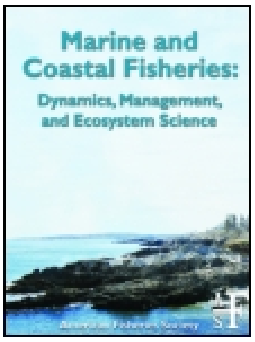

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ARTICLE

Spatial and Temporal Patterns in Smolt Survival of Wild and Hatchery Coho Salmon in the Salish Sea

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Abstract

Understanding the factors contributing to declining smolt-to-adult survival (hereafter "smolt survival") of Coho Salmon *Oncorhynchus kisutch* originating in the Salish Sea of southwestern British Columbia and Washington State is a high priority for fish management agencies. Uncertainty regarding the relative importance of mortality

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operating at different spatial scales hinders the prioritization of science and management activities. We therefore examined spatial and temporal coherence in smolt survivals for Coho Salmon based on a decision tree framework organized by spatial hierarchy. Smolt survival patterns of populations that entered marine waters within the Salish Sea were analyzed and compared with Pacific coast reference populations at similar latitudes. In all areas, wild Coho Salmon had higher survival than hatchery Coho Salmon. Coherence in Coho Salmon smolt survival occurred at multiple spatial scales during ocean entry years 1977–2010. The primary pattern within the Salish Sea was a declining smolt survival trend over this period. In comparison, smolt survival of Pacific coast reference populations was low in the 1990s but subsequently increased. Within the Salish Sea, smolt survival in the Strait of Georgia declined faster than it did in Puget Sound. Spatial synchrony was stronger among neighboring Salish Sea populations and occurred at a broader spatial scale immediately following the 1989 ecosystem regime shift in the North Pacific Ocean than before or after. Smolt survival of Coho Salmon was synchronized at a more local scale than reported by other researchers for Chinook Salmon *O. tshawytscha*, Pink Salmon *O. gorbuscha*, Chum Salmon *O. keta*, and Sockeye Salmon *O. nerka*, suggesting that early marine conditions are especially important for Coho Salmon in the Salish Sea. Further exploration of ecosystem variables at multiple spatial scales is needed to effectively address linkages between the marine ecosystem and Coho Salmon smolt survival within the Salish Sea. Since the relative importance of particular variables may have changed during our period of record, researchers will need to carefully match spatial and temporal scales to their questions of interest.

During their ocean residence, Pacific salmon *Oncorhynchus* spp. travel thousands of kilometers through spatially and temporally dynamic environments. Survival in the marine environment plays a major role in determining the numbers of adult Pacific salmon recruiting to fisheries and returning to freshwater to spawn (Pearcy 1992). Most Pacific salmon “marine survival” estimates cover the period from when smolts leave their spawning stream to when they return and, therefore, include some freshwater effects; hereafter we refer to these as “smolt survival” estimates. Understanding factors that influence smolt survival and using this information to predict Pacific salmon run sizes has proven to be a challenging undertaking (Dorner et al. 2013; Irvine and Akenhead 2013). When smolt survival patterns are compared among populations and species, results can provide important insight into the factors contributing to survival. When smolt survival patterns are similar across broad geographic regions, this suggests that broad-scale climate conditions are affecting survival (Mantua et al. 1997; Beamish et al. 1999b; Mueter et al. 2007; Peterman and Dorner 2012). In comparison, synchronous smolt survival patterns found only for populations within a limited geographic region suggest that local factors, disconnected from broad-scale drivers, are having the greatest influence on survival (Pyper et al. 2005; Beamish et al. 2012). Furthermore, when smolt survival patterns differ between species or regions, these contrasts can inform hypotheses and future study of the key factors affecting survival.

The marine environment is linked to the survival of Pacific salmon, such as Coho Salmon *Oncorhynchus kisutch*, at many spatial scales. For example, at the broadest scale, Coho Salmon populations entering the Gulf of Alaska Current north of Vancouver Island have had different smolt survival patterns than those entering the California Current south of this location (Coronado and Hilborn 1998a; Hobday and Boehlert 2001; Teo et al. 2009). At the scale of the California Current, smolt survival among Coho Salmon populations exhibit some synchrony (Beamish et al. 2000; Botsford and Lawrence 2002); however, several studies have noted different smolt survival patterns for populations that enter the California Current but originate inside versus outside the Salish Sea (Coronado and Hilborn 1998a; Hobday and Boehlert 2001; Beetz 2009). The Salish Sea encompasses the network of inland marine waters from the northern extent of the Strait of Georgia within British Columbia to the southern extent of Puget Sound in Washington State and includes the Strait of Juan de Fuca that connects the Salish Sea to the California Current (Figure 1A). The Strait of Georgia basin can be divided into northern, central, and southern subbasins based on physical factors, such as water depth, salinity, turbidity, and currents (Thomson 2014). Similarly, Puget Sound basin is comprised of four major subbasins, Whidbey Basin, Central Puget Sound, South Puget Sound, and Hood Canal (Babson et al. 2006; Moore et al. 2008b). Smolt survival differences at this subbasin scale have not been demonstrated.

In recent decades, several salmonid species that spawn in watersheds draining into the Salish Sea (e.g., Coho Salmon, Chinook Salmon *O. tshawytscha*, and steelhead *O. mykiss*) have returned in increasingly low numbers (Coronado and Hilborn 1998b; Scott and Gill 2008; Beamish et al. 2010), whereas other species (e.g., odd-year returning Pink Salmon *O. gorbuscha*) have returned in unprecedented high numbers (Irvine et al. 2014). Understanding factors contributing to these declines is a high priority for fish management agencies in the Pacific Northwest. Uncertainty in the relative importance of mortality operating at different spatial scales hinders the prioritization of science and management activities. This paper focuses on smolt survival of Coho Salmon in the Salish Sea and adds more than a decade of information to previous analyses for this species (Coronado and Hilborn 1998a; Beamish et al. 2000), explores heterogeneity within the Salish Sea, and provides a framework for future investigation of explanatory factors.

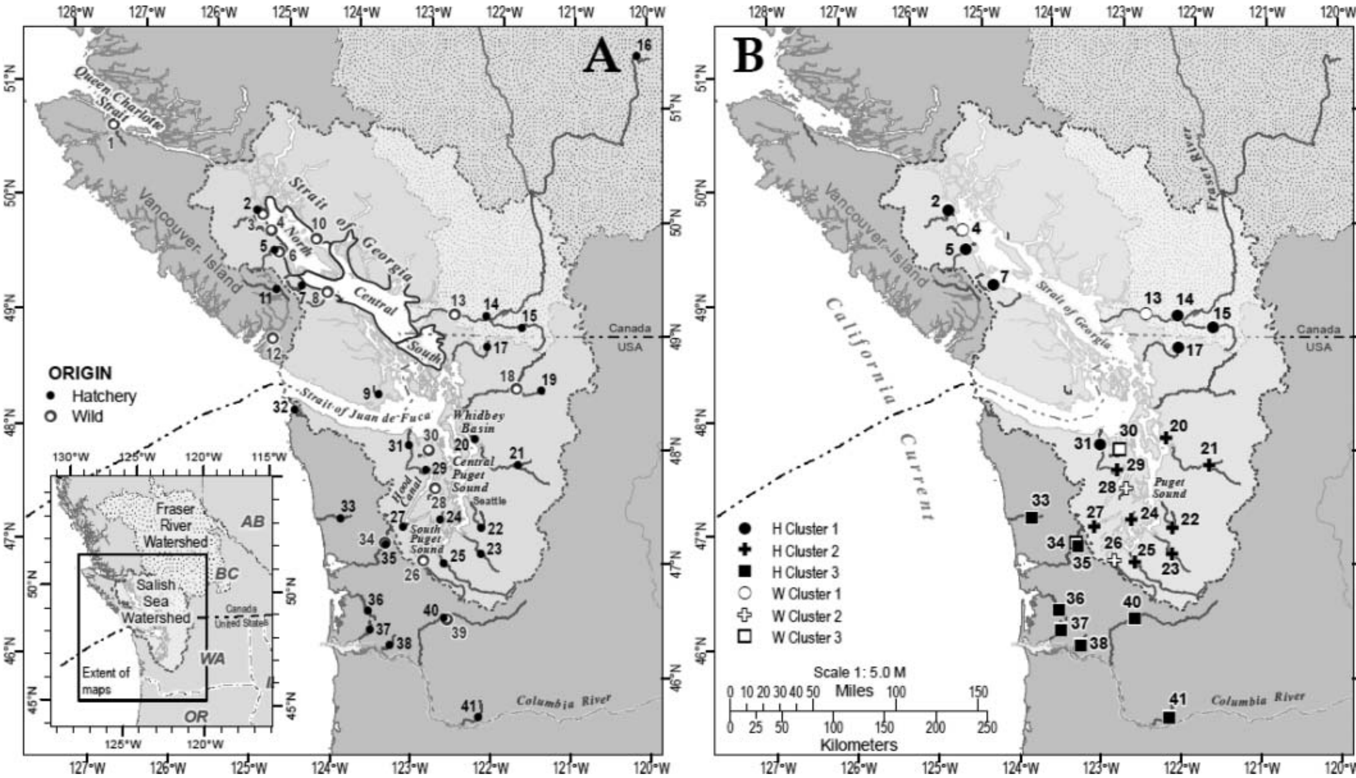

FIGURE 1. Study area showing **(A)** the major oceanographic areas and locations of Coho Salmon populations (open circle = wild, filled circle = hatchery) and **(B)** the spatial organization of cluster analysis groupings for the Strait of Georgia (circles), Puget Sound (crosses), and the Pacific coast (squares). Numbers correspond to population information provided in Table 1.

The primary objectives of this study were to examine patterns of spatial and temporal coherence in smolt survival for wild and hatchery Coho Salmon populations within the Salish Sea and to identify appropriate spatial scales for the subsequent identification of key ecosystem variables. These objectives were addressed using a decision tree framework (Figure 2) that connects the scale of survival patterns within multiple populations entering the California Current to the scale of ecosystem variables. In addition to populations within the Salish Sea, we also examined smolt survivals for Pacific coast reference populations from the Columbia River, Washington coast, and western and northeastern coasts of Vancouver Island. Since only populations originating from the Salish Sea spend time rearing and growing in the inland sea environment, survival differences between Salish Sea and Pacific coast reference populations were likely attributable to their early marine behavior and ecology. Coho Salmon smolt survival was also compared between and within the two primary basins of the Salish Sea (Puget Sound versus Strait of Georgia) and the subbasins within each primary basin.

Five separate analyses were used in combination to examine the patterns of spatial and temporal coherence in smolt survival of hatchery and wild Coho Salmon. The first two analyses investigated the smolt survival patterns without prior geographic assignment. A cluster analysis identified population groupings based on smolt survival. An exponential decay model examined the strength of survival correlations as a function of distance for the entire time series and for three preassigned time periods corresponding to major climatic regimes in the North Pacific Ocean. The next three analyses investigated smolt survival patterns at preassigned spatial scales identified in the decision tree (Figure 2). A regional mixed-effects model tested the contribution of geographic regions (Salish Sea versus outside the Salish Sea, Strait of Georgia versus Puget Sound) to Coho Salmon smolt survival. Linear regression and structural change analysis identified temporal trends and whether breakpoints occurred at these spatial scales. Residuals from this regional model were used in a second mixed-effects model to test whether smolt survival of Salish Sea populations covaried with Pacific coast populations (California Current scale) and whether survival differed at the subbasin scale. Finally, we calculate effect sizes to compare the relative contributions of patterns at multiple scales with the overall variation in survival.

METHODS

Populations.—Stream populations, identified by their stream of origin and the location of monitoring activities, were

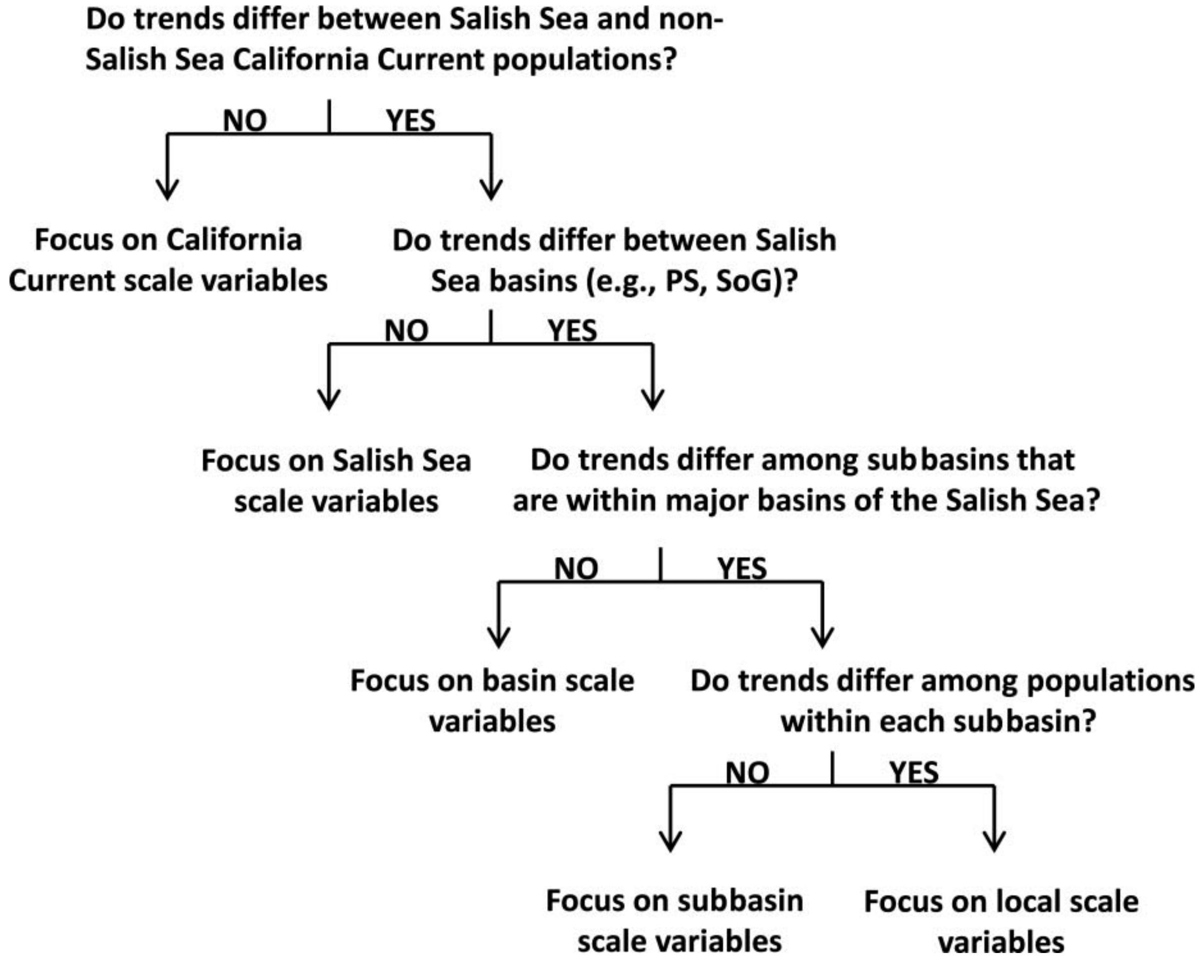

FIGURE 2. Decision tree showing the series of dichotomous questions regarding survival patterns that are used to infer an appropriate scale for considering environmental variables associated with the observed patterns (SoG = Strait of Georgia, PS = Puget Sound).

groups of fish produced either by natural spawning ("wild") or in hatcheries and represented the major areas within the Salish Sea, as well as locations on the western and northeastern coasts of Vancouver Island, the Olympic Peninsula, southwestern Washington, and the lower Columbia River (Figure 1; Table 1). One population (Louis Creek) in the Thompson River (tributary to the Fraser River) watershed originates outside the terrestrial geographic boundaries of the Salish Sea but migrates into and through the Salish Sea and was therefore included with the Strait of Georgia populations.

Smolt survival estimates.—Our measures of smolt survival included survival from the release location in freshwater, which was often upstream of the marine entry point; therefore, we chose not to use the term marine survival. Smolt survival was the estimated number of 3-year-old Coho Salmon caught in all fisheries plus the number of 3-year-old Coho Salmon escaping fisheries to return to the rivers or hatchery to spawn divided by the number of smolts that produced these adults. Age 3 is the typical age of returning spawners in the Salish Sea region (Sandercock 1991; Labelle et al. 1997) and represented the majority of the adult returns in most of our datasets. Jacks (precocious 2-year male Coho Salmon) were not included in the analysis because they rarely contribute to fisheries; their small size makes them difficult to enumerate (Irvine et al. 1992), resulting in estimates of unknown accuracy and precision.

The primary method to estimate smolt survival was based on the release and subsequent recovery of coded-wire-tagged (CWT) Coho Salmon smolts (Table 1). Tag data for U.S. populations were retrieved from the coastwide CWT database (www.rmpc.org). Tag data for Canadian populations were retrieved from the Mark Recovery Program database (Kuhn et al. 1988) and regional agency datasets (S. Baillie, Fisheries and Oceans Canada in Nanaimo, British Columbia, personal communication). A second estimation method relied on estimates of smolts leaving a system during the spring and adults returning during the fall and winter 18 months later. Smolt survival estimates using this second approach will be biased high if there are significant numbers of Coho Salmon subyearlings leaving the system in fall that survive to adulthood, as was found for some streams in our study area (Craig et al. 2014; Bennett et al. 2015). For this second method, spawner escapement estimates were expanded by exploitation rate, either modeled or calculated using tag recoveries of a nearby population, in order to include the fish retained in fisheries in the survival estimates. Modeled exploitation rates (CoTC 2013) were estimated using either a mixed-stock model based on annual CWT recoveries or using backwards runs of the Fishery Regulation Assessment Model. The Fishery Regulation Assessment Model is a comprehensive fishery model used to plan and assess the impacts of mixed-stock ocean fisheries on Coho Salmon stocks from Alaska to California (PFMC 2008).

Selection criteria were developed in order to remove the CWT codes that were likely to be affected by year-specific factors other than marine conditions. Tag codes from Puget Sound populations were ignored prior to 1977 releases due to concerns about incomplete fishery and escapement sampling. Additional criteria for excluding CWT codes included no sampling data from major fisheries impacting that population, missing escapement recoveries for age-3 returns, incorrectly cut tag lengths, known disease noted for smolts upon release, poor environmental conditions noted at release, fish that were part of a sterilization experiment and genetically altered (e.g., triploid), or release at the fry rather than smolt life stage. Net pen or sea pen releases were not used, as fish escaping terminal fisheries were not likely to be well documented (one exception was three tag codes from the Big Qualicum Estuary sea pen releases in 1989 because estimated smolt survival was similar to the releases from Big Qualicum Hatchery). Eighty-four percent of the tag codes met these criteria and were summed by year and watershed (hatchery and wild separately).

Groupings in smolt survival without prior assignment.—A cluster analysis identified population groups with similar patterns in smolt survival. Because this analysis did not use prior information about geographic regions, the results could be used to objectively examine whether patterns in smolt survival were associated with population characteristics, including geography and origin (i.e., hatchery versus wild). The time series used in this analysis included 28 populations (including 7 wild) that spanned ocean entry years (OEYs) 1977–2010 (Table 1). Datasets had a minimum of 19 years that met the selection criteria and were not truncated on either extreme (e.g., a time series with 19 years beginning in 1992 would not be included in this analysis, whereas a time series with 19 years of data beginning in 1980 would be included).

Ward's hierarchical cluster analysis, which minimizes within-group variance among clusters, described associations among populations based on Euclidian distances between annual smolt survival estimates (Legendre and Legendre 2012). Prior to analysis, all data were logit transformed and scaled to a mean of 0 and standard deviation of 1. As a result of these transformations, the cluster analysis identified similarities in data trends (e.g., high and low years), removing among-population differences in the magnitude of smolt survival. Statistical support for the cluster groupings was examined with a multiscale bootstrap resampling technique using the pvclust package in R version 3.1 (Suzuki and Shimodaira 2006). The approximately unbiased P-value from this analysis represented the statistical support for each branch of the dendrogram based on N = 10,000 bootstraps. A P-value greater than or equal to 95% was considered to be strong support.

Smolt survival correlations over distance and time.—Correlograms and correlation-by-distance analyses were conducted on the entire data series and the data series divided into three OEY time periods (1977–1988, 1989–1997, and 1998–2010). These time periods were selected because they have been identified as regimes in the physical climate of the North Pacific Ocean (Overland et al. 2008). The end of the last time period (1998–2010) represented the end of the time series, not an identified regime break. These analyses tested whether time periods associated with broad-scale (i.e., climate) environmental changes could be linked to different scales of smolt survival correlations among Coho Salmon populations.

Correlograms visually displayed the strength and direction of the correlations (Pearson's product-moment correlation coefficients) among populations for the entire data set and among the three time periods. Smolt survival data were logit transformed and scaled prior to analysis. Correlations among a single set of populations with overlapping data in all three time periods were used so that patterns could easily be compared across time periods. At least 5 years of overlapping data within each time period were required, resulting in 17 populations being included in the display.

The rate of decay in pairwise correlations was modeled as a function of distance between populations. All populations with overlapping smolt survival estimates in a given time period were used. A geographic information system (GIS) was used to create a series of path distance arrays and to calculate distance over sea between points of entry into the marine environment. Data were fit with an exponential decay model (Myers et al. 1997; Pyper et al. 2005):

$$\rho(d) = \rho_o e^{-d/v},$$

where $\rho(d)$ was the survival correlation measure and d the distance between marine entry locations. The intercept, ρ_o, represented the correlation between neighboring populations, and the parameter v (e-folding scale) was the distance at which the population correlations were reduced by 37% (i.e., $e^{-1} \times 100\%$). The fit of the exponential decay model was weighted by the number of years of data for each population, and parameters were estimated with nonparametric bootstrap sampling with replacement (1,000 iterations) using the stats package in R version 3.1 (R Development Core Team 2014). In order to compare results from this study with those previously published (Pyper et al. 2005; Teo et al. 2009; Kilduff et al. 2014), the analysis was first conducted allowing the intercept (ρ_o) to vary and then conducted while constraining the intercept to a constant value of 1. The fit of the unconstrained and constrained models to the data was compared using Akaike information criteria corrected for small sample size (AIC_c; Burnham and Anderson 2002). For all analyses, models were considered to have strong support when the difference in AIC_c values between the best (lowest AIC_c) and a given model was less than three.

Smolt survival patterns at Salish Sea and basin scales.—A model selection process was used to evaluate the differences in smolt survival among geographic regions. Linear mixed-effect models evaluated the fixed effects explicitly accounted for in the study design, while taking into account the random effects that were not strictly controlled for in the analysis (Stroup 2012). The model evaluated whether geographic region (Table 1; Pacific coast, Strait of Georgia, or Puget Sound), origin (wild or hatchery origin), and year explained variation in smolt survival; population was a random effect in all analyses. All populations with available data were included in the regional analysis, except for three populations as explained below. This analysis was restricted to OEYs $\geq$ 1977 because this was the first year of data for many populations.

Several of the populations did not fall neatly into any of the three regions in the first analysis. The Keogh River (number 1 in Table 1; Figure 1A) was assigned to the Pacific coast region, as this population enters marine waters (Queen Charlotte Strait) at the north end of Vancouver Island that connect most directly with the Pacific Ocean. Goldstream River (number 9), Snow Creek (number 30), and Dungeness River (number 31) populations enter the Strait of Juan de Fuca, which has oceanographic characteristics more similar to the Pacific Ocean shelf than the inland waters of the Strait of Georgia (Johannessen et al. 2006; Masson and Pena 2009). Because the Strait of Juan de Fuca lies within the geographic boundaries of the Salish Sea but did not obviously assign to either the Puget Sound or Strait of Georgia region, these populations were excluded in the mixed-effects model analysis.

A series of models examined whether geographic region, origin (hatchery or wild), year, and possible two-way interactions predicted variation in smolt survival. The AIC was used to compare the model probabilities given the data. Akaike information criteria values were not corrected for small sample size as the number of samples (independent survival estimates) were well above the threshold where small sample size issues are a problem. (Burnham and Anderson 2002). The strength of support for each model was based on model weights. Year was modeled as a linear covariate to determine trend. An autoregressive error structure with a 3-year lag was used for all analyses, as this structure matched the dominant 3-year Coho Salmon life cycle and resulted in the lowest AIC values when compared with the same model with other possible autoregressive and autoregressive moving-average variance structures. Unlike the cluster analysis, in which data were logit transformed and scaled (mean of 0, standard deviation of 1), the mixed-effects model analyses were performed on logit-transformed but nonscaled data. Consequently, the two analyses explored smolt survival patterns in different ways; the mixed-effects model focused on differences in the magnitude of smolt survival among explanatory variables, whereas the cluster analysis focused on similarities in smolt survival trends (high years versus low years).

The regional model evaluated whether smolt survival differed among the three geographic regions (Pacific coast, Strait of Georgia, and Puget Sound) but did not determine how smolt survival differed at these two scales in our decision tree (Figure 2). Furthermore, the use of year as a covariate in the regional model assumed smolt survival trends were consistent over time. A temporal shift in smolt survival trends might be expected given the reported shifts in climate regimes during the time series (Overland et al. 2008; Perry and Masson 2013).

In order to simultaneously evaluate the differences between the Salish Sea and the Pacific coast and between the Strait of Georgia and Puget Sound, linear regressions were applied to smolt survival time series from the Pacific coast, Strait of Georgia, and Puget Sound and structural changes in these time series were investigated using the strucchange package in R (Zeileis et al. 2002). Smolt survival data used in this analysis were the annual predicted smolt survival values (hatchery and wild combined) from the regional mixed-effects model for the Pacific coast, the Strait of Georgia, and Puget Sound. This analysis allowed both the intercept and slope of the time series segments to vary and tested whether a “shift,” or a change in trend, was supported by the data. A comparison of AIC_c values was used to determine whether one breakpoint was more likely than no breakpoints in the data set. The fit of a breakpoint to the data set was determined with an F-test calculated from the ordinary least-squares residuals of segmented and nonsegmented models (Zeileis et al. 2003). Analysis was conducted on logit-transformed smolt survival data. Differences between Pacific coast, Strait of Georgia, and Puget Sound time series were supported if the slope for one regression was outside the 95% confidence interval of the regression slope for the contrasting region. For time series in which more than one linear trend was identified, the breakpoint year and associated confidence intervals were calculated.

Regional coherence and smolt survival patterns at a subbasin scale.—The results from the mixed-effects model of regional variation and structural change analysis did not address whether smolt survival differed among subbasins within the Salish Sea or whether covariation in survival between Salish Sea and Pacific coast reference populations was significant. In order to investigate smolt survival patterns at both these spatial scales, primary trends identified in the regional model were removed from the survival data. Residual annual smolt survival for each Salish Sea population was the response variable in a mixed effects model and was the difference between the annual population estimates and annual predictive smolt survival from the best regional model. Subbasin and Pacific coast residual survivals were the fixed effects and population was the random effect. Subbasins included seven subbasin delineations within Puget Sound

TABLE 1. List of Coho Salmon populations used for the analysis of smolt survival patterns. Location is listed by biogeographic region (PC = Pacific coast, SS = Salish Sea), Salish Sea basin (SoG = Strait of Georgia, PS = Puget Sound, JDF = Strait of Juan de Fuca), Salish Sea subbasin, and watershed. The watershed number refers to the map number in Figure 1. The origin is either hatchery (H) or wild (W). Ocean entry years (OEYs) include the first and last year of data, the number in parentheses is the number of years of data (excluding gaps) within the range. Method describes the way in which smolt survival was calculated. Method 1 was based on a coded wire tag reconstruction. Method 2 was smolt and spawner counts from weirs expanded by an exploitation rate that was either modeled (2.1) or based on coded wire tag recoveries from a neighboring population (2.2).

Region	Salish Sea basin	Salish Sea subbasin	Watershed	Origin	OEY	Method
PC			1. Keogh River	W	1997–2010 (14)	2.1
SS		Northern SoG	2. Quinsam River	H	1976–2010 (35)	1
SS	SoG	Northern SoG	3. Simms Creek	W	1998–2008 (11)	2.1
SS	SoG	Northern SoG	4. Black Creek	W	1978–2010 (27)	1
SS	SoG	Northern SoG	5. Puntledge River	H	1978–2004 (25)	1
SS	SoG	Northern SoG	6. Millard Creek	W	1999–2006 (8)	2.1
SS	SoG	Central SoG	7. Big Qualicum River	H	1973–2010 (37)	1
SS	SoG	Central SoG	8. Englishman River	W	1998–2010 (9)	2.1
SS	JDF		9. Goldstream River	W	1998–2010 (12)	1
SS	SoG	Northern SoG	10. Myrtle Creek	W	2001–2010 (9)	1
PC			11. Robertson Creek	H	1998–2010 (13)	1
PC			12. Carnation Creek	W	1998–2010 (13)	2.2
SS	SoG	Central SoG	13. Salmon River	W	1986–2007 (17)	1
SS	SoG	Central SoG	14. Inch Creek	H	1984–2010 (27)	1
SS	SoG	Central SoG	15. Chilliwack River	H	1982–2004 (20)	1
SS	SoG	Central SoG	16. Louis Creek	H	1990–2007 (14)	1
SS	SoG	Southern SoG	17. Nooksack River	H	1982–2009 (28)	1
SS	PS	Whidbey	18. Baker River (Skagit)	W	1991–2010 (18)	1
SS	PS	Whidbey	19. Skagit River	H	1995–2010 (16)	1
SS	PS	Whidbey	20. Tulalip Bay	H	1980–2010 (30)	1
SS	PS	Whidbey	21. Skykomish River	H	1983–2010 (27)	1
SS	PS	Central PS	22. Green River	H	1977–2010 (31)	1
SS	PS	Central PS	23. Puyallup River	H	1979–2010 (32)	1
SS	PS	South PS	24. Minter Creek	H	1979–2009 (14)	1
SS	PS	South PS	25. Kalama Creek	H	1979–2010 (20)	1
SS	PS	South PS	26. Deschutes River	W	1977–2008 (24)	1
SS	PS	Hood Canal	27. Skokomish River	H	1979–2010 (32)	1
SS	PS	Hood Canal	28. Big Beef Creek	W	1977–2010 (34)	1
SS	PS	Hood Canal	29. Quilcene River	H	1979–2010 (26)	1
SS	JDF		30. Snow Creek	W	1985–2010 (22)	2.1
SS	JDF		31. Dungeness River	H	1977–2010 (17)	1
PC			32. Sooes River	H	1982–2010 (23)	1
PC			33. Quinault River	H	1977–2010 (34)	1
PC			34. Bingham Creek	W	1982–2010 (29)	1
PC			35. Satsop River	H	1973–2010 (34)	1
PC			36. Willapa River	H	1973–2010 (24)	1
PC			37. Grays River	H	1977–2010 (29)	1
PC			38. Elochoman River	H	1985–2008 (22)	1
PC			39. Upper Cowlitz River	W	2001–2010 (8)	2.1
PC			40. Cowlitz River	H	1982–2010 (26)	1
PC			41. Washougal River	H	1977–2010 (28)	1

and the Strait of Georgia (Table 1; Figure 1A) and tested whether there were differences in smolt survival patterns among subbasins within the Salish Sea. Subbasin differences were further examined using Bonferonni multiple comparisons and were considered different when the P-value was less than an alpha of 0.05. Residuals of smolt survival for Pacific coast reference populations were detrended values of annual survival outside the Salish Sea and were calculated as the mean residual survival among Pacific coast populations for each year. Residuals for each population were calculated from the best regional model. Inclusion of this factor tested whether similar trends could be detected between the California Current populations in the Salish Sea and those outside the Salish Sea (top bifurcation in decision tree; see Figure 2). This analysis was conducted for the entire time series, as well as for subdivisions of the full time series as identified from the results of the structural change analysis.

*Effect sizes of multiple spatial scales.—*Effect sizes from the two sets of mixed-effects models were computed in order to compare the relative importance of factors explaining variation in smolt survival. Effect sizes were the parameter estimate divided by its standard error, akin to Cohen's D effect-size calculation. For a given factor, these values were summed for multiple comparisons (e.g., multiple subbasin contrasts). Comparing effect size between the regional mixed-effects model and the subsequent analysis of residual survival was complicated by the fact that the second analysis started with a substantial amount of variation explained by factors in the regional mixed-effects model, including variation from Pacific coast populations. Therefore, we adjusted the effect sizes of parameters in each model by the initial variation in the Salish Sea. For the regional mixed-effects model, this adjustment used residuals of a model that included only a constant and the process error generated by random effects and correlation structure. For the residual survival model, this adjustment used residuals of the best regional mixed-effects model. In both adjustments, we focused on the variance generated by Salish Sea populations only. We then weighted relative effect sizes by the amount of variance each model sought to explain.

RESULTS

Groupings of Smolt Survival According to Cluster Analyses

Populations clustered into two major geographical groupings, (mostly) Salish Sea (Puget Sound and the Strait of Georgia) and (mostly) Pacific coast (Figures 1B, 3). Wild populations clustered with hatchery populations from their respective geographic regions. The Salish Sea cluster included a Puget Sound cluster and a Strait of Georgia cluster (bootstrap support for these groupings was 100%). The Puget Sound cluster included populations from all four subbasins (Table 1; Figure 3). The Strait of Georgia cluster included populations from all three subbasins of the Strait of Georgia and the Dungeness River (Strait of Juan de Fuca). The Pacific coast cluster was split into two groups (lower Columbia River and coastal

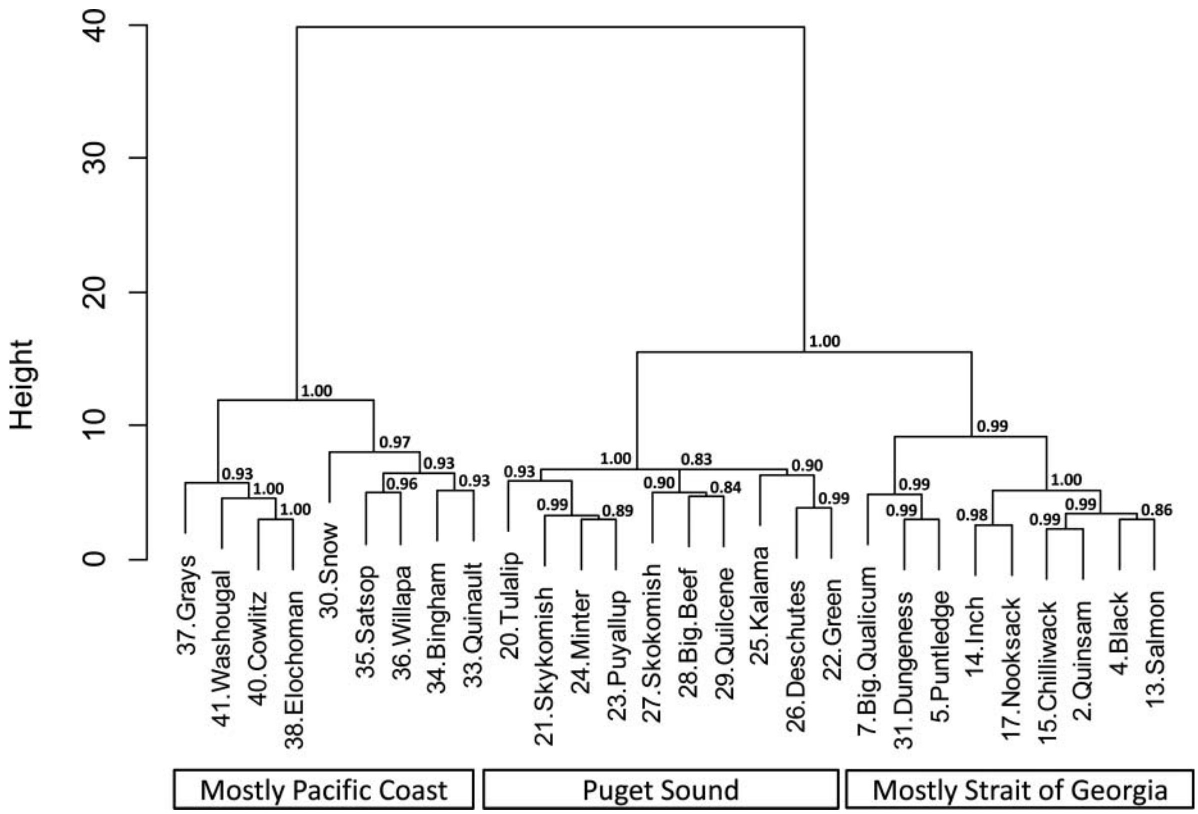

FIGURE 3. Dendrogram showing the results of Ward's hierarchical cluster analysis of smolt survival estimates for Coho Salmon populations in the Salish Sea and neighboring watersheds, ocean entry years 1977–2010. The vertical line height represents the Euclidean distance (magnitude of difference) between pairs of populations. Bootstrap support for each cluster is provided as an approximately unbiased P-value (significance, $P \geq 0.95$).

Washington) that were also strongly supported by the bootstrap analysis (bootstrap support for these groupings was 100%). The one geographic exception to membership in the Pacific coast cluster was the Snow Creek population, which enters the marine environment in the Strait of Juan de Fuca.

Smolt Survival Correlations over Distance and Time

Correlograms showed that smolt survival correlations were spatially structured among the Pacific coast, Strait of Georgia, and Puget Sound regions but that the strength of the correlations changed over time (Figure 4). For the entire time series,

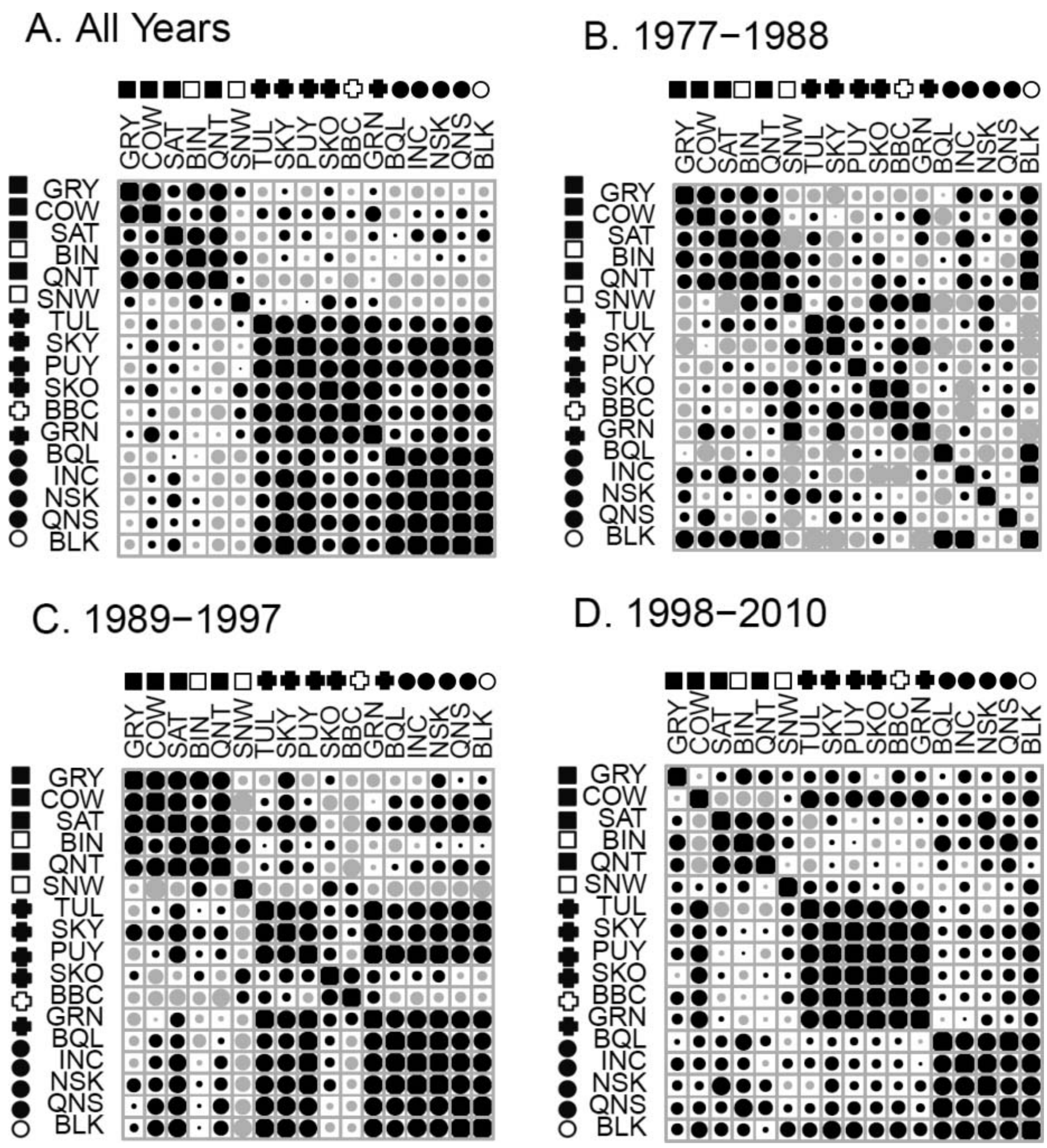

FIGURE 4. Pairwise correlations in Coho Salmon smolt survival over different ocean entry year time periods shown as a correlogram for **(A)** the entire time series**, (B)** 1977–1988, **(C)** 1989–1997, and **(D)** 1998–2010. Correlogram results are mirrored above and below the diagonal, with larger circles representing stronger correlations than smaller circles. Within the correlogram, black circles are positive correlations and gray circles are negative correlations. The first six populations listed are from the Pacific coast (squares): Grays (GRY), Cowlitz (COW), Satstop (SAT), Bingham (BIN), Quinault (QNT), and Snow (SNW). The second six populations are from Puget Sound (crosses): Tulalip (TUL), Skykomish (SKY), Puyallup (PUY), Skokomish (SKO), Big Beef (BBC), and Green (GRN). The final five populations are from the Strait of Georgia (circles): Big Qualicum (BQL), Inch (INC), Nooksack (NSK), Quinsam (QNS), and Black (BLK). For the population labels, filled symbols are hatchery fish and open symbols are wild populations.

correlations in Coho Salmon smolt survival were strong and positive within the Strait of Georgia and the Salish Sea (Puget Sound and Pacific coast), as well as between the Strait of Georgia and Puget Sound. However, they were generally weak or negative between the Pacific coast and the Strait of Georgia or Puget Sound (Figure 4A). During the first period (OEYs 1977–1988), smolt survival was weakly correlated among populations in the Salish Sea region but positively correlated among populations in the Pacific coast region (Figure 4B). Two populations from the Strait of Georgia (Inch Creek [number 14] and Black Creek [number 4]) were positively correlated with Pacific coast populations during the first time period. During the second period (OEYs 1989–1997), smolt survival was positively correlated within the Salish Sea and Pacific coast regions but not between them (Figure 4C). Exceptions during this period were the Skokomish River and Big Beef Creek (numbers 27 and 28, respectively, in the Hood Canal subbasin of Puget Sound), which were positively correlated with each other but weakly correlated with the rest of the Salish Sea populations. During the third period (OEYs 1998–2010), smolt survival was positively correlated within the Strait of Georgia and Puget Sound basins. However, between these basins, only Black Creek in the Strait of Georgia was positively correlated with Puget Sound populations (Figure 4D). Populations in the Pacific coast region were weakly correlated with Salish Sea populations during this third time period.

The correlations among populations declined with distance, and the shape of the exponential decay curve fit to the data differed among time periods (Figure 5). The *e*-folding scale (v), representing the extent of spatial synchrony, was three to four times greater for the second two time periods (OEYs 1989–1997 and 1998–2010) than the earliest time period (OEYs 1977–1988; Table 2). The intercept parameter (ρ_o), representing the correlation between neighboring populations at a theoretical separation distance of 0, was nearly two times higher (stronger) in the second (OEYs 1989–1997) time period than the first (OEYs 1977–1988) or third (OEYs 1998–2010) time periods (Table 2). For each time series, the exponential decay model that included an intercept parameter was a better fit to the data than when the intercept was fixed at a value of 1 (full time series: $\Delta AIC_c = 5.5$; OEYs 1977–1988: $\Delta AIC_c = 10$; OEYs 1989–1997: $\Delta AIC_c = 5.8$; and OEYs 1998–2010: $\Delta AIC_c = 91.4$).

Regional Differences in Smolt Survival

The mixed-effects model including region, origin (hatchery or wild), year, and an interaction between region and year was overwhelmingly supported by the data (model weight = 0.977, Model 9; Table 3). Two other potentially contending models (Models 2 and 3) added an additional interaction term to these four effects but did not reduce the negative log likelihood, suggesting these additional terms were predictively neutral. All parameter values in the best model differed from 0. The region × year interaction indicated that annual trends in smolt survival differed among regions. Across all regions, annual smolt survival was consistently higher for wild than hatchery Coho Salmon.

Recognizing that highly variable smolt survival is the norm in Pacific salmon populations (e.g., Teo et al. 2009), we visualized predictions for each year by using the structure of the best model but including year as a categorical variable rather than a covariate (Figure 6). Predictions were back-calculated to nontransformed values for ease of interpretation. Modeled predictions of annual smolt survival of hatchery Coho Salmon ranged from 0.6% to 16.6% inside the Strait of Georgia, 0.6% to 15.7% in Puget Sound, and 0.1% to 4.6% on the Pacific coast. In comparison, annual smolt survival of wild Coho Salmon ranged from 1.1% to 30.8% for the Strait of Georgia, 1.3% to 25.7% for Puget Sound, and 0.2% to 10.4% for the Pacific coast.

Smolt Survival Patterns at Salish Sea and Basin Scales

Survival trends differed within regions of the California Current (in the Salish Sea versus outside the Salish Sea) and between basins of the Salish Sea (Table 4; Figure 7). The Strait of Georgia and Puget Sound time series were best fit with single regression models, whereas two separate linear trends were supported for the Pacific coast time series, with a break occurring in OEY 1991 (95% confidence interval = 1986–1992). A lack of structural change in the two Salish Sea time series was supported by AIC_c model comparisons of one versus two linear models ($\Delta AIC_c < 3$) and by *F*-tests ($P > 0.05$). However, smolt survival trends differed between Salish Sea basins, with survival declining more rapidly in the Strait of Georgia than in Puget Sound (regression slopes were outside the 95% confidence intervals calculated for the other basin). The break in the Pacific coast time series was supported by AIC_c model comparisons of one versus two linear models ($\Delta AIC_c = 13.6$) and the *F*-test ($P < 0.05$) used to test goodness of fit for the model. For OEYs 1977–1991, the temporal trend for the Pacific coast region did not differ from a slope of 0. Following a decrease in smolt survival in the early 1990s, survival of Pacific coast populations increased through 2010 (Table 4; Figures 6, 7).

Regional Coherence and Smolt Survival Patterns at a Subbasin Scale

Based on the entire time series, residual smolt survival of Salish Sea populations covaried with Pacific coast reference populations ($F = 7.51$, $P = 0.006$) but did not differ among subbasins ($F = 1.68$, $P = 0.18$). Overall, residual smolt survival values were predominantly negative in the 1990s and again in the mid-2000s and positive during other portions of the time series (Figures 7, 8). Results differed when the time

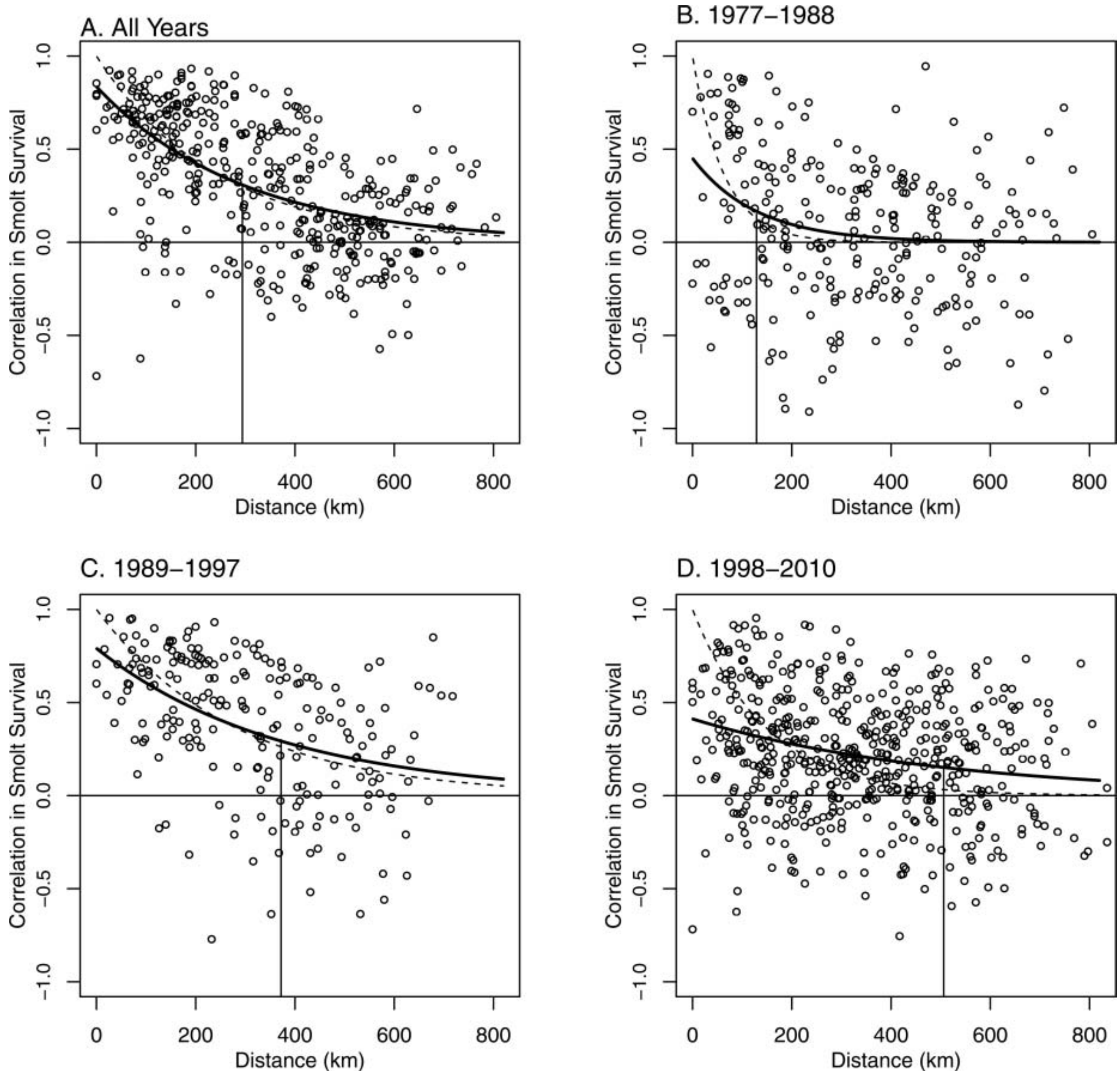

FIGURE 5. Pairwise correlations of Coho Salmon smolt survival as a function of distance between populations. Panels represent **(A)** the entire time series dataset and three time periods: **(B)** 1977–1988, **(C)** 1989–1997, and **(D)** 1998–2010. Each point represents an individual pairwise correlation. The curvilinear lines represent an exponential decay function fit to the data with an estimated intercept (solid line) and an intercept fixed at a value of 1 (dashed line). The vertical thin line represents the distance at which pairwise correlations decrease by 37% (*e*-folding scale) for the nonlinear function with an estimated intercept.

TABLE 2. Parameter values for exponential decay models, $\rho(d) = \rho_o e^{-d/v}$, which described the relationship between the strength of the survival correlation, $\rho(d)$, and the ocean entry distance (d) among populations.

	ρ_o (Intercept)		v (*e*-folding scale)	
Time period	Estimate	95% CI	Estimate	95% CI
All years	0.84	0.75–0.93	294 km	246–354 km
1977–1988	0.46	0.22–0.73	129 km	64–307 km
1989–1997	0.79	0.65–0.94	372 km	287–518 km
1998–2010	0.41	0.34–0.50	506 km	367–747 km

series was divided into two periods based on identified breakpoints for the Pacific coast region (1977–1991, 1992–2010). In the first time period (1977–1991), neither Pacific coast smolt survival nor subbasin was a good predictor of residual smolt survival of Salish Sea populations ($F < 0.8$, $P > 0.5$, Figure 9A). However, between 1992 and 2010 the residual smolt survival of Salish Sea populations covaried with the residual smolt survival of Pacific coast populations and differed among subbasins ($F = 3.91$ and $F = 3.71$, respectively, $P < 0.05$; Figure 9b). In the 1977–1991 time period, Bonferroni multiple comparisons indicated contrast between residual smolt survival of just two subbasins (Hood Canal and Whidbey). In the

TABLE 3. Factors contributing to Coho Salmon smolt survival from ocean entry years 1977 to 2010. An "X" indicates fixed-effect variables included in linear mixed-effects models predicting variation in smolt survival. Factors include region (Strait of Georgia, Puget Sound, or Pacific coast), origin (hatchery or wild), and year (ocean entry year). Population (not shown) was included in the model as a random effect. The differences in AIC values from the model with the lowest AIC score (ΔAIC) were used to compare models. An asterisk indicates the best model.

Model	Intercept	Region	Origin	Year	Region × year	Origin × year	Origin × region	Log likelihood	ΔAIC	Model weight
1	X	X						1,110.2	48.9	0.000
2	X		X					1,112.0	50.5	0.000
3	X			X				1,102.1	30.8	0.000
4	X	X		X				1,101.2	32.9	0.000
5	X		X	X				1,099.7	27.9	0.000
6	X	X	X					1,109.0	48.6	0.000
7	X	X	X	X				1,097.7	28.1	0.000
8	X	X	X	X		X		1,101.5	37.6	0.000
9*	X	X	X	X	X			1,081.7	0.0	0.977
10	X	X	X	X			X	1,098.3	33.2	0.000
11	X	X	X	X	X		X	1,084.3	9.1	0.010
12	X	X	X	X	X	X		1,085.1	8.7	0.012
13	X	X	X	X		X	X	1,102.1	42.7	0.000

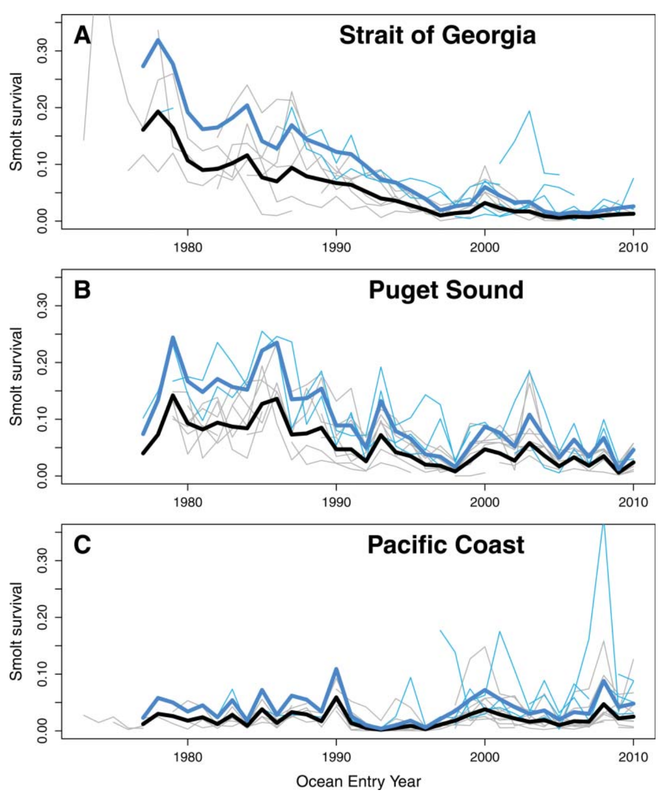

FIGURE 6. Smolt survival time series for Coho Salmon from ocean entry years 1977 to 2010. The values shown are not transformed (logit transformation was used in the analysis to account for heterogeneous variance among years). Panels represent the three geographic regions: (**A**) the Strait of Georgia, (**B**) Puget Sound, and (**C**) the Pacific coast. The thin lines represent individual populations: the thin gray lines are hatchery populations and the thin blue lines are wild populations. The thick lines show the predicted survival for hatchery (black) and wild (blue) populations in each region from the best mixed-effects regional model (Model 9 in Table 3), with year incorporated as a categorical variable to highlight annual variation in smolt survival.

1992–2010 time period, five strong contrasts existed, all between South Puget Sound and the five subbasins with above-average residual smolt survival. Across the two time periods, the South Puget Sound subbasin went from having high smolt survival relative to other subbasins to the lowest survival relative to other subbasins. The reverse occurred for Hood Canal and southern Strait of Georgia subbasins.

Effect Sizes of Multiple Spatial Scales

The comparison of relative effect sizes (Figure 10) revealed how Coho Salmon smolt survival was explained at different spatial scales (Figure 2). The largest spatial scale was regionwide coherence of Salish Sea and Pacific coast populations. This source of variation had a much lower relative effect for Salish Sea populations than any other parameter. The next smaller spatial scale was the region-specific scale, i.e., the differences between Salish Sea (Strait of Georgia and Puget Sound) populations and Pacific coast populations. These patterns, represented by the Region and Region × Year terms, exhibited the largest effect size. The next smaller spatial scale was the basin scale (Strait of Georgia versus Puget Sound). These patterns, represented by the Year and Region × Year terms, exhibited the second largest effect sizes. Variation at the subbasin scale was modest compared with these larger spatial scales. The finest spatial scale includes population-specific factors, including hatchery or wild origin, as well as within-population temporal variation. This latter source of variation could not be assigned a relative effect size but includes much of the variation not explained by any model. Given the relative effect sizes of origin alone, population-specific variation may be on the same order of magnitude as subbasin effects.

TABLE 4. Linear model parameters (95% confidence intervals in parentheses) and breakpoints identified for Coho Salmon smolt survival time series from Strait of Georgia, Puget Sound, and Pacific coast regions. Analysis was conducted using predicted smolt survival (hatchery and wild combined) based on the best regional mixed-effects model. Slope parameters correspond to logit-transformed survival time series. Strait of Georgia and Puget Sound time series did not have a significant breakpoint (only one segment).

Region	Breakpoint years	First segment slope	Second segment slope
Strait of Georgia		−0.09 (−0.08 to −0.10)	
Puget Sound		−0.06 (−0.04 to −0.08)	
Pacific coast	1991 (1986 to 1992)	0.03 (−0.03 to 0.10)	0.13 (0.07 to 0.20)

DISCUSSION

This study provides evidence for coherence in Coho Salmon smolt survival at multiple spatial scales for OEYs 1977–2010. Covariation at the Salish Sea scale (versus Pacific coast) was supported by the cluster analysis, which did not rely on a priori geographic assignment, and the mixed-effects model, which tested differences among preassigned geographic regions. The primary Salish Sea scale pattern was declining smolt survival over the entire period of record. This pattern contrasted with Pacific coast reference populations, which had lower smolt survival than the Salish Sea populations in the 1970s and 1980s, but similar smolt survival in recent years. Smolt survival for Pacific coast populations was consistently low in the early 1990s, but subsequently increased. Within the Salish Sea, major basins shared a similar

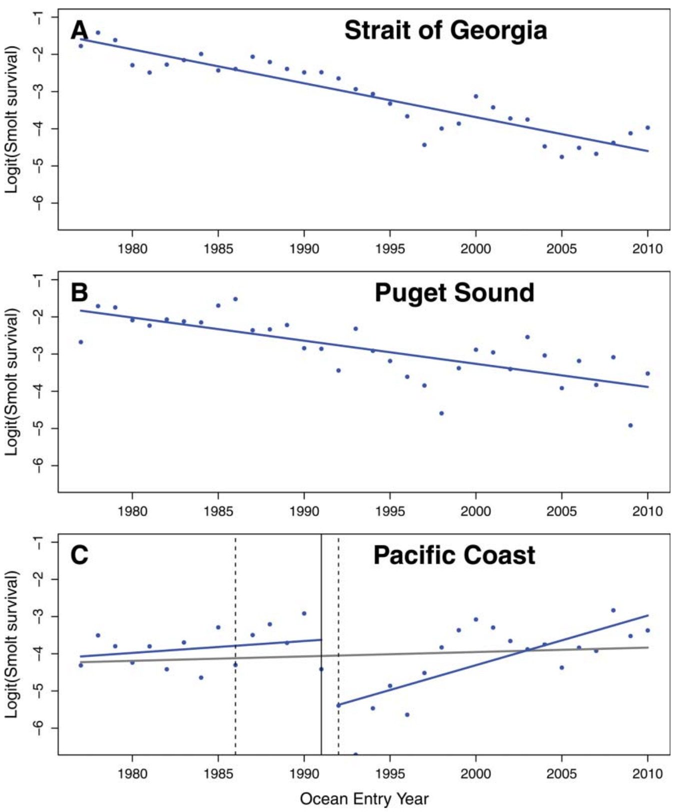

FIGURE 7. Trends in smolt survival for Coho Salmon from ocean entry years 1977 to 2010. The values shown are logit transformed. The panels represent the three geographic regions: **(A)** the Strait of Georgia, **(B)** Puget Sound, and **(C)** the Pacific coast. Points represent the average smolt survival each year for each region (hatchery and wild combined). The thick blue lines are best-fit linear regressions based on breakpoint analysis. The vertical lines are the breakpoint and 95% confidence intervals (solid and dashed lines, respectively). No breakpoints were identified for the Strait of Georgia or Puget Sound. The thick gray line in panel (C) is the best-fit linear regression model with no breakpoints and is provided for comparison.

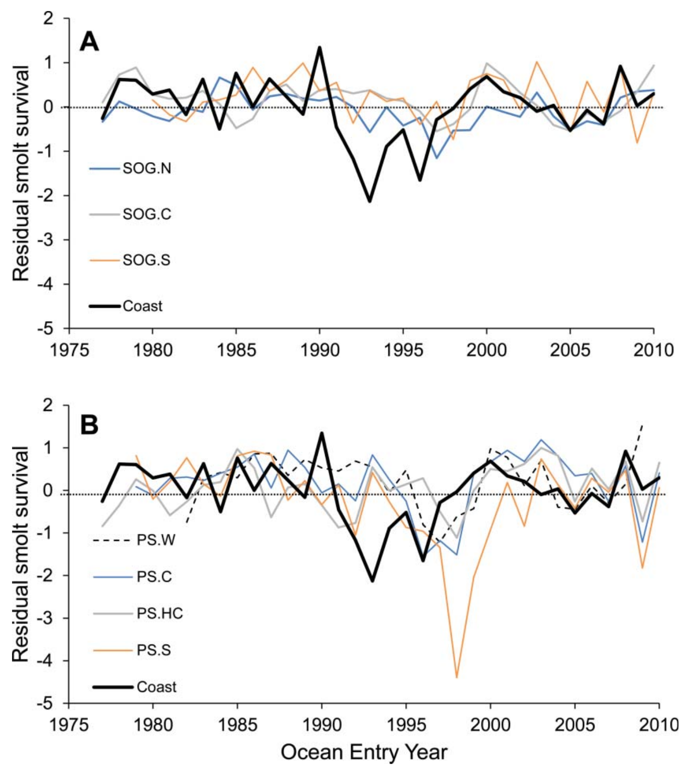

FIGURE 8. Smolt survival residuals from ocean entry years 1977 to 2010. Residuals were calculated from the best regional model in Table 3. The values shown were averaged by subbasin within **(A)** the Strait of Georgia (SOG; solid colored lines in panel A) and **(B)** Puget Sound (PS; dashed and colored lines in panel B) and along the Pacific coast (thick solid black line in both panels). Subbasin abbreviations are as follows: N = North, C = Central, S = South, HC = Hood Canal, and W = Whidbey.

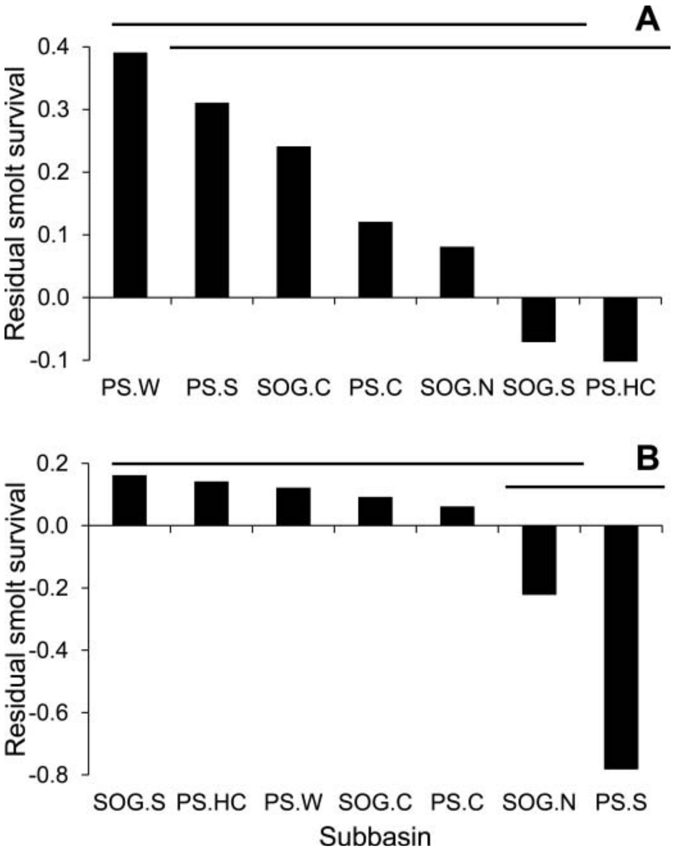

FIGURE 9. Mean smolt survival residuals for each subbasin of the Salish Sea for two time periods: ocean entry years **(A)** 1977–1991 and **(B)** 1992–2010. Residuals were calculated from the best regional model (Table 3) and represent variation in survival after main effects in the time series were removed. Subbasins are shown for the Strait of Georgia (SOG) and Puget Sound (PS). Horizontal lines link subbasins lacking significant differences as determined by Bonferroni multiple comparisons. Subbasin abbreviations are as follows: N = North, C = Central, S = South, HC = Hood Canal, and W = Whidbey. Note that the order of the subbasins and the range of the *y*-axis changes between panels.

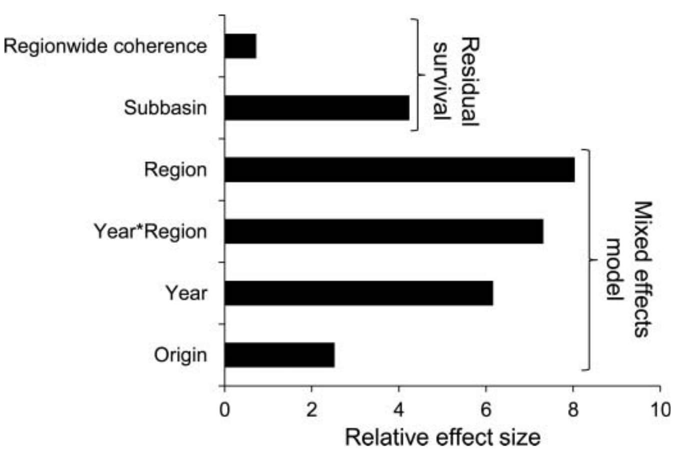

FIGURE 10. Relative effect sizes of multiple factors contributing to smolt survival of Coho Salmon in the Salish Sea. The effect size was calculated from the best regional mixed-effects model and subsequent analysis of residual survival.

declining survival trend but the decline was steeper in the Strait of Georgia than Puget Sound. Smolt survival differences at the subbasin scale were apparent only after the primary Salish Sea scale trend was removed from the data and were distinct only for the Whidbey and Hood Canal subbasins early in the time series and the South Puget Sound subbasin later in the time series. Although differences between populations in the Salish Sea and outside the Salish Sea were significant, both regions had low smolt survival in the early 1990s.

Our results are consistent with previous studies that demonstrated Coho Salmon smolt survival patterns at the scale of the California Current (Beamish et al. 2000; Botsford and Lawrence 2002; Beamish et al. 2004b; Teo et al. 2009), the Salish Sea (Coronado and Hilborn 1998a; Hobday and Boehlert 2001; Beetz 2009) and between basins of the Salish Sea (Coronado and Hilborn 1998a). However, these previous studies did not resolve the issue of multiple scales and arrived at seemingly conflicting results with respect to the importance of factors affecting smolt survival at different scales. For example, how could patterns differ between the Salish Sea and Pacific coast (Coronado and Hilborn 1998a; Hobday and Boehlert 2001) if a shared climate regime was affecting both patterns (Beamish et al. 2000; Beamish et al. 2004b)?

The time frames for each study have contributed to different conclusions regarding spatial scale. Coronado and Hilborn (1998a) investigated Coho Salmon smolt survival for OEYs 1971–1990 and concluded that Salish Sea populations (termed “BC South Coast” and “Puget Sound”) had declining survival trends compared with a lack of temporal trend observed for Washington coast or Columbia River populations. With an additional 4 years of information, Beamish et al. (2000) demonstrated a synchronous and declining trend for California Current populations originating both inside and outside the Salish Sea. This result was driven by the synchronous low smolt survival that occurred in the 1990s (Figure 7C), data not available at the time Coronado and Hilborn (1998a) conducted their analysis. The breakpoint (OEY 1991) identified in our analysis for the Pacific coast time series was consistent with the low smolt survival period during the early 1990s (Beamish et al. 2000; Peterson et al. 2006). However, with an additional 15 years of information, our results show that smolt survival of Pacific coast populations has increased since the 1990s, whereas there is no evidence for increasing smolt survival in the Salish Sea through OEY 2010. This perspective helps to reconcile the identified differences between the Salish Sea and Pacific coast with the identified coastwide similarities in smolt survival.

Spatial Scale is Time Dependent

The temporal scale determined what spatial pattern in smolt survival was identified. For example, when the entire time series was examined, smolt survival patterns were similar within the Salish Sea but differed from Pacific coast reference populations (Figures 3, 4A). However, when this same time series was subdivided, spatial coherence within the Salish Sea was weak in the first time period (Figure 4B; OEYs 1977–1988), synchronous in the second time period (Figure 4C; OEYs 1989–1997), and stronger within basins than across the entire Salish Sea in the third time period (Figure 4D; OEYs 1998–2010).

The *e*-folding parameter (v) described the scale, and the intercept (ρ_o) of the exponential decay model described the strength of spatial synchrony. The *e*-folding scale value itself has no specific biological relevance but rather provides a common metric to compare scales of spatial synchrony in smolt survival among species. The intercept can be interpreted as shared environmental effects among neighboring populations (Pyper et al. 2005). A comparison among time periods revealed broader spatial synchrony in smolt survival since OEY 1989 and stronger shared environmental effects for OEYs 1989–1997 than in the other two time periods.

In addition, our results suggest that spatial synchrony among Coho Salmon populations occurs at a more localized scale than for other Pacific salmon species, implying that local marine conditions are particularly important for Coho Salmon within the Salish Sea. The *e*-folding scale estimated for the entire time series was 294 km (95% CI = 246–354 km), approximately one-third the value for Chinook Salmon (1,069 km; Kilduchumff et al. 2014) and one-half to three-quarters the values for Pink Salmon (431 km; Pyper et al. 2001) and Chum Salmon *O. keta* (564 km; Pyper et al. 2002). Calculation of an *e*-folding scale for Sockeye Salmon *O. nerka* does not appear to have been made; however, Pyper et al. (2005) found that the 50% scale for Sockeye Salmon was slightly larger than that for Pink and Chum salmons. Some caution is needed when comparing estimates for Chum, Sockeye, and Pink salmons with those of Coho and Chinook salmons, as the former were based on spawner-recruit residuals that incorporated a greater degree of freshwater influence than the smolt survival estimates for Coho and Chinook salmons.

The *e*-folding scale in this study was slightly larger than that reported in a previous coastwide study of Coho Salmon populations (217 km; Teo et al. 2009). This difference can be explained by how the intercept (ρ_o) was selected for analysis. Teo et al. (2009) found that model fit was not improved by estimating the intercept and therefore constrained the intercept (ρ_o) to a value of 1. In our analysis, model fit was substantially improved by estimating the intercept; allowing the intercept to be < 1 changed the shape of the exponential decay function and increased the estimated *e*-folding scale.

Importance of Early Marine Environment

Different smolt survival patterns between Salish Sea and Pacific coast populations suggest that the early marine environment determines interannual differences in smolt survival. By itself, this result cannot distinguish between effects of the early marine environment versus effects of marine environments encountered during population-specific ocean migration routes (Weitkamp and Neely 2002). However, the importance of the early marine environment to Coho Salmon smolt survival is broadly supported by other studies. For example, across the range of Coho Salmon, smolt survival was better explained by ocean conditions following ocean entry than by those at later life stages (Hobday and Boehlert 2001). On the outer coastal continental shelf adjacent to the Columbia River, catches of juvenile Coho Salmon in the first month of ocean residence were strongly correlated with hatchery jack returns, which were, in turn, strongly correlated with hatchery adult returns (Pearcy 1988). Other studies have pointed to the importance of growth in the early marine environment. Early marine growth was correlated with smolt survival of wild Coho Salmon from Carnation Creek on the western coast of Vancouver Island (Holtby et al. 1990), and Beamish et al. (2004a) proposed that growth to a critical size during the early marine rearing period determines the overall survival trajectory for Coho Salmon in the Strait of Georgia.

Growth and survival are integrated responses to ecosystem conditions. In order to explain survival patterns in the Salish Sea, we must answer the following question: what has changed during the last 30 years and what drove those changes? Ultimately, this question may require an ecosystem research program, such as that implemented off the coast of Washington and Oregon (Brodeur et al. 2000) and recently extended from the Strait of Georgia (Masson and Perry 2013) to include Puget Sound in the Salish Sea (Riddell et al. 2009; U.S. Salish Sea Technical Team 2012). Retrospective analyses such as ours provide valuable insights on changing conditions. Based on the survival patterns identified in this study, we briefly summarize below the ecosystem processes recognized at spatial scales identified in the decision tree framework (Figure 2). These preliminary hypotheses should provide guidance for future ecosystem research within the Salish Sea, as well as for future development of predictive ecosystem indicators for these populations.

North Pacific Ocean and California Current Scales

The geographic scope of this study did not allow us to contrast patterns within regions of the North Pacific Ocean, but these have been described by other researchers (Coronado and Hilborn 1998a; Hare et al. 1999; Teo et al. 2009). For the purpose of this discussion, environmental factors at the North Pacific Ocean scale will be considered as they are manifested in the northern California Current, which was the geographic scope of our study populations.

Our study encompassed three climate regimes reported in the North Pacific Ocean (Hare and Mantua 2000; Overland et al. 2008). Coho Salmon smolt survival in the Salish Sea declined throughout this period. Some similarities within and outside the Salish Sea were detected in the detrended time series due to lower-than-average smolt survival in all regions during the 1990s, corresponding with an extended El Nino period from 1990 to 1996 (Peterson et al. 2006). North Pacific Ocean climate indices useful in predicting Coho Salmon smolt survival for coastal populations include the Pacific Decadal Oscillation Index, North Pacific Gyre Oscillation Index, and Multivariate El Nino Southern Oscillation Index (Rupp et al. 2012). Ocean climate changes may be linked to the Salish Sea ecosystem through tidal mixing and the introduction of seasonally varying nutrient- and oxygen-rich waters, as well as changes in stream flows (Mantua et al. 1997), temperature (Ebbesmeyer et al. 1989; Moore et al. 2008b), and wind patterns (Beamish et al. 1999a).

Salish Sea Scale

The inland sea environment of the Salish Sea is unique with respect to oceanography and has historically supported higher smolt survival rates of Coho Salmon than the outer coast continental shelf. On the outer coast continental shelf, increased productivity is associated with a deeper mixed layer and delivery of nutrients to the photic zone (Povolina et al. 1995). In the Strait of Georgia, increased productivity is associated with increased stratification and light exposure (Yin et al. 1997; Collins et al. 2009; Masson and Pena 2009) and nutrients are not thought to be limiting (Mackas and Harrison 1997; Johannessen et al. 2014). In addition to the physical environment, zooplankton communities in the Strait of Georgia are composed of large lipid-rich taxa belonging to a subarctic zoogeographic range (Mackas et al. 2013) and are mostly devoid of the southern-origin copepods associated with low smolt survival of Coho Salmon on the outer coast continental shelf (Peterson 2009).

The Salish Sea has undergone significant changes during the period of study that are related to Coho Salmon smolt survival in ways that are not fully understood. At present, temporal trends in the Strait of Georgia ecosystem have been better studied than those in Puget Sound and the Strait of Juan de Fuca. Over multiple decades in the Strait of Georgia, seawater and river water temperatures have increased, deep water oxygen has declined, sea level has risen, and timing of the Fraser River freshets has changed (Riche et al. 2013). These changes can be organized into major regime shifts occurring in the late 1970s and mid-1990s (Perry and Masson 2013), with a major shift in the zooplankton community in 1998–1999 (Li et al. 2013) and the mean vertebrate trophic level decreasing since the 1980s (Preikshot et al. 2013). After 1990, the biomass of zooplankton, calanoid copepods, and Pacific Herring *Clupea pallasii* were the best indicators of early smolt survival for Coho Salmon in the Strait of Georgia (Araujo et al. 2013).

Based on current understanding, freshwater inflows and wind speed, which are associated with stratification depths and primary productivity (Denman and Gargett 1983; Yin et al. 1997; Moore et al. 2008b; Preikshot et al. 2013), and zooplankton biomass and composition, which are indicators of smolt survival (Peterson 2009; Araujo et al. 2013), may serve as important indicators of early marine conditions at the scale of the Salish Sea.

Basin Scale

The major difference observed between basins of the Salish Sea was the rate at which smolt survival declined over the past three decades. Interpreting these differences with respect to ecosystem processes is limited by a lack of detailed studies comparing the oceanography of the Strait of Georgia with that of Puget Sound. In general, the Strait of Georgia is deep, greatly influenced by freshwater input from the Fraser River, and connected to the Pacific Ocean at both its southern and northern boundaries. In comparison, Puget Sound is relatively shallow, influenced primarily by freshwater from the Skagit River, and connected to the Pacific Ocean only at its northern boundary.

One potential hypothesis to explain differences in Coho Salmon smolt survival in the Strait of Georgia versus Puget Sound is that populations in the two basins have different abilities to respond to changing ecosystem states based on genetically predisposed migration behavior or innate growth potential. The migration behavior of Coho Salmon and the duration of time spent within the Salish Sea ecosystem are better described for the Strait of Georgia than for Puget Sound. Migrations out of the Salish Sea have been observed for populations originating in both basins (Weitkamp and Neely 2002; Morris et al. 2007), but trawl surveys suggest that Coho Salmon from Puget Sound leave the Salish Sea earlier that those from the Strait of Georgia (R. J. Beamish, Fisheries and Oceans Canada, personal communication). In addition, a large portion of Coho Salmon historically overwintered within the Strait of Georgia and contributed to active recreational and troll fisheries in this basin. In 1991, for the first time on record, returning Coho Salmon were rarely caught in active recreational and troll fisheries within the Strait of Georgia (Simpson et al. 2000, especially Figure 9), and reduced catches were concluded to be the result of shifts in distribution to predominantly outside the Salish Sea (Beamish et al. 1999a). Residency of Coho Salmon has also been observed in the Puget Sound basin (Allen 1959; Rhode et al. 2013); however, a detailed comparison between the two basins has not been conducted.

Subbasin Scale

The ability to understand Coho Salmon smolt survival at a subbasin scale is critical to managing terminal fisheries in these areas. Subbasin scale variation in the Salish Sea ecosystem has been identified for temperature and salinity (Babson et al. 2006; Moore et al. 2008b), oxygen (Johannessen et al. 2014), nitrogen (Sutton et al. 2013), and chlorophyll (Masson and Pena 2009), which may be linked with early marine growth and survival. Moore et al. (2008a) found that subbasin scale oceanographic properties were better predicted by local air temperatures and river flows than climate-scale indices. In addition to oceanographic properties, the influence of urbanization, toxic chemicals (e.g., polychlorinated biphenyls), harmful algal blooms (e.g., *Heterosigma*; Rensel et al. 2010), and disease (e.g., *Nanophyetus*) are most likely to vary at a subbasin scale. Heterogeneity among the Salish Sea subbasins provides a natural laboratory to examine the relative impacts of these factors on Coho Salmon smolt survival and will require investment in a research program to collect the needed time series.

Our results indicate that subbasin scale differences in smolt survival were small in magnitude compared with basin scale or Salish Sea scale patterns. However, the ability to detect subbasin differences suffered from low statistical power (few populations per subbasin, few long-term smolt survival time series). The South Sound subbasin of Puget Sound was the most distinctive in that smolt survival in this subbasin was relatively high in the early portion of the time series and very low in the latter portion of the time series. South Sound, which is a series of shallow inlets separated from the remainder of Puget Sound by a sill at the Tacoma Narrows, is distinctive from other Puget Sound subbasins by its large temperature ranges (Moore et al. 2008b), low stratification (Moore et al. 2008a), and salinity that is more strongly influenced by freshwater inputs than is the salinity in the Strait of Juan de Fuca (Babson et al. 2006).

Conclusions

A desired outcome of this study was to guide the development of ecosystem indicators of Coho Salmon smolt survival, with specific reference to survival within the Salish Sea. We found a more localized scale of synchronized survival than reported by other researchers for Chinook, Pink, Chum, and Sockeye salmons, suggesting that early marine conditions are especially important for Coho Salmon within the Salish Sea. Within the geographic scope of our study, the dominant pattern in smolt survival occurred at the scale of the Salish Sea. Explaining this pattern will require future study on mechanistic links between the observed ecosystem changes and Coho Salmon growth and survival. We highlight the importance of the early marine environment to help focus future investigation. The ability to predict secondary patterns from the scale of the California Current to the scale of individual subbasins will be equally relevant to contemporary management concerns, such as climate change and run-size forecasting. For example, in an era characterized by low smolt survival, average smolt survival in Puget Sound over the past decade ranged by an order of magnitude, greater than that observed within the Strait of Georgia. Further exploration of ecosystem variables at multiple spatial scales is needed to effectively address linkages between the marine ecosystem and Coho Salmon smolt survival within the Salish Sea. Since the relative importance of particular variables may have changed during our period of record, researchers will need to carefully match spatial and temporal scales to their questions of interest.

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