

Context-dependent responses of juvenile Atlantic salmon (*Salmo salar*) to forestry activities at multiple spatial scales within a river basin

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Abstract: We used classification trees and regression trees to relate the incidence and density of juvenile Atlantic salmon (*Salmo salar*) to forestry activities measured at four spatial scales (subbasin and 8, 2, and 0.5 km radii upstream of study sites) and environmental features in 120 stream reaches of the Cascapedia River basin, Québec, Canada. At all scales, incidence increased with reach size and accessibility to the reach from the river mainstem. Incidence declined with areal coverage of logging at all scales, but only in larger reaches. The time horizon over which logging effects were detected increased with spatial scale. At all scales, density in salmon-bearing reaches increased with accessibility. Density in more accessible reaches was negatively related to logging over the preceding 9 years at the subbasin and 8 km scales, but no effects of logging on density were detected at the 2 and 0.5 km scales. Overall, apparent effects of logging activities on salmon incidence and density were mostly negative and strong, but were both markedly scale-dependent and conditional on environmental context.

Résumé : Nous avons utilisé les arbres de classification et de régression pour relier l'incidence et la densité de saumons de l'Atlantique (*Salmo salar*) à l'environnement et aux activités forestières quantifiées à quatre échelles spatiales (le sous-bassin et des rayons de 8, 2 et 0,5 km en amont de chaque tronçon) dans 120 tronçons du bassin versant de la rivière Cascapédia, Québec, Canada. A toutes les échelles, l'incidence du saumon augmentait avec la taille des tronçons et l'accessibilité depuis la rivière principale et diminuait avec une augmentation du pourcentage de superficie coupée. Les effets des coupes étaient détectables sur des horizons temporels croissants avec l'augmentation de l'échelle spatiale. La densité de saumons augmentait avec l'accessibilité à toutes les échelles. Dans les tronçons plus accessibles, la densité diminuait avec une augmentation du pourcentage de superficie coupé au cours des 9 années précédentes aux deux plus grandes échelles du sous-bassin et de 8 km. Aucun effet des coupes sur la densité de saumons n'était détectable aux deux plus petites échelles de 2 et 0,5 km. Les effets apparents des coupes sur l'incidence et la densité de saumons juvéniles étaient forts et négatifs, mais dépendant de l'échelle spatiale et du contexte environnemental.

Introduction

The responses of aquatic organisms to human activities such as logging can be conditional on environmental context. For example, removal of riparian vegetation by logging in Oregon streams led to greater increase of periphyton and invertebrate abundance in small reaches than in large ones, apparently because riparian forest had greater influence on stream production in the small reaches (Murphy and Hall 1981). Logging also had a context-dependent effect on winter abundance of salmonid fry in Alaskan streams: fry abundance at logged sites declined if woody debris was removed, but increased otherwise (Murphy et al. 1986). Accounting for environmental context can lead to clearer understanding of the impacts of logging on stream fish populations and

help develop preventive or remedial measures tailored to specific environmental conditions. Nonetheless, few studies have explicitly considered potential interactions between logging and the environmental context when assessing impacts of logging on fish populations (e.g., Murphy and Hall 1981; Murphy et al. 1986).

Logging activities affect stream fish populations by modifying key environmental features that structure these populations at various spatial scales. At the local habitat scale, removal of riparian canopy by logging can increase water temperature and light penetration (Davies and Nelson 1994), resulting in increased invertebrate abundance (Kiffney et al. 2003). At the drainage basin scale, logging can increase the load of suspended sediments and the magnitude of freshet discharge (Macdonald et al. 2003), as well as water yield

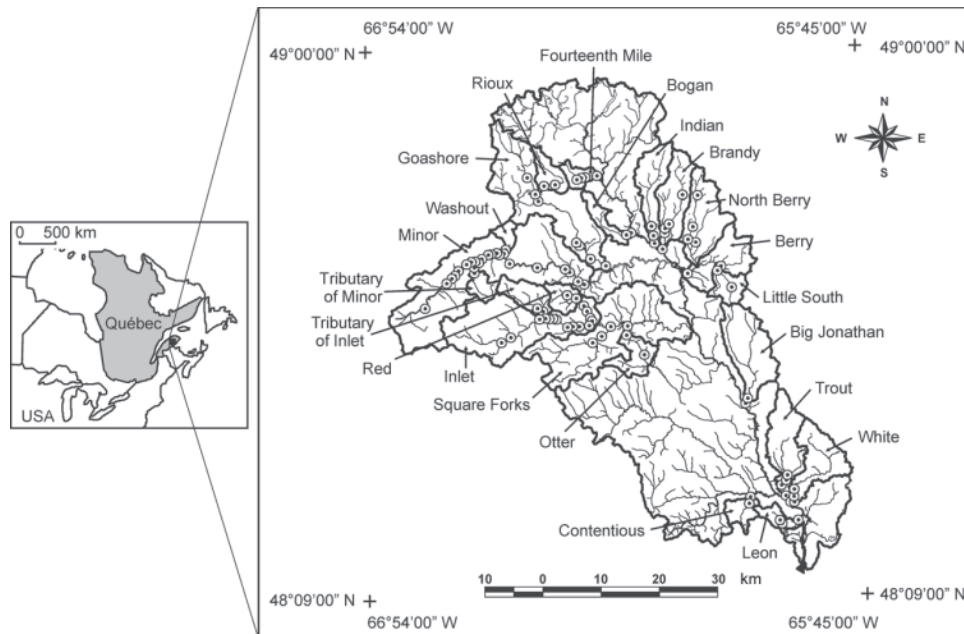
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Fig. 1. Location of the 120 sampling sites distributed among 22 tributary streams in the Cascapedia River basin, Québec, Canada.



and nutrient concentrations (Lamontagne et al. 2000; Martin et al. 2000). Because fish relate to their local or proximal environment differently than to larger-scale characteristics of the basin (Armstrong et al. 1998; Folt et al. 1998), effects of logging on fish abundance may also differ across scales.

It is not clear which scale, local habitat or drainage basin, is most useful for understanding potential context-dependent effects of logging on fish populations. Logging has been suggested to have maximum impact at a scale of tens to hundreds of hectares (Carignan and Steedman 2000). However, basin-wide studies at larger scales may allow for more effective assessment of the cumulative effects of logging by integrating a multitude of small disturbances over a large basin (Hicks et al. 1991). Direct comparison of results and conclusions from studies conducted at different spatial scales can be misleading because patterns found at smaller scales do not necessarily extrapolate to larger scales (Wiens 1989; Hicks et al. 1991). Multiscale studies can therefore help identify the most appropriate spatial scales for understanding the impacts of logging activities on fish stream populations.

Logging effects on stream ecosystems have been examined mostly by comparing biotic or physical features of streams between logged and unlogged sites (e.g., Rowe et al. 2002; Death et al. 2003; Latterell et al. 2003). However, the areal coverage of logged patches within different age classes may be a more precise and informative measure of impact than simply the presence or absence of logging. For example, population densities of smaller fish species in Oregon streams declined with increases in coverage of recent (1–3 years) logging, whereas larger species declined with increase in coverage of older (4–8 years) logging (Rutherford et al. 1992).

This study examines responses of juvenile Atlantic salmon (*Salmo salar*) to forestry activities occurring 0–19 years before the study, measured at four spatial scales (subbasin and 8, 2, and 0.5 km radii upstream of study sites). Two biologi-

cal metrics, incidence and population density in salmon-bearing reaches, were used as measures of population responses. Specifically, we compared the usefulness of proximate and larger-scale measurements of forestry activity for understanding the impacts of forestry on Atlantic salmon and examined whether those impacts were mitigated or accentuated by specific combinations of environmental conditions (i.e., whether forestry effects were context-dependent).

Materials and methods

The incidence and population density of Atlantic salmon and a host of environmental variables were quantified at 120 sampling sites distributed among 22 tributary streams in the Cascapedia River basin (3179 km²), Québec, Canada (Fig. 1). The basin topography is hilly: 49% of the basin area has terrain slopes $\leq 15^\circ$; 28% has slopes $> 30^\circ$, and 23% has intermediate slopes. Plant cover consists primarily of fir–spruce forest (conifers, 66%; mixed, 23%; scattered deciduous, 2%), with the remaining area accounted for by shrubs, rocks, and other nonforest cover (9%; includes 2% in agricultural and urban land). The basin is sparsely populated but is subject to intensive forestry activities. Of the 120 sites in the present study, 116 were in subbasins exposed to logging in the 19 years preceding the study. Substantial portions of the subbasins upstream from the study sites (subbasin area: median = 70.1 km², range = 8.1–337.9 km²) were affected by intensive logging (percentage of upstream area covered by cuts: median = 18.0%, range = 0.0%–37.6%) over this period. Governmental regulations have required forestry operations in the basin to leave an unharvested 20 m buffer strip (60 m when Atlantic salmon is present) along permanent streams since 1988.

Sites were visited in random sequence during low flow from mid-June to late August in 2000 (24 sites), 2001 (48 sites), and 2002 (48 sites). Sampled areas covered the entire

Table 1. Median, interquartile range, and variable codes for 25 environmental variables describing fish habitat at 120 sites in the Cascapedia River basin.

Variable name	Code	Median	Quartiles, 25%–75%
Accessibility index	AI	0.8	0.3–1.0
Altitude (m)	AL	240.0	167.5–315.0
Overhead opening (°)	OO	95.7	75.4–113.5
Cover index	CI	2.4	1.4–3.0
Distance to mainstem (km)	DM	9.1	2.5–21.7
Distance to mouth (km)	DO	75.5	52.8–82.4
Entrenchment (%)	EN	10.0	5.0–15.0
Height increment at flood (m)	HI	0.5	0.4–0.7
Mean current velocity (cm·s ⁻¹)	MC	34.9	26.0–48.9
Mean depth (cm)	MD	24.6	18.8–29.4
Mean substratum size	MS	5.3	4.9–5.8
Mean temperature (°C)	MT	10.5	9.0–12.0
Mean wetted width (m)	MW	9.3	6.3–14.1
Pools (number)	PO	0.0	0.0–1.5
Stream gradient (°)	SG		
Subbasin		2.1	0.6–3.3
8 km		1.1	0.5–2.3
2 km		1.0	0.5–1.7
0.5 km		1.1	0.3–2.0
Stream order	SO	3.0	3.0–4.0
Stream slope (°)	SS	1.0	0.6–1.3
Subbasin area (km ²)	SA	70.1	25.5–151.0
Terrace width ^a (m)	TW	107.8	81.3–163.5
Units of large woody debris (number)	UW	3.5	1.0–8.5
Vegetation abundance index	VA	1.0	1.0–1.8
Width increment at flood ^a (m)	WI	2.6	1.9–4.0

Note: Variable codes for Fig. 4 are also given.

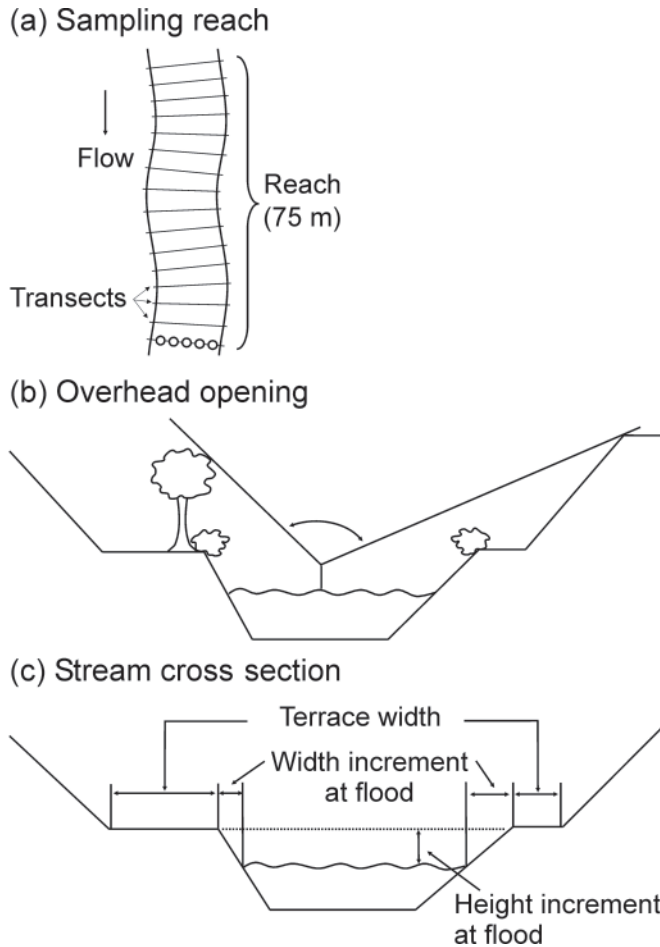
^aSum of measures from right and left margins.

stream width in completely wadable reaches and ranged 5 m from one bank, chosen randomly, towards the opposite bank in deeper reaches. Fish were sampled by single-pass electrofishing (Smith-Root D-15) in an upstream direction within open stream sections (Lobón-Cerviá and Utrilla 1993; Jones and Stockwell 1995). All captured fish were identified, measured, weighed, and returned to the stream site of capture. Salmon density was calculated as total captures divided by section area (numbers·100 m⁻²). Because capture efficiency was not 100%, this measure underestimates true density but should be proportional to it if efficiency is comparable across reaches. All reaches were sampled at base flow, and therefore variation in depth, water velocity, cover, and substratum size among reaches was limited (Table 1). Abundance estimates obtained by one-pass electrofishing have been shown to correlate well with those from multiple-pass removal experiments in homogeneous geographic areas (e.g., small mountain streams (Kruse et al. 1998); small warmwater streams (Edwards et al. 2003)), including estimates for juvenile Atlantic salmon in areas similar to those sampled in the present study (Hedger et al. 2005; M.A. Rodríguez, unpublished data).

In all, 25 environmental variables were quantified (Table 1). Water depth and substratum size were recorded at five equidistant points along each of 16 transects perpendicular to streamflow (Fig. 2a). Substratum size was assigned a numerical code reflecting the dominant size category (modi-

fied Wentworth scale: 1, ≤0.0625 mm; 2, 0.0625–2 mm; 3, 2–16 mm; 4, 16–32 mm; 5, 32–64 mm; 6, 64–256 mm; 7, >256 mm; 8, bedrock). Current velocity (pigmy-type meter, Scientific Instruments 1205) was measured at five equidistant points along every third transect starting with the second transect from the downstream end. Wetted width was measured at each transect. Abundance of submerged vegetation (moss or macrophytes) and overall availability of structural cover (rocks, woody debris, undercut bank, and overhanging vegetation) were estimated visually and assigned ordinal values reflecting areal coverage (1, ≤5%; 2, 6%–15%; 3, 16%–45%; 4, >45%). Overhead opening (angle between riparian canopy or hilltops blocking incident sunlight at the centre of the stream; Fig. 2b) and slope over the stream reach were measured with a handheld clinometer (Suunto PM-5). The increment in stream height and width at flood (from annual flood marks) and terrace width (distance between stream bank and piedmont) were measured on site (Fig. 2c). Water temperature (midpoint of maximum and minimum recorded while electrofishing) was measured (maximum–minimum thermometer, Barigo). Entrenchment (mean gradient ≤100 m away from stream bank), subbasin area, stream order (Strahler), and altitude were obtained from 1:20 000 topographic maps, as were distances by waterway from each reach to the Cascapedia River (“distance to mainstem”) and from the mouth of each stream to the mouth of the Cascapedia River (“distance to mouth”)

Fig. 2. Schematic views illustrating field measurements of (a) depth and substratum size, recorded at sampling points (circles) along all transects, and current velocity, recorded at sampling points along every third transect starting from the second-most downstream transect; (b) overhead opening (angle between structures blocking direct sunlight); (c) terrace width, height increment at flood, and width increment at flood.

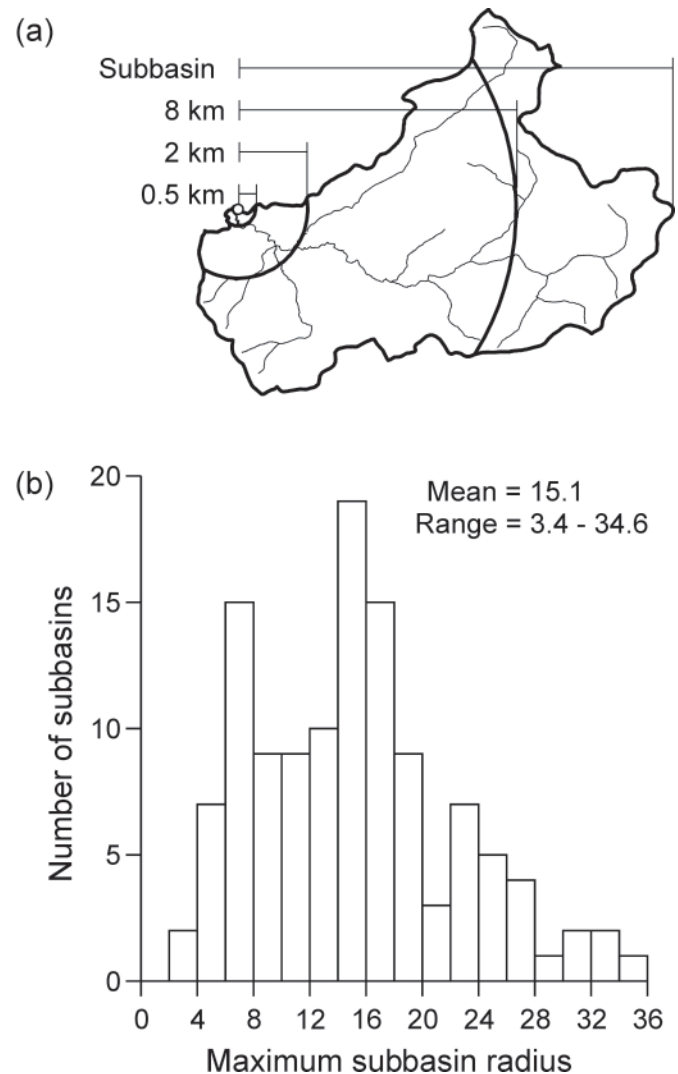


(planimeter, Calculated Industries 6125). Units of large woody debris (>10 cm diameter) and pools were counted within each reach. Physical barriers potentially affecting upstream migration of fish along a tributary were assessed from field observations and topographic maps, and their effectiveness was coded as an integer value, B , ranging from 0 (no visible barrier) to 4 (insurmountable barrier) and reflecting the height, type (beaver dams, log jams, culverts, falls), and configuration of the barrier. An index of accessibility combining multiplicatively all potential barriers for each site was calculated as

$$\text{accessibility} = \prod_{i=1}^N \left(1 - \frac{B_i}{4}\right)$$

where N is the number of visible barriers and B_i is the effectiveness of barrier i downstream from the site. Accessibility was assigned the value 1 in the absence of visible barriers. The index thus ranged from 0 to 1, taking a value of 0 if at least one barrier was insurmountable ($B_i = 4$).

Fig. 3. (a) Schematic representation of zones used to quantify landscape features and forestry activities at four spatial scales: subbasin and 8, 2, and 0.5 km radii upstream of the sampling sites. The concentric curves are delimited by watershed boundary lines. (b) Frequency distribution of the radius from the study reach to the most distant upstream point within the subbasin of the reach (km).



A geographic information system (ArcGIS, v. 8.2, ESRI, Redlands, California) was used to measure logging activities at four spatial scales: subbasin and semicircular zones of 8, 2, and 0.5 km radii upstream of each site (Fig. 3a), as well as the total subbasin area upstream of the site, and stream gradient (mean slope from the site to upstream boundary), the percentage of the subbasin area affected by spruce budworm outbreaks, and the density of roads (primary, secondary, tertiary, and total; $\text{km}\cdot\text{km}^{-2}$). GIS maps were based on 1:20 000 forest maps (Ministère des Ressources naturelles du Québec), annual logging records, and photo-interpretation (Société de la faune et des parcs du Québec). All but 25 of the study reaches had subbasins that extended beyond the 8 km radius (Fig. 3b). Logging activities were grouped into three categories reflecting the harvesting procedures employed by forestry companies: intensive (clearcut harvesting, protection of

Table 2. Median and interquartile range for 35 forestry variables measured at four spatial scales in the Cascapedia River basin.

Variable name	Code	Spatial scale			
		Subbasin	8 km	2 km	0.5 km
Spruce budworm outbreaks	sb	22.6 (18.8–27.8)	25.8 (17.3–32.2)	21.3 (6.5–37.8)	9.7 (0.0–23.4)
Road density					
Total	rt	1.9 (1.4–2.3)	1.8 (1.5–2.1)	1.5 (1.0–2.2)	1.6 (0.6–2.8)
Primary	r1	0.2 (0.1–0.3)	0.1 (0.0–0.3)	0.0 (0.0–0.4)	0.0 (0.0–0.9)
Secondary	r2	0.8 (0.2–1.6)	0.4 (0.1–1.2)	0.2 (0.0–0.8)	0.0 (0.0–0.0)
Tertiary	r3	0.6 (0.2–1.0)	0.8 (0.3–1.4)	0.8 (0.2–1.4)	0.0 (0.0–1.6)
Intensive logging (years)					
0–1	i1	1.0 (0.0–2.8)	0.3 (0.0–4.6)	0.0 (0.0–2.3)	0.0 (0.0–0.0)
0–2	i2	2.5 (0.0–3.5)	1.9 (0.0–5.4)	0.0 (0.0–5.8)	0.0 (0.0–0.0)
0–3	i3	2.8 (0.7–4.3)	2.4 (0.0–5.6)	0.0 (0.0–9.0)	0.0 (0.0–2.2)
0–4	i4	3.1 (0.8–5.6)	2.3 (0.0–7.9)	0.0 (0.0–10.0)	0.0 (0.0–4.0)
0–9	i9	8.6 (2.9–14.2)	5.1 (2.2–18.9)	2.4 (0.0–24.5)	0.0 (0.0–5.4)
0–14	i14	13.1 (4.0–22.4)	11.4 (4.0–23.8)	6.3 (0.3–25.1)	0.0 (0.0–11.5)
0–19	i19	16.4 (4.5–23.8)	17.8 (4.8–25.6)	8.7 (1.3–25.5)	0.0 (0.0–17.4)
Partial logging (years)					
0–1	p1	0.1 (0.0–2.2)	0.0 (0.0–0.3)	0.0 (0.0–0.0)	0.0 (0.0–0.0)
0–2	p2	0.6 (0.0–3.1)	0.1 (0.0–1.6)	0.0 (0.0–0.0)	0.0 (0.0–0.0)
0–3	p3	0.9 (0.0–3.9)	0.1 (0.0–2.8)	0.0 (0.0–0.0)	0.0 (0.0–0.0)
0–4	p4	1.5 (0.0–5.8)	1.0 (0.0–5.1)	0.0 (0.0–0.5)	0.0 (0.0–0.0)
0–9	p9	3.8 (0.8–8.5)	2.3 (0.1–6.9)	0.0 (0.0–3.1)	0.0 (0.0–0.0)
0–14	p14	6.1 (0.9–11.1)	4.3 (0.1–9.0)	0.0 (0.0–6.7)	0.0 (0.0–0.0)
0–19	p19	7.2 (0.9–13.4)	4.9 (0.1–9.1)	0.0 (0.0–7.2)	0.0 (0.0–0.3)
Combined logging (years)					
0–1	c1	2.7 (0.3–5.5)	2.7 (0.0–6.3)	0.0 (0.0–7.1)	0.0 (0.0–1.5)
0–2	c2	3.9 (2.6–7.2)	4.0 (2.1–8.4)	0.0 (0.0–13.2)	0.0 (0.0–3.6)
0–3	c3	5.1 (2.9–8.9)	5.5 (2.5–9.4)	0.0 (0.0–16.2)	0.0 (0.0–4.4)
0–4	c4	7.8 (3.7–12.5)	5.8 (3.3–13.4)	5.1 (0.0–17.1)	0.0 (0.0–9.7)
0–9	c9	15.4 (6.7–23.0)	10.6 (5.7–22.6)	8.8 (0.6–31.1)	0.0 (0.0–11.7)
0–14	c14	18.3 (10.3–29.5)	18.5 (7.3–30.0)	12.6 (1.8–31.9)	3.9 (0.0–21.4)
0–19	c19	21.5 (11.1–35.4)	23.6 (7.7–31.2)	18.7 (2.9–34.5)	4.4 (0.0–24.5)

Note: Road densities are expressed as km-km⁻². Spruce budworm outbreaks and logging data are given as percent of total subbasin area. Variable codes for Fig. 4 are also given.

regeneration, seed tree, and patch cutting), partial (partial harvesting, thinning, strip harvesting, selection cutting, harvesting within green strips, and diameter-limit cutting), and combined (intensive plus partial) logging. The logging variables used in the analyses quantified the percentage of the total land area at a given distance upstream that was logged (either intensively, partially, or combined) in the following time intervals preceding the study: 0–1, 0–2, 0–3, 0–4, 0–9, 0–14, and 0–19 years (Table 2).

We used classification trees (CT) and regression trees (RT) to examine the context-dependent response of salmon populations to forestry variables measured at multiple scales. CT and RT are robust tools for ecological modelling that can effectively represent nonlinear relationships between a single response variable (qualitative in CT and quantitative in RT) and a set of predictor variables. Additionally, they can reveal nonadditive effects and complex interactions between predictors without requiring a priori specification of the form of these interactions (Breiman et al. 1984; De'ath and Fabricius 2000). This ability to detect interactions is particularly relevant in studies focusing on context-dependent effects, which by definition are interactive. CT and RT use binary recursive

partitioning (Breiman et al. 1984) to split the data into progressively smaller and more homogeneous subgroups. Beginning with the entire data set, at each step this algorithm examines all possible splits for each possible value of the predictor variables and selects the candidate split (the “splitting value”) that maximizes the homogeneity within the two resulting subgroups with respect to the response variable. Similar to parametric methods such as multiple regression, in CT and RT strong colinearity among predictor variables can complicate the interpretation of effects of individual predictors. However, in CT and RT only one predictor is allowed to enter the model at any given split, and as the data are split into smaller subgroups, the relations among predictors may change. Therefore, predictors that are highly correlated over the whole data set may not be as strongly correlated in subgroups of the data (Lawler and Edwards 2002).

Salmon incidence and density were treated separately because salmon were absent from 51 of the 120 reaches. CT were used to analyse salmon incidence in all 120 reaches, whereas RT were used to analyse salmon density only in the 69 salmon-bearing reaches. Although RT are invariant to the

distribution of predictor variables, they are not invariant to the distribution of the response variable (Atkinson and Therneau 2000). Salmon density was therefore transformed as $\ln(X)$ to reduce the potential influence of outliers. CT and RT were produced for each spatial scale separately.

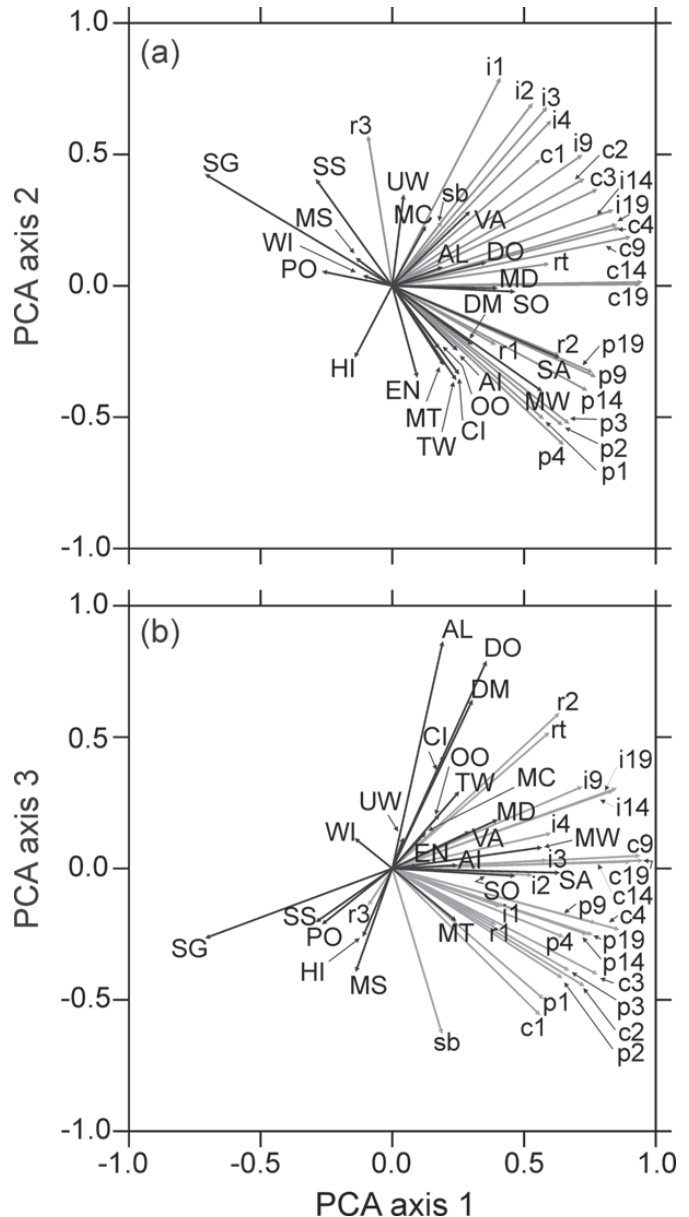
Model specification and cross-validation followed Turgeon and Rodríguez (2005). The Rpart software library (Atkinson and Therneau 2000) was used for all calculations (S-PLUS program, v.7.2, Insightful Corporation, Seattle, Washington). Because recursive partitioning sometimes leads to excessive splitting, producing trees that are too large and overfit the data, we used "pruning" and cross-validation (an alternative to conventional parametric inference for model assessment) to select optimal trees (Atkinson and Therneau 2000; De'ath and Fabricius 2000). First, we generated a sequence of trees of increasing size, using a cost-complexity parameter (CP), to eliminate ("prune off") splits that were obviously not worthwhile, i.e., that did not improve the fit by at least the value of CP ($= 0.01$ for all trials) (Atkinson and Therneau 2000). Then, 10-fold cross-validation was used to estimate prediction error, and final tree size was determined by the 1 SE rule, which favours the largest tree for which the cross-validated error falls within 1 standard error (SE) of the minimum relative error determined by cross-validation (Atkinson and Therneau 2000). The influence of individual predictor variables was gauged by the proportional reduction in error (PRE; a measure of the variation accounted for by the splits associated with each predictor in the tree), an approach similar to the use of partial R^2 to assess the contribution of individual predictors in multiple regression. Additionally, we used the correct classification rate (CCR; percentage of all cases correctly predicted), sensitivity (percentage of observed presences correctly predicted), and specificity (percentage of observed absences correctly predicted) to evaluate the accuracy of CT. Empirical odds ratios, calculated as

$$OR = \frac{P_1 A_2}{P_2 A_1}$$

where P_x and A_x represent numbers of reaches where salmon was present (P) or absent (A) under condition x , were used to compare salmon incidence under different environmental conditions determined by the CT, e.g., in reaches with wetted width < 8.7 m vs. reaches with wetted width ≥ 8.7 m. A small constant (0.5) was added to values of P and A to avoid null denominators.

We conducted a preliminary principal components analysis (PCA; based on the correlation matrix) to examine the relationships between the environmental and forestry variables (measured at the subbasin scale) and check for multicollinearity among these variables. Variables were transformed as required to reduce the influence of outliers and linearize relationships. We did not retain a reduced set of components from the PCA for subsequent inclusion as predictors in CT and RT because of the difficulties in interpreting composite variables and because using linear composites of variables as predictors can reduce predictive power and mask interactions among the original variables (Muñoz and Felicísimo 2004).

Fig. 4. Loadings from a principal component analysis (PCA) of environmental (solid arrows, uppercase codes) and forestry (shaded arrows, lowercase codes) variables measured at the subbasin scale. Plots are presented for (a) axes 1 (30.6% of total variance) and 2 (13.8%) and (b) axes 1 and 3 (11.6%). Linear correlations between variables are represented approximately by the length and alignment of their respective arrows. Variable codes are as in Tables 1 and 2.



Results

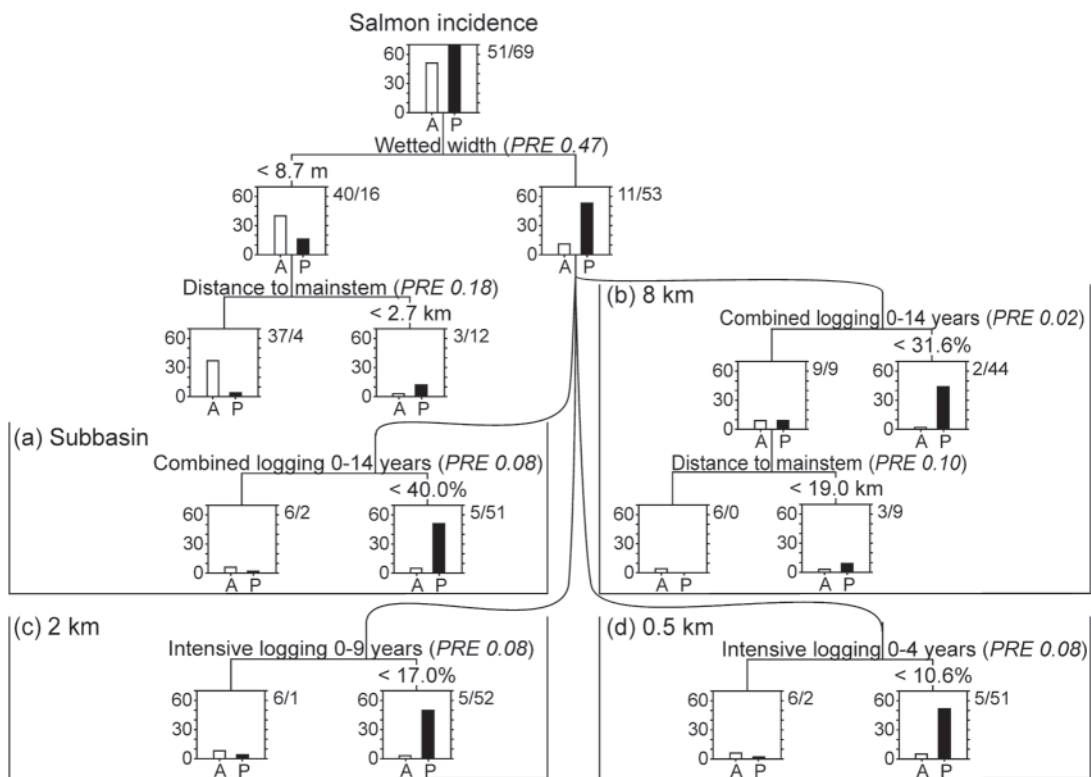
The PCA of environmental and forestry variables showed little relationship between the areal coverages of intensive and partial logging in the Cascapedia River basin (Fig. 4). Combined logging, given by the sum of intensive and partial logging, was positively related to both these variables, as would be expected. Within each of these three sets of logging variables, correlations reflected the overlap in temporal coverage between pairs of variables, e.g., strong correlation

Table 3. Classification success (CCR, specificity, and sensitivity) and proportional reduction in error (PRE) of classification tree models and PRE of regression tree models by spatial scale.

Spatial scale	Classification trees				Regression trees
	CCR	Specificity	Sensitivity	PRE	PRE
Subbasin	88.3	84.3	91.3	72.5	68.7
8 km	90	84.3	94.2	76.5	68.4
2 km	89.2	84.3	92.8	72.5	57.5
0.5 km	88.3	84.3	91.3	72.5	49.1

Note: All values are percentages.

Fig. 5. Classification tree models for salmon incidence. Models are composed of a common part (top, left) and a part specific to each scale (open boxes; bottom): (a) subbasin, (b) 8 km, (c) 2 km, and (d) 0.5 km. Vertical bars represent the number of reaches with (solid) or without (open) salmon at each node. Splitting rules and proportional reduction in error (PRE) are given on the branches of each tree. The number of reaches with and without salmon are given alongside the boxes for each node.



between 0- to 14-year and 0- to 19-year cuts (14-year overlap), but weaker correlation between 0- to 14-year and 0- to 1-year cuts (1-year overlap). Among the environmental variables, the strongest correlations were between wetted width and subbasin area (Pearson $r_p = 0.86$), altitude and distance to mouth ($r_p = 0.84$), altitude and distance to mainstem ($r_p = 0.77$), stream gradient and subbasin area ($r_p = -0.74$), and stream gradient and wetted width ($r_p = -0.70$) (Fig. 4); all other correlations were ≤ 0.63 . The strongest correlation between environmental and logging variables was between stream gradient and 0- to 19-year combined cuts ($r_p = -0.62$). Logging variables were generally related positively to subbasin size and wetted width and negatively to stream gradient (Fig. 4), perhaps reflecting greater accessibility and ease of manoeuvring for forestry equipment in large expanses of flat lowland terrain.

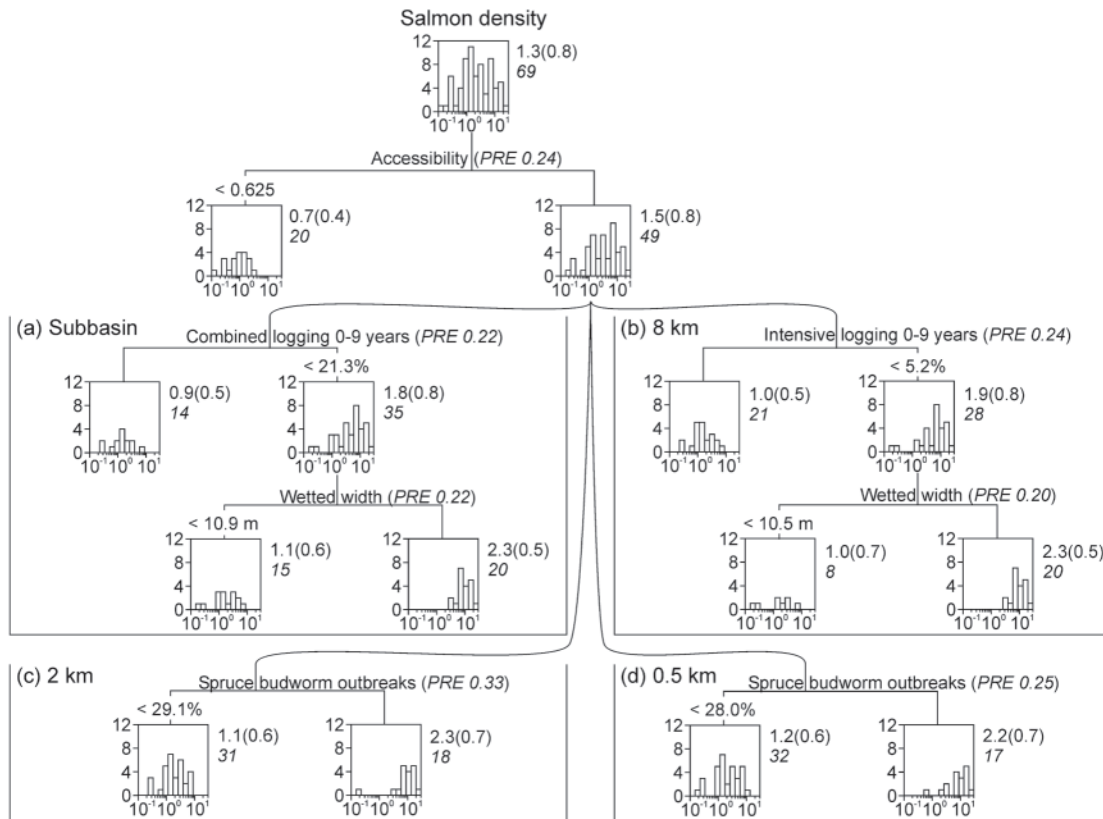
A total of 1539 salmon were captured over the three years of sampling. Salmon were present in 69 of the 120 reaches

and 14 of the 22 streams sampled. The ability of final CT models to classify reaches correctly on the basis of incidence (CCR) differed little across scales and ranged from 88.3% at the subbasin scale to 90.0% at the 8 km scale (Table 3). All models had a greater ability to correctly classify salmon-bearing reaches (sensitivity) than reaches without salmon (specificity). For CT models, the proportional reduction in error varied little across scales (72.5%–76.5%).

Although CT models were built for each spatial scale separately, two environmental predictors, wetted width and distance to the mainstem, were retained in the final models at all scales (Fig. 5). Smaller reaches (wetted width < 8.7 m) had lower incidence than larger reaches (odds ratio (OR) = 11.4). Among smaller reaches, salmon incidence was greater in reaches nearer (< 2.7 km) to the Cascapedia River mainstem than in more distant reaches (OR = 29.8) (Fig. 5).

Among larger reaches (wetted width ≥ 8.7 m), salmon incidence was negatively related to logging at all scales

Fig. 6. Regression tree models for population density (numbers·100 m⁻²) in salmon-bearing reaches (*X* axis). Models are composed of a common part (top) and a part specific to each scale (open boxes, bottom): (a) subbasin, (b) 8 km, (c) 2 km, and (d) 0.5 km. Vertical bars represent the density distribution of salmon at each node. Splitting rules and proportional reduction in error (PRE) values are given on the branches of each tree. The mean (SD) of ln-transformed density and the number of observations (in italics) are given alongside the boxes representing terminal nodes.



(Figs. 5a–5d). Salmon incidence was negatively related to combined logging in the preceding 14 years at both the subbasin (OR = 24.3) and 8 km scales (OR = 17.8) (Figs. 5a, 5b). Salmon incidence also was negatively related to intensive logging in the preceding 9 years at the 2 km scale (OR = 41.4) and to intensive logging in the preceding 4 years at the 0.5 km scale (OR = 24.3) (Figs. 5c, 5d). At the two smaller scales, declines in salmon incidence were apparent at relatively low threshold values for intensive logging (17.0% at the 2 km scale; 10.6% at the 0.5 km scale). The fact that salmon incidence was negatively related to logging only in larger reaches points to an interaction between logging and stream size that is independent of scale (Fig. 5).

Final RT models for salmon density in salmon-bearing reaches retained only two or three predictor variables. The proportion of variation in salmon density accounted for by the models increased with spatial scale, ranging from 49.1% at the 0.5 km scale to 68.7% at the subbasin scale (Table 3). Accessibility was a major predictor of salmon density at all scales (Fig. 6). Mean salmon density in readily accessible reaches (accessibility ≥ 0.625) was approximately twice that in less accessible ones (Fig. 6).

Relationships between salmon density and logging were only detected in readily accessible reaches, at the two largest spatial scales (Fig. 6). At the subbasin scale, mean salmon density in reaches having <21.3% of combined logging in the preceding 9 years was 2.5 times that in reaches with

greater values of combined logging (Fig. 6a). Among the former reaches, those having wetted width ≥ 10.9 m had greater salmon density than narrower ones. At the 8 km scale, mean salmon density in reaches having <5.2% of intensive logging in the preceding 9 years was 2.5 times that in reaches with greater values of intensive logging (Fig. 6b). At this scale, mean salmon density was greatest in reaches having <5.2% of intensive logging in the preceding 9 years and wetted width ≥ 10.5 m. Final RT models were similar for the 2 km and 0.5 km scales. At these scales, salmon density was greatest in readily accessible reaches subject to spruce budworm outbreaks having areal coverage $\geq 28\%$ –29.1% (Figs. 6c, 6d). Similar to the models for incidence, an interaction involving logging and an environmental predictor was apparent. Salmon density was negatively related to logging only in readily accessible reaches but, contrary to the models for incidence, only at the two largest spatial scales (Figs. 6c, 6d).

Discussion

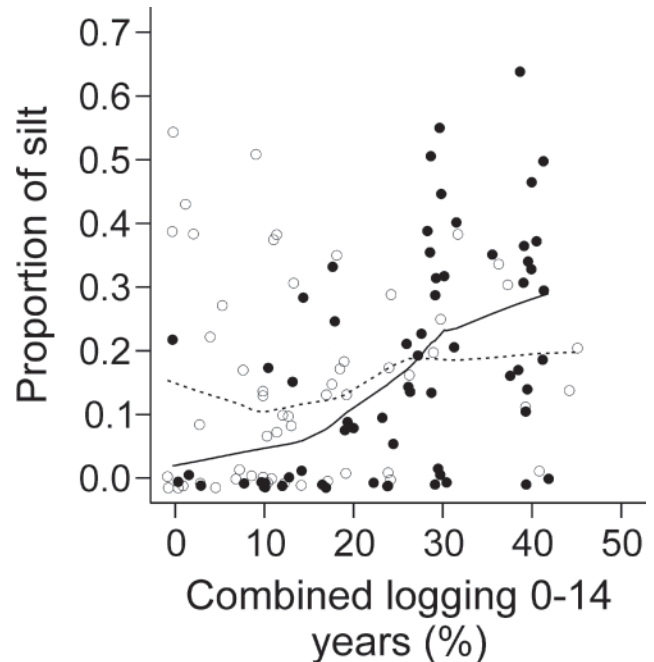
At all spatial scales, logging appeared to have context-dependent effects: incidence declined only in large reaches and density declined only in readily accessible reaches. Logging impacts on periphyton, invertebrates, and physical characteristics in Oregon streams varied as a function of stream width and gradient and resulted in greater abundance

of periphyton and invertebrates in small, high-gradient reaches than in large, low-gradient ones (Murphy and Hall 1981). Canopy removal resulted in a smaller reduction in shading, and thus less enhancement of primary production, in large reaches than in small reaches. Furthermore, sediment deposition was greater in large reaches because of their lower gradient and transport capacity relative to small reaches. Increased sedimentation offset any beneficial effect of increased light exposure in larger reaches (Murphy and Hall 1981). In the Cascapedia River basin, the effect of logging on salmon incidence in large reaches may have been linked to decline in habitat quality mediated by increased deposition of fine sediments. Because reach width and gradient were negatively correlated (Spearman rank correlation, $r_s = -0.66$), small reaches likely were less susceptible to accumulation of fine sediments than large ones, possibly explaining why no effect of logging on salmon incidence was apparent in small reaches. The proportion of silt increased with logging in larger reaches but not in smaller ones (analysis of covariance (ANCOVA) term for the interaction between stream width and logging, $p = 0.007$; Fig. 7), lending support to this interpretation. The apparent context-dependent effect of logging on salmon density may be a consequence of restriction of fish movement by barriers such as log jams, beaver dams, culverts, or waterfalls in less accessible reaches, which may hinder adjustment of local densities to match spatial differences in habitat quality induced by logging. In contrast, salmon in accessible reaches may move more freely and avoid areas impacted by logging, creating density differentials that better reflect habitat quality.

The cumulative effects of logging on salmon incidence seemed to be integrated over longer time horizons at larger spatial scales. Fine sediments produced by logging have been reported to rapidly increase in reaches immediately downstream of the logged area and subsequently decline within 1 to 3 years after the disturbance (Macdonald et al. 2003; Haggerty et al. 2004). However, redistribution and transport of deposited sediments to reaches further downstream may continue for many years. For example, in the Big Beef Creek basin (USA), mass influx of sediments arising from forestry activities between 1850 and 1930 produced a sediment wave that was transported over 18 km of main stream channel and an artificial lake (≈ 1 km in length) (Quinn and Peterson 1996) before arriving near the downstream limit of the creek by 1970 (Madej 1982). This wave was then transported over a distance of 6 km between 1970 and 1976 (Madej 1982). Logging effects on downstream reaches may therefore be detectable for many decades after the actual disturbance (e.g., Madej 1982; Swank et al. 2001). Transport of fine sediments from upstream to downstream reaches over a span of decades may explain why logging effects appeared to be integrated over longer time periods at larger spatial scales. These long-term effects seem akin to the “ghost of the land use past”, where past agricultural activity in North Carolina basins determined present-day fish and invertebrate diversity, independently of riparian reforestation (Harding et al. 1998).

In contrast with salmon incidence, logging effects on salmon density were only apparent at the two largest spatial scales. When fine sediments from multiple headwater

Fig. 7. Relative abundance of silt (particle size <0.0625 mm; transformed as arcsine square-root) vs. percent areal coverage of 0–14 years of combined logging, at the subbasin scale. Circles represent reaches in two categories of wetted width derived from CT models (Fig. 4): ≥ 8.7 m (solid circles) and < 8.7 m (open circles). Lines are lowest regression curves for the two categories: ≥ 8.7 m (solid line) and < 8.7 m (dotted line). A small amount of random jitter was added to improve the visibility of overlapping symbols.



sources accumulate in downstream reaches, effects of logging on fish populations may be magnified in those reaches that receive the impact of distant upstream sources and thus be apparent only at larger spatial scales. Salmon density was positively related to areal coverage of spruce budworm outbreaks at the two smaller scales, 2 km and 0.5 km. Loss of riparian canopy caused by defoliation can result in increased light exposure, local temperature, and productivity (Swanston 1991; Kiffney et al. 2003, 2004). The influence of defoliation on salmon density seems to be local (Swanston 1991) and may thus be more readily detectable at smaller spatial scales.

In summary, apparent effects of logging activities on salmon incidence and density were mostly negative and strong, but were both markedly scale-dependent and conditional on environmental context. The two biological metrics used to quantify the responses to logging, incidence and density, differed in their sensitivity to spatial scale, capacity to detect logging impacts, and integration of effects over time. Examining the variation in salmon incidence and density over multiple spatial scales helped us understand the context-dependent responses of salmon populations to logging and pointed to potential limitations of studies focusing on single scales and biological metrics. For example, the apparent absence of logging effects on salmon density at the two smaller spatial scales suggests that future study designs should consider the possibility that large-scale disturbances arising from logging may not be detectable at smaller spatial

or temporal scales. Potential effects of logging should therefore be examined with a view to detection of downstream effects, particularly as concerns transport of sediments from headwaters to downstream reaches. Because biotic responses to logging can differ across geomorphic settings, future studies may benefit from considering environmental context explicitly when assessing the effects of logging on fish populations.

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