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Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract: We evaluated the relative importance of "bottom-up" (production-limited) and "top-down" (predator-mediated) processes during early marine residence in a population of Chinook salmon (*Oncorhynchus tshawytscha*) from the upper Columbia River, USA. We examined length, mass, and condition index of age-0 juveniles collected in the ocean during June and September across 11 years in relation to conditions in the river, estuary, and coastal ocean and to future adult returns. Characteristics of juveniles in September, but not June, were related to adult returns. During years when coastal waters were relatively cool and productive, juveniles captured in September displayed relatively low condition and reduced otolith growth compared with years when coastal waters were relatively warm and unproductive; this contrast indicates that top-down effects such as selective mortality or competition are important during early marine residence. Key physical (river plume volume during emigration) and biological (condition) variables and their interaction accounted for >95% of the variation in adult returns. Future research should focus on evaluating predators and competitors and understanding how river plume structure influences survival.

Résumé : Nous avons évalué l'importance relative des processus ascendants (limités par la production) et descendants (modulés par les prédateurs) au début du séjour en mer dans une population de saumons quinnat (*Oncorhynchus tshawytscha*) du cours supérieur du fleuve Columbia (États-Unis). Nous avons examiné la longueur, la masse et l'indice d'embonpoint de juvéniles de 0 an prélevés en océan durant les mois de juin et septembre pendant 11 ans, par rapport aux conditions dans le fleuve, l'estuaire et le littoral océanique, ainsi qu'aux retours d'adultes subséquents. Les caractéristiques des juvéniles en septembre, mais non en juin, étaient reliées aux retours d'adultes. Durant les années où les eaux côtières étaient relativement froides et productives, les juvéniles capturés en septembre présentaient des indices d'embonpoint et des taux de croissance des otolites relativement faibles par rapport à ceux des juvéniles capturés durant les années d'eaux côtières relativement chaudes et non productives. Ces différences indiquent que des effets descendants tels qu'une mortalité sélective ou la concurrence sont importants au début du séjour en mer. Des variables physiques (volume du panache fluvial durant l'émigration) et biologiques (embonpoint) clés et leur interaction expliquaient >95 % de la variabilité des retours d'adultes. Les travaux de recherche futurs devraient se pencher sur l'évaluation des prédateurs et des concurrents et la compréhension de l'influence de la structure du panache fluvial sur la survie. [Traduit par la Rédaction]

Introduction

A major focus of fisheries research is to identify factors regulating the productivity of biological populations. Regulatory mechanisms are often identified as processes directly related to prey productivity (bottom-up) or predation (top-down) (Murdoch 1994; Munch et al. 2005). One empirical approach to identify regulatory mechanisms is to compare population characteristics before and after a critical period in the life history (Checkley et al. 1988; Wright and Gibb 2005; Meekan et al. 2006). Changes in key biological attributes, such as size or condition, within a cohort over time can provide insight on the relative importance of bottom-up versus top-down processes (Meekan et al. 1998; Beamish and Mahnken 2001; Searcy and Sponaugle 2001).

Growth and survival can be directly influenced by fluctuations in prey productivity or abundance or by competition from abundant conspecifics and (or) co-occurring species. If variation in size or growth is primarily and directly regulated by prey availability, we expect positive relationships with indices of prey productivity (Worm and Myers 2003). In contrast, if size or growth is largely influenced by competition, we expect negative relationships with estimates of prey abundance or fish abundance. Top-down processes can also result in negative relationships between size or growth and survival, such as when size-dependent predation leads to disproportionately higher survival of larger individuals in poor growth and survival environments (Booth and Hixon 1999; MacDonald et al. 2002; Meekan et al. 2006).

Pacific salmon (*Oncorhynchus* spp.) are primarily semelparous species with highly variable life histories and large fluctuations in population size (Healey 1991). Our ability to explain patterns of production and abundance has been improved by increasing recognition that variation in ocean conditions influences productivity and survival (Hare et al. 1999; Beamish and Mahnken 2001; Mueter et al. 2002). However, unpredicted fluctuations in salmon productivity continue to cause economic and conservation challenges (Lindley et al. 2009).

The Columbia River (CR) watershed supports many populations of Pacific salmon, including five populations of Chinook salmon

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Fig. 1. (*a*) Columbia River watershed with locations of the mainstem dams and gaging station referred to in text. (*b*) Transect and station locations for ocean collections used in this study.
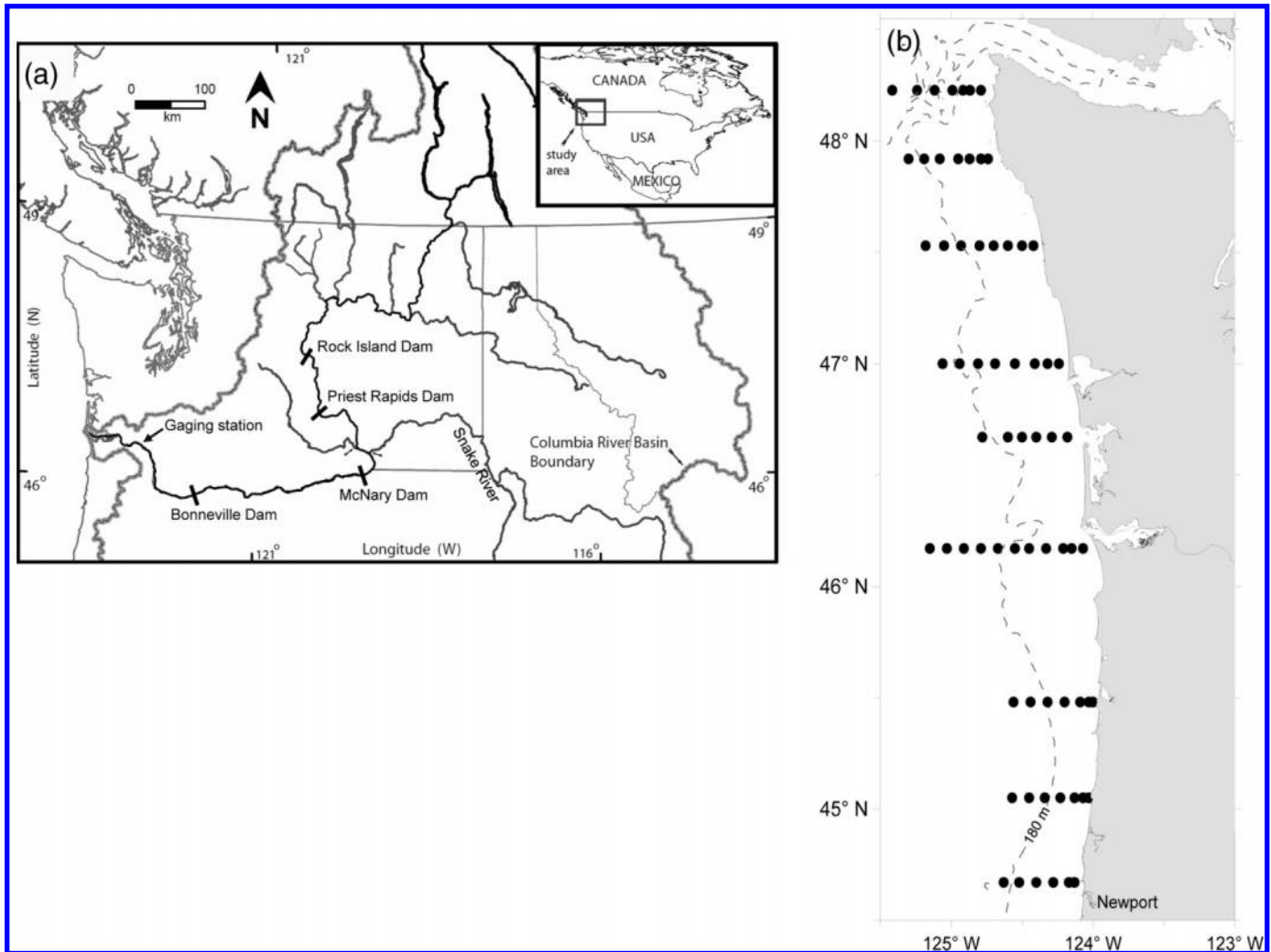
(*Oncorhynchus tshawytscha*) that are protected under the Endangered Species Act (Ford 2011). River plume environments, particularly associated frontal structures, result in aggregations of larval and juvenile fishes and potential predators. Although plume environments can be favorable for growth (Bowman and Esaias 1978; De Robertis et al. 2005; Morgan et al. 2005), they can also increase predation pressure (Bakun 2006). Plume aspects, such as size and orientation, can influence the distribution (De Robertis et al. 2005) and survival (Burla et al. 2010*a*) of juvenile salmonids during early marine residence.

Covariation between salmon survival in the Northeast Pacific Ocean and indicators of basin-scale ocean variation, such as the Pacific Decadal Oscillation (PDO), has been recognized for over 20 years (Beamish and Bouillon 1993; Mantua et al. 1997; Hare et al. 1999). Strong relationships between ocean conditions during early marine residence and survival support the hypothesis that this is a critical period for Chinook salmon (Beamish and Mahnken 2001; Duffy et al. 2005; Sharma et al. 2012). Potential mechanisms regulating survival are poorly understood and include (*i*) enhanced growth and survival during periods of cooler sea surface temperature (SST) (i.e., negative PDO values) due to local and regional variation in currents, which enhances nutrient availability and primary and secondary production (Mantua et al. 1997; Di Lorenzo et al. 2008); (*ii*) decreased predation intensity during cooler periods due to reduced overlap between juvenile salmon and warmer water predators, such as

Pacific hake (*Merluccius productus*) (Emmett et al. 2006; Emmett and Krutzikowsky 2008); or (*iii*) a combination of these factors.

Ocean surveys to identify the factors regulating the abundance of CR salmon populations have been conducted in coastal waters of the northwestern USA since 1998 (Brodeur et al. 2003). We examined an abundant genetic stock group collected in those surveys — upper CR summer–fall-run Chinook salmon — to determine if variation in size, growth, and condition of juveniles collected in June and September for 11 years provided evidence of bottom-up or top-down effects on survival. We compared juveniles collected at the beginning (June) and end (September) of the critical early marine period to determine if those attributes were related to (*i*) the density of conspecifics in the river and coastal ocean during emigration and (or) (*ii*) variation in river, plume, and (or) ocean conditions. We further evaluated the relative importance of key physical and biological variables during early marine residence in relation to survival using a multimodel inference approach.

Methods

Juvenile collection and genetic stock identification

From 1998 to 2008, surveys occurred off the coasts of Washington and Oregon during late May, late June, and late September (Fig. 1). A Nordic 264 rope trawl was towed in surface waters (3–4 km·h⁻¹ for 15–30 min; Daly et al. 2009). Trawl catches were

standardized to density (fish·km⁻¹) based on the distance towed. On board, fish were identified, measured (fork length (FL), mm), and frozen. In the laboratory, fish were remeasured and weighed (±0.1 g).

Juvenile Chinook salmon were genotyped at 13 microsatellite DNA loci following Teel et al. (2009) and assigned to stock groups using a standardized genetic database (Seeb et al. 2007; Barnett-Johnson et al. 2010), the program ONCOR (Kalinowski et al. 2007), and the likelihood model of Rannala and Mountain (1997). From 1998 to 2008, >7000 juvenile Chinook salmon (74–400 mm FL) were collected. Of these, 33% were assigned to the upper Columbia River summer–fall (UCSF) stock group. The UCSF stock group is composed of fish originating upstream of McNary Dam (MCN), although some hatcheries below the dam use the stock for production of fall Chinook salmon. UCSF juveniles emigrate to the ocean primarily as subyearlings. Hatchery production of Chinook salmon in the upper CR basin began in 1899, expanded during the Grand Coulee Fish Maintenance Project, and continues today with >11 000 000 summer and fall hatchery subyearlings released annually (Regional Mark Information System Database, Pacific States Marine Fisheries Commission, Portland, Oregon; http://www.rmpc.org).

Our analyses focused on subyearlings, which accounted for 74% of the UCSF juveniles collected in the ocean surveys. Of those subyearlings, an average of 20% were marked with an adipose fin clip, passive integrated transponder (PIT), or coded wire tag (CWT), indicating likely hatchery origin. Subyearlings were ≤120 mm FL in May (7% of catch), ≤140 mm FL in June (24% of catch), and <250 mm FL in September (69% of catch) (De Robertis et al. 2005; Fisher et al. 2007). Subyearlings collected in May were excluded because of low abundance. Mean posterior probability for genetic assignment averaged 87% (±15% SD) for the 1604 individuals included in this study.

Juvenile size, condition, growth, and abundance

We generated a series of metrics to describe the size, condition, and growth of subyearling Chinook collected in the ocean surveys. We calculated mean FL (mm) and mass (M, g) for the UCSF subyearlings captured in June and September for each year (1998–2008). Size data were ln-transformed to obtain normality and homogeneous variance. We then used the monthly residuals from the relationship between ln-transformed FL and M as an index of body condition independent of body size (Cone 1989; Jakob et al. 1996), hereafter referred to as "condition indices" or "CI". We estimated marine growth rate in September using otolith structural analyses. Mean increment width (MIW) during the 14 days prior to capture was selected to indicate interannual growth variation after the first summer at sea. June collections were excluded from this analysis because otolith sample sizes were limited in some years (Table A1).

The June and September collections represent the UCSF genetic stock group during the beginning and the end of their first ocean summer, respectively. Data on the abundance and genetic stock composition of juvenile Chinook migrating through the lower CR estuary from 2009 to 2011 indicate that 20% of annual catch of UCSF subyearlings occurred by 25 June and >80% of the annual catch occurred by 25 September (L. Weitkamp, NOAA Fisheries, Newport, Oregon, unpublished data). Furthermore, prior analyses indicate that the majority of the UCSF stock group remains off Washington and Oregon during their first year at sea (Trudel et al. 2009; J. Fisher, Oregon State University, Corvallis, Oregon, unpublished data). Therefore, individuals collected in June ocean surveys represent recent migrants, whereas those collected in September could have spent weeks or months in coastal waters. Available CWT information indicates that a mix of hatcheries are represented in both June and September collections (Table A2).

We sought an index of the relative abundance of subyearlings to evaluate the potential for density-dependent responses in UCSF juveniles. Therefore, we estimated the annual in-river and marine abundance of all Chinook salmon subyearlings. In-river abundance was estimated from the number of subyearlings migrating annually past MCN (Fig. 1) (http://www.cbr.washington.edu/dart/dart.html). Marine density (mean fish·km⁻¹) of all subyearling Chinook salmon caught in June and September surveys was used to indicate the abundance of conspecifics. Yearling Chinook and coho (*Oncorhynchus kisutch*) salmon were not considered because they emigrate earlier than subyearling Chinook (April–May versus July–August, respectively) and are primarily out of the study area by late June (Fisher et al. 2007).

Fish growth is strongly influenced by temperature. In seasonal upwelling regions, more productive conditions are associated with cooler water temperatures (Mantua et al. 1997; Di Lorenzo et al. 2008). Therefore, it is important to evaluate the effect of seasonal and interannual variation in water temperature on subyearling growth. We calculated the percent realized growth (RG), which provides an indication of the variation in growth that is not directly attributable to temperature (Hurst et al. 2010). To estimate RG, we divided observed growth (OG) by potential growth (PG) and multiplied by 100.We estimated OG as

$$OG = [\ln(M_{Sept}) - \ln(M_{June})]/(t_2 - t_1) \cdot 100$$

where M_{Sept} = mean mass (g) of subyearlings in September, M_{June} = mean mass (g) of subyearlings in June, t_1 = 25 June, and t_2 = 25 September, which are the midpoints of the June and September surveys. The daily PG from t_1 to t_2 was estimated using laboratory determination of temperature-dependent growth for juvenile Chinook salmon (%·day⁻¹ in g) at maximum ration (Brett et al. 1982) and coastal water temperature data (see below).

$$PG = \ln[\text{Growth rate } (\%\cdot\text{day}^{-1})] = 0.691(\pm0.082) \cdot \ln(\text{Temp}) - 0.870(\pm0.224)$$

The overall PG from 25 June to 25 September, given observed temperature variation, was then determined for each year. This analysis allows us to determine if the interannual pattern in realized growth is attributable to variation in water temperature.

Columbia River, plume, and coastal ocean environment

Environmental data were obtained from SATURN (Science and Technology University Research Network), an observatory designed to serve as scientific infrastructure for interdisciplinary studies in the CR coastal margin (Baptista et al. 2008). SATURN integrates a real-time observation network, a modeling system, and a web-based information system. The modeling system ("Virtual Columbia River", http://www.stccmop.org/datamart/virtualcolumbiariver) is anchored by 3D unstructured-grid numerical models of water circulation (Zhang et al. 2004; Baptista et al. 2005; Zhang and Baptista 2008).

The SATURN simulation databases include water levels and 3D velocity, salinity, and temperature fields. For this study, we relied on the output of simulation database DB14 to characterize the variability of plume size (area of the plume surface and volume of the 3D plume) and location (expressed in terms of coordinates of the centroid of the surface plume). We defined the plume using a cutoff salinity of 28 PSU. Burla et al. (2010b) demonstrated that the majority of variation in the coastal surface salinity field is accounted for by variation in river discharge (43%) and prevailing winds (21%). Data on daily discharge in the lower river were obtained from the USGS (Fig. 1: site 14246900 at 46°10′53″N, 123°10′56″W; http://waterdata.usgs.gov).

We used two basin-scale environmental indices to characterize variability in ocean conditions: the PDO and the North Pacific Gyre Oscillation (NPGO), which are statistically independent modes of variation in ocean SST and sea level height (SLH), respectively. The PDO is defined as the leading principal component of North Pacific monthly SST variability poleward of 20°N (Hare et al. 1999). In general, negative values of the PDO indicate cooler SST

Table 1. Pearson's correlation coefficients for comparisons between biological and physical indices related to juvenile upper Columbia River summer–fall Chinook salmon and their early marine residence.

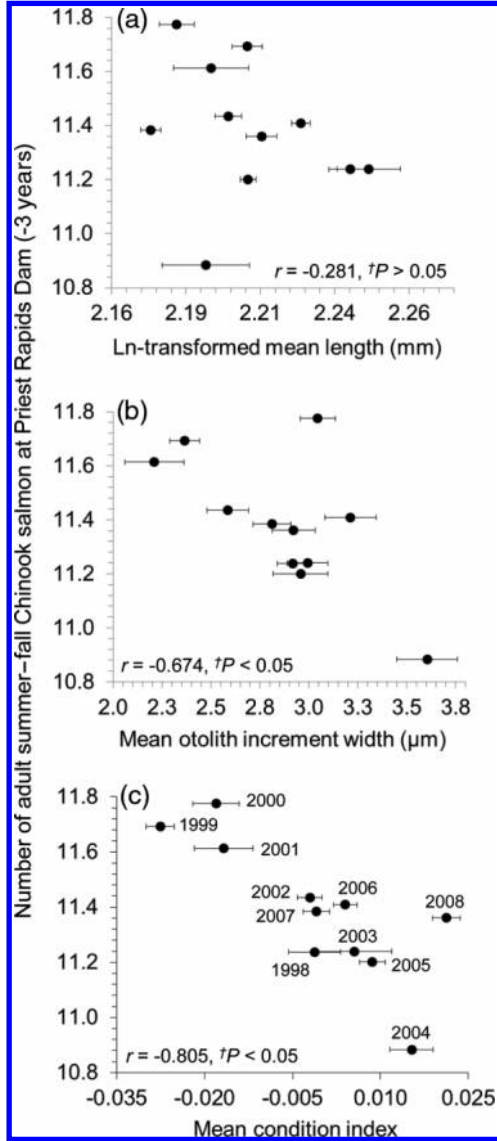|	June			September				SuFa adults PRD (−3 years)
	FL (mm)	M (g)	CI	FL (mm)	M (g)	CI	MIW (μm)	
Biological indices								
1. June marine density (fish·km^{-1})	−0.400	−0.350	0.282	0.595	**0.640**	0.513	0.405	−0.393
2. Sept. marine density (fish·km^{-1})	0.292	0.222	−0.049	−0.072	0.029	0.215	−0.405	0.211
3. Subyearlings past MCN	−0.124	−0.177	−0.355	−0.002	−0.104	−0.563	−0.193	0.113
Physical indices								
4. Columbia River flow$_{4\_7}$ (m^3·s^{-1})	0.467	**0.736**	**0.771**	0.281	0.133	−0.144	0.133	0.122
5. Plume volume$_{4\_7}$ (km^3)	0.628	**0.689**	0.507	−0.121	−0.183	−0.313	−0.050	0.543
6. PDO$_{7\_9}$	−0.335	−0.313	0.107	0.076	0.135	0.353	0.451	**−0.669**
7. NPGO$_{4\_6}$	0.375	0.354	−0.100	−0.329	−0.410	−0.557	−0.509	**0.692**
8. SST$_{4\_7}$	−0.574	−0.548	0.113	−0.031	−0.061	0.496	**0.782**	**−0.763**
9. SuFa adults PRD (−3 years)	0.504	0.443	−0.144	−0.281	−0.369	**−0.805**	−0.675	**1.000**

Note: FL, fork length (mm); M, mass (g); CI, condition index; MIW, mean otolith increment width (μm); SuFa, summer–fall Chinook salmon; PRD, Priest Rapids Dam; MCN, McNary Dam; PDO, Pacific Decadal Oscillation; NPGO, North Pacific Gyre Oscillation; SST, sea surface temperature. Subscripts indicate months used to calculate average values (i.e., PDO$_{7\_9}$ is mean PDO from July to September). Significant values are indicated in bold (†$P < 0.05$). Degrees of freedom for statistical comparisons are adjusted for autocorrelation (see text for details). $n = 11$ for all comparisons except those with plume characteristics ($n = 10$, no data for 1998). FL and M and indices (4) and (9) were ln-transformed to obtain normality and homogeneous variance.

Fig. 2. Percent frequency histograms for juvenile metrics during years with good (open bars) and poor (solid bars) ocean conditions. Metrics include subyearling fork length (mm) and mass (g) (ln-transformed) and condition indices for ocean collections in June (a–c) and September (d–f). $n = 201$ for good years in June; $n = 224$ for poor years in June; $n = 298$ for good years in September; $n = 871$ for poor years in September. Asterisks (*) indicate significant differences between groups at $P < 0.05$.
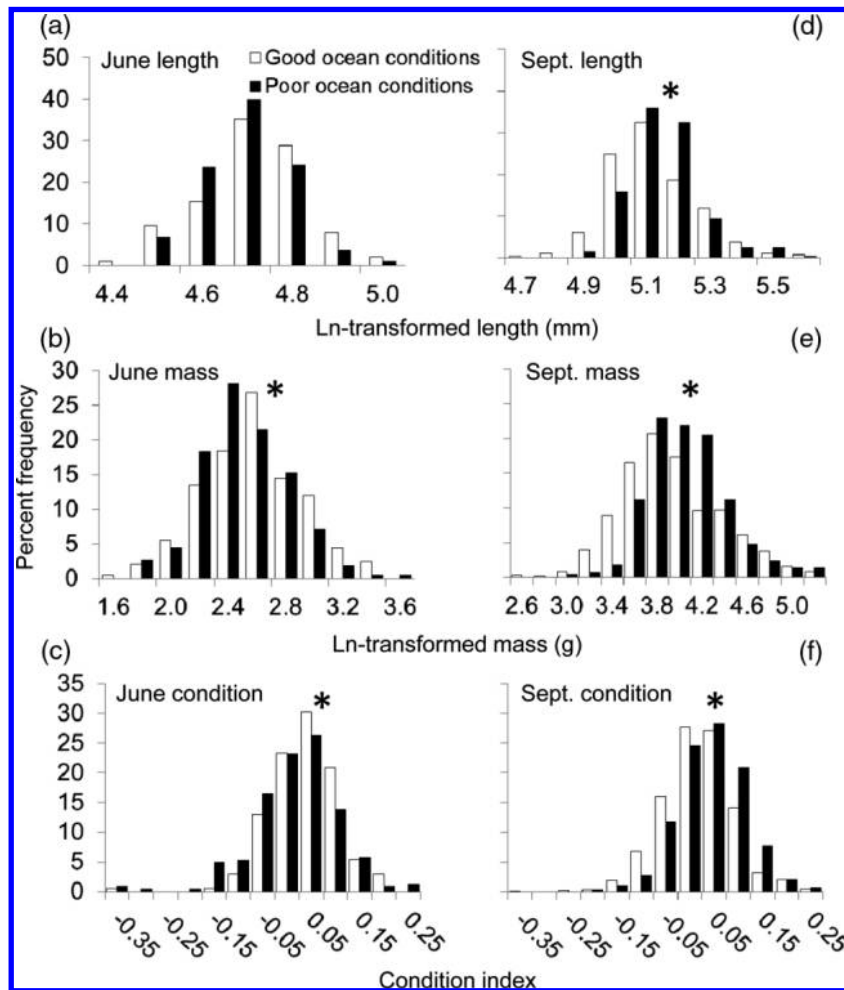
and relatively high salmon production off the west coast of North America (Hare and Mantua 2000; Mantua and Hare 2002). The NPGO is the second leading principal component of variability in North Pacific SLH that is related to salinity, nutrients, and chlo-rophyll (Di Lorenzo et al. 2008). If variation in primary productivity was the primary driver of variation in salmon growth and survival during early marine residence, then we expect salmon size, condition, and survival to be greater during years with con-

Fig. 3. Relationship of adult returns to Priest Rapids Dam (PRD) (−3-year lag) vs. subyearling attributes in September, 1998–2008, including mean (±SE) for (*a*) fork length at capture (mm), (*b*) otolith increment width (μm) during the 14 days prior to ocean capture, and (*c*) condition index. Symbols represent years. Refer to Appendix Table A3 for annual adult return values. See text for explanation of adjusted significance ($^{†}P$).
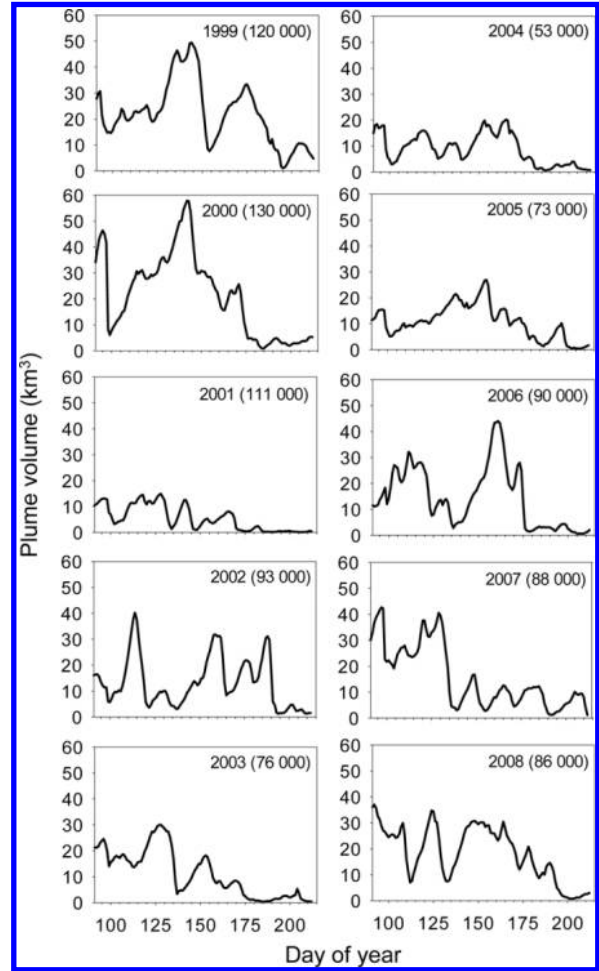

Fig. 4. Columbia River plume volume (km³) from 1 April (Day 91) to 31 July (Day 212) in 1999–2008. Subsequent adult returns of upper Columbia River summer–fall Chinook salmon (−3-year lag) are indicated in parentheses. Peak estuarine catches of the upper Columbia River summer–fall stock group occur between 15 June and 31 July. No data are available for 1998.

sistently negative values of the PDO and positive values of the NPGO. Monthly mean values for these indices were downloaded from http://www.o3d.org/npgo/data/NPGO.txt and http://jisao. washington.edu/pdo/PDO.latest. Finally, SST data taken at 2 m depth during biweekly visits to a station 5 miles (1 mile = 1.609 km) offshore of Newport, Oregon (NH05: 44.651°N, 124.181°W) were used to indicate variation in water temperature during the first ocean summer. This dataset was selected because it provided the longest time series available in coastal waters (<15 km from shore), where the majority of subyearlings are collected.

Survival indicators

There are limitations associated with all survival estimates. Given the available information, we concluded that the number of adult summer and fall Chinook salmon passing Priest Rapids Dam (PRD), which is located on the CR mainstem upstream of the confluence with the Snake River, provided the best available indica-

tor of relative survival for the UCSF stock group (see Appendix B for details) (Fig. 1). The dominant age-at-maturity of interior summer–fall Chinook salmon is 0.3 (i.e., individuals emigrate to marine waters in their first year and spend 3 years in the ocean prior to reproducing; Myers et al. 1998). Therefore, we lagged adult returns by 3 years for comparison with conditions during emigration. Given that the second most abundant age-at-maturity is 0.4, we also lagged adult returns by 4 years for comparison with conditions during emigration; however, we observed no significant relationships and those data are not presented.

Statistical analyses

We compared physical attributes of juveniles in two ways. First, we pooled emigration years into two groups based on observed variation in ocean conditions. Since 1998, researchers have ranked 16 physical and two biological criteria in terms of their likely effect on survival of juvenile salmon emigrating from the CR (1 = best conditions for survival, 14 = worst; Burke et al. 2013; http://www.nwfsc.noaa.gov/research/divisions/fed/oeip/g-forecast. cfm). A mean rank, which indicates ocean conditions relative to other years, is then generated for each year. To compare juvenile attributes during periods when ocean conditions were favorable and unfavorable for survival, we classified emigration years as "poor" (mean rank > 9) or "good" (mean rank < 9) in terms of

Fig. 5. Mean values for (*a*) Pacific Decadal Oscillation (PDO) in July to September and (*b*) North Pacific Gyre Oscillation (NPGO) in April to June from 1950 to 2008. Black line indicates period covered by this study. See text for data sources.
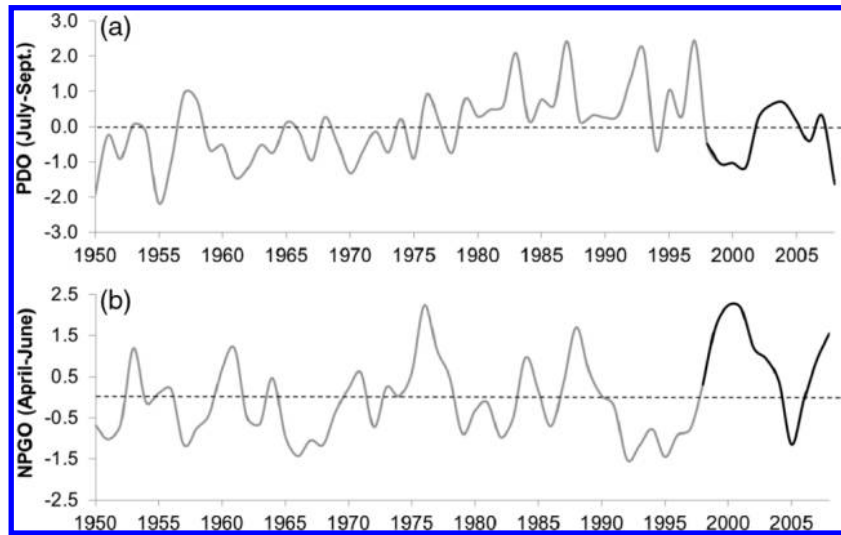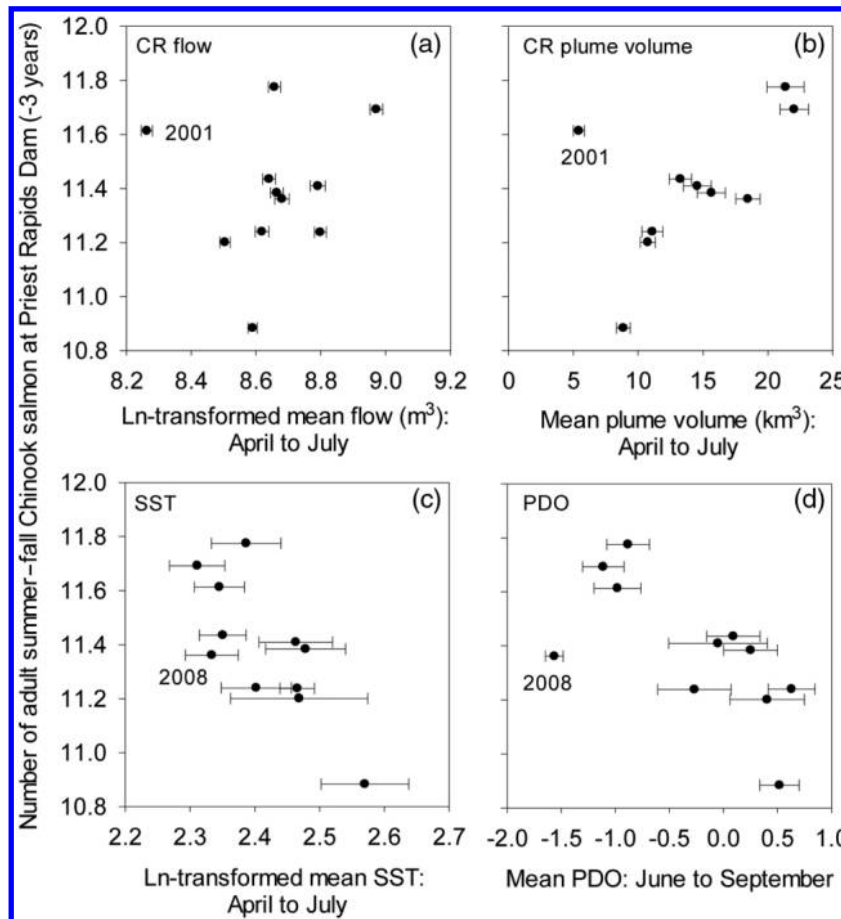

Fig. 6. Relationship between ln-transformed adult returns to Priest Rapids Dam (−3-year lag) and (*a*) ln-transformed mean flow (m³) during April to July; (*b*) mean plume volume (km³) from April to July; (*c*) mean nearshore SST (°C) in April to July; and (*d*) mean PDO from June to September.

ocean conditions (Table A3). We then combined juveniles from poor and good years and compared the frequency distributions of their length, mass, and condition using Kolmogorov–Smirnov tests. Second, we compared mean attributes of juveniles in June and September in relation to physical and biological variables across all years (1998–2008) using correlation analyses. Physical indices were averaged across seasons (January to March, April to June, etc.) to identify the most appropriate periods. Variables were transformed when needed to obtain normality and homoscedasticity. Short time series can be autocorrelated, which can increase type I error rates.

Table 2. Pearson's correlation coefficients for seasonal comparisons of biological and physical indices.

Columbia River discharge (1998–2008)

	JFMA	MJJA	AMJJ	SOND
CI_{June}	**0.692**	**0.790**	**0.828**	0.446
CI_{Sept}	−0.295	0.125	0.114	−0.252
PRD SuFa adults	0.281	0.020	0.079	−0.059

Columbia River discharge (1998–2008 excluding 2001)

	JFMA	MJJA	AMJJ	SOND
CI_{June}	0.427	0.530	0.607	0.336
CI_{Sept}	**−0.745**	−0.267	−0.338	−0.407
PRD SuFa adults	0.665	0.440	0.611	0.040

Plume volume (1999–2008 excluding 2001)

	JFMA	MJJA	AMJJ	SOND
CI_{June}	0.107	−0.325	0.194	−0.266
CI_{Sept}	−0.506	−0.432	−0.628	−0.371
PRD SuFa adults	**0.708**	0.509	**0.836**	0.047

SST (1998–2008)

	JFM	AMJ	AMJJ	JAS	OND
CI_{June}	0.009	−0.110	−0.164	−0.007	−0.194
CI_{Sept}	0.259	0.510	0.508	0.259	0.341
PRD SuFa adults	−0.564	**−0.758**	**−0.759**	−0.572	−0.332

SST (1998–2007)

	JFM	AMJ	AMJJ	JAS	OND
CI_{June}	0.101	−0.063	0.041	0.006	−0.275
CI_{Sept}	0.651	**0.806**	**0.824**	0.413	0.186
PRD SuFa adults	−0.657	**−0.806**	**−0.816**	−0.577	−0.337

PDO (1998–2007)

	JFM	AMJ	JAS	JJAS	OND
CI_{June}	−0.122	−0.079	0.239	0.199	0.400
CI_{Sept}	0.590	**0.777**	**0.890**	**0.936**	0.498
PRD SuFa adults	−0.634	**−0.677**	**−0.816**	**−0.839**	−0.279

NPGO (1998–2007)

	JFM	AMJ	AMJJ	JAS	OND
CI_{June}	−0.125	−0.139	−0.098	−0.075	−0.075
CI_{Sept}	−0.664	**−0.778**	**−0.747**	−0.652	**−0.771**
PRD SuFa adults	0.548	**0.713**	**0.679**	0.551	**0.790**

Note: CI, condition index; PRD SuFa adults, summer–fall Chinook salmon adult return to Priest Rapids Dam at a –3-year lag; SST, sea surface temperature; PDO, Pacific Decadal Oscillation; NPGO, North Pacific Gyre Oscillation. Abbreviations indicate months used to calculate mean (i.e., JFMA = January–April). Degrees of freedom for statistical comparisons are adjusted for autocorrelation (see text for details). Significant values are indicated in bold ([†]$P < 0.05$).

Therefore, we adjusted degrees of freedom when determining significance (indicated by "[†]P") for Pearson correlation coefficients as recommended by Pyper and Peterman (1998).

To quantify the relative importance of physical and biological variables during emigration, we performed multivariate linear regression analysis to hindcast adult returns. No plume simulations were available for 1998; therefore, we used the emigration years 1999–2008 to directly compare alternative models. Variables for model inclusion were selected based on visual inspection and correlation analysis. Model residuals were examined for normality and independence, and we calculated Akaike information criteria adjusted for small sample size (AIC_c) to evaluate models (Burnham and Anderson 2002). Normalized likelihood values (w_i) were calculated using the following:

$$w_i = \frac{\exp(-0.5 \cdot \Delta_i)}{\sum_{r=1}^{r} \exp(-0.5 \cdot \Delta_r)}$$

Table 3. Observed growth (OG), potential growth (PG), and percent realized growth (RG) between June and September for subyearling Chinook salmon juveniles collected in the coastal ocean from 1998 to 2008.

Year	OG ($\%\cdot day^{-1}$, g)	PG ($\%\cdot day^{-1}$, g)	RG (%)
1998	**2.04**	**2.02**	**100.9**
1999	0.86	2.01	42.8
2000	1.29	2.07	62.2
2001	1.72	2.18	78.7
2002	1.42	2.06	68.7
2003	**1.96**	**2.08**	**94.3**
2004	**1.63**	**2.50**	**65.1**
2005	**1.58**	**2.30**	**68.7**
2006	1.72	2.17	79.2
2007	1.17	2.35	49.9
2008	1.53	2.18	70.2

Note: Years classified as "poor ocean conditions" during emigration are indicated in bold. The remaining years were classified as "good ocean conditions".

where w_i are Akaike weights for model i, the numerator is the likelihood for model i, and the denominator is the sum of the relative likelihoods for the other models. Δ_i represents the difference between the AIC_c of the best model and the others.

Results

Seasonal and interannual variation in juvenile characteristics

Over 1600 UCSF subyearlings were collected between 1998 and 2008 (Table A1). Mean juvenile length, mass, and condition in June were not significantly correlated with mean values in September ($r < 0.53$, [†]$P > 0.05$). However, mean mass (g) in September was positively related to marine density in June (Table 1).

Juveniles that emigrated during "good" ocean conditions were longer and heavier than those that emigrated during "poor" ocean conditions in June ($P < 0.05$), but CI did not differ between groups ($P > 0.05$). However, by September, juveniles that emigrated during good ocean conditions were significantly shorter and lighter and had lower CI compared with those that emigrated in poor ocean conditions ($P < 0.05$; Fig. 2).

When all emigration years (1998–2008) were examined individually, future adult returns were significantly related only to juvenile attributes in September (Table 1). Adult returns were significantly and negatively correlated with MIW and CI of individuals collected in September 3 years prior (Fig. 3). The MIW was positively correlated with mean CI in September ($r = 0.662$, [†]$P = 0.05$) but not with mean FL or M ($r < 0.250$, [†]$P > 0.05$).

Columbia River flow, plume, and coastal ocean environment

For June collections, mean CI was positively correlated with freshwater discharge (Table 1) and was greater when the CR plume was positioned southwesterly (north–south: $r = -0.675$ and east–west: $r = -0.837$, [†]$P \leq 0.05$), which indicates upwelling favorable winds. In contrast, for September collections, mean CI was negatively correlated with river flow in winter and early spring, except for the 2001 drought year (Table 1). Mean CI in September was also negatively correlated with plume volume and area, except in 2001 and 2008 ($r > -0.964$, [†]$P < 0.05$). For these years, 2001 was a drought year (Fig. 4) with relatively good ocean conditions (cool and productive), whereas 2008 was a high flow year with productive ocean conditions (the most negative summer PDO observed during this study; Fig. 5).

Adult returns were positively related to plume area ($r = 0.836$, [†]$P < 0.05$, $n = 10$) and volume (Fig. 6b) during emigration except in the drought year 2001. A similar, but weaker, correlation between adult returns and river discharge was observed ($r = 0.685$,

Table 4. Top ten model results for hindcasting adult returns (2002–2011) of upper Columbia River summer–fall Chinook salmon based on conditions during juvenile emigration (1999–2008).

Model	RSS	AIC_c	Δ_i	w_i	R^2
CI_{Sept}, $PlVol_{4\_7}$, $CI_{Sept} \times PlVol_{4\_7}$	0.021	−36.750	0.000	0.727	0.966
CI_{Sept}, PDO_{7_9}, $CI_{Sept} \times PDO_{7\_9}$	0.027	−34.049	2.701	0.188	0.955
CI_{Sept}, PDO_{7_9}	0.099	−30.167	6.583	0.027	0.837
CI_{Sept}, SST_{4_7}, $CI_{Sept} \times SST_{4\_7}$	0.041	−30.075	6.674	0.026	0.933
CI_{Sept}, SST_{4_7}	0.104	−29.619	7.130	0.021	0.828
CI_{Sept}, $PlVol_{4\_7}$	0.143	−26.506	10.243	0.004	0.765
CI_{Sept}, $NPGO_{4\_6}$	0.157	−25.523	11.226	0.003	0.741
MIW, $PlVol_{4\_7}$, MIW $\times PlVol_{4\_7}$	0.074	−24.121	12.629	0.001	0.818
CI_{Sept}, $CRFlow_{4\_7}$	0.195	−23.376	13.374	0.001	0.679
$PlVol_{4\_7}$, SST_{4_7}	0.219	−22.203	14.546	0.001	0.634

Note: $PlVol_{4\_7}$, mean plume volume from April to July; CI_{Sept}, mean condition index of juveniles collected in September; PDO_{7_9}, mean value of Pacific Decadal Oscillation from July to September; SST, sea surface temperaturel; NPGO, North Pacific Gyre Oscillation; MIW, mean otolith increment width; and $CRFlow_{4\_7}$, mean Columbia River flow from April to July; RSS, residual sum of squares, AIC_c, Akaike's information criteria adjusted for small sample size. Δ_i represents the difference between the AIC_c of the best model and the others. w_i indicates the relative likelihood of the model given the data.

[†]$P < 0.05$, $n = 10$). Adult returns were also greater when ocean waters were cool and productive during emigration (lower SST, negative PDO, and positive NPGO; Table 1).

In September, MIW and CI were greater when basin-scale indices indicated that coastal waters were relatively warm and unproductive (Tables 1 and 2). Based on the hypothesis that observed marine growth is directly related to productivity, we expected growth to be higher in years with colder SST. Estimates of RG allowed us to examine interannual growth variation after accounting for temperature. From June to September, RG averaged between 42% and 100% of the PG (Table 3). There were no significant correlations between RG and SST ($r = 0.279$) or between RG and adult returns ($r = -0.340$, [†]$P > 0.05$, $n = 11$).

Hindcast model of adult returns

Correlation analysis was used to determine the appropriate time step for averaging physical variables to include in the hindcast model of adult returns (Rupp et al. 2012; Table 2). The following variables were included in model selection: $CRFlow_{4\_7}$, $PlVol_{4\_7}$, PDO_{6_9}, $NPGO_{4\_6}$, SST_{4_7}, CI_{Sept}, and MIW, and variables that were cross-correlated ($r \geq 0.60$) were not included in the same model. Plume volume and area were highly correlated; however, volume was used in model development because of its stronger relationship with adult returns. We evaluated 30 models, and the most parsimonious model included $CRFlow_{4\_7}$, CI_{Sept}, and an interaction term (Table 4). In general, adult returns were greater when plume volume was relatively high during juvenile emigration and when the PDO values were negative during early marine residence. The mean CI of juveniles collected in September appeared in 8 of the 10 top models (Table 4). An interaction between mean CI and plume volume, PDO, or SST was present in all models that accounted for >90% of the variation in adult returns (Table 4).

Discussion

In this 11-year retrospective study, we did not find evidence for direct bottom-up effects; neither growth nor condition of subyearling Chinook salmon during early marine residence was positively related to indices of ocean productivity. Instead, subyearlings had significantly lower condition indices during years with relatively cool and productive coastal waters. Estimates of realized growth indicated that temperature variation could not account for the pattern of lower growth during cool, productive summers. At the same time, condition indices of juveniles after the first ocean summer were negatively related to survival and were the best univariate predictor of adult returns. Therefore, these observations indicate that top-down processes, such as selective mortality in poor survival years, or competition during periods of high survival may exert a stronger influence during early marine residence than direct bottom-up processes, such as prey production.

Several studies have documented a reduction in mean size or condition during high survival years for Pacific salmon (Ruggerone and Nielson 2004; Moss et al. 2005) as well as other marine species (Sponaugle and Cowen 1997; Booth and Hixon 1999; Hoey and McCormick 2004). One explanation for these observations is that when mortality is biased towards individuals that are smaller or in lower condition, survivors are relatively larger or display higher body condition (i.e., "the bigger-is-better hypothesis"; Litvak and Leggett 1992; Sogard 1997; Meekan et al. 2006). Therefore, body size and (or) condition are greater in comparatively low survival environments or years compared with high survival environments or years.

An alternative explanation for the reduced body condition during years with apparently high survival is that competition for prey resources increases as cohort survival, and hence abundance, increases. The smaller size and CI of juveniles observed in September during years with good ocean conditions could represent negative effects associated with greater juvenile abundance. If more juveniles survive when estuary and ocean conditions are favorable, competition for prey could increase even though primary productivity is relatively high (see Ruggerone and Nielson 2004 for review). However we did not observe a density-dependent response in juvenile attributes in relation to abundance in river or in coastal waters. This observation may be due to (i) relatively low juvenile abundance and, hence, limited capacity for intraspecific competition; or (ii) inadequate spatial coverage of ocean sampling (i.e., a substantial portion of subyearlings may be in waters shallower than those accessible by survey vessels). Alternatively, favorable ocean conditions may lead to enhanced survival of other competitors. Finally, interannual variation in survival may simply lead to a reduced overall mean condition in high survival years because of the survival of greater numbers of fish with differential condition. In this instance, one might expect higher variance or negative skewness in the distributions of size or condition indices during high survival years compared with low survival years. However, we did not observe the expected pattern of higher variance or negative skewness in the distributions of size or condition indices during high compared with low survival years.

It is worthwhile to note that for populations of spring Chinook salmon in the interior CR basin, which migrate to marine waters as yearlings, significant, positive relationships exist between adult returns and yearling growth during early marine residence (Tomaro et al. 2012; J.A. Miller, unpublished data). These findings contrast with the negative relationships between adult returns and subyearling body condition that we observed in this study. This contrast between subyearling and yearling life histories may reflect differences in stage-specific mortality rates. Populations that emigrate as yearlings would experience a greater proportion of their lifetime mortality prior to marine entry than populations

that emigrate primarily as subyearlings and, therefore, may be influenced by different mechanisms. Munch et al. (2005) noted that top-down processes predominate early in the life history, while bottom-up processes are more common later, and thus, our ability to detect either process can be influenced by when in the life history we sample the population.

Our study is not the first to observe a positive relationship between survival and basin-scale indicators of cool and productive ocean waters (e.g., Hare et al. 1999; Rupp et al. 2012). Our study differed in the finding of significant relationships between survival and plume conditions. Variation in plume size displayed stronger relationships with survival than river discharge alone, which is perhaps not surprising given that SATURN circulation simulations integrate conditions in the river, estuary, and coastal ocean (Burla et al. 2010b). Others have observed positive relationships between survival and river flow (Petrosky and Schaller 2010) or plume volume (Burla et al. 2010a) in Snake River spring Chinook salmon and CR steelhead, respectively. Postulated mechanisms of reduced mortality during periods of higher flow and (or) larger plume include enhanced in-river survival due to more rapid passage through the hydropower system (Petrosky and Schaller 2010; Haeseker et al. 2012). A related hypothesis is that residence time (and related predation) in the lower river, estuary, and plume are also reduced during years with high flow and plume volume. Although this hypothesis remains to be fully evaluated, the opposite appears to be the case for two potential predators. Caspian tern (*Hydroprogne caspia*) and double-crested cormorant (*Phalacrocorax auritus*) consumption of juvenile salmonids during the study period was greater during high flow and plume volume conditions (Lyons 2010; J.A Miller and A. Baptista, unpublished data). Another potential explanation is that the area or volume of the plume, which is positively related to flow, influences overall productivity on the continental shelf. The plume delivers macronutrients (nitrate, iron, and silica) to the shelf and has been linked to enhanced primary and secondary production in coastal waters (Hickey and Banas 2003). Therefore, it is plausible that enhanced production results in higher survival during years with greater plume volume. Under these scenarios, enhanced survival of juvenile salmon, their potential competitors, or reduced predation pressure during conditions of high flow and plume area and volume could result in lower mean body condition of UCSF subyearlings by the end of their first ocean summer.

Two emigration years can be considered anomalous in terms of river and plume (2001) and ocean (2008) conditions. The relatively high survival of the 2001 emigrants despite the drought conditions indicates that poor river conditions may be modulated, to some extent, by relatively good ocean conditions (but see Haeseker et al. 2012). Furthermore, the relatively low survival of the 2008 emigrants despite the apparently positive plume (high area and volume) and ocean (negative PDO) conditions suggests that favorable conditions in the plume and ocean are a necessary, but not wholly sufficient, component of high survival. Although it is not clear why the adult returns associated with the 2008 emigration year were relatively low, mean CI in September provided the most robust univariate indicator of that reduced survival.

Our data indicate that selective mortality and (or) competition may exert a stronger influence than direct prey limitation on the growth and survival of UCSF subyearling Chinook salmon during early marine residence. Furthermore, the mean condition of juveniles at the end of their first ocean summer accounted for more of the variation in subsequent adult returns than any other variable examined. Combined, these observations suggest that interannual variation in survival for this population may be well established a few months after marine entry and prior to widespread ocean migration. Additional research on potential predators and competitors as well as the generation of stock-specific abundance estimates at additional periods and locations during emigration could further elucidate regulatory mechanisms. Given that river discharge and hatchery releases in the CR basin are largely controlled, future effort to coordinate experimental releases of marked juveniles during periods of varying plume and ocean characteristics could improve our understanding of how river conditions, plume structure, and ocean characteristics interact and influence juvenile salmon survival.

References

Bakun, A. 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. Sci. Mar. **70**: 105–122.

Baptista, A.M., Zhang, Y.L., Chawla, A., Zulauf, M., Seaton, C., Myers, E.P., Kindle, J., Wilkin, M., Burla, M., and Turner, P.J. 2005. A cross-scale model for 3D baroclinic circulation in estuary–plume–shelf systems: II. Application to the Columbia River. Cont. Shelf Res. **25**(7–8): 935–972.

Baptista, A., Howe, B., Freire, J., Maier, D., and Silva, C.T. 2008. Scientific exploration in the era of ocean observatories. Comput. Sci. Eng. **10**(3): 53–58. doi:10.1109/MCSE.2008.83.

Barnett-Johnson, R., Teel, D.J., and Casillas, E. 2010. Genetic and otolith isotopic markers identify salmon populations in the Columbia River at broad and fine geographic scales. Environ. Biol. Fish. **89**: 533–546. doi:10.1007/s10641-010-9662-5.

Beamish, R.J., and Bouillon, D.R. 1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci. **50**(5): 1002–1016. doi:10.1139/f93-116.

Beamish, R.J., and Mahnken, C. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog. Oceanogr. **49**(1–4): 423–437. doi:10.1016/S0079-6611(01)00034-9.

Booth, D.J., and Hixon, M.A. 1999. Food ration and condition affect early survival of the coral reef damselfish, *Stegastes partitus*. Oecologia, **1218**: 364–336.

Bowman, M.J., and Esaias, W.E. 1978. Oceanic fronts in coastal processes. Springer-Verlag, New York.

Brett, J.R., Clarke, W.C., and Shelbourn, J.E. 1982. Experiments on thermal requirements for growth and food conversion efficiency of juvenile Chinook salmon *Oncorhynchus tshawytscha*. Can. Tech. Rep. Fish. Aquat. Sci. No. 1127.

Brodeur, R.D., Myers, K.W., and Helle, J.H. 2003. Research conducted by the United States on the early ocean life history of Pacific salmon. N. Pac. Anadr. Fish Comm. Bull. **3**: 89–131.

Burke, B.J., Peterson, W.T., Beckman, B.R., Morgan, C., Daly, E.A., and Litz, M. 2013. Multivariate methods of adult Pacific salmon returns. PLoS ONE, **8**(1): e54134. doi:10.1371/journal.pone.0054134. PMID:23326586.

Burla, M., Baptista, A.M., Casillas, E., Williams, J.G., and Marsh, D.M. 2010a. The influence of the Columbia River plume on the survival of steelhead (*Oncorhynchus mykiss*) and Chinook salmon (*Oncorhynchus tshawytscha*): a numerical exploration. Can. J. Fish. Aquat. Sci. **67**(10): 1671–1684. doi:10.1139/F10-083.

Burla, M., Baptista, A.M., Zhang, Y.L., and Frolov, S. 2010b. Seasonal and interannual variability of the Columbia River plume: a perspective enabled by multiyear simulation databases. J. Geophys. Res. Oceans, **115**. doi:10.1029/2008JC004964.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Checkley, D.M.J., Raman, S., Maillet, G.L., and Mason, K.M. 1988. Winter storm effects on the spawning and larval drift of a pelagic fish. Science, **335**: 356–348.

Cone, R.S. 1989. The need to reconsider the use of condition indices in fishery science. Trans. Am. Fish. Soc. **118**: 510–514. doi:10.1577/1548-8659(1989)118<0511:TNTRTU>2.3.CO;2.

Daly, E., Brodeur, R., and Weitkamp, L. 2009. Ontogenetic shifts in diets of juvenile and subadult coho and Chinook salmon in coastal marine waters: important for marine survival? Trans. Am. Fish. Soc. **138**: 1420–1438. doi:10.1577/T08-226.1.

De Robertis, A., Morgan, C.A., Schabetsberger, R.A., Zabel, R.W., Brodeur, R.D., Emmett, R.L., Knight, C.M., Krutzikowsky, G.K., and Casillas, E. 2005. Columbia River plume fronts. II. Distribution, abundance, and feeding ecology of juvenile salmon. Mar. Ecol. Prog. Ser. **299**: 33–44.

Di Lorenzo, E., Schneider, N., Cobb, K.M., Franks, P.J.S., Chhak, K., Miller, A.J., McWilliams, J.C., Bograd, S.J., Arango, H., Curchitser, E., Powell, T.M., and

Riviere, P. 2008. North Pacific Gyre Oscillation links ocean climate and eco-system change. Geo. Res. Lett. **35**. doi:10.1029/2007GL032838.

Duffy, E.J., Beauchamp, D.A., and Buckley, R.M. 2005. Early marine life history of juvenile Pacific salmon in two regions of Puget Sound. Estuar. Coast. Shelf Sci. **64**(1): 94–107. doi:10.1016/j.ecss.2005.02.009.

Emmett, R.L., and Krutzikowsky, G.K. 2008. Nocturnal feeding of Pacific hake and jack mackerel off the mouth of the Columbia River, 1998–2004: Implications for juvenile salmon predation. Trans. Am. Fish. Soc. **137**(3): 657–676. doi:10.1577/T06-058.1.

Emmett, R.L., Krutzikowsky, G.K., and Bentley, P. 2006. Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: Relationship to oceanographic conditions, forage fishes, and juvenile salmonids. Prog. Oceanogr. **68**(1): 1–26. doi:10.1016/j.pocean.2005.08.001.

Fisher, J., Trudel, M., Ammann, A., Orsi, J.A., Piccolo, J., Bucher, C., Harding, J.A., Morris, J., Brodeur, R., Casillas, E., MacFarlane, B., and Welch, D. 2007. Comparisons of the coastal distributions and abundances of juvenile Pacific Salmon from central California to the Northern Gulf of Alaska. *In* The ecology of juvenile salmon in the northeast Pacific Ocean: regional comparisons. *Edited by* C.B. Grimes, R.D. Brodeur, L.J. Haldorson, and S.M. McKinnell. American Fisheries Society, Bethesda, Md. pp. 31–80.

Ford, M.J. 2011. Status review update for Pacific salmon and steelhead listed under the Endangered Species Act: Pacific Northwest [online]. NOAA Tech. Memo NMFS-NWFSC-113. Available from http://www.nwfsc.noaa.gov/assets/25/7962_01312012_150050_SRUpdateSal&SteelheadTM113WebFinal.pdf [accessed on 1 January 2012].

Haeseker, S., McCann, J.A., Tuomikoski, J., and Chockley, B. 2012. Assessing freshwater and marine environmental influences on life-stage-specific survival rates of Snake River spring–summer Chinook salmon and steelhead. Trans. Am. Fish. Soc. **141**: 121–138. doi:10.1080/00028487.2011.652009.

Hare, S.R., and Mantua, N.J. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog. Oceanogr. **47**(2–4): 103–145. doi:10.1016/S0079-6611(00)00033-1.

Hare, S.R., Mantua, N.J., and Francis, R.C. 1999. Inverse production regimes: Alaska and West Coast Pacific salmon. Fisheries, **24**(1): 6–14.

Healey, M.C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. UBC Press. pp. 313–393.

Hickey, B.M., and Banas, N.S. 2003. Oceanography of the U.S. Pacific Nortwest coastal ocean and estuaries with application to coastal ecology. Estuaries, **26**(4B): 1010–1031.

Hoey, A.S., and McCormick, M.I. 2004. Selective predation for low body condition at the larval–juvenile transition of a coral reef fish. Oecologia, **139**(1): 23–29. doi:10.1007/s00442-004-1489-3.

Hurst, T.P., Abookire, A.A., and Knoth, B. 2010. Quantifying thermal effects on contemporary growth variability to predict responses to climate change in northern rock sole (*Lepidopsetta polyxystra*). Can. J. Fish. Aquat. Sci. **67**(1): 97–107. doi:10.1139/F09-171.

Jakob, E.M., Marshall, S.D., and Uetz, G.W. 1996. Estimating fitness: a comparison of body condition indices. Oikos, **77**: 61–67. doi:10.2307/3545585.

Kalinowski, S.T., Manlove, K.R., and Taper, M.L. 2007. ONCOR A computer program for genetic stock identification [online]. Department of Ecology, Montana State University, Bozeman, Mont. Available from http://www.montana.edu/kalinowski/Software/ONCOR.htm [accessed on 1 January 2011].

Lindley, S., Grimes, C., Mohr, M., Peterson, W., Stein, J., Anderson, J., Botsford, L., Bottom, D., Busack, C., Collier, T., Ferguson, J., Garza, J., Grover, A., Hankin, D., Kope, R., Lawson, P., Low, A., MacFarlane, R., Moore, K., Palmer-Zwahlen, M., Schwing, F., Smith, J., Tracy, C., Webb, R., Wells, B., and Williams, T. 2009. What caused the Sacramento River fall Chinook stock collapse [online]? NOAA_TM_SWFSC-447. Available from http://swr.nmfs.noaa.gov/media/SalmonDeclineReport.pdf [accessed on 1 January 2012].

Litvak, M.K., and Leggett, W.C. 1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. Mar. Ecol. Prog. Ser. **81**: 13–24. doi:10.3354/meps081013.

Lyons, D.E. 2010. Bioenergetics-based predator-prey relationships between piscivorous birds and juvenile salmonids in the Columbia River estuary. Fisheries and Wildlife, Oregon State University, Corvallis.

MacDonald, D.W., Newman, C., Stewart, P.D., Domingo-Roura, X., and Johnson, P.J. 2002. Density-dependent regulation of body mass and condition in badgers (*Meles meles*) from Wytham Woods. Ecology, **83**(7): 2056–2061. doi:10.1890/0012-9658(2002)083[2056:DDROBM]2.0.CO;2.

Mantua, N.J., and Hare, S.R. 2002. The Pacific decadal oscillation. J. Oceanogr. **58**(1): 35–44. doi:10.1023/A:1015820616384.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., and Francis, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Am. Meteorol. Soc. **78**(6): 1069–1079. doi:10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2.

Meekan, M.G., Dodson, J.J., Good, S.P., and Ryan, D.A.J. 1998. Otolith and fish size relationships, measurement error, and size-selective mortality during the early life of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **55**(7): 1663–1673. doi:10.1139/f98-047.

Meekan, M.G., Vigliola, L., Hansen, A., Doherty, P., Halford, A., and Carleton, J.H.

2006. Bigger is better: size-selective mortality throughout the life history of a fast-growing clupeid, *Spratelloides gracilis*. Mar. Ecol. Prog. Ser. **317**: 237–244. doi:10.3354/meps317237.

Morgan, C.A., De Robertis, A., and Zabel, R.W. 2005. Columbia River plume fronts. I. Hydrography, zooplankton distribution, and community composition. Mar. Ecol. Prog. Ser. **299**: 19–31.

Moss, J.H., Beauchamp, D.A., Cross, A.D., Myers, K.W., Farley, E.V., Murphy, J.M., and Helle, J.H. 2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Trans. Am. Fish. Soc. **134**(5): 1313–1322. doi:10.1577/T05-054.1.

Mueter, F.J., Ware, D.M., and Peterman, R.M. 2002. Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the northeast Pacific Ocean. Fish. Oceanogr. **11**(4): 205–218. doi:10.1046/j.1365-2419.2002.00192.x.

Munch, S.B., Snover, M.L., Watters, G.M., and Mangel, M. 2005. A unified treatment of top-down and bottom-up control of reproduction in populations. Ecol. Lett. **8**(7): 691–695. doi:10.1111/j.1461-0248.2005.00766.x.

Murdoch, W.W. 1994. Population regulation in theory and practice. Ecology, **75**(2): 271–287. doi:10.2307/1939533.

Myers, J.M., Kope, R.G., Bryant, G.J., Teel, D., Lierheimer, L.J., Wainwright, T.C., Grant, W.S., Waknitz, F.W., Neely, K., Lindley, S.T., and Waples, R.S. 1998. Status review of Chinook salmon from Washington, Idaho, Oregon, and California. NOAA Tech. Memo NMFS-NWFSC-35.

Petrosky, C.E., and Schaller, H.A. 2010. Influence of river conditions during seaward migration and ocean conditions on survival rates of Snake River Chinook salmon and steelhead. Ecol. Freshw. Fish, **19**: 520–536. doi:10.1111/j.1600-0633.2010.00425.x.

Pyper, B.J., and Peterman, R.M. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. Can. J. Fish. Aquat. Sci. **55**(9): 2127–2140. doi:10.1139/f98-104.

Rannala, B., and Mountain, J.L. 1997. Detecting immigration by using multilocus genotypes. Proc. Natl. Acad. Sci. **94**: 9197–9201. doi:10.1073/pnas.94.17.9197. PMID:9256459.

Ruggerone, G.T., and Nielson, J.L. 2004. Evidence for competitive dominance of Pink salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. Rev. Fish Biol. Fish. **14**: 371–390. doi:10.1007/s11160-004-6927-0.

Rupp, D., Wainwright, T., Lawson, P., and Peterson, W. 2012. Marine environment-based forecasting of coho salmon (*Oncorhynchus kisutch*) adult recruitment. Fish. Oceanogr. **21**(1): 1–19. doi:10.1111/j.1365-2419.2011.00605.x.

Searcy, S.P., and Sponaugle, S. 2001. Selective mortality during the larval–juvenile transition in two coral reef fishes. Ecology, **82**(9): 2452–2470. doi:10.1890/0012-9658(2001)082[2452:SMDTLJ]2.0.CO;2.

Seeb, L.W., Antonovich, A., Banks, M.A., Beacham, T.D., Bellinger, M.R., Blankenship, S.M., Campbell, M.R., Decovich, N.A., Garza, J.C., Guthrie, C.M., Lundrigan, T.A., Moran, P., Narum, S.R., Stephenson, J.J., Supernault, K.J., Teel, D.J., Templin, W.D., Wenburg, J.K., Young, S.F., and Smith, C.T. 2007. Development of a standardized DNA database for Chinook salmon. Fisheries, **32**: 540–552. doi:10.1577/1548-8446(2007)32[540:DOASDD]2.0.CO;2.

Sharma, R., Velez-Espino, L.A., Wertheimer, A.C., Mantua, N., and Francis, R.C. 2012. Relating spatial and temporal scales of climate and ocean variability to survival of Pacific Northwest Chinook salmon (*Oncorhynchus tshawytscha*). Fish. Oceanogr. **22**(1): 14–31.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. **60**(3): 1129–1157.

Sponaugle, S., and Cowen, R.K. 1997. Early life history traits and recruitment patterns of Caribbean wrasses (Labridae). Ecol. Monogr. **67**(2): 177–202. doi:10.1890/0012-9615(1997)067[0177:ELHTAR]2.0.CO;2.

Teel, D.J., Baker, C., Kuligowski, D.R., Friesen, T.A., and Shields, B. 2009. Genetic stock composition of subyearling Chinook salmon in seasonal floodplain wetlands of the lower Willamette River, Oregon. Trans. Am. Fish. Soc. **138**(1): 211–217. doi:10.1577/T08-084.1.

Tomaro, L., Teel, D.J., Peterson, W.P., and Miller, J.A. 2012. Early marine residence of Columbia River spring Chinook salmon: when is bigger better? Mar. Ecol. Prog. Ser. **452**: 237–252. doi:10.3354/meps09620.

Trudel, M., Fisher, J., Orsi, J.A., Morris, J.F.T., Thiess, M.E., Sweeting, R.M., Hinton, S., Fergusson, E.A., and Welch, D.W. 2009. Distribution and migration of juvenile Chinook salmon derived from coded wire tag recoveries along the continental shelf of western North America. Trans. Am. Fish. Soc. **138**: 1369–1391. doi:10.1577/T08-181.1.

Worm, B., and Myers, R.A. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology, **84**(1): 162–173. doi:10.1890/0012-9658(2003)084[0162:MAOCSI]2.0.CO;2.

Wright, P.J., and Gibb, F.M. 2005. Selection for birth date in North Sea haddock and its relation to maternal age. J. Anim. Ecol. **74**(2): 303–312.

Zhang, Y.-L., and Baptista, A.M. 2008. SELFE: a semi-implicit Eulerian–Lagrangian finite-element model for cross-scale ocean circulation. Ocean Modell. **21**(3–4): 71–96. doi:10.1016/j.ocemod.2007.11.005.

Zhang, Y.-L., Baptista, A.M., and Myers, E.P. 2004. A cross-scale model for 3D baroclinic circulation in estuary–plume–shelf systems: I. Formulation and skill assessment. Cont. Shelf Res. **24**: 2187–2214.

Appendices A and B appear on the following pages.

Appendix A

Table A1. Mean density (fish·km⁻¹) and mean (±SE) mass (g), fork length (FL, mm), and condition index (CI) at capture for upper Columbia River summer–fall (UCSF) subyearling Chinook salmon collected in coastal waters off Oregon and Washington in June and September.

	June					September						
Year	Fish·km⁻¹	Mass (g)	FL (mm)	CI	n	Fish·km⁻¹	Mass (g)	FL (mm)	CI	n	MIW	n
1998	0.73	10.4 (0.4)	100.7 (1.0)	−0.001 (0.004)	52	1.32	67.6 (3.7)	175.2 (2.9)	−0.001 (0.004)	58	2.92 (0.08)	20
1999	0.06	23.0 (3.2)	128.3 (6.8)	−0.005 (0.024)	4	2.83	50.8 (2.3)	162.2 (2.0)	−0.028 (0.002)	145	2.37 (0.08)	19
2000	0.37	12.4 (0.4)	107.4 (1.2)	−0.013 (0.005)	38	0.73	40.6 (2.4)	152.6 (2.2)	−0.018 (0.004)	42	3.05 (0.09)	25
2001	0.17	11.2 (1.1)	105.9 (3.2)	−0.040 (0.003)	8	3.28	54.3 (6.4)	159.6 (5.1)	−0.017 (0.005)	50	2.21 (0.15)	16
2002	0.52	13.6 (0.8)	107.9 (1.9)	−0.005 (0.021)	43	2.32	50.0 (2.0)	159.4 (1.7)	−0.002 (0.002)	146	2.59 (0.11)	19
2003	1.80	12.2 (0.4)	106.3 (0.9)	−0.014 (0.004)	115	1.03	74.0 (7.9)	177.9 (4.8)	0.006 (0.006)	28	2.99 (0.10)	17
2004	0.58	11.8 (0.6)	104.4 (1.7)	−0.006 (0.006)	48	0.56	52.8 (7.6)	157.6 (5.7)	0.015 (0.004)	23	3.60 (0.15)	16
2005	0.23	12.0 (1.1)	107.1 (3.3)	−0.029 (0.011)	10	2.80	51.4 (1.2)	161.2 (1.0)	0.009 (0.002)	190	2.96 (0.14)	22
2006	0.90	12.1 (0.6)	104.4 (1.5)	0.007 (0.004)	72	2.58	58.9 (1.4)	168.2 (1.2)	0.004 (0.002)	199	3.21 (0.13)	18
2007	0.78	13.4 (1.0)	109.1 (2.3)	−0.008 (0.007)	20	2.63	39.4 (1.3)	149.6 (1.3)	−0.001 (0.002)	132	2.81 (0.10)	22
2008	0.62	14.7 (1.3)	110.6 (3.5)	0.015 (0.008)	24	5.96	60.0 (2.6)	164.1 (2.0)	0.021 (0.002)	157	2.92 (0.11)	11

Note: Mean (±SE) daily otolith increment width (MIW, μm) during the 14 days prior to capture is included for individuals collected in September. Sample size (n) is indicated.

Table A2. Source, number, and mean size at release (fork length (mm) in parentheses) for subyearlings that were collected in coastal waters in June (J) and September (S) from 1998 to 2008 and genetically identified as upper Columbia River (CR) summer–fall Chinook salmon.

	1998		1999		2000		2001		2002		2003		2004		2005		2006		2007		2008	
Source	J	S	J	S	J	S	J	S	J	S	J	S	J	S	J	S	J	S	J	S	J	S
Hanford Reach																						1
Klicktat Hatchery YKFP	2																					
Little White Salmon NFH			1		1 (94)																	
Lower CR																			1 (79)			
North Oregon Coast						1										2		1				
Priest Rapids	3		1		1		1 (86)		1 (87)	1 (96)							2 (84)	3 (84)				3 (101)
Ringold Springs Hatchery		1									1 (93)											
Snake River fall Chinook			1		1				1 (69)	1 (69)	4 (91)		2		1 (77)		9 (93)	3 (98)	1 (114)	1 (85)	5 (89)	
South Oregon Coast										1												
Umatilla River													5		2					5		
Upper CR			1 (64)										1			2	1 (88)		1 (90)		1	
Washington Brights									5				4				3		2	3		
Wells Hatchery		2	1								1						3	5	3		9 (90)	

Note: Data presented are only for fish with coded wire tags (CWT). Source is the hatchery, stock, or river of origin and was obtained from the Regional Mark Information System Database (Pacific States Marine Fisheries Commission, Portland, Oregon; http://www.rmpc.org). Mean fish size at release for each source in each month is included when available. Size data are not available for all CWT individuals. YKFP, Yakima Nation Fisheries Project; NFH, National Fish Hatchery; CR, Columbia River. Note that some fish from outside of the upper CR are included, which is expected based on probability of assignment to genetic stock group (87% ± 15% SD).

Table A3. Ocean conditions during emigration and adult returns of summer–fall Chinook salmon to Priest Rapids Dam (PRD) on the Columbia River 3 years after juvenile emigration.

Emigration year	Ocean indicators mean rank	Ocean classification	Return year	Adult returns
1998	11.3	Poor	2001	75 947
1999	4.6	Good	2002	119 660
2000	4.8	Good	2003	129 988
2001	5.7	Good	2004	110 573
2002	4.6	Good	2005	92 516
2003	10.2	Poor	2006	76 087
2004	10.8	Poor	2007	53 294
2005	12.3	Poor	2008	73 186
2006	8.8	Good	2009	90 140
2007	6.5	Good	2010	87 900
2008	3.1	Good	2011	85 901

Note: Rankings for ocean conditions are based on 14 years of data (1998–2012) and available from http://www.nwfsc.noaa.gov/research/divisions/fed/oeip/g-forecast.cfm [accessed 30 December 2012]. See text for details on classification.

Appendix B

Indicators of survival

There are limitations associated with any survival estimate. For salmon populations in the Columbia River (CR), the presence of mainstem dams with sophisticated detection facilities creates opportunities to census juvenile and adult fish during downstream and upstream passage, respectively. Numbers of fish can be estimated at certain facilities, and some of those facilities can also collect information on origin and age for fish with passive integrated transponder (PIT) tags. A common metric of survival is the ratio of adults to juveniles based on detections of PIT tags at particular dams. These estimates are limited to discrete groups of fish, such as production from specific hatcheries or individuals above a certain dam, and are often based on relatively few adults. Most estimates of smolt to adult return ratio (SAR) rely on PIT tag data and are thus available for specific regions or hatcheries (Tuomikoski et al. 2012). Another estimate of cohort-specific survival can be generated by adjusting annual or seasonal counts of adults at specific dams based on age estimates for a subset of those adults, which are usually derived from scale analysis, and some

Table B1. Available information on age-at-maturity and exploitation rate for the Upriver Bright Complex (URB) of Chinook salmon and estimates of smolt-to-adult return ratio (SAR) for wild and hatchery subyearling Chinook salmon tagged at Rock Island Dam (RIS).

Brood year	Subyearling emigration year	URB proportion contribution by age-at-maturity					URB exploitation rate	Subyearlings passed MCN (10³)	Subyearlings passed RIS (10³)	Subyearlings PIT-tagged at RIS	RIS SAR
		1	2	3	4	5					
1990	1991	0.22	0.21	0.31	0.25	0.01					
1991	1992	0.20	0.15	0.44	0.20	0.01					
1992	1993	0.15	0.18	0.39	0.27	0.01					
1993	1994	0.18	0.28	0.28	0.25	0.00					
1994	1995	0.08	0.16	0.45	0.28	0.01					
1995	1996	0.15	0.16	0.41	0.27	0.00					
1996	1997	0.11	0.09	0.54	0.25	0.00			17		
1997	1998	0.12	0.19	0.41	0.27	0.01	0.44	11 443	28		
1998	1999	0.12	0.12	0.43	0.32	0.01	0.49	7 645	14		
1999	2000	0.15	0.19	0.40	0.24	0.01	0.58	10 662	23	4 073	2.01
2000	2001	0.10	0.26	0.38	0.25	0.01	0.33	10 778	25	4 484	0.00
2001	2002	0.16	0.27	0.41	0.15	0.00	0.53	8 397	28	4 800	1.06
2002	2003	0.13	0.26	0.35	0.25	0.01	0.48	7 682	26	4 388	0.28
2003	2004	0.17	0.20	0.42	0.21	0.00	0.47	8 414	22	3 183	0.03
2004	2005	0.13	0.29	0.39	0.18	0.00	0.60	6 929	32	3 547	0.59
2005	2006						0.60	4 069	16	4 208	0.62
2006	2007						0.57	4 723	16	3 596	0.36
2007	2008						0.55	2 411	16	3 678	1.06
2008	2009								8	1 889	0.37

Note: The number of subyearlings passing downstream at RIS and the number of subyearlings included in PIT-tag estimates of SARs are included. Age-at-maturity indicates time since hatching, not egg deposition. MCN, McNary Dam.

Table B2. Number of spring Chinook salmon adults passing over Priest Rapids Dam (PRD) and smolt-to-adult return ratio (SAR) for two hatchery populations within the upper Columbia River.

Emigration year	Adult passage PRD (−2-year lag)	Smolt-to-adult return ratio (SAR)	
		Cle Elum Hatchery ($r = 0.83$)	Leavenworth Hatchery ($r = 0.91$)
2000	34 066	3.81	1.83
2001	17 441	0.28	0.24
2002	13 521	1.37	0.36
2003	14 148	0.59	0.43
2004	8 535	1.54	0.34
2005	6 708	0.66	0.09
2006	12 178	1.25	0.89
2007	13 469	1.01	0.46
2008	30 539	3.12	1.91
2009	15 246	1.78	0.57
2010	19 495	1.49	0.75

Note: The majority of spring Chinook emigrate as yearlings and return after 2 years in the ocean (Myers et al. 1998). Adult returns were lagged −2 years. Correlations between lagged adult returns and SARs are included in parentheses for each group. Cle Elum Hatchery is on the Yakima River, and Leavenworth Hatchery is on the Wenatchee River.

estimation of exploitation rate. These age-specific estimates of adult abundance are available for only certain CR dams where adults are sampled in a systematic manner. It is important to note that these estimates do not exist for genetic stock groups. Therefore, these approaches generate information on adult return by species, time of passage, and age based on the location of specific dams rather than for genetic stock groups.

There is extensive stock-specific life history variation in Chinook salmon (Waples et al. 2001). Ecological studies focused on specific stocks have greater potential to provide ecologically meaningful results than studies of mixed-stock groups. With the development of genetic baselines, the genetic stock of origin for individuals collected in mixed-stock groups can now be estimated with a high level of confidence. However, there is currently a spatial mismatch between the traditional methods used to estimate survival and the level of genetic resolution attainable with current baselines. Therefore, we compiled life history data and passage information most relevant to the UCSF genetic stock group to generate estimates of survival for this study. The information is summarized below.

(1) Priest Rapids Dam (PRD) is located on the upper CR, upstream of its confluence with the Snake River, and provides an estimate of the number of adults entering the upper CR region. Ideally, these adult counts would be modified using data on juvenile production, age structure of returning adults, exploitation rate, and in-stream adult mortality. This detailed level of comprehensive information is available for very few groups of salmon and, to our knowledge, no genetic stock group.

(2) Age-specific adult return data require repeated collections of adults. This level of sampling occurs for the CR Upriver Bright complex (URB), which includes all fall Chinook from areas upstream of McNary Dam (MCN) and the Deschutes River. Therefore, this group contains a substantial number of individuals from populations other than the UCSF population but provides an indication of age-at-maturity and exploitation rate. The available data on age structure for subyearling URB Chinook salmon indicate that the dominant age-at-maturity is 3 years old (i.e., have spent 3 years in the ocean) (40% ± 0.06% SD from 1990 to 2003) and that the variation in the proportion of 3-year-olds is low (CV = 15.5% from 1990 to 2003) (S. Ellis, Columbia River Inter-Tribal Fish Commission, Portland, Oregon). Similarly, the contribution of 4-year-olds is relatively consistent (mean = 27%, CV = 15%; Table B1).

(3) The exploitation rate for the URB complex was consistent (mean = 51.3% ± 8% SD) during the study period, 1998–2008 (PFMC 2011).

(4) There are recent estimates of SARs for upper CR wild and hatchery subyearling Chinook salmon tagged at Rock Island Dam (RIS) from 2000 to 2010 (Tuomikoski et al. 2012). The RIS is in the upper CR, upstream of nearly all of fall Chinook salmon populations, and therefore accounts for a relatively small proportion of the UCSF production (~14% of summer and fall run adults counted at MCN after subtracting fish destined for the Snake River based on dam counts). These SARs are based on an average of 3770 (±238 SE) smolts per

year. Therefore, these estimates provide a useful metric for trend determination but have limited application to the overall UCSF genetic stock group. From 2000 to 2010, SARs for subyearling Chinook tagged at RIS were positively correlated with adult returns to RIS at a –3-year lag ($r = 0.59$) and a –4-year lag ($r = 0.70$). When the 1 year with an estimated SAR of 0 (2001) is removed, the correlations increase to 0.79 for a –3-year lag and 0.86 for a –4-year lag. These data indicate that adult returns to geographically relevant dams can provide estimates of survival similar to other estimates, such as SARs, that are often spatially or ecologically limited (Table B1).

(5) There are no estimates of juvenile passage at PRD, which means that there are no data available for relevant, direct comparisons of juvenile production at this location with subsequent adult passage. Downstream passage of juveniles over other dams in the upper CR provides an estimate of interannual variation in production. Internannual variation in the number of subyearlings passing RIS (CV = 33%) is much lower that the variation associated with SARs based on these same juveniles (2000–2008 CV = 83%; Table B1). Interannual variation in the number of subyearling passed MCN is similar to RIS (CV = 38%).

(6) For upper CR spring Chinook salmon, which have a less variable age structure than summer and fall populations, SAR estimates are positively correlated with the number of adults migrating past PRD (Table B2; Tuomikoski et al. 2012). In these cases, PIT tag detections at MCN were used to generate SARs. However, MCN is downstream of the confluence with the Snake River, and thus, adult passage at that dam includes Snake River spring Chinook. Therefore, we compared estimates of SARs for two Upper CR hatchery spring Chinook salmon populations with adult passage over PRD, which provides a more appropriate geographic comparison.

(7) There is extensive information available for salmon populations within the CR basin that can provide meaningful proxies for survival and aid our understanding of the mechanisms regulating survival. Given the available information, we conclude that adult returns of summer and fall adults to PRD provide a robust indicator of relative survival for the UCSF stock group.

References

Pacific Fisheries Management Council. 2011. Preseason Report I: Stock Abundance Analysis and Environmental Assessment Part 1 for 2011 Ocean Salmon Fishery Regulations Pacific Fishery Management Council, Portland, Oregon, USA.

Tuomikoski, J., McCann, J., Chockley, B., Schaller, H., Haeseker, S., Fryer, J., Petrosky, C., Tinus, E., Dalton, T., and Ehlke, R. 2012. Comparative survival study (CSS) of PIT-tagged 717 spring/summer Chinook and summer steelhead Comparative Survival Study of PIT-tagged spring/summer/fall Chinook and summer steelhead, and sockeye [online]. Fish Passage Center, Portland, Oregon, USA. Available from http://www.fpc.org/documents/CSS/2012%20CSS%20Annual%20Report–Final.pdf [accessed on 12 December 2012].

Waples, R.S., Gustafson, R.G., Weitkamp, L.A., Myers, J.M., Johnson, O.W., Busby, P.J., Hard, J.J., Bryant, G.J., Waknitz, F.W., Neely, K., Teel, D., Grant, W.S., Winans, G.A., Phelps, S., Marshall, A., and Baker, B. 2001. Characterizing diversity in salmon from the Pacific Northwest. J. Fish Biol. **59**(Suppl. A): 1–41.