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Relationships between oceanic conditions and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from California, Washington, and Alaska, USA

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ABSTRACT

We model age-specific growth rates of Chinook salmon (*Oncorhynchus tshawytscha*) with two life-history behaviors from Alaska (i. Situk and ii.Taku Rivers), Puget Sound, Washington (iii., iv. Skagit River), and California (v. Smith River) relative to oceanic conditions in those regions. By analyzing over 20 yr of biological and physical data from the NE Pacific downwelling, upwelling, and transition zones, we are able to determine the factors affecting growth across much of the species' range and between life-history behaviors. With scale increment data from returning fish, we use path analysis and partial least squares regression to quantify the relationships between growth and regional- and large-scale oceanic conditions (e.g., sea level height, sea surface temperature, upwelling). Alaskan fish with both ocean- and stream-type behaviors were fit best by the environmental data from the winter in Alaska waters. Specifically, coastal and gyre factors such as sea surface temperature, river flow, and Ekman pumping positively correlated to growth, indicating a productive and strong Alaska Current promoted growth. Growth of fish from California was fit by local factors such as increased upwelling, lower coastal sea surface temperature, and wind stresses during summer and spring, indicating a productive and strong California Current promoted growth. For Puget Sound, Washington, growth of fish that migrate to sea in their first year was generally negatively correlated to a strong California Current. Puget Sound fish that spend a year in freshwater before migrating to sea were modeled well with environmental data from their source region for the first 2 yr at sea and by data from Alaska waters in their third year at sea. Results suggest that conditions in which the transition zone is dominated by neither the Alaska nor California Currents are best for increased growth of Puget Sound fish.

Key words: Chinook salmon, ENSO, environment, northern oscillation index, pacific decadal oscillation

INTRODUCTION

The northeast Pacific coast can be divided into three general regions of productivity: upwelling south of Vancouver Island, BC, downwelling north of Vancouver Island, and the transition between the two (hereinafter referred to as the transition zone; Fig. 1; Favorite *et al.*, 1976; Hickey, 1979; Ware and McFarlane, 1989). The population dynamics and growth of fishes across these regions are often asynchronous (e.g., Hobday and Boehlert, 2001; Wells *et al.*, 2006). For instance, the production of Pacific salmon (*Oncorhynchus* spp.) is negatively correlated between the upwelling and downwelling regions (Hare *et al.*, 1999). In light of this, it becomes important to quantify those ocean environmental factors that influence vital rates so that the ecology and dynamics of widely distributed species can be understood. Ultimately, such an understanding can be used to improve fishery management (King *et al.*, 2001; Rothschild and Shannon, 2004; King and McFarlane, 2006). Specific examples include improved estimation of ocean abundance, maturation rates (Wells *et al.*, 2007), and return numbers to appropriately set harvest rules. Here, we describe the relationship of growth of Chinook salmon (*Oncorhynchus tshawytscha*) from southeast Alaska to California to the regional and larger-scale environment they encounter while at sea.

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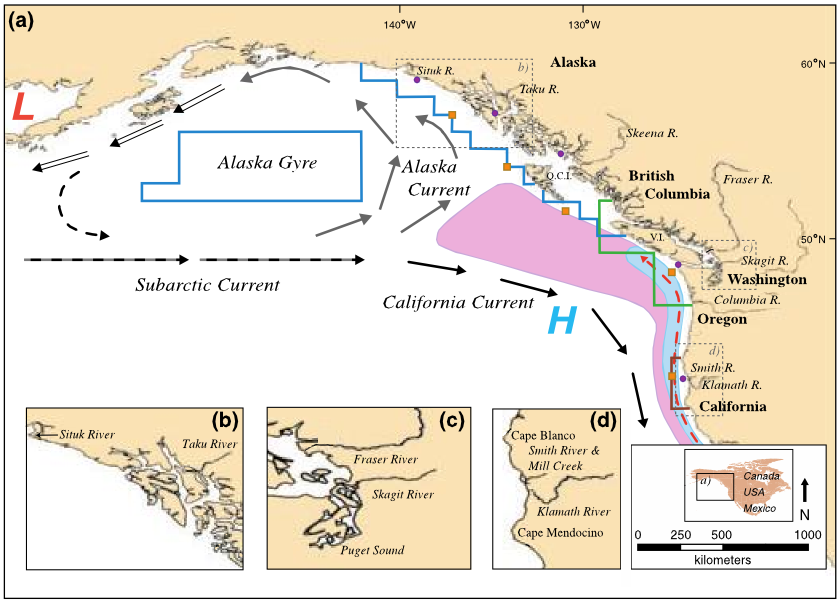
Figure 1. Major currents of the (a) North Pacific: the Subarctic Current (gray-black dash), bifurcating into the California Current (black) and the Alaska Current (gray). The Alaska Stream is double tailed. The red-dashed arrow represents the Davidson Current, which may surface during the winter. Conversely, during the spring the Davidson Current deepens (to become the California Undercurrent; Freeland *et al.*, 1984), the California Current strengthens, and the coastal region is characterized by upwelling. Favorite *et al.* (1976) referred to this region as the Upwelling Domain (light blue). Favorite *et al.* (1976) also identified the oceanic region influenced by freshwater plumes as the Dilute Domain (magenta). Also included are the rough locations of the Aleutian low pressure cell (red 'L') and the North Pacific high pressure cell (blue 'H'; Strub and James, 2002). Fish scales were collected from the Situk and Taku Rivers (inset b), the Skagit River (inset c), and the Smith River (Mill Creek, inset d). For Alaska fish we used the Comprehensive Ocean Atmosphere Data Set to characterize environmental values from the blue bordered coastal region and gyre waters. We also used sea level height stations (magenta circles) and Pacific Fisheries Environmental Laboratory shore stations (orange squares). River flow data were obtained for the Skeena River. Similar regional-specific environmental data were consolidated for the Skagit River fish (green border) and the Smith River fish (brown border). Queen Charlotte Island (Q.C.I.) and Vancouver Island (V.I.) are shown.



The physical dynamics of the coastal ecosystems are dramatically different along the Alaska Current, California Current, and the transition zone. Along the California Current coastal productivity is driven by upwelling during the spring and summer when the current strength and northerly winds are stronger (Hickey, 1979; Ware and McFarlane, 1989). Interannually, during years when upwelling intensity is at optimal values, productivity is expected to be enhanced (Cury and Roy, 1989; Mann and Lazier, 1991). In contrast, the southeast Alaska coast is a downwelling system and, therefore, regional coastal upwelling plays a less significant role in nutrient supply while river inputs and deep water mixing play a stronger role (Favorite *et al.*, 1976; Peterson *et al.*, 2005). Generally, as the Aleutian low pressure cell strengthens, the Alaska Current becomes stronger (Beamish and Bouillon, 1993). With this increased Alaska Current strength, Ekman pumping in the gyre increases. Also associated with increased Alaska Current and upwelling of gyre waters, more nutrients and trace elements are exchanged between the gyre and coastal waters by onshore flow and eddies (Francis *et al.*, 1998; Whitney and Robert, 2002; Johnson *et al.*, 2005; Peterson *et al.*, 2005). Increased eddy number and size are associated with years when the Alaska Current is strong, as well as during El Niño – Southern Oscillation (ENSO) events (Mysak, 1985). The transition zone located at the bifurcation of the Alaska and California Currents is dominated by the dynamics of the two currents intra- and inter-annually (Freeland *et al.*, 1984). Specifically, this region exists at the northern-most extent of the upwelling zone and is centered in a lower-salinity region (Fig. 1; Favorite *et al.*, 1976). During the winter, circulation along Vancouver Island may be dominated by a northward flowing current from Washington and Oregon, but as northerly winds and the California Current strengthen in spring and summer, the undercurrent deepens and the surface current along the edge of the shelf turns southeastward (Freeland *et al.*, 1984). This change in current direction is associated with a switch from relatively strong downwelling to weak upwelling along the coast (Freeland *et al.*, 1984; Sackmann *et al.*, 2004).

Because the strengths of the Alaska and California Currents are driven, in large part, by the relative strength of the Aleutian low pressure cell and North Pacific high pressure cell (Fig. 1, Strub and James, 2002), the currents are negatively correlated to one another both intra- and inter-annually. During the winter, the Alaska Current strengthens and the California Current weakens (Strub and James, 2002). Between years, and during specific regimes (Hare *et al.*, 1999), the relative condition between the two currents often has one current stronger than its long-term average and the other weaker (Hickey, 1979; Ware and McFarlane, 1989).

It follows that productivity and survival of salmon originating from these regions would also be negatively correlated (Hare *et al.*, 1999; Mueter *et al.*, 2002). However, Chinook salmon growth rate differences from across these regions are not correlated (Wells *et al.*, 2006), partly because the migratory behavior of Chinook salmon often places the fish from one region into another (e.g., Columbia River Chinook salmon migrate to Alaska waters, Healey, 1991). However, for Chinook salmon populations that are restricted to their source region where growth across their oceanic lives can be regressed against their known environmental exposure, Wells *et al.* (2007) demonstrated that growth is correlated to the environment in a similar manner to survival. Namely, years of good productivity and survival in a given region are also associated with increased growth for resident Chinook (Wells *et al.*, 2006, 2007).

Salmonids are fast growing, relatively short-lived fish whose dynamics are profoundly impacted by size and growth rates. For instance, it is postulated that Chinook salmon return to spawn when a threshold size is reached so that slow growth delays maturation (Healey, 1991). In contrast, for Atlantic salmon (*Salmo salar*) variations in the growth rate affect the return timing (Jonsson *et al.*, 2003). Either of these relationships may exist for Chinook salmon maturation, 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 (Healey and Heard, 1984), 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. Finally, the amount of cohort mixing may increase or decrease through time with varying growth. The existence of these growth-related life-history and population traits make it clear that appropriate models of the effects of the ocean environment on growth are needed to estimate variability in fitness.

The role of regional and basin-scale environmental variability in Chinook salmon abundance has been investigated (e.g., Hare *et al.*, 1999; Mueter *et al.*, 2002). Yet, research on growth related to a variable environment is lacking. Until recently, understanding of return size as it relates to basin-scale factors was based on a single ENSO event (Pearcy and Schoener, 1987; Johnson, 1988). Expanding on this approach, Wells *et al.* (2006) demonstrated that the return sizes of more than 20 cohorts of Chinook salmon throughout their 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. Wells *et al.* (2007) also examined the effects of regional environment on growth of California Chinook salmon. It was determined that growth rate and maturation were correlated with sea surface temperature, winds, and upwelling in the same fashion as productivity of the system, i.e., wind-driven upwelling, and retention of nutrients along the coast were positively correlated to growth and maturation. Here, we extend that study to include fish from a large portion of their range and across life-history behaviors. Two life-history types for Chinook salmon are examined here, i.e., stream and ocean type based on juvenile rearing behavior. The similarities and differences across regions and life-history behaviors offer us the opportunity to evaluate the effects of the environment on growth across regions and life-history behaviors.

The objective of this work was to use a novel combination of modeling techniques to describe the relationship of Chinook salmon growth to the ocean environment as described by regional- and large-scale environmental variables. We present results from three regions along the United States West Coast encompassing the larger portion of Chinook salmon's natural range (Alaska, Washington, and California) and from two life-history behaviors for the purposes of making regional comparisons to understand growth dynamics and environmental relationships.

METHODS

Life-history behavior

Ocean and stream life-history types are considered distinct genetic lineages; however this nomenclature does not apply for Skagit River Chinook salmon that are considered to be ocean-type (Myers *et al.*, 1998) or Situk River fish which are genetically stream-type but have an ocean-type behavior. Here, ocean-type Chinook salmon are those that migrate to sea before the first winter in freshwater (Healey, 1991). They remain in estuarine waters for a period of days to several months. Afterward, the majority are believed to grow to maturation in near-shore and coastal waters and the remaining proportion in open ocean and Alaska coastal and gyre waters (Healey, 1991). Stream-type Chinook salmon migrate to sea after at least one winter in freshwater, passing through estuarine waters to reside in coastal marine waters until late summer or autumn. By the end of autumn most have migrated farther along the coast than ocean-type fish, as well as into the open ocean and Alaska Gyre waters (Healey, 1991; Beamish *et al.*, 2005).

Scale collections

Scale samples were removed from the dorso-lateral region of females captured during the terminal fisheries on (i) ocean-type Situk River (1982–2003, N = 1139, Johnson *et al.*, 1992), (ii) stream-type Taku River (1982–2003, N = 1092), Alaska, and (iii) ocean- (1980–2003, N = 1427) and (iv) stream-type (1980–2003, N = 972) Skagit River, Washington Chinook salmon (Table 1, Fig. 1). Terminal fisheries occurred at the river mouths and/or up river. Fish samples representing the age, size, and sex structure of the terminal catch (systematic and random sampling) were taken by Alaska Department of Fish and Game and Washington Department of Fish and Wildlife throughout each run year. From these samples, scales from females were randomly selected. Approximately 60 fish were selected for each year unless there were too few fish or more samples were needed to fill out the

Table 1. Sample sizes of 1, 2, 3, 4, and 5 ocean-winter (OW) female Chinook salmon (*Oncorhynchus tshawytscha*) collected each return year from the terminal fisheries of Situk and Taku Rivers, Alaska, and Skagit River, Washington. The Smith River, California, fish were collected on their spawning grounds (Fig. 1).

	Alaska									Washington								California				
	Situk R. Ocean				Taku R. Stream					Skagit R. Ocean				Skagit R. Stream				Smith R. Ocean				
Year	2	3	4	5	1	2	3	4	5	1	2	3	4	1	2	3	4	1	2	3	4	5
1980										1	6	46	3	3	65	19						
1981											5	45	7	7	34	27	1		2	25	4	
1982	5	18	8				14	39	7	1	9	51	3		38	15			2	25	3	
1983		18	5					54	3		7	50	4	1	3	22			4	15	4	1
1984		7					23	33	2	1	27	42	6	2	30	4			2	24	3	
1985	9	15	5				21	37	1		5	51	4		28	11				48	12	
1986	5	8	3				11	47	1		3	41	17	2	9	39			7	25	5	
1987		18	5				5	51	4		3	37	20	1	5	8			5	29	1	
1988	1	2	7		3	19	5	30	2		6	48	11	2	45	12		1	4	65	8	
1989						1	22	32	3		19	38	15		37	42				9	8	
1990					2		32	25			4	72	7	2	26	21				2		
1991	3	63	12	1		4	6	7	1		21	36	22		44	38			3	9	3	
1992	10	11	24							1	4	59	9	4	46	15			2	17	6	1
1993	6	57	46	1							10	39	4	3	35	30				2	2	
1994	6	22	30				4	51	3		22	32	4	5	31	18			1	13	3	1
1995	5	178	23				13	43		4	23	32	7	3	56	9			2	12	5	
1996		36	39	1			44	15												14		
1997		29	31				15	45				26	4		6	5			3	18	12	
1998		34	26			1	9	48	1		6	60	9		3	5			2	18	6	
1999	2	45	11				5	18	1	1	30	22	18		25	2			2	12	5	
2000		52	9			1	29	29	1	3	12	49	5	1	5	3			11	33	8	1
2001		19	45				35	17	1		2	24	8		2	4			9	11	2	
2002	4	50	7				46	13				27	9			2			1	17	3	
2003	1	55	3			5	40	15			22	38	8	3	4	2	2					
Total	57	737	339	3	5	31	379	649	31	12	246	965	204	39	577	353	3	1	62	443	103	4

age distribution (e.g., 1995 Situk River samples). From a 2.7-km stretch of Mill Creek, a tributary of the (v) Smith River, California, we sampled scales from all returning ocean-type females (1981–2002, N = 613, Table 1, Fig. 1, see Wells *et al.*, 2007).

Scale samples from (i, ii) Alaska and (iii, iv) Washington fish were prepared as acetate impressions by representative laboratories. We then digitized the impressions. Scales from (v) California fish were cleaned and secured between glass slides and were digitized (Fig. 2, Wells *et al.*, 2003). Using image analysis software (Optimas 6.5), the location of each winter annulus was marked and the distance between each annulus, along a 20° line relative to the maximum scale length, was calculated as a measure of the growth of that fish during that given year (Clutter and Whitesel, 1956; Reimers, 1973; Schluchter and Lichatowich, 1977). In addition to the lead author, each scale was aged by the laboratory from which it came. When there was disagreement (<5% for all populations) in ocean ages, the scale was removed from the analysis. The average annulus widths were calculated for all growth years of each cohort. These average annulus widths were used to determine the effect of environment on growth. Because each scale was used to estimate growth in years prior its capture the sample sizes may be greater than the number of years sampled (e.g., older fish captured during the first year of sampling can be used to estimate growth in earlier years).

Because of uncertainty in determining the time of movement of fish from the freshwater to the estuary and the estuary to the ocean from scales, we combined the first year of growth in the analyses. Importantly, it has been demonstrated that some Chinook salmon populations have substantial inter-annual variation in their period of estuarine residence that is dependent on some of the same environmental variables we are examining (MacFarlane *et al.*, 2005). However, the majority of first-year growth occurs in the ocean environment. Finally, population-specific inter-annual variation in size at migration to ocean waters is small relative to the total first year growth. In all, we believe that our approach has measured ocean growth allowing us to examine the relationship between variation in ocean environment and growth, although for estimates of the first year at sea the relationship will be confounded somewhat by variation in early growth.

For all populations, erosion of the scale margin typical of anadromous fish required that we only measure to the final annulus and ignore the most recent growth. This made it impossible to develop meaningful population-specific scale⁄fish length

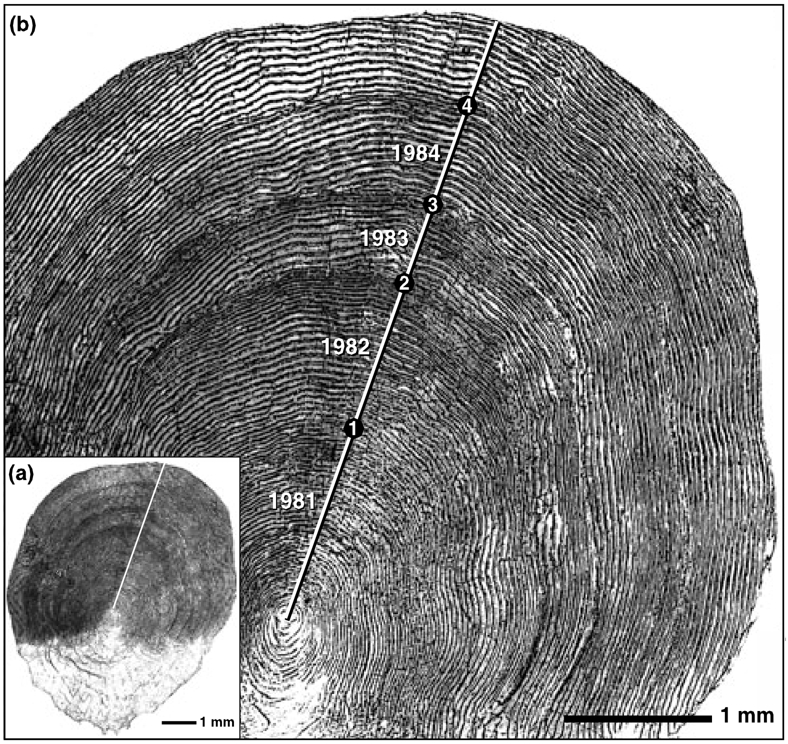


Figure 2. A dorso-lateral scale collected from a four ocean-winter Smith River, California spawned female Chinook salmon (*Oncorhynchus tshawytscha*) collected in December 1985. Inset (a) shows the entire scale with the 20° ageing transect. A magnified image of the ageing transect is shown in (b) including the four ocean winters and growth years.

relationships (i.e., correlations of determination were 0.39, 0.32, 0.61, and 0.28 for fish from Situk, Taku, Skagit, and Smith Rivers, respectively). However, Bilton (1985) showed correlations of determination greater than 0.80 using scales that were complete.

Ocean distribution

Although relatively little is confirmed about the specific ocean distribution of the stocks we used in the study, Healey (1991) showed that fish tagged within the inside waters of Alaska were rarely captured south of British Columbia. Thedinga *et al.* (1998) reported that Situk River fish spend up to a month in the tidally influenced lower region of the Situk River before completing migration to the sea. Limited tag-return data regarding Situk River Chinook salmon indicate that after the short period in the estuary, the majority do not rear in the inside or near-shore waters of southeast Alaska; apparently they move rapidly through these waters to more distant rearing areas in the Gulf of Alaska. However, limited tagging and genetic analyses indicate some Taku River Chinook salmon remain inside Southeast Alaska waters for the first year before moving to the shelf. As they age, some Taku River Chinook salmon, representing the stream-type behavior, may move as far westward as the Aleutian Islands and southern Bering Sea. Also, neither of these Alaska populations return to near-shore waters near their natal streams until the spawning migration in the final spring of their lives (McPherson *et al.*, 2000; A. Wertheimer, NMFS Auke Bay Fishery Laboratory, Juneau, Alaska, personal communication; M. Trudel, Fisheries and Oceans Canada, Pacific Biological Laboratory, Nanaimo, BC, personal communication).

California Chinook salmon have a much more restricted distribution. Wells *et al.* (2007) reported on a contact rate analysis of the ocean fishery to show that fish of northern California origin reside largely in northern California waters between Cape Mendocino and Cape Blanco (Fig. 1). Puget Sound, Washington, Chinook salmon spend their first year at sea near their source (e.g., Duffy *et al.*, 2005). However, as they age, a portion migrate north, and are rarely found south of Vancouver Island (Healey, 1991). Further, their distribution may be dependent on the relative strengths of the Alaska and California Currents (e.g., Pearcy and Schoener, 1987; Brodeur *et al.*, 2004). Therefore, in addition to modeling growth with data from the transition zone, we modeled growth of Puget Sound, Washington, fish after the first year at sea using data from Alaska waters.

Cross-correlation of growth patterns between stocks

We used cross-correlation as a starting point to compare the time series of variation in average annulus widths between different stocks at each growth period (i.e., first, second, third, and fourth years at sea). To reduce auto-correlation and calculate degrees of freedom (Pyper and Peterman 1998), time series were linearly detrended across time and missing data were filled with the detrended mean (Table 1 shows missing values). Time trends in the data were either insignificant or weak and in all cases there was no need to adjust the degrees of freedom (Pyper and Peterman 1998). The cross-correlation allowed us to evaluate similarities and dissimilarities between growth patterns of the fish across their distribution and life histories. Neither imputed nor detrended data were used in further analyses.

Environmental data

Environmental regions were defined using a combination of what is understood about the distribution of Chinook salmon populations along their range (Healey, 1991; Beamish *et al.*, 2005; Wells *et al.*, 2007), and the physical oceanography of the northeast Pacific coast (Favorite *et al.*, 1976; Hickey, 1979; Freeland *et al.*, 1984; Ware and McFarlane, 1989; Hobday and Boehlert, 2001; Strub and James, 2002). For instance, Alaska Chinook salmon reside largely in the coastal and central Alaskan waters south to the Subarctic Current (Fig. 1). The southeast Alaska coastal region we defined is similar to the downwelling production domain demonstrated in Ware and McFarlane (1989); however, we extend the southeast coastal range to include coastal waters of Queen Charlotte Island. Importantly, the physical environment of the Queen Charlotte Island region affects the Alaska coast and central waters dramatically (i.e., Skeena River flow drives Haida Eddy formation, Di Lorenzo *et al.*, 2005), and therefore may control much of the production potential in the region. We did not specifically use variables from the Alaska Stream waters, which are less frequently inhabited by southeast Alaska Chinook salmon (Healey, 1991), but the environmental variables we examined from the remainder of the Alaska system capture much of the environmental variation of the entire Alaska system (Beamish and Bouillon, 1993). Puget Sound, Washington, Chinook salmon spend the majority of their first year in waters around Vancouver Island (Duffy *et al.*, 2005). The region is characterized by the equatorward and poleward deflections of the Subarctic Current, to become the California and Alaska Currents. This physical dynamic leads to high intra- and inter-annual environmental variability (Fig. 1; Favorite *et al.*, 1976; Hickey, 1979; Ware and McFarlane, 1989; Sackmann *et al.*, 2004). The region is also centered in the Dilute Domain, characterized by the retention of lower salinity plumes discharged from the Columbia River, Strait of Juan de Fuca, Queen Charlotte Sound and Dixon Entrance (Fig. 1; Favorite *et al.*, 1976). Therefore, to capture intra- and inter-annual variability and the geographic extent of the environmental influences on the transition zone, we used environmental data from the Columbia River to north of Vancouver Island (52°N). Finally, the California coastal region between Cape Mendocino and Cape Blanco, the region inhabited by northern California salmon (Wells *et al.*, 2007), is environmentally distinct from other regions along the California Current coast (Fig. 1, Koslow *et al.*, 2002; Huyer *et al.*, 2005). In total, our analysis includes the coastal and gyre conditions from Yakutat Bay, AK to northern California, encompassing most of the distribution of Chinook salmon in this study (Fig. 1).

The environment of central to southeast Alaskan coastal waters was described using the values for coastal northerly and easterly pseudo wind stresses, scalar winds, wind stress curl, upwelling, coastal sea surface temperature, sea level height, and Skeena River, British Columbia flow (Table 2). The coastal environment was determined offshore to approximately the 500–1000 m isobath (Fig. 1). The gyre waters were characterized by values for Ekman pumping and sea surface temperature (Fig. 1, see fig. 8 in Strub and James, 2002). Finally, the strength of the Aleutian low pressure cell, as represented by the Aleutian low pressure index (ALPI), was included to represent the overall Alaska climatic condition

Table 2. Environmental variables used to characterize the oceanic environment from each region (Fig. 1) were collected from various sources for the years 1976–2002.

Variable description	Identifier	Alaska	Washington[¶¶]	California
Aleutian Low Pressure Index*	ALPI	+	+	
Northern Oscillation Index[†]	NOI		+	+
easterly pseudo-wind stress[‡]	EPseudo	+	+	+
northerly pseudo-wind stress[‡,§]	NPseudo	+	+	+
non-directional wind speed[‡]	Scalar	+	+	+
Ekman pumping[¶]	Ekman	+	+	
sea surface temperature in gyre[‡]	SSTGyre	+	+	
upwelling**	Upwelling	+	+	+
wind stress curl[§,**]	Curl	+	+	+
sea surface temperature along coast[‡]	SSTCoast	+	+	+
sea level height[††]	SLH	+	+	+
Skeena River flow[‡‡]	Skeena	+	+	
Fraser River flow[‡‡]	Fraser		+	
Klamath River flow[§§]	Klamath			+

Variables were averaged within the region, and then into warm (May, June, July, August, September) and cold (November, December, January, February, March) seasons. These seasonal values 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. The variables, identifiers used in Figs 3, 4, 6, 8, 9, 11, 13, and 14, their sources, and associated noteworthy comments are listed. Positive signs indicate which variables were used to model populations from each state.

*Source: Beamish and Bouillon, 1993.

[†] Source: Schwing *et al.*, 2002.

[‡] 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: National Center for Environmental Prediction.

**Source: Pacific Fisheries Environmental Laboratory (Fig. 1).

[††] Source: University of Hawai'i Sea Level Center (Fig. 1).

[‡‡] Source: Canada Hydrological Survey (Stations #08EF001 & #08MF005; Fig. 1).

[§§] Source: United States Geologic Survey (Station #11530500; Fig. 1).

[¶¶] After the first growth year Washington fish were modeled using Alaska and transition zone data separately.

(Beamish and Bouillon, 1993). Data were averaged within each region to obtain a value for each month of each year. These monthly regional averages were averaged into warm (May, June, July, August, and September) and cold (November, December, January, February, and March) seasons. We avoided data from April and October because examination of the data showed that these months, on average, represented the transition of seasonal conditions.

Environmental conditions were also characterized for the coastal ocean and inshore waters around Vancouver Island south to the Columbia River (transition zone; Fig. 1). To represent this region, we used values of northerly and easterly wind stress, scalar wind, upwelling, wind stress curl, coastal sea surface temperature, sea level height, Fraser River, British Columbia flow and the strength of the North Pacific high pressure cell represented by the northern oscillation index (NOI; Schwing *et al.*, 2002). We also characterized the ocean environment between Cape Mendocino and Cape Blanco using the same environmental indices as used for the transition zone but we replaced Fraser River flow data with that of the Klamath River, California (Fig. 1).

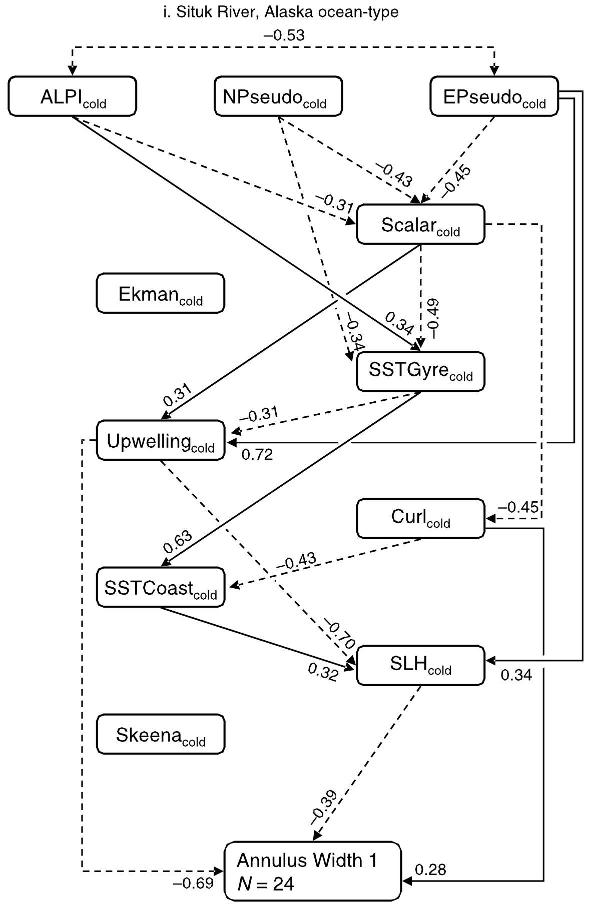
The variables we examined are correlated to each other and cannot be used as independent variables in a multiple regression model of growth. Therefore, we used a path analysis to examine direct and indirect relationships of each variable on growth and to identify variables to use in a model fitted simultaneously with multiple variables (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).

Path analysis and partial least squares regression

We used path analysis to determine the direct, indirect, and total effects of the environmental variables on growth (Wright, 1934). 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. Simply, path analysis is used to determine the collinearity of variables in a system to identify possible mechanistic connections. At the start of a path analysis the variables of interest are arranged in a hierarchical fashion (structure) representing the demonstrated causative relationships between variables (e.g., wind stresses drive, in part, upwelling) and/or accumulated variance (e.g., sea level height represents the accumulated variance of many factors including upwelling and wind stresses). Importantly, Mitchell (1992) and Petraitis *et al.* (1996) advised 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. Once a defendable path structure is defined *a priori*, successive stepwise regressions can be used to test the significance of relationships between the variables and, hence, define the paths. See Wright (1934), Mitchell (1992), Petraitis *et al.* (1996), and Hox and Bechger (1998) for a more complete description of these analyses. Importantly, while path analysis quantifies the degree of colinearity between variables, it does not correct for it.

Path models were built for each age at sea and the effects of each season were analyzed separately. The exogenous variables (variables in the path model with no explicit causes or measurement error term) were ALPI or NOI, and coastal northerly and easterly wind stresses. We also included variables representing the Alaska Gyre, and arranged the path structure for Alaska to reflect variability along the coast (Fig. 3, the environment used by most northern-origin Chinook salmon, Healey, 1991). Coastal scalar wind, Ekman pumping, sea surface temperature of the gyre, coastal upwelling, wind stress curl, coastal sea surface temperature, and Skeena River flow were endogenous variables (intervening variables that are modeled both as independent and dependent). As is proper for path analysis, the structure of the Alaska model was *a priori*, and arranged hierarchically so that each successive endogenous variable included a portion of the variation of the previous variables, as well as unmeasured effects. Specifically, coastal scalar winds mediate variation in wind stresses and ALPI. Ekman pumping is driven by the wind strength and direction. Sea surface temperature in the gyre varies with the amount of Ekman pumping. Coastal upwelling covaries with coastal winds and gyre strength. Sea surface temperature along the coast is dependent, in part, on the winds, upwelling, and curl. Sea level height represents the concomitant effect of the variation in all the previous variables, as well as current speed. Skeena River flow represents the largest geographic scale of variation by covarying with both atmospheric and terrestrial conditions. Finally, annulus width, if it does relate to the environment, is dependent on the entire structure of the model. Similar path models were built for the other regions examined. However, gyre data were dropped and river flow data were replaced with more regional flow data.

Figure 3. Path analysis of the cold period environmental variables and the annulus width in the first growth year for Situk River, Alaska ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). Results demonstrate that cold conditions are related to first-year annulus width. For each season, 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 regressions with a $P < 0.05$ were considered significant. A $P < 0.05$ was also used to evaluate the significance of correlations between exogenous variables. Solid and dashed arrows indicate positive and negative path coefficients respectively.


i. Situk River, Alaska ocean-type

Successive stepwise regressions on standardized data (mean = 0, standard deviation = 1) for each endogenous variable starting with annulus width, as the first dependent variable, were used to define the paths between variables. An independent variable was retained in each regression step if it was significant at $\alpha = 0.15$, yet only regressions that were significant at $\alpha = 0.05$ were considered significant. Once the paths were determined, the path model was evaluated relative to the covariance structure of the observed data by use of the chi-square test of a structural equation modeler (SAS Institute., 1989; PROC CALIS). After confirmation that the path model developed was not significantly different from the structure of the observed data ($P > 0.05$; Mitchell, 1992; Petraitis *et al.*, 1996), the direct, indirect, and total effects of each variable on annulus width were calculated. The total effect of each variable on annulus width was determined by multiplying standardized coefficients along each direct path and summing the cumulative correlations across paths. Univariate statistics and pairwise comparisons demonstrated that all assumptions of linearity were met across the years we examined.

We used partial least squares regressions to fit growth data with environmental variables (Abdi, 2003). Environmental variables that were shown to have direct or indirect relationships to growth were combined across seasons and were included in the independent data set. This multivariate approach can result in a testable model because the methodology accounts for collinearity. 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 analogous 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 data sets are decomposed simultaneously such that the latent variables of the independent data matrix are uncorrelated to one another, but are correlated to the dependent data set. Further, each latent variable determined is progressively less correlated with the dependent variable. We used the non-linear iterative partial least squares algorithm to determine the latent variables (Geladi and Kowalski, 1986). Separate partial least squares models were developed for each age spent at sea.

Similar to principal component loadings, the weights for each environmental variable loaded in the first latent variable can be used to determine the amount of variation accounted for by a particular variable within the environmental data set. Latent variable weights are determined directly from the unstructured data and not from an analysis dependent on an *a prior*, determined path structure therefore, they can yield support for or against the calculated effects from the path models we develop.

RESULTS

Cross-correlation analysis of growth rates indicated that none of the five different Chinook salmon groups were correlated with one another, suggesting that either growth was relatively randomly determined or that the factors affecting growth were different among the groups. This finding is supported by Wells *et al.* (2006). All path models were concordant to the observed data ($P > 0.05$). Also, all partial least square regressions resulted in randomly distributed residuals indicating that the linear fits were appropriate. Table 3 shows the global results of the partial least squares and path analyses, wherein sign relationships between all variables examined and growth of all populations and ages are presented. Table 3, however, should be viewed in the context of the associated figures for proper interpretation of correlation strengths.

Ocean-type Alaska Chinook salmon

Situk River ocean-type Chinook salmon growth related to environmental data during the four analyzed periods. Figure 3 is an example of the path structure we used to examine growth of Chinook salmon from the Situk River. During the first year of growth, winter coastal conditions related directly to growth ($P = 0.024$, $N = 24$), i.e., lower sea level height, reduced upwelling, and increased curl enhanced growth (Figs 3 and 4a). During the second growth year, both the cold ($P = 0.018$, $N = 24$) and warm ($P = 0.013$, $N = 24$) seasons related to growth (Fig. 4b), i.e., specifically, during the cold season, reduced upwelling, reduced wind stress curl, and

Table 3. Signs of the weights from partial least squares regressions (black is negative and grey is positive) for each environmental variable used to model 1, 2, 3, and 4 ocean-winter growth of female Chinook salmon (*Oncorhynchus tshawytscha*) collected from Alaska, Washington, and California.

	Alaska								Washington							California			
	Situk Ocean				Taku Stream				Skagit Ocean			Skagit Stream				Smith Ocean			
Variable	1	2	3	4	1	2	3	4	1	3	4*	1	2	3	3*	1	2	3	4
ALPI$_{\mathrm{cold}}$	▒	▒	▒ ●		▒	▒									■ ●				
NOI$_{\mathrm{cold}}$									■ ●	■ ±		■	▒	▒					■
EPseudo$_{\mathrm{cold}}$	■	▒			■ ●				■	■		■ ●	■	■	■ ±				
NPseudo$_{\mathrm{cold}}$	■ ±	▒ ±			■ ●	■			■	■ ●		▒	±	▒ ●	■				■
Scalar$_{\mathrm{cold}}$	■	■ ±			▒ ●	■				▒			■ ●		▒ ●±				▒ ●±
Ekman$_{\mathrm{cold}}$		▒			▒ ●										▒				
SSTGyre$_{\mathrm{cold}}$	▒	▒ ●				▒									▒ ●				
Upwelling$_{\mathrm{cold}}$	■ ●	■ ●			■ ●±				■ ±	■		▒	■	▒ ±	■ ±				■ ●
Curl$_{\mathrm{cold}}$	▒ ●	■ ●		▒ ●		■			■	■		▒ ●	■ ●	■ ●	■ ●				
SSTCoast$_{\mathrm{cold}}$	▒ ±					▒ ●			▒ ●	▒ ±									
SLH$_{\mathrm{cold}}$	▒ ●±								■ ●						■ ●				
Skeena$_{\mathrm{cold}}$			■ ●	▒ ●		■ ●													
Fraser$_{\mathrm{cold}}$									▒ ●±	■ ●				■ ●±					
Klamath$_{\mathrm{cold}}$																			
ALPI$_{\mathrm{warm}}$			▒				▒ ●	▒ ●			■ ±				■ ±				
NOI$_{\mathrm{warm}}$												■ ●				▒		▒	
EPseudo$_{\mathrm{warm}}$			■ ●				■ ●	■ ●±							■ ●	±		▒	■ ●±
NPseudo$_{\mathrm{warm}}$		▒	■ ●±		■ ●	■ ●	■ ●	■			▒	■			▒ ±	■	▒	▒	■ ●
Scalar$_{\mathrm{warm}}$		■ ●					▒ ●				■ ±				▒	■		■	■ ●
Ekman$_{\mathrm{warm}}$			▒ ±					▒ ●			■				■				
SSTGyre$_{\mathrm{warm}}$							▒	■			■				■				
Upwelling$_{\mathrm{warm}}$											▒	▒			▒	■ ●	▒ ●	▒	■ ●±
Curl$_{\mathrm{warm}}$		■ ●														■		▒	
SSTCoast$_{\mathrm{warm}}$							▒ ●	■ ●				■ ●				■ ●		■	
SLH$_{\mathrm{warm}}$											■ ●				■ ●			■ ●	
Skeena$_{\mathrm{warm}}$			▒ ●			■ ●	■ ●												
Fraser$_{\mathrm{warm}}$																			
Klamath$_{\mathrm{warm}}$																			

A dot (•) indicates a variable that had a direct effect in path analysis and positive⁄negative (±) indicates that the weight of a variable was a different sign from the effect calculated in path analysis. Asterisks indicate Washington fish modeled with Alaska data. Figures 4, 6, 9, 11, and 14 show these results in greater detail.

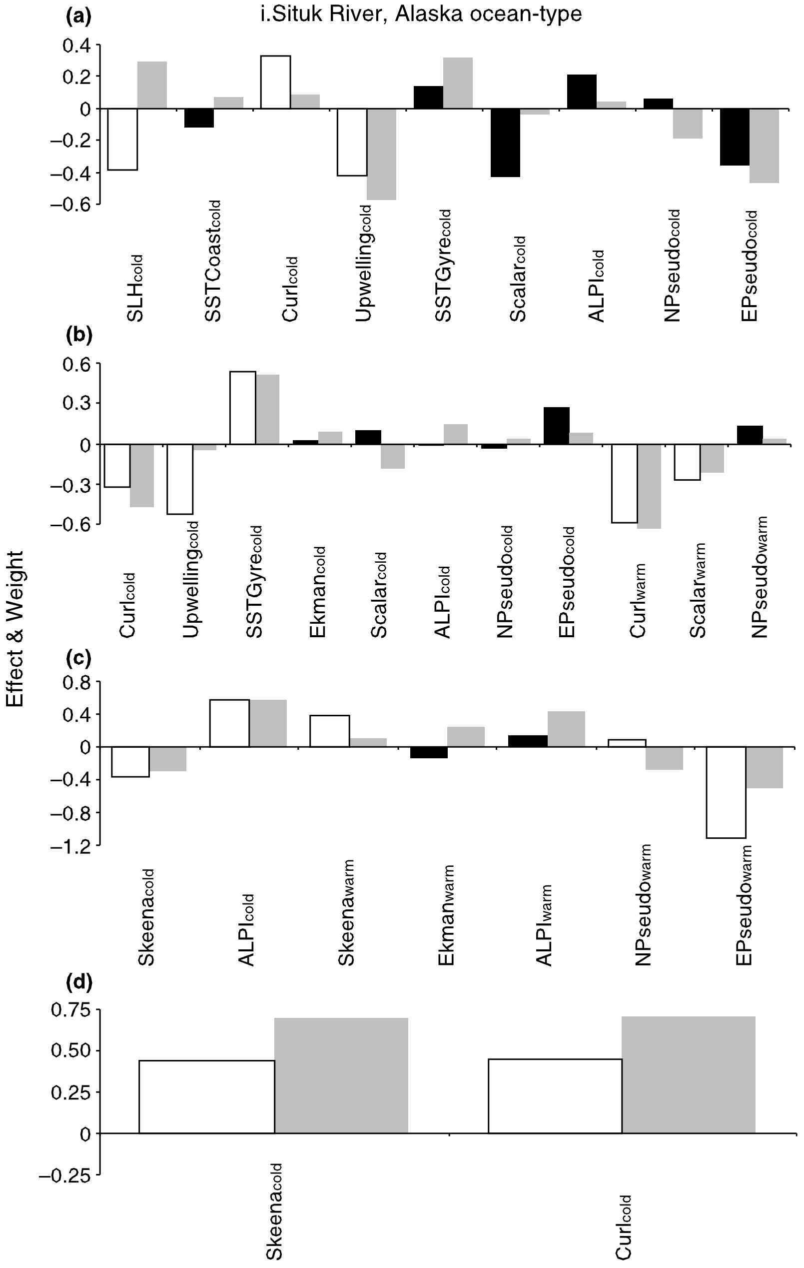
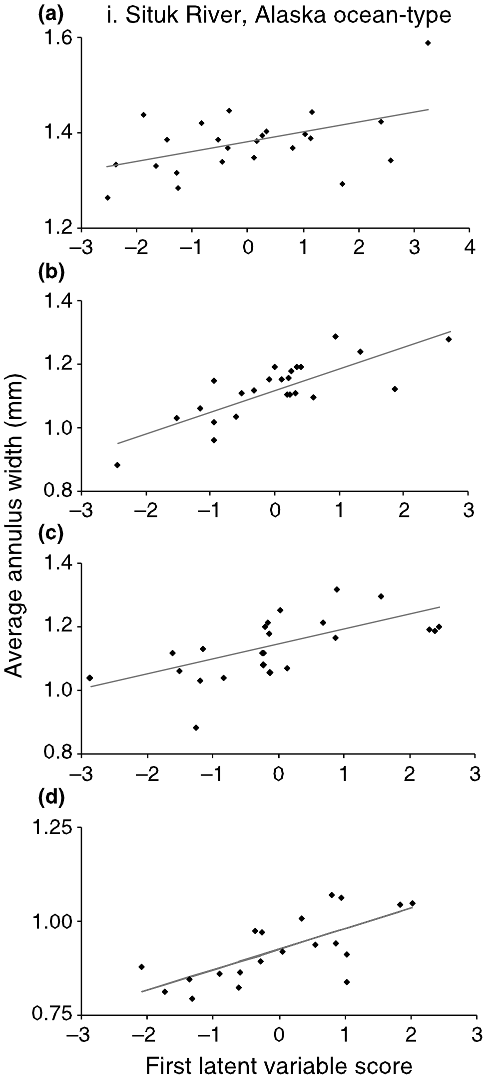


Figure 4. Results from the cold and warm season path analyses for the (a) first, (b) second, (c) third, and (d) fourth years at sea of Situk River, Alaska ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). The total effects of each variable on annulus width were determined by multiplying standardized coefficients along each direct path and summing the cumulative correlations across all paths. The total effects are shown as white and black bars. A white bar indicates that the variable had a direct effect and a black bar indicates that it had only indirect effects. 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 grey bars.

increased sea surface temperature in the Alaska Gyre increased growth (Fig. 4b). During the warm season, increased coastal wind stress curl and mixing retarded growth. During the third year of growth, Skeena River flow negatively related to growth in the cold season (P = 0.0039, N = 23) and positively in the warm season (P = 0.0062, N = 23, Fig. 4c). The strength of the Aleutian low pressure cell was positively related to growth. However, easterly wind stress along the coast was strongly negatively related to growth. During the fourth growth season, the fit of growth to cold season environmental variables was significant (P = 0.023, N = 20), but only two variables, Skeena River flow and coastal wind stress curl, drove the positive relationship to growth (Fig. 4d).

The partial least squares regression for Situk River fish during their first year at sea was significant but the fit was relatively poor (R^2 = 0.24, P = 0.015, N = 24, Fig. 5a). Environmental variable weights on the first latent variable were typically not similar to the effects calculated from the path analysis indicating that the model represented by the path analysis was somewhat insufficient (Fig. 4a). During the second growth year at sea, the combination of variables across seasons loaded into a single latent variable fit the growth data very well (R^2 = 0.47, *P* = 0.0002, *N* = 24, Fig. 5b), and the pattern of weights and effects between environmental variables was similar between techniques (Fig. 4b). Similarly, growth during the third (R^2 = 0.40, *P* = 0.0011, *N* = 23, Fig. 5c) and fourth growth years (R^2 = 0.51, *P* = 0.0004, *N* = 20, Fig. 5d) fit by partial least squares regression and the factor weights across the variables were similar to the pattern of effects calculated by the path analyses (Fig. 4c,d).

Figure 5. Fits of the average annulus widths for Situk River, Alaska ocean-type Chinook salmon (*Oncorhynchus tshawytscha*) in the (a) first, (b) second, (c) third, and (d) fourth years at sea to the first latent variable score calculated using partial least squares regression.



Stream-type Alaska Chinook salmon

The stream-type Chinook salmon from the Taku River were fit significantly by the environmental data from along the Alaska coast and gyre waters. The structure of the model was similar to that shown for the ocean-type fish of the Situk River (Fig. 3), i.e., the same variables were used and were arranged in the same hierarchical fashion from the standpoint of environmental variability along the coast. However, the factors that were determined to be significant differed between populations. During the first year at sea, growth was related to both the cold (*P* = 0.0015, *N* = 25) and warm (*P* = 0.0040, *N* = 25, Fig. 6a) seasons. During the cold season coastal upwelling, Ekman pumping, and coastal scalar winds were directly, positively related to growth, while coastal wind stress was directly, negatively related to growth (Fig. 6a). Warm-season coastal northerly wind stress was directly, negatively related to growth. During the second year of growth, both the cold (*P* = 0.0001, *N* = 25, Fig. 6b) and warm (*P* = 0.0300, *N* = 25) seasons were related to growth. During the second cold season, Skeena River flow was directly, negatively related to growth, while coastal sea surface temperature was directly, positively related to growth, but during the warm season Skeena River flow and northerly wind stress were directly, negatively related to growth (Fig. 6b). During the third year at sea, growth was related to environmental conditions during the warm season (*P* = 0.0033, *N* = 24, Fig. 6c). Specifically, Skeena River flow was directly, negatively related to growth and coastal sea surface temperature, coastal scalar wind, and the ALPI were directly, positively related to growth. During the last year at sea, growth was related to the environment during the warm season (*P* = 0.0115, *N* = 22, Fig. 6d), i.e., coastal sea surface temperature was negatively related directly to growth, and Ekman pumping, the ALPI, and coastal easterly wind stress were positively related to growth.

Findings from the partial least squares regression approach demonstrate that growth during the first year at sea fit significantly with the first latent variable as an independent variable (R^2 = 0.49, *P* = 0.0001, *N* = 25, Fig. 7a) and, except the sign for coastal upwelling during the cold season, the pattern of

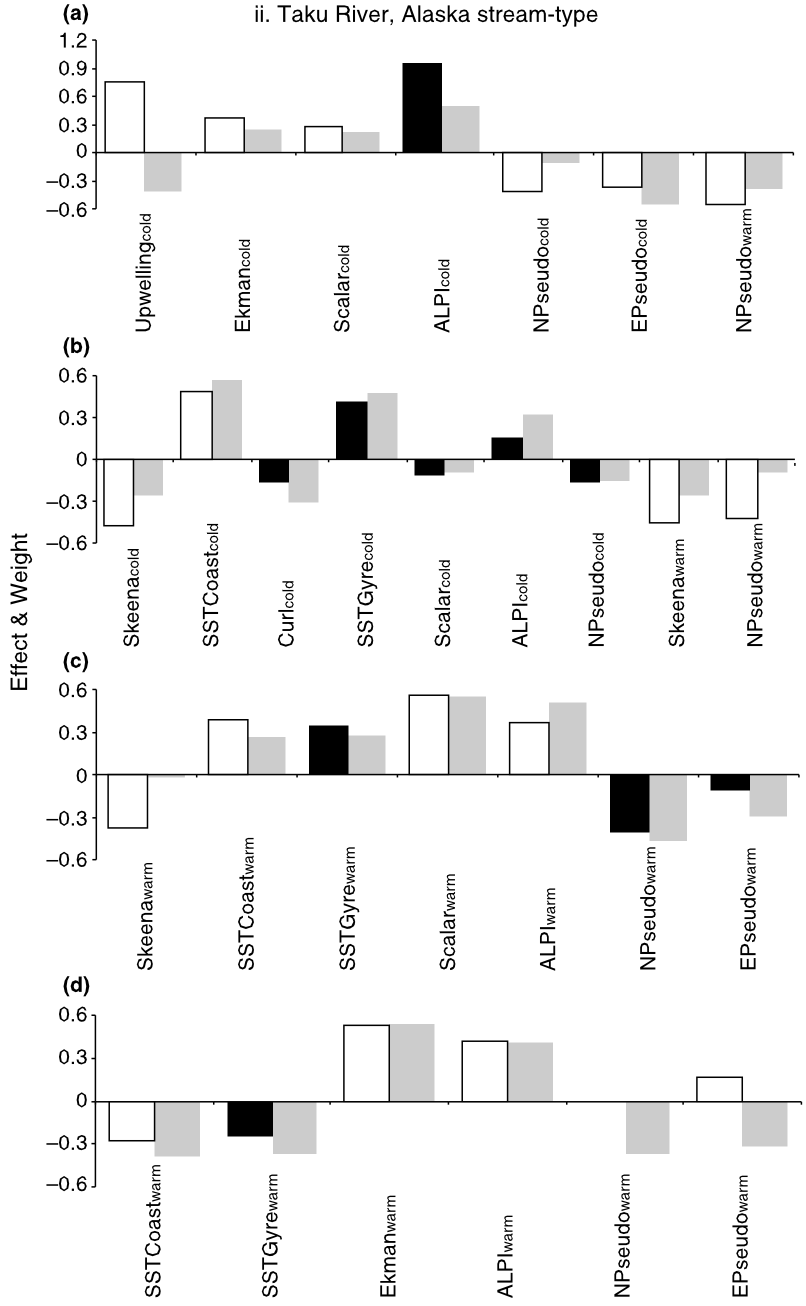


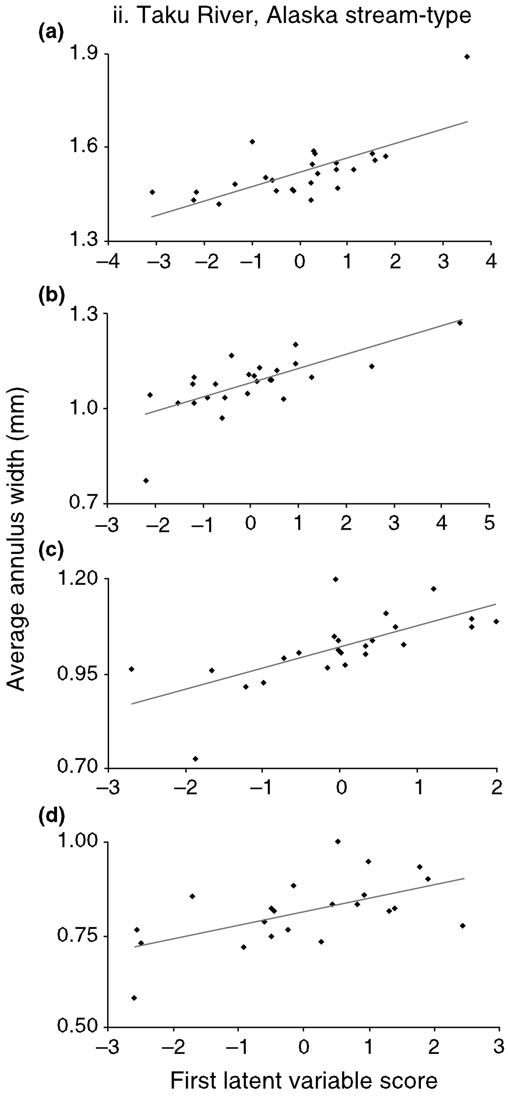
Figure 6. Calculated effects from the cold and warm season path analyses and weights from the partial least squares regressions for the (a) first, (b) second, (c) third, and (d) fourth years at sea of Taku River, Alaska stream-type Chinook salmon (*Oncorhynchus tshawytscha*). The arrangement of variables in the path analyses is similar to that in Fig. 3 and the figure description similar to that for Fig. 4.

weights was similar to the pattern of environmental effects determined from the path analysis (Fig. 6a). The second year of growth was also fit significantly by the partial least squares regressive approach (R^2 = 0.51, P = 0.0001, N = 25, Fig. 7b), and the pattern of weights across all variables loaded into the first latent variable was similar to the pattern of effects calculated from the path analysis (Fig. 6b). Likewise, growth during the third year at sea was fit significantly to the first latent variable (R^2 = 0.47, P = 0.0002, N = 24, Fig. 7c), and growth during the fourth year at sea was modeled significantly by the first latent variable (R^2 = 0.33, P = 0.0052, N = 21, Fig. 7d).

Ocean-type Washington Chinook salmon

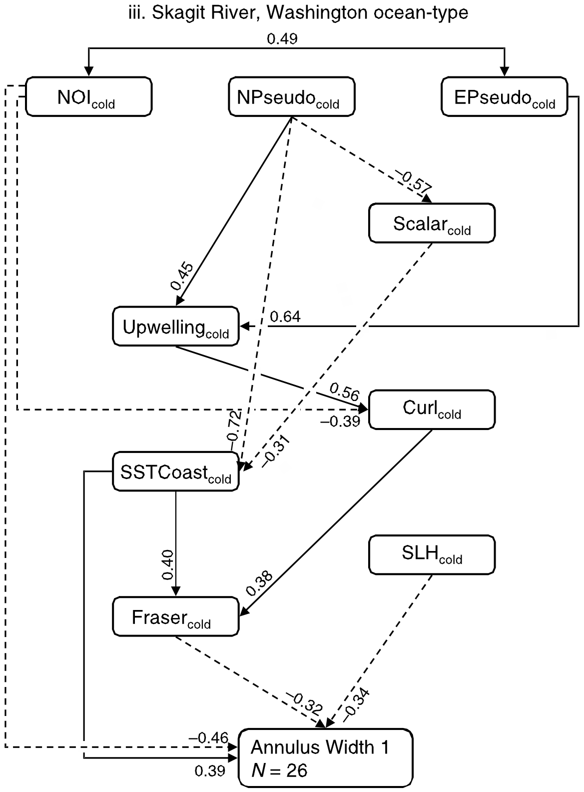
Chinook salmon with ocean-type behavior from the Skagit River fit the environmental data from the

Figure 7. Fits of the average annulus widths for Taku River, Alaska stream-type Chinook salmon (*Oncorhynchus tshawytscha*) in the (a) first, (b) second, (c) third, and (d) fourth years at sea to the first latent variable score calculated using partial least squares regression.



transition zone well during the first and third year at sea. During the first growth year, the variables from the cold season related to growth ($P = 0.0093$, $N = 26$, Fig. 8); Fraser River flow, sea level height, and the NOI were negatively related to growth, and coastal sea surface temperature was positively related to growth (Fig. 9a). Growth during the third year at sea related to conditions during the cold season ($P = 0.0048$, $N = 25$, Fig. 9b). The second and fourth growth years were not fit significantly with the environmental data from the transition zone.

Figure 8. Path analysis of the environmental variables and the annulus width in the first growth year for Skagit River, Washington ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). Results demonstrate that cold conditions are related to first-year annulus width. Description of results is similar to Fig. 3.



Generally, growth of ocean-type Skagit River fish did not fit as well using environmental data from Alaska ($P > 0.05$). However, during the fourth growth year at sea, when fish may have moved north of the transition zone, environmental data from Alaska fit the growth data well. Fish growth was related to warm season Alaska Current environmental variables ($P = 0.0232$, $N = 23$, Fig. 9c). Specifically, sea level height, sea surface temperature in the gyre, and Ekman pumping were negatively related to growth and upwelling and northerly wind stress were positively related to growth. Interestingly, these conditions typically result from a weaker Alaska Current.

We also modeled growth with the partial least squares regression approach using environmental data from the transition zone. The partial least squares regression for the growth in the first year at sea fit significantly ($R^2 = 0.39$, $P = 0.0004$, $N = 26$, Fig. 10a). Also, the pattern of variable weights on the

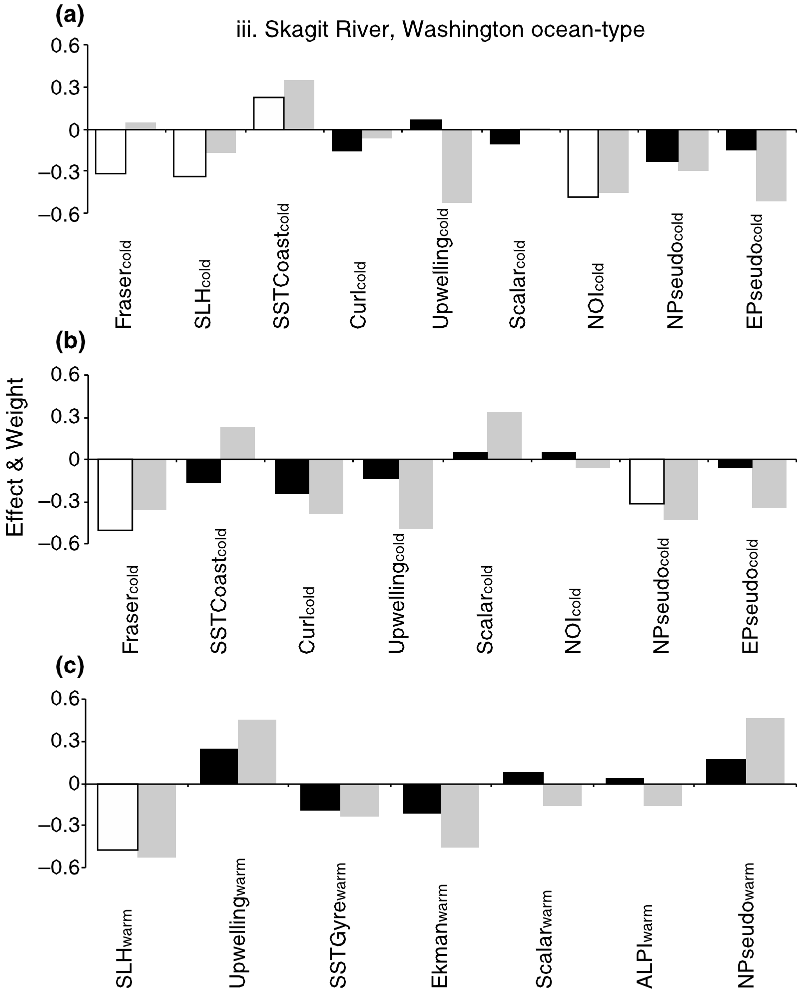


Figure 9. Calculated effects from the cold and warm season path analyses and weights from the partial least squares regressions for the (a) first and (b) third years at sea of Skagit River, Washington ocean-type Chinook salmon (*Oncorhynchus tshawytscha*) using environmental data from the transition zone and (c) the fourth year of growth modeled with Alaska data. Otherwise, the figure description is similar to that for Fig. 4.

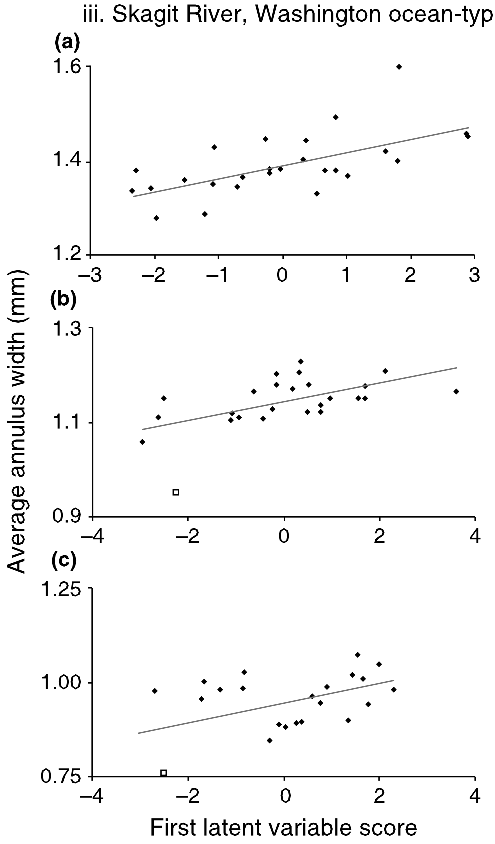
first latent variable was similar to that for the effects calculated with the path analysis, except Fraser River flow was weighted slightly positively and upwelling during the cold season was weighted negatively (Fig. 9a). Growth in the third year at sea was fit significantly using the partial least squares approach (R^2 = 0.32, P = 0.0032, N = 25, Fig. 10b). However, growth data in 1995, when growth was very low, was an outlier.

We fit the fourth year of growth at sea to environmental data from Alaska and the fit was poor (R^2 = 0.24, P = 0.0180, N = 23), and driven by the exceptionally low growth in 1983. That 1983 was a poor growth year is counter to the interpretation from the path analysis which suggested that a weaker Alaska Current promotes growth. The weak relationship we detected suggests that these analyses are not informative about what environmental conditions affect the fourth year of growth at sea.

Stream-type Washington Chinook salmon

Growth of Chinook salmon with stream-type behavior from the Skagit River was significantly related to the environment in the transition zone for the three years of growth data available (Table 1). The structure of the path models was similar to that used for the ocean-type Skagit River fish (Fig. 8); however the variables that were determined to be significant were different. During the first year at sea, the environment during both cold (P = 0.0001, N = 26) and warm (P = 0.0200, N = 26, Fig. 11a) seasons fit growth data significantly. Specifically, during the cold season, curl had a direct positive relationship and easterly wind stress had a direct negative effect. Coastal sea surface temperature and NOI during the warm season were directly, negatively related to growth (Fig. 11a). Growth during the second year at sea was fit significantly with data from the cold season (P = 0.0001,

Figure 10. Fits of the average annulus widths for Skagit River, Washington ocean-type Chinook salmon (*Oncorhynchus tshawytscha*) in the (a) first and (b) third years at sea related to the first latent variable score calculated using partial least squares regression and environmental data from the transition zone, and (c) the average annulus widths for the fourth year of growth at sea related to the first latent variable score calculated using partial least squares regression and environmental data from the Alaska data. Open square in (b) represents 1995 and open square in (c) represents 1983.



N = 25, Fig. 11b), i.e., curl and scalar winds were directly negatively related to growth (Fig. 11b). Finally, during the third year at sea, growth was described by environmental data from the cold season (P = 0.015, N = 23, Fig. 11c), i.e., directly, Fraser River flow and northerly wind stress were positively related to growth while curl was negatively related to growth.

During the third year at sea, the environment of the Alaska Current and gyre waters also fit the growth data well (P = 0.0037, N = 23, Fig. 11d). Specifically, both cold and warm season variables were significantly related to growth. Generally, conditions indicative of a weaker current during the cold and warm seasons (e.g., decreased sea level height, ALPI, winds and increased coastal upwelling) promoted growth. Although examination of the individual variables suggests that this is a simplified interpretation (e.g., Ekman pumping was positively related to growth in the cold season).

Again using environmental data from the transition zone as the independent data set, we modeled the growth of stream-type Skagit River fish using partial least squares regression and produced significant models of growth for the first year at sea (R^2 = 0.53, P = 0.0001, N = 26, Fig. 12a). The weights of the variables on the first latent variable had a similar pattern to calculated effects from the path analysis (Fig. 11a). Similarly, growth during the second (R^2 = 0.51, P = 0.0001, N = 24, Fig. 12b) and third (R^2 = 0.34, P = 0.0035, N = 23, Fig. 12c) years at sea were modeled significantly using the first latent variable as the independent variable.

We also modeled stream-type Skagit River fish growth during their third year at sea using Alaskan environmental conditions. The resulting fit was excellent (R^2 = 0.64, P = 0.0001, N = 23, Fig. 12d), and the pattern of variable weights on the first latent variable was somewhat similar to those obtained by path analysis except that scalar winds, upwelling, and easterly wind stress during the cold season all had small indirect effects calculated from the path model.

Ocean-type California Chinook salmon

Smith River Chinook salmon growth was fit significantly with the environmental data collected from northern California waters (Fig. 1). Growth during the first year at sea was directly and negatively related to coastal sea surface temperature and upwelling during the warm season (P = 0.023, N = 24, Figs 13 and 14a). During the second growth year at sea, upwelling and northerly wind stress during the warm season were positively related to growth (P = 0.0136, N = 24, Fig. 14b). During the third year at sea, the sea level height during the warm season had a direct negative relationship to growth (P = 0.0250, N = 25, Fig. 14c). Growth during the fourth year at sea was fit well by both cold and warm season data (P = 0.0186, P = 0.0001, N = 20, respectively). During the cold season, upwelling and scalar wind were negatively related to growth (Fig. 14d). During the warm season scalar wind and northerly wind stress were directly negatively related to growth, and upwelling and easterly wind stress were directly positively related to growth (Fig. 14d).

Using the partial least squares regressive approach, growth during the first year at sea was fit significantly

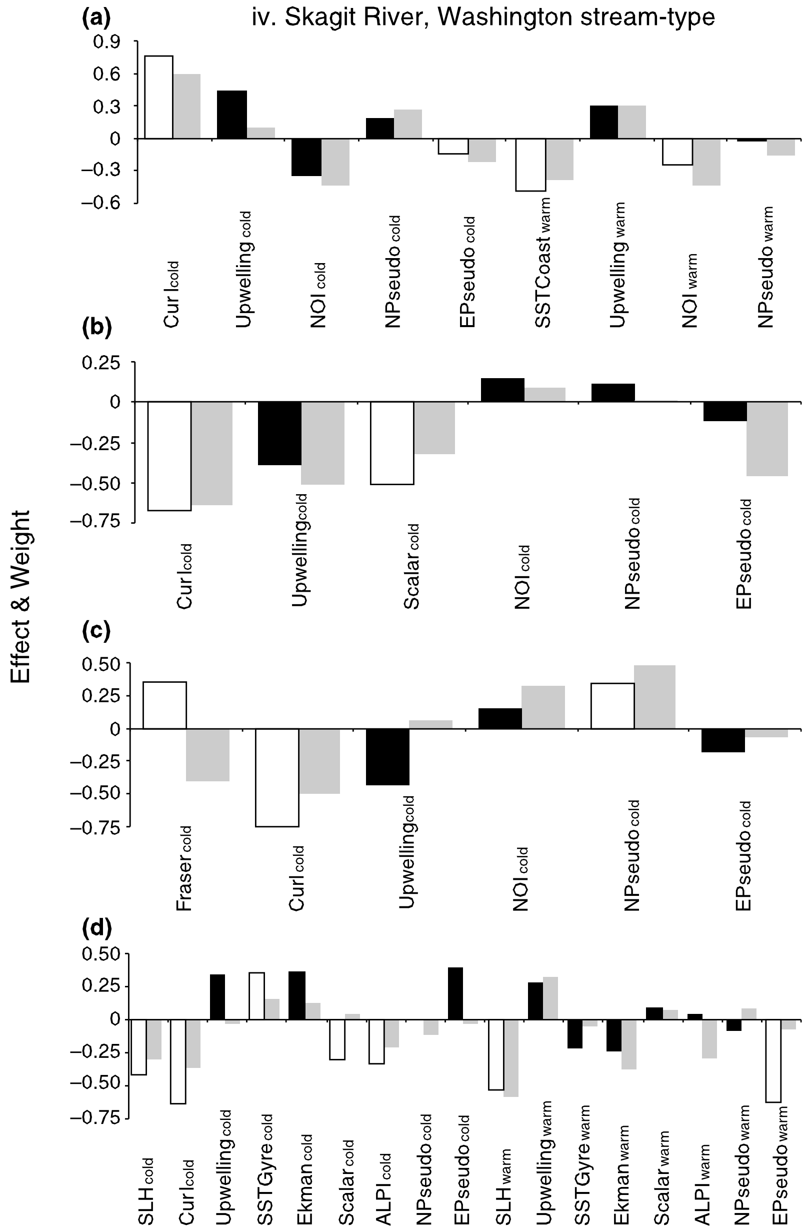


Figure 11. Calculated effects from the cold and warm season path analyses and weights from the partial least squares regressions for the (a) first, (b) second, and (c) third years at sea of Skagit River, Washington stream-type Chinook salmon (*Oncorhynchus tshawytscha*) modeled with environmental data from the transition zone and (d) the third year at sea modeled with Alaska data. The arrangement of variables in the path analysis is similar to that in Fig. 8 and the figure description is similar to that for Fig. 4.

(R^2 = 0.35, P = 0.0023, N = 24, Fig. 15a), and the variable weights had a similar pattern to the pattern of effects described by the path analysis (Fig. 14a). Growth during the second year at sea was fit significantly by the first latent variable (R^2 = 0.24, P = 0.0142, N = 24, Fig. 15b). However, when the growth data from 2001, an exceptional growth year, was removed the relationship was insignificant. Like the growth model for the second growth year, the third growth year was also poorly fit by the first latent variable (R^2 = 0.23, P = 0.0197, N = 23, Fig. 15c). Data for the fourth growth season fit the first latent variable well (R^2 = 0.48, P = 0.0007, N = 20, Fig. 15d).

DISCUSSION

We used a combined approach of first identifying environmental factors correlated to growth by path analysis, then describing the strength of the relationships by fitting partial least squares regressions. Path analysis was used to detect the correlations of environmental variables indirectly and directly to the growth rates. Path analyses showed that the *a priori*, determined structure and the paths between environmental variables and the growth rates were concordant with the structure of the observed data. For the most part, the structure of our path models were further

Figure 12. Fits of the average annulus widths for Skagit River, Washington stream-type Chinook salmon (*Oncorhynchus tshawytscha*) in the (a) first, (b) second, and (c) third years at sea related to the to the first latent variable score calculated using partial least squares regression and environmental data from the transition zone and (d) the average annulus widths for the third year of growth at sea related to the first latent variable score calculated using partial least squares regression and environmental data from the Alaska data.

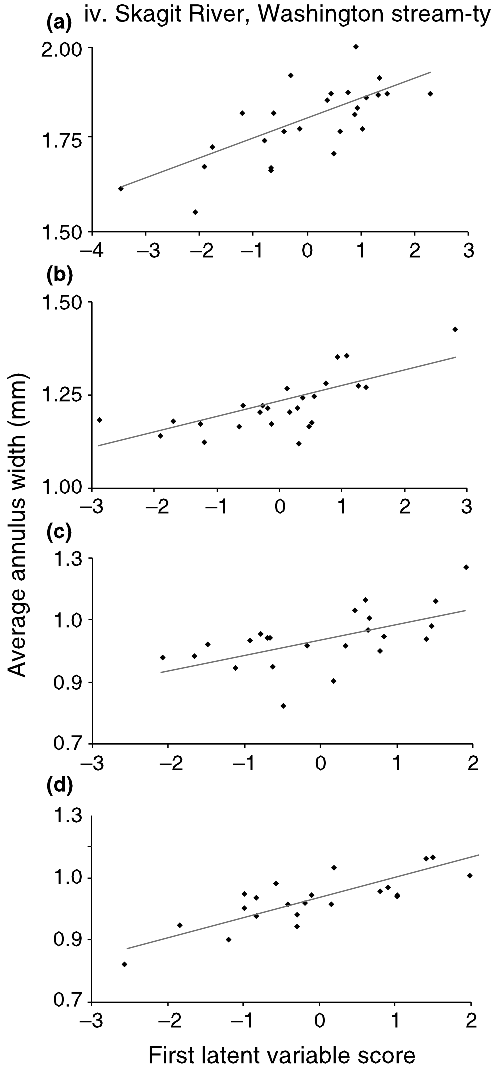
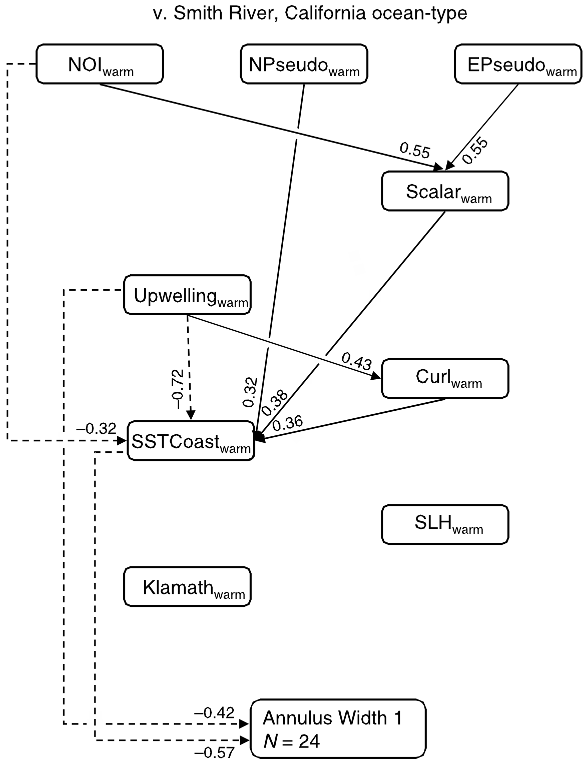


Figure 13. Path analysis of the environmental variables and the annulus width in the first growth year for Smith River, California ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). Results demonstrate that warm conditions are related to first-year annulus width. Description of results is similar to Fig. 3.



validated by the unstructured loadings of the environmental variables on the first latent variable of the partial least squares approach.

We are careful not to imply a causation model with any of our detected relationships (Wright, 1934; Petraitis *et al.*, 1996). 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 distribution of fish in each year analyzed. Rather, we built models based on correlations that represented average multivariate relationships between environmental variables in the area occupied on average by the fish. However, biophysical mechanisms have been demonstrated between the environmental variables we used and productivity of the system, survival and distribution of prey species as well as survival and early growth of Chinook salmon.

The environmental variables were selected for the analyses because they are correlated with production and biological dynamics in the ocean environment (Parsons *et al.*, 1984; Mann and Lazier, 1991; Miller, 2004). Further, these variables are correlated with survival and early growth of Pacific salmon (Hobday and Boehlert, 2001; Koslow *et al.*, 2002; Logerwell *et al.*, 2003). The NOI and ALPI represent large-scale forces driving, in part, the structure of winds over the Gulf of Alaska and along the California coast.

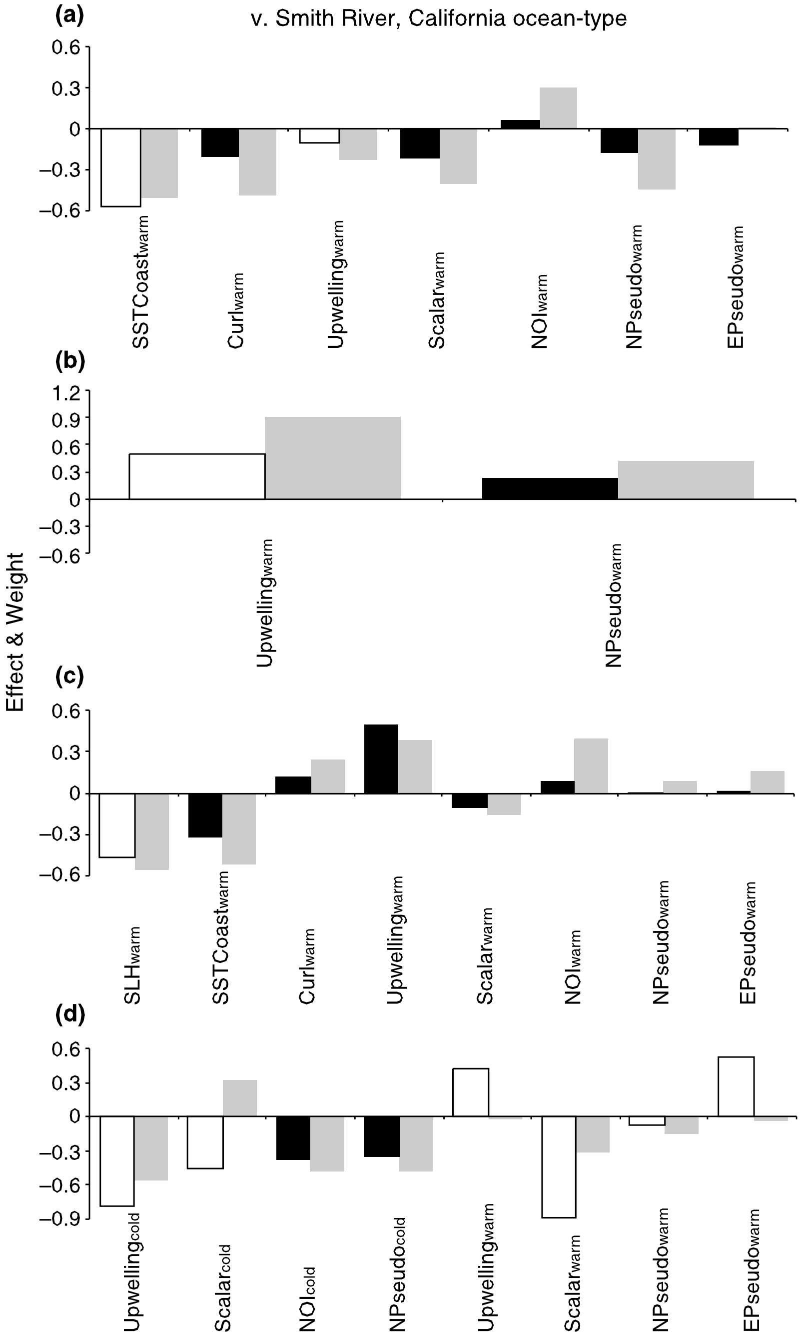
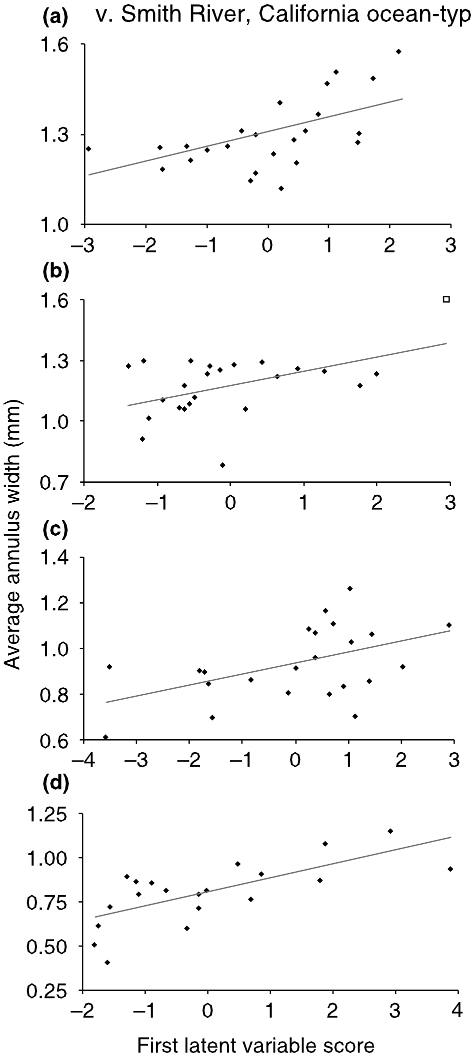


Figure 14. Calculated effects from the cold and warm season path analyses and weights from the partial least squares regressions for the (a) first, (b) second, (c) third, and (d) fourth years at sea of Smith River, California ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). Otherwise, the figure description is similar to that for Fig. 4.

Northerly and easterly pseudo-wind stresses provide the force driving upwelling and downwelling along the Pacific coast. Scalar wind is a measure of the non-directional wind speed and indexes the degree of turbulence in surface waters. Ekman pumping is a measure of wind divergence over open water which drives open-ocean upwelling. In open oceans and along the coast, upwelling provides nutrients to surface waters. Wind stress curl is a measure of the wind shear off the coast, and along the Alaska Current, strong wind stress curl (relatively reduced wind speeds offshore) indicates accelerating onshore flow locally, and weaker wind stress curl indicates that the onshore flow is decelerating. However, along the California Current, increased wind stress curl results in increased retention of water moving off shore. Wind-driven upwelling magnitude and frequency covary with sea surface temperature regionally. Sea level height varies

Figure 15. Fits of the average annulus widths for Smith River, California ocean-type Chinook salmon (*Oncorhynchus tshawytscha*) in the (a) first, (b) second (open square represents 2001), (c) third, and (d) fourth years at sea to the first latent variable score calculated using partial least squares regression.



at a large spatial and temporal scale and relates to current speed and all of the previous variables discussed. Finally, river flow represents the degree of locally imported freshwater and nutrients and is correlated with the terrestrial response to large-scale variability patterns. Skeena River flow, specifically, is positively correlated to the formation of Haida Eddies which can transport nutrients along the coastal and central waters of the Gulf of Alaska (Whitney and Robert, 2002; Di Lorenzo *et al.*, 2005). Generally, sea level height and river flow are confounded representations of overall productivity.

The occurrence of relatively low coefficients of determination in our models indicates that other sources of variation in growth were not accounted for by these environmental variables. We envision two primary reasons for the substantial variation we noted. First, we modeled scale growth as opposed to fish growth. While scale growth is linearly related to fish length (Bilton, 1985), there is variation introduced by scale shape, size, microstructure, and interpretation. Secondly, process error is present in our models because we quantified the relationship between the environment and growth as though it were direct. More likely, relationships act indirectly through complex ecosystem interactions (e.g., prey dynamics). 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 believe we have conservatively measured some of the underlying effects of various oceanographic features and multivariate conditions on growth.

The overall conclusion of this study is that the growth rate of Chinook salmon relates to the environment, and the relationship is region- and life-history specific. We could have anticipated this from our cross-correlation analysis and the results of Wells *et al.* (2006), i.e., growth in none of the sampled populations was correlated with that in any other, but did relate to their respective regional environments.

Alaska fish were fit best by the environmental data. Specifically, both regional- and large-scale factors, as well as Alaska coastal and gyre factors fit the data well. For the most part, Alaska Chinook salmon with both ocean- and stream-type behaviors remain in the Gulf of Alaska, not moving south into the California Current (Healey, 1991). They may use not only the Alaska coastal system but also a fraction of the populations that apparently reside in the Alaska Gyre and Alaska Stream waters (Healey, 1991; Beamish *et al.*, 2005). Therefore, it is understandable that their growth fitted well to the environmental data from the Alaska Gyre and coast.

Fish from California were fit by regional-scale factors; however, the fits were not very good. Poor fits may have resulted from combining the growth season of California fish into one season as opposed to separating the growth season into spring and summer. In fact, Wells *et al.* (2006, 2007) demonstrated that growth rate, maturation, and length at return were more strongly tied to spring conditions than summer. Along the California Current, upwelling is strongest in the spring and influences the potential productivity along the coast for the remainder of the growth season. Ultimately, our results indicate that to model growth of California Current Chinook salmon, a shorter time frame should be used relative to that required for fish from Alaska where the productivity during the growth season is largely dependent on winter conditions. However, the results of path analyses on growth for the first 3 yr at sea for California fish show a similar pattern of total effects calculated from Wells *et al.* (2007), which indicates conservation of the main effects.

Puget Sound, Washington, Chinook salmon originate from a region dominated by substantial intra- and inter-annual variability (Favorite *et al.*, 1976). Likely as a result of the dynamic physical nature of the region, growth of some age groups was not modeled well by the environmental data. However, of those models that were significant, it was evident that growth of Puget Sound fish with ocean-type behavior was negatively related to a stronger California Current. Specifically, ocean-type Puget Sound fish were negatively related to the NOI and upwelling. Possibly, growth is reduced because in years when the California Current is strong the northward winter extension of the Oregon and Washington current has less effect along the coast of Vancouver Island, so that less of its nutrient-rich waters are advected into the region (Favorite *et al.*, 1976; Freeland *et al.*, 1984). Interestingly, ocean-type Puget Sound fish were not modeled significantly better by Alaska environmental data, suggesting that the relationship we detected with environmental data from the transition zone was not caused solely by covariation between regions. First-year stream-type Puget Sound fish were also negatively related to the NOI, positively related to upwelling and northern wind stress and negatively to sea surface temperature, suggesting that growth of stream-type Puget Sound fish was not as adverse to a strong California Current strength as it was for ocean-type fish. During the second and third years at sea, the relationship of growth to NOI, upwelling and curl was entirely opposite that detected for the first year at sea. Such a finding suggests that a portion of the stream-type Puget Sound fish may have moved into Alaska waters (Healey, 1991) where similar environmental factors are out of phase with the California Current system (see Wells *et al.*, 2006; Fig. 5). Somewhat contrary to this argument, few Puget Sound fish have been recovered in Southeast Alaska fisheries. Regardless, stream-type fish from Puget Sound in their third year at sea were modeled equally well or better by Alaskan environmental data, but the results suggested that a productive and strong Alaska Current was not the primary factor promoting growth. Specifically, growth was negatively related to ALPI and sea level height along the coast. Ultimately, it appears that these stream-type fish may be highly migratory from the source region, and/or the dominance of one current in the transition zone sets up conditions for poor growth. The biological and physical dynamics appear to be too complicated to address entirely with this data set.

There were dramatic seasonal differences in growth models between the populations. California fish were fit almost exclusively to warm-season data and were only related to the cold season if they remained at sea for four growth seasons. During the fourth winter at sea, the relationship to the environment in the cold season was weaker than that to the warm season and could be the result of correlation between variables from the two seasons. In contrast, all of the northern populations were modeled better with cold season data. In the Gulf of Alaska, nutrient transfers between the Alaska Gyre and the coast are more intense during the winter. Therefore, much of the potential productivity of the system during the growth season may be established during the winter (Strub and James, 2002; Di Lorenzo *et al.*, 2005).

River flow was a significant variable for modeling growth of northern Chinook salmon. We included Skeena River flow as a measure that captured the variability in Haida Eddy formation and strength (Di Lorenzo *et al.*, 2005), and, therefore, model the effect of nutrient and trace metal flow into the Gulf of Alaska. River flow from other regions was intended to balance models and test our assumptions about the role of Skeena River flow. That Skeena River flow was more often positively related to growth of Taku River Alaskan fish supports the idea that Skeena River flow is correlated with nutrient transfers to the Alaska Gyre waters and along the coast. However, this interpretation is complicated by the negative relationship between growth of Situk River fish during their second winter at sea and Skeena River flow. This conflict indicates either a spurious result, or points to a difference in the distributions of the two populations. Puget Sound fish were more often negatively related to Fraser River flows. Together these results indicated that the role of river flow is likely greater than that of simply seeding eddies. California fish, for which growth was not related to river flow, reside in an area where river flow is discharged directly onto a narrow continental shelf where any impact of freshwater input is dispersed.

While populations from these regions responded differently to individual environmental variables and physical conditions, the Alaska and California populations seem to respond similarly to production in their respective systems. Along the California Current, California Chinook salmon growth was enhanced by conditions conducive to increased productivity. Specifically, cool temperatures, increased upwelling, a stronger North Pacific high pressure system, and reduced sea level height related positively to growth. Similarly, Alaska salmon with both ocean- and stream-type behaviors had enhanced growth during periods in which the physical environment was conducive to nutrient availability in the Alaska Gyre and along the coast and transfer of those nutrients between environments. In the first year of growth for ocean-type Alaska fish, the results from the path analysis and unstructured partial least squares regression were divided on the effect of sea level height, which did not appear as a significant variable in any other path models. Otherwise, our results generally indicated that strong ALPI, warm waters, and reduced coastal upwelling (onshore transport along the coast) promoted growth.

Generally, Puget Sound, Washington, fish growth was negatively related to a strong California Current, and had a limited and complex relationship to the strength of the Alaska Current. In other words, conditions conducive to increased productivity in the California Current were negatively related to growth of Puget Sound fish. However, fish from Puget Sound appeared to have had increased growth when neither the Alaska nor California Currents were strong enough to dominate the transition zone. The results from fish with ocean-type behavior during the first and third years at sea suggest that their growth was negatively related to a strong California Current. That is, growth was negatively related to the NOI and upwelling in the transition zone, which may act to deepen the undercurrent and reduce northern advection of nutrients to the surface. However, during the fourth season growth was positively related to a weakened Alaskan Current (e.g., decreased coastal sea level height and Ekman pumping, and increased upwelling coastally). Puget Sound fish with the stream-type behavior presented a more complicated case when put in the context of the boundary currents. Specifically, during the first year at sea, growth was positively related to upwelling in the transition zone, and negatively to the NOI. As both upwelling in the transition zone (Fig. 1) and the NOI are positively related to the California Current strength, these results are not simply indicative of the strength of the California Current. In the second year at sea, growth was negatively related to regional upwelling, perhaps a result of reduced nutrient input to the area, but growth was positively related to the NOI. Alaska environmental data did not fit the growth data for the second year at sea well, which supports the suggestion that this was not simply a model result dependent on correlation between regional environments. Using environmental data from the transition zone to model, growth during the third year resulted in similar patterns noted for the second year of growth at sea. However, there was a better fit using environmental data from Alaska in the third year of growth at sea. Examination of the relationships between individual variables from Alaska and growth in that third year shows conditions indicative of a weaker Alaska Current during the cold and warm seasons promoted growth. Clearly, the relationship between Puget Sound Chinook, specifically those with a stream-type behavior, and likely productivity in either the California or Alaska Currents is not obvious. This is important when considering the simplified model in which northern and southern salmon population productivities are considered to be negatively correlated. The transition zone represents a complex arena in which Chinook salmon growth, and possibly productivity, is only partly dependent on the relative strengths and productivity of the Alaska and California Currents.

We made certain assumptions in the models presented. These included the following: (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 apparent variation in growth is not predominantly related 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 distribution of the fish is relatively static.

As for variation in fishing pressures, we argue that our results are robust despite the variation introduced by variations in fishing pressure and that there is no evidence fishing practices track the variables examined in this data set. However, had fishing practices varied similarly in relation to the environment as did growth rate, our results would be inflated.

Relative to modeling growth following the first ocean winter (assumption 2), the period before the first ocean winter is considered to be the time when the selective mortality on smaller fish is greatest (Beamish and Mahnken, 2001; Beamish *et al*., 2004). If the fish experience significant size-selective mortality, we would be overestimating growth and underestimating the negative impacts of the environment during the first year at sea. Ultimately, our estimates for the first year of growth are a confounded representation of growth in fresh water, growth in salt water, and size related mortality. 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 effects from size-selective mortality on growth estimation after the first ocean winter.

We considered hatchery fish and wild fish to relate similarly to the environment (assumption 3). Importantly, for three of the stocks we examined, Situk, Taku, and Smith River, there were no hatchery fish. For Skagit River the contribution of hatchery fish was small relative to the number of wild fish. However, we left possible hatchery fish anonymous in our sample. This requirement was driven primarily by a lack of known-origin fish in samples with which to make a discrimination rule. Because we were interested in the ocean growth period and Chinook salmon are generally released with little scale growth (fish from this study very rarely had more than 1/3 of their first year of growth before apparent ocean entry), the possible impact of differences in early growth rate was likely not significant.

In our analysis, we combined the growth occurring before and after ocean entry due to the often unclear and indistinct checks indicating the estuary and ocean entry (assumption 4). However, for a given stock, variation in the size at ocean entry is limited relative to the degree of variation in ocean growth.

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). It follows that non-stationary environmental conditions, likely resulting in varying distributions of fish, put into question our approach of a static definition of regions and a spatially unvarying application of at-age models. However, supporting our approach, any attempt we made to model variables together across larger regions than those used here (in an attempt to capture the full distribution of the fish) increased the variation of the models significantly and failed to identify significant models. This was particularly evident for California and Puget Sound Chinook salmon.

In summary, we have demonstrated a biologically relevant model for describing the growth of Chinook salmon in relation to the environment along a large portion of their natural range during ocean residence. In doing so, we have advanced knowledge beyond simple growth models, and identified specific oceanographic features that influence growth of Chinook salmon across their natural range and life-history variability.

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