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ARTICLE

Increasing Dominance of Odd-Year Returning Pink Salmon

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Abstract
The hypothesis that abundance patterns differ between even- and odd-year returning Pink Salmon *Oncorhynchus gorbuscha* was examined using data from the eastern and western North Pacific Ocean, northern and southern British Columbia, and biologically based conservation units, which are Canadian groupings of salmon that are genetically and/or ecologically distinct from each other. Detailed data from (mostly) southern British Columbia were examined to test hypotheses that the differences between even- and odd-year broodlines were due to fishing, broodline interactions, limitations in freshwater or the ocean, and/or density dependence. The odd-year broodline has become increasingly predominate over the genetically distinct even-year broodline on both sides of the Pacific and in five of six British Columbia regions. Five analytical approaches revealed abundances were generally increasing for odd-year conservation units and declining or stable for even-year conservation units. Recent increases in odd-year spawner abundance in southern British Columbia were correlated with decreased fishery exploitation, but exploitation was higher for odd-year than for even-year salmon, refuting the hypothesis that differential exploitation is responsible for the changing dominance. Significant negative interactions between even- and odd-year broodlines were found in several of the British Columbia regions tested, but there was little evidence of competition between broodlines in the marine environment. Odd-year populations in the Fraser River increased despite density-dependent reductions in freshwater production, while there was no indication of changes in marine productivity. Our results, combined with literature findings indicating a more southerly glacial refugium for odd-year than for even-year Pink Salmon and temperature-related survival differences between these broodlines, suggest that recent climate conditions are benefiting odd-year returning Pink Salmon more than even-year salmon, especially in the southern part of their range.

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Pacific Salmon (genus *Oncorhynchus*) are typically anadromous and semelparous, meaning that they spend part of their lives in the ocean, spawn in freshwater, and die shortly after spawning (Groot and Margolis 1991). Salmon have a complex hierarchical population structure extending from taxonomic species to groups at individual spawning sites (Riddell 1993). Their relatively precise homing to natal rivers and death after spawning restricts gene flow among spawning locations. Persistent spawning locations (demes) can be aggregated into populations that often exhibit local adaptations (Irvine and Fraser 2008). In Canada, wild Pacific Salmon are increasingly being managed and assessed as biologically based conservation units (CUs), each of which is a group of salmon living in an area and sufficiently isolated from other groups that if the salmon in the area were to become extirpated it is unlikely that the area would be recolonized naturally in an acceptable period of time (e.g., a human lifetime; DFO 2005). Individual CUs tend to be genetically and/or ecologically distinct from other CUs and often occupy separate freshwater spawning and/or rearing habitats (Holtby and Ciruna 2007).

Pink Salmon *O. gorbuscha*, the most abundant species of Pacific Salmon, are especially interesting because their strict 2-year life cycle makes them the only species with complete genetic isolation between fish that spawn in even-numbered years and fish that spawn in odd-numbered years; these separate lineages are known as broodlines. Pink Salmon are plentiful throughout the North Pacific Ocean, ranging from northern Washington State and southern British Columbia north to western Alaska and the North American Arctic in the east and from the coast of the Sea of Japan north to the East Siberian Sea in the west (Heard 1991). The less precise homing of Pink Salmon (and Chum Salmon *O. keta*) relative to other Pacific salmon species, which may be related to their shorter juvenile period of freshwater residency and an associated lower level of imprinting in their natal rivers (Quinn 1993), results in their CUs occupying relatively large freshwater areas. A recent workshop examining reasons for the increasing abundance of Pink and Chum Salmon failed to determine precisely why these increases are occurring (Davis and Beamish 2012).

It has long been known that sympatric even- and odd-year returning Pink Salmon broodlines can have very different run sizes. For example, near the southern extent of their range in the eastern Pacific Ocean, Pink Salmon have very large runs in the Fraser River, British Columbia, and Washington State in odd years but are almost absent in even years (Heard 1991). In northern British Columbia, Bristol Bay, and western Alaska as well as the North American Arctic, returns of Pink Salmon tend to be greater in even years than in odd years (Ricker 1962; Craig and Haldorson 1986; Heard 1991). In Hokkaido (northern Japan), odd-year Pink Salmon have usually been dominant (Nagata et al. 2007), while in Russia odd-year Pink Salmon are most abundant on the east coast of the Kamchatka Peninsula while even-year Pink Salmon dominante on the west coast (Radchenko et al. 2007). Climate-related changes appear to have been playing a role in increasing the overall abundances of Pink Salmon (Irvine and Fukuwaka 2011), but detailed comparisons of even- and odd-year broodlines have rarely been made. Although it has been more than 50 years since Ricker (1962) proposed eight hypotheses to explain the differences in run size between even- and odd-year Pink Salmon, consensus on the explanations for these differences is lacking (Krkošek et al. 2011).

The purpose of the research reported in this paper was to evaluate the trends in abundance for even- and odd-year Pink Salmon broodlines and to test several hypotheses for the differences found. Time series for Pacific Salmon abundance are available at various temporal, spatial, and biological scales. To test the hypothesis that abundance patterns differ for even- and odd-year Pink Salmon, we compared time series of even- and odd-year abundance in the western and eastern halves of the North Pacific Ocean and in (primarily) British Columbia, where we evaluated differences between the northern and southern areas and between even- and odd-year CUs. We used detailed data from (mostly) southern British Columbia to further test hypotheses that the differences between even- and odd-year Pink Salmon abundance trends are due to fishing, broodline interactions, limitations in freshwater or ocean productivity, and/or density dependence.

METHODS

Data

Catch as an abundance index for western and eastern North Pacific Pink Salmon (Table 1, category 1; *1925–2011).*—We analyzed commercial catch data maintained by the North Pacific Anadromous Fish Commission to evaluate Pink Salmon abundance trends in the western and eastern North Pacific (Irvine et al. 2012). The North Pacific catch data were separated into two periods: 1925–1950 (to overlap with cannery-based catch estimates; Table 1, category 2) and 1951–2011 (to align with CU escapement data; Table 1, category 3).

Catch as an abundance index for northern (Skeena–Nass rivers) and southern (Fraser River) British Columbia Pink Salmon populations (Table 1, category 2; *1900–1950).*—Reconstructed British Columbia catch estimates were used for the first half of the 20th century, a period when few reliable spawner escapement estimates are available (Argue and Shepard 2005). Argue and Shepard examined two main types of information: estimates of canned salmon and estimates of salmon processed by other methods (e.g., pickled, smoked, and salted). These estimates were converted to landed weights by species based on information in annual reports, then to numbers of salmon based on average weights by species from 1951 to 1954. We report only data from canneries near the Fraser and the Skeena–Nass rivers, reasoning that most of the fish processed at these canneries would be fish returning to those rivers.

Spawner numbers as an abundance index for non-Fraser CUs (Table 1, category 3; *1950–2011).*—Non-Fraser River

TABLE 1. Summary of abundance indices and other data types used to assess Pink Salmon.

Category	Index	Years	Region	Product	Source
1	NPAFC commercial catch (pieces)	1925–2011	Western and eastern North Pacific Ocean	Figures 1, 2, 3A, 3B	Irvine et al. (2012)
2	Catch estimated from landed weight	1900–1950	Northern (Skeena–Nass) and southern (Fraser) British Columbia	Figures 3C, 3D	Argue and Shepard (2005)
3	Escapement by conservation unit	1950–2011	British Columbia CUs excluding Fraser River	Tables 3, 4, A2.1; Figures 4, 5, 6	NuSeds database (see text)
4	Escapement, catch, returns, exploitations	1954–2011	Fraser River CU, non-Fraser southern British Columbia, Puget Sound	Figure 7	Publications in text, C. J. G. Michielsens (unpublished)
5	Fry production	1962–2011	Fraser River; southern British Columbia	Figures 8, 9B, 10A	B. A. White (unpublished), P. Van Will (DFO, personal communication)
6	Fry production	1986–2011	Puget Sound	Figures 8, 9B, 10B	White (unpublished), Adicks (personal communication)
7	Fecundity, sex ratio	1961–2001	Fraser River	Figures 9A, 10A	White (unpublished)
8	Adult fish weight	1961–2011	British Columbia, Fraser River, Puget Sound	Figure 12	British Columbia: Irvine et al. (2012); Fraser and Puget Sound: White (unpublished), Adicks (personal communication)

escapement time series downloaded from the Department of Fisheries and Oceans Canada (DFO) salmon escapement database (NuSEDS; January 7, 2013) were available for many rivers and CUs beginning in the early 1950s. We acknowledge the variability in methods used to estimate spawner abundances. According to NuSEDS, the most common methods were peak live-plus-dead counts and area-under-the-curve estimations. Other methods included fence counts, mark–recapture, test fisheries, visual surveys from the ground and air, and expert opinion (Cousens et al. 1982; Jantz et al. 1990; Irvine and Nelson 1995).

Escapements, returns, and exploitation for southern Pink Salmon (Table 1, category 4; *1954–2011*).—The DFO estimated odd-year Pink Salmon escapement to the Fraser River watershed from the 1950s until 1991 using an extensive mark–recapture program with visual counts in smaller tributaries (PSC 1994). Between 1993 and 2001, escapements were estimated by mark–recapture in the lower river (PSC 2005; Schubert et al. 1997). From 2003 to 2007, escapement estimates were derived as run sizes (estimated from test fisheries) minus the total catches in fisheries (PSC 2007, 2009, 2012). In 2009 and 2011, hydroacoustic assessments in the lower Fraser River were used to generate Fraser River Pink Salmon escapements (Xie et al. 2013). Because of the various methodological changes, the Pacific Salmon Commission has given considerable thought to the validity of the Fraser River estimates and made changes as appropriate. Escapement estimates for Washington State rivers from K. Adicks (Washington Department of Fish and Wildlife, personal communication) are on file (B. A. White, unpublished).

For fisheries intercepting Fraser River, Washington State, and other southern stocks, genetic stock identification analyses were used to differentiate the various Pink Salmon populations from which fish were caught (Beacham et al. 1985, 2012). The adult return migration of Fraser River Pink Salmon was assessed by the Pacific Salmon Commission for several decades by adding stock-specific catch estimates to spawning adult estimates (PSC 2012). Escapement and catch data were used to compute exploitation rates (catch/[catch + escapement]) for the Fraser River odd-year and southern British Columbia (non-Fraser River) odd- and even-year broodlines. Odd-year catch estimates for non-Fraser River Pink Salmon were only available from 1989 onwards, as this was when genetic stock identification became available to partition catches among CUs.

Fraser River and Washington State fry abundance estimates (Table 1, categories 5, 6).—In the Fraser River, Pink Salmon fry production from odd-year spawning adults has been assessed in even years since 1962 (Vernon 1966). Sampling was conducted from a vessel at Mission, British Columbia, from approximately late February to late May. Fry were trapped using a surface inclined-plane trap and a vertical trap. The vessel sampled sequentially at three stations across the river. Catches of fry stratified by depth, gear type, and sample period were expanded to generate daily estimates of Pink Salmon fry migration and the total fry out-migration by the end of the sampling period. Similarly, starting in 1986 fry abundance estimates were available for some Washington State Pink Salmon stocks (Skagit, Stillaguamish, and Snohomish).

Fecundity, sex ratios, and fish weight (Table 1, categories 7, 8).—In the Fraser River, fecundity data were collected by the DFO from 1961 to 2001, after which the spawning ground enumeration program was no longer conducted. The weights of Pink Salmon caught in British Columbia fisheries were computed from data on commercial catches in Irvine et al. (2012). The weights of fish returning to the Fraser River and the Skagit and Stillaguamish rivers (Adicks, personal communication) were on file (White, unpublished).

Analyses

Hypothesis: abundance differs between even- and odd-year brood lines.—Two methods were used to test this hypothesis: simple regression analysis and time series comparisons of the ratio of even- to odd-year abundance estimates. For the former, the null hypothesis that the correlation between the variable of interest and time (in years) did not differ from zero, was tested using least-squares regression (two-tailed tests). The results consisted of correlation coefficients (r) and probability (P-values). For the latter method, we needed to account for the 1-year mismatch between even and odd years. To generate ratios for even years, we divided the log-transformed even-year abundance by the log-transformed average of the previous and next odd-year values. For the odd-year comparisons, we divided the log-transformed average of two adjacent even years by the log-transformed value of the separating odd year. These two methods were applied to the even- and odd-year time series of North Pacific catch data (Table 1, category 1), northern and southern British Columbia cannery-based catch estimates (Table 1, category 2), and non-Fraser River escapement estimates for individual CUs (Table 1, category 3).

While the catch data were complete (i.e., there were no missing estimates), the time series of Pink Salmon escapement were incomplete for many rivers and CUs. We excluded rivers from our trend analysis if they were missing more than one-third of the years of data and/or more than two of the most recent 5 years.

An algorithm provided by Brown (1974) was used to impute missing escapement values. Before running the in-filling algorithm, we transformed the data by $\log_{10}(E_{ij} + 1)$, where E_{ij} is the escapement count in river i and year j. After imputation, we back-transformed each value to its original value for records (E) in river i and year j. The imputation algorithm was developed in R (R Core Team 2012) and is provided in Supplement A in the online version of this article.

We assumed that the catch-based abundance estimates for even and odd years in the western and eastern North Pacific were appropriate indices of total abundance. However, to compare even- and odd-year escapement time series, we expanded our indices of abundance because sampling effort may have varied between these broodlines. Most rivers excluded from the previously described trend analyses had escapement estimates in some years, though many were not regularly sampled because the numbers of Pink Salmon were low. Using the available data, a CU-specific scalar value was calculated as

$$S_a = \frac{\sum_{i=1}^{N} EM_i}{\sum_{i=1}^{n} EM_i},$$

where S_a is the scalar for CU a, EM_i is the median escapement of CU a in river i, N is the total number of rivers in CU a, and n is the number of rivers in CU a with imputed estimates. Scaled escapements (E_S) were then calculated for each year j by

$$E_{Sj} = S_a \sum_{i=1}^{n} E_{Uaij},$$

where E_{Uaij} is the unscaled escapement for CU a in river i in year j. Annual escapement estimates for all rivers in each CU were then summed to obtain CU-specific abundance time series.

Five approaches were used to examine the time series patterns of the abundance data. As much as practicable, these approaches were aligned with the developing regional methodology (Holt et al. 2009; Grant et al. 2011; Grant and Pestal 2012; Porszt et al. 2012; see Appendix 1 for details). Within each approach, the resulting abundance trends were color coded as green (increasing slope or abundance), amber (little or no change), or red (decreasing) (Table 2).

All five approaches were used to analyze the North Pacific catch and British Columbia escapement data (1951–2011). For the North Pacific catch data for 1925–1950, the analysis was restricted to approaches 2, 3, and 4 since we were not focused on the most recent part of the time series, which was the basis of approaches 1 and 5.

In some instances, the freshwater distribution of even-year CUs overlapped spatially with that of odd-year CUs, while in other instances they did not. In this latter case, we grouped the CUs into similar geographic areas when comparing the abundance time series of returning fish during even and odd years (Table 3).

Hypothesis: fisheries exploitation drives differences between even- and odd-year broodlines.—The only data available to test

TABLE 2. Analytical approaches used to categorize the status of Pink Salmon from time series on abundance. Three approaches (2, 3, and 4) were used for the North Pacific catch data (1925–1950) and all five were used for the other catch data (1950–2011) and Pink Salmon CU escapement data. The shaded segments of the circles indicate the approaches used to obtain the results shown in Figures 2 and 4.

Approach	1925–1950 catches	Other data	Metric	Upper benchmark (green)	Lower benchmark (red)
1			Slope during the last 20 years	Positive slope and $P < 0.1$	Negative slope and $P < 0.1$
2			Slope of the entire time series	Negative slope and $P < 0.1$	Negative slope and $P < 0.1$
3			Ratios between geometric means of the most recent 1 or 5 generations and the entire time series	≥0.75 (see text and Table A1.1)	≤ 0.5 (see text and Table A1.1)
4			Ratio between the geometric mean of most recent 3 generations and the first 3 generations of the time series	≥ 0.75	<0.3
5			Slope of the percent change during the last 20 years	< 15% decline	≥30% decline

this hypothesis were from Fraser River Pink Salmon (odd-year) and non-Fraser River southern British Columbia Pink Salmon (odd- and even-year). For Fraser River Pink Salmon, the time series only contained exploitation data for odd years (1959–2011), as even-year Fraser River Pink Salmon are rare. For non-Fraser southern British Columbia stocks, the odd-year exploitation time series was much shorter (1989–2011) than the even-year time series (1954–2010), restricting the usefulness of these time series when comparing differences in exploitation rates between odd and even years. We therefore explored whether the exploitation rate time series for odd-year Fraser River Pink Salmon could be used as a proxy for non-Fraser River odd-year southern British Columbia Pink Salmon to allow us to better test the hypothesis that there was no difference in exploitation rates between even- and odd-year southern British Columbia Pink Salmon during 1959–2011.

TABLE 3. Regions with even- and odd-year escapement data. The regions include CUs identified by number (Figure 4; Table A2.1 in Appendix 2); T is the total number of rivers within the region in the NuSEDs database, and S is number of rivers used in the autocorrelation analysis (Table 4).

	Even year			Odd year		
Region	Number	T	S	Number	T	S
North Coast	3	164	19	16–18	154	22
Central Coast	4–5	248	83	19–23	257	75
Middle Upper Skeena	7	57	2	24	65	3
East Haida Gwaii	10	100	18	27	58	3
Hecate Lowlands	11	178	37	28	181	34
Strait of Georgia	12	66	7	29	72	9

Even- and odd-year exploitation ratios were estimated and compared using the same process as described for abundance estimates (imputing intermediate years by calculating the average of the exploitation rate of the previous and next years), except that the data were not log transformed. Since exploitation rate data were not normally distributed (Shapiro–Wilk test of normality; $P < 0.05$), a paired-sample Wilcoxon signed rank test was used to evaluate the hypothesis that there was no difference in exploitation rates between even and odd years for southern British Columbia Pink Salmon.

Hypothesis: The abundance of even-year broodlines impacts odd-year broodlines and vice versa.—Broodline interactions may be caused by delayed density-dependent processes. To test this hypothesis, we used autocorrelation analyses lagged by 1 year to explore the interactions between even- and odd-year broodlines using log-transformed escapement time series of the various Pink Salmon populations. We also computed autocorrelations lagged by 2 years to examine the interactions within broodlines.

Hypothesis: Freshwater productivity, marine productivity, and/or density dependence drive changes in abundance.—Because data to test the impact of these drivers on Pink Salmon abundance were only available for odd-year stocks in the Fraser River and Washington State, it was not possible to evaluate the impact of these drivers on the differences between the odd- and even-year broodlines. Instead, the available data only allowed us to evaluate the importance of these drivers on the trends in abundance. Freshwater productivity was expressed in terms of the number of fry/spawner or the number of fry/egg. To evaluate ocean productivity, we used the adults/fry ratio, which included fish in the brief postfry stage in the river prior to entering the ocean.

Freshwater productivity for both Fraser River and Washington State Pink Salmon was explored further by examining density-dependent processes within river environments. We determined whether a Ricker stock–recruit model (Ricker 1975) that explicitly accounted for density dependence explained the trends in freshwater productivity (fry/spawner). This was done by comparing Ricker models with density-independent estimates (average ln[fry/spawner]). To evaluate whether there were trends in freshwater productivity that could not be explained by the Ricker model and the assumed density dependence, a Kalman filter model (Peterman et al. 2000; Peterman and Dorner 2012) assuming an underlying time trend in the alpha parameter of the Ricker model was applied to the Fraser River data (the only time series of sufficient length to detect underlying trends).

RESULTS

Abundance Patterns and Differences between Even- and Odd-Year Broodlines

Pink Salmon in the North Pacific Ocean are at record high abundance levels, with no indication of declines. On average, the abundance (catch) of Pink Salmon in the western North Pacific (Asia) was 65% of that in the eastern North Pacific (North America), and odd-year catches exceeded even-year catches by 14% and 48% in the western and eastern areas, respectively (Figure 1). Odd-year Pink Salmon increased in abundance during 1925–1950 on both sides of the North Pacific, while even-year Pink Salmon were stable or declining over that time period (Figure 2). During the more recent time period 1950–2011, the abundance of both even- and odd-year Pink Salmon broodlines increased (Figure 2). A period of even-year dominance on both sides of the Pacific until about 1935 shifted to odd-year dominance by about 1950 (Figure 3A, B). Since then, odd-year Pink Salmon have predominated in the catches in the western North Pacific. In the east, there was a shift back to even-year dominance from the mid-1950s until the mid-1970s, followed by a trend toward increasing odd-year catches through to the present time. The overall tendency to increasing dominance of odd-year fish from 1925 to 2011 was significant in both areas (Figure 3A, B; slope < 0).

The catch data for the northern and southern areas of British Columbia predate the North Pacific time series. During the first half of the 20th century, even-year fish predominated in northern British Columbia (Skeena–Nass rivers), outnumbering odd-year fish in 33 of 46 years (Figure 3C). There was no shift toward changing proportions of broodlines (the slope was not significantly different from zero) in the Skeena–Nass rivers. Interestingly, there were modest catches of even-year Pink Salmon in the Fraser River during the early part of the 20th century (Argue and Shepard 2005), although odd-year Pink Salmon become increasingly predominant in the time series (Figure 3D).

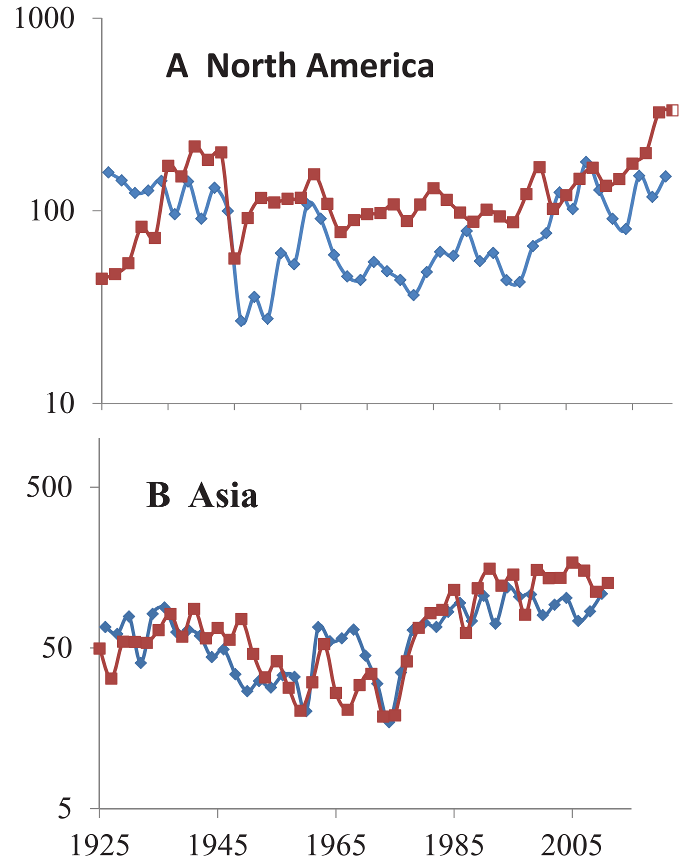

FIGURE 1. Commercial catch (millions of fish) of odd-year (squares) and even-year (diamonds) Pink Salmon from **(A)** the eastern North Pacific Ocean (North America) and **(B)** the western North Pacific Ocean (Asia) from 1925 to 2011. [Figure available online in color.]

Ten of the 13 CUs with data for even years and 14 of the 20 CUs with data for odd years had sufficient data for us to analyze trends (Figure 4; Table A.2). Overall, even-year CUs show predominantly decreasing trends in abundance or no trend at all (more amber and red than green; Figure 4A), while odd-year CUs show predominantly increasing trends (mostly green; Figure 4B). There was no clear north–south pattern.

Of the six regions with even- and odd-year escapement data (Table 3), even-year Pink Salmon were more abundant than odd-year fish in East Haida Gwaii, Central Coast, and Hecate Lowlands, although this pattern has shifted in the latter two cases in recent years (Figure 5A–C). During most years, odd-year Pink Salmon were more abundant than even-year fish in the Middle Upper Skeena River and Strait of Georgia (not including the Fraser River) (Figure 5E, F). The North Coast was the exception, with even- and odd-year populations each being most abundant about half the time (Figure 5D).

East Haida Gwaii was the only British Columbia region where even-year Pink Salmon increased in dominance (i.e., have a positive slope). In each of the five other regions (North Coast, Central Coast, Hecate Lowlands, Middle Upper Skeena River,

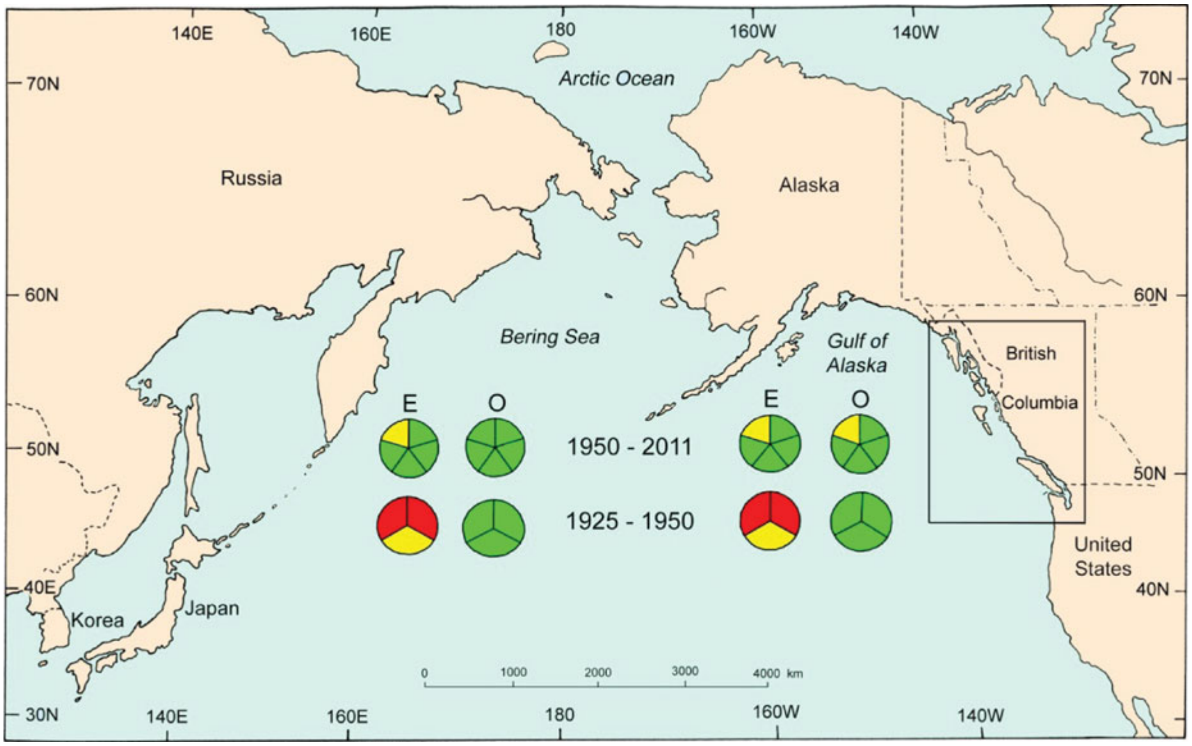

FIGURE 2. Results of the abundance analyses for Pink Salmon caught in even (E) and odd (O) years in Asia (left circles) and North America (right circles). The three-piece circles represent the results based on approaches 2, 3, and 4 (see Table 2) using data from 1925 to 1950; the five-piece circles show the results from all five approaches using data from 1950 to 2011. Green indicates an increasing trend, amber little or no change, and red a decreasing trend. The inset shows the location of the map shown in Figure 4.

and Strait of Georgia), the slopes were significantly negative, indicating the increasing dominance of odd-year Pink Salmon (Figure 6).

Effects of Fishery Exploitation

The paired-sample Wilcoxon signed rank test indicates that prior to 2000 (1989–1999), the exploitation rate (H) on southern British Columbia Pink Salmon from areas other than the Fraser River was greater during odd years than during even years ($H_{odd} = H_{even} + 0.14$; $\alpha = 0.025$, $P = 0.019$; see Table A2.2 for data). Since 2000, there has been no difference in exploitation between the odd-and even-year broodlines ($P = 0.97$). This indicates that the drop in the exploitation rate for Pink Salmon returning to non-Fraser River systems has been larger during odd than even-years.

The correlation between the exploitation rate of odd-year Fraser River and other odd-year southern British Columbia Pink Salmon is significant ($r^2 = 0.83$, $r^2_{adj} = 0.66$, $P = 0.007$). In addition, the paired-sample Wilcoxon signed rank test indicates no significant difference in exploitation rates between odd-year Fraser River Pink Salmon and other odd-year southern British Columbia Pink Salmon between 1989 and 1999 ($P = 0.15$) and thereafter ($P = 0.24$). The odd-year Fraser River Pink Salmon exploitation rate time series was therefore considered an acceptable proxy for the shorter non–Fraser River odd-year exploitation rate time series, which enabled us to extend the even–odd comparison back to 1959.

When we compared the exploitation rates of odd-year Fraser River Pink Salmon (as a proxy for other odd-year Pink Salmon) and even-year southern British Columbia Pink Salmon from 1959 to 1999 (Figure 7; Table A2.2), we found (paired-sample Wilcoxon signed rank test) that the exploitation rate on southern British Columbia Pink Salmon was higher in odd years than in even years ($H_{odd} = H_{even} + 0.16$; $P = 0.000$). Odd-year Pink Salmon experienced higher exploitation rates until 1999, and consequently there was a greater decrease in exploitation rates when they dropped to similar, much lower levels in 2000.

Broodline Interaction Effects

Autocorrelation analysis of the escapement time series (Table 4) indicated significant negative interactions between the abundances of even- and odd-year populations in two of six regions for the entire time series and the last 20 years, and significant positive interactions for the North Coast for the entire time series. In contrast, significant positive interactions were found for five of six regions within broodlines using the entire time series, although only one of six regions in the last 20 years. When Fraser River odd-year Pink Salmon were included

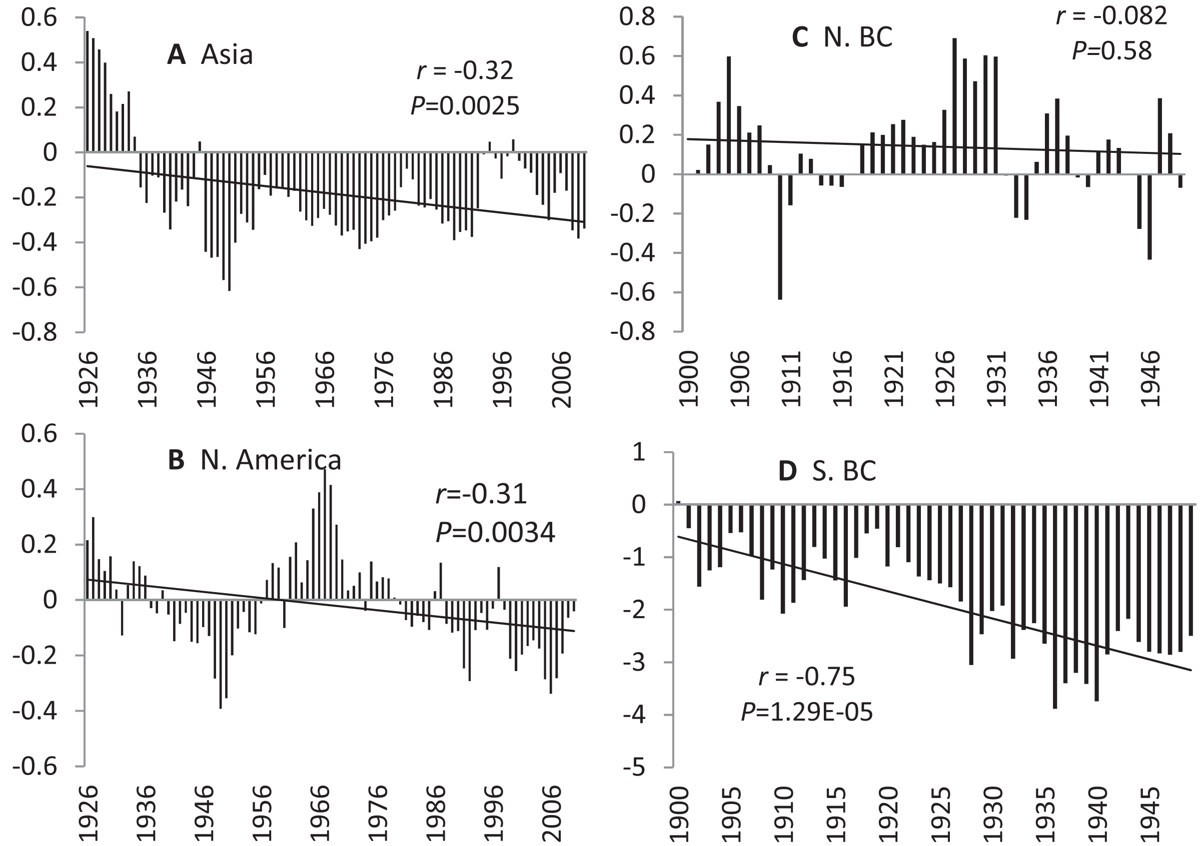

FIGURE 3. Time series of the ratio of the commercial catch of even-year to odd-year Pink Salmon (log scaled) for **(A)** the western North Pacific (Asia) and **(B)** the eastern North Pacific (North America) from 1926 to 2010, as well as for **(C)** northern British Columbia (the Skeena and Nass rivers) and **(D)** southern British Columbia (the Fraser River) from 1900 to 1950. Positive ratios (those above the horizontal axis) represent even-year dominance, while negative ratios indicate odd-year dominance.

with other Strait of Georgia salmon, the interactions between broodlines were significantly negative while the interactions within broodlines were significantly positive (Table 4, bottom row).

TABLE 4. Results of the autocorrelation analysis (*r*) of the escapement time series exploring the interaction between odd and even years (lag 1) and the impact of escapement in the brood year on the escapement of the next generation (lag 2). Sample sizes are given in Table 3; asterisks denote statistical significance ($P < 0.05$).

	All years		Last 20 years	
Region	Lag 1	Lag 2	Lag 1	Lag 2
North Coast	0.26*	0.18	0.19	−0.04
Central Coast	0.01	0.39*	0.06	0.16
Mid Upper Skeena	−0.06	0.42*	−0.47*	0.21
East Haida Gwaii	−0.64*	0.75*	−0.66*	0.73*
Hecate Lowlands	−0.26*	0.27*	−0.03	0.15
Strait of Georgia	0.15	0.30*	−0.07	0.15
Strait of Georgia and Fraser River	−0.34*	0.78*	−0.60*	0.71*

Freshwater versus Marine Effects

Analysis of the time series of freshwater and postfry (largely marine) productivity for Fraser River and Washington State Pink Salmon showed a significant decreasing trend in freshwater productivity (fry/spawner) over the entire time series for Fraser River Pink Salmon (1961–2011; $P = 0.00$) but no trend for Washington State Pink Salmon (although data were only available for recent years [1985–2011]; $P = 0.63$) (Figure 8A). There was also no trend in freshwater productivity for Fraser River Pink Salmon during 1985–2011 ($P = 0.46$), showing that the results for the two populations are not contradictory. To explain the overall declining trend in freshwater productivity, we explored the sex ratio and fecundity time series for Fraser River Pink Salmon (not adjusted for length) that were available until 2001. Overall, the results indicate that there was no significant trend in sex ratios ($P = 0.29$) but that there was a significant decline ($P = 0.003$) in fecundity (Figure 9A). Declining fecundity (eggs/female) could possibly explain 19% of the trend in the fry/spawner time series ($P = 0.03$; Figure 9B), while declining fry/egg could explain 94% of this trend ($P = 0.00$). No significant trends were detected for postfry productivity for Fraser

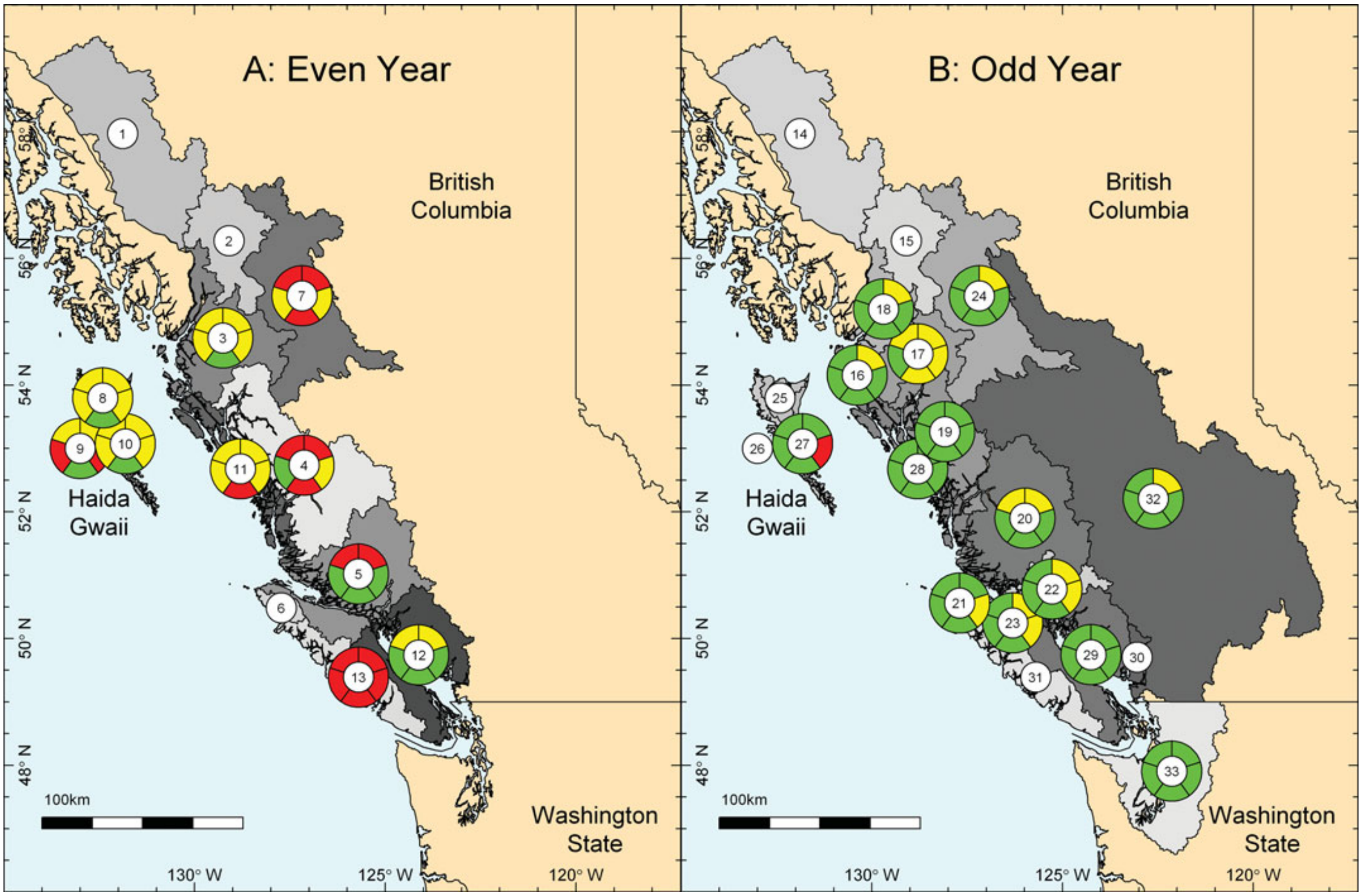

FIGURE 4. Status of **(A)** even-year and **(B)** odd-year conservation units (CUs) of Pink Salmon depicted by five-piece circles in which the central number is the number of the CU and each piece shows the results from one approach (see Table 2). The colors are used as in Figure 2. Each circle is placed in the area of the freshwater distribution of that CU (see Table A2.1 for CU names).

River and Washington State Pink Salmon ($P = 0.69$ and 0.12, respectively; Figure 8B).

Density Dependence

Density-dependent impacts on freshwater productivity were explored by comparing Ricker model fits with the average freshwater productivity (average ln[fry/spawner]) (zero anomaly lines; Figure 10). The Ricker model prediction anomalies were smaller than the density-independent anomalies based on the average for both Fraser River and Washington State Pink Salmon stocks, indicating density dependence during the freshwater phase of their life history. Application of a Kalman filter model (Peterman et al. 2000) indicates that there are some further signs of change in freshwater productivity once density dependence has been taken into account. Figure 11 shows the trend in the standardized productivity parameter of the Ricker stock–recruit relationship with a Kalman filter model fitted to Fraser River Pink Salmon stock–recruit data. Changes in productivity in addition to the changes that can be attributed to density dependence seemed to have occurred only in the freshwater environment, not during the postfry stage. Overall, the detected variability in freshwater productivity was minor (mean productivity = 4.86, standard deviation = 0.21) and did not impact the overall productivity of Fraser River Pink Salmon (freshwater and marine combined). The freshwater productivity first decreased before increasing again in the new millennium. Density dependence in the freshwater environment is also apparent in the time series of the average weight of Fraser River and Washington State Pink Salmon; mean body weights declined until the early 1990s, similar to the pattern for the even- and odd-year broodlines in the British Columbia catch (Figure 12).

DISCUSSION

To carry out our analyses, it was necessary to use a wide variety of data sets, some of unknown accuracy and precision. Our first assumption was that catch was an appropriate index of abundance. Commercial catch is often used to index salmon abundance over large spatial scales (e.g., Irvine and Fukuwaka 2011; Noakes and Beamish 2011; Radchenko et al. 2007). For

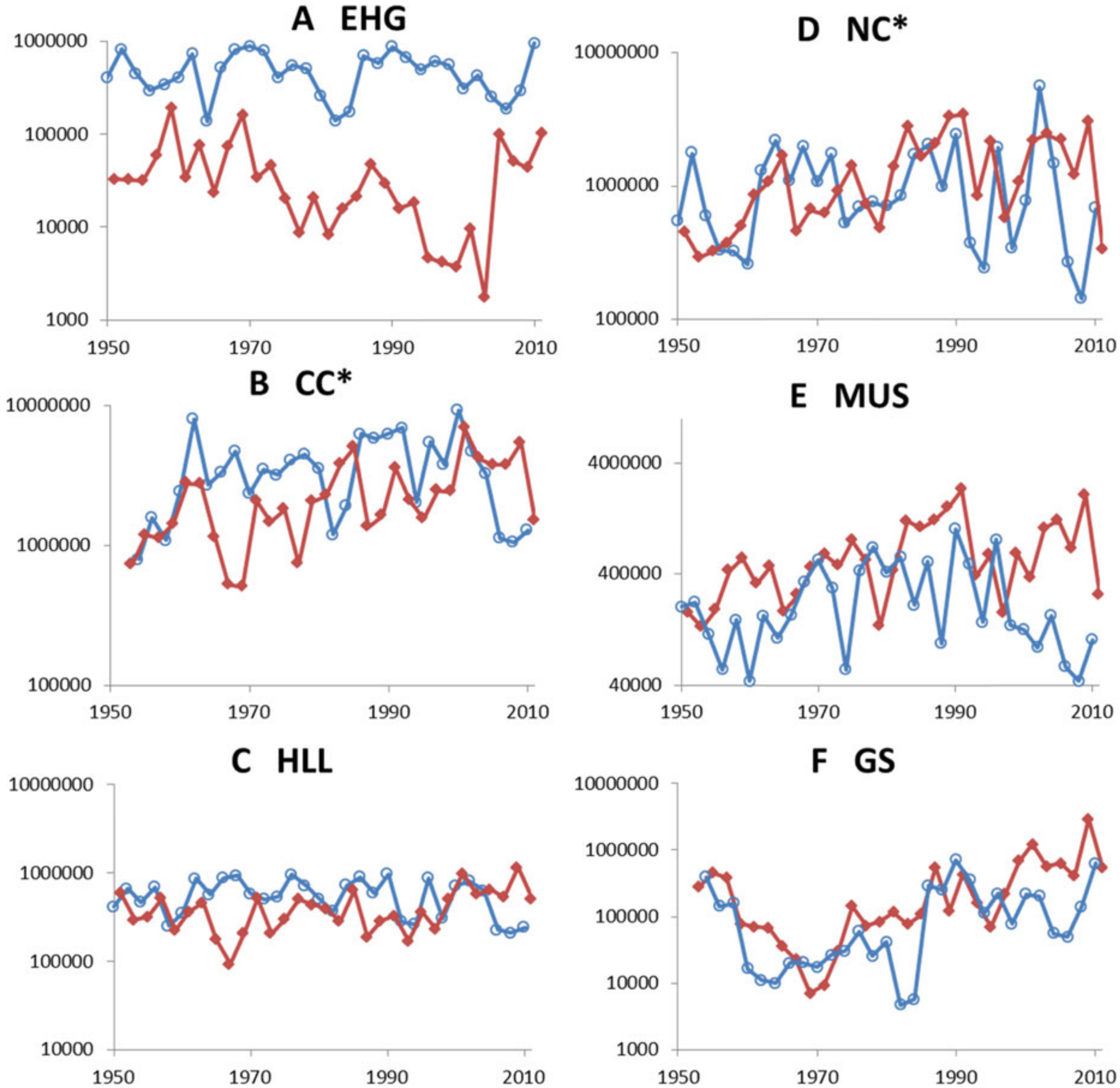

FIGURE 5. Pink Salmon escapement (numbers of fish; $\log_{10}$ scale) for CUs and regions (the latter identified by asterisks) during even (circles) and odd years (diamonds) from 1950 to 2011. Panels are as follows: **(A)** East Haida Gwaii, **(B)** Central Coast, **(C)** Hecate Lowlands, **(D)** North Coast, **(E)** Middle Upper Skeena, and **(F)** the Strait of Georgia. Table A2.1 provides the corresponding CU numbers, Figure 4 the locations, and Figure 6 the data as ratios of even- and odd-year broodlines. [Figure available online in color.]

Pink Salmon, Antonov (2005) and Varnavskaya et al. (1995) (both cited by Radchenko et al. 2007) found that commercial catches of Pink Salmon were highly correlated with returns (i.e., escapement plus catch). Therefore, we considered catch to be a reasonable index of abundance for large geographic regions. A second concern was that spawner numbers were estimated using a variety of methods. Non-Fraser River CU data were analyzed using five separate approaches, each yielding similar results, giving us confidence that the trends that we documented were real. Exploitation rate data were only available for southern British Columbia, and we did not apply these estimates to populations outside this area. Estimates of freshwater and marine productivity for Fraser River Pink Salmon were uncertain because of the small proportion of the fry population sampled (although the methodology was reasonably consistent) as well as methodological changes reflected in the escapement time series. We concluded that the potential benefits of partitioning the life cycle into two stages and evaluating the role of factors in freshwater versus the ocean as well as density dependence outweighed these concerns.

A common theme emerged from the analysis of more than a century's data on Pink Salmon abundance at several scales. Pink Salmon returning to spawn in odd-numbered years became increasingly abundant relative to those returning in even years,

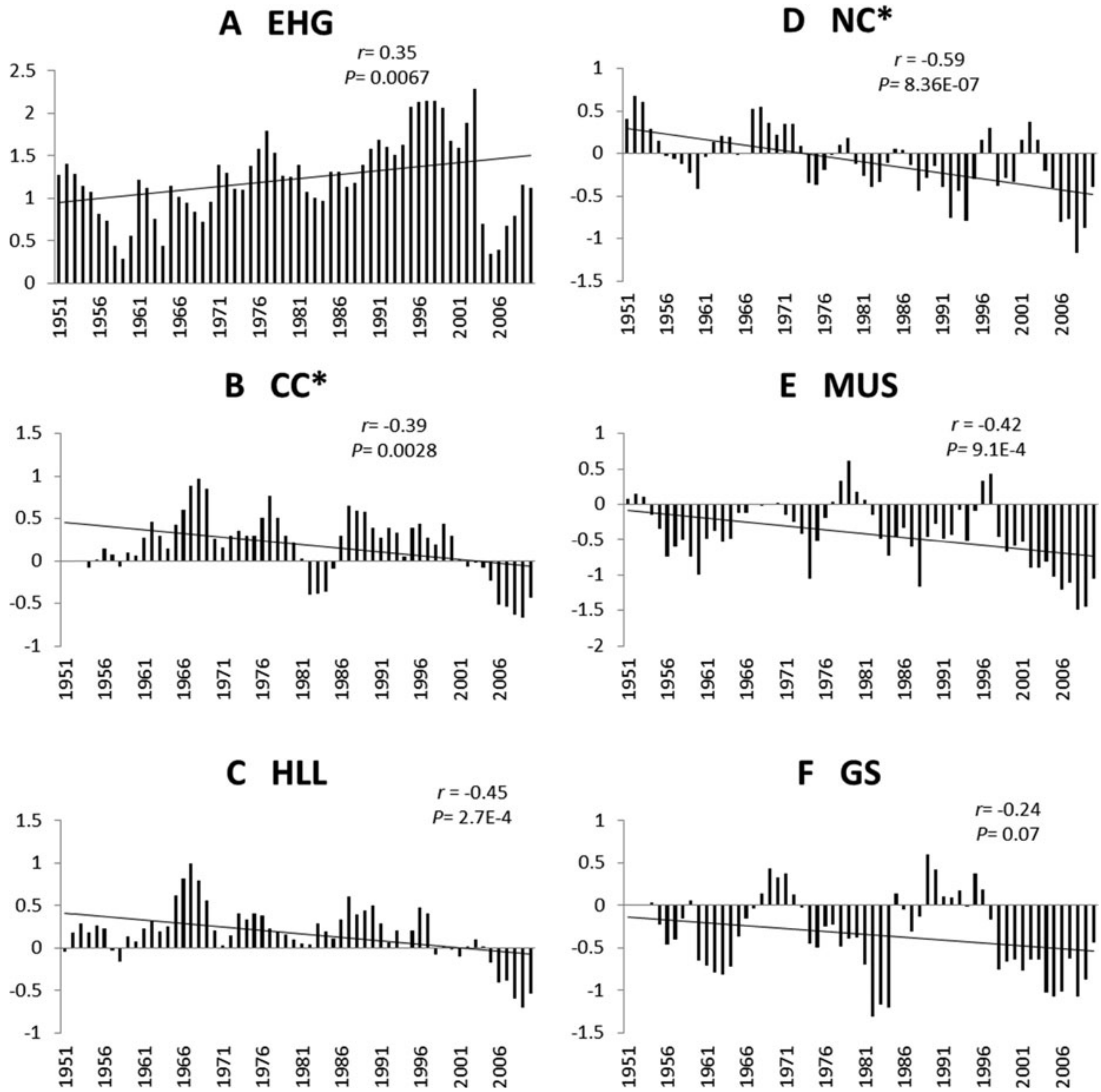

FIGURE 6. Time series of the ratios of the escapement of even-year to odd-year Pink Salmon (log scaled) for the CUs and regions shown in Figure 5 from 1951 to 2010. Positive ratios (those above the horizontal axis) indicate the dominance of even-year fish, negative ratios that of odd-year fish.

and this seemed to be particularly true in the southern areas. This is illustrated by recent record-high Pink Salmon catches on both sides of the North Pacific in which fish returning in odd-numbered years currently dominante; early in this time series (1925–1935), even-year catches often exceeded those of odd years. The same theme is illustrated by the results for British Columbia Pink salmon populations. Of the two data sets in British Columbia in which the even- to odd-year catch ratios in the first half of the 20th century could be examined, there was no temporal pattern for the northern Skeena–Nass rivers while for the more southerly Fraser River the increasing dominance of odd-year Pink Salmon was significant. Of the six areas of British Columbia for which we were able to examine even- to odd-year escapement ratios from 1950 to 2011, there was a significant pattern of increasing dominance for odd-year Pink Salmon in five areas, the exception being Eastern Haida Gwaii, another northern British Columbia area. In addition, evaluation of the escapement-based status of Pink Salmon using five abundance time series approaches shows that it was overwhelmingly positive for 14 odd-year CUs but neutral or negative for 10 even-year CUs.

To explain why odd-year Pink Salmon were generally increasing in dominance, several of Ricker's (1962) hypotheses about the differences between even- and odd-year broodlines were tested with data from the southeastern portion of the species' distribution (primarily British Columbia). Our finding

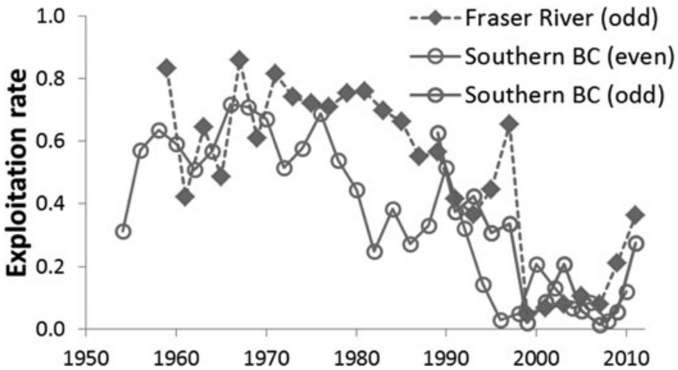

FIGURE 7. Time series of exploitation rates for odd-year Pink Salmon from the Fraser River, other odd-year Pink Salmon from southern British Columbia, and even-year Pink Salmon from southern British Columbia.

that fishery exploitation was higher on odd- than on even-year populations despite the fact that the former had stronger recent returns refutes the hypothesis that differential fishing was responsible for the changing abundance patterns, at least in southern British Columbia. Heard (1991) also discounted mortality

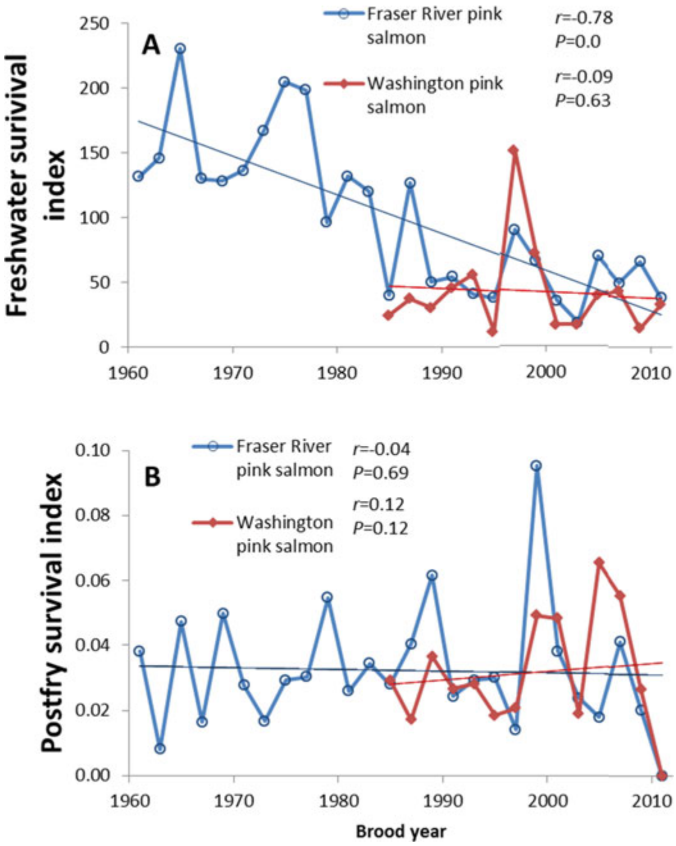

FIGURE 8. **(A)** Freshwater and **(B)** postfry survival indices for Pink Salmon from the Fraser River (fry/spawner and adults/fry, respectively; circles) and Washington State ([fry × 10]/spawner and adults/[fry × 10], respectively; diamonds) from 1961 to 2011. [Figure available online in color.]

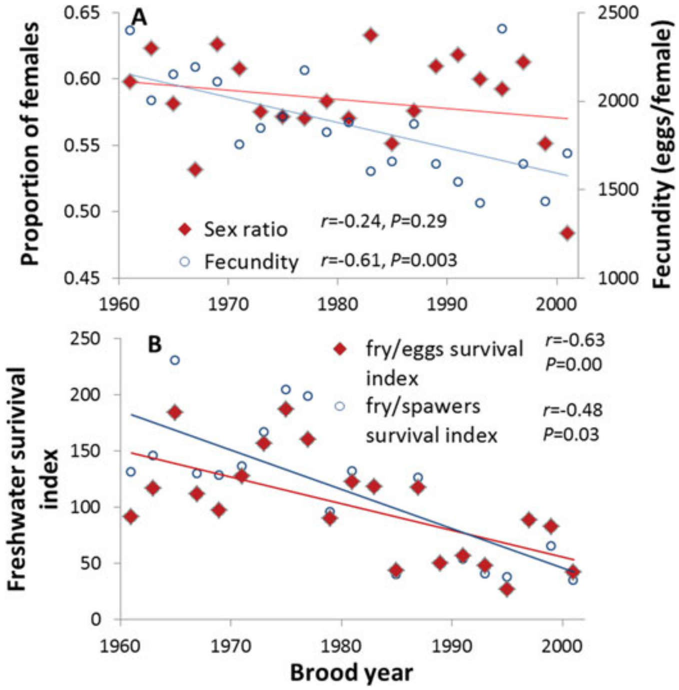

FIGURE 9. Time series of **(A)** the sex ratio (proportion of females) and fecundity and **(B)** freshwater survival indices for Fraser River Pink Salmon from 1961 to 2001. [Figure available online in color.]

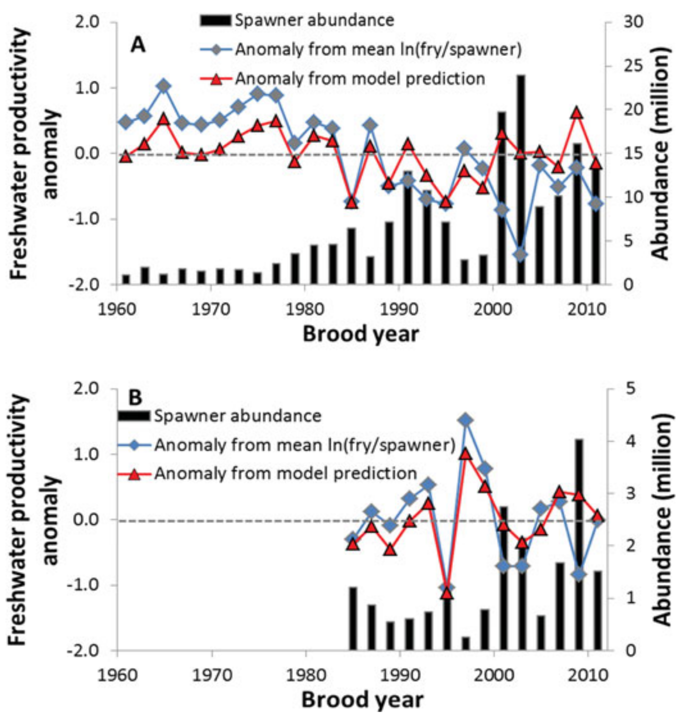

FIGURE 10. Freshwater productivity anomalies from the average (ln[fry/spawner]) and Ricker stock–recruit model predictions from 1961 to 2011 for **(A)** Fraser River and **(B)** Washington State Pink Salmon. Smaller anomalies indicate that the model explained the changes in freshwater productivity better. [Figure available online in color.]

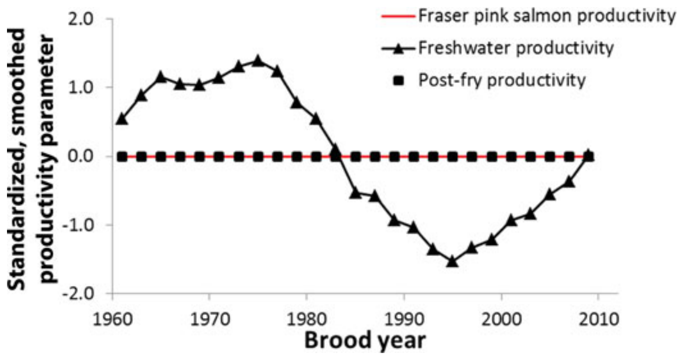

FIGURE 11. Trends in Kalman filter time series of Ricker stock–recruit productivity parameter values representing overall productivity (returning adults/spawner), productivity during the freshwater life history phase (fry/spawner), and productivity during the postfry phase (recruits/fry). [Figure available online in color.]

from fishing, noting that the dominance patterns occurred before the onset of industrial fishing.

Additional hypotheses by Ricker (1962) involved suppressive interactions between broodlines, either through cannibalism, competition for food, or degradation of the freshwater habitat. Krkošek et al. (2011) confirmed that such delayed density-dependent interactions between broodlines, exacerbated by environmental stochasticity, could be most important in determining the differences in abundance between even and odd years. In our study, we found significant negative interactions between even- and odd-year Pink Salmon in two out of six British Columbia regions. In addition, when odd-year Pink Salmon from the Fraser River were included in the Strait of Georgia region, even- and odd-year interactions were significant, probably because of the large numbers of Fraser River salmon. Fraser River Pink Salmon only come in contact with even-year Strait of Georgia Pink Salmon when they are both in the marine environment, primarily the Strait of Georgia. The huge disparity in the numbers of young Pink Salmon in the Strait of Georgia and Puget Sound in alternating years, which is chiefly the result of large numbers of odd-year Pink Salmon from the Fraser River, also correlate with the survival patterns for other salmon species, such as Coho Salmon *O. kisutch* (Beamish et al. 2008) and Chinook Salmon *O. tshawytscha* (Ruggerone and Goetz 2004).

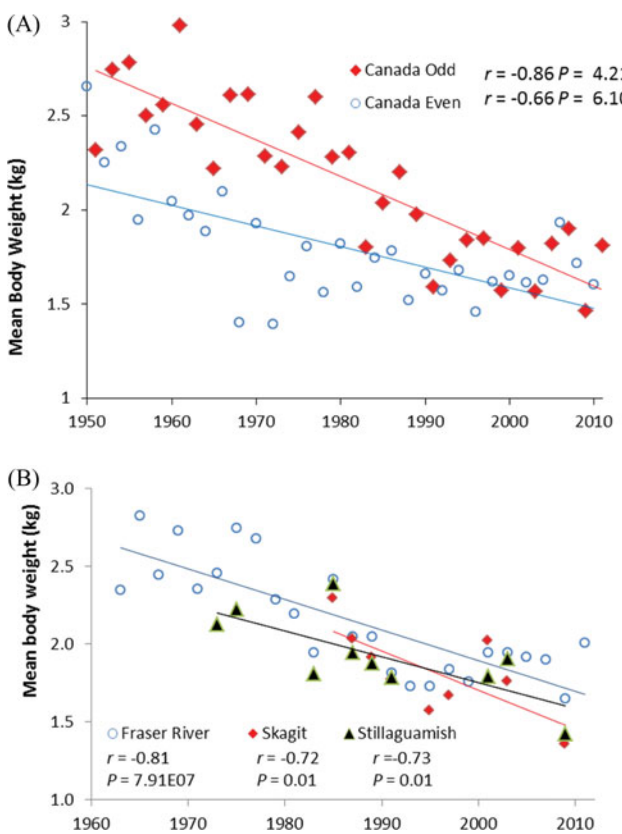

FIGURE 12. Time series and trends in the average body weight of **(A)** British Columbia even- and odd-year Pink Salmon and **(B)** odd-year fish returning to the Fraser River and Washington State (Skagit and Stillaguamish rivers) from 1961 to 2011. [Figure available online in color.]

The mechanism causing broodline interactions has been difficult to identify. Evidence to support the suppression of one broodline by the other by competition for food in the marine environment is limited (Krkošek et al. 2011). In the Sea of Okhotsk, adult Pink Salmon feed on the adult form of a hyperiid amphipod that in its juvenile form may be an important food resource for young Pink Salmon, possibly depleting this food resource for young salmon (Andrievskaya 1970). In the subarctic North Pacific, large numbers of odd-year Pink Salmon decreased the amount of zooplankton in odd years and thereby increased the phytoplankton from April to June (Shiomoto et al. 1997), although this was not demonstrated to lead to competition between odd- and even-year Pink Salmon. Further, the relationships between Pink Salmon and other salmon species in the same areas are poorly understood. For instance, Beamish et al. (2010) found that the growth of young odd-year Pink Salmon in the Strait of Georgia was most rapid during years when the dominant brood of Fraser River Sockeye Salmon *O. nerka* was also present. In summary, although the large numbers of adult (or juvenile) odd-year Fraser River Pink Salmon may deplete food resources for juvenile (or adult) even-year Strait of Georgia populations, we have no direct evidence of this.

Krkošek et al. (2011) also proposed the hypothesis of differential adaptations to geographic clines, citing as evidence the tendency for even-year Pink Salmon to be more abundant in the north and odd-year Pink Salmon to be more abundant in the south. Beacham et al. (2012) found much greater genetic differentiation between even- and odd-year populations of Pink Salmon than regional differentiation within these broodlines. They concluded that the geographic distribution of genetic differentiation for North American Pink Salmon was consistent with dispersal from a northern glacial refugium for even-year Pink Salmon and dispersal from a southern refugium for odd-year Pink Salmon, as proposed by Aspinwall (1974). Churikov and Gharrett's (2002) analysis of mitochondrial DNA variation in Pink Salmon suggests that there were different colonization routes for these separate broodlines. In contrast, Hawkins et al. (2002) concluded from an analysis of allozyme data that even- and odd-year Asian Pink Salmon probably originated from a single population. Beacham et al. (2012) related the spawning distributions of even- and odd-year Pink Salmon to the greater suitability of even-year fish to a colder environment (Beacham and Murray 1988).

Nagata et al. (2007) found that odd-year Pink Salmon from the coast of Hokkaido in the Sea of Okhotsk survived better than even-year fish in warmwater conditions. Before the 1990s, odd-year Pink Salmon were predominant, but beginning in the early 1990s the returns of even-year Pink Salmon surpassed those of odd-year fish. Dominance then appeared to switch back to odd-year fish for the 2002 and 2004 brood years (Nagata et al. 2007). This latter switch corresponds to an increase in the water temperatures encountered by the odd-year line, suggesting that coastal sea surface temperature played a role (Nagata et al. 2007).

A shift toward the increasing dominance of odd-year Pink Salmon in northern British Columbia was not found in the Skeena–Nass rivers during 1900–1950 or in East Haida Gwaii during 1950–2010. Fine-resolution data from Alaska and Russia were not available for this analysis, but we project that in these northerly areas a shift toward increased dominance of odd-year Pink Salmon will be weak or lacking. Differences in the run strength of the even- and odd-year broodlines in Kamchatka were not related to latitude (Radchenko et al. 2007).

Our analysis of Fraser River Pink Salmon data provides insight into the dominance patterns. Using data from Argue and Shepard (2005), it was shown that in the early 20th century significant numbers of Pink Salmon returned to the Fraser River in even years, although odd-year fish were always predominant. Millions of Pink Salmon spawned upstream of the Fraser Canyon prior to their extirpation when large quantities of rock were dumped into the river during railway construction in 1913 and from a rock slide in 1914 (Ricker 1989). During 1939–1949, odd-year Pink Salmon destined for the Fraser River and Puget Sound outnumbered even-year fish by a ratio of 266:1 (Neave 1952). Yet self-sustaining odd-year Pink Salmon runs above the Fraser Canyon did not become reestablished until 1–2 generations following the completion of the Fraser River fishways at Hells Gate in 1947 (Roos 1991; Ricker 1989). Even-year returns of Pink Salmon to the Fraser River decreased to around 1,000 or fewer fish after 1947 (Argue and Shepard 2005), and observations of Pink Salmon in even years are now rare.

The density-dependent reductions in Fraser River freshwater productivity (fry produced per adult) are likely associated with increased concentrations of spawning Pink Salmon in the lower Fraser River. Escapements to the Fraser River have increased in recent years due to reduced exploitation. Yet spawning remains concentrated in the lower river a full century following the depositions of rock in 1913–1914 (Ricker 1989; Pess et al. 2012). For instance, salmon escapement surveys conducted by the DFO in odd years from 1985 to 1991 indicate that over 80% of the spawning occurred in the lower Fraser River. Reduced fecundities, caused by smaller body size, also played a role in the declining freshwater productivity of Fraser River Pink Salmon. Our finding of smaller returning Pink Salmon, which coincided with increasing spawner numbers, corroborates results by other researchers (e.g., Ricker 1981; Bigler et al. 1996). Declining body size was significant for both odd- and even-year British Columbia Pink Salmon as well as odd-year Fraser River and Washington State Pink Salmon. In conclusion, escapements to the Fraser River have increased in recent years in spite of declines in freshwater productivity. It is not possible to speculate on the role of freshwater changes in productivity in other areas.

In summary, odd-year Pink Salmon are increasing their dominance on both sides of the North Pacific Ocean and in several regions of British Columbia, including areas where the separate broodlines share freshwater environments. The increased dominance of odd-year Pink Salmon in southern British Columbia does not appear to be due to differential fishing on the separate broodlines. Odd-year populations in the Fraser River and Puget Sound increased in response to declining exploitation, despite density-dependent reductions in freshwater production. The tendency for even-year Pink Salmon to be most predominant in the northern part of their range and odd-year salmon in the southern part is consistent with the even-year broodline being better adapted to cool conditions (Beacham et al. 2012). The negative density-dependent interactions between broodlines found by Krkošek et al. (2011) and this study could result from competition in the marine environment, but there is little evidence for this. The recent increasing dominance of odd-year Pink Salmon in the south could also be explained by negative interactions if warming is occurring and odd-year fish are favored under warming conditions. Beamish et al. (2004) found clear links between marine survival and climate regimes for odd-year Fraser River Pink Salmon. We encourage detailed examination of the survival patterns of even- and odd-year Pink Salmon from other areas and possible associations between these patterns and climate change as a way to better understand the abundance patterns of this intriguing species.

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Appendix 1: Approaches to Examining the Time Series Patterns of Abundance Data

As noted in the text, five different approaches were used to examine the time series data on the abundance of Pink Salmon. In the first and second approaches, the aggregate annual abundance for each region or conservation unit (CU) was $\log_{10}$ transformed, and then the significance of the slope (least-squares regression) for the most recent 20 years (approach 1) or the entire time series (approach 2) was determined. The slope of the regression line designated the unit as green (increasing abundance), amber (unchanged abundance), or red (decreasing abundance) (Table 2).

In the third approach, the geometric mean catch or escapement for the most recent generation (i.e., 2 years) and the most recent five generations was divided by the geometric mean for the entire time series. The resulting ratios determined status: red if the ratio was <0.5, green if it was ≥ 0.75, and amber if it fell between these benchmarks. These two scores were combined into a single score based on Table 2 and Table A1.1.

The fourth approach used the earliest part of the time series as a historical baseline with which to compare the unit's current status (Table 2). This approach is similar to one found to be among the most accurate in identifying population units at risk of decline while avoiding false positives (i.e., characterizing the abundance as declining when it is not; Porszt et al. 2012).

In the fifth approach, the percentage change in the $\log_{10}$ transformed data over the most recent 20 years (e.g., 1991—2011 or 1990–2010 for escapement data) was computed (Table 2).

TABLE A1.1. Method of combining the ratio of the geometric mean of the most recent generation to the geometric mean of the entire time series with the corresponding ratio for the geometric mean of the last five generations in approach 3 (Table 2; L. B. Holtby, DFO, personal communication).

Most recent five generations	Most recent generation		
	Red	Amber	Green
Red	Red	Red	Red
Amber	Red	Amber	Green
Green	Amber	Green	Green

APPENDIX REFERENCE

Porszt, E. J., R. M. Peterman, N. K. Dulvy, A. B. Cooper, and J. R. Irvine. 2012. Reliability of indicators of decline in abundance. Conservation Biology 26:894–904.

Appendix 2: Detailed Data

TABLE A2.1. Even-year (left-hand side) and odd-year (right-hand side) CU numbers and codes, number of rivers per CU in the NuSEDs database (T), number of rivers in lagged correlation analysis (S), first year of data collection, and inverse of the scalar used to generate the total estimate.

No.	CU code[a]	T	S	First year	Inverse of scalar	No.	CU code[a]	T	S	First year	Inverse of scalar
1	TranFjs	1	0			14	TranFjs	1	0		
2	UpNass	6	0			15	UpNass	5	0		
3	NSE	164	19	1950	0.69	16	NSE	36	9	1951	0.36
4	HSFjs	146	61	1950	0.84	17	LOSK	58	3	1951	0.62
6	NWVI	35	0			18	NPO	60	10	1951	0.70
						19	HSFjs	104	49	1951	0.88
7	MUS	57	2	1950	0.68	20	HKSRBCD	69	10	1951	0.94
8	NHG	16	7	1950	0.88	21	Nahwitti	24	3	1953	0.82
9	WHG	66	8	1950	0.78	22	SFjs	48	11	1953	0.91
10	EHG	100	18	1950	0.91	23	EVIJS	12	2	1951	0.62
11	HLL	178	37	1950	0.62	24	MUS	65	3	1951	0.68
12	GS	66	7	1954	0.74	25	NHG	13	0		
13	WVI	85	6	1954	0.12	26	WHG	39	0		
						27	EHG	58	3	1951	0.71
						28	HSLL	181	34	1951	0.56
						29	GS	72	9	1953	0.34
						30	EHSBI	13	0		
						31	WVI	67	0		
						32	Fraser	1	1	1961	
						33	Wash[b]	1	1	1959	

[a]See Figure 4 for CU freshwater locations. Even-year CUs are as follows: 1 = transboundary fjords, 2 = upper Nass River, 3 = Nass–Skeena estuary, 4 = Hecate Strait fjords, 5 = southern Ffjords, 6 = northwest Vancouver Island, 7 = middle–upper Skeena River, 8 = North Haida Gwaii, 9 = West Haida Gwaii, 10 = East Haida Gwaii, 11 = Hecate Lowlands, 12 = Strait of Georgia, and 13 = West Vancouver Island; odd-year CUs are as follows: 14 = transboundary fjords, 15 = upper Nass River, 16 = Nass–Skeena estuary, 17 = lower Skeena River, 18 = Nass–Portland Observatory, 19 = Hecate Strait fjords, 20 = Homathko-Klinaklini-Smith-Rivers-Bella Coola-Dean, 21 = Nahwitti River, 22 = southern fjords, 23 = East Vancouver Island–Johnstone Strait, 24 = middle–upper Skeena River, 25 = North Haida Gwaii, 26 = West Haida Gwaii, 27 = East Haida Gwaii, 28 = Hecate Strait Lowlands, 29 = Strait of Georgia, 30 = East Howe Sound–Burrard Inlet, 31 = West Vancouver Island, 32 = Fraser River, and 33 = Washington State (primarily Puget Sound).

[b]Not technically a CU, though treated like one for this analysis.

TABLE A2.2. Exploitation rates for Fraser River and even- and odd-year southern British Columbia Pink Salmon populations, 1954–2011 (see Figure 7 in the main text); NA = not available.

		Southern British Columbia	
Year	Fraser River	Even year	Odd year
1954		0.31	
1955	NA		NA
1956		0.57	
1957	NA		NA
1958		0.63	
1959	0.83		NA
1960		0.59	
1961	0.42		NA
1962		0.51	
1963	0.64		NA
1964		0.57	
1965	0.49		NA
1966		0.72	
1967	0.86		NA
1968		0.71	
1969	0.61		NA
1970		0.67	
1971	0.82		NA
1972		0.51	
1973	0.74		NA
1974		0.58	
1975	0.72		NA
1976		0.69	
1977	0.71		NA
1978		0.54	
1979	0.75		NA
1980		0.45	
1981	0.76		NA
1982		0.25	
1983	0.70		NA
1984		0.38	
1985	0.66		NA
1986		0.27	
1987	0.55		NA
1988		0.33	
1989	0.56		0.63
1990		0.52	
1991	0.42		0.38
1992		0.32	
1993	0.37		0.42
1994		0.14	
1995	0.44		0.31
1996		0.03	
1997	0.65		0.34
1998		0.05	
1999	0.05		0.02
2000		0.21	
2001	0.07		0.09
2002		0.13	
2003	0.08		0.21
2004		0.07	
2005	0.11		0.06
2006		0.08	
2007	0.08		0.01
2008		0.03	
2009	0.21		0.06
2010		0.12	
2011	0.36		0.28

TABLE A2.2. Continued.