Quantifying the effects of wind, upwelling, curl, sea surface temperature and sea level height on growth and maturation of a California Chinook salmon (*Oncorhynchus tshawytscha*) population

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ABSTRACT

We used retrospective scale growth chronologies and return size and age of female Chinook salmon (*Oncorhynchus tshawytscha*) from a northern California, USA, population collected over 22 run years and encompassing 18 complete cohorts to model the effects of oceanographic conditions on growth during ocean residence. Using path analyses and partial least squares regressive approaches, we related growth rate and maturation to seven environmental variables (sea level height, sea surface temperature, upwelling, curl, scalar wind, northerly pseudo-wind stress and easterly pseudo-wind stress). During the first year of life, growth was negatively related to summer sea surface temperature, curl and scalar winds, and was positively related to summer upwelling. During the second, third and fourth growth years growth rate was negatively related to sea level height and sea surface temperature, and was positively related to upwelling and curl. The age at maturation and the fork length at which three ocean-winter fish returned were related to the environment experienced during the spring before the third winter at sea (the year prior return). Faster growth during the year before return led to earlier maturation and larger return size.

Key words: Chinook salmon, curl, growth, maturation, turbulence, upwelling

INTRODUCTION

Developing a quantified size-at-age model is fundamental to modeling fish population dynamics. This basic information is required for calculations, such as cohort age at maximum biomass, spawning stock biomass, yield per recruit, fecundity relationships, and age-length keys (Beverton and Holt, 1957; Ricker, 1975). For long-lived fishes, environmentally related variation in growth is most apparent in early life before it becomes asymptotic. As the fish ages and variation in growth rate is decreased, above or below average growth years may interact less with vital rates.

Here, we model the impact of the California oceanic environment on the growth rates of a northern California Chinook salmon (*Oncorhynchus tshawytscha*) population. Chinook salmon is a fast growing, relatively short-lived fish. Cohorts typically do not reach asymptotic size but mature if they are fast growing and/or reach a given size before the next spawning season (Loeffel and Wendler, 1969; Healey, 1991; Hankin *et al.*, 1993). Therefore, the influence of the ocean environment on the size at age and possibly return dynamics of a cohort could be dramatic.

Salmonid population dynamics are profoundly impacted by size at age and growth rate. For instance, it is postulated that Chinook salmon return to spawn when a threshold size is reached so that slow average growth is associated with delayed maturation (Healey, 1991). By contrast, variation in the growth rate of Atlantic salmon (*Salmo salar*) affects their return timing, whereby a reduction in growth cues the return timing of the fish (Jonsson *et al.*, 2003). Either of these relationships between growth and California Chinook salmon maturation may be true, or it is possible that a threshold size associated with a reduction in growth rate cues maturation (Hankin *et al.*, 1993). Fecundity is also strongly tied to size at age (Healey and Heard, 1983), as is egg size and early survival (Heath *et al.*, 1999). Size may also have an effect on competition for redd sites and timing of arrival to spawning grounds (Dickerson *et al.*, 2005). Finally, the amount of cohort

mixing may increase or decrease through time with varying growth. Such growth-related life-history and population traits make it clear that appropriate growth models are necessary to estimate the ecological aspects of these fish.

Little has been done to include environmental variation in growth rate and maturation models for salmonids along the California Current system (Hobday and Boehlert, 2001; Snover *et al.*, 2005). However, quantifying the relationships of ocean environmental variation to growth is important for incorporating environmental variables into adaptive management models. Specifically, environmental features that covary with life-history traits (e.g. growth rate, maturation and survival) may be predictors of population dynamics that are traditionally hindcast.

Generally, for Pacific salmon (*Oncorhynchus* spp.) along their California Current range, only the effects of large-scale events, such as El Niño–Southern Oscillation (ENSO), on growth have been explored (Pearcy and Schoener, 1987; Johnson, 1988; Wells *et al.*, 2006). For example, the 1982/83 ENSO resulted in a 30% reduction in the fecundity of coho salmon (*Oncorhynchus kisutch*) in Oregon, USA, and, at that time, was the most dramatic reduction recorded in the size of Chinook salmon returning to Oregon spawning sites (Johnson, 1988). Expanding on this approach, Wells *et al.* (2006) demonstrated that the return sizes of more than 20 cohorts of coho and Chinook salmon throughout their eastern Pacific ocean range were correlated with large-scale factors, such as ENSO, Pacific Decadal Oscillation (Mantua *et al.*, 1997) and the strength of the north Pacific high pressure system. On a more regional scale, Hobday and Boehlert (2001) showed that mixed-layer depth and other factors such as sea surface temperature influenced survival and growth of coho salmon. These studies did not present a model with which to estimate the effect of environment on growth rate throughout the life of the fish, but, importantly, they identified likely candidate variables for such a model.

The objectives of this paper are to quantify the effects of environmental variation on age-specific growth, and to determine if variation in the ocean environment relates to variation in age and size at return of California Chinook salmon. We accomplish our objectives by relating regional and large-scale ocean environmental variation to retrospective scale growth chronologies and return size of Chinook salmon collected over 22 run years (1981–2002) encompassing 18 complete cohorts from brood years 1980–97.

METHODS

Biological data

Chinook salmon data were collected from a 2.7-km privately owned segment of Mill Creek (~10% of total stream length; Fig. 1), a tributary of the Smith River in northern California, USA. This segment was topographically and hydrologically representative of the creek and was censused weekly for recently spawned carcasses beginning with the heavy rains of November and continuing through to mid-March for run years 1981–2002 (Table 1). In doing this, cohorts from brood years 1980–97 were represented in the sample. From each returning female, the fork length was measured, numerous scales were collected from the dorso-lateral region, and scales were stored dry in envelopes. Each fish was jaw marked to avoid repeated sampling.

Mill Creek has a self-sustaining population of ocean-type Chinook salmon (i.e. populations with juveniles that do not over-winter in freshwater; Healey, 1991). Juveniles emigrate to the ocean during May–June and after two or more years return to spawn beginning in late autumn or early winter with an extended run to mid-February. While there is a hatchery on the Smith River, the numerical impact of the hatchery fish is minimal on the Mill Creek population. Of ~340 000 externally marked juveniles released in Smith River over the years 1978, 1979, 1995, 1996 and 1999, no adults (male or female) were later reported in Mill Creek by us or any user groups (A. VanScoyk, unpublished data).

Because scales were collected from post-spawned fish, there was some erosion at the scale edge. This erosion was never enough to eliminate the last annulus, but it did eliminate the possibility of modeling the final partial year of growth using scale data. Regardless, without an accurate assessment of the circuli deposition timing (Fisher and Pearcy, 1990; Wells *et al.*, 2003), we would remain restricted to the final annulus in our analysis. However, the erosion did negate regressing fish length to scale radius for back calculation of fish size (Fig. 2). Therefore, in this study all growth measures, unless otherwise stated, relate to scale growth. We are confident that the scale growth patterns of Chinook salmon mirror those of the fish in a linear fashion (Bilton, 1985).

Scales were cleaned with deionized water and mounted between glass slides (Wells *et al.*, 2003) and examined for growth patterns. Each was magnified 100× and the image was captured with a digital camera (resolution 3840 × 3072; Fig. 2). An image analysis system (Optimas 6.5) was then used to age fish and

Figure 1. (a) Map of the primary range inhabited by ocean-type northern California Chinook salmon (*Oncorhynchus tshawytscha*). Wind stresses, scalar winds and sea surface temperatures collected from the Comprehensive Ocean Atmosphere Data Set were averaged in the area encompassing waters of northern California and southern Oregon offshore to 125°W. This region is indicated by the gray boundary offshore between Cape Mendocino and Cape Blanco. The open black square represents the sea level height station used in this analysis (Crescent City, CA). The closed black square represents the station used to calculate curl and upwelling values (Pacific Fisheries Environmental Laboratory; 42°N, 125°W). Inset (b) shows Mill Creek, Smith River, and Klamath River, California.
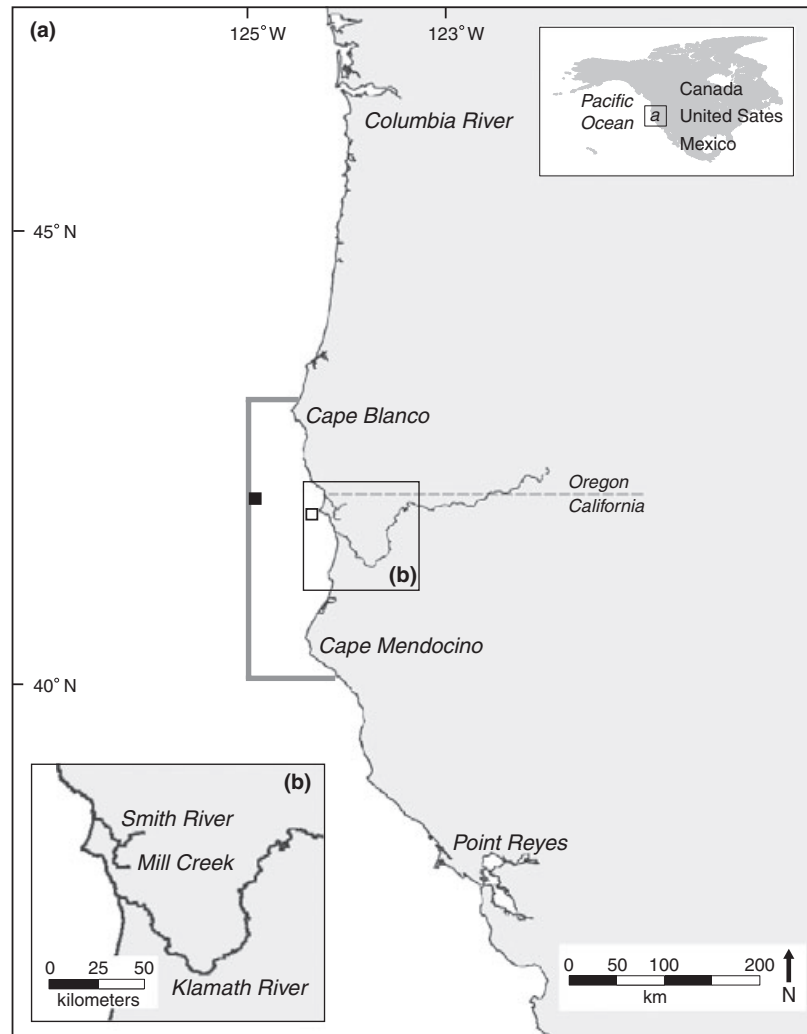
measure annual growth widths. Annual widths were considered an accurate estimate of annual growth rate of the fish. All measures were made along a 20° line from the perpendicular axis (Clutter and Whitesel, 1956; Reimers, 1973; Schluchter and Lichatowich, 1977).

Typically fish migrated to the ocean with fewer than 20 circuli, accounting for one-third of the total growth in the first year. However, we could not examine ocean growth separate from that which occurred in freshwater and the estuary because the transition from freshwater to ocean growth was not always obvious. We have no data to estimate the temporal variability or the influence of estuarine residence on overall growth, but MacFarlane *et al.* (2005) demonstrated that climatic conditions do affect residence and growth in an estuary and its associated plume waters. In the Smith River estuary residence times for juveniles have been estimated to vary between 1 and 5 weeks (Zajanc, 2003). Because of these uncertainties, we combined the entire first year of growth in our analysis.

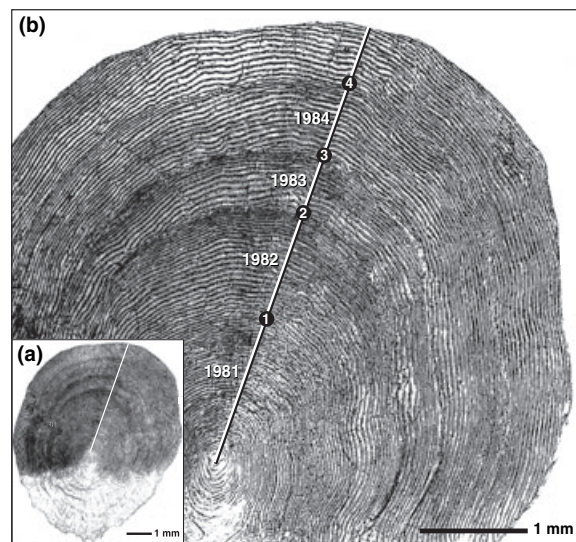*Distribution of Mill Creek Chinook salmon in the ocean environment*

To apply regional environmental data to a growth model, it is critical that the population's distribution across various environmental landscapes be quantified. In the review of Chinook salmon distribution by Healey (1991), it was apparent that the overwhelming proportion of Chinook salmon with California, USA, origins remain within California Current waters. Also, coded wire-tagged fish from Smith River recovered in coastal and high seas fisheries ($N = 102$, run years 1981–2002; Pacific States Marine Fisheries Commission's Regional Mark Processing Center)

Table 1. Sample sizes of 1, 2, 3, 4 and 5 ocean-winter (OW) female Chinook salmon (*Oncorhynchus tshawytscha*) collected each return year from Mill Creek, CA, USA (Fig. 1).

Return year	1 OW	2 OW	3 OW	4 OW	5 OW
1981		2	25	4	
1982		2	25	3	
1983		4	15	4	1
1984		2	24	3	
1985			48	12	
1986		7	25	5	
1987		5	29	1	
1988	1	4	65	8	
1989			9	8	
1990			2		
1991		3	9	3	
1992		2	17	6	1
1993			2	2	
1994		1	13	3	1
1995		2	12	5	
1996			14		
1997		3	18	12	
1998		2	18	6	
1999		2	12	5	
2000		11	33	8	1
2001		9	11	2	
2002		1	17	3	
Total	1	62	443	103	4

Figure 2. A dorso-lateral scale collected from a four ocean-winter Mill Creek, California, spawned female Chinook salmon (*Oncorhynchus tshawytscha*) collected in December 1985. Inset (a) shows the entire scale with the 20° ageing transect. A magnified image of the ageing transect is shown in (b) including the four ocean winters and growth years. This fish experienced poor growth during the 1983 year. Interestingly, during its fourth growth year (1984) the growth rate exceeded that in its third.

indicated the majority of fish released from the Smith River hatchery remain resident in waters off northern California and Oregon, USA. We extend this interpretation by including fish from all coded wire-tagged recoveries of hatchery Chinook salmon that had been released in California waters north of Cape Mendocino for years 1981–2002. A total of 2436 fish with origins from California waters north of Cape Mendocino were recovered in the coastal and high seas fisheries. The age composition of recoveries was 2, 65, 32 and 1% each of 1, 2, 3 and 4 ocean-winter fish respectively. Of all recoveries combined, only 2% of these fish were recovered north of the Columbia River mouth, 35% were recovered between Columbia River and Cape Blanco, 13% were recovered in our source region (Cape Mendocino to Cape Blanco), 50% were recovered between Cape Mendocino and Point Reyes, and an insignificant number were captured between Point Reyes and Point Conception (Fig. 1). Importantly, 63% of recoveries south of Cape Mendocino were collected from ports within ~20 km of the source region (Fig. 1). The distribution of recoveries was independent of age. These data tentatively argue that fish originating from northern California remain within northern California and southern Oregon waters but the numbers are uncorrected raw counts and, therefore, represent only the range of the fish.

We examined recovery data with an effort and contact rate correction, thus allowing an interpretation of distribution. Contact rate is the proportion of the cohort encountered by a fishery and is a function of the number of fish remaining in the cohort, effort incurred by the fishery, selectivity and the relative abundance of the fish. Assuming selectivity is similar and covaries across regions, the regional effort values can be divided out of the confounded variable (i.e. number of tagged fish observed in a region divided by the amount of effort on those fish within the region). The proportion of a given cohort within specific regions out of all regions within the range can then be estimated. To determine this relative abundance, we used an analysis of data from 1984 to 2002 coded wire-tagged recoveries of two and three ocean-winter fish with origins from Klamath River, CA, a large river immediately south of Smith River (M. Mohr, unpublished data; http://www.pcouncil.org/salmon/ salsafe.html; Fig. 1). Only the ocean fishery data were used. The same regions were examined as that for the raw recovery analysis presented before. Of all the two

ocean-winter Klamath River fish alive in the ocean environment, 59% were present between Cape Blanco and Cape Mendocino during May–August. Similarly, of all the three ocean-winter Klamath River fish present in the ocean environment, 61% were between Cape Blanco and Cape Mendocino. For both age classes, the fish that were not present in the source region (∼40%) were evenly allocated north to Columbia River and south to Pt Reyes. This finding indicates that the mean and mode of the distribution during the third and fourth growth seasons (ages 2 and 3 ocean winters) is located between Cape Blanco and Cape Mendocino.

There are too few catch data on fish during their first, second and fifth growth seasons (ages 0, 1 and 4 ocean winters) to use an effort-corrected analysis of distribution. As for fish distribution before the first ocean winter, studies on ocean-type Chinook populations demonstrate that they commonly remain near their natal systems (e.g. Beamish *et al.*, 2004; MacFarlane *et al.*, 2005). We cannot imply from our catch analysis that fish during their second year at sea remain largely resident in waters between Cape Blanco and Cape Mendocino. However, there is evidence that California Chinook salmon migrate farther from their natal source as they age (Healey, 1991). Based on our interpretations of the distribution of two and three ocean-winter fish during their third and fourth growth seasons, Chinook salmon with northern California origins may also reside near their source during the second growth season. During their fifth growth season (return year for four ocean-winter fish), fish have the opportunity to migrate from our defined region undetected. However, our models incorporate larger scale environmental variables (sea level height) suggesting that we should be able to develop a first pass model on our limited return data for four ocean-winter fish.

Overall, we are confident that environmentally related age-specific growth models for northern California Chinook salmon can be fit based on environmental data from the area encompassing waters off of Cape Blanco to Cape Mendocino (Fig. 1) at least through the fourth growth season. As for modeling relationships in the fifth growth season, we do not have a sufficient sample size to justify exploring the fit of data from other regions and, instead, we simply present a first pass at modeling these fish using environmental data from our defined region (Fig. 1).

Environmental variables

Appropriate environmental variables with which to model growth must meet a minimum of characteristics. First, the relationship, if one exists, between the

environmental variable and growth needs to have a biologically relevant interpretation. Secondly, the environmental variable must have associated data for a significant portion of the growth time series. Biologically relevant data, such as chlorophyll, nitrate and prey abundance, are often temporally insufficient. Therefore, while simple biological models may be inferred from these factors as they relate to growth, the data are too sporadic. However, data on factors correlated to production, such as upwelling, curl and sea surface temperature, can be examined. Biologically relevant models can be inferred by relating these physical factors to primary, secondary and tertiary production (Miller, 2004). Seven environmental variables met the criteria we set out: northerly and easterly pseudo-wind stresses, scalar winds, upwelling, curl, sea surface temperature and sea level height. The sources for each of these variables are listed in Table 2.

Table 2. Seven environmental variables used to characterize the oceanic environment between Cape Mendocino and Cape Blanco off shore to 125°W (Fig. 1) were collected from various sources for the years 1977–2002.

Variable description	Variable identifier
Easterly pseudo-wind stress*	EPseudo
Northerly pseudo-wind stress*†	NPseudo
Non-directional wind speed; scalar wind speed*	Scalar
Upwelling‡	Upwelling
Curl†‡§	Curl
Sea surface temperature*	SST
Sea level height¶**	SLH

Variables were averaged within the region and into spring (March, April and May) and summer (June, July and August) values. These seasonal values (14 variables in total) were included in age- and season-specific path analyses and those variables with effects were included in partial least squares regression analyses to model variation in growth rate, size at maturity and age at maturity. The variables, identifiers used in Figs 3–6, 8 and 10, their sources, and associated noteworthy comments are listed.

*Source: Comprehensive Ocean Atmosphere Data Set using 1° resolution averages.
†Typically negative values indicate stronger NPseudo and more Curl, but for ease of interpretation we have reversed the scale (=index value × −1).
‡Source: Pacific Fisheries Environmental Laboratory station 42°N, 125°W (Fig. 1).
§Spring values in 1978 were unavailable.
¶Source: University of Hawaii Sea Level Center station at Crescent City, CA, USA.
**Spring values in 1979 were unavailable.

Koslow *et al.* (2002) used a principal component analysis on a larger set of variables, in which these seven were a subset, to demonstrate that the region encompassing the majority of northern California Chinook salmon, as determined by the previously discussed tag analysis, is environmentally coherent and distinct from the area north or south of it. Furthermore, Huyer *et al.* (2005) demonstrated that there exists two separate upwelling domains in the region between the Columbia River and Cape Mendocino. Specifically, there exists a distinct upwelling domain between the Columbia River mouth and Cape Blanco and another between Cape Blanco and Cape Mendocino. Together, the evidence supports that the region inhabited by northern California Chinook salmon is environmentally distinct from other regions and ultimately suggests that confining our analysis to this spatial scale describes a complex and distinct environment.

The values for the seven environmental variables representing ocean conditions between Cape Blanco and Cape Mendocino were averaged into a spring (May–June) and summer (June–August) period for each year. These periods are considered the primary growth seasons for other California salmon (Fisher and Pearcy, 2005). Once averaged, our analysis included 14 separate variables with which to model growth.

The variables we examined are correlated to each other and cannot be used as independent variables in a multiple regression model of growth. Therefore, we used a path analysis to examine direct and indirect relationships of each on growth and identify variables to use in a predictive model (Mitchell, 1992; Petraitis *et al.*, 1996; Hox and Bechger, 1998). Those variables that covaried directly and indirectly with growth were entered into a partial least squares regression (Geladi and Kowalski, 1986).

Statistical analysis of growth

For each scale, the annulus widths (AW) were measured up through the annulus formed the last winter before return. Then, we related AW at each growth period (first, second, third and fourth) to environmental condition. The relationships between all variables were linear. Durbin–Watson tests indicated that autocorrelations for the variables were minimal. However, given extremely high curl values during the last few years of sampling, summer curl was skewed ($P < 0.01$) and transformations failed to bring the data into normality. Importantly, residuals from all significant models, including those incorporating summer curl values, were randomly distributed indicating that linear models fit the data through its range of values.

We used path analysis to evaluate the relationships of the 14 environmental variables on growth. Models were built for each growth period and the effects of spring and summer environmental conditions were evaluated separately. The exogenous variables (variables in the path model with no explicit causes or measurement error term) were northerly and easterly pseudo-wind stresses. Scalar winds, upwelling, curl, sea surface temperature and sea level height were endogenous variables (intervening variables that are modelled both as independent and dependent). The ultimate dependent variable was AW. Here, structure refers to the arrangement of variables and the order in which they are included in the determination of paths. Paths are the standardized slope coefficients between variables in the model. Path model is the term we use to describe the complete model with all significant paths determined. Because values for spring curl in 1978 and spring sea level height in 1979 were missing, these years were removed from the analyses. The removal of these data only affected estimation of growth during the first and second growth seasons.

The structure of the model was *a priori*, determined wherein each successive endogenous variable encompassed a portion of the variation of the previous variables, as well as unmeasured effects. Specifically, scalar winds mediated variation (was dependent on or covaried with) of wind stresses, upwelling mediated variation of scalar winds and wind stresses, and curl mediated upwelling and winds. Sea surface temperature mediated variation of winds, upwelling and curl. Sea level height represented the concomitant effect of the variation of all the previous environmental variables. Finally, AW, if it does relate to the environment, was dependent on the structure and paths of the model. Once insignificant paths are rejected the model can be used to describe the relationships between variables to one another and the ultimate dependent variable. Importantly, Mitchell (1992) and Petraitis *et al.* (1996) advise that a single structure be decided upon and all of the paths be tested within that structure. Otherwise, the exploration of alternative model structures corrupts tests of significance. See Wright (1934), Mitchell (1992), Petraitis *et al.* (1996) and Hox and Bechger (1998) for a more complete description of these analyses.

Six successive stepwise regressions on standardized data (mean 0, standard deviation 1) were used to define the paths between variables. The first stepwise regression modeled the biological parameter as a dependent variable and the remaining endogenous and exogenous variables were independent variables. Once variables were determined to relate directly to

the biological parameter, those variables were then included in a stepwise regression as dependent variables, and all variables above them in the structure of the model (e.g. Fig. 3) were included as independent variables. This procedure was then repeated until the only remaining variables were the exogenous

Figure 3. (a) Results of the path analyses of the environmental variable relationships to one another and the annulus width (AW) in the first growth year demonstrated that summer conditions are related to first-year AW. Models were built for spring and summer separately. For each season, six successive stepwise regressions on standardized data (mean 0, standard deviation 1) were used to define the paths between endogenous variables. Variables were retained in each stepwise regression if they had a $P < 0.15$ but only models with a $P < 0.05$ were considered significant. A $P < 0.05$ was also used to evaluate the significance of correlations between exogenous variables. (b) The total effect of each variable on AW was determined by multiplying standardized coefficients along each direct path and summing the cumulative correlations across all paths. These total effects are shown as black bars. Those variables with an effect were used in a partial least squares regression and the weight of each variable on the first latent variable is shown by the gray bars.
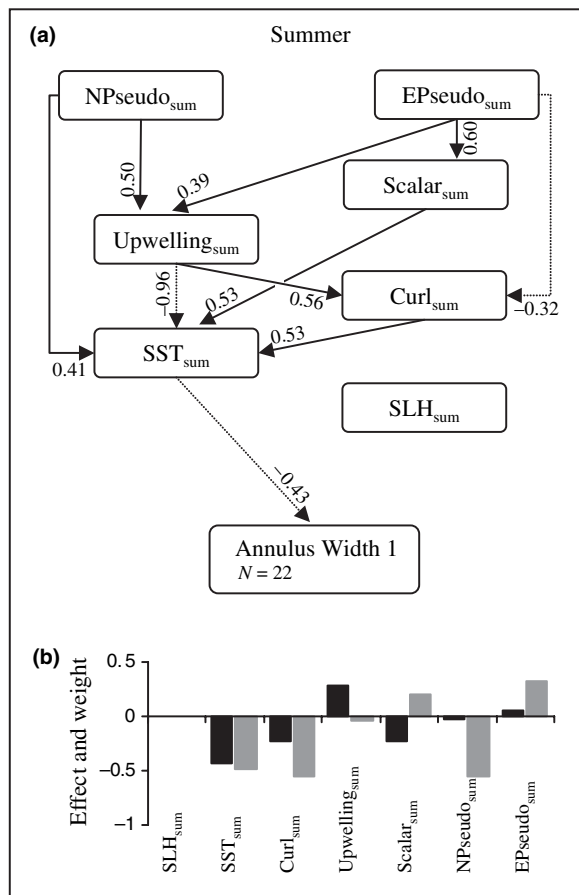
variables. All slopes that were found to be significant are included in the path models. Variables were retained in each stepwise regression if they had a $P < 0.15$ but only models with a $P < 0.05$ were considered significant. A value of $P < 0.05$ was also used to evaluate the significance of correlations between exogenous variables. Once the paths were determined, the model was evaluated relative to the covariance structure of the observed data by use of a structural equation modeler (SAS Institute, 1989; PROC CALIS).

After confirmation that the model developed was not significantly different from the structure of the observed data (chi-squared, $P > 0.05$; Mitchell, 1992; Petraitis *et al.*, 1996), the direct, indirect and total effects of each variable on AW were calculated. The total effect of each variable on AW was determined by multiplying standardized coefficients along paths leading to the biological parameter and summing the cumulative correlations across all paths leading to the biological parameter. Importantly, while path analysis quantifies the degree of colinearity between variables it does not correct for it; therefore, unless only one variable is determined to have a direct effect, path analyses results cannot be used as predictive models.

We used partial least squares regression to fit models of environmental variables to AW. Separate partial least squares models were developed for each growth period. Variables with a calculated effect from path analysis were combined across seasons and were included in the independent dataset. The data from 1978 and 1979 (during which spring curl or sea level heights were not available) were used in the development of regression models for the first growth season because only the summer environmental values were required.

The partial least squares regression approach is particularly useful when there is a single dependent variable and a larger number of predictor variables and there is multicolinearity between those independent variables. Partial least squares regression searches for a set of components (called latent variables) that performs a simultaneous decomposition of independent and dependent variable sets (see Abdi, 2003 and Geladi and Kowalski, 1986 for a more complete description of this technique). Roughly, the latent variables are synonymous with principal components in that they are reduced dimension, uncorrelated, linear representations of the data matrices. The primary difference from principal component analysis is that in partial least squares regression the independent and dependent datasets are decomposed simultaneously such that the latent variables of the independent data

matrix are uncorrelated to one another but are correlated to the dependent dataset. Further, the latent variables determined are progressively less correlated to the dependent variable. We used the nonlinear iterative partial least squares algorithm.

The latent variable weights can be used to describe the influence of each variable on the latent variable score. Similar to principal component loadings, the latent variable weights can be used to determine the amount of variation encompassed by a particular variable within the environmental and biological datasets. Further, these latent variable weights are determined directly from the unstructured data and not from an analysis dependent on an *a priori*, determined path structure.

The latent variable scores of the independent data matrix were then used as independent variables in a multiple regression to model growth rate. We used a cross-validation procedure to choose the optimal number of latent variables to include for predicting the AW (Geladi and Kowalski, 1986). Specifically, the mean square error of prediction (MSEP) was calculated to estimate the predictive power of the models. To accomplish this, the average AW for a removed year was predicted based on a model determined from the remaining years of data and the difference between the predicted and observed AW values was the residual. The procedure was continued through the number of years for which there were data. Finally, the residuals were squared and averaged.

Size and age at return

Because a representative sample of the Mill Creek population was taken each run year, the impact of the environment on return age and size could be evaluated in a number of ways. We examined two aspects of a cohort's maturity. First, we evaluated how the environment correlated to the age at maturity of a cohort (three ocean winters or greater). Secondly, we examined the variation in size at age of returning three and four ocean-winter fish.

We examined how the proportion of three ocean-winter returns varied with the environment across 18 complete cohorts. Before analysis, the two ocean-winter fish (10%) and one ocean-winter fish (<1%) were removed from the dataset. Therefore, we addressed the question of whether, minus the few early returns, the environment affecting fish during their third growth year and return year could be used to predict the proportion of three ocean-winter fish returning. Specifically, we regressed the arcsin-transformed age ratio against the conditions experienced during the third final full year of growth and during the

return year to determine the point at which the proportion of fish returning after the third ocean winter, as opposed to later, was related to the environment. A path analysis, similar to that described for modeling growth, was used to determine the effect of environmental variables on the proportion of the fish in a cohort returning after three ocean winters. Variables with direct and indirect relationships to maturation were combined across seasons and were used as independent variables in a partial least squares regression.

Using a similar combination of path analysis and partial least squares regression as done for modeling growth rate and maturity, we examined the influence of the ocean environment the year prior to and during return on size at age of 3 and 4 ocean-winter spawning females. These two age groups represented the largest proportion of returns. Fork length at return was modeled with variables from the third full year of growth, the fourth full year of growth and the year of return. In doing this, we could determine the period at which the return size of each age group is related to the environment. Rather than a cohort-specific approach, as done in maturation analysis, we used a time-specific approach with this analysis (return years 1981–2002).

RESULTS

Path analysis fits to annulus widths

Growth rates (AWs) representing the first year at sea had a negative relationship to summer sea surface temperature, curl, and scalar winds and a positive relationship to summer upwelling (Fig. 3a,b), and the path model was not significantly different from the observed data ($P = 0.82$).

Growth rate during the second year at sea related to spring and summer conditions. Path models for spring ($P = 0.39$) and summer ($P = 0.87$) were not significantly different from the structure of the observed data (Fig. 4). Specifically, growth rate was negatively related to sea level height and sea surface temperature and positively to curl and upwelling during the spring and summer. Growth was positively related to scalar winds and wind stresses during the spring but negatively or not significantly during the summer.

Growth rate during the third year at sea was related to the environment during the spring and the path model was not significantly different from that of the observed data ($P = 0.25$; Fig. 5). Growth was negatively related to sea level height, sea surface temperature and scalar winds and positively to curl, upwelling, and northerly wind stresses.

Figure 4. (a and c) Results of the path analyses of the environmental variable relationships to one another and the annulus width (AW) in the second growth year indicated both spring and summer were related to second-year AW. Models were built for spring and summer separately. (b and d) The total effect of each variable on AW was determined by multiplying standardized coefficients along each direct path and summing the cumulative correlations across all paths. These total effects are shown as black bars. Those variables with an effect were used in a partial least squares regression and the weight of each variable on the first latent variable is shown by the gray bars.
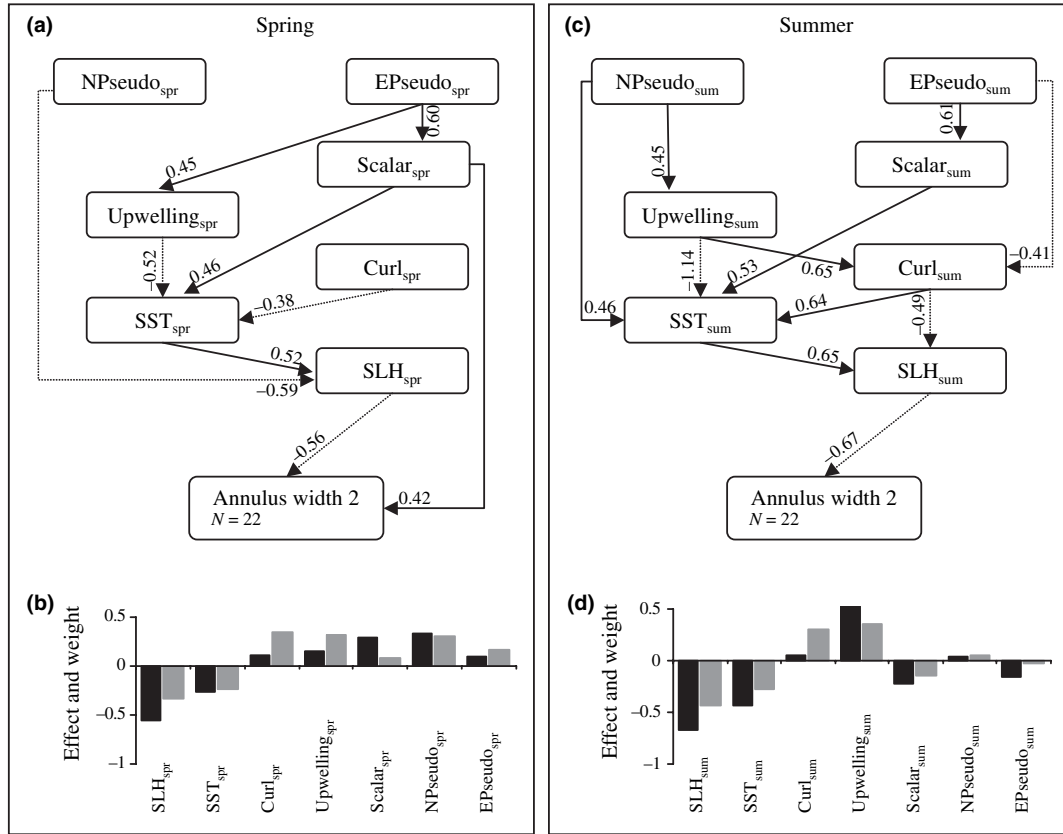
Growth rate in the fourth year at sea could be modeled with spring and summer conditions (Fig. 6). Path models for both spring ($P = 0.33$) and summer ($P = 0.95$) were not dissimilar to the structure of the observed data. The total effects of spring and summer sea level height, scalar winds, and, to a lesser degree, easterly wind stresses on growth rate were negative. Growth rate was positively related to spring and summer upwelling and northerly wind stress. Summer sea surface temperature and curl had no significant relationship with growth.

*Partial least squares regression fit to annulus width data*

The first year of growth was fit with the partial least squares regression. The MSEP indicated that using more than the first latent variable did not result in a better fit. The regression of growth rate to that latent variable was significant ($P = 0.0005$; $r^2 = 0.31$;

MSEP = 0.011; Table 3; Fig. 7a). The weights for the environmental variables in the first latent variable had a similar pattern as demonstrated for the total effects calculated from the path analysis. However, in the latent variable summer scalar winds loaded positively and northerly wind stress had a much stronger negative relationship with growth rate (Fig. 3b).

The second year of growth was related to the first latent variable ($P = 0.003$; $r^2 = 0.49$; MSEP = 0.020; Table 3; Fig. 7b) and using additional latent variables did not improve the fit. The pattern of weights for all variables loaded in the latent variable was similar to the effects calculated from the path analysis (Fig. 4b,d).

The first latent variable was sufficient to model the growth rate in the third year ($P = 0.021$, $r^2 = 0.30$; MSEP = 0.021; Table 3; Fig. 7c). Generally, the

Figure 5. (a) Results of the path analyses of the environmental variable relationships to one another and the annulus width (AW) in the third growth year demonstrated that spring conditions are related to third-year AW. Models were built for spring and summer separately. (b) The total effect of each variable on AW was determined by multiplying standardized coefficients along each direct path and summing the cumulative correlations across all paths. These total effects are shown as black bars. Those variables with an effect were used in a partial least squares regression and the weight of each variable in the first latent variable is shown by the gray bars.
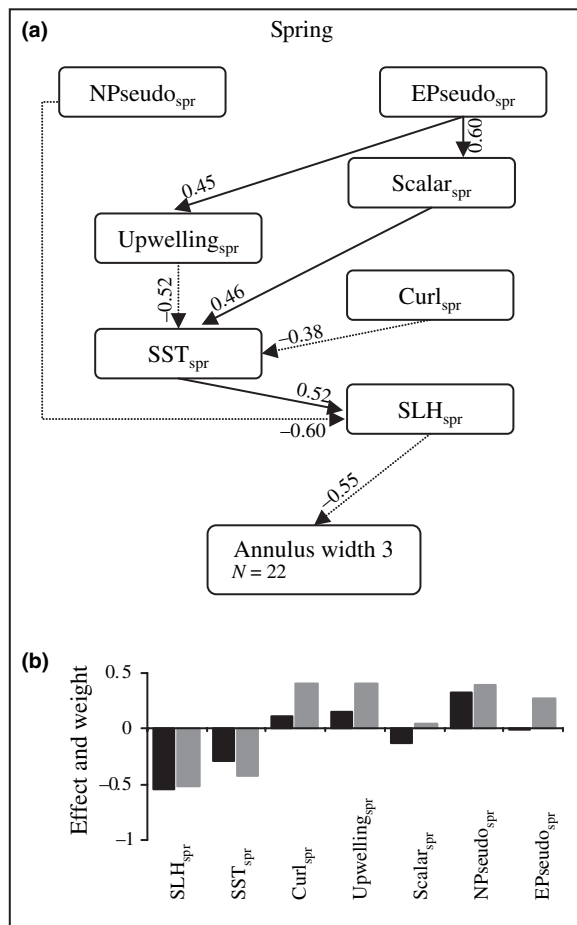
loadings for variables in the latent variable were similar in pattern to the calculated effects from the path analysis. However, upwelling, curl and easterly wind stress loaded more strongly positive in the latent variable (Fig. 5b).

While data for the fourth year of growth was limited, the first latent variable was significantly related to growth rate data ($P = 0.005$; $r^2 = 0.37$; MSEP = 0.025; Table 3; Fig. 7d). Variable loadings in the first latent variable had a similar pattern to the total effects

calculated from the path analysis. However, spring scalar wind had a strong negative calculated effect in the path analysis and did not load significantly on the first latent variable (Fig. 6b).

Maturation

The proportion of fish from a cohort returning after the third ocean winter was related to conditions experienced during the spring before the third winter at sea. The path model was not significantly different from the structure of the observed data ($P = 0.22$, Fig. 8a). The arcsin-transformed proportion of three ocean-winter fish returning was related negatively to sea level height, sea surface temperature and scalar winds and positively to curl, upwelling and northerly wind stresses during the spring before the third winter at sea (Fig. 8b).

Variables with effects were used as independent variables in the partial least squares regression. Maturation data were fit well by the first latent variable ($P = 0.011$; $r^2 = 0.34$; Table 3; Fig. 9) and additional latent variables did not improve the fit. The MSEP representing untransformed proportions of return numbers was 0.051 for the partial least squares regression. Excepting the positive weight for the easterly wind stress, the loadings for the variables in the first latent variable had a similar pattern to that observed from the path analysis (Fig. 8b).

The factors affecting maturation were similar to those affecting growth rate during the third growth period. In fact, there was a significant relationship between the arcsin-transformed proportion of fish maturing after the third winter (prop. 3 OW) and the AW representing the third growth season (Eqn 1).

$$\arcsin(\sqrt{(\text{prop.3OW})}) = (0.85 \pm 0.331\text{SE})\text{AW},$$
$$\text{df} = 17, P = 0.02, r^2 = 0.36. \tag{1}$$

It was evident that our fits of maturation to the environmental data failed to capture the limited number of three ocean-winter fish from the 1987 cohort returning in 1990 (33%, Fig. 9). Reduced proportions may have been an artifact of a small number returning from the 1987 cohort ($N = 6$ for fish returning at or older than three ocean winters), but examination of all age groups demonstrated that growth was dramatically reduced in 1990 (Fig. 7). In addition, growth of fish in their third growth season was very low in 1989 (Fig. 7c). Results from the current work demonstrated that the proportion of three ocean-winter fish maturing relates to the growth

Figure 6. (a and c) Results of the path analyses of the environmental variable relationships to one another and the annulus width (AW) in the fourth growth year indicated both spring and summer were related to fourth-year AW. Models were built for spring and summer separately. (b and d) The total effect of each variable on AW was determined by multiplying standardized coefficients along each direct path and summing the cumulative correlations across all paths. These total effects are shown as black bars. Those variables with an effect were used in a partial least squares regression and the weight of each variable in the first latent variable is shown by the gray bars.
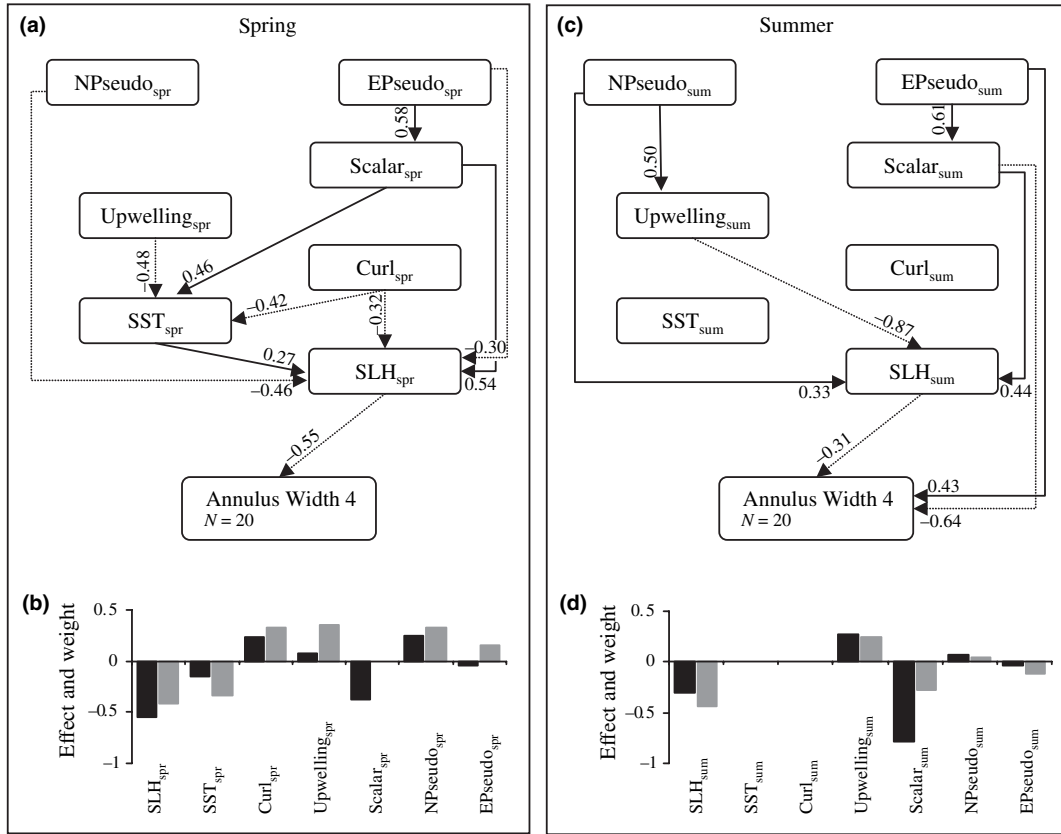

Table 3. Partial least squares regressions for California Chinook salmon (*Oncorhynchus tshawytscha*) growth rates, maturation and return length were developed with environmental data from the region between Cape Blanco and Cape Mendocino (Table 1; Fig. 1).
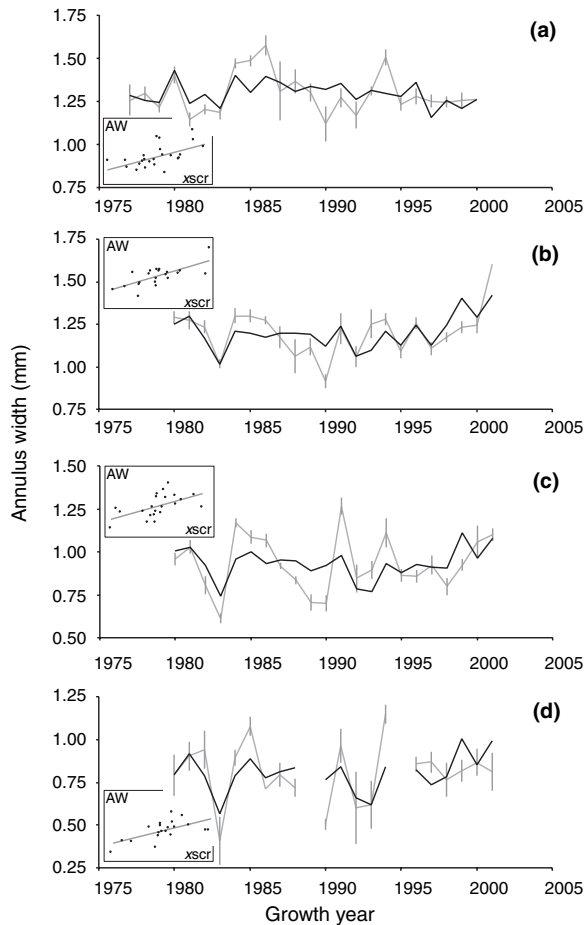
Ind. variable	Slope (±1 SE)	Intercept	df	P-value	r^2	MSEP
GR_1	0.052 (±0.012)	1.297 (±0.020)	23	0.0016	0.31	0.011
GR_2	0.046 (±0.010)	1.203 (±0.021)	20	0.0003	0.49	0.020
GR_3	0.054 (±0.019)	0.933 (±0.030)	21	0.0008	0.30	0.021
GR_4	0.054 (±0.017)	0.803 (±0.033)	19	0.0004	0.37	0.025
arcsin($\sqrt{}$(prop 3OW))	0.097 (±0.034)	1.094 (±0.054)	17	0.0110	0.34	0.055 (0.051)
FL of 3OW	13.81 (±4.61)	871.26 (±7.33)	21	0.0010	0.31	1377

Shown are the models for the first (GR_1), second, third and fourth growth years, the proportion of three ocean-winter fish returning from a cohort [arcsin($\sqrt{}$(*prop3OW*))], and fork length of three ocean-winter returns (FL of 3OW). In all models the mean square error of prediction (MSEP) indicated that the first latent variable was sufficient to model the dependent variable. Associated statistics include slope for the first latent variable (±1 standard error), intercept (±1 standard error), degrees of freedom (df), P-value, coefficient of variation (r^2) and MSEP. The MSEP calculated for the proportion of three ocean-winter fish returning was calculated from transformed values and, shown in parentheses, from untransformed values.

period the season before the final winter. Together, the few fish maturing after the third winter and returning in 1990 was likely not an outlier. However,

to determine the effects of the 1990 return year on the partial least squares regression models, we re-evaluated them with the 1990 data removed. The fit of

Figure 7. Shown are the fits of the annulus widths (AW) in the (a) first, (b) second, (c) third and (d) fourth growth years with the environmental data using partial least squares regression displayed across the time series and as inset scatter plots showing the fit of the data to the first latent variable (*xscr*). Gray time series show the observed average AWs across the growth years for which there were data (±1 standard error) for each age group, and black time series show the predicted AWs from the partial least squares regression. For each age group is also shown a scatter plot of the observed average AWs to the first latent variable and, within each of these insets, the gray line represents the fitted relationship of observed data to the first latent variable.
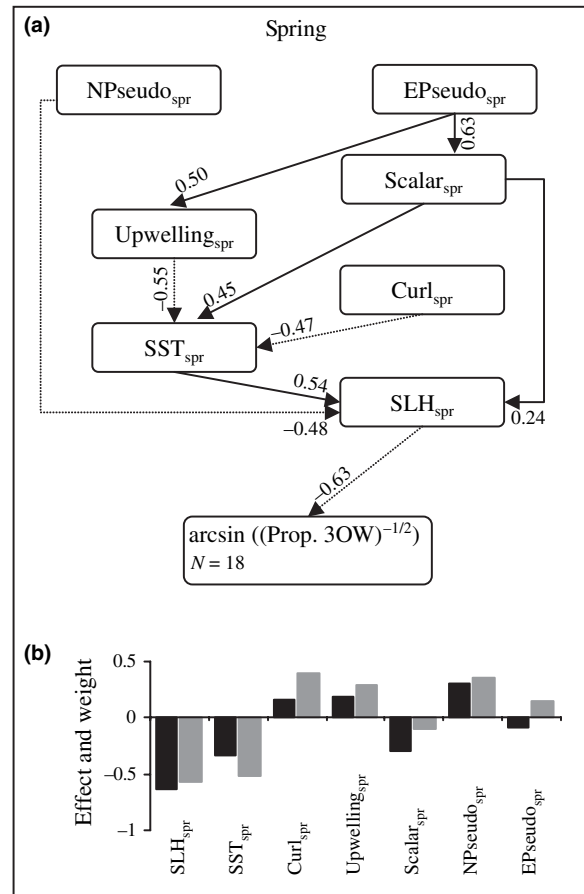
Figure 8. (a) Results of the path analyses of the environmental variable relationships to one another and the arcsin-transformed proportion of three ocean-winter fish returning to spawn (Prop. 3OW) demonstrated that spring conditions before the last winter at sea are related to maturation. Models were built for spring and summer for the last full season of growth and the return year separately. (b) The total effect of each variable on maturation was determined by multiplying standardized coefficients along each direct path and summing the cumulative correlations across all paths. These total effects are shown as black bars. Those variables with an effect were used in a partial least squares regression and the weight of each variable in the first latent variable is shown by the gray bars.

maturation rate was not improved after removal of the 1990 return data (Fig. 9).

Length at return

Path analysis demonstrated that the only significant relationship between return length and the environment was that between the fork length at return of three ocean-winter fish and the environment experi-
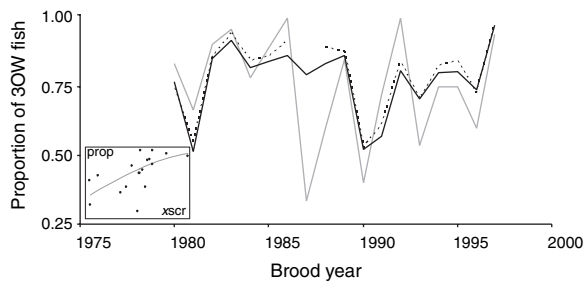
enced in the spring before the final winter at sea ($P = 0.02$; $r^2 = 0.34$; Fig. 10a). The path model was not significantly different from the observed data covariance ($P = 0.22$). Length at return of three ocean-winter fish was negatively related to sea level height and sea surface temperature and was positively related to curl, upwelling and wind stresses (Fig. 10b).

Partial least squares regression was used to fit the fork length at return of three ocean-winter fish to

Figure 9. Fit of the proportion of three ocean-winter (3OW) fish maturing with the environmental data from the spring before the last winter at sea using partial least squares regression displayed across the time series and as an inset scatter plot showing the fit of the arcsin-transformed data to the first latent variable (*xscr*). Gray time series show the observed proportion of three ocean-winter fish across the brood years for which there was data, and black time series show the predicted maturation from the partial least squares regression. The inset scatter plot shows the observed arcsin-transformed proportion of three ocean-winter fish (prop) fit with the first latent variable and, within the inset, the gray line represents the fitted relationship of observed arcsin-transformed data to the first latent variable.

Figure 10. (a) Results of the path analyses of the environmental variable relationships to one another and the fork length of returning three ocean-winter fish (FL of 3OW) demonstrated that spring conditions before the last winter at sea are related to the length of returning three ocean-winter fish. Models were built for spring and summer for the last full season of growth and the return year separately. (b) The total effect of each variable on length was determined by multiplying standardized coefficients along each direct path and summing the cumulative correlations across all paths. These total effects are shown as black bars. Those variables with an effect were used in a partial least squares regression and the weight of each variable in the first latent variable is shown by the gray bars.
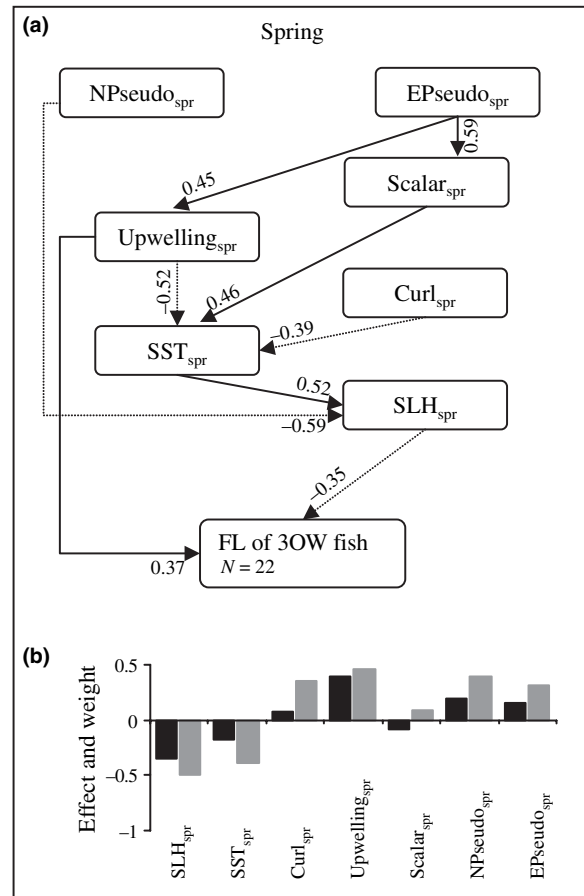

environmental variables that had been shown to have an effect. The first latent variable fit the length data significantly ($P = 0.0061$; $r^2 = 0.31$; MSEP = 1377; Table 3; Fig. 11). The variables loaded into the first latent variable yielded similar results to the total effects calculations from the path analysis. However, the weight of scalar winds was modestly positive (Fig. 10b).

DISCUSSION

We are careful not to imply a causation model with any of our detected relationships. Such a step would be in advance of our actual knowledge of the linkages between the environment, productivity of the system and ultimate effect on the fish. It would also imply that we have a complete knowledge of the fish's distribution across each year analyzed. Rather, we built models based on correlations that represented average multivariate relationships between environmental variables in the area occupied, on an average, by the fish. However, consider that the path structure, and resulting path models, were based on both mechanistic understanding and spatial and temporal variability of the data. That the calculated effects of variables in the *a priori* determined structural models were largely similar to the pattern of weight loadings from the

unstructured partial least squares approach lends support to our models.

The environmental variables were selected for the analysis because they are correlated with production and biological dynamics in the ocean environment (Miller, 2004). Further, these variables are correlated with survival and early growth of Pacific salmon in California Current waters (Hobday and Boehlert, 2001; Koslow *et al.*, 2002; Logerwell *et al.*, 2003).

Figure 11. Shown is the fit of the average fork lengths (FL) of returning three ocean-winter fish with the environmental data from the spring before the last winter at sea using partial least squares regression displayed across the time series and as an inset scatter plot showing the fit of the data to the first latent variable (xscr). Gray time series show the observed average fork lengths (±1 standard error) of three ocean-winter fish across the return years for which there were data, and black time series show the predicted average fork lengths from the partial least squares regression. The inset scatter plot shows the observed average fork lengths of three ocean-winter fish fit with the first latent variable and, within the inset, the gray line represents the fitted relationship of observed data to the first latent variable.
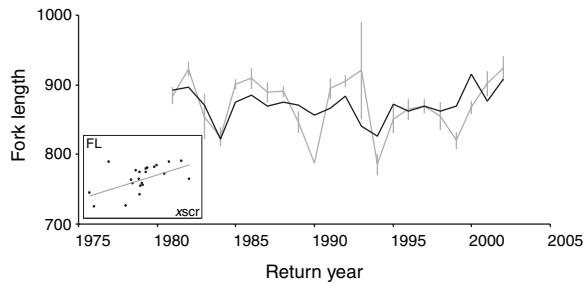
Northerly and easterly pseudo-wind stresses are often associated with storms and enhanced mixing, and also provide the forces driving upwelling. Scalar wind is a measure of the non-directional wind speed and represents the degree of turbulence in surface waters. Upwelling provides nutrients to surface waters and curl is a measure of the retention or advection of surface waters from the shore. Mueter *et al.* (2002) demonstrated that coastal sea surface temperatures, during the upwelling season, are spatially correlated at a scale of ∼500 km. Therefore, at a scale similar to our sample area, sea surface temperature covaries with regional conditions during the Chinook salmon growth season. Specifically, wind-driven upwelling magnitude and frequency covary with sea surface temperature in that region. Finally, sea level height represents variation at the largest temporal and spatial scale examined here with values highly correlated along the California Current. Sea level height relates to current speed and it is dependent to some degree on all of the previous variables discussed. Generally, sea level height is a confounded representation of the productivity of the California Current system.

Path analysis indicated that growth during the first season at sea was weakly but significantly related to summer conditions. Chinook salmon migrated during late spring so our model fits well with what would be expected. Sea surface temperature was determined to have a direct negative relationship with growth, likely as a result of the negative correlation between sea surface temperature and upwelling and productivity. However, importantly we related the first year of growth to the environment retrospectively. It is during the first year at sea that the effects of size-selective mortality (Beamish and Mahnken, 2001; Beamish *et al.*, 2004) and possibly density dependence (Martin and Wertheimer, 1989; Greene and Beechie, 2004) are greatest. We also had a degree of uncertainty in our models related to freshwater and estuarine growth that was not separated out of the analyses. In all, our somewhat poor fits and prediction for the first growth season were to be expected.

During the second, third and fourth growth seasons, the patterns of correlation between the spring ocean environmental variables and growth were similar. Specifically, the sea level height had a direct negative relationship with growth. On a more regional level, sea surface temperature was negatively related to growth while curl and upwelling were positively related to growth. Generally, in the spring, environmental variables positively associated with large- and regional-scale productivity were also positively related to growth. Likewise, those variables with negative relationships to productivity were also negatively related to growth. In addition to the correlation of growth to spring conditions, growth rates during the second and fourth seasons were also related to summer conditions.

While we noted a relationship between summer conditions and growth in the first, second and fourth seasons, we did not note one for the third season. While this may have been the actual mechanism occurring in the system, it is also possible that we introduced a bias by pooling all return ages together in our models. As the proportion of three ocean-winter fish from a cohort returning was related to spring and not summer conditions it is likely that the three ocean-winter fish we examined (72% of the sample, Table 1) were those that were destined to return without regard to the summer conditions. However, to determine if there was an effect of summer conditions on growth in the third season, we would have had to analyze the third season of growth from the four ocean-winter fish separately (17% of the sample; Table 1). Sample size did not accommodate such a rigorous examination.

Unlike other variables examined, path analysis and partial least squares approaches almost consistently yielded an opposite relationship between scalar wind and the biological parameters. Namely, the structure of our path models resulted in scalar winds having an estimated negative affect on the biological parameters while partial least squares, an unstructured approach,

estimated that scalar winds were positively related to the biological parameters. Scalar winds have been shown to have a direct causal relationship on Chinook salmon prey abundance (Cury and Roy, 1989; Roy *et al.*, 1992; Ainley *et al.*, 1993). However, the relationship is complicated because it is nonlinear and also because it is confounded by the positive benefits of upwelling on production. Specifically, a scalar wind speed between ~5–6 m s^{-1} is optimal for the production of many Chinook salmon prey species (MacKenzie, 2000) and anything less or more leads to suboptimal production (e.g. Cury and Roy, 1989; Roy *et al.*, 1992). In our study region we found that the minimum spring scalar wind speed was 6.2 m s^{-1} between 1977 and 2002. Therefore, we expected a negative relationship between scalar winds in the spring and growth of Chinook salmon. In fact, that is what we found for all path analysis models except the one representing the spring period of the second growth year. Importantly, the path analysis approach examined the role of scalar winds within the context of its relationship to each oceanographic feature. Perhaps the path models allow a more appropriate means by which to examine the effects of such a troublesome variable. Interestingly, upwelling, which is associated with increased scalar winds (Cury and Roy, 1989), was always positively related to growth suggesting that the models were able to separate the positive impact of upwelling on production from the possible negative impact of increased turbulence.

However, ultimately path analysis demonstrated that sea surface temperature or sea level height could often be used alone to fit roughly the relationships between environment and growth rates (these variables had singular direct relationships). In part, this is due to large-scale variability confounding smaller scale variability but likely also represents movement of fish across environmental landscapes. For example, for growth in the first year, during which time the fish likely remain along the coast near their natal system, we showed that sea surface temperature and not sea level height were related negatively to growth. However, as the fish age they follow optimal temperatures by using deeper waters (Hinke *et al.*, 2005). Also, while we demonstrated that they remain within the source region on average, there is likely interannual variability in their distribution along the coast (e.g. Pearcy and Schoener, 1987; Brodeur *et al.*, 2004). Therefore, as the fish age, sea level height, a factor representing conditions along the entire California Current system, fits growth best. The partial least squares regressions introduced the other environmental forces into the growth models, and, because it was

not restricted by an *a priori*, determined model structure, demonstrated that variables such as upwelling, curl and northern wind stress were weighted relatively greater than the effects calculated from the path analysis. Most importantly, partial least squares regression is capable of using all variables in a predictive model. The additional environmental variables improved the fits. For instance, modeling growth in the first year using only sea surface temperature as an independent variable resulted in an $r^2 = 18\%$. By including the remaining variables that were shown to have an effect into a multivariate approach the r^2 increased to 0.31 (Table 3).

We used partial least squares regressions to evaluate the ability of our models to predict growth rates of fish at large and to forecast maturation rate one year ahead of the returning stock. However, without a model of causation between the environmental variables and the vital rates, we leave ourselves open to spurious results and variation introduced from changing ocean conditions and unstable inter-variable relationships (e.g. regimes). For instance, we noted a dramatic change in the strength of summer curl occurring at about the same time as a switch in oceanic conditions, whereby coastal water retention was exceptionally high beginning in 1998 (Peterson and Schwing, 2003). Nevertheless, for the 22-year period for which we fit environmental data to biological data, models were capable of predicting missing data reasonably well (Table 3, MSEP values). For instance, we captured 34% of the variation in the maturation data and estimated the proportion of fish returning after the third ocean winter with relatively low error (MSEP = 0.051).

What we see as the most significant finding in this work is the development of a model describing environmental mechanisms correlated to the age of maturity of Chinook salmon. The proportion of fish returning following the third ocean winter, as opposed to older fish, was fitted significantly to environmental variables affecting the fish during the spring of the last full year of growth (that prior the third ocean winter). Specifically, we demonstrated that those environmental factors positively related to growth (e.g. upwelling, curl) were positively related to maturing after three ocean winters. In keeping with this finding, there was a significant relationship between the AW and three ocean-winter return ratio. While we demonstrated that the environment experienced in the last full year of growth may have related to maturation, we note that it is also likely that early life-history experiences (before and during initial ocean entry) may relate to age at maturation (Hobday and Boehlert,

2001). We could not be confident about early-life patterns in scale morphology or the confounding of early-life habitat use and environment. As a result, we confined our results to the complete first year of growth and, therefore, were unable to explore the effects of early life on maturation.

In addition to quantifying the relationship between the environment and age at return, we also demonstrated that the size at which three ocean-winter fish returned was related to the environment the year prior return. Ultimately, in combination with the results related to age at maturation, this suggests that the probability of returning during the fall after the third ocean winter is based, in part, on length at the onset of the final winter at sea. These findings are supported by Wells *et al.* (2006) in which the return size of California Current coastal Chinook salmon was more highly correlated to the environment experienced during the last full year of growth than any other time period. Generally, we have shown that spring upwelling, spring curl and cool waters were positively related to return size for three ocean-winter fish. Growth rates and return sizes of these three ocean-winter fish were dependent on similar conditions as is overall spring productivity of the California Current system.

None of the length-at-return models we examined demonstrated a significant relationship between the environment and length of four ocean-winter fish. Perhaps for four ocean-winter returns, the inherent growth rate was great enough that, if left unmediated by the environment, it would have been sufficient to mandate return at four ocean winters. In support, few fish returned beyond the four ocean winters and those that did may have been considered anomalies. This suggests that after four ocean winters, the fish was bound to return regardless of growth or environmental conditions experienced during that year following the third ocean winter.

We showed that, over the 18 cohorts examined, the average length of return of three ocean-winter fish varied approximately 25%, suggesting fish return on average between 775 and 925 mm fork length (Fig. 11). Such a wide variation in return size may be conferred to variation in fecundity (Healey, 1991) and egg size (Nicholas and Hankin, 1988) and ultimately variation in the fitness of the population. Healey and Heard (1983) demonstrated that the relationship between fecundity is exponential. However, Johnson (1988) showed that a significant reduction in the average size of Chinook salmon during the 1983 ENSO was not met with a significant decrease in fecundity. We argue, as did Johnson (1988), that the

decrease in fecundity may have been noted had the analysis been age specific (i.e. fluctuations in relative abundance of age classes was not taken into account). In support, Quinn *et al.* (2004), having used a size-adjusted fecundity estimate, showed that fecundity increased with marine growth of Chinook salmon. Findings by Nicholas and Hankin (1988) also suggest that egg size may be affected by a reduction in fish size and condition. As egg number is related to potential recruitment and egg size is related to individual survival (Heath *et al.*, 1999), the impact of a 25% reduction in return size at age may be significant. The observed variation in age at maturation, whereby fish are exposed to more or less ocean mortality between three and four ocean-winter periods, coupled with variation in return length, suggests the mechanisms we present here may relate to substantial variation in recruitment and to the spawner–recruit relationships.

The low coefficients of variation about our models indicated that other sources of variation in growth were not accounted for by our environmental variables. We envision two primary reasons for the substantial variation we noted. First, in examining the variation around our fitted relationships, it is important to consider we modeled scale growth as opposed to fish growth. While scale growth is linearly related to fish length (Bilton, 1985), variation is introduced by scale shape, size, micro-structure and interpretation. Secondly, a degree of variation is introduced into our models because we quantified the relationship between the environment and growth as though it were direct. Rather, this relationship is conferred indirectly through complex ecosystem interactions. Ultimately, the mechanisms determining growth are more complicated than can be modeled with environmental variables alone. This is not to imply that the findings we present are insignificant to the larger scheme of describing growth. Rather, we have conservatively quantified some of the relationships between various oceanographic features and multivariate conditions on growth.

By quantifying the relationships between salmon growth and maturation and the environment, we could evaluate the need to adapt management across different environmental regimes (e.g. Peterson and Schwing, 2003; Swartzman and Hickey, 2003) and along environmental trends such as global warming (e.g. Bakun, 1990). For instance, estimates of escapement for California Chinook salmon are based on an invariant maturation schedule. Our models could potentially be used to adjust escapement estimates. However, we had variable success in fitting the

environmental data to the growth and maturation data.

We successfully captured the negative effects of the 1983 ENSO event on growth yet we missed the drastic reduction in growth that occurred during the 1990 growth season. Examination of the environmental data from these two years elucidates why we did not capture the reduction in growth and maturation during 1990. Likely, interannual variation in the inter-relationships between variables may have led to the poor fits in 1990. Sea level height was at its greatest during the 1983 growth season and was only slightly above average during 1990. Sea level height variability had a strong relationship to growth and maturation and was paramount to fitting biological data with environmental data. Therefore, we did not capture the reduced growth in 1990 because sea level height was at an average state. Sea surface temperature was also substantially higher in 1983 than 1990. In fact, across all of the variables examined for 1983 the conditions were correlated with very poor production. It follows that we detected and predicted poor growth in 1983, but for 1990 none of the environmental variables were at the extreme ends of their distribution. However, sea surface temperature for the spring of 1990 was ranked fifth lowest within our time series. Theoretically, considering the relationship between growth and sea surface temperature to be negative and linear (across the range of values we examined), growth would have been exceptional in 1990. The residuals for all of our models were linear and random and, of the cooler years (1985, 1991, 1999 and 2002), none resulted in such poor growth as in 1990. Ultimately, it does bring into question the liberal or untested use of environmentally mediated models to fit biological vital rates (Haeseker *et al.*, 2005).

We made the following assumptions in the models presented: (1) fishing pressures and selectivity were not correlated to the same environmental variables used as independent variables in our models; (2) after the first ocean winter we modeled growth predominantly as opposed to size-selective mortality; (3) hatchery and wild fish related similarly to the ocean environment; (4) the effect of growth before ocean entry was insignificant or synchronous with open ocean model results; and (5) the average spatial distribution of the fish is relatively static.

As for variation in fishing pressure, we argue that our results are representative despite the variation introduced by variations in fishing pressure (assumption 1) and that there is no evidence fishing practices track the variables examined in this dataset. In fact, examination of fishing effort in California demon-

strates that there was no correlation between effort and the environmental variables, nor between effort and any of the observed vital rates (B. Wells, unpublished data, http://www.pcouncil.org/salmon/salsafe05/salsafe05.pdf). However, for future applications, if fishing practices vary similarly to the environment as do vital rates the results would represent a colinearity between the environment and fishing practices and would falsely identify the environment as the important component relating to the vital rate.

Relative to modeling growth following the first ocean winter (assumption 2), the period before the first ocean winter is considered the period during which the greatest size-selective mortality occurs (Beamish and Mahnken, 2001; Beamish *et al.*, 2004). If first-year size-selective mortality was substantial then we would have overestimated growth rates and underestimated the negative relationships between growth and the environment. Chinook salmon are mobile predators and are significantly larger when they enter the second winter than during the first. Therefore, it seems unlikely that there would be substantial size-selective mortality after the first ocean winter.

As for assumption 3, we left any possible hatchery fish anonymous in our sample. The requirement to make this assumption was driven primarily by a lack of known-origin fish with which to validate a discrimination rule. Without validation studies, and often with them, discrimination is poor. Regardless, being of similar size and timed to emigrate at a similar time, hatchery fish from the Smith River are released in such a way as to mimic wild populations. They are also spawned from wild brood stock. As we were interested in the ocean growth period and Chinook salmon were released at and emigrate at ∼100 mm fork length (12–20 scale circuli) the impact of differences in early growth rate were likely not of concern. However, importantly, differences between the return dynamics of hatchery fish can occur if there is a substantial difference in the potential growth in the ocean environment. In all, the concerns are that variation in release size of salmonids can lead to variation in return dynamics (e.g. Wells *et al.*, 2006), fish were released in a way as to maximize their survival, and there may be differences in potential growth. However, the numerical contribution of hatchery fish on the wild Mill Creek population was likely non-existent or was minimal. Consider that of ∼340 000 fish marked in the nearest hatchery none were ever recovered in Mill Creek.

In our analysis, we combined the growth periods occurring before and after ocean entry due to the often

nebulous discrimination of the ocean entry check (assumption 4). It is not unlikely that variation in estuarine residence could relate to the overall environmental conditions, thus creating varying degrees of apparent ocean entry periods on the scales (gradual width increases versus immediate shifts in growth rate). Our methodology may have confounded the models of early growth somewhat. Regardless, we demonstrated a significant model, even if there is no legitimate mechanism for determining if the freshwater/estuarine growth related similarly to, or oppositely to, the environment relative to the ocean growth period.

Finally, it has been demonstrated that the distribution of salmon (Pearcy and Schoener, 1987; Brodeur et al., 2004) and salmon prey (Brodeur et al., 2003, 2004) covary with oceanic condition (Chelton and Davis, 1982; see Fig. 5 of Wells et al., 2006). It follows that non-stationary environmental conditions, concomitant with varying distributions of fish, put into question our approach of an inherently static definition of regions and a spatially unvarying application of at-age models. Importantly, any attempt we made to model variables together across larger regions (in an attempt to capture the full distribution of the fish) increased the variation about the models significantly, failed to identify significant models, and/or made the interpretation of the models unrealistic. This was to be expected given the findings of Koslow et al. (2002), who demonstrated that the degree of variation between regions was significantly greater than within, and that numerous like-variables between regions may either be uncorrelated or negatively correlated. Importantly, the inclusion of sea level height as a large-scale variable incorporated variation across the range of Chinook salmon residing within the California Current system. That sea level height consistently had a direct affect on 2, 3 and 4 ocean-winter fish may have indicated a varying distribution over the period for which we have samples. All five of our assumptions have little opportunity to negate or bias our results other than to add a degree of variation around the model.

In summary, we have demonstrated environmentally mediated models for describing the growth of Chinook salmon during ocean residence. We also showed how and when the age and length at maturation relate to the ocean environment. Ultimately, we have advanced knowledge of simple inherent growth models and identified specific oceanographic features related to important vital rates of a California Chinook salmon population.

ACKNOWLEDGEMENTS

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