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Idiosyncratic responses of Pacific salmon species to land cover, fragmentation, and scale

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Keywords: Chinook salmon (*Oncorhynchus tshawytscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), pink salmon (*O. gorbuscha*), sockeye salmon (*O. nerka*), forest management, forest pattern, GIS, land cover, remote sensing, Landsat.

Abstract. Salmon are critical to the ecology and livelihood of the Pacific Northwest, and are declining throughout much of their range. While much of their life cycle occurs in open ocean, freshwater conditions also contribute to population trends. Because stream habitats are connected to uplands by water flow, salmon can be influenced by the characteristics of terrestrial systems. We analyzed the relationships between the population trends of Pacific salmon (1953-2006) and land cover, fragmentation, and forest age derived from remotely-sensed, landscape level datasets. Analyses included 425 populations of all native salmon species in 156 watersheds on Vancouver Island, British Columbia, Canada. Vancouver Island salmon escapements exhibited general patterns of decline, which may be largely controlled by broad-scale marine conditions. The spatial variation in these population trends was related to landscape variables at watershed and riparian scales with regression trees. Results were found to be species specific, but characteristics indicating a legacy of historic and current forest management (such as fragmented forests and non-forested or early-successional forest cover) generally had negative effects, driven by a small subset of highly fragmented watersheds. Chum and coho had strong negative relationships with fragmentation, pink had a strong positive relationship with wetland abundance, and Chinook and sockeye were most closely related to geomorphology. There was no “single best” scale of analysis. Salmon trends were generally more closely related to variables estimated over the entire watershed, however, the relative importances of watershed and riparian level predictors varied by both variable and species. Efforts to restore salmon habitat will be complicated by marine and freshwater processes, terrestrial conditions throughout watersheds, and the idiosyncratic requirements of each species.

Introduction

Salmon (*Oncorhynchus* spp.) are an integral component of many ecosystems, cultures, and economies of North America’s Pacific Northwest. However, many salmon populations in the region are exhibiting declines relative to historic levels. Nehlson et al. (1991) determined that 214 populations in the western continental U.S. are at risk of extinction; this estimate was subsequently raised to 314 (Allendorf et al. 1997). North of the border, 1074 Canadian populations were identified as at risk or extinct (Slaney et al. 1996). Although this is only 11% of Pacific Canadian populations, it is probably a conservative estimate as data were insufficient to assess nearly half of all populations and many in British Columbia have declined substantially since the early 1990s when these assessments were made (e.g., Welch et al. 2000). Today, 31 evolutionarily significant units of Pacific Salmon (out of 51 total) are listed as endangered, threatened, or of concern under the United States Endangered Species Act (NOAA 2010). In Canada, four populations have been identified as endangered or threatened by the Committee on the Status of Endangered Wildlife in Canada, although none have legal status under the Species at Risk Act (Irvine et al. 2005, COSEWIC 2010). Roughly one-third of all Pacific salmon populations are now estimated to be extinct (Gustafson et al. 2007) and dialogue continues over how best to manage and recover this resource (Bisson et al. 2009, Bottom et al. 2009, Healey 2009, Ruckelshaus et al. 2002, Schwindt et al. 2003).

There is thus strong motivation to identify the mechanisms of recent salmon declines. However, salmon have complex and diverse life cycles (Groot and Margolis 1991), greatly challenging attempts to understand population trends. Salmon incubate in freshwater; rear in

either freshwater or estuaries; migrate to the ocean where they feed and grow, either traveling to the open ocean or remaining in coastal waters; and finally return to their natal streams to spawn and die. The amount of time spent in each habitat ranges from months to years, and varies both within and between species and within and between populations (Groot and Margolis 1991). Debate continues over the relative influence of freshwater and marine conditions on salmon dynamics: Some researchers (e.g., Welch et al. 2000) believe that the dominant controls on salmon abundance are marine, however, in a review of life-stage specific survival rates, Bradford (1995) found freshwater survival to have a slightly stronger contribution to overall survival.

A number of freshwater factors influence salmon survival and viability. Further, because streams integrate the flows of water, energy, and materials throughout a drainage, salmon populations and their habitat are functions not only of local conditions, but also of watershed-scale land cover and disturbance. Terrestrial land use/land cover (e.g., Allan 2004, Bradford and Irvine 2000, Inoue et al. 1997), land use change (e.g., Bilby and Mollet 2008) and geomorphology (e.g., Brazner et al. 2004, Regetz 2003) thus have potentially strong impacts on fishes and their habitats (e.g., Richards and Host 1994). Freshwater habitat degradation, resulting from local and landscape processes, is believed to contribute to the decline of more than 90% of the imperiled U.S. populations (Nehlsen et al. 1991), as well as to many of the Canadian ones (Slaney et al. 1996).

The effects of forest harvest on salmon are of especial concern, since salmon and timber are the prime, frequently co-occurring resources in the Pacific Northwest (e.g., Burnett et al. 2007, Hartman et al. 1996, Reeves et al. 1993, Scrivener and Brownlee 1989). Forest management has a variety of consequences to streams (Chamberlin et al. 1991) and associated impacts on biota (Hicks et al. 1991, Richardson 2008). Forest harvest tends to increase runoff and stream flow, especially peak flow (Macdonald et al. 2003, Matheussen et al. 2000, Nagasaka and Nakamura 1999), but effects in large basins and during large storm events remain controversial (Beschta et al. 2000, Jones and Grant 1996, Thomas and Megahan 1998). Flow alterations can increase the number of eggs swept away in a flood event (Heard 1991, Healey 1991, Montgomery et al. 1999, Sandercock 1991). Forest harvest also tends to increase water temperatures (Johnson and Jones 2000, Pollock et al. 2009, Welsh et al. 2005), which may harm salmon if temperatures rise above tolerated levels (Nagasaka and Nakamura 1999), or may cause short-term benefits by increasing primary productivity and food supply (Hicks et al. 1991). Another side effect of forest harvest and roads is increased sedimentation (Croke and Hairsine 2006, May 2002, Opperman et al. 2005, Scrivener and Brownlee 1989). Elevated fine sediment in spawning gravel negatively influences salmon by reducing dissolved oxygen flow to eggs, blocking fry emergence (Groot and Margolis 1991), and reducing availability of the preferred prey of juvenile salmon (Suttle et al. 2004). Increased turbidity may also alter feeding behavior and success (Hicks et al. 1991). Forest harvest reduces allochthonous inputs of organic matter, especially coarse woody debris, to streams (Bilby and Ward 1991), reducing habitat complexity and the number and diversity of fish species that can be supported (Reeves et al. 1993, Sharma and Hilborn 2001). Finally, the above changes in flow characteristics, sediment, and coarse woody debris can all, alone and in concert, alter stream geomorphology, with consequent changes to stream habitats (Chen and Wei 2008, Mellina and Hinch 2009, Wood-Smith and Buffington 1996).

Most investigations of forestry related effects are detailed studies conducted in one to a few small, intensively modified basins. An increasing number of broad-extent studies over a large number of watersheds relate land use/land cover to stream habitat and species (as

summarized below). However, these have mostly been conducted in mixed use systems, finding strong effects of urban and agricultural land use (Allan 2004). Investigations in forest dominated systems are less common and effects may be more subtle. Several landscape studies have confirmed the effects of forestry on fish and fish habitat using harvest area as a test variable (Deschênes et al. 2007, Hemstad and Newman 2006, Kershner et al. 2004, Woodcock et al. 2006). In contrast, Van Sickle et al. (2004) failed to find an effect of forest land cover, in lieu of direct forest management variables, on stream status. It may be that land cover variables lack sensitivity in forest dominated systems. Measures of landscape configuration (such as patch size and shape attributes or the prevalence of patch edges in a region), capturing the spatial arrangement and fragmentation of forest cover, may provide a better indication of terrestrial condition as it affects streams. Moreover, forest harvest has strong, characteristic effects on these fragmentation metrics, for example, decreasing forest patch sizes while increasing the number of forest patches and the amount of edge (Franklin and Formann 1987, Mladenoff et al. 1993, Ripple et al. 1991). Yet, to our knowledge, fragmentation metrics have not yet been included in studies of landscape effects on streams, although this practice has been encouraged (Gergel et al. 2002, Johnson and Gage 1997, Kearns et al. 2005, Steel et al. 2010).

It is now widely recognized that upland processes can have notable effects on fish, and calls for multi-scale analyses are becoming routine (e.g., Durance et al. 2006, Poff and Huryn 1998). In studies of aquatic habitat and biota, questions of scale typically revolve around the extent of terrestrial habitat potentially influencing the stream, most commonly contrasting effects of conditions measured in the local riparian zone with those measured over the entire watershed. Researchers have found, variously, that local and riparian level parameters (Lammert and Allan 1999, Sandin and Johnson 2004) and watershed level characteristics (Creque et al. 2005, Feist et al. 2003, 2010, Opperman et al. 2005, Roth et al. 1996, Wang et al. 1997) are more relevant, depending on the extent of the study; that different stream habitat properties are most sensitive to different scales and different terrestrial characteristics operate most strongly at different scales (Richards et al. 1996, Strayer et al. 2003); and that the relative explanatory power of the two scales varies over time (Pess et al. 2002) and between species (Pont et al. 2005). Wang et al. (2006) hypothesized that such scale dependence may be an effect of anthropogenic disturbance and that local characteristics are more important than watershed land cover to fish in relatively undisturbed, heavily forested systems. However, forest harvest, even at relatively low levels, generally relates most strongly to fish and stream condition when estimated over the entire watershed rather than simply along the riparian network (Burnett et al. 2006, Deschênes et al. 2007, Hemstad and Newman 2006, Woodcock et al. 2006).

Existing studies of landscape effects to streams offer temporal snapshots. They relate spatial variation in fish abundance, in-stream habitat variables, etc. to spatial variation in landscape composition. Yet they do not provide a real test of effects of changing land use/land cover, and predicting such effects by interpolating their results requires a space for time substitution. Therefore, although evaluations with static measures of abundance are often used to support hypothesized mechanisms of salmon decline, they provide no specific link to population trends.

The major objective of this study is to explicitly link temporal trends of spawning salmon abundance on Vancouver Island, British Columbia, Canada to forest pattern, as characterized by landscape metrics of land cover, forest fragmentation, and forest age structure. Individual objectives are to (1) estimate temporal trends of salmon spawners overall and by population; (2) relate population trends to the characteristics of the riparian networks and watersheds in which

they spawn; (3) determine the relative performance of variables estimated over riparian and watershed extents, and assess whether models constructed with variables from both scales best explain salmon trends; and (4) by considering all five species of native Pacific salmon – Chinook (*Oncorhynchus tshawytscha*), chum (*O. keta*), coho (*O. kisutch*), pink (*O. gorbuscha*), and sockeye (*O. nerka*) – assess the extent to which terrestrial influences are species specific or common to all Pacific salmon.

Materials and methods

Study area

We assessed the relationships between salmon trends and terrestrial landscape characteristics over Vancouver Island. Vancouver Island is part of the Pacific Northwest region of North America, located off the southwest coast of mainland British Columbia, Canada (Figure 1). Bedrock is predominantly igneous. The climate is temperate maritime, with mild, wet winters and cool, dry summers. Precipitation primarily falls as rain. Coniferous forests are the dominant land cover. Land use on the island is 89% forest; only 1% and 2.6%, respectively, is under agricultural or urban development. Vancouver Island ownership is 12% provincial parks; 27% private (a legacy of historic crown grant to railroad concession, municipal development, agriculture, etc.); and 55% provincial crown land. Much of the private and crown land is managed forests. The remaining 6% is divided between a variety of types of small holdings. Vancouver Island is 32,134 km² in area and contains 2093 third order or higher watersheds (mapped at 1:50,000 scale; Ministry of Sustainable Resource Management 2004) and over 65,000 km of rivers and streams. Over 250 of these watersheds support salmon. Many of the salmon populations at risk in British Columbia and the Yukon identified by Slaney et al. (1996) are found disproportionately on Vancouver Island.

Datasets

Salmon abundance was taken from annual escapement counts (Fisheries and Oceans Canada). Escapements are the number of adults returning to spawn. Over 1300 populations are monitored on Vancouver Island, including 230 Chinook, 236 chum, 241 coho, 225 pink, and 229 sockeye. (Here and throughout we use “population” to refer to salmon of a given species spawning in the same watershed, although strict population distinctions have not been established in all cases.) Although escapement records extend from 1953 to present, not all populations have been sampled consistently over this time period. Wiley et al. (1997) found that 10 generations of data are required to accurately characterize temporal trends in salmonid populations, which would be 20-50 year time series for Pacific salmon species. These guidelines can be restrictive, and conservation assessments often require only three generations of data to determine population trends (e.g., Irvine et al. 2005). We retained all populations containing more than 20 years of observations, which included records from 156 Vancouver Island waterbodies (Table 1). On average, populations each contained 39.5±10.0 years of observations, spanning a 47.4±6.6 year period. This ensures at least three generations for each population, and 10 for coho and pink salmon populations, and has been found to afford sufficient power to detect trend differences in single and paired watershed studies (Korman and Higgins 1997). Escapement counts were ln+1 transformed and expressed as proportions of the population mean over the time series.

Many researchers have expressed reservations over the use of escapement time series to detect responses to environmental change. Such data reflect many sources of variation, including variation in freshwater and marine survival, age at maturity, fishing mortality (Pella

and Myren 1974), and measurement-error (Cousens et al. 1982, Holt and Cox 2008, Shardlow et al. 1987), which vary within and between watersheds and years and may all but obscure the relationships of interest (Bradford et al. 2005, Pella and Myren 1974). However, they are often the only data available that characterize salmon abundance over large areas and long periods. Moreover, our analyses have been designed to not require confidence in any specific escapement record while capitalizing on the strengths (i.e., duration and extent) of the escapement database.

Landscape level metrics of forest pattern were derived from national datasets of land cover, fragmentation (Wulder et al. 2008a, b), and forest inventory (Leckie and Gillis 1995). All were characterized over two scales of observation: the entire watershed and the riparian area, defined by a 100 m buffer surrounding all waterbodies in a watershed. This buffer distance was chosen to correspond to the spatial resolution of the fragmentation dataset. Waterbodies were mapped at 1:50,000 scale (Natural Resources Canada 2008).

The Earth Observation for Sustainable Development of forests (EOSD, Wulder et al. 2008a) dataset maps land cover from circa year 2000 Landsat satellite imagery with products generated at a spatial resolution of 25 m. Land cover classes are described in Table 2. Land cover information was extracted as the proportion by area of each land cover class within the watershed and riparian buffer. We also calculated three secondary products: the total proportion of wetland (sum of herb, shrub, and forested wetlands), and the number and evenness of forested classes. Because the timing, size, quality, and longevity of debris inputs varies with forest type, diverse forested landscapes (e.g., high richness and evenness) are expected to provide more diverse food supplies and increase structural diversity, supporting a larger number of fishes (Franklin 1992).

The national forest fragmentation dataset (Wulder et al. 2008b) calculated over 90 landscape metrics from the map of EOSD land cover (converted to a binary forest/non-forest classing) at four spatial scales. We chose six metrics calculated on a 1 km² grid to represent forest fragmentation within watersheds and five metrics calculated on a 1 ha grid to represent forest fragmentation in the riparian buffers. These fragmentation variables have known relationships with forest harvest activities, and are listed in Table 3. Metrics were aggregated by mean, standard deviation, and maximum values by watershed and the mean and standard deviation within riparian buffers. Maximum values did not vary at the riparian scale, except for in the forest/non-forest join variable. At this level, the sums of forest/forest and forest/non-forest joins were also used.

We included information on forest age distributions from forest inventory data (British Columbia Ministry of Sustainable Resource Management 2002). The proportion of each watershed and riparian buffer in five forest age classes was extracted (Table 2; Gillis et al. 2003). Forest inventory coverage is limited to areas of crown managed forest, so analyses with forest age could only be performed for a subset of watersheds on Vancouver Island (Figure 1, Table 1). Watersheds without forest inventory data are nonrandomly distributed, largely occurring in the southeast of Vancouver Island and encompassing the areas of urban development, private forest lands, sedimentary bedrock, and most major salmon hatcheries. Relationships observed over the subset of watersheds with forest age information may thus not be equivalent to those over the entire dataset. As a result, we present the results from analyses both with and without forest age data.

Additional geomorphic variables included in the watershed set are listed in Table 2. Elevation mean, variability, and stream gradient were measured from the 25m GeoBase digital elevation data product (Government of Canada 2007). Stream gradient was calculated as the

mean slope value for all pixels containing a stream within a watershed. Slopes were calculated in 3x3 pixel windows. The position of the watershed centroid in UTM coordinates (m), distance from the centroid of the watershed to the coast (km), watershed area (m²), and stream density (m⁻¹) were measured in a geographic information system. Bedrock geology was expressed as the proportion of each watershed and riparian buffer in four major rock types (intrusive, volcanic, metamorphic, sedimentary), as mapped at 1:250,000 scale by Massey et al. (2005a, b).

Analyses

Overall trends for each salmon species were determined with linear mixed effects models (Pinheiro and Bates 2000) modeling standardized escapement counts with time as a random variable and error variances grouped by population. Mixed models were performed in R (R Core Development Team, <http://www.r-project.org>) using the add-on package nlme (Pinheiro et al. 2009). Population-specific trends were estimated with simple linear regression of the standardized escapement counts as a function of time by population. The slope of this relationship for each population was used to characterize the temporal trend of spawner abundance for a given species in a given waterbody. These analyses were performed in STATISTICA 8.0 (StatSoft, Inc., Tulsa, OK, USA).

Escapement trends were related to watershed- and riparian-scale land cover, fragmentation, forest age, etc. with regression tree models (Breiman et al. 1998) using the R package tree (Ripley 2007). Regression trees are appealing because they are nonparametric techniques that place no distributional requirements on the data; accommodate both continuous and categorical predictor variables; and are powerful variable selection tools capable of identifying the most important explanatory variables from large, interdependent datasets (Breiman et al. 1998, De'Ath and Fabricius 2000). Regression trees recursively split a dataset along simple thresholds of the independent variables to minimize the heterogeneity within the two resulting subgroups. Our analyses used deviance, or the sum of the squared residuals between the observations in a group and the group mean, as the heterogeneity criterion to identify splitting rules. Consequently, trees implicitly handle nonlinearities and interactions. Although the context-dependence of ecological processes, including forestry effects on streams (Deschênes et al. 2007, Kaufmann and Hughes 2006, Williams et al. 2002), is well known, interactions are often omitted from standard regression models because they result in a multiplicative increase in the number of variables. Further, regression trees are well suited to the vagaries of the escapement time series, which are more reliably indicative of general trends than of absolute abundances or rates of change (Larkin and Slaney 1997). Effectively, regression trees group populations into the generalized bins (e.g., increasing, moderately declining, steeply declining) that are statistically supported by the dataset. Trees were pruned to the optimal tree size as determined by 10-fold cross-validation and evaluated by residual deviance. Separate models were created for all salmon and for each species individually, and using watershed and riparian level predictors individually and in combination. Model fit was assessed with the proportion by which trees reduced the deviance of the salmon trends. Variable usage was summarized by the number of times a variable was selected over all trees and the mean proportional deviance reduction by each node at which that variable was used. The presence of spatial autocorrelation in tree residuals was evaluated with Mantel tests (Legendre and Legendre 1998), which tested if similarity between residuals was correlated to the geographic distance between watershed centroids. The R package vegan (Oksanen et al. 2008) was used to calculate distance matrices and perform Mantel tests.

We also investigated whether the presence of hatcheries within a watershed influenced salmon trends. The locations (Figure 1) and species of major hatcheries were taken from MacKinlay et al. (2004). As only very few hatchery streams were present in our sample ($n = 21$ augmented populations in 7 watersheds), we chose not to include a dummy hatchery variable in the analyses and watersheds and populations with hatcheries were included in all analyses. Vancouver Island hatcheries typically augmented Chinook ($n = 7$ hatchery populations), coho ($n = 6$), and chum ($n = 5$) salmon; only three major hatcheries released pink salmon, and none enhanced sockeye populations. The effect of hatcheries on population trends was tested in STATISTICA with a Mann-Whitney U test of population trends and with contingency tables of the proportion of populations exhibiting positive, negative, and nonsignificant trends. Hatchery effects on non-target species were not considered.

Results

Across Vancouver Island, all salmon species but sockeye showed a general declining trend from 1953 to 2006 (Figure 2). Populations targeted by hatcheries had significantly higher trends (mean \pm standard error: $\text{trend}_{\text{hatchery}} = 0.001 \pm 0.002$ vs. $\text{trend}_{\text{no_hatchery}} = -0.013 \pm 0.001$ standardized spawners/year; Mann-Whitney U, $p < 0.0001$) and were more likely to have positive or stable trends (Pearson $\chi^2 = 8.82$, $df = 2$, $p < 0.01$; Table 4). Multivariate regression trees successfully modeled salmon trends as a function of forest composition, fragmentation, and age, reducing deviances of the observed slopes by 12.9-77.5% (Figure 3). Regression tree residuals tended not to be spatially autocorrelated; weak, albeit significant ($p < 0.05$), autocorrelation was observed for coho trend residuals when modeled with riparian and watershed variables both with (Mantel $r = 0.07$) and without forest age (Mantel $r = 0.05$), and with watershed variables without forest age (Mantel $r = 0.06$), and for pink trend residuals in the subset of watersheds containing forest age data when modeled with riparian (Mantel $r = 0.16$) and both riparian and watershed variables (Mantel $r = 0.16$). Independent variables were moderately intercorrelated. In general, the strongest pairwise correlations ($|r| \geq 0.75$) occurred between variables that are intuitively related: fragmentation variables within and between scales formed a cluster of highly correlated metrics, and land cover, forest age, and geology variables were closely related to their between-scale counterpart. Additionally, in both the full and forest age watershed sets, larger watersheds were farther from the coast, the proportion of dense coniferous forest increased to the north, the wetland sum term was dominated by forested wetlands, and forest evenness was inversely related to the abundance of open coniferous forests. In the entire watershed set, several land cover variables were correlated with forest fragmentation in the riparian buffer: nonforest and forest patch sizes increased with the abundance of riparian herb and open conifer cover, respectively.

Trends tended to be least predictable when pooling all species, and the most variance was explained for pink salmon (Figure 3). When modeling salmon trends as a function of land cover and fragmentation, watershed level predictors had greater explanatory power than forest pattern in the riparian buffer for chum, and sockeye; the reverse was true for pink; and the two scales had similar explanatory power for coho and Chinook (Figure 3). The performance of riparian-level models relative to watershed models was improved for chum and sockeye when forest age variables were included, but weakened for Chinook (Figure 3). The relative performance of individual variables between scales showed similar patterns (Tables 5 and 6). Variables calculated over the entire watershed generally yielded greater deviance reductions than those estimated for the riparian buffer. However, different variables were often selected from the two

scales. Including both watershed and riparian predictors in the same model increased explanatory power for Chinook, pink, and, slightly, coho trends, but only in the analyses including forest age (Figure 3). Models required 1-5 decisions to model trends (Figure 3).

Decision trees for the simultaneous watershed-riparian models are diagrammed in Figures 4 (without forest age variables) and 5 (with forest age variables). The importance of individual landscape variables to salmon trends and, in some cases, even the sign of the response, differed by species (Tables 7 and 8). In general, chum and coho salmon trends were most associated with forest fragmentation. These patterns were driven by a few highly fragmented watersheds with steeply declining salmon populations. Across all models, chum trends were most strongly and negatively related to edginess. The strongest responses of coho trends in the full watershed set were to the fragmentation metrics summarizing forest cover: as overall forest cover declined, so too did coho populations. Coho also experienced strong negative effects of sparse broadleaf forest cover and old growth forests. Pink salmon trends were strongly positively associated with the proportion of wetland present. Sockeye and Chinook were generally less consistent between the two watershed sets, which may be due to the limited sample sizes for these species. Both of these species tended to respond strongly to geomorphic variables. When pooling all salmon species, edginess dominated models, which is probably due to the dominant number of coho and chum records in the escapement dataset (Table 1).

Discussion

Salmon trends

Escapement records of all Pacific salmon species except sockeye exhibited declining numbers of spawning adults throughout Vancouver Island. This agrees with the determination that many populations at risk occur on Vancouver Island (Slaney et al. 1996). Overall declines were moderate and gradual over the time frame of the escapement database. Our analyses have focused on the influence of terrestrial conditions on salmon populations, via their effects on freshwater life stages. However, salmon are subject to a wide variety of stressors, including marine conditions, predation, and fishing pressure. For example, studies of alternate datasets have also found recent declines in salmon populations, particularly on the east coast of Vancouver Island, which has been attributed to a shift in marine conditions (Beamish et al. 1999, Smith and Ward 2000, Welch et al. 2000). We have ignored these effects in this work because marine survival functions on a larger spatial scale (500-1000km; Mueter et al. 2002) than the watershed analysis units due to mixing of populations while at sea and broader, regional scale climate drivers. Therefore, it should be relatively constant over the extent of Vancouver Island. General trends of Vancouver Island salmon populations may be determined by temporal variation in marine conditions and harvest rate, but the spatial variation of this trend, which is the focus of this study, should be a function of the freshwater conditions in individual watersheds. This assumption may not be appropriate if broad climatic differences exist between watersheds; if fishing pressure is spatially heterogeneous, for example differing between the west coast of Vancouver Island and the Strait of Georgia; or if adverse effects from hatchery populations, such as competition or sea lice (e.g., Krkošek 2010), which occur over limited scales in coastal waters, are present. However, these influences would most likely be apparent in the regression tree analyses or in spatial autocorrelation of the residuals. The geographic locations of the watersheds were included in all analyses, and were almost never significant or included in final models. If population trends strongly varied between regions, it should be manifested in a relationship with the geographic coordinates, and be well modeled by the linear thresholding

approach of the regression trees. Failing that, regional patterns that are not captured by the models are expected to leave a signal of spatial autocorrelation in the residuals. Yet spatial autocorrelation of the residuals was negligible (in all cases Mantel $r < 0.2$).

Terrestrial influences on salmon trends

Terrestrial land cover clearly has a strong influence on salmon, and fish in general, which is in agreement with much previous research (cited in the introduction). We found strong associations between salmon trends and forest fragmentation and land cover. Although we relate salmon trends over up to five decades to environmental variables observed in year 2000, to some extent the forest pattern metrics integrate contemporary and historical land use. Because forest communities pass through recognized successional stages as they develop, current land cover and forest age contain information on past disturbance. Moreover, current forest management practices on Vancouver Island target already disturbed forests for harvest to preserve those that are more pristine (Bunnell and Dunsworth 2009). Consequently, current fragmentation is indicative of historic conditions and the legacy of anthropogenic impacts.

This is the first study that we know of that has related salmon trends to terrestrial fragmentation. Fragmentation metrics merit wider use in freshwater studies (Kearns et al. 2005). They provide information beyond that contained in popular land cover summaries, and may be more sensitive to landscape differences in regions with little variation in land cover, such as heavily forested systems. Most models of salmon trends included forest fragmentation variables, and these were generally in the direction of more rapid declines under greater fragmentation. In particular, chum, coho, and all species together were most strongly related to fragmentation. As fragmentation increases, these species decline more steeply.

We assume that fragmentation is a metric of forest harvest (e.g., Franklin and Formann 1987, Mladenoff et al. 1993), which is known to be detrimental to salmon (Burnett et al. 2007, Hartman et al. 1996, Reeves et al. 1993, Scrivener and Brownlee 1989). Relationships with land cover also support the hypothesis that forest harvest influences salmon: the non-forested shrub class has consistently negative relationships with salmon trends, occurring in models of all species and chum; when common, herbaceous cover was negatively related to salmon trends; and the early-successional broadleaf classes also tend to have negative relationships with coho trends. Unlike Welsh et al. (2005), we found herbaceous cover to have a general positive effect on coho. However, the level of herbaceous cover over which this pattern occurred was very low (i.e., thresholds of 0.3-0.4% herbaceous land cover in Figures 4 and 5).

Collectively, therefore, our results corroborate experimental studies of the impacts of forest harvest on salmon physiologies and populations performed at limited spatial and temporal scales, and extend their conclusions to the regional level. Similarly, they confirm studies investigating the abundance and habitat preferences of salmon, as influenced by landscape composition, and extend them to salmon population dynamics. It is important to note that this is an expression of historic trends; current practices, in recognition of the effects of forest harvest on fish and stream habitat, restrict harvest in riparian areas (British Columbia Forest and Range Practices Act, Davies and Nelson 1994, Rashin et al. 2006).

Our results also agree with many studies that wetland habitat is important to fish (Feist et al. 2003, Pess et al. 2002, Richards et al. 1996, Roth et al. 1996, Strayer et al. 2003, Wang et al. 1997). Wetlands may provide spawning and rearing habitats to salmon, and may also modify characteristics of the mainstem habitat, for example by filtering out sediments or nutrients or raising water temperatures. We observed positive relationships between wetlands and abundance trends for pooled species, Chinook, and pink salmon; wetland variables were selected more often

when considering the abundance of wetlands within the riparian buffer rather than within the entire watershed.

Forest age variables contributed to multivariate models of all salmon species but chum (Table 8). Surprisingly, coho trends tended to be negatively related to the abundance of old growth forest. Old growth forest is expected to promote salmon by providing greater inputs of large woody debris and, consequently, greater habitat complexity (Bilby and Ward 1991, Burnett et al. 2007, Paulsen and Fisher 2001, Reeves et al. 1993). Our results may contradict these expectations because, on Vancouver Island, abundant old growth forests tend to occur in some of the most fragmented watersheds as protected patches amongst actively managed forests (Wulder et al. 2009). Coho also had negative relationships with forest fragmentation, thus, the apparent effect of old growth forest may instead be a signal of fragmentation. Alternatively, salmon responded negatively to old growth forests only at relatively high thresholds of old growth abundance. Where old growth forests were rare, positive relationships were observed with this variable (e.g., the model of coho trends with both watershed and riparian predictors, Figure 5). Reduced light inputs under old growth canopies may negatively affect salmon by lowering water temperatures and limiting food production (Hicks et al. 1991). Steel et al. (2004) also observed positive relationships between salmonids and the abundance of young forests.

Scale

We found salmon trends to generally be modeled better with variables estimated over the entire watershed. However, it would not be appropriate to label this the dominant scale over which terrestrial landscape processes influence streams. The relative performance of the two scales differed by species (Figure 3) and by variables (Tables 5 and 6). Indeed, this quest to determine the “single best” scale neglects its multi-scale justification that different processes operate over different scales. For example, while both the riparian zone and the entire catchment can be sources of materials to streams, the riparian zone can also filter the materials that enter a stream, potentially moderating the influence of the upland. Moreover, different scales may contribute water and material to streams at different times of year (the variable source area concept, Naiman et al. 1992), and may thus have different effects on stream biota, depending on the life history stage influenced. Treating scales separately makes logistical sense in the framework of traditional field data collection, but not given the remotely-sensed inputs that are more commonly used in such analyses. It follows that variables measured at multiple scales should be included simultaneously in analyses of fishes and streams but, like Feist et al. (2010), we found combined scale models to afford little additional explanatory power over those constructed with a single scale. More promising approaches include using path analysis or covariance structure analysis to link variables expressed along a scale hierarchy with mechanistic hypotheses (Burcher et al. 2007, Infante et al. 2006, Wehrly et al. 2006, Zorn and Wiley 2006) or variance partitioning to identify the independent and joint effects of variables measured at different scales (Gido et al. 2006, Sandin and Johnson 2004, Wang et al. 2003, Weigel et al. 2006).

Idiosyncratic species responses

A common thread throughout our analyses is the lack of a common thread between Pacific salmon species. Species responded idiosyncratically to characteristics of the terrestrial environment surrounding freshwater habitat. The relative importance of riparian and watershed level features also varied by species. Different species responded most strongly to different variables, and in different directions to the same variables (although this covaried with variable importance). As noted above, chum salmon exhibited a strong negative relationship between

trends in spawner abundance and forest fragmentation, and pink escapement trends had a strong positive association with wetland habitat. Conversely, chum had a negative, though less important, association with wetlands, and pink a positive, and again, less important relationship with fragmentation. Pooling all species together greatly diminished explanatory power by combining variable, potentially contradictory responses within a dataset. Several researchers have also noted differential responses by salmon species to forest harvest (Bisson et al. 1992, Hartman et al. 1996, Hicks et al. 1991). However, these species have not been equally well studied. Coho salmon are the most extensively researched; relatively little is known about the remaining Pacific salmon species and their responses to forest management (Hicks et al. 1991).

The differences observed between species may be related to differing life history strategies. Sockeye salmon have a long freshwater life stage (one year for Vancouver Island populations, Burgner 1991), and trends of its abundance were well explained by land cover characteristics surrounding the freshwater habitat (Figure 3). However, the results for pink salmon, especially, are unexpected. It is strange that pink salmon, which spend very little time in freshwater (Heard 1991), tended to be best explained by terrestrial features (Figure 3). Furthermore, they were found to be most influenced by wetlands, although they are not known to use wetland habitat. However, wetlands are valuable landscape elements and their importance is due to far more than direct habitat provision. Wetlands improve downstream water quality by filtering out sediment and nutrients (Johnston 1991, Whigham et al. 1988) and mediate stream temperatures (Wehrly et al. 2006). They also export invertebrates (Hood 2002) and phytoplankton (Lehman et al. 2008), directly and indirectly benefiting salmon via trophic interactions (Eaton and Simenstad 2009). Since pink salmon tend to spawn far downstream (Heard 1991), they thus may experience the most integrated effects of watershed characteristics, resulting in strong correlations with landscape structure and the opportunity for the presence or absence of upstream wetlands to have important effects. Pink salmon are also exhibiting the steepest decline (Figure 2), which may contribute to the increased explanatory power for this species.

Conclusions

Escapement data indicate that Pacific salmon populations are in general decline throughout Vancouver Island, British Columbia. Spatial variation in decline rates can be attributed to factors operating during the freshwater stage of their life cycle. Freshwater conditions are strongly controlled by terrestrial land cover and forest fragmentation in the riparian areas and watersheds surrounding salmon streams, as may be measured by remotely-sensed land cover and fragmentation products. Our research presents an unprecedented analysis of all five species of Pacific salmon over a large number of watersheds. Although expected relationships were observed, including negative responses by salmon to proxies of forest harvest and positive effects of wetlands, these patterns were highly species specific. Moreover, there was no “single best” scale of analysis. The relative importance of variables measured at the riparian and watershed scales varied over both variables and species. Different processes operate over different scales, and thus, multiple scales should be considered simultaneously in landscape analyses. Although current forest management practices restrict forest harvest in riparian zones, greatly reducing the negative impacts of forest harvest (Davis and Nelson 1994, Hicks et al. 1991, Rashin et al. 2006), we find that watershed-wide activities may influence salmon. Restoration of freshwater habitats, including a recognition of the importance of landscape features potentially distant from a stream, cannot but benefit salmon populations, but it is

unlikely that populations will recover without integrated attention to both freshwater and marine processes (e.g., Bisson et al. 1992, Hill et al. 2010, Kareiva et al. 2000). Moreover, freshwater restoration will be challenged by the diverse needs of different species.

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Table 1. Sample sizes of Vancouver Island salmon populations with ≥ 20 years of escapement records for both the complete set of watersheds and those containing forest inventory data of forest age composition.

	n (total)	n (with forest inventory)
Chinook	50	38
Chum	148	118
Coho	145	108
Pink	57	47
Sockeye	25	19
Total	425	330

Table 2. Land cover, forest age, and geomorphology data products used in salmon trend analyses. Land cover descriptions taken from Wulder and Nelson (2003) and forest age classes are derived from Gillis et al. (2003). Land cover and forest age data were summarized at both watershed and riparian levels. Fragmentation variables are described in Table 3.

Variable	Description
<i>Land Cover – Proportion of the watershed or riparian buffer in each of the following classes</i>	
snow.ice	Glacier/snow
rock.rubble	Bedrock, rubble, talus, blockfield, rubblely mine spoils, or lava beds.
exposed	< 5% vegetation. River, pond or lake sediments; exposed soils; reservoir margins, beaches, landings, burned areas, roads, mudflats, cutbanks, moraines, gravel pits, tailings, railways, buildings and parking, etc.
shrub	At least 20% ground cover which is $\geq 1/3$ shrub.
herb	Vascular plant without woody stem (grasses, crops, forbs, gramminoids). Minimum of 20% ground cover or 1/3 of total vegetation must be herb.
wetl.tree	Land with a water table near, at, or above soil surface for enough time to promote wetland or aquatic processes. The majority of vegetation is trees.
wetl.shrub	Land with a water table near, at, or above soil surface for enough time to promote wetland or aquatic processes. The majority of vegetation is shrub.
wetl.herb	Land with a water table near, at, or above soil surface for enough time to promote wetland or aquatic processes. The majority of vegetation is herb.
wetl.sum	Union of the three above wetland types.
conif.dense	> 60% crown closure. Coniferous trees are $\geq 75\%$ of total basal area.
conif.open	26-60% crown closure. Coniferous trees are $\geq 75\%$ of total basal area.
conif.sparse	10-25% crown closure. Coniferous trees are $\geq 75\%$ of total basal area.
brdlf.dense	> 60% crown closure. Broadleaf trees are $\geq 75\%$ of total basal area.
brdlf.open	26-60% crown closure. Broadleaf trees are $\geq 75\%$ of total basal area.
brdlf.sparse	10-25% crown closure. Broadleaf trees are $\geq 75\%$ of total basal area.
mixed.sparse	10-25% crown closure. Neither coniferous nor broadleaf trees account 75% or more of total basal area.
forest.richness	Total number of forest classes in a watershed.
forest.evenness	Simpson's evenness index calculated from the proportions of each forest class within a watershed.
<i>Forest Age – Proportion of the watershed or riparian buffer in each of the following classes</i>	
age0	No forest present
regeneration	Forest aged 1-20 years
immature	Forest aged 21-120 years
mature	Forest aged 121-240 years
oldgrowth	Forest aged > 240 years
<i>Geomorphology</i>	
stream.density	Length of rivers and streams (m) per unit area (m ²) of watershed
elev.MEAN	Average elevation (m) of the watershed
elev.STD	Standard deviation of elevations (m) within a watershed
stream.gradient	Average slope of all stream pixels within a watershed
coast distance	Straight-line distance from the centroid of the watershed to the coast (km)
XCENTROID	Geographic location of the watershed centroid in UTM zone 10 eastings (m)
YCENTROID	Geographic location of the watershed centroid in UTM zone 10 northings (m)
AREA	Watershed area (m ²)
<i>Bedrock Geology – Proportion of the watershed or riparian buffer in each of the following classes</i>	
Intrusive	
Igneous	
Metamorphic	
Sedimentary	

Table 3. Fragmentation metrics calculated over the entire watershed (at a 1 km² resolution) and within the 100-m riparian buffer (at a 1 ha resolution).

Landscape characteristic	Watershed-level metric	Riparian buffer metric
Forest cover	frarea (% by area) fprop (% by patch) fpatch (n forest patches)	fprop (% by area)
Patch size	fmarea (mean patch size, ha) fsarea (sd patch size, ha)	sfarea (sum of squared forest patch sizes, m ²) snarea (sum of squared non-forest patch sizes, m ²)
Edge	fdense (edge density, m/ha)	ffcount (number of forest/forest joins) fncount (number of forest/non-forest joins)

Table 4. Contingency table of salmon population trends (significantly increasing, no significant trend, significantly decreasing) by the presence of a major hatchery for that species in the same watershed. Counts as well as percentages (by column, in parentheses) are given.

Trend	No hatchery	Hatchery
Increasing	22 (5%)	2 (10%)
No trend	212 (52%)	17 (81%)
Decreasing	170 (43%)	2 (10%)

Table 5. Variable usage summary of all regression tree models of salmon trends in the full set of watersheds comparing the importance of variables when estimated over the entire watershed or within the riparian buffer. Variables are grouped into geomorphic, land cover, fragmentation, and bedrock geology sets. Variables that were never used in models are omitted. Variable importance is indicated by the deviance reduction (as a proportion of the initial deviance) resulting from each node at which a variable occurs and the number of nodes (n) at which a variable is used. Deviance reductions presented are averages over all models in which a variable occurs. Each variable at each scale was available for use in 12 models (specific extent and combined extent models for 6 species). The directions (dir) of the relationships between salmon trends and each variable are also given. Variable that were used inconsistently are indicated by ‘~’, but the strongest, most common direction of their effects are also given.

variable	watershed			riparian		
	Δ deviance	n	dir	Δ deviance	n	dir
elev.mean	0.3734	2	+			
coast distance	0.0845	2	+			
exposed	0.3188	2	+	0.0563	1	-
shrub				0.0691	1	-
herb	0.0772	4	+	0.0589	2	~+
wetl.shrub				0.1145	1	+
wetl.herb	0.3598	2	+	0.2680	1	+
wetl.sum				0.1822	2	+
conif.dense				0.0467	1	-
conif.open	0.0216	1	-			
brdlf.sparse				0.1763	1	-
forest.evenness	0.1281	2	-	0.1025	1	-
forest cover	0.1139	7	~+			
forest cover sd				0.1048	1	-
patch size	0.0756	2	+			
patch size sd	0.1551	2	+			
edge	0.2688	2	-	0.0833	6	~-
edge sd				0.0202	1	-
intrusive	0.2300	2	~+	0.1240	2	~+
volcanic				0.0640	2	-

Table 6. As in Table 5, but for the subset of watersheds containing forest age data. Variables are grouped into geomorphic, land cover, fragmentation, and forest age sets.

variable	watershed			riparian		
	Δ deviance	n	dir	Δ deviance	n	dir
elev.mean	0.1275	2	+			
coast distance	0.3115	2	+			
x	0.0288	2	-			
shrub				0.2096	1	-
herb	0.0767	4	+			
wetl.herb				0.0984	3	~+
wetl.sum				0.4161	2	+
conif.dense				0.0881	1	-
conif.open	0.0284	1	-			
conif.sparse				0.032	1	+
brdlf.open				0.1395	2	~-
brdlf.sparse	0.1090	5	~+			
forest.evenness	0.5192	2	-	0.1441	1	+
forest cover sd				0.0166	1	+
edge	0.2221	4	-	0.0709	2	~-
age0	0.1694	1	+	0.2020	3	+
immature	0.1155	3	~-	0.1350	1	+
mature	0.4098	1	-			
oldgrowth	0.0783	1	+	0.2008	3	-

Table 7. Variable usage summary of all regression tree models of salmon trends in the full set of watersheds comparing the importance of variables between species. Variables are grouped into geomorphic, land cover, fragmentation, and bedrock geology sets. Generally, each variable for each species was available for use in 4 models (the 2 individual extent models, plus an opportunity for each extent in the combined extent model). The exception is the geomorphic variables, which were only estimated at the watershed extent. Column definitions follow Table 5.

variable	all			chinook			chum			coho			pink			sockeye		
	Δ deviance	n	dir	Δ deviance	n	dir	Δ deviance	n	dir	Δ deviance	n	dir	Δ deviance	n	dir	Δ deviance	n	dir
elev.mean																0.3734	2	+
coast distance							0.0845	2	+									
exposed				0.3188	2	+				0.0563	1	-						
shrub	0.0691	1	-															
herb	0.0792	4	~+							0.0548	2	+						
wetl.shrub													0.1145	1	+			
wetl.herb				0.2680	1	+							0.3598	2	+			
wetl.sum	0.0179	1	+										0.3466	1	+			
conif.dense										0.0467	1	-						
conif.open	0.0216	1	-															
brdlf.sparse										0.1763	1	-						
forest.evenness				0.1025	1	-							0.1281	2	-			
forest cover	0.0255	3	~-							0.1801	4	+						
forest cover sd													0.1048	1	-			
patch size	0.0756	2	+															
patch size sd				0.1551	2	+												
edge	0.0210	1	+	0.0819	1	-	0.2223	3	-	0.0775	2	-	0.1127	1	+			
edge sd	0.0202	1	-															
intrusive													0.0568	1	-	0.2171	3	~+
volcanic				0.0678	1	-							0.0602	1	-			

Table 8. As in Table 7, but for the subset of watersheds containing forest age data. Variables are grouped into geomorphic, land cover, fragmentation, and forest age sets.

variable	all			chinook			chum			coho			pink			sockeye		
	Δ deviance	n	dir	Δ deviance	n	dir	Δ deviance	n	dir	Δ deviance	n	dir	Δ deviance	n	dir	Δ deviance	n	dir
elev.mean																0.1275	2	+
coast distance				0.3115	2	+												
x	0.0288	2	-															
shrub							0.2096	1	-									
herb	0.0471	2	+							0.1064	2	+						
wetl.herb							0.0788	1	-				0.1082	2	+			
wetl.sum													0.4161	2	+			
conif.dense							0.0881	1	-									
conif.open	0.0284	1	-															
conif.sparse	0.032	1	+															
brdlf.open				0.2116	1	-	0.0673	1	+									
brdlf.sparse							0.0884	2	+	0.1227	3	-						
forest.evenness																0.3942	3	~-
forest cover sd							0.0249	1	+									
edge	0.116	2	-				0.3283	2	-	0.0823	1	-	0.0594	1	+			
age0	0.0438	1	+							0.0884	1	+	0.1694	1	+	0.4737	1	+
immature				0.1555	1	-							0.1086	3	~+			
mature													0.4098	1	-			
oldgrowth	0.1133	1	-							0.1892	3	~-						

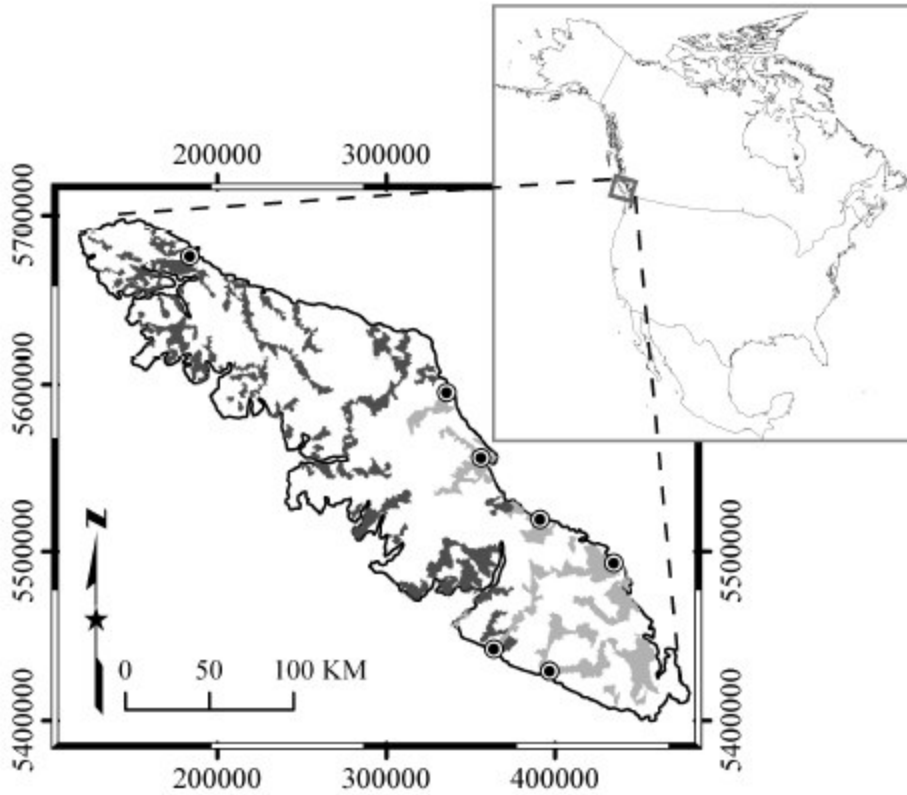


Figure 1. Locator map of Vancouver Island, British Columbia, Canada, showing the watersheds studied. Watersheds containing land cover, forest fragmentation, and forest age data are shown in dark grey. Those in light grey are not included in the forest inventory dataset, and do not have forest age data. Watersheds with major salmon hatcheries are indicated by points at their outlets. Geographical coordinates (UTM zone 10N, NAD1983) are also provided.

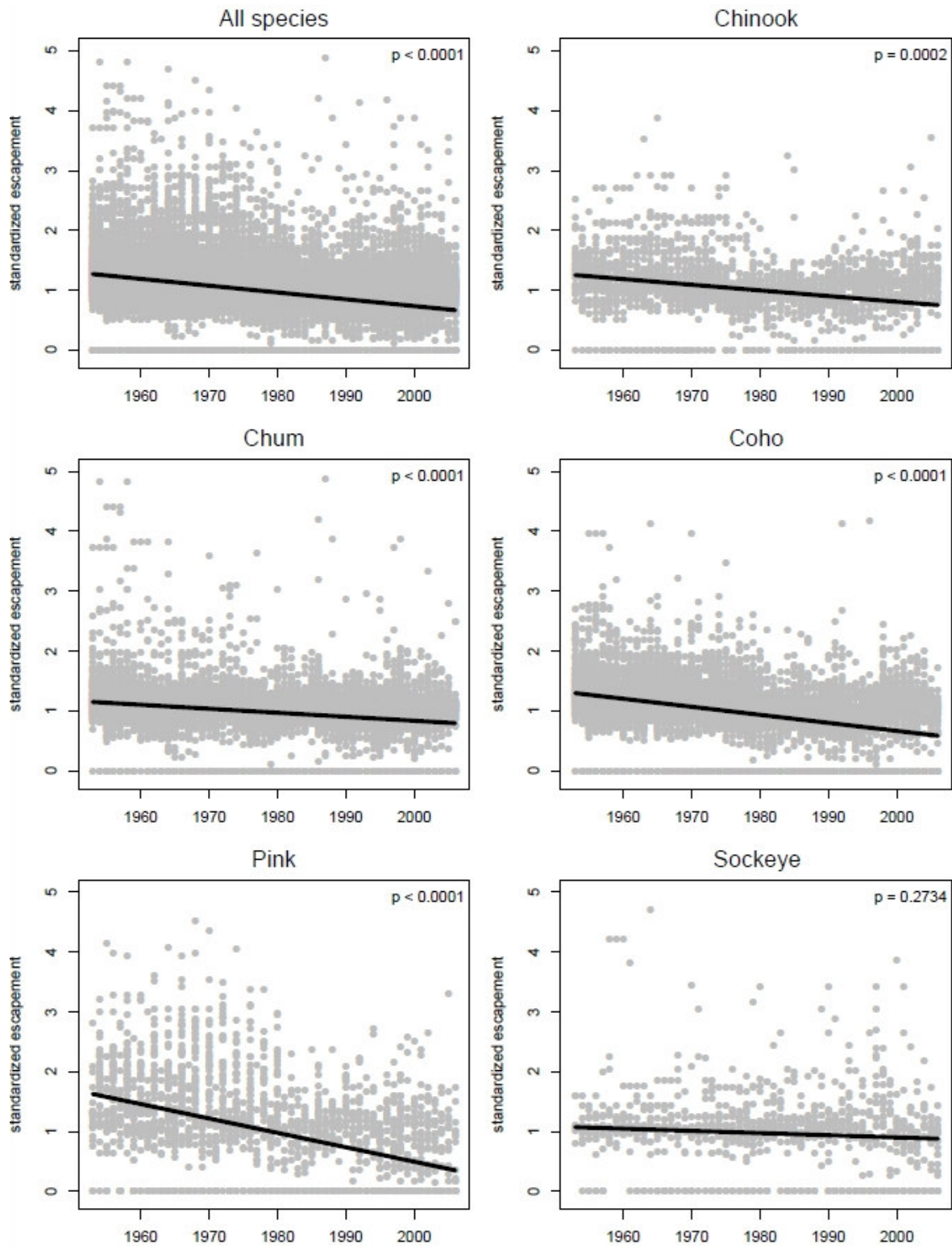


Figure 2. General trends of salmon on Vancouver Island presented both collectively and for individual species. Spawner escapement abundances have been $\ln+1$ transformed and standardized by the population mean to facilitate interpopulation comparisons.

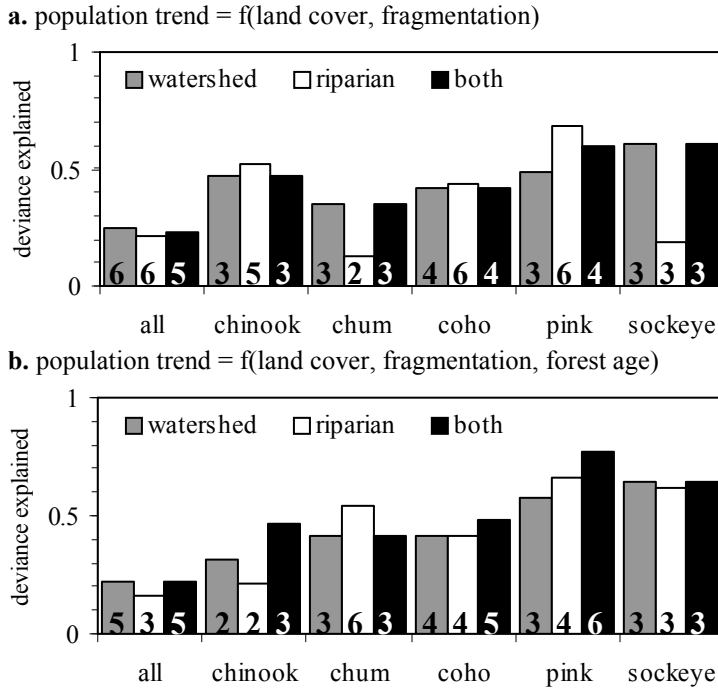
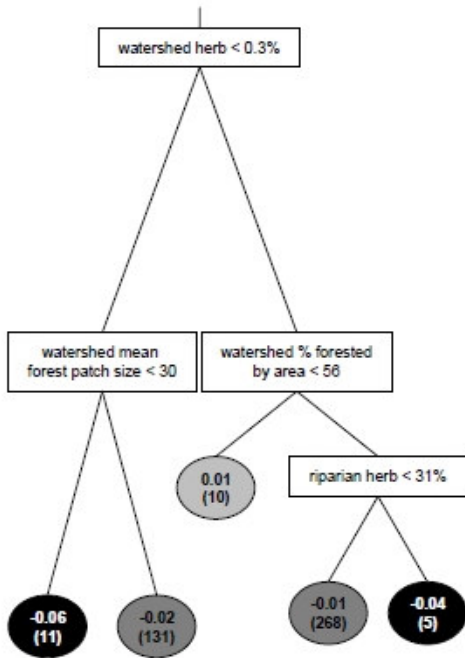
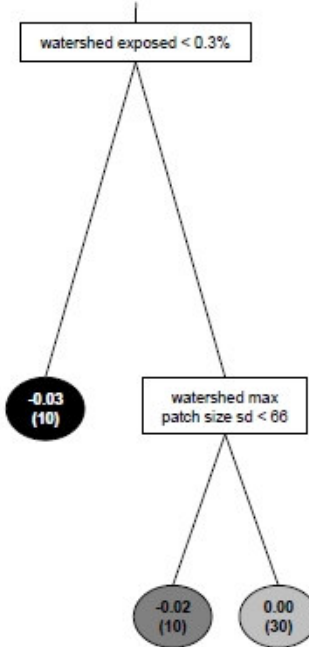


Figure 3. Proportion of salmon trend deviances explained by the regression tree models (bars) and the size (number of terminal nodes) of each regression tree (numbers at the base of the bars). Results are presented for models of watershed- and riparian-level predictors, considered both independently and simultaneously. Results shown in **a** modeled salmon trends as a function of land cover and forest fragmentation; those in **b** also include forest age among the explanatory variables.

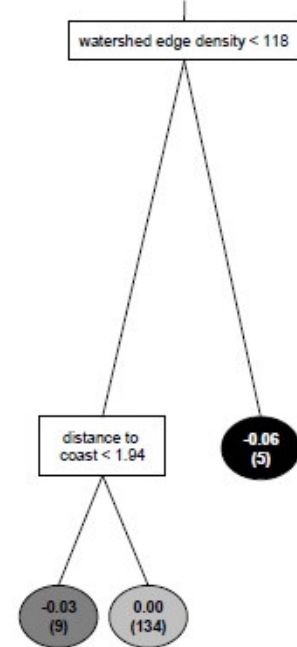
A. All salmon



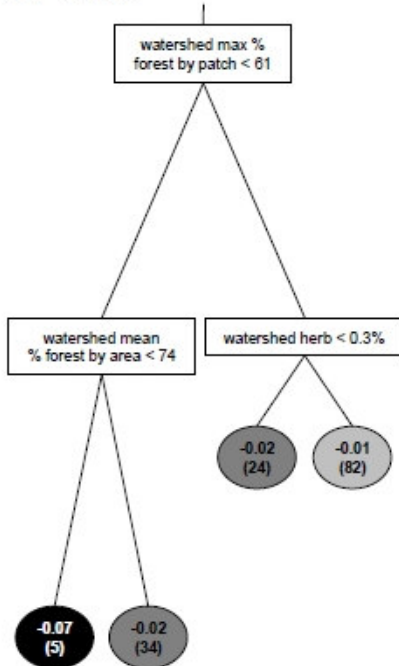
B. Chinook



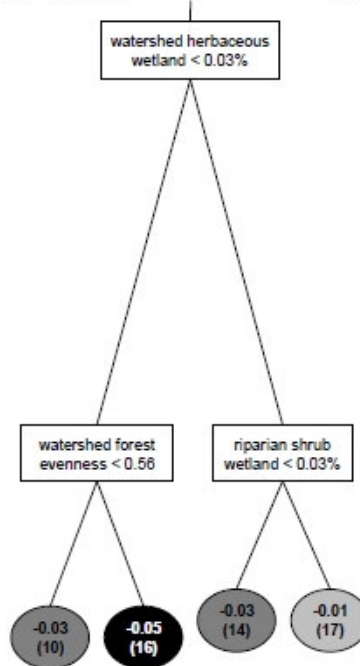
C. Chum



D. Coho



E. Pink



F. Sockeye

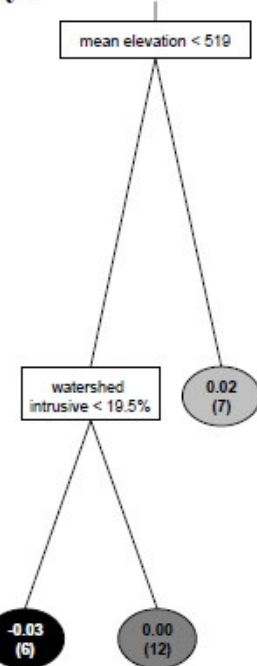


Figure 4. Regression tree models of salmon trends as a function of land cover and forest fragmentation estimated over both watershed and riparian scales. At each internal node, watersheds follow the branch to the left (right) if the decision is evaluated as true (false). The numbers at the terminal nodes (leaves) are the mean trends (the slope of standardized salmon abundance vs. time) of the populations within that node with the number of populations at each node in parentheses. Population trends are also indicated by the shading of the terminal node.

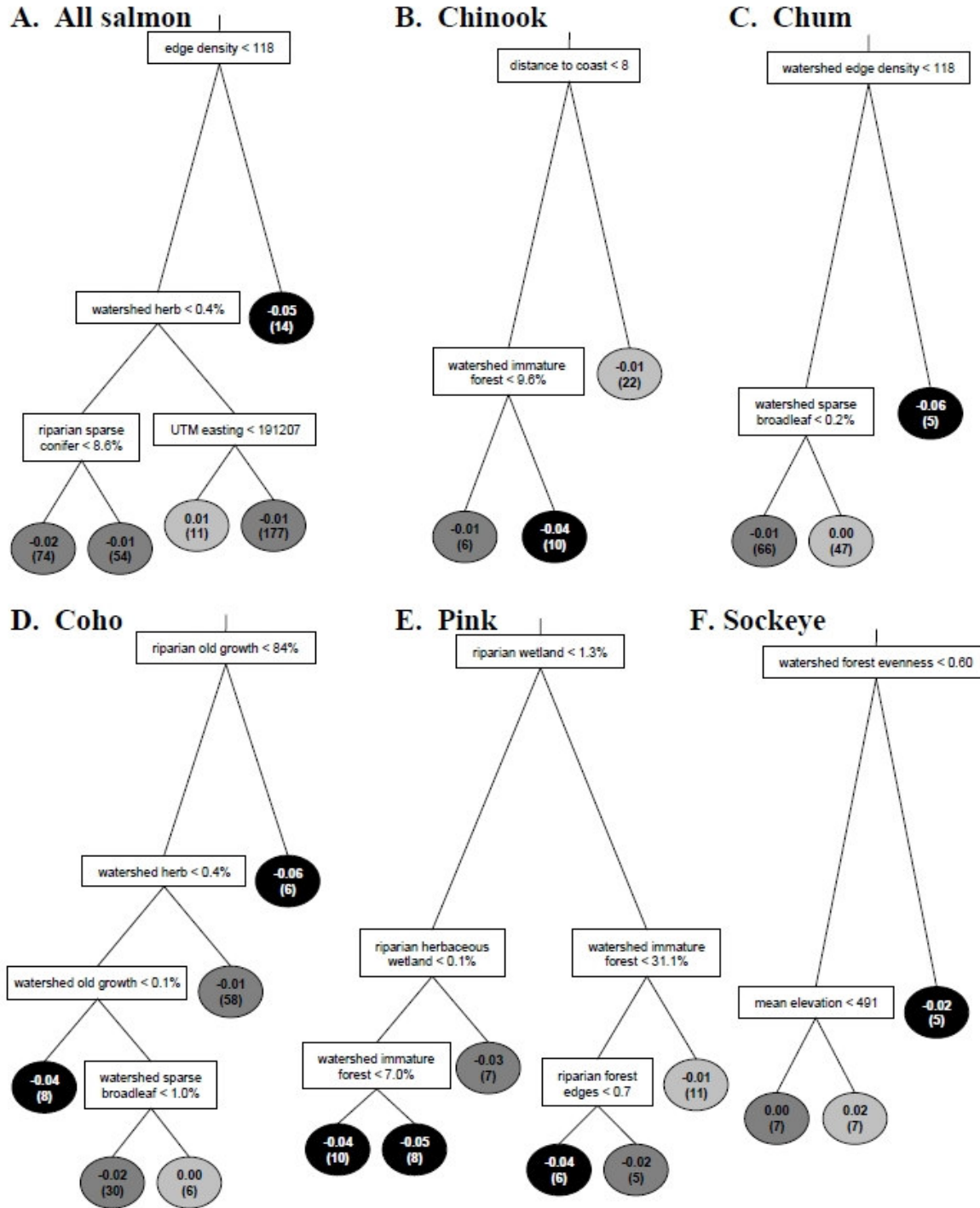


Figure 5. Regression tree models of salmon trends as a function of land cover, forest fragmentation, and forest age estimated over both watershed and riparian scales. At each internal node, watersheds follow the branch to the left (right) if the decision is evaluated as true (false). The numbers at the terminal nodes (leaves) are the mean trends (the slope of standardized salmon abundance vs. time) of the populations within that node with the number of populations at each node in parentheses. Population trends are also indicated by the shading of the terminal node.