

RECONSTRUCTION OF PACIFIC SALMON ABUNDANCE FROM RIPARIAN TREE-RING GROWTH

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Abstract. We use relationships between modern Pacific salmon (*Oncorhynchus* spp.) escapement (migrating adults counted at weirs or dams) and riparian tree-ring growth to reconstruct the abundance of stream-spawning salmon over 150–350 years. After examining nine sites, we produced reconstructions for five mid-order rivers and four salmon species over a large geographic range in the Pacific Northwest: chinook (*O. tshawytscha*) in the Umpqua River, Oregon, USA; sockeye (*O. nerka*) in Drinkwater Creek, British Columbia, Canada; pink (*O. gorbuscha*) in Sashin Creek, southeastern Alaska, USA; chum (*O. keta*) in Disappearance Creek, southeastern Alaska, USA; and pink and chum in the Kadashan River, southeastern Alaska, USA. We first derived stand-level, non-climatic growth chronologies from riparian trees using standard dendroecology methods and differencing. When the chronologies were compared to 18–55 years of adult salmon escapement we detected positive, significant correlations at five of the nine sites. Regression models relating escapement to tree-ring growth at the five sites were applied to the differenced chronologies to reconstruct salmon abundance. Each reconstruction contains unique patterns characteristic of the site and salmon species. Reconstructions were validated by comparison to local histories (e.g., construction of dams and salmon canneries) and regional fisheries data such as salmon landings and aerial surveys and the Pacific Decadal Oscillation climate index. The reconstructions capture lower-frequency cycles better than extremes and are most useful for determination and comparison of relative abundance, cycles, and the effects of interventions. Reconstructions show lower population cycle maxima in both Umpqua River chinook and Sashin Creek pink salmon in recent decades. The Drinkwater Creek reconstruction suggests that sockeye abundance since the mid-1990s has been 15–25% higher than at any time since 1850, while no long-term deviations from natural cycles are detected for salmon in the Kadashan River or in Disappearance Creek. Decadal-scale cycles in salmon abundance with periods of 25–68 years were detected in all of the reconstructions. This novel approach provides river-specific, long-term perspectives on salmon abundance and cycles. Additionally, it provides a new frame of reference for maintaining and rebuilding individual stocks and for striking a balance between societal demands and the limited, always-changing salmon resource.

Key words: dendroecology; nutrients; *Oncorhynchus*; Pacific Northwest; Pacific salmon; paleoecology; reconstruction; riparian; tree rings.

INTRODUCTION

Population dynamics of Pacific salmon (*Oncorhynchus* spp.) prior to the rise of industrial fisheries and the ubiquitous land use changes of the last century are poorly understood. This lack of historical context underlies many current salmon management and conservation challenges, including difficulties in understanding moving baselines and in determining reasonable goals for spawner abundance (escapement) and the rebuilding of stocks (Lichatowich 1997, Rosenburg et al. 2006). The unique biophysical features of

each river system and each salmon population add to the complexity of problems faced by managers. In the absence of objective, data-based perspectives, establishing goals and baselines becomes politicized, compromising the long-term welfare of salmon and the people and other animals that rely on salmon. Reconstruction of long-term patterns in individual salmon populations can considerably improve management by providing a clearer understanding of natural baselines and cycles and allowing more objective analyses of fishery declines.

Current understanding of long-term patterns in salmon abundance is based on two primary sources: climate–salmon links and paleoecology. Regional-scale salmon abundance over the last ~90 years has been linked to sea surface temperatures in the North Pacific (Mantua et al. 1997) and described by the Pacific Decadal Oscillation (PDO) climate index. Positive (warm) phases of the PDO are associated with higher ocean survival and returns of salmon in their northern

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range (central British Columbia, Canada, to Alaska, USA) and lower rates of survival and returns in the southern range where salmon forage in the California Current System (central British Columbia to California, USA). The reverse is true when polarity is negative (cool phase). Tree-ring-based reconstructions show that PDO cycles have affected climate patterns over North America for at least 400 years, but also suggest that the nature of the PDO has changed over time. For example, during the 1800s the PDO transitioned to a more energetic regime, and in the last century the time period between reversals in polarity has lengthened (Biondi et al. 2001, Gedalof and Smith 2001). Although regional salmon abundance has tracked PDO over the last 80–90 years, this period includes only two to three polarity reversals (~1.5 full cycles), making the case for cyclicity difficult to demonstrate. Additionally, historical catch records are used to approximate salmon abundance, but these are modern observations, limited to human-modified systems. It is unknown whether the PDO has always been linked to salmon abundance. Last, while the PDO may drive salmon abundance at large regional scales, it frequently does not capture the important features of smaller populations or individual stocks with distinct life history strategies and adaptations to local conditions. For example, sockeye salmon (*O. nerka*) populations within Bristol Bay show asynchronous production over time related to changing climate and hydrology of spawning and nursery habitats (Hilborn et al. 2003).

Paleolimnological reconstructions of sockeye (Finney et al. 2000, 2002) provide a second source of information about long-term salmon abundance. In lakes where salmon contributions are large enough to affect the nutrient mass balance and where flushing rates are relatively low (Holtham et al. 2004), nutrients imported by sockeye can drive primary productivity and affect N isotope composition in food webs. The nutrient contribution varies considerably over time with sockeye abundance and is reflected in sediment microfossil assemblage and $\delta^{15}\text{N}$ signals. Lake-sediment-based reconstructions show that sockeye abundance in two Alaskan lakes (Akalura and Karluk) has been lower in the last 30 years than at any time in 1000+ years (Finney et al. 2002). The reconstructions also show that modern low abundances are not unprecedented; from A.D. 0–600 sockeye abundances in both lakes were even lower than modern populations and shifted to consistently higher numbers around A.D. 800.

Lake sediment approaches work well for reconstructing some sockeye populations, but other species spawn almost exclusively in rivers, for which continuous, high-quality sediment records are rarely available. Environmental conditions on rivers can, however, be reconstructed potentially from riparian tree-ring records, offering an approach targeting stream-spawning salmon (including pink [*O. gorbuscha*], chum [*O. keta*], chinook [*O. tshawytscha*], coho [*O. kisutch*] stream-spawning

sockeye stocks, and Asian and Atlantic species). Similar limitations may also apply, i.e., the salmon nutrient contribution to riparian forests must be large enough and be retained in the system long enough to affect tree productivity. Tree rings generally offer a better temporal resolution (annual) than sediments (approximately decadal). Tree rings are easier to date accurately but are usually limited to time spans ≤ 500 years in the Pacific Northwest, while sediments can span thousands of years. Lake-sediment-based reconstructions and climate-based inference provide valuable long-term perspectives. Nevertheless, additional methods for reconstructing salmon abundance, especially in streams, are of great value and utility.

Here we present and evaluate a novel approach to reconstructing salmon abundance in individual rivers based on links between salmon and riparian tree-ring growth. We described initial evidence of this link in a pilot study (Drake et al. 2002) and expand upon those findings, incorporating data from mechanistic studies, improved reconstruction methods, and additional sites from a larger geographic area.

In general, retrospective analyses now provide broadly useful perspectives for many conservation issues. The work we present here adds to a growing diversity of approaches in reconstructing fisheries and related environmental patterns; for example, the biomass of Atlantic cod prior to industrial fisheries was estimated using historic observations in fishing logs (Rosenberg et al. 2006), nearshore ocean temperature over ~130 years was reconstructed using growth patterns in the valves of geoduck clams (*Panopea abrupta*; Strom et al. 2004), and “biochronologies” indicative of both biotic (food supply) and abiotic (temperature) factors have been reconstructed from scales and otoliths of long-lived fishes (e.g., Pereira et al. 1995). Creative new approaches such as these can provide objective estimates of past abundance and improve our collective understanding of links between environmental conditions and the abundance and natural dynamics of fishery resources now in decline.

Salmon and riparian trees

A large and still growing body of literature describes the transport of salmon carcasses and nutrients into the riparian forest by predators and scavengers and by physical processes such as floods (e.g., Cederholm et al. 1989, Ben-David et al. 1998, Hilderbrand et al. 1999). Additionally, a number of studies provide consistent evidence that salmon N is incorporated into riparian trees and other vegetation (e.g., Bilby et al. 1996, Ben-David et al. 1998, Helfield and Naiman 2001, Bartz and Naiman 2005). Here we build upon previous work and use dendroecological approaches to examine potential nutrient effects over time.

Are riparian trees affected by salmon-derived nutrients in a way fundamentally similar to lakes? Can varying annual salmon nutrient contributions (i.e.,

varying numbers of spawners) affect primary productivity (i.e., tree growth) from year to year? We first examined potential mechanistic links between salmon and tree growth in two companion studies (Drake et al. 2005, 2006). We found that NH_4^+ was the major nitrogenous product of bacterial decay, that ~50% of the total N in salmon carcasses was contributed directly to riparian soils as NH_4^+ and NO_3^- during an ~11-week decay process, that NH_4^+ and NO_3^- moved laterally through soils at least 50 cm, and that the relatively fast decay of soft tissues and slow decay of bones results in bioavailability of NH_4^+ within weeks, NO_3^- within months, and P ions and Ca^{+2} over months to years (Drake et al. 2005). We also used a $^{15}\text{NH}_4^+$ tracer to simulate decay of salmon carcasses, quantifying movements and fate of NH_4^+ in soils and trees of a riparian forest over one year. Conifer roots began to take up the $^{15}\text{NH}_4^+$ tracer almost immediately after addition in the autumn (coincident with salmon spawning), and uptake continued throughout the winter. By spring, ~37% of the tracer was found in trees and had been largely allocated to foliage and stems (Drake et al. 2006). These studies describe nutrient pathways from salmon carcass to riparian trees that could mediate a tree growth response within one year.

Tree rings and fertilization

Relatively little dendroecology research has been conducted in riparian forests. This is, in part, because tree-ring–climate relationships are most easily identified at the latitudinal and elevational limits of species ranges where trees respond strongly to precipitation and temperature limitation. For example, precipitation and temperature accounted for 75–95% of the variance in the rings of slow-growing trees on well-drained soils (Garfinkel and Brubaker 1980), and climate signals in the rings of mountain hemlock (*Tsuga mertensiana*) were stronger in trees at the upper and lower elevational limits of the species distribution than trees growing at middle elevations (Peterson and Peterson 2001). Most mature riparian trees are less likely than their upland counterparts to be limited by water availability or harsh climate conditions, and therefore nutrient effects may be more easily identified in their annual growth patterns.

Tree growth will only respond to salmon nutrients if the trees are nutrient limited. While temperature and water availability essentially determine species' distributions, nutrient availability can strongly affect forest productivity in the Pacific Northwest. Silvicultural nutrient additions are widely known to increase xylem (wood) production in Pacific Northwest forests: growth responses are observed in >80% of Douglas-fir (*Pseudotsuga menziesii*) stands fertilized with N (Gessel et al. 1969), and the rate of xylem cell (wood) formation can potentially double the year following fertilization (Brix and Mitchell 1980). Nutrient requirements of coniferous species are less than half that of hardwoods, and, unlike most hardwoods, conifers retain their foliage over many

years. These are both notable advantages in Northwest forests, where soils are relatively low in nutrients and cation exchange capacity (CEC) and nutrient (usually N) limitation of tree growth occurs widely (Cole and Gessel 1992).

Therefore, since nutrient limitation occurs widely in the Northwest, tree-ring growth responses to fertilization are well documented in forestry science, and there is mechanistic evidence linking salmon abundance and riparian tree growth, we used an empirical approach to compare salmon escapement records to non-climatic patterns in tree-ring growth. We then used the comparisons as calibration sets to reconstruct salmon abundance in specific rivers and validated the reconstructions using historical fisheries data. This approach provides new perspectives on cycles of salmon abundance over the last several hundred years and has potential utility in setting restoration goals for threatened and endangered stocks.

STUDY SITES, DATA, AND METHODS

The pilot study

Our pilot work (Drake et al. 2002) was based on tree-ring increment cores collected from two southeastern Alaska sites for an evaluation of total basal area growth (see Helfield and Naiman 2001). We used the 9–13 increment cores collected at each site to simply compare indexed growth at salmon and reference sites to salmon escapement, historical precipitation and temperature data, and the PDO index. Growth index was positively correlated with escapement (lag of one year) at both salmon sites, but at neither of the reference sites. Climate variables were not correlated with salmon abundance and, therefore, could not be responsible for a false salmon signal. Regressions relating escapement to the tree-ring growth index were used to calculate preliminary reconstructions of salmon abundance.

Site selection and characteristics

Three primary criteria were used to select additional sites for salmon abundance reconstruction: (1) the availability of 20+ years of high-quality salmon escapement records counted at weirs or dams (we use the management terms “escapement” to describe the number of salmon that escape modern fisheries or pass artificial barriers to spawn in a given system and “abundance” to describe natural, pre-industrial populations); (2) riparian trees >150 years old; and (3) availability of a nearby, ecologically comparable reference site on a reach of river inaccessible to salmon (usually upstream of a barrier to salmon passage). Nine suitable site pairs on mid-order streams were identified, including the pilot study sites (Table 1, Fig. 1). The salmon-influenced sites were selected first, usually with guidance from regional fishery biologists. We then located a nearby, visually similar reference site supporting the same tree species, on similar terrain, but upstream of barriers to salmon passage.

TABLE 1. Site pair characteristics.

| River | Reference site | Distance between salmon and reference sites | Salmon species† |
|-------------------------|---------------------------------------|---|---------------------------|
| Southern Oregon | | | |
| North Fork Umpqua River | Clearwater River tributary to Umpqua | upstream ~13 km | chinook (100%) |
| Rogue River | Rogue River | upstream ~20 km | chinook (95%), coho (5%) |
| British Columbia | | | |
| Big Qualicum River | Englishman River | ~25 km | chum (90%), chinook (10%) |
| Drinkwater Creek | Drinkwater Creek | upstream ~3 km | sockeye (89%), coho (11%) |
| Southeast Alaska | | | |
| Disappearance Creek | Unnamed tributary of Chomondley Sound | <2 km | chum (94%), pink (6%) |
| Lake Creek | Nugget Creek | ~7 km | sockeye (94%), pink (6%) |
| Sashin Creek | Sashin Creek | upstream ~3 km | pink (99%), chum (1%) |
| Kadashan River | Kadashan River | upstream ~4 km | pink (74%), chum (26%) |
| Indian River | Indian River | upstream ~5 km | pink (94%), chum (6%) |

Note: "Escapement" refers to the number of salmon counted entering the system each year. Mean escapement was calculated for species of interest (e.g., chinook only at the Rogue River). Steelhead were excluded from analyses because of generally low numbers and variable rates of survival after spawning. The abbreviation "ADFG" stands for "Alaska Department of Fish and Game."

† Data in parentheses indicate the percentage of spawning area.

Field and laboratory methods

We collected a minimum of 22 increment cores (5.1 mm diameter) from each new site using increment borers (Haglöf, Madison, Mississippi, USA). Additional cores (10–16) were collected from three of the four pilot study sites and added to pilot study materials to increase sample size to at least 22 cores (sample size was determined using a power analysis, described in *Quantitative tree ring analyses*). We targeted trees most likely to respond to salmon-derived nutrients by avoiding species distributional limits and atypical microsites. All cores were collected from dominant or subdominant trees growing within 50 m of the active channel in relatively wide floodplain reaches. Salmon sites were located within ~100 m of known salmon spawning areas; salmon remains (scattered bones and partial carcasses) were generally abundant at the salmon sites (Appendix A). Diameter at breast height (dbh; measured at ~1.4 m above the ground surface) and horizontal distance to the active channel were recorded for each tree, along with site characteristics such as tree and understory species present (Appendix A). Red alder (*Alnus rubra*) is an abundant N-fixer in Pacific Northwest forests, and its contribution of N to soils could potentially interfere with a salmon nutrient signal in tree rings. However, red alder is an early successional, shade-intolerant, short-lived (~100 years) species (Franklin and Dyrness 1988) and was absent or uncommon in the established forests (all >150 years old) of this study.

Four soil samples were collected at each site. Organic soil was removed to the A horizon using a hand shovel and shears (for cutting fiber and roots) from within a 22 cm diameter guide ring. Mineral soil was collected by driving a 4.8 cm diameter stainless steel cylinder into the A horizon to a depth of 10 cm. All soil samples were weighed fresh, passed through a 4-mm sieve in the field,

and stored at ~5°C. Organic and mineral soil samples (four of each from each site) were processed separately. Subsamples (~10 g) were dried at 100°C for at least 48 hours to determine gravimetric moisture and then combusted at 550°C for one hour to determine organic matter content. Soil pH was determined for each sample from ~10 g fresh soil mixed with 20 mL deionized water (Robertson et al. 1999). Remaining soils were composited by site for CEC determination (performed by Columbia Analytical Services, Kelso, Washington, USA) using Environmental Protection Agency methods EPA 9081 and 6010B (U.S. EPA 1983). Cations in ammonium acetate were measured via emission spectrophotometry (Jarrel Ash ICP, Grand Junction, Colorado, USA) at the University of Washington. Effective CEC (ECEC) was determined from 1 mol/L ammonium acetate soil extracts by summing the exchangeable cations (Robertson et al. 1999). The ECEC overestimates CEC because it includes ions in the soil solution and was corrected using a factor of 0.9.

Increment cores were air-dried, mounted, and sanded using standard dendroecology methods (Phipps 1985). Ring widths were measured to 0.001 mm on a Velmex measuring system (Velmex, Bloomfield, New York, USA).

Quantitative tree-ring analyses

Minimum sample size (20 trees from each site) was determined with a power analysis of the pilot study materials. We cross-dated increment cores from each site using the program COFECHA (Holmes 1983; see Appendix B for a more detailed description of software and quantitative approaches) and standardized series from each site into relative, dimensionless growth index chronologies (with an mean of 1) using the program ARSTAN (Cook 1985). As many as three series from a

TABLE 1. Extended.

| Escapement years | Escapement data source | Mean escapement | Range of escapement | Tree species used | Aspect |
|---------------------------------|--------------------------------------|-----------------|---------------------|-------------------|-----------|
| 1946–1998 | Winchester Dam | 5650 | 1503–11 694 | Douglas-fir | northwest |
| 1942–1998 | Gold Ray Dam | 27 876 | 8875–61 233 | Douglas-fir | west |
| 1966–2001 | Big Qualicum Hatchery counting fence | 123 521 | 21913–217 780 | western redcedar | northeast |
| 1969–1998 | Stamp River Ladder (DFO) | 7410 | 1797–15 461 | western hemlock | southeast |
| 1965–1967, 1968–1984 | ADFG weir counts | 31 693 | 7696–65 581 | Sitka spruce | north |
| 1971–1983, 1992–2001 | ADFG weir counts | 6194 | 2065–17 909 | Sitka spruce | southeast |
| 1934–1980, 1995–2003 | ADFG weir counts | 23 729 | 0–154 958 | Sitka spruce | northeast |
| 1969–1987 | ADFG weir counts | 161 713 | 39003–294 734 | Sitka spruce | northeast |
| 1967–1969, 1971–1980, 1982–1996 | ADFG surveys | 7685 | 381–46 200 | Sitka spruce | south |

site were discarded if they were damaged or if their correlation with other series was <0.20 . The program ARSTAN derives chronologies by removing age-related (low-frequency) growth trends from individual series and then using bi-weight robust means to convert all series into a single chronology representing growth patterns common to the site (Cook and Briffa 1990). The user defines parameters for detrending. In the interest of preserving high-to-mid-frequency variation (trends less than a century in length) and removing growth-related trends, we used a 100-year spline with a 50% frequency response. We chose to use resulting site-wide autoregressive (ARS) chronologies for the analyses and reconstructions. The AR process was intentionally retained in the series because it is likely to include multiyear effects of salmon fertilization. Additionally, regional-scale/climate-linked AR process should be removed in the differencing process. We determined the pairwise similarity of the ARS chronologies (pair intercorrelation) with COFECHA, using both 32-year and 100-year splines.

Basal-area growth describes the radial production of wood (xylem) and proved to be an important measure in a parent study (Helfield and Naiman 2001). We calculated basal-area growth of individual trees over the most recent 50 years (BA_{50}) using the equation

$$BA_{50} = (\pi \times r^2) - [\pi \times (r - RW_{50})^2] \quad (1)$$

where radius (r) = (dbh/2) – bark width and RW_{50} = the sum of ring width measurements over the last 50 years of growth. An interval of 50 years was chosen so that short series could be included in the analysis while avoiding the juvenile growth phase in calculations and so that all sites were comparable. Mean BA_{50} of each salmon site was compared to its corresponding reference site using t tests assuming unequal variance ($\alpha = 0.05$).

We used “differencing” to remove climate signals (and other potential regional-scale disturbances such as disease or storm damage) from the salmon site

chronologies. Differencing was first applied to changes in tree-ring growth attributable to air pollution (Nash et al. 1975) but has also been used to assess episodes of infestation (Swetnam et al. 1985, Swetnam and Lynch 1989, 1993). The variance of each reference site chronology was rescaled to approximate the variance of the corresponding salmon site using the ratio of standard deviations (after Swetnam et al. 1985; see Appendix B for details):

$$CRW_r = \left[\frac{SD(r)}{SD(s)} \times (RW_r - \text{mean } r) \right] + RW \quad (2)$$

$$RWd_t = RW_{s_t} - CRW_{r_t} \quad (3)$$

Rescaling variance makes the chronologies directly comparable. Non-climatic variation, i.e., differenced ring width (RWd), was then extracted from the salmon chronologies (RWs) by subtracting reference site chronology index values (RW_r). The index values were calculated first and then differenced. For presentation, we added 1 to each RWd value so that differences would, like the chronologies, vary around a mean of 1.

Comparing salmon escapement and differenced ring width

Annual RWd values were initially compared to escapement using nonparametric Spearman’s rank correlation (Spearman’s ρ ; SPSS version 14, SPSS, Chicago, Illinois, USA); when both variables change in the same direction, a concordance (0 to 1) is calculated, while negative values (0 to –1) indicate a discordance or negative relationship. We continued with analyses and reconstructions only for the systems in which the initial Spearman’s ρ was significant ($P < 0.05$).

Multiyear fertilization effects from salmon should be contained in RWd series autocorrelation. Forestry science studies show that fertilization can affect tree-ring growth for several successive years; e.g., Douglas-fir needle production is highest two to three growing seasons after silvicultural N applications (Brix 1981).

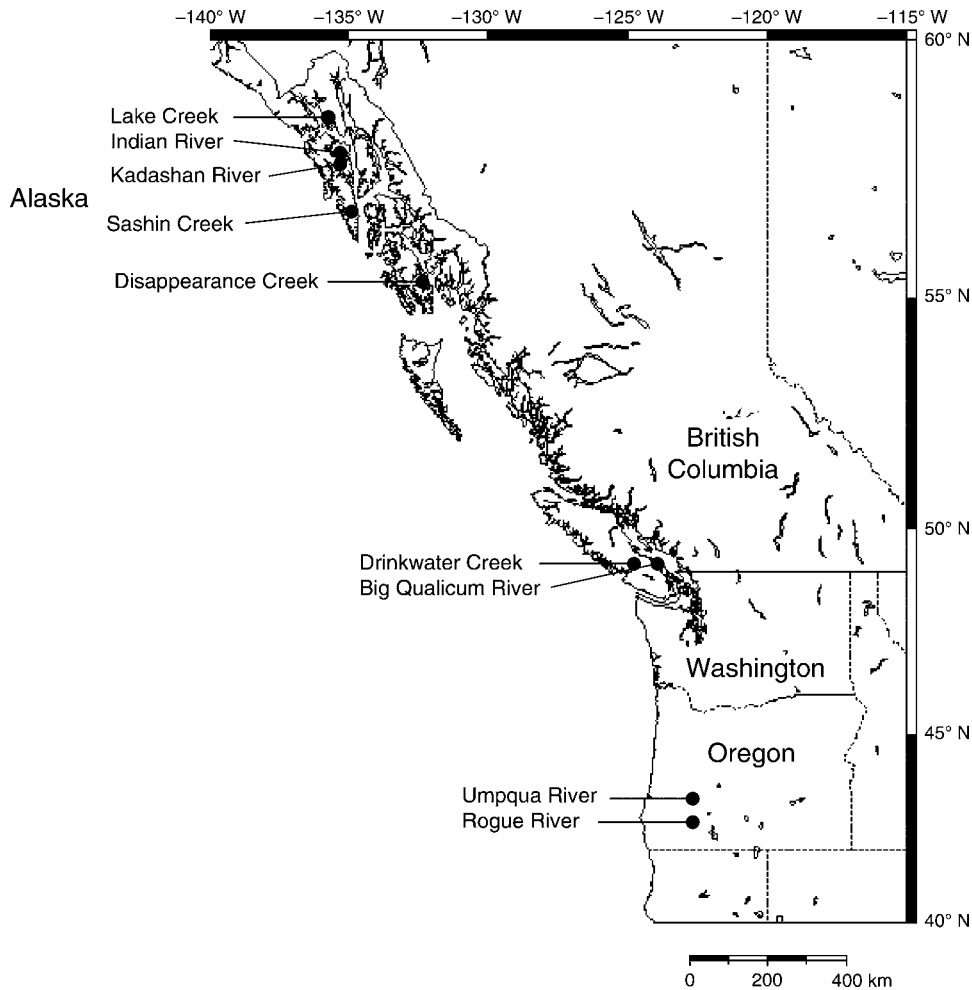


FIG. 1. Study site locations. Each site includes both a salmon site and a nearby reference site upstream of a barrier to salmon passage.

Forest fertilization guidelines developed for the Pacific Northwest (in the interest of producing wood) suggest an N application (220 kg/ha) every 5–10 years (Cole 1995; Environment Canada, data *available online*),² providing an indication of the time frame over which a pulse fertilization is expected to increase wood production. Although mechanistic evidence from the carcass decay and ¹⁵N tracer studies (Drake et al. 2005, 2006) and the pilot study (Drake et al. 2002) suggest that salmon fertilization is most likely to affect tree-ring growth the following year (a lag-1 relationship), we also examined the RWd series for evidence of longer-term fertilization effects. We calculated simple autocorrelation (AC) and partial autocorrelation (PAC) coefficients to describe autoregressive patterns and potential lagged growth effects in RWd chronologies (SPSS version 14.0).

We used expectations based on our mechanistic studies and evidence from the AC/PAC analyses to formulate potential predictors for a tree-ring growth response, and we compared these to the chronologies using exploratory Spearman's ρ correlation analyses to identify general relationships and best approaches for reconstructions. Three potential tree-ring-based predictors of salmon abundance in year t (differenced ring width [RWd], minimally smoothed, three-year moving averages [RWd_{3ma}], and summed RWd for years 2–7 [RWd_{s2-7}]) were compared to escapement ($\text{Esc}_{\text{lag}0}$, $\text{Esc}_{\text{lag}1}$, and $\ln(\text{Esc}_{\text{lag}1})$) at each site pair. Because growth responses of trees may be lagged for at least two years, we also compared RWd and RWd_{3ma} to weighted Esc_{t-1} ($\text{Esc}_{w,t-1}$), with a 30% influence of escapement from year $t-2$:

$$\text{Esc}_{w,t-1} = [\text{Esc}_{t-1} + (0.3 \times \text{Esc}_{t-2})]/1.3. \quad (4)$$

Esc_{t-1} was used alone when Esc_{t-2} was not available (at the ends of and breaks in the escapement series; Table

² (<http://www.cccma.bc.ec.gc.ca/>)

1). The 0.3 weight of year $t - 2$ was based on the results of the related ^{15}N tracer study (Drake et al. 2006). These predictors were determined a priori based on known time frames of fertilization response and our own mechanistic studies. We attempted to minimize bias by subjecting all site pairs to the same analyses and comparisons (e.g., 100-year splines were used to detrend all series).

We used additional correlation analyses to compare RWs, RWr, and RWd to climate variables (seasonal mean low temperature and precipitation from the Western Regional Climate Center) and to the PDO index (1920–1998) from Mantua (data *available online*).^{3,4} The climatic manifestations of warm phase (positive) PDO are warmer sea surface temperatures in the northeastern Pacific, resulting in decreased winter precipitation, snowpack, and stream flow at all of our study sites. Correlation analysis of the PDO index and RWd is complicated somewhat by covariation of PDO and salmon abundance. If PDO-related climate does drive tree-ring growth, we expect to see correlations between PDO and reference site (RWr) chronologies, and these can be removed by differencing. We used correlation analyses to compare climate variables (seasonal temperature, precipitation, and PDO) to tree-ring series before (RWr, RWs) and after (RWd) differencing and to evaluate the effectiveness of differencing method removing climate signals. Exploratory correlation analyses were also used to identify potential covariation between climate and escapement.

Regression model development

We hypothesize that an $\text{RWd}_{3\text{ma}}$ response curve under a full range of salmon escapement (0 to infinity) should have an S-shape (Fig. 2). The curve should approach a lower limit of 0, where growth is equal at the reference site and the salmon site, and approach an upper limit as adding more nutrients no longer increases tree-ring growth and other factors begin to limit growth. Most of our sites, however, have not experienced a full range of salmon escapement over the last 20–50 years, and observed relationships over this period are likely to be some portion of an S-shaped curve. For example, curves for rivers with small or depleted salmon populations may contain only the initial departure from the lower threshold as a shallow curve. Therefore, we tested the fit of S-shaped, exponential, inverse, linear, and logarithmic curves to RWd or $\text{RWd}_{3\text{ma}}$ vs. Esc_{t-1} , or Esc_{w-1} of each RWd chronology, and chose the best-fit curve for regression equations (Table 4) using curve-fitting software (SPSS version 14.0). We excluded years 1964–1970 from the Umpqua River curve-fitting procedure; these were noted years of very high, but uncounted, chinook returns to the Rock Creek hatchery during which it was not possible to determine how many spawners reached the site and how many left the system for the hatchery

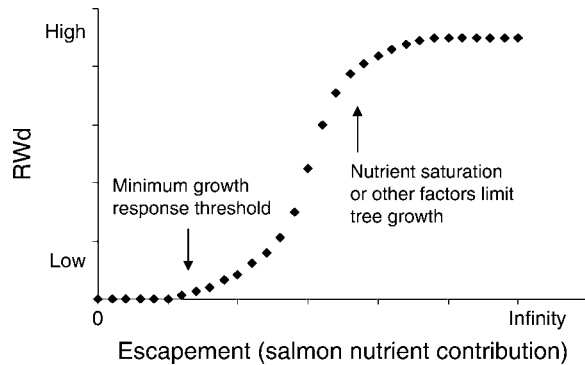


FIG. 2. Theoretical response of differenced ring width (RWd) to increasing salmon escapement in nutrient-limited riparian trees. In the absence of salmon, the difference between tree ring growth index at the reference site and the salmon site (RWd) = 0. As nutrient contributions from salmon increase, a growth response becomes apparent at a minimum threshold. The response also approaches an upper limit as adding more nutrients no longer increases tree ring growth. Each of our escapement data sets only encompasses a portion of this curve.

(Winchester Dam, *unpublished data*). High hatchery returns in later years were counted and were subtracted from the Winchester Dam counts. We also excluded the years 1971–1974 from the Sashin Creek curve-fitting procedure. A temporary weir built on Sashin Creek in 1971 flooded the salmon site during this time and resulted in very low tree-ring growth. Finally, we used spectral analysis of the RWd chronologies (SPSS version 14.0) to identify underlying periodicities in the chronologies.

Validation of the reconstructions was accomplished by comparing reconstructed salmon abundance to records of landings (Department of Fisheries and Oceans Canada), aerial surveys in Alaskan streams (Heinl et al. 2003), historically noted years of very good or very poor regional salmon catch (Pacific Fisherman 1915, 1939, National Fisherman 1972), historical PDO index (Mantua et al. 1997), reconstructed PDO index (Gedalof and Smith 2001), and known impacts to salmon escapement such as constructions of dams and salmon canneries on the rivers.

RESULTS

Chronology characteristics

The chronologies varied in length from 122 to 512 years. Raw series intercorrelation (similarity of series within any given salmon or reference site) was lowest (0.27) among the trees at the Big Qualicum River salmon site and highest (0.596) at the Nugget, Alaska, reference site (Table 2). Most intercorrelation values were close to 0.50; i.e., all trees growing at any one site shared ~25% of the mid- to high-frequency variation (calculated with a 32-year spline). Site pair chronology characteristics were comparable, with the exception of the Big Qualicum–Englishman pair. The Englishman River was the closest and best of potential reference sites but ultimately this

³ <http://www.wrcc.dri.edu/CLIMATEDATA.html>

⁴ <http://jisao.washington.edu/pdo/PDO.latest>

TABLE 2. Tree-ring chronology characteristics at each site.

| Site pair | Series (<i>n</i>) | Series length (yr) | | Series | | | Mean BA ₅₀ (cm ²) | Mean dbh (cm) |
|---------------------------|------------------------|--------------------|------|------------------|-------------|------------------|---|------------------|
| | | Maximum | Mean | intercorrelation | Sensitivity | Intercorrelation | | |
| Pair 1, Douglas-fir | | | | | | 0.451, 0.420 | | |
| Umpqua River | 25 | 673 | 236 | 0.53 | 0.187 | | 2178 ± 256 | 88 |
| Clearwater River | 20 | 439 | 163 | 0.5 | 0.16 | | 897 ± 115 | 83 |
| Pair 2, Douglas-fir | | | | | | 0.565, 0.541 | | |
| Rogue River | 22 | 175 | 120 | 0.556 | 0.189 | | 1157 ± 127 | 67 |
| Rogue River | 21 | 328 | 231 | 0.455 | 0.152 | | 1774 ± 154* | 106 |
| Pair 3, Western red cedar | | | | | | 0.194, 0.199 | | |
| Big Qualicum River | 24 | 202 | 91 | 0.271 | 0.242 | | 4854 ± 384* | 106 |
| Englishman River | 21 | 324 | 127 | 0.465 | 0.196 | | 1474 ± 109 | 69 |
| Pair 4, Western hemlock | | | | | | 0.354, 0.357 | | |
| Drinkwater Creek | 22 | 162 | 137 | 0.508 | 0.264 | | 1902 ± 176* | 75 |
| Drinkwater Creek | 20 | 238 | 200 | 0.357 | 0.273 | | 1395 ± 142 | 74 |
| Pair 5, Sitka spruce | | | | | | 0.524, 0.546 | | |
| Disappearance Creek | 19 | 292 | 212 | 0.497 | 0.205 | | 2847 ± 481 | 111 |
| Disappearance Creek | 19 | 293 | 141 | 0.381 | 0.228 | | 2107 ± 299 | 87 |
| Pair 6, Sitka spruce | | | | | | 0.669, 0.680 | | |
| Lake Creek | 23 | 225 | 128 | 0.501 | 0.172 | | 1889 ± 187* | 82 |
| Nugget Creek | 25 | 122 | 107 | 0.596 | 0.165 | | 1102 ± 99 | 59 |
| Pair 7, Sitka spruce | | | | | | 0.385, 0.312 | | |
| Sashin Creek | 25 | 512 | 280 | 0.526 | 0.195 | | 848 ± 126 | 92 |
| Sashin Creek | 21 | 354 | 138 | 0.550 | 0.224 | | 1896 ± 201* | 83 |
| Pair 8, Sitka spruce | | | | | | 0.457, 0.461 | | |
| Kadashan River | 24 | 365 | 215 | 0.527 | 0.191 | | 1532 ± 219 | 96 |
| Kadashan River | 7 | 249 | 145 | 0.341 | 0.210 | | 1202 ± 392 | 54 |
| Pair 9, Sitka spruce | | | | | | 0.666, 0.607 | | |
| Indian River | 20 | 196 | 124 | 0.427 | 0.193 | | 2404 ± 293* | 78 |
| Indian River | 19 | 323 | 162 | 0.439 | 0.185 | | 867 ± 126 | 48 |

Notes: The first site listed for each pair is the salmon site, and the second is the reference site. Two values for series intercorrelation (similarity of tree-ring chronologies between each site pair) were derived using 32- and 100-year splines, respectively. Basal area growth over the last 50 years (BA₅₀) is given as mean ± SE; asterisks (*) indicate the statistically higher of the pair ($P < 0.05$). Diameter at breast height (dbh) was measured at ~1.4 m above the ground surface. See Table 1 for site information.

was not a well-matched pair. The climate gradient between the sites was steep and soils were relatively dissimilar; e.g., Englishman River soils contained less organic matter (a ~30% difference) and had a much lower CEC (a 110 mol_c/100 g difference; Appendix A).

We identified positive, significant (Spearman's ρ $P < 0.05$) relationships between RWd and local escapement records at five of the nine sites (Umpqua, Drinkwater, Disappearance, Sashin, and Kadashan; Table 3, Appendix C). Correlations at three of the remaining sites were not significant, and at the Indian River site, the RWd vs. Esc relationship was negative. Results presented below are restricted to the six sites for which significant (positive or negative) correlations between escapement and RWd were identified.

Was the climate signal effectively removed from chronologies?

All study sites were located in relatively moist, sheltered river valleys and were not near species distribution limits, so we did not expect the chronologies to contain strong

climate signals. But site pair intercorrelation analyses suggested common, ostensibly climatic, patterns within each pair (Spearman's $\rho = 0.35$ –0.67; Table 2). Site pair intercorrelation is most easily attributable to local climate, but may also reflect disturbances such as insect infestation that can drive growth patterns at a scale of kilometers. Comparison of seasonal precipitation and mean low temperature (40–57 years of climate data) to the RWs, RWr, and RWd chronologies suggest that climate (mostly temperature-related) signals were removed by differencing at all sites except the Indian River (Appendix C). While we may not have identified the most important climatic drivers of tree-ring growth at the sites, possibly degree-days or insolation during certain critical periods, our goal was to eliminate a climate signal rather than to describe its source.

The PDO was positively correlated with temperature records at all sites, conforming to expectations for the region. The PDO was also positively correlated with escapement at four sites, although this was not necessarily expected because escapement to individual

rivers frequently doesn't reflect regional-scale salmon abundance (e.g., Hilborn et al. 2003). The PDO index was significantly correlated with RW_r at the Umpqua River, Drinkwater Creek, and the Indian River (Table 4; Appendix C), suggesting that PDO-related climate drives tree-ring growth at these sites. Douglas-fir, Sitka spruce, and western hemlock growing in low-elevation riparian forests may respond differently to climatic drivers, so the existence of both negative and positive correlations is not unexpected. RW_d (the non-climatic signal) was positively correlated with the PDO index only at the four sites where PDO and escapement were also positively correlated, suggesting that the RW_d signal is salmon-related rather than climate-related (Tables 3 and 4). At the Indian River, a strong, positive relationship between RW_r and PDO and a weaker positive relationship at the salmon site between RWs and PDO result in a RW_d chronology that is negatively correlated with salmon escapement. We conclude that this is an artifact of strong PDO–RW_r (climate-based) relationship rather than a salmon fertilization signal and excluded the Indian River from further analyses. We also conclude that differencing effectively removed climate variability from RW_d chronologies at the remaining sites, leaving non-climatic growth patterns that contain a salmon abundance signal, if it exists.

Exploratory analyses linking salmon escapement and tree-ring growth

Statistical comparisons indicate a relationship between RW_d and escapement records that is strong enough to warrant salmon abundance reconstruction at five of the nine sites (Table 3, Fig. 3). Salmon escapement was reflected most strongly in tree-ring growth in the year following escapement (a lag-1 relationship) in all systems except Drinkwater Creek, where the lag-0 correlation was approximately equal to the lag-1 correlation ($\rho = 0.520$ and $\rho = 0.450$, respectively; Appendix C). Positive relationships between one-year lagged escapement and RW_d were improved by using a three-year moving average (RW_d_{3ma}; Appendix B) at all sites except Drinkwater Creek, where unsmoothed RW_d was most closely correlated with escapement (Appendix C).

Positive autocorrelation (AC) persisted from two to six years in the RW_d chronologies, and partial autocorrelation (PAC) values suggest that autoregressive model orders (AC controlled for previous years) are 1–2 years in each chronology (Appendix D). In other words, salmon escapements are positively correlated with RW_d for up to six years, but within each chronology, 1-year lagged effects are not independent from 2–6-year lagged effects.

Derivation of equations relating RW_d to escapement

The relationship between Umpqua River chinook and RW_d_{3ma} was best described by the nearly straight portion of an exponential curve. Relative to the other

sites, Umpqua River escapement is low, and the range of escapement is small (Table 1), with a more-or-less straight-line relationship over this range of observations. However, if the variation in annual escapement was higher, upper and lower limits might become apparent. Both RWs and RW_r are positively correlated with the PDO at the Umpqua River, but removal of the climate signal (differencing) results in an RW_d chronology that is neutral with respect to the PDO. Differenced ring width is positively correlated with escapement over the last ~50 years and is not correlated with the PDO during this period.

Drinkwater Creek RW_d chronologies were compared to sockeye escapement counted at the downstream Stamp River fish ladder. Sockeye in Drinkwater Creek proper were counted in 1990 and 2000 in snorkel surveys and accounted for ~5% of the Stamp River sockeye migration in those years. We assume that escapement to Drinkwater Creek reflects overall Stamp River escapement from 1953 to 1998 and use Stamp River escapement as a proxy for Drinkwater Creek. Historical salmon abundance in the Stamp River is more variable than the Umpqua River, but escapement to Drinkwater Creek is still relatively low (Table 1). The Drinkwater Creek relationship was best described by an exponential curve, showing a lower response limit (asymptote approaching zero), but no upper limit. The Drinkwater Creek salmon and reference sites are well-matched: both are pure, even-aged stands of western hemlock growing in wet streamside areas at the base of steep slopes, interspersed with pools of standing water and skunk cabbage (*Lysichiton americanum*). Reference site ring width index (RW_r) is negatively correlated with the PDO index ($\rho = -0.591$, $P < 0.01$) and neutral with respect to escapement. Salmon site ring width index (RWs) is neutral in respect to the PDO and positively correlated with escapement ($\rho = 0.354$, $P = 0.05$; Table 3). Salmon site ring width index (RWs) is theoretically affected by the same PDO climate-based forcing as RW_r, but the signal is muted by a salmon fertilization pattern of the opposite sign (the PDO and escapement are strongly, positively correlated; $\rho = 0.708$, $P < 0.01$). Removal of the climate signal (calculation of RW_d) strengthens the positive relationship between RW_d and escapement ($\rho = 0.551$, $P < 0.01$; curve fit $r^2 = 0.425$).

The three Alaskan streams examined here currently support much larger populations of salmon than the Umpqua River and Drinkwater Creek (Table 1). At Disappearance Creek (a small but extremely productive chum salmon system) the curve has an inverse shape (Table 3), suggesting that salmon nutrient fertilization approaches a maximum or saturation point in years of high escapement. This is reasonable for a small river supporting a large, dense salmon run. Sashin Creek is dominated by pink salmon (~99%) and a strong biannual pattern is seen in much of the weir count record (1934–2003 with a few interruptions), reflecting the two-year life cycle of this species. Weighting the

TABLE 3. Correlation of escapement (number of salmon counted entering the system each year) in each system with the salmon, reference, and differenced index chronologies lagged by one year (RWs, RWr, and RWd, respectively), a longer-term growth effect (summed growth for years 2–7; RWd_{s2-7}), the Pacific Decadal Oscillation Index (PDO), and a suite of climate variables.

| Site | RWs | | | RWr | | | RWd | | |
|---------------------------|-------------|-------------------|----------|-------------|-------------------|----------|-------------|-------------------|----------|
| | Correlation | Spearman's ρ | <i>P</i> | Correlation | Spearman's ρ | <i>P</i> | Correlation | Spearman's ρ | <i>P</i> |
| Umpqua River | 0 | | | 0 | | | + | 0.451 | <0.01 |
| Drinkwater Creek | + | 0.354 | <0.05 | 0 | | | + | 0.551 | <0.01 |
| Disappearance Creek | 0 | | | – | –0.595 | <0.01 | + | 0.708 | <0.01 |
| Sashin Creek | + | 0.481 | <0.01 | 0 | | | + | 0.481 | <0.01 |
| Kadashan River | 0 | | | 0 | | | + | 0.529 | <0.02 |
| Indian River [‡] | + | 0.295 | 0.05 | + | 0.643 | <0.01 | – | –0.375 | <0.05 |

Notes: Appendix C contains full correlation matrices. See Table 1 for site information.

[†] Negative correlation suggests that escapement is lower in years when spring (average monthly low) temperatures (temps) are higher.

[‡] Escapement estimated using regional (southeastern Alaska) pink and chum salmon catch.

[§] Autumn precipitation.

escapements (Eq. 4) smoothed the biannual pattern, after which an exponential curve provided the best fit for Sashin Creek. The Kadashan River escapement–RWd relationship was best described by an S-shaped curve, suggesting both a lower response limit and an upper saturation point.

We compared residuals from the regressions to summed RWd (lagged by 2–6 years, as indicated by AC analyses; Table 4), but the addition of a second term did not improve estimation of escapement at any site. The best-fit equations (Table 5) were applied to RWd chronologies to produce reconstructions (Fig. 4).

Tree growth over the last 50 years, as measured by mean BA₅₀, varied by approximately fivefold among all sites; the lowest value, surprisingly, was 848 cm²/yr at the Sashin Creek salmon site. The highest BA₅₀ was 4854 cm²/yr at the Big Qualicum River salmon site (Table 2). Mean BA₅₀ was significantly greater at the salmon sites in five of the nine pairs, significantly greater at the reference site in two pairs, and statistically equal at two pairs.

Soil characteristics

Descriptive soil analyses show a wide range of soil conditions (Appendix A) but no consistent pattern is attributable to the presence or absence of salmon. Cation exchange capacity, a measure of soils capacity to hold nutrients, varied considerably, but was generally

lower at the southern sites (i.e., those in Oregon; Appendix A). The lowest CEC was 11.6 mol_c/100 g at the southernmost reference site (the Clearwater River, Oregon), while the highest CEC was 447.8 mol_c/100 g at the Drinkwater Creek, British Columbia, salmon site.

Higher CEC at the northern sites is largely attributable to higher soil organic matter (OM) content, a result of cooler summer conditions that slow soil OM decay.

Validation of the reconstructions

It is instructive to compare site-specific histories and several regional-scale benchmark years in Pacific salmon fisheries to the reconstructions. The PDO is linked to several notable extremes in regional Pacific salmon fisheries; 1915 was an excellent year for Oregon and Washington salmon fisheries and a poor year in Alaska (Pacific Fisherman 1915). The reverse occurred in 1939, with a poor salmon fishery in Washington and Oregon and record high catch in Alaska (Pacific Fisherman 1939). A poor salmon catch marked 1972 in southeastern Alaska, and the largest run of spring chinook on record in the southern region occurred in that same year (National Fisherman 1972). We also compare our reconstructions to historic PDO reversals in 1947, 1977 (Mantua et al. 1997), and 1998 and PDO reversals reconstructed by Gedalof and Smith (2001) in 1662 (–), 1680 (+), 1696 (–), 1712 (+), 1734 (–), 1758 (+), 1798 (–), 1816 (+), 1840 (–), and 1923 (+).

TABLE 4. Spearman's correlations comparing the Pacific Decadal Oscillation Index (PDO) to the unmodified salmon, reference, and differenced growth indices (RWs, RWr, and RWd, respectively), and climate variables.

| Site | RWs | | | RWr | | |
|---------------------|-------------|-------------------|----------|-------------|-------------------|----------|
| | Correlation | Spearman's ρ | <i>P</i> | Correlation | Spearman's ρ | <i>P</i> |
| Umpqua River | + | 0.46 | <0.01 | + | 0.39 | <0.01 |
| Drinkwater Creek | 0 | | | – | –0.35 | 0.05 |
| Disappearance Creek | 0 | | | 0 | | |
| Sashin Creek | + | 0.28 | <0.02 | 0 | | |
| Kadashan River | + | 0.41 | <0.01 | 0 | | |
| Indian River | + | 0.23 | <0.05 | – | –0.59 | <0.01 |

Notes: Appendix C contains full correlation matrices, including specific seasonal and annual correlations between climate variables (temp, temperature; precip, precipitation) and PDO. See Table 1 for site information.

TABLE 3. Extended.

| RWd _{s2-7} | | | PDO | | | Temp/precip | | |
|---------------------|-------------------|----------|-------------|-------------------|----------|-------------|-------------------|----------|
| Correlation | Spearman's ρ | <i>P</i> | Correlation | Spearman's ρ | <i>P</i> | Correlation | Spearman's ρ | <i>P</i> |
| + | 0.494 | <0.01 | 0 | | | - | spring low temps† | <0.05 |
| + | 0.466 | <0.02 | + | 0.708 | <0.01 | 0 | | |
| 0 | | | 0 | | | 0 | | |
| 0 | | | + | 0.403 | <0.01 | 0 | | |
| 0 | | | + | 0.505 | <0.03 | 0 | | |
| + | 0.498 | <0.01 | + | 0.500 | <0.01 | + | temps and precip§ | <0.05 |

Umpqua River, southern Oregon.—Reconstructed Umpqua River salmon abundance varies considerably over time and appears to be cyclic from 1750 until an interruption in the late 1800s coinciding with the construction of (1) a salmon cannery on the Umpqua River in 1878 (Lichatowich 1999) and (2) the Winchester Dam in 1890 (Fig. 4A). Cannery activities peaked in 1911, after which declining catch led to closure by ca. 1920. The dam was a “definite barrier” to salmon passage at low flows, but higher flows allowed some passage through a modified spillway/fish ladder (FCO and OSGC 1946). The period of interruption lasted until at least 1920, when cycles resembling the earlier portions of the reconstruction appear, but they are of smaller (~50%) amplitude. Reconstructed escapement maxima prior to 1890 were substantially higher than in more recent times; two of the early maxima (in years 1815 and 1765) are beyond the upper limit of our calibration set.

The benchmark years compare well to the reconstruction; 1915, although within the period of interruption, corresponds to a peak in reconstructed Umpqua chinook abundance. Likewise, 1939 corresponds to a relatively low point in the reconstruction. The largest run of chinook on record in the southern salmon range was seen in 1972, and this corresponds to a peak in the reconstruction and with Winchester Dam counts.

The reconstruction shows a general downward trend in chinook abundance from 1942 to 1964. Declining salmon returns in the Umpqua River during the 1940s and 1950s are attributed to increased summer water temperatures and winter flooding and the consequences of extensive logging in the watershed (Johnson et al.

1994). The fish ladder was improved in the early 1980s (Johnson et al. 1994). The hatchery started producing salmon in 1925, with limited success, and was closed from 1975 to 1979.

Patterns in both escapement records and the reconstruction are consistent with expectations for the region based on historic and reconstructed PDO index. Positive-phase PDO from 1977 to 1998 corresponds to a sustained decline in both historic escapement and reconstructed salmon abundance, and the 1998 reversal marks the first of several years of increasing chinook abundance. Positive-phase PDO is also associated with two of three long-term declines (1765–1795 and 1815–1839), although the reconstructed PDO index and salmon abundance from 1750 to 2002 are not statistically correlated. A third decline in reconstructed salmon abundance occurs from 1858 to 1877, a period of relative neutrality in PDO oscillations (Gedalof and Smith 2001). The PDO phase reversals in 1923 and 1946 occur during the interruption (by the dam and cannery) and are not associated with particular features of the reconstruction.

Reconstructed chinook abundance prior to 1905 shows clear maxima at ca. 1765, ca. 1815, ca. 1858, and possibly ca. 1785. Minima are seen at ca. 1772, 1795, 1838, and 1877 (Fig. 4A). Spectral analysis suggests that the time series contains two low-frequency periodic components at 40 and 15 years (Appendix E). The 40-year cycle is a visually dominant feature in the reconstruction, while the 15-year cycle is less obvious (Fig. 4). Reconstructed PDO cycles have an average period of ~23 years, with longer (30–70 years) periods common prior to 1850 (Gedalof and Smith 2001). Spectral analysis also suggests periodicity at 4–5 years, possibly reflecting the four-year life cycle of chinook salmon; a four-year period is also evident in the escapement data (not shown).

Salmon may not be the only mediators of a tree fertilization response. Annual lamprey (*Lampetra* sp.) counts at Winchester Dam have declined from ~477 000 in 1966 to <50 in recent years. Lamprey, like salmon, are anadromous and die after spawning (Moyle 1976) and represent a substantial upstream movement of nutrients. Lamprey have failed to inspire the type of intense research currently lavished on salmon, but they

TABLE 4. Extended.

| RWd | | | Climate | |
|-------------|-------------------|----------|-------------|-------------|
| Correlation | Spearman's ρ | <i>P</i> | Correlation | Variable |
| 0 | | | + | temp/precip |
| + | 0.36 | 0.05 | + | temp/precip |
| 0 | | | + | temp |
| + | 0.21 | 0.06 | + | temp |
| + | 0.27 | <0.02 | + | temp |
| + | 0.51 | <0.01 | + | temp |

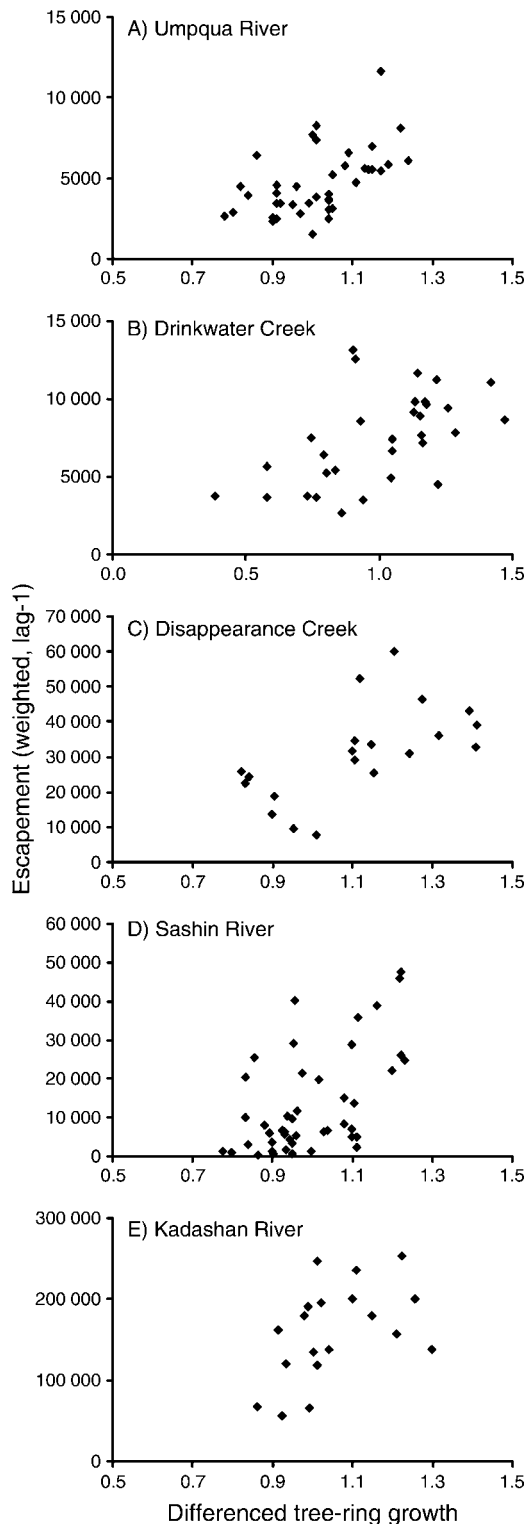


FIG. 3. Plots of differenced tree-ring growth (RWd_{3ma} varying around mean = 1) vs. escapement (weighted, lag-1; see Eq. 2) at the five sites where a positive relationship between tree-ring growth and salmon escapement was detected. Note that the x-axis scale varies among panels.

may have contributed to the dramatic cycles seen in the Umpqua River reconstruction.

Drinkwater Creek, Central Vancouver Island, British Columbia.—The Drinkwater Creek reconstruction shows relatively stable sockeye abundance in the system from 1850 to 1939, a slight increase from 1940 to ca. 1955, followed by a marked decrease, reaching a minimum in 1972, and then increasing abundance until the present (Fig. 4B). Trends after 1969 follow Stamp River escapement closely and follow southern British Columbia sockeye landings records (1952–2002) somewhat less closely (see footnote 5). The reconstruction suggests that escapement to Drinkwater Creek since the early 1990s has been, on average, 15–20% higher than at any time since 1850.

A flow regulation dam was built at the outlet of Great Central Lake (of which Drinkwater Creek is a tributary) in 1956; this partially blocked salmon passage despite addition of a fishway in 1957 and is a likely contributor to the apparent decline in sockeye abundance beginning in the late 1950s. The Canadian Department of Fisheries and Oceans (DFO) began to take a more proactive role in improving salmon passage and production in the greater Barkley Sound system at this time. Habitat protection and fishing gear and area restrictions were implemented, fishways and hatcheries were built, and Great Central Lake was fertilized from 1970 to 1973 and from 1977 to 1998 (Hyatt 1999). The stability of reconstructed sockeye abundance prior to 1940, however, suggests that both the decline in the 1950s and the increase since 1972 are anthropogenic in nature.

The Drinkwater Creek reconstruction is difficult to compare to the fisheries' benchmark years. Located in southern British Columbia (Fig. 1), it is geographically central to the northern and southern Pacific salmon populations that vary with PDO. Reconstructed escapement shows a small abundance peak in 1915 and a negative spike in 1940, in mild agreement with the Washington and Oregon extremes. But more recent, longer-term trends (a minimum in 1972 followed by increases until the mid-1990s) more closely resemble the northern cycle.

Sockeye landings from 1952 to 1968 in southern British Columbia (prior to Stamp River record keeping) suggest that sockeye populations were depressed in the area during this time, but our reconstruction shows relatively high abundance during these years. Within this period, regional catch was highest in 1958 (~21 000 Mg) and was lowest in 1963 (~3400 Mg); the reconstruction corroborates this with high abundance in 1958 (and the period maximum in 1959) and low abundance in 1963 (minimum in 1965).

Although the reconstruction does not contain visually obvious cycles, spectral analysis suggests a distinct underlying periodicity of 33 years (Appendix E) and less distinct periodicities of perhaps 5–6 years and 2 years.

TABLE 5. Regression equations used for the reconstructions (see *Study sites, data, and methods: Comparing salmon escapement and differenced ring width* for explanations of variables).

| Site | Curve shape | Equation | r^2 | P | Second term |
|---------------------|-------------|--|-------|-------|----------------|
| Umpqua River | exponential | $Escw_{t-1} = 603.1 \times (e^{1.957} \times RWd_{3ma})$ | 0.372 | 0.000 | RWd_{lag2-6} |
| Drinkwater Creek | exponential | $Escw_{t-1} = 1569 \times (e^{1.463} \times RWd)$ | 0.425 | 0.000 | RWd_{lag2-4} |
| Disappearance Creek | inverse | $Escw_{t-1} = 76\,362 + (-49\,026/RWd_{3ma})$ | 0.379 | 0.004 | RWd_{lag2-3} |
| Sashin Creek | exponential | $Escw_{t-1} = 10^{-1.714+(RWd_{3ma} \times 4.777)}$ | 0.359 | 0.000 | RWd_{lag2} |
| Kadashan River | S-shaped | $Escw_{t-1} = e^{14.01+(-2.192/RWd_{3ma})}$ | 0.301 | 0.015 | RWd_{lag2-3} |

The relationship between salmon and tree rings at Drinkwater Creek is unusual in that salmon nutrients are correlated with tree-ring growth within one growing season. Sockeye may spawn earlier in the growing season in Drinkwater Creek than chinook, pink, and chum at the other sites. Alternatively, the growing season for western hemlock on Vancouver Island may extend later in the year than Douglas-fir in southern Oregon and Sitka spruce in Alaska; cambial growing seasons are highly variable and can only be determined precisely by site-specific studies.

Disappearance Creek, southeastern Alaska.—Disappearance Creek is probably the most natural of the nine study sites. Little old-growth forest remains on Prince of Wales Island but a remnant is preserved in the Disappearance Creek drainage, perhaps because it supports a chum stock locally famous for large adult sizes and because many hatcheries have used the Disappearance Creek chum for broodstock (P. Doherty, *personal communication*). The height of human encroachment occurred in 1966–1984, when the Alaska Department of Fish and Game operated a weir on the river to count annual chum returns. Escapement varied from ~1800 to 15 500 during the 18 years of weir counts (Table 1).

Weir counts in Disappearance Creek (years 1966–1984) do not closely follow regional trends. Differenced ring width, however, is strongly correlated with salmon escapement from 1966 to 1984. Minima in the reconstruction (Fig. 4C) occurred in 1754, 1772, 1796, 1847, 1912, 1960, and 1989 and contain an underlying periodicity of 25–33 years (Appendix E). Contrary to expectations, positive phases of the PDO are weakly associated with long-term declines in reconstructions. Many other points in the reconstruction also oppose expectations, including several within the period of record. For example, although escapement in the benchmark year 1972, a disastrous year for southeastern Alaskan fisheries, was also the year of lowest escapement in Disappearance Creek (<8000 fish), the system diverged strongly from regional patterns in the following years, with the highest recorded escapements of 52 000 fish in 1973 and 60 000 fish in 1974. The 1970s were generally poor for Alaskan salmon fisheries but began to increase in 1977 with a PDO reversal. Nevertheless, both Disappearance Creek escapement records and the reconstruction contradict expectations based on the

PDO; maximum escapement in 1974 was followed by decreasing escapement until 1985.

The period of high pink and chum salmon landings in southeastern Alaska, 1931–1939 (data from Mantua et al. 1997), corresponds to a period of nearly average abundance in the reconstruction. The reconstruction also shows average abundance in the regionally poor benchmark year 1915. Aerial surveys are rough estimates of annual abundance made from fixed-wing aircraft on one day per year by the Alaska Department of Fish and Game (ADFG; Heintz et al. 2003). They were conducted at Disappearance Creek from 1985 to 2002 and show that 1998 and 1999 were years of relatively high escapement, corresponding with a peak (with a maximum value in 2000) in the reconstruction.

Sashin Creek, southeastern Alaska.—Reconstructed Sashin Creek pink-salmon abundance is visually quite different from the other reconstructions, with a low baseline interspersed with periodic, high-amplitude peaks in abundance (Fig. 4D). This pattern is also an essential feature of the weir counts; e.g., 1934–1939 escapement averaged ~8000 per year, 1940–1949 escapement averaged ~57 000, and 1950–1958 escapement averaged only ~2000 per year. Sashin Creek escapement was more variable than any other site, ranging from 0 to ~155 000. The relationship between escapement and RWd was described by an exponential curve; no upper limit of a fertilization effect was detected. The reconstruction follows weir counts reasonably well, with the exception of 1977–1980, during which high escapement was counted at the weir but only a very small peak was reconstructed (RWd during this time was low).

Major maxima (>70 000 spawners) in the reconstruction occurred in 2003, 1942, 1908, 1858, 1826, in a cluster at the turn of the 19th century (1813, 1801, 1790, 1780), 1753, 1745, 1706, 1685, and 1657, and these maxima were interspersed with many smaller peaks. Spectral analysis suggests at least three distinct periodicities in the reconstruction at 68, 21, and 2.1 years (Appendix E). Pacific Decadal Oscillation reversals (1758, 1798, 1816, 1946, 1977, 1998) are all associated with peaks in reconstructed abundance, but the peaks in the reconstruction are so close together that a relationship with PDO is not visibly apparent. The 2.1-year periodicity in the reconstruction may reflect the 2-year pink-salmon life cycle. The benchmark 1915 salmon

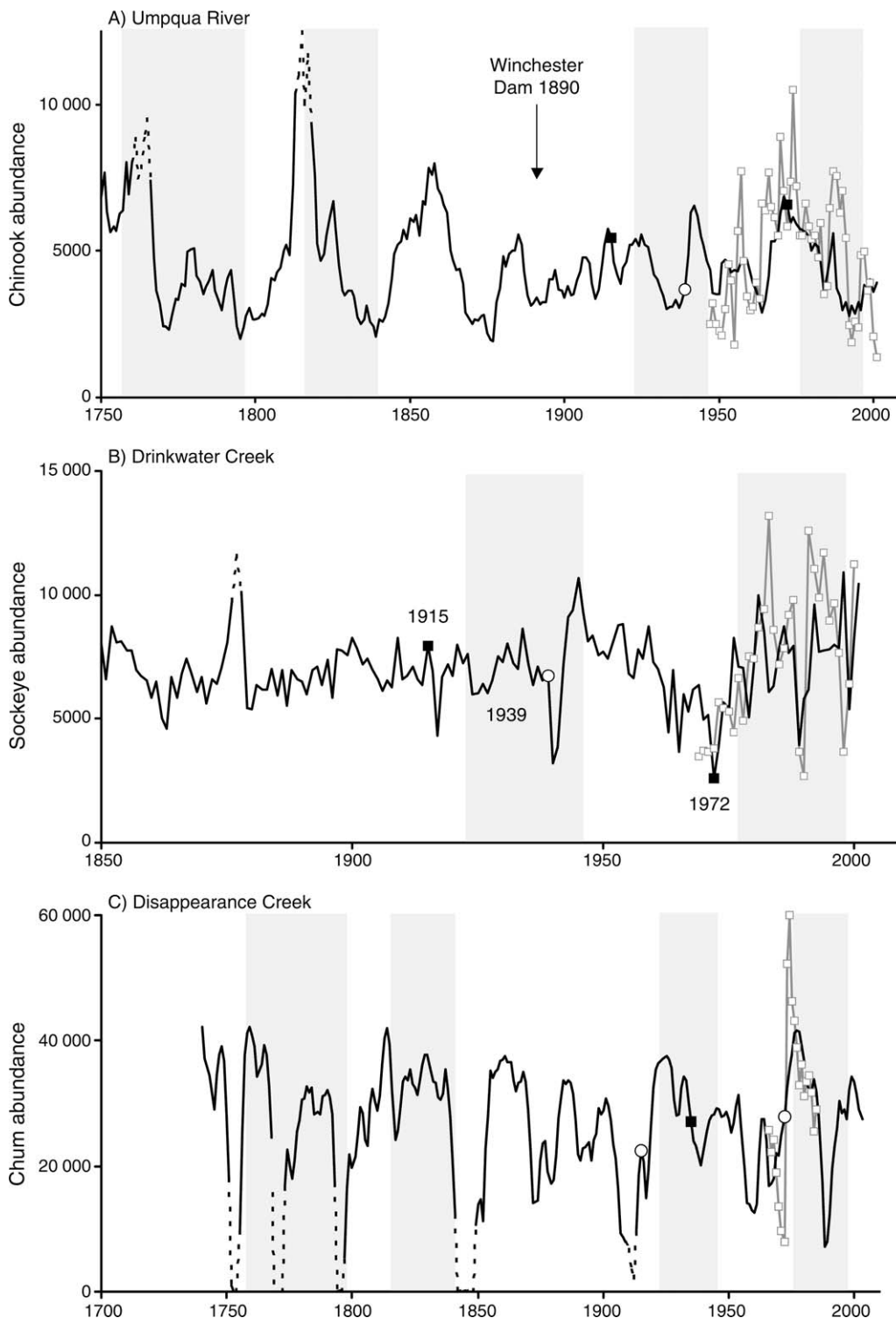


FIG. 4. Reconstructed salmon abundance (solid line), including extrapolated values outside of the calibration range (dashed line), and weighted escapement (gray line with open squares). The (A) Umpqua River, in Oregon, lies within the southern Pacific salmon range, (B) Drinkwater Creek is central, and all Alaskan sites, (C) Disappearance Creek, (D) Sashin Creek, and (E) Kadashan River, lie within the northern salmon range. Benchmark years, or historic “boom” (solid square) and “bust” (open circle) years in regional salmon fisheries are marked. The year of 1915 was one of very high salmon catch/abundance in Washington and Oregon and very low catch/abundance in southeastern Alaska. The year of 1939 was the reverse, generally poor catch in Washington and Oregon (Pacific Fisherman 1939), while 1933–1935 were peak years for pink and chum catch/abundance in

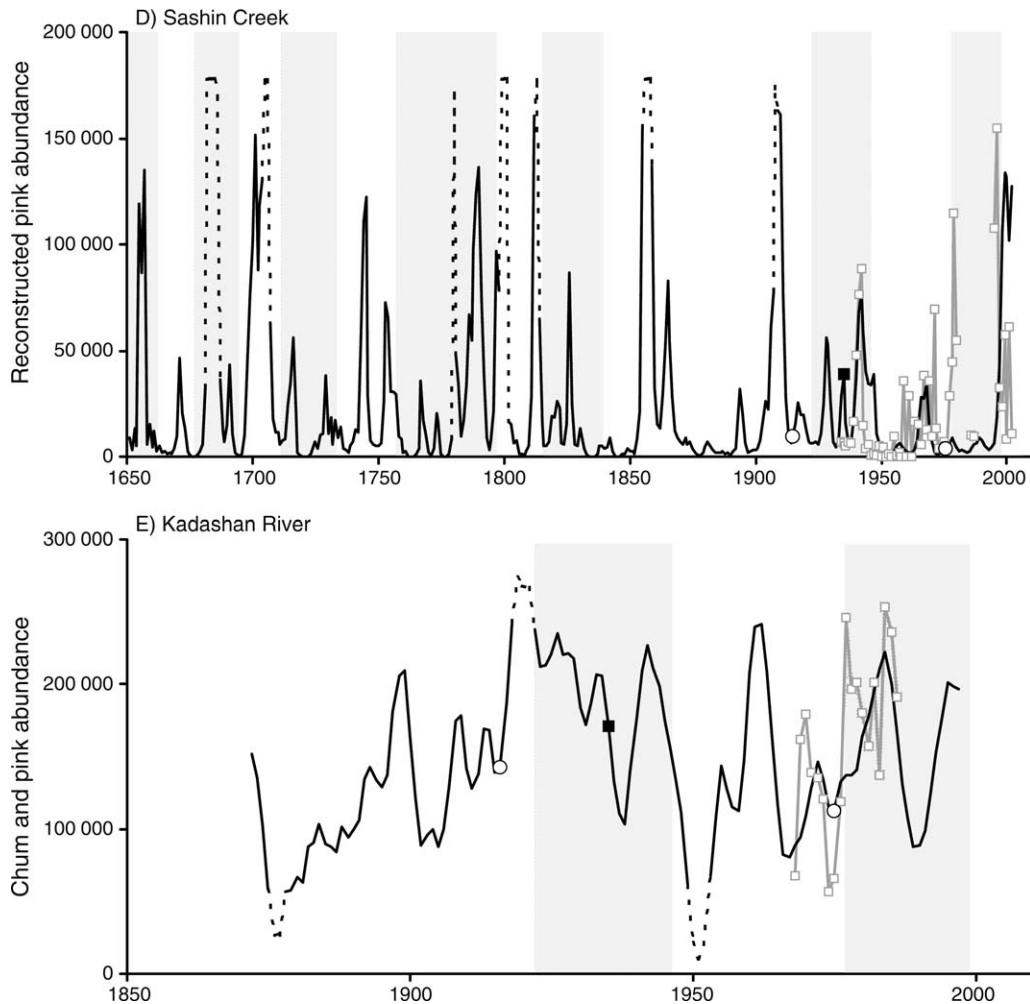


FIG. 4. Continued.

fishery (poor in southeastern Alaska) corresponds with a low point in the reconstruction, and the period of 1931–1939 (years of high regional catch) corresponds to a definite (but not large) peak in abundance.

The three most recent peaks in Sashin Creek pink abundance are substantially lower than most reconstructed maxima prior to ca. 1915. Since the Sashin Creek watershed is protected and remains in a relatively natural state, smaller maxima since ca. 1915 are likely attributable to fisheries; this is supported by historical evidence. By the 1920s there was widespread overfishing on the early portions of southeastern Alaska pink runs (Alexandersdottir 1987). In Sashin Creek, specifically, later spawning was linked to decreased egg survival and

fry production (Skud 1958). The Sashin Creek escapement cycle maximum in 1996 was the highest of three in ~70 years of weir count records, perhaps reflecting recent improvements in management of the fishery. But four maxima (1682, 1704, 1798, and 1856) prior to the weir count history are far higher than the highest values in our calibration set; if we extrapolate from existing data these were approximately four times larger than the 1996 maximum of 155 000 returns.

Kadashan River, southeastern Alaska.—The Kadashan River was a pilot study site at which RWs and salmon escapement were positively correlated (Drake et al. 2002). Increased sample size (~15 additional increment cores from the salmon site) and differencing substan-

← southeastern Alaska (Mantua et al. 1997). A year of very high chinook catch in the southern range occurred in 1972 (National Fisherman 1972), and 1970–1975 were poor years for chum and pink catch in southeastern Alaska. Shaded areas mark periods when the Pacific Decadal Oscillation (PDO) was at its positive/warm phase (pre-1925 values are from Gedalof and Smith [2001], and post-1925 values are from Mantua et al. [1997] and Biondi et al. [2001]). Note that the span of years shown on the x-axis varies among the panels.

tially improved the initial relationship. The new curve is S-shaped, suggesting both a lower and an upper threshold response, and replaces a linear fit in the pilot study (with undifferenced RWs). The S-shaped curve produced a fundamentally similar reconstruction to the pilot study, but with less-pronounced extremes (Fig. 4E).

The Kadashan River reconstruction contains minima at 1875–1882, 1902–1906, 1949–1953, ca. 1967, and 1989–1990. The benchmark year 1915 (low catch in the region) corresponds with average reconstructed abundance; the period of 1931–1939 (years of high regional catch) corresponds to a definite, although not particularly large, peak in reconstructed abundance. The early 1970s, with poor chum and pink fisheries in southeastern Alaska, were also relatively low in the reconstruction. Spectral analysis did not indicate any distinct low-frequency periodicity in the reconstruction and only a relatively weak, broad peak at 2–3 years, again potentially reflecting the life cycle of pink and chum salmon.

Tenakee Inlet, a rich salmon-fishing ground that includes the Kadashan and Indian rivers, supported three salmon canneries from 1916 to 1974. Despite fairly intense fisheries over this period, the reconstruction suggests that chum abundance was relatively high from 1910 to 1945. The ADFG aerial surveys of salmon in streams during spawning migrations on one day each year provide a relative estimate of annual escapement (Heinl et al. 2003) and corroborate our Kadashan River reconstruction closely. For example, the 1996 aerial survey count was ~10 times greater than average, and 1996 is also a maximum in the reconstruction. Additionally, 1989–1991 were years with the lowest aerial counts and correspond with a minimum in the reconstruction.

Indian River, southeastern Alaska.—Our interpretation of the salmon–tree-ring relationship at the Indian River changed substantially from the pilot study. Increased sample size strengthened patterns that show a strong correlation between Indian River RWr and PDO-related climatic drivers. The reference site ring width index now follows PDO ($\rho = 0.589$, $P < 0.01$) and is positively correlated with seasonal low temperatures. The increased sample size and differencing revealed that climate is the primary driver of both RWr and RWs at the Indian River and that the resemblance of the RWs chronology to escapement is likely a result of covariation between the PDO index and escapement rather than a salmon nutrient signal, as suggested in the pilot study (Drake et al. 2002).

It is surprising that we see a strong climate signal in both RWs and RWr at the Indian River site but at none of the other sites. This may be a result of the site's southern aspect (Table 1) affecting soil moisture, growing season temperature, or insolation more strongly or possibly more porous subsoil leading to greater summer water stress.

DISCUSSION

We have presented a repeated pattern of positive correlations between wild salmon escapement and non-climatic riparian tree-ring growth. Our study is the first to test this relationship in a comprehensive way, and positive relationships at the most fundamental level were identified at about half (five of nine) of the sites. When moving-average models and response curves were used to refine and quantify the relationships, salmon escapement accounted for 30–43% of non-climatic tree-ring variation. These relationships are, ostensibly, a tree growth response to salmon nutrients and are mechanistically supported by forest fertilization studies, a related salmon carcass decay study, and a ^{15}N tracer study describing pathways and fate of a late-season NH_4^+ pulse (simulated salmon contribution) in riparian soils and trees. The reconstructions capture essential, sub-decadal-scale variation and cycles (e.g., those associated with salmon species life cycles) and longer periodicities of 25–40 years in three of the reconstructions and 68 years in the longest reconstruction at Sashin Creek. The reconstructions underestimate years of extremely high abundance and overestimate years of extremely low abundance, i.e., reconstructed extremes are dampened. Although these are indirect estimates of past salmon abundance, they are the first available for salmon that spawn in streams and they provide unique perspectives on relative abundance, cycles, and effects of interventions over time.

Identification of a sub-decadal, nutrient-based relationship between trees and salmon at multiple sites demonstrates ecosystem-scale links between salmon and riparian forests and is an important ecological finding in itself. Additionally, each reconstruction contains unique features characteristic of the site. For example, there is a strong ~40-year cyclicity in the Umpqua River chinook, relative stability in Drinkwater Creek sockeye, and periodic, high-amplitude peaks of abundance in Sashin Creek pink salmon. This is not unexpected since considerable variability in the biophysical characteristics exists among the >200 river valleys in the Pacific Coastal Ecoregion (Naiman and Anderson 1997) and their salmon populations (Quinn 2005). The reconstructions presented here are of single species (two species in the Kadashan River) in relatively small rivers and suggest striking differences even in relatively closely spaced systems. These comparisons highlight the importance of site-specific approaches and add an element of complexity to our understanding of “pre-impact” population dynamics. Over the largest scales salmon abundance may be determined by global climatic drivers; e.g., the PDO index was significantly correlated with escapement in four of the five systems we examined in detail. But there are also many deviations in both recorded escapement and in the reconstructions from the PDO index. The effects of climatic drivers may not be homogenous within regions, and river-specific variability may exert a strong influence over salmon survival,

especially over shorter periods. Although it is tempting to generalize about pre-impact patterns in salmon abundance, the variability in our reconstructions suggests resisting this urge and emphasizing instead the distinctive features of individual salmon stocks.

An important additional consideration is that tree-ring growth is a relatively conservative response to fertilization; overall tree growth, including roots and leaves, is probably underestimated by tree-ring growth alone. This is potentially important in long-term site development that includes the effects of trees on riparian soil formation and salmon-forest feedbacks, including shading (stream temperature regulation) and production of organic matter and wood (see Naiman et al. 2005*a, b*).

Our comparison of radial growth of individual trees over the last 50 years (BA_{50}) in salmon vs. reference sites is equivocal. We observed higher radial growth at salmon sites in five of the nine site pairs, but BA_{50} is not a time series and is much less powerful than chronological analyses. Although trees at the salmon sites may not always grow faster than their reference site counterparts, our chronology data suggest that they almost certainly grow faster when salmon are abundant than they would in the absence of salmon. The growth rate of individual riparian trees is important in that it relates to the supply of "key pieces" of large wood in forested rivers, logs large enough to stick in the channel and form jams and pools, increasing habitat complexity and sediment retention (Beechie and Sibley 1997, Montgomery et al. 2003). The role of key pieces in providing habitat for the freshwater life stages of salmon (e.g., Solazzi et al. 2000, Roni and Quinn 2001) is a fundamental link in a potential positive feedback between salmon and the riparian forest. Large-wood-mediated retention of spawning gravel is ostensibly important for all salmonid species, even those not rearing in freshwater.

A dispassionate consideration of tree-ring-salmon approaches

Over the last decade many attempts have been made to reconstruct salmon abundance using N isotopes in tree rings (using an approach similar to lake sediment $\delta^{15}\text{N}$), but salmon abundance has not been related to $\delta^{15}\text{N}$ over time in any peer-reviewed publication and, to our knowledge, no negative results have been published. The failure to detect a salmon-related $\delta^{15}\text{N}$ signal in tree rings is likely due to two basic factors: first, because N is frequently a limiting resource, trees conserve it through tight internal recycling (for example, N may be withdrawn from tree ring A and then deposited in tree rings B-D). Second, sap contains a majority of the N found in wood and is highly mobile between many different rings, so sap must be removed to analyze N bound in the structure of wood, a labor-intensive process that leaves N-poor materials for mass spectroscopy analyses.

Advantages of using tree-ring growth as an indicator of salmon abundance include the relative ease of including a large number of trees (we incorporated growth information from ~360 trees and ~90 000 tree rings). Additionally, growth responses may be an "integrative" indicator of the effects of the many nutrients contributed by salmon; for example, phosphorus or calcium may co-limit growth or interact synergistically with nitrogen during uptake or growth.

The methods and approach described here are relatively simple and somewhat intuitive, providing an advantage in understandability and applicability. It may be possible to develop more advanced models relating historic salmon abundance to growth but complex models are frequently difficult to justify biologically, and increased specialization may limit the number of potential users.

Some of the most severely limiting disadvantages of the "growth" approach include a lack of good study sites (meeting all criteria listed in *Study site, data, and methods*) and difficulty in accounting for covariates (e.g., potential changes over time in N fixation rates). Age detrending of tree-ring series, although necessary for chronology calculations, may remove some of the longest-term, lowest-frequency trends associated with salmon decline, resulting in underestimation of abundance in the earlier portions of the reconstructions.

Study site selection and other considerations for future work

The best predictor of the presence of a salmon signal appeared to be the physical closeness of salmon and reference sites; salmon signals were derived from site pairs that were 2, 3, 4, and 13 km apart. Additionally, the closest site pairs, Drinkwater and Disappearance Creeks, produced the closest relationship between RW_d and salmon escapement. The site pairs that failed to produce salmon signals were 7, 25, and 26 km distant (Lake Creek, Big Qualicum River, and Rogue River, respectively; Table 1). Close proximity means, of course, that the salmon and reference sites are more likely to be subject to the same conditions (other than salmon) over time, such as microclimate or damage from insects or storms. Soil characteristics, which undoubtedly mediate fertilization effects, are also more likely to be similar at physically close salmon and reference sites, although we found no consistent predictor of tree-ring growth response in the soil characteristics measured. We initially suspected that soils with relatively low CEC would be more likely to produce a tree-ring-salmon signal; i.e., trees growing in soils with low nutrient storage capacity would be more likely to reflect nutrient availability over short (sub-decadal) time scales, but this was not the case. Salmon signals were identified at sites with both relatively low (Umpqua River) and high (Drinkwater, Disappearance, and Sashin Creeks) CEC. Cation exchange capacity is affected by pH, and low soil pH decreases the availability of nutrients to plants. Soil

pH at most of the Alaskan sites was relatively low (although soil pH > 4.0 at all sites; Appendix A). Ultimately, the comparisons are limited to nine site pairs, too few from which to draw general conclusions while accounting for interaction effects between the many soil characteristics affecting nutrient availability. Tree species, surprisingly, does not appear to be an important factor for site selection; reconstructions were produced from Sitka spruce, Douglas-fir, and western hemlock.

Realistically, it is probably not reasonable to expect a fertilization response in every riparian forest bordering a salmon stream; other limiting factors such as summer water availability or light limitation may drive patterns in tree-ring growth much more strongly or overwhelm a subtle fertilization signal. Salmon nutrient additions must also be large enough to affect soil nutrient availability, i.e., salmon nutrients must change the mass balance of available nutrients in soils, in at least some years, to affect tree growth.

Dendroecological reconstructions require high-quality, long-term escapement records, old trees, and nearby reference sites. These criteria are difficult to meet today and will preclude the salmon-reference site differencing approach in many systems. The widespread loss of old-growth riparian trees has not only diminished stream quality and degraded salmon habitat, but it has also eliminated an important source of information about the history of individual stream systems. This study provides another reason for the continued and improved conservation of riparian forests and enforcement of no-logging buffer zones around streams. If climate signals can be accounted for and removed in other ways, such as by using upland site chronologies, the reference site restriction, at least, may be reduced.

CONCLUSIONS

Policy makers and managers currently struggle to balance the demands of society and industry with the limited and always-changing capacity of the environment to produce living resources. Populations and population dynamics of fishery resources are, in most cases, only poorly understood: today's expectations are based on perceptions and records limited to an era of intense exploitation from industrial fisheries. Long-term perspectives, such as those presented here, can allow a more objective analysis of fishery declines and a clearer understanding of natural baselines and cycles. The salmon abundance reconstructions suggest that management and restoration of the world's remaining salmon fisheries will require a thoughtful approach for each stock, but we can also draw some general conclusions.

First, the reconstructions provide additional evidence that salmon populations are, by nature, cyclic over time, not only at large scales (as ocean conditions change), but also at much smaller scales (by stock) that are not always in step with large-scale climate patterns (e.g.,

Levin 2003). All of the reconstructions contain evidence of cyclic patterns extending up to 350 years before present. (Long-term cyclicality is also seen in paleolimnological reconstructions by Finney et al. [2000, 2002].) Second, reconstructions can be used to help identify primary drivers of salmon decline and, by extension, best approaches for restoration. Although many factors may contribute to decline of an individual stock, describing the timing of declines or interruptions in cyclicality can help identify the relative influence of disturbances and may provide a framework for setting priorities in restoration. Third, the reconstructions can be used to assess management and stock-rebuilding efforts of the past.

Our belief is that the growing body of retrospective knowledge, including the reconstructions presented here, will foster a modification of expectations and promote logic-based decisions about this intrinsically, culturally, and commercially valuable resource in the future.

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APPENDIX A

A table presenting soil characteristics and site and vegetation descriptions (*Ecological Archives* A017-060-A1).

APPENDIX B

A description of software and quantitative approaches (*Ecological Archives* A017-060-A2).

APPENDIX C

A table presenting correlation analyses of tree ring chronologies, seasonal climate variables, Pacific Decadal Oscillation climate index, and escapement (*Ecological Archives* A017-060-A3).

APPENDIX D

Figures presenting autocorrelation (ACF) and partial autocorrelation (PACF) analyses of differenced ring width (RWd) chronologies (*Ecological Archives* A017-060-A4).

APPENDIX E

Figures presenting spectral analyses of reconstructed salmon abundance (*Ecological Archives* A017-060-A5).