L.E. 1987. Stream channels: the link between forests and fishes. *In* Streamside management: forestry and fishery interactions. *Edited by* E.O. Salo and T.W. Cundy. College of Forest Resources, University of Washington, Seattle, Wash. pp. 39–97.

Swanston, D.N. 1991. Natural processes. Am. Fish. Soc. Spec. Publ. 19. pp. 139–179.

Thedinga, J.F., Murphy, M.L., Heifetz, J., Koski, K.V., and Johnson, S.W. 1989. Effects of logging on size and age composition of juvenile coho salmon (*Oncorhynchus kisutch*) and density of presmolts in southeast Alaska streams. Can. J. Fish. Aquat. Sci. **46**: 1383–1391.

Toews, D.A.A., and Moore, M.K. 1982. The effects of streamside logging on large organic debris in Carnation Creek. Land Management Rep. No. 11, Research Branch, British Columbia Ministry of Forests, Victoria, B.C.

Tripp, D.B., and Poulin, V.A. 1986. The effects of mass wasting on juvenile fish habitats in streams on the Queen Charlotte Islands. Land Management Rep. No. 45, Research Branch, British Columbia Ministry of Forests, Victoria, B.C.

Tripp, D.B., and Poulin, V.A. 1992. The effects of logging and mass wasting on juvenile salmonid populations in streams on the Queen Charlotte Islands. Land Management Rep. No. 80, Research Branch, British Columbia Ministry of Forests, Victoria, B.C.

Warren, D.R., and Kraft, C.E. 2003. Brook trout (*Salvelinus fontinalis*) response to wood removal from high-gradient streams of the Adirondack Mountains (N.Y., USA). Can. J. Fish. Aquat. Sci. **60**: 379–389. doi:10.1139/f03-031.

Wilzbach, M.A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream dwelling cutthroat trout (*Salmo clarki*). Can. J. Fish. Aquat. Sci. **42**: 1668–1672.

Young, K.A., Hinch, S.G., and Northcote, T.G. 1999. Status of resident coastal cutthroat trout and their habitat twenty-five years after riparian logging. N. Am. J. Fish. Manage. **19**: 901–911. doi:10.1577/1548-8675(1999)019<0901:SORCCT>2.0.CO;2.

Appendix A. Sample calculation of postlogging responses from studies using before–after - control–impact (BACI) designs

Table A1. Data for large wood number (per 100 m; from De Groot et al. (2007)).

Stream	Prelogging value	Postlogging value
Control	69.5	106
Treatment (observed)	85.0	81.0
Treatment (expected)	n/a	121.5

The expected value for the treatment stream (treatment (expected)) during the postlogging period if no logging effect had occurred is calculated by applying the same difference between the pre- and post-logging values for the control stream to the treatment stream. This is shown graphically below.
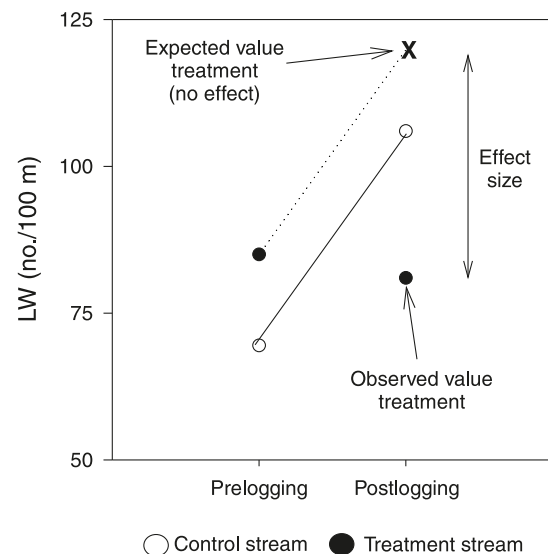
The difference between pre- and post-logging periods for the control stream is $106 - 69.5 = 36.5$.

Because the control stream experienced an increase of 36.5 units from the pre- to the post-logging period, the same would be expected of the treatment stream had no logging occurred.

Treatment (expected) during the postlogging period = treatment (observed) prelogging + expected difference if no effect had occurred

$= 85.0 + 36.5$

$= 121.5$

The postlogging response is calculated as [(observed value for logged stream – expected value for logged stream) / expected value for logged stream] $\times$ 100

Response = [(81 – 121.5) / 121.5] $\times$ 100

$= -33.3\%$

Reference

De Groot, J.D., Hinch, S.G., and Richardson, J.S. 2007. Effects of logging second-growth forests on headwater populations of coastal cutthroat trout: a 6-year, multi-stream, before-and-after field experiment. Trans. Am. Fish. Soc. **136**: 211–226. doi:10.1577/T04-232.1.