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Relating spatial and temporal scales of climate and ocean variability to survival of Pacific Northwest Chinook salmon (*Oncorhynchus tshawytscha*)

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ABSTRACT

Pacific Northwest Chinook, *Oncorhynchus tshawytscha*, have exhibited a high degree of variability in smolt-to-adult survival over the past three decades. This variability is summarized for 22 Pacific Northwest stocks and analyzed using generalized linear modeling techniques. Results indicate that survival can be grouped into eight distinct regional clusters: (1) Alaska, Northern BC and North Georgia Strait; (2) Georgia Strait; (3) Lower Fraser River and West Coast Vancouver Island; (4) Puget Sound and Hood Canal; (5) Lower Columbia Tules; (6) Columbia Upriver Brights, Willamette and Cowlitz; (7) Oregon and Washington Coastal; and (8) Klamath River and Columbia River Summers. Further analysis for stocks within each of the eight regions indicates that local ocean conditions following the outmigration of smolts from freshwater to marine areas had a significant effect on survival for the majority of the stock groups analyzed. Our analyses of the data indicate that Pacific Northwest Chinook survival covaries on a spatial scale of 350–450 km. Lagged time series models are presented that link large-scale tropical Pacific conditions, intermediate-basin scale northeastern Pacific conditions, and local sea surface temperatures to survival of Pacific Northwest stocks.

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INTRODUCTION

Chinook salmon (*Oncorhynchus tshawytscha*) is a high valued species for recreational and commercial fisheries, and is of high cultural significance for Native American tribes in the northwest Pacific region of North America (Hunn, 1990). Large variability in adult returns has created substantial challenges for managing Chinook salmon fisheries. Because most Chinook salmon fisheries are now supported by large-scale hatcheries that release a known number of juveniles each year and monitoring programs provide estimates for natural smolt abundances in major production basins, a better understanding for how stock specific marine survival responds to ocean conditions could lead to better models of recruitment and therefore better informed management.

Numerous papers on *Oncorhynchus* spp. have related recruitment and marine survival covariation with respect to marine environmental conditions (Hare and Francis, 1995; Hare *et al.*, 1999; Magnusson, 2002; Mueter *et al.*, 2002; Peterman *et al.*, 2003; Beamish *et al.*, 2004). However, studies of Chinook salmon have been either focused on particular wild populations (e.g., Skagit River, U.S.A. by Greene *et al.*, 2005; or Snake River, U.S.A. by Hinrichsen and Fisher, 2009), dominated by hatchery populations (Magnusson, 2002) or limited to catch data (Hare and Francis, 1995). While results from these studies specific to Chinook salmon have helped identify marine environmental conditions that are likely important drivers of Chinook salmon population dynamics (i.e., survival and maturation), to our knowledge there is no geographically extensive research linking the marine environment with Chinook salmon recruitment and survival over time.

From southeast Alaska to northern California, Chinook salmon smolts typically leave the freshwater environment to enter an ocean that is either in or near

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a state of transition from winter to spring conditions (Quinn, 2005). Depending on the timing of this spring transition, outmigrants could encounter spring-like conditions characterized by a coastal ocean that has experienced significant upwelling, supporting nutrient enrichment and elevated primary productivity, or winter-like conditions characterized by downwelling, favoring low nutrients and low primary productivity, or a transition between the two (Bakun, 1996). Immediately after ocean entry, juvenile Chinook salmon spend a large amount of time on the coastal shelf either migrating along the coast or staying close to their natal rivers (Trudel *et al*., 2009). This early marine life history phase has been shown to be extremely important, with many studies linking interannual variations in different aspects of ocean conditions, such as upwelling and water temperature, with indicators of *Oncorhynchus* spp. marine survival (Logerwell *et al*., 2003; Peterson and Schwing, 2003; Lawson *et al*., 2004; Peterson *et al*., 2006). This paper focuses on conditions occurring during this early marine life cycle phase, with the intent of assessing the degree to which marine environmental variables can explain observed variability in marine survival of Pacific Northwest (PNW) populations of Chinook salmon from the Klamath River in the south to southeast Alaska in the north.

We examined covariation of marine survival at different spatial scales to determine the relative effects of broad-scale, regional, and local conditions on the interannual variation in survival of selected PNW Chinook salmon stocks. We then evaluated the hypotheses that: (i) ocean productivity as expressed by sea surface temperature (SST) anomalies (positive or negative) are inversely related to marine survival of Chinook salmon across our study area; and (ii) that large scale ocean–atmospheric processes such as the El Niño Southern Oscillation (ENSO; Wolter and Timlin, 1998) and the Pacific Decadal Oscillation (PDO; Mantua *et al*., 1997) impact the local conditions in near-shore coastal waters and thus also affect the survival of Chinook salmon. These hypotheses are assessed by relating patterns in SST, ENSO, and PDO to survival anomalies for multiple Chinook salmon stocks coastwide. Our analyses focus on tagged stocks that were either natural populations or the best representation of natural populations (i.e., hatchery tagging programs that are managed to mimic wild fish behavior). We also built lagged time series models to demonstrate how climate conditions associated with the tropical ENSO could be used to predict Chinook salmon marine survival in the short-term (at lead times of 1–2 yr).

MATERIALS AND METHODS

Coded wire tag data

The Chinook Technical Committee (CTC) of the Pacific Salmon Commission tracks 36 indicator stocks using coded wire tags (CWT; Johnson, 1990; Lapi *et al*., 1990) to evaluate exploitation rates in the ocean. We chose 21 of these stocks (see Table 1 and Fig. 1) for which the tagging data had adequate escapement sampling and a time series of more than 20 yr in length. In addition, we analyzed data for Klamath River Chinook salmon in southern Oregon/northern California. This stock is not managed under the jurisdiction of the Pacific Salmon Commission but it is important for salmon harvest management off the coast of Oregon and California, and has adequate sampling and tag data. Abundances of age-2 cohorts were reconstructed using a virtual population technique (cohort analysis), similar to the approach used by Coronado and Hilborn (1998).

From the CWT data, age-2 ocean abundances were constructed using Eqn (1):

$$\mathrm{O}_{a,t} = \frac{\mathrm{OC}_{a,t} + TC_{a,t} + E_{a,t} + \mathrm{O}_{a+1,t+1}}{1 - NM_{a,t}} \qquad (1)$$

where O is the ocean cohort, OC is the ocean catch, TC is the terminal catch, *E* is the escapement, and NM is natural mortality. Subscripts *a* and *t* indicate age and time, respectively. NM is assumed to occur in each age class before fishing mortality occurs and is assumed to be 40% to age-2 before fishing, 30% from age-2 to age-3, 20% from age-3 to age-4, and 10% from age-4 to age-5. Note that Eqn (1) is used recursively starting at an assumed final age (age-5 was used).

Corresponding survival to age-2 of fish released as sub-yearlings was computed using Eqn (2):

$$S_{2,t} = \frac{\mathrm{O}_{2,t}}{Rel_{t-2}} \qquad (2)$$

where S_2 is survival to age-2 associated with brood year releases (*Rel*) at time *t*–2 for a specific CWT group. In the case of yearling releases, survival and brood year releases change to $S_{3,t}$ (1^{st} ocean age) and Rel_{t-3}, respectively.

Ocean environmental data

We examined measures of coastal ocean conditions from April to July, the primary months of ocean entry of Chinook salmon smolts for the stocks evaluated in this study. We used monthly mean Bakun Upwelling Indices from April to July in the smolt year, obtained

Table 1. Exploitation rate indicator stocks, location, run type, and age of smolt at release.

Origin	Stock name	Location	Stock acronym	Run type	Smolt age
S.E. Alaska	Alaska Spring	Southeast Alaska	AKSP	Spring	Age-1
British Columbia	Kitsumkalum	North/Central BC	KLM	Summer	Age-1
	Robertson Creek	WCVI	RBT	Fall	Age-0
	Quinsam	Georgia Strait	QNSAM	Fall	Age-0
	Puntledge	Georgia Strait	PUNTL	Summer	Age-0
	Big Qualicum	Georgia Strait	BQR	Fall	Age-0
	Chilliwack (Harrison Stock)	Lower Fraser River	CHILLIWAC	Fall	Age-0
Puget Sound	Stillaguamish Fall Fingerling	Central Puget Sound	STL	Summer/Fall	Age-0
	George Adams Fall Fingerling	Hood Canal	GAD	Summer/Fall	Age-0
	South Puget Sound Fall Fingerling	South Puget Sound	SPSF	Summer/Fall	Age-0
	Nisqually Fall Fingerling	South Puget Sound	NIS	Summer/Fall	Age-0
Washington Coast	Queets Fall Fingerling	North Wash. Coast	QTS	Fall	Age-0
Columbia River	Cowlitz Tule	Columbia River (Lower WA)	CWF	Fall Tule	Age-0
	Spring Creek Tule	Columbia River (Mid)	SPR	Fall Tule	Age-0
	Columbia Lower River Hatchery	Columbia River (Lower OR)	LRH	Fall Tule	Age-0
	Upriver Bright	Upper Columbia River (Hanford)	URB	Fall Bright	Age-0
	Lewis River Wild	Lower Columbia River	LRW	Fall Bright	Age-0
	Lyons Ferry*	Snake River	LYF	Fall Bright	Age-0
	Willamette Spring	Willamette	WSH	Spring	Age-1
	Summers	Columbia River (Upper WA)-Wells Dam	SUM	Summer	Age-1
Oregon Coast	Salmon River	North Oregon Coast	SRH	Fall	Age 0
Southern Oregon/CA	Klamath River	Southern OR coast/ Northern CA coast	KLAM	Fall	Age 1

*Lyons Ferry was not used in the analysis because of insufficient number of years.

from the Pacific Fisheries Environmental Laboratory (PFEL: http://www.pfeg.noaa.gov/products/las/docs/global_upwell.html; Schwing *et al.*, 1996). We used monthly average gridded SST from April to July in the smolt year from NOAA extended reconstructed sea surface temperature data described by Smith and Reynolds (2004) (http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.ersst.html). Station locations were along the coastal shelf from 42° to 60°N at 2° intervals along the coast (see map Fig. 1). Additional nearshore SST data were obtained from BC lighthouse stations for Canadian waters (http://www-sci.pac.dfo.mpo.gc.ca/osap/data/SearchTools/Searchlighthouse_e.html).

Relationships between marine survival and region

Regional groupings of stocks were derived from standard cluster analysis techniques based on hierarchical agglomeration algorithms (Gordon, 1981) of marine survival rates. The model examined included year as the main effect, and analyzed year and stock, and year and region interactions (Eqn 3). The regional groupings were assessed for statistical differences among regions using an ANOVA of the following linear model:

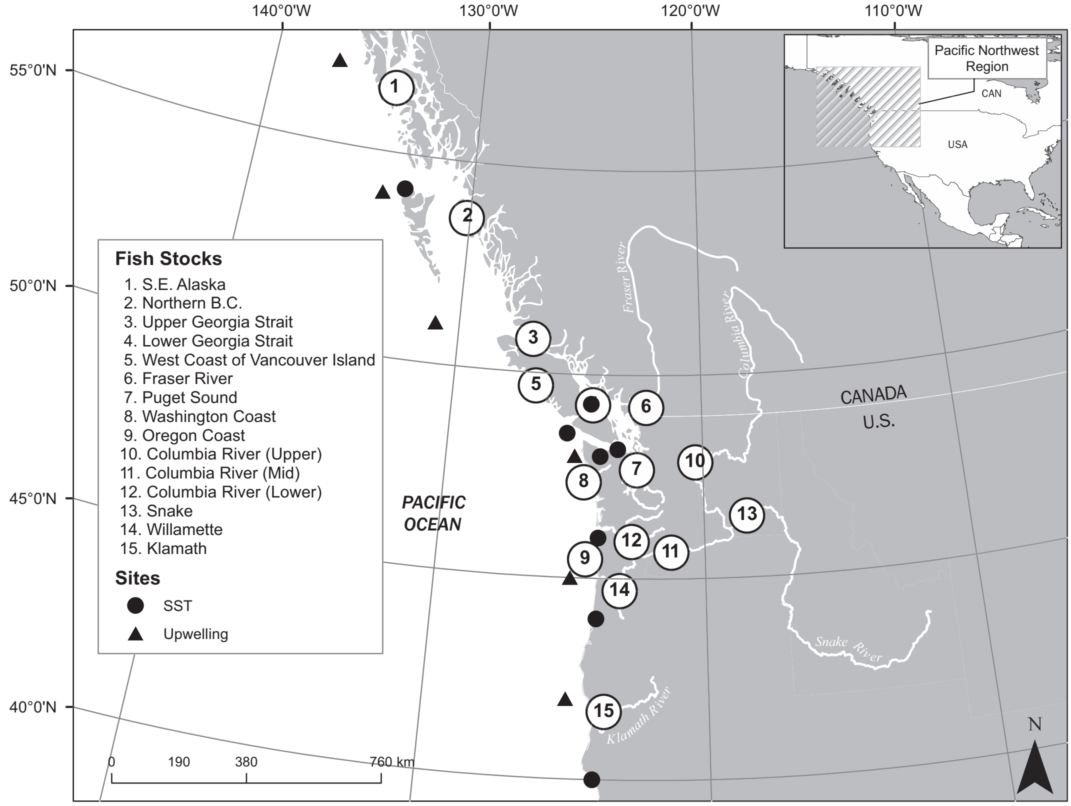
$$\ln(S_{2,q,t}) = \alpha + \omega_t Y + Y\sum_{i=1}^{n}\chi_i R_i + Y\sum_{i=1}^{n}\phi_i q_i \quad (3)$$

where Y is the year-effect, R_i represents the region estimated from the cluster analysis, q_i the stock, and S is the standardized survival to age-2 over time and over all stocks (R) and years (t). In this model, $\chi_i = \varphi_i = 0$ under the null hypothesis, and $\chi_i \neq 0$ and/or $\varphi_i \neq 0$ under the alternate hypothesis. α is the intercept in the model. The survival data used in this analysis are standardized survival, as the absolute differences in survival vary by an order of magnitude across stocks.

Relationships between local physical ocean conditions and Chinook salmon survival to age-2

We examined the correlation of two measures of physical ocean conditions during the initial marine residency of Chinook salmon smolts with the marine survival of 21 stocks of Chinook salmon (Snake River was excluded due to incomplete sampling in 1992 to

Figure 1. Chinook Populations tracked with coded wire tags. Sites used in the analysis are indicated by SST (circle) or Upwelling (Triangle) which were analyzed with respect to survival variation.



1994, 1996 and 1997). These measures were the Bakun UPI and SST for the spring transition period (April through July).

An initial correlation analysis was examined between SST, upwelling and survival. Because we found no consistent patterns of correlations between marine survival and the monthly averaged upwelling indices, further analysis was limited to the influence of SST on survival. We constructed linear regressions between time series of survival and SST time series from the geographical stations closest to the river mouth in the year of smolt outmigration for each stock. The linear regressions were expressed as:

$$S_{2,s,t} = \alpha + \beta V_{s,t} + \varepsilon_{s,t} \quad (4)$$

where $S_{2,s,t}$ represents survival to age-2 for stock (s) at time (t) in ocean entry year, $V_{s,t}$ is the independent ocean variable (SST) at time t, α is a constant, β is the slope parameter of the variable ($V_{s,t}$), and ϵ is the normal additive error of stock (s) and time (t).

Rather than using a traditional approach of statistical inference, i.e., testing for significance of a particular variable (in this case the value of the β parameter in Eqn 4), we performed a likelihood profile analysis (Hilborn and Mangel, 1997; Sharma and Hilborn, 2001) to quantify the uncertainty of the effect of SST. The likelihood profiles were generated using Eqn (5):

$$L(S_{2,s,t}|\alpha,\beta) = \frac{1}{\sqrt{2\pi\sigma^2}}\exp\left[-\frac{\left(S_{2,s,t}-\hat{S}_{2,s,t}\right)^2}{2\sigma^2}\right] \quad (5)$$

Lag-based time series analyses

Based on results obtained in the local scale analysis of survival and SST, we performed lag-based time series analyses linking ENSO, a global-scale phenomenon, to large basin-scale phenomena (i.e., the PDO), and then linking the PDO to the local SST potentially affecting Chinook salmon survival in the short-term. These relationships were incorporated into a series of models to determine how phenomena occurring on different spatial scales affect local ocean conditions and therefore the survival of a particular stock of Chinook salmon. These models were tested for two stocks, Oregon Coastal and Columbia Upriver Brights. The models are described in Eqn (6–8):

$$\mathrm{PDO}_t = \alpha_1 + \beta_1 \mathrm{ENSO}_{t-a} + \varepsilon_s \quad (6)$$

where PDO is the Pacific Decadal Oscillation (Mantua *et al*., 1997) estimated at time (t); ENSO is the El Niño Southern Oscillation Index as estimated through multivariate techniques (Wolter and Timlin, 1998) measured at time (t–a); and α_1 and β_1 are the intercept and slope parameters. Multiple time lags were examined from a = 6 months to a = 12 months, at 1-month intervals. The best predictor was based on these multiple lag-time relationships.

The model relating PDO to SST had the form:

$$\mathrm{PCSST}_t = \alpha_2 + \beta_2 \mathrm{PDO}_{t-a} + \varepsilon_s \quad (7)$$

where PCSST is the first principal component (PC) of local SST from four stations on the coastal shelf of Oregon and Washington for the months of April to July, from 42°N,124°W to 48°N,124°W at 2°N intervals. These stations were used to summarize local SST conditions affecting the Columbia River Bright and Oregon coastal Chinook stocks. This approach served as an intermediate step relating near shore ocean conditions to the PDO as well as the local SST station that is biologically relevant to survival of a particular stock.

Multiple time-lags were also examined for Eqn (7) with a = 1 to a = 12 months at 1-month intervals. The best predictor based on these multiple lag-time relationships was a = 1 month relating PDO to localized conditions on coastal Oregon and Washington. The local SST at the station closest to the river mouth for stock s was then related to PCSST by

$$\mathrm{SST}_t = \alpha_3 + \beta_3 \mathrm{PCSST}_{t-a} + \varepsilon_s \quad (8)$$

Multiple time lags were examined for a = 0 to a = 12 months at 1-month intervals for Eqn (8). The best lag was for a = 0 to relate the coastal Oregon and Washington stations to the SST stations that are off biological relevance to Columbia River Bright and Oregon coastal Chinook stocks.

Outputs from Eqn (6–8) were then used in Eqn (4) to predict the effect of ENSO events on survival of two Chinook salmon stocks.

RESULTS

Chinook salmon survival to age-2 by region

The groupings of stocks identified by a cluster analysis were: (1) Alaska, Northern BC, and North Georgia Strait; (2) Georgia Strait; (3) Lower Fraser River and West Coast of Vancouver Island (WCVI); (4) Puget Sound and Hood Canal; (5) Lower Columbia Tules [Spring Creek and Columbia Lower River Hatchery (LRH)]; (6) Columbia Upriver Brights, Willamette, and Cowlitz; (7) Oregon Coastal (Salmon River) and Washington Coastal (Queets); and, (8) Klamath River and Columbia River Summers (these two populations are currently depressed). Survivals to age-2 ocean recruits (using absolute measures of survival) are shown for these groups in Figure 2.

Results of the ANOVA for Eqn (3) indicated that year effects drive most of the variation in stocks over time, and that year effects were common across all groups (Table 2). We tested the full model including the year × region and the year × stock interactions to evaluate the effects of region and stock, with the year effect. The year × stock interaction was not significant, but the year × region interaction was significant. This test also indicated significant differences in survival between regions (Fig. 2). Residual diagnostics indicated the model did not appear to be overfitting, and the quartile plot (not shown) indicated that using a normal error structure was valid and the data were neither under- or over-dispersed. There were no outliers, and Cook's distance (Neter *et al*., 1996) was <1.0 for all data points.

Correlations of survival between individual stocks also indicated regional synchrony. Figure 3 displays a summary of pairwise correlations of survival in relation to distance between stocks. The number positive correlations >0.4 occurred at higher frequencies for stocks with streams of origin entering the ocean at distances <400 km apart.

Chinook salmon survival in relation to upwelling and SST

We analyzed the upwelling data and SST data with respect to survival for Chinook salmon stocks across multiple locations (Table 3). This broad-scale spatial analysis showed no consistent relationship between upwelling and survival of stocks across different regions: approximately equal numbers of negative and positive correlations >0.4 were observed. In contrast, SST tended to be negatively correlated with survival; all correlations >|0.4| were negative (Table 3), indicating that colder water tended to have a positive effect on survival. Although some correlations (positive for upwelling or negative for SST) do occur for some stocks that are not geographically proximate to the ocean stations (Table 3), our intent here is to evaluate the relationship between survival and environmental conditions on local scales. The hypothesis being tested relates April to July SST and upwelling from local stations of importance to survival for the

Figure 2. Time series of absolute survival for regional groups of Chinook salmon stocks from the north Oregon coast to southeast Alaska (STL is missing due to insufficient tag recoveries in early years).

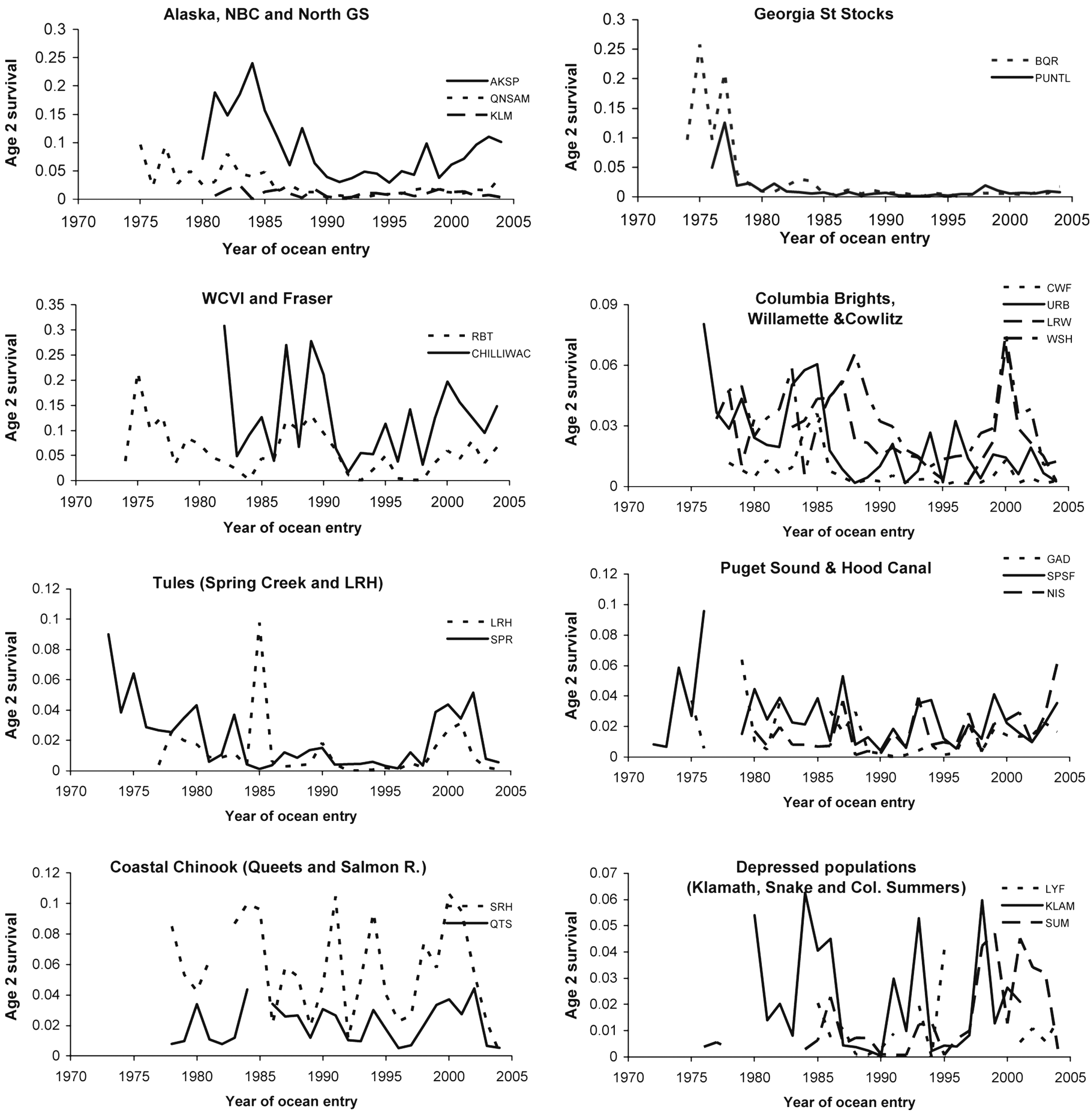
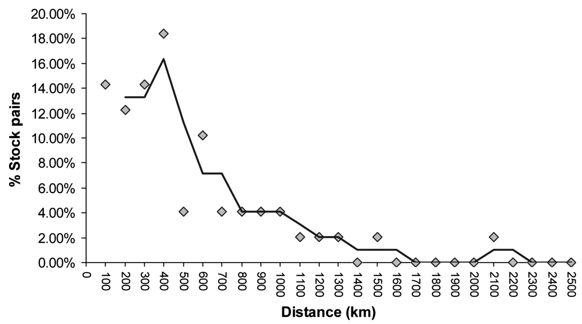


Table 2. ANOVA tests to estimate effects of Region and Stock on survival variation over time, accounting for year-effects.

Variable	d.f.	Deviance Resid.	d.f.	Resid. Dev	*F*	P (>*F*)
NULL			503	39.154		
Year (Y)	26	9.39	477	29.77	7.67	<2.2e-16*
Year (Y):Region (R)	186	16.07	291	13.70	1.93	1.697e-06*

*Significant $\alpha = 0.05$. Deviance Residual is the amount of deviance explained by adding the variable. The Residual Deviance is the remainder in the model not explained by adding the variable.

Figure 3. Results of correlation analysis displaying correlation ranking of survival (number of stock pairs with r > 0.4) between stocks and regions as a function of distance (km). Proportion of stock pairs with $r > 0.4$ as a function of distance (km) between river mouths. The solid line represents the second-order moving average. The solid line represents the moving average across these rankings by 4-yr distance blocks.



stock from the geographical region of closest proximity to these stations. The other information presented in this table is for illustrative purposes only.

Localized effects on survival

We tested for localized SST effects on survival using data for one stock from each group. The stocks examined were Alaska Spring, Big Qualicum River, Columbia Upriver Brights, Salmon River (Oregon Coastal), WCVI, Spring Creek, South Puget Sound, and Klamath (Figs 4 and 5). This analysis was carried out for the months of April through September, which corresponds to the period of initial marine residency after the smolts move from freshwater into the ocean environment.

For most stocks there was a statistically significant effect of SST at a certain time and area on survival. These effects are local in nature (Figs 4 and 5), and even though the relationships may not have a high r^2, they are significant for the majority of stocks (Table 4). The relationships shown in Figures 4 and 5, and the likelihood plots in Figure 6 indicate that the effect of a 1° change in SST in either the positive or negative direction could have a large effect on survival. For example, a 1°C increase in SST in July at 44°N,124°W would lead to a 0–4% decrease in survival for Oregon Coastal Chinook, with the most likely decrease at around 2% (Fig. 6).

In five of the eight stocks, there is a statistically significant ($P < 0.05$) fit for the linear model (Eqn 4). For stocks for which this relationship is not significant, i.e., Klamath, south Puget Sound, and Alaska Spring, likelihood profiles (Fig. 6) suggested that survival will increase or decrease in survival corresponding with a decrease or increase in SST, although the distribution overlaps the zero point. The linear model fit the data well based on residual diagnostics.

Building lagged models of survival for two stocks

We investigated whether survival for two stocks, Columbia Upriver Brights and Oregon Coastal, was related to local conditions in a lagged fashion using the data shown in Figures 4 and 5. We used Eqn (6), in which ENSO conditions in the tropical Pacific in May–June are used to predict PDO conditions in the following year in June (Fig. 6a). This model was statistically significant ($P = 0.01$; Table 5). The June PDO results were then used to predict the leading principal component based on PCA of the gridded SST data in June at 42°N,124°W, 44°N,124°W, 46°N,124°W, and 48°N,124°W (Fig. 6b). This model was also statistically significant ($P < 0.001$; Table 5). Finally, using Eqn (8), the principal component (July) was related to SST in July for 44°N,124°W and 48°N,124°W, the two stations that are important for survival for the Oregon Coastal Chinook salmon and Columbia Upriver Bright Chinook salmon (Fig. 6c,d). This model was also statistically significant ($P < 0.001$; Table 5). We used the output of these lagged models as input to Eqn (4) to forecast expected survival for spawning Chinook that out-migrate the following year based on ENSO conditions in the tropical Pacific in the year that they spawn. We used bootstrap techniques on parameter estimates obtained in each of the steps described in Eqn (6) through (8) to graphically show the range of effects of positive or negative ENSO for Oregon Coastal Chinook (Fig. 8).

DISCUSSION

Survival and scale

Studies similar to this one have examined the effect of large-scale and local-scale phenomena on sockeye, chum, and pink salmon (Mueter *et al.*, 2002; Peterman *et al.*, 2003; Pyper *et al.*, 2005). Bradford *et al.* (1997) and Malick *et al.* (2009) found that large-scale factors affect coho smolt survival. In addition, catch data analyzed by Hare *et al.* (1999) indicated a north–south regime shift in terms of salmon catches from Alaska to Oregon that oscillated in concordance with the PDO. Our study employs many of the same general techniques used in these studies but applies them to Chinook salmon survival.

While there is significant synchrony in the marine survival of the Chinook salmon stocks evaluated across a broad geographic scale, survival rates covary more closely at a regional level. Our results indicate

Table 3. Correlation of stock survival (excluding Snake River) with environmental station showing a positive ($r > 0.4$; dark gray) or negative ($r < -0.4$; light gray) relationship.

Primary environmental indicator	Month	Lat long location	Stock: AKSP	KLM	RBT	QNSM	PUNTL	BQR	ILLIW	GAD	SPSF	MS	WRY	QTS	WSH	CWF	SPR	LRH	LRW	URB	SUM	SRH	KLAM
Upwelling	April	A42N125W	−0.06	0.08	0.12	−0.08	0.28	−0.09	0.01	0.11	0.11	−0.11	0.17	0.57	0.06	0.03	0.49	0.13	0.01	0.04	0.57	0.18	−0.01
		A45N125W	0.08	0.07	0.38	0.14	0.27	0.17	0.23	0.24	0.04	−0.22	0.21	0.51	0.32	0.09	0.38	0.21	0.09	0.00	0.28	0.22	−0.13
		A48N125W	0.17	0.03	0.41	0.23	0.25	0.22	0.27	0.27	0.03	−0.21	0.20	0.39	0.36	0.12	0.31	0.26	0.07	−0.02	0.18	0.21	−0.12
		A51N131W	0.18	0.02	0.31	0.16	0.25	0.10	0.13	0.22	−0.25	−0.33	0.13	0.20	0.30	0.01	0.35	0.24	−0.08	−0.06	0.30	0.10	−0.19
		A54N134W	0.21	−0.02	0.03	−0.02	0.10	0.08	−0.11	−0.05	−0.55	−0.38	0.11	−0.02	0.08	−0.06	0.30	0.06	−0.28	0.00	0.15	−0.07	−0.18
		A57N137W	0.23	−0.06	−0.08	−0.12	0.08	0.08	−0.29	−0.14	−0.48	−0.40	0.22	0.00	−0.12	−0.01	0.20	0.01	−0.41	0.12	0.12	−0.12	−0.11
		A60N146W	0.35	0.37	−0.06	0.24	0.38	0.29	0.08	0.16	0.05	−0.18	0.26	0.27	−0.02	0.23	0.49	0.31	−0.11	0.31	0.55	0.22	0.06
		A60N149W	0.25	0.39	0.09	0.13	0.42	0.30	0.15	0.12	0.02	−0.15	0.23	0.29	0.11	−0.01	0.56	0.09	−0.12	0.13	0.60	0.26	−0.06
	May	M42N125W	−0.21	0.07	−0.01	0.13	0.05	−0.01	0.19	0.03	0.08	0.14	−0.29	−0.13	−0.15	−0.28	0.23	−0.05	−0.16	−0.21	0.32	−0.01	−0.28
		M45N125W	−0.23	0.12	−0.08	0.20	−0.06	0.07	0.14	−0.15	0.00	−0.06	−0.31	−0.32	−0.14	−0.25	−0.03	−0.08	−0.20	−0.14	−0.02	−0.04	−0.31
		M48N125W	0.02	0.42	0.12	0.50	0.07	0.42	0.37	−0.03	0.15	−0.09	−0.14	−0.35	0.12	−0.06	0.07	0.06	−0.04	0.08	−0.11	0.00	−0.28
		M51N131W	−0.40	−0.03	0.02	0.09	0.05	0.03	0.13	−0.41	0.00	0.12	−0.51	−0.41	−0.17	−0.24	−0.08	−0.01	−0.33	−0.18	−0.17	−0.17	−0.17
		M54N134W	−0.05	−0.24	−0.13	0.07	−0.09	0.07	−0.08	−0.38	−0.26	−0.08	−0.28	−0.43	−0.24	0.04	−0.37	−0.07	−0.31	0.05	−0.54	−0.27	0.09
		M57N137W	0.02	−0.27	−0.14	0.04	−0.08	0.10	−0.12	−0.38	−0.27	−0.11	−0.18	−0.36	−0.27	0.10	−0.44	−0.13	−0.28	0.09	−0.59	−0.30	0.16
		M60N146W	−0.10	−0.16	−0.07	0.05	0.23	−0.15	0.10	−0.20	−0.24	0.05	−0.34	−0.27	−0.33	−0.04	−0.27	0.06	−0.28	−0.21	0.07	−0.42	0.30
		M60N149W	−0.08	−0.09	−0.13	0.04	0.35	−0.12	−0.03	−0.15	−0.25	−0.04	−0.23	−0.20	−0.27	−0.13	−0.23	0.01	−0.32	−0.20	0.28	−0.28	0.35
	June	J42N125W	−0.09	0.00	−0.19	0.09	0.14	−0.08	−0.08	−0.13	−0.03	0.04	−0.28	−0.20	−0.17	0.00	−0.21	0.03	0.10	−0.06	0.16	0.01	0.31
		J45N125W	0.27	0.27	−0.10	0.54	0.17	0.25	0.18	0.20	0.19	−0.05	−0.05	−0.13	0.05	0.25	−0.20	0.21	0.24	0.13	0.09	0.15	0.44
		J48N125W	−0.06	0.01	−0.21	0.07	0.38	−0.03	−0.13	−0.18	−0.10	−0.11	−0.21	−0.09	−0.08	−0.14	−0.21	−0.11	−0.13	−0.22	0.29	0.09	0.47
		J51N131W	−0.01	0.04	−0.41	0.05	0.30	0.02	−0.22	−0.24	−0.28	−0.16	−0.10	−0.20	−0.21	−0.13	−0.21	−0.14	−0.33	−0.14	0.19	0.01	0.45
		J54N134W	0.00	0.04	−0.54	−0.04	0.28	−0.03	−0.36	−0.29	−0.39	−0.20	−0.08	−0.20	−0.32	−0.13	−0.11	−0.13	−0.46	−0.07	0.28	0.01	0.38
		J57N137W	−0.10	−0.22	−0.59	−0.19	0.13	−0.21	−0.46	−0.36	−0.46	−0.23	−0.19	−0.21	−0.43	−0.13	−0.19	−0.11	−0.52	−0.06	0.13	−0.02	0.31
		J60N146W	−0.11	−0.24	−0.53	−0.15	0.11	−0.21	−0.36	−0.32	−0.46	−0.23	−0.24	−0.21	−0.38	−0.14	−0.18	−0.11	−0.53	−0.09	0.09	−0.02	0.28
		J60N149W	−0.54	−0.29	−0.09	−0.45	−0.09	−0.44	−0.14	−0.13	−0.13	0.46	−0.38	0.02	−0.26	−0.47	0.33	−0.14	−0.29	−0.47	0.45	−0.20	−0.03
	July	JU42N125W	−0.10	−0.14	−0.21	−0.35	0.15	−0.35	−0.14	−0.02	−0.19	0.14	−0.09	0.17	−0.21	−0.21	0.34	−0.06	−0.09	−0.18	0.65	0.13	0.13
		JU45N125W	−0.02	−0.26	−0.27	−0.30	0.03	−0.33	−0.27	−0.27	−0.28	−0.23	−0.07	0.25	−0.46	0.10	−0.06	0.09	−0.12	0.20	0.19	0.13	0.03
		JU48N125W	0.31	−0.12	−0.04	0.01	0.10	−0.17	−0.10	−0.06	−0.08	−0.36	0.18	0.28	−0.18	0.47	−0.21	0.40	0.16	0.37	−0.05	0.14	0.06
		JU51N131W	−0.24	−0.15	−0.23	−0.30	0.21	−0.40	−0.20	−0.49	−0.04	−0.05	−0.14	−0.12	−0.28	−0.13	−0.15	−0.09	−0.13	−0.20	0.03	−0.19	−0.11
		JU54N134W	−0.17	0.13	0.00	−0.09	0.27	−0.26	0.05	−0.40	0.28	0.09	−0.10	−0.20	−0.08	−0.01	−0.17	0.08	0.10	−0.16	0.03	−0.08	−0.01
		JU57N137W	−0.32	0.21	0.21	−0.09	0.17	−0.36	0.16	−0.25	0.33	0.18	−0.18	−0.33	0.11	−0.12	−0.13	0.22	0.14	−0.25	0.03	−0.14	−0.20
		JU60N146W	−0.17	0.09	0.16	−0.16	0.16	−0.36	0.19	−0.16	0.07	0.08	0.07	−0.15	0.06	−0.16	−0.16	−0.02	0.13	−0.37	0.06	−0.21	0.01
		JU60N149W	−0.08	−0.03	0.18	−0.12	0.35	−0.40	0.30	0.02	−0.03	−0.01	−0.03	0.00	0.19	−0.19	0.18	0.02	0.16	−0.34	0.30	−0.10	−0.16
Sea_surface temperature	September	40N124 WSSTSEP	0.04	0.02	−0.26	0.20	−0.03	0.34	0.04	−0.07	0.03	0.08	−0.02	−0.22	−0.31	0.05	0.03	0.03	−0.36	0.29	−0.27	−0.07	−0.20
	July	44N124 WSSTJUL	−0.19	0.02	−0.04	−0.03	−0.35	0.08	−0.02	−0.03	−0.20	0.10	−0.09	−0.41	−0.02	−0.27	0.00	−0.12	−0.36	−0.28	−0.28	−0.44	−0.24
	April	46N124 WSSTAPR	−0.16	−0.08	−0.25	−0.19	−0.03	0.05	−0.36	−0.32	−0.25	−0.05	0.00	−0.42	−0.12	−0.35	−0.33	−0.42	−0.23	−0.29	−0.28	−0.36	−0.14

Table 3. (Continued).

Primary environmental indicator	Month	Lat long location	Stock AKSP	KLM	RBT	QNSM	PUNTL	BQR	ILLIW	GAD	SPSF	MS	WRY	QTS	WSH	CWF	SPR	LRH	LRW	URB	SUM	SRH	KLAM
	July	48N124 WJUL	−0.41	0.07	−0.08	−0.15	−0.29	0.04	0.02	−0.19	−0.16	0.20	−0.23	−0.40	0.01	−0.46	0.13	−0.28	−0.36	−0.40	−0.18	−0.33	−0.27
	June	RR-June	−0.14	0.30	−0.10	0.00	−0.07	0.05	0.00	0.15	−0.09	0.18	0.14	−0.18	0.12	−0.25	0.13	−0.04	−0.03	−0.27	0.15	−0.26	0.04
	June	Amphitrite Pt-June	0.06	−0.13	−0.34	−0.08	−0.11	0.17	−0.39	−0.25	−0.10	0.06	−0.01	−0.51	−0.08	−0.13	−0.28	−0.28	−0.25	0.03	−0.45	−0.17	−0.09
	August	Chrome Island-August	−0.14	−0.17	−0.24	−0.04	0.24	−0.01	−0.23	−0.02	0.11	0.26	−0.01	−0.09	−0.28	−0.25	−0.11	−0.30	−0.28	−0.18	0.17	−0.30	0.27
	September	Langara Island Sep	−0.10	−0.36	−0.15	−0.11	0.34	−0.06	0.02	−0.17	−0.14	−0.01	−0.33	−0.25	−0.37	−0.39	−0.08	−0.38	−0.57	−0.18	0.05	−0.12	−0.42

that there is a positive correlation in survival rates among Chinook salmon stocks that occur at a geographic scale of 350–450 km (Fig. 3), the strength of which decreases as distance increases between stocks increases. This is consistent with other studies showing regional covariation in survival for pink, chum, and sockeye salmon, with correlations between survival rates being greater at distances <500 km (Mueter *et al.*, 2002, Pyper *et al.*, 2005).

Broad-scale and regional concordance in survival rates demonstrate that shared environmental conditions impact Chinook salmon stocks at these scales. However, most of the variation in survival between stocks is not explained at these scales, indicative of a large influence of some combination of local ocean conditions or stock specific responses to similar environmental conditions impacting survival (e.g., Hilborn *et al.*, 2003). This observation is consistent with the paradigm of Pacific salmon biology that conditions during early marine residency are important determinants of marine survival and year-class strength (Groot and Margolis, 1991; Quinn, 2005). Factors influencing survival during the early marine phase are a complex interaction of physical and biological processes, including temperature, upwelling, lower-trophic level production, competition, and predation (Holtby *et al.*, 1990; Koslow *et al.*, 2002; Briscoe *et al.*, 2005; Malick *et al.*, 2009). We used local measures of SST as a proxy for early marine conditions encountered by the stock groups of Chinook salmon evaluated. We found that marine survival generally decreased with increases in SST across stocks, although the relationship was not statistically significant for all stocks evaluated.

We did not see a strong relationship between local monthly averaged upwelling during the early marine residency of Chinook salmon and survival in this analysis. Ruzicka *et al.* (2011) concluded that upwelling has an inconsistent relationship with survival because it does not characterize the mechanisms that underlie the biological underpinnings affecting survival, so they developed an alternative upwelling-driven meso-zooplankton index for the Oregon shelf ecosystem that has a better correspondence to survival for Oregon coho salmon than the simple upwelling index we used. Biological mechanisms for characterizing the juvenile Chinook salmon's apparent affinity towards colder water and species, such as cold neritic copepods (Bi *et al.*, 2011), could indirectly be related to Chinook survival, although investigating these mechanisms was beyond the scope of the current analysis.

Figure 4. Relationship between survival and SST for Klamath, Salmon River (Oregon Coastal Chinook), Spring Creek Tules (Columbia), and the Columbia Upriver Brights. The SSTs were obtained from COADS database for locations near the coastal shelf and were the most highly correlated with survival during the first few months after smolts emigrate into the ocean. Stations reported are 40°N,124°W, 44°N,124°W, 46°N,124°W and 48°N,124°W.

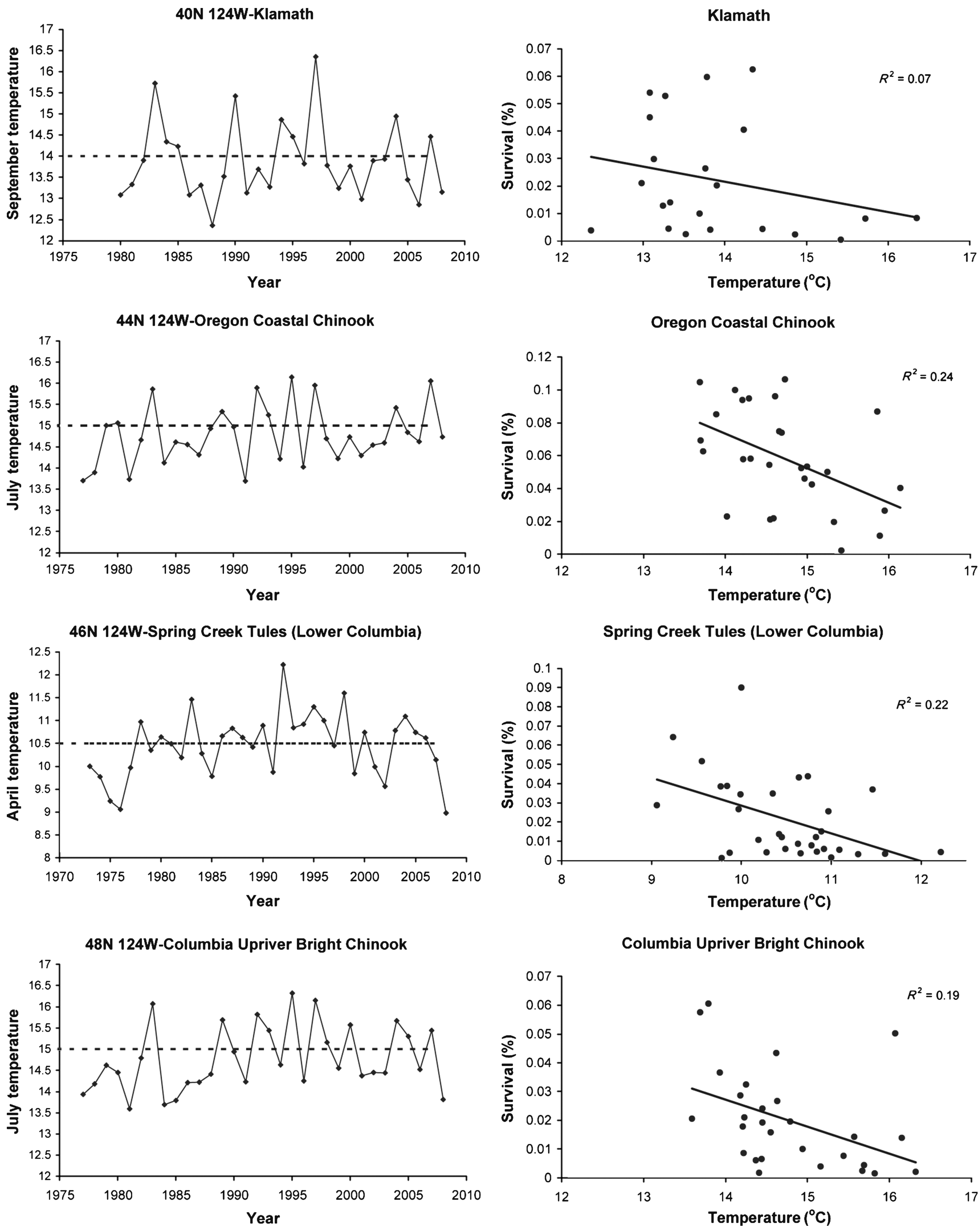


Figure 5. *Relationship between survival and SST for Puget Sound, West Coast of Vancouver Island (WCVI), Georgia Strait, and southeast Alaska (SEAK). The SSTs were obtained from BC lighthouse database for nearest locations that could be used as surrogates for these systems.*

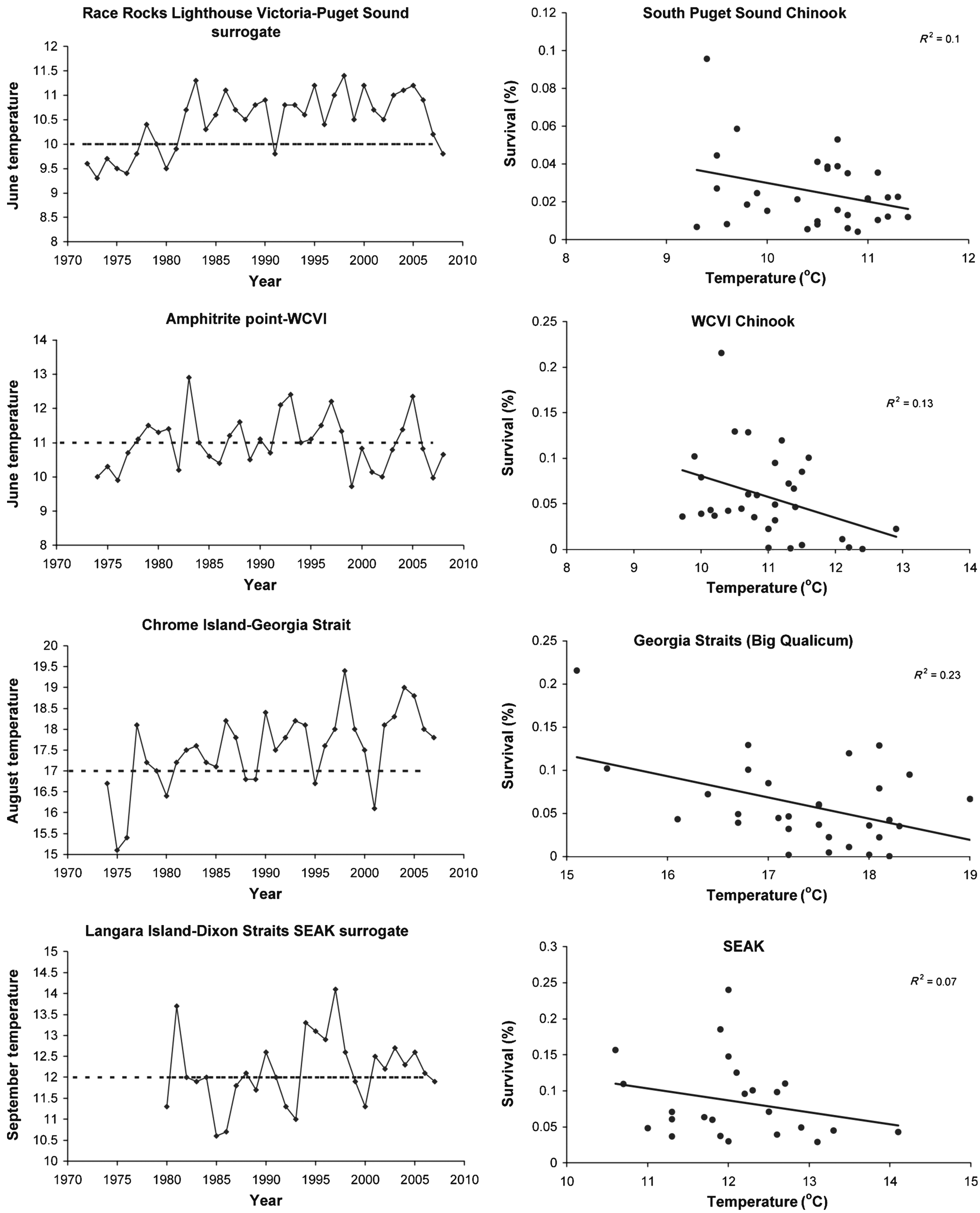


Table 4. ANOVAs using Eqn (4), indicating significance of ocean variable SST in months indicated in Figures 4 and 6. As described in Methods, the SST data set used for each stock is different.

	d.f.	SS	MSE	*F*	P (>*F*)		d.f.	SS	MSE	*F*	P (>*F*)
Klamath						South Puget Sound					
SST	1	0.0006	0.0006	1.43	0.25	SST	1	0.001	0.001	3.07	0.09
Residuals	20	0.0086	0.0004			Residuals	29	0.010	0.000		
Oregon Coast						West Coast of Vancouver Island					
SST	1	0.0058	0.0058	7.9	0.01	SST	1	0.009	0.009	4.44	0.04
Residuals	26	0.0192	0.0007			Residuals	29	0.060	0.002		
Spring Creek (Lower Columbia Tules)						Georgia Straits (Big Qualicum River)					
SST	1	0.003	0.003	8.35	0.01	SST	1	0.016	0.016	8.65	0.01
Residuals	30	0.011	0.000			Residuals	29	0.053	0.002		
Upriver Brights						Alaska Spring Chinook					
SST	1	0.001	0.001	6.02	0.02	SST	1	0.004	0.004	1.51	0.23
Residuals	26	0.006	0.000			Residuals	22	0.063	0.003		

Our finding of a consistent inverse relationship between survival and SST throughout the geographic range examined differs somewhat from other Pacific salmon species. Significant relationships between localized measures of SST and marine survival have also been shown for pink, chum, and sockeye salmon (Mueter *et al.*, 2002, 2005; Pyper *et al.*, 2005). However, for these species the relationship was generally positive for northern British Columbia and Alaska stocks, and negative for more southerly stocks. Also, marine survival of coho salmon covaries from southern British Columbia to southeast Alaska, but not with more southerly stocks from Washington to California (Coronado and Hilborn, 1998; Hobday and Boehlert, 2001). These results indicate that Chinook salmon are an exception to the overall increase in Alaska salmon production associated with warmer conditions under the inverse production regimes noted by Hare *et al.* (1999) and that productivity of Chinook salmon stock groups from as far north as southeast Alaska may be negatively impacted by warming of the North Pacific Ocean and Gulf of Alaska.

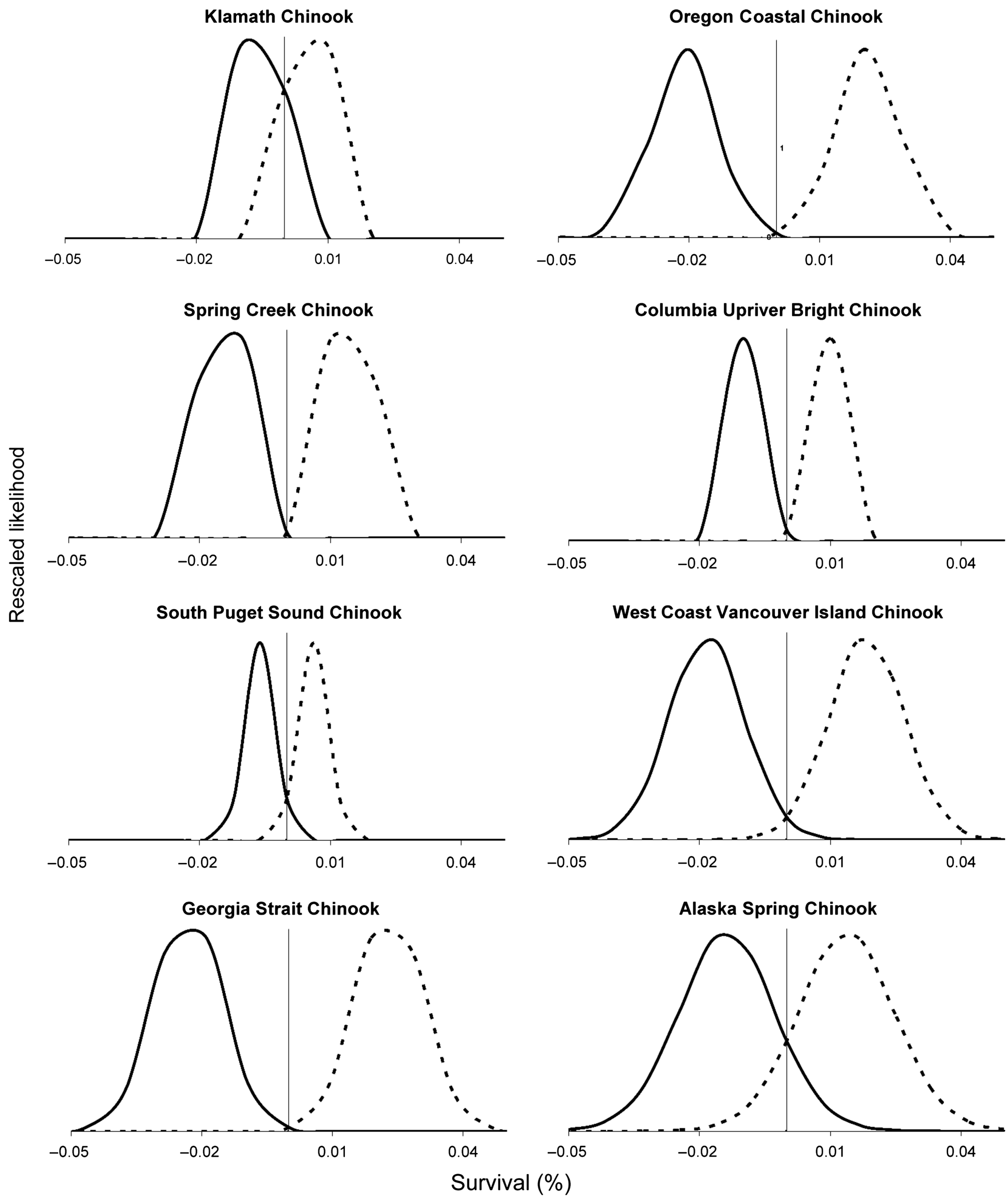
We demonstrate how the relationships between indices of ocean conditions could be used on various spatial scales to forecast survival (Figs 7 and 8). Thus, this study relates issues of spatial and temporal scales to Chinook salmon survival in the way that Levin (1992) and Mackas *et al.* (1985) did for other marine organisms. Figure 2 indicates this information could also be integrated with other biological indicators (Trudel *et al.*, 2005; Peterson *et al.*, 2006; Bi *et al.*, 2011) to understand the ecosystem interactions that affect survival of salmon across these scales. Survival of PNW Chinook is strongly linked to global climate patterns, and this study demonstrated these connections empirically by relating a derived species-scale parameter (survival) to processes that occur on a variety of scales.

Large-scale environmental conditions in the PNW

Survival of Chinook salmon stocks coastwide has oscillated over time across the entire PNW (Fig. 2). An examination of 4 years (1983, 1985, 1992, and 1999) provides more evidence for this pattern some context to explain the variability in these rates over time. In these years, anomalous SSTs were observed in the Pacific Ocean (Fig. 9). Both 1983 and 1992 exhibited lingering effects of a prolonged El Niño which brought warm water to the coastal shelf, leading to low productivity and shifts in species composition at lower trophic levels such as euphausiid species with lower caloric and fat content than the typical north Pacific species (Peterson *et al.*, 2006). Average survivals of Chinook salmon stocks examined for 1983 and 1992 ocean entry years were 3.5% and 1.0%, respectively. In contrast, the cooler conditions in 1985 and 1999 were associated with average standardized survivals of 5% in 1985 and 1999, respectively, for the stocks examined in this paper. Although 1983 does not stand out as a large anomaly, the prolonged conditions in the NE Pacific in 1981 that preceded the El Niño starting in 1982 and extending till 1983, had an adverse effect on survival between 1981 and 1983 (Peterson *et al.*, 2006).

The survival and SST models provide a mechanism for predicting the impacts of regional and local environmental conditions on survival. The SST in the North Pacific Ocean has varied greatly from 2005 to 2008 (Fig. 10). Poor ocean conditions in 2005 had an adverse effect coastwide on Chinook salmon survival (PSC, 2008). Based on our results, we predicted higher than average survival for 2008 outmigrants, with larger

Figure 6. Rescaled likelihood profiles of the Beta parameter as a function of a 1° change in SST at each of the locations specified in Figures 5 and 6. A 1°C increase in SST (solid line) indicates the absolute amount of decrease in overall survival might be expected for the stock, whereas a 1°C decrease in SST (dashed line) indicates the absolute increase in survival that might be expected for a particular stock. These figures assume a linear fit.

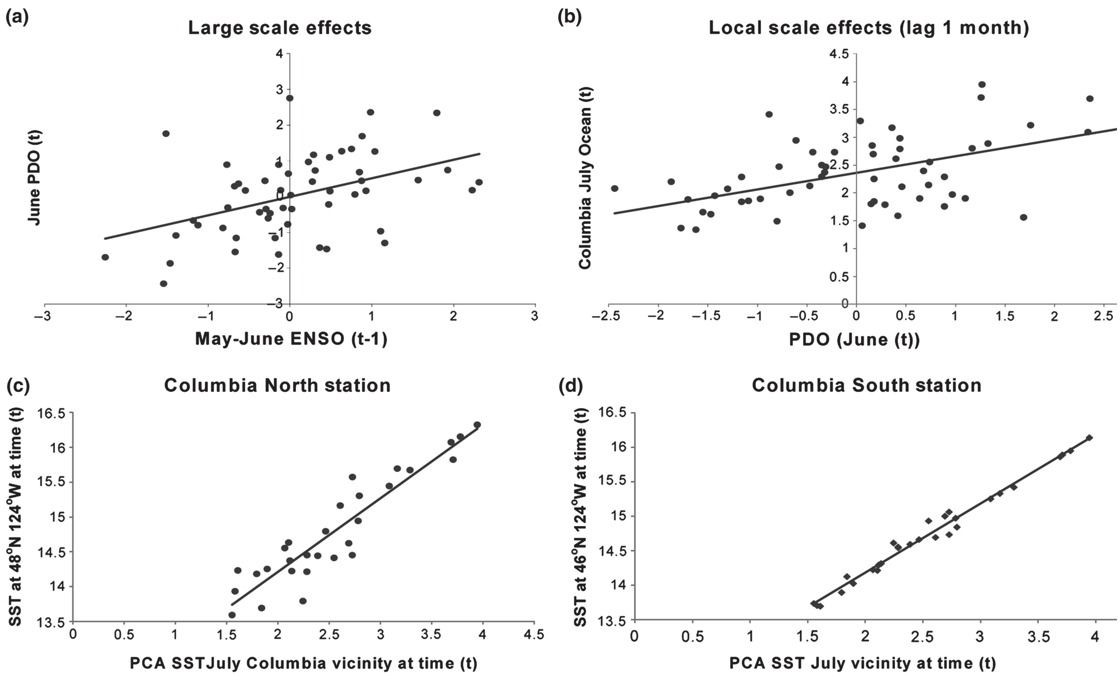


than average runs in 2010, 2011 and 2012 (for the 3-, 4-, and 5-yr-olds for ocean-type Chinook, and 4-, 5-, and 6-yr-olds for stream-type Chinook). These are the types of spatial and temporal patterns that can be used to infer trends in survival over the near-term. Observed survival in 2010 from outmigrating smolts indicated a stronger than average return for the 3-yr-old ocean-type fish and 4-yr-old stream-type fish from Oregon to British Columbia, demonstrating that broad-scale ocean conditions are useful indicators of overall marine survival for Chinook coastwide. These predictions could be taken a step further by using the lag-linked models relating ENSO to the PDO, which in turn affects regional conditions on the shelf and

Table 5. ANOVAs using Eqns (6–8) demonstrating significance of ENSO in predicting PDO; the PDO in predicting conditions of the Columbia, Washington and Oregon coasts; and of the PCA off the Columbia in predicting SST at the Oregon coast stations at 44°N,124°W and 48°N,124°W.

	d.f.	SS	MS	*F*	P (>*F*)
ANOVA on Eqn (6)					
ENSO(t−1)	1	13.67	13.67	12.94	0.001
Residual	53	56.00	1.06		
ANOVA on Eqn (7)					
PDO(t)	1	6.47	6.47	20.24	3.67E-05
Residual	54	17.27	0.32		
ANOVA on Eqn (8)					
Columbia (t)	1	13.00	13.00	1515.84	2.93E-25
Residual	27	0.23	0.01		

Figure 7. Lag time effects from different scales affecting SST at the local scale affecting survival of the Columbia River Bright and Oregon coast Chinook stocks. The top left panel (a) relates ENSO conditions the previous year to PDO conditions in the current year, the top right panel (b) relates June PDO conditions in the NE Pacific to conditions off the Washington and Oregon coast in the vicinity of the Columbia, and the bottom two panels (c and d) relate conditions off the Columbia to sea surface temperatures that are related to survival of Columbia River Bright and Oregon coastal Chinook salmon stocks.



thus survival of Chinook coastwide. Thus an ENSO value in May–June would relate to a PDO value in June of the following year that would relate to local effects for the region in question. In the example we presented for the Oregon coastal and Columbia River Chinook stock, temperatures at stations near the Columbia River mouth are key locations to relate to survival of the Columbia River Bright and Oregon coastal Chinook salmon stocks. The magnitude of this effect and its uncertainty can be quantified with an ENSO index value for Oregon coastal Chinook (Fig. 8).

Figure 8. The effect of a positive or negative ENSO on Oregon Coastal Chinook survival (a linear model relating survival to SST, or a non-linear exponential model relating survival to SST, based on data shown in Fig. 4).

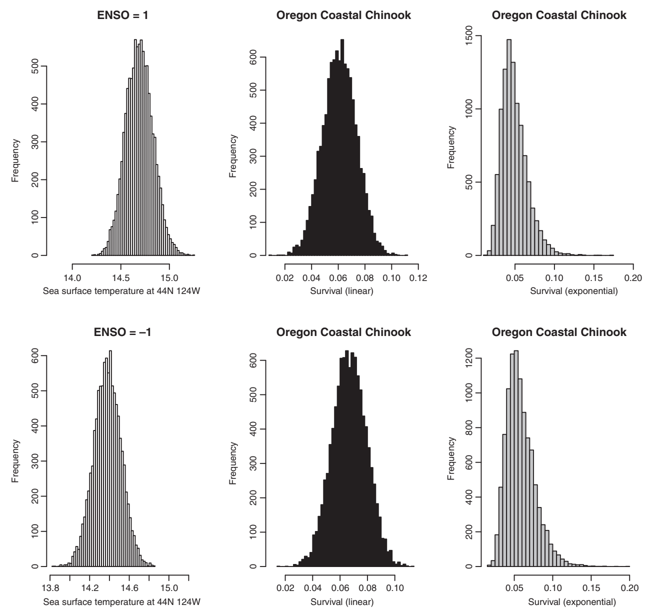
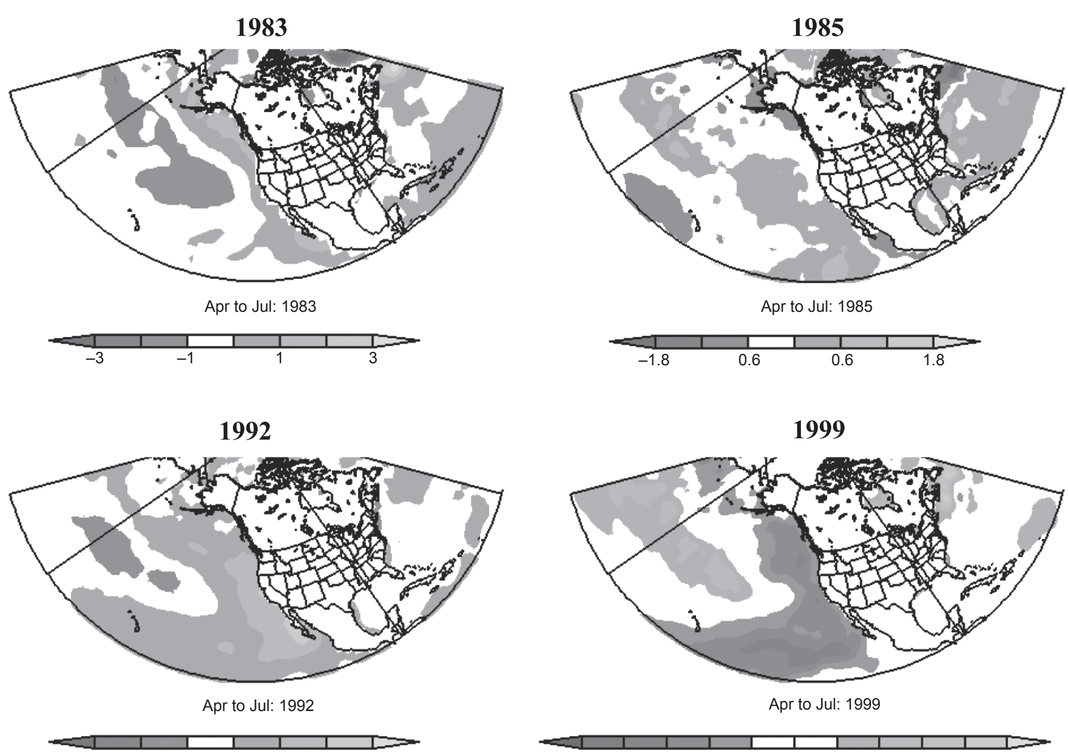


Figure 9. Four distinct patterns of environmental conditions that may have consequential impacts on PNW Chinook survival during the spring transition period (April through July). The upper and lower left hand panels show warmer than average conditions (anomalies), indicating poor upwelling in 1983 and 1992 impacting survival coast-wide. The right hand panels indicate cooler than average conditions (anomalies) in 1985 and 1999 that had a positive effect on survival coastwide (data and figures generated from http://www.esrl.noaa.gov).



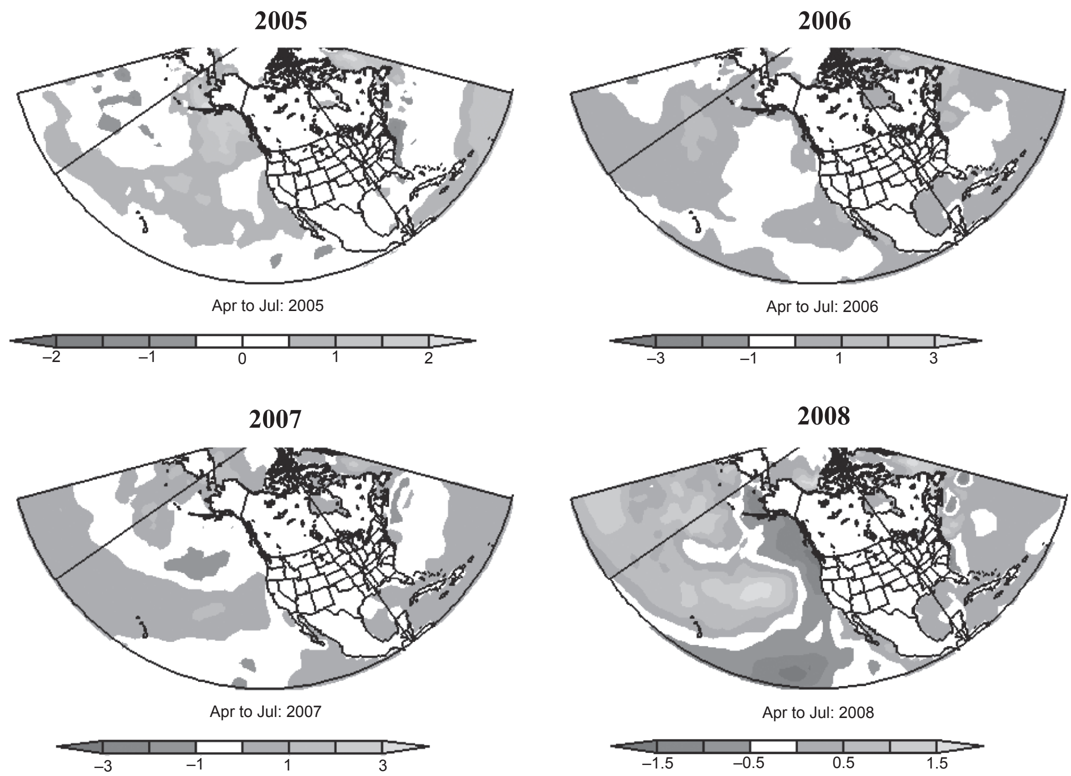


Figure 10. Conditions along the northeast Pacific Ocean rim in 2005–2008 during spring (April through July) period of early marine residency of Chinook salmon (data and figures generated from http://www.esrl.noaa.gov).

CONCLUSIONS

This paper provides an analysis of coastwide Chinook survival trends from northern California to southeast Alaska. Results indicate that survival can be grouped into eight distinct regional clusters that are primarily geographically based. Further analysis for stocks within each of the eight regions indicates that local ocean conditions as characterized by SST following the timing of outmigration of smolts from freshwater to marine areas had a significant effect on survival for the majority of the stock groups analyzed. In addition, the analysis indicates there is weak coherence (colder than average SSTs are positively correlated with an increase in survival all along the coast) on an annual basis coastwide that drives Chinook survival from SEAK to northern California. While upwelling data do not indicate an effect on survival of Chinook, SST shows an inverse relationship with survival over the time series analyzed. Analyses of the survival data spatially shows that Pacific Northwest Chinook survival typically covaries on a spatial scale of 350–450 km.

We found evidence that survival of Chinook salmon stocks from the north California coast to southeast Alaska is affected by environmental conditions at ocean basin, regional, and local scales. In addition, we analyzed environmental conditions that occur across different temporal and spatial scales, and presented lagged time-series models to link them to survival of specific Chinook salmon stocks. This approach could be used to formulate early predictions of Chinook survival coastwide and contribute to an adaptive management framework based on these projections. Principles of precautionary management (FAO 1996, Richards and Maguire, 1998) could be used as guidelines, and risk to the resource could be reduced by setting lower fishing targets when conditions are expected to be poor. Conversely, fishing targets could be increased when ocean conditions indicate that survival rates would be better than average. The models presented are useful for projecting survival for Chinook coastwide, and for developing a strategy that optimizes long-term sustainability of the resource. Finally, assuming that the SST–survival relationships identified here are indicative of a robust mechanism that will persist in a changing climate, the effect of climate change can be inferred for Chinook based on the relationship with SST. A 1° increase in SSTs during the key transition period (April through July) from freshwater to ocean environments could result in a reduction in survival of 1–4% across the species range.

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