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Effects of early-life stage and environmental factors on the freshwater and marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in rivers of Southeast Alaska

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Abstract—Highly variable recruitment and declines in productivity of Chinook salmon (*Oncorhynchus tshawytscha*) have created economic and cultural hardships throughout Alaska. Therefore, it is necessary to understand the factors influencing these declines. In this study, principal component analysis and regression were used to determine how biological and environmental factors have influenced freshwater survival, smolt production, and marine survival of Chinook salmon in the Chilkat River (brood years 1999–2009) and marine survival in the Stikine River (brood years 1998–2009). Smolt production in the Chilkat River was higher in years when parr had shorter average mid-eye fork lengths, river discharge was low in the fall (P=0.05), and river temperatures and discharge were high in early spring (P=0.03), indicating density-dependent growth in fresh water and the importance of river conditions to annual growth and abundance of this species. Marine survival of fish in the Stikine River was positively related to smolt length, indicating higher survival in years when smolts were larger (coefficient of multiple determination [R^2]=0.26). Greater marine survival of salmon in the Chilkat River occurred in years when smolt migrations ended later in the month of May, smolts were larger, and discharge was lower (R^2=0.5) than in other years. These results indicate the importance of the early marine period in determining year-class strength and highlight the variation in mechanisms that influence survival of stocks of Chinook salmon.

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Survival of salmon species (*Oncorhynchus* spp.) of the Pacific Ocean varies with life stage. As a result, identifying critical periods of mortality that determine brood strength can lead to more specific analyses of biotic and abiotic factors that may affect stocks. Although life history strategies vary by species and stock, most salmon undergo single or multiple freshwater wintering periods before migrating to the marine environment (McCormick et al., 1998; Quinn, 2005). The freshwater overwinter and early marine entry periods are frequently recognized as critical periods and bottlenecks for survival in the life history of salmon species in the Pacific Ocean (Beamish and Mahnken, 2001).

In fresh water, parr must survive at least one winter period of freezing water temperatures, low river discharge, surface ice, and low productivity (Biro et al., 2004; Huusko et al., 2007). Results of previous research indicate that overwinter survival of juvenile salmonids is related to body size, with larger individuals having higher survival rates than smaller ones (Zabel and Achord, 2004). Larger, faster-growing individuals can better escape size-selective mortality (such as that resulting from predation), have a larger gape size (enabling the consumption of a greater diversity of prey that are larger and have higher energy), have greater lipid reserves, and have a lower relative metabolic rate, all of which help to sustain them during winter months (Houde, 1987; Sogard, 1997; Biro et al., 2004; Thompson and Beauchamp, 2014). Larger body sizes may also enable these individuals to secure higher quality winter habitats (Quinn and Peterson, 1996; Zabel and Achord, 2004).

Environmental conditions before, during, and after winter can also influence survival (Cunjak, 1988; Lawson et al., 2004). Low water temperatures (<0°C) reduce metabolic rates, reducing feeding efficiency, capability to avoid predators, and ability to respond to shifting ice conditions (Brown et al., 2011). Stressors from environmental conditions can cause metabolic deficits that lead to starvation or increased predation due to forage-based, risk-taking behaviors (Cunjak, 1988; Biro et al., 2003). Reductions in river discharge during the fall, when fish are moving to overwintering sites, and during winter can limit habitat accessibility and availability, and higher river discharge generally increases suitable habitat and carrying capacity of fish, reducing competitive interactions among juveniles (Lawson et al., 2004; Huusko et al., 2007). However, events of extremely high winter discharge can flush parr from winter habitats, restrict areas for effective drift foraging, and cause ice-related events of fish mortality (Lawson et al., 2004; Huusko et al., 2007; Neuswanger et al., 2014). Increases in turbidity that result from high discharge can further reduce the foraging ability of parr by limiting visibility but can protect fish from visual predators as well (Lawson et al., 2004; Neuswanger et al., 2014).

Following winter, parr undergo behavioral and physical changes, known as smoltification, and become adapted to living in a marine environment (Healey, 1991). Early marine entry is a critical period for juvenile salmon that can determine strength of brood years (BYs) (Beamish and Mahnken, 2001; Mueter et al., 2002a). Movements of salmon smolts from fresh to marine waters follows the evolutionary concept of risk and reward, the notion that it is energetically advantageous yet riskier to migrate to and feed in the ocean than it is to remain in resource-limited fresh waters (Jonsson and Jonsson, 1993; Quinn, 2005). Results of previous research on smolt migration indicate that large variability in marine survival may be due to migration timing and a match or mismatch between smolt arrival in the ocean and nearshore marine conditions, including food availability (Rikardsen et al., 2004; Hvidsten et al., 2009). Smolt body size and changes in river conditions, such as increases in temperature and river discharge, have been linked to the timing of smolt migration (Bohlin et al., 1993; Vega et al., 2017). Environmental changes, such as increases in water temperature, trigger migratory movements, but river discharge may augment migration as higher flows allow some passive transportation downstream (Bohlin et al., 1993; McCormick et al., 1998).

Correlations between body size, early marine growth, and survival have been observed in most species of salmon in the Pacific and Atlantic Oceans (Holtby et al., 1990; Koenings et al., 1993; Mortensen et al., 2000; Antonsson et al., 2010; Murphy et al., 2013). The critical size and critical period hypothesis is that, for Pacific salmon (*Oncorhynchus* spp.), the majority of natural mortality in marine environments occurs during 2 periods: 1) mortality of fish due to predation in the early marine period and 2) mortality of fish smaller than a critical size due to their inability to meet minimum metabolic requirements during their first year at sea (Beamish and Mahnken, 2001). Larger, faster-growing individuals are able to capture larger prey at an earlier age, resulting in improved metabolic efficiency and greater growth (Quinn, 2005). Fish typically have an optimal temperature range, within which metabolic rate is most efficient and growth is maximized (Wootton, 1998). Regional ocean conditions, including upwelling and advection, affect water temperatures and prey abundances and distributions; in turn, these conditions may benefit or hinder growth and survival (Cole, 2000; Mortensen et al., 2000; Mueter et al., 2002b). Body size of juveniles during the early marine period is more influential during years when mortality is high and marine survival is below average, indicating that having a large body size is more important when marine conditions are suboptimal for growth and survival (Holtby et al., 1990; Graham et al., 2019).

Although results of previous research indicate the importance of physical and environmental conditions to the survival of stocks of Pacific salmon in fresh water during the early marine period, the factors influencing variability in recruitment and survival can be unique to each stock and remain unknown for many stocks (Malick et al., 2009). Chinook salmon (*O. tshawytscha*) in Alaska support important and diverse subsistence, commercial, recreational, and personal use fisheries. In Southeast Alaska (SEAK), declines in abundance and catch of stocks of Chinook salmon, increased variability in productivity, and overfishing over the past 60 years have led to fishing restrictions, which have created cultural, social, and economic hardships for communities in this region (ADFG CSRT[1]). With impending threats, including climate change and mine development, it is imperative to understand the basic mechanisms affecting survival and recruitment of this species.

The objectives of this study were 1) to examine influences of biological (parr length) and local environmental (temperature and discharge) factors on freshwater overwinter survival and smolt production of Chinook salmon in the Chilkat River, in SEAK near Juneau; 2) to determine how biological factors, such as smolt body size and migration timing, and local environmental factors, including regional sea-surface temperatures (SSTs) and river discharge and temperatures, influenced marine survival of Chinook salmon in the Chilkat River; and 3) to determine how a biological factor, smolt body size, and local environmental factors, including regional SSTs and river discharge, influenced marine survival of Chinook salmon in the Stikine River, further southeast in SEAK. This research helps clarify the factors that influence freshwater overwinter and marine survival of Chinook salmon and will allow managers to develop more accurate and reliable catch forecasts.

Materials and methods

Study sites

The Chilkat and Stikine Rivers were selected for this study because they support important regional stocks

[1] ADFG CSRT (Alaska Department of Fish and Game Chinook Salmon Research Team). 2013. Chinook salmon stock assessment and research plan, 2013. Alaska Dep. Fish Game, Special Publ. 13–01, 56 p. [Available from website.]

of Chinook salmon and long-term data exists for both systems. These rivers are 2 of the 11 indicator systems selected by the Alaska Department of Fish and Game (ADFG) and Fisheries and Oceans Canada to be sampled and studied as part of in-depth stock assessments for Chinook salmon (ADFG CSRT[1]). This monitoring program was initiated because of statewide and regional stock declines for this species and the need for increased information for run forecasting (ADFG CSRT[1]).

The Chilkat River is a moderately sized, glacially fed river that originates at the Chilkat Glacier in British Columbia, Canada, and drains into Lynn Canal near Haines, Alaska (ADFG CSRT[1]; Elliott and Peterson[2]) (Fig. 1). This river supports the fifth-largest stock of Chinook salmon in SEAK, with an annual spawning run of about 4000 large (>660 mm in mid-eye fork length) fish (ADFG CSRT[1]). Adult Chinook salmon from the Chilkat River typically grow in the inside marine waters of northern SEAK (Elliott and Peterson[2]).

The Stikine River is a transboundary river originating in British Columbia and draining near Wrangell, Alaska. Chinook salmon in this system are jointly managed by the ADFG and Fisheries and Oceans Canada (Jaecks et al.[3]) (Fig. 1). The Stikine River supports the second-largest stock of Chinook salmon in SEAK, with an annual spawning run of about 22,000 large fish (Pahlke[4]; ADFG CSRT[1]). Adult Chinook salmon from the Stikine River primarily grow in the Gulf of Alaska and the Bering Sea (Pahlke et al.[5]).

Chinook salmon in both rivers have a stream-type life history, where juveniles reside in fresh water for 1 year before migrating downstream as age-2 smolts (Quinn, 2005; ADFG CSRT[1]). The age structure for returning adults was similar for Chinook salmon from the Stikine and Chilkat Rivers, with most adults returning to fresh water after 2–4 years in the marine environment (Chapell[6]). Sampling effort and design of surveys to estimate smolt abundance and adult return were similar for work in both rivers. However, surveys of freshwater juvenile Chinook salmon conducted in the fall and spring in the Chilkat River allowed assessment of additional freshwater processes (overwinter survival and smolt production); as a result, data from each river system were analyzed separately.

Chilkat River

Biological data We estimated values for several biological attributes for Chinook salmon in the Chilkat River by using data from 2 efforts conducted by the ADFG: a tagging study in which coded-wire tags (CWTs) are attached to juveniles in both the fall and spring (we used data for the period 2000–2011) and a mark-recapture program that targeted adults (we used data for the period 2002–2016) (Elliott and Power[7]; Elliott and Peterson[2]). The biological factors estimated were marine survival, the rate of survival from freshwater emigration to return for spawning (BYs: 1999–2009); smolt abundance, the number of juvenile salmon in the spring; smolt mean mid-eye fork length (in millimeters); parr abundance, the number of juvenile salmon in the fall; parr mean mid-eye fork length (in millimeters); and overwinter survival, the survival rate of juvenile salmon from the fall to the spring.

The mark-recapture survey was executed by using a 2-event sampling scheme for a closed population. For the first sampling event, adult Chinook salmon were captured and marked between 10 June and 24 July of each survey year in the lower Chilkat River. For the second sampling event, adults were captured from August through mid-September in each survey year in the 3 principal spawning tributaries of the Chilkat River, the Kelsall, Tahini, and Klehini Rivers. Chinook salmon captured during sampling events were measured to the nearest 5-mm interval of mid-eye fork length, their sex was determined, scales were sampled, and the fish were inspected for the presence or absence of an adipose fin (small fin located between the dorsal and caudal fins). Fish that did not have an adipose fin were processed and scanned with a CWT detector (Elliott and Power[7]).

Data from both sampling events were tabulated, and Petersen estimators were used to estimate abundance, given that all assumptions of the model were met during sampling (Seber, 1982). Size, age, and sex selectivity in sampling data were evaluated by using Kolomogorov–Smirnov tests. If selectivity was present in data from either the first or second sampling event, a stratified Petersen model was used to eliminate variability in capture probability (Elliott and Power[7]). Adult abundance was estimated by using results from both the mark-recapture and CWT surveys. Marked adult fish from the Chilkat River were primarily recovered in seasonal troll, SEAK sport, drift gill-net, or purse seine fisheries during annual surveys conducted by the ADFG, which aims to sample 20% of the catch of Chinook salmon in SEAK (Elliott and Peterson[2]). Marine survival was calculated by using the estimated values for smolt and adult abundance associated with each BY.

The CWT survey of juvenile Chinook salmon was initiated in 2000 to estimate parr and smolt abundance, smolt emigration, and marine catch of the stock in the Chilkat

[2] Elliott, B. W., and R. L. Peterson. 2018. Production and harvest of Chilkat River Chinook and coho salmon, 2018–2019. Alaska Dep. Fish Game, Reg. Oper. Plan SF.1J.2018.10, 47 p.. [Available from website.]

[3] Jaecks, T., P. Richards, S. J. H. Power, P. Etherton, and I. Boyce. 2015. Estimation of smolt production and harvest of Stikine River Chinook salmon, 2015. Alaska Dep. Fish Game, Reg. Oper. Plan SF.1J.2015.04, 18 p. [Available from website.]

[4] Pahlke, K. A. 2010. Escapements of Chinook salmon in Southeast Alaska and transboundary rivers in 2008. Alaska Dep. Fish Game, Fish. Data Ser. 10-71, 38 p. [Available from website.]

[5] Pahlke, K. A., P. Richards, and P. Etherton. 2010. Production of Chinook salmon from the Stikine River, 1999–2002. Alaska Dep. Fish Game, Fish. Data Ser. 10-03, 16 p. [Available from website.]

[6] Chapell, R. S. 2013. Production, escapement, and juvenile tagging of Chilkat River Chinook salmon in 2010. Alaska Dep. Fish Game, Fish. Data Ser. 13-25, 48 p. [Available from website.]

[7] Elliott, B. W., and S. J. H. Power. 2015. Chilkat River Chinook salmon escapement studies in 2015. Alaska Dep. Fish Game, Reg. Oper. Plan SF.1J.2015.13, 31 p. [Available from website.]

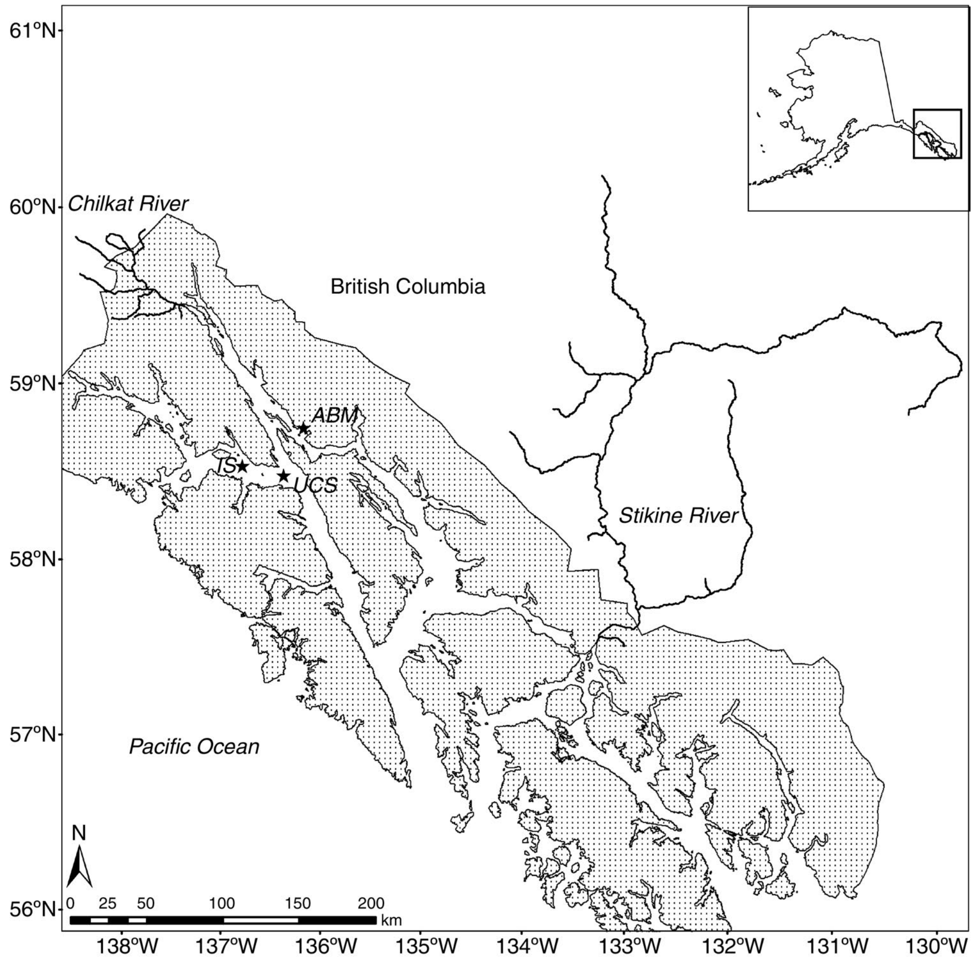

Figure 1

Map of the Chilkat and Stikine Rivers in Southeast Alaska and in British Columbia, Canada. The influence of environmental and biological factors on marine survival, freshwater overwinter survival, and smolt production of Chinook salmon (*Oncorhynchus tshawytscha*) from these rivers was examined. Chinook salmon sampled from the Chilkat River were from the brood years 1999–2009 and those sampled from the Stikine River were from the brood years 1998–2009. The stars indicate the 3 locations where sea-surface temperatures were collected monthly from May through August during 1997–2015: Auke Bay Monitor (ABM), Upper Chatam Strait (UCS), and Icy Strait (IS).

River (Chapell[6]). The tagging of juveniles occurred from mid-September through October for parr and from April through May for smolts. The fall sampling period began in September at upriver locations and moved downstream as the season progressed, ending at the lower portion of the main stem of the Chilkat River. Spring sampling started in April and was conducted entirely on the lower portion of the main stem of the Chilkat River. In both sampling periods, juvenile Chinook salmon were captured each day by using 100 Gee minnow traps (Cuba Specialty Manufacturing[8], Fillmore, NY) baited with disinfected salmon roe (Chapell[6]). The ADFG fit a statistical model to CWT data from both sampling events to estimate parr abundance, smolt abundance, and overwinter survival (Elliott and Peterson[2]). Estimates of total annual abundance of smolts were used to represent freshwater smolt production.

Data from the spring sampling of the CWT program in the Chilkat River were used to create indices of smolt migration timing. The number of minnow traps and catches of Chinook salmon were used to calculate the daily catch per unit of effort over the spring sampling period (early April–late May) for each reach of the river (Elliott and Peterson[2]). The daily catch per unit of effort in the lower Chilkat River was used as a proxy for the total number of fish migrating to the ocean each day. To capture differences in annual migration timing, the ordinal date

[8] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

when 95% of smolts had been captured was used to define the end of the outmigration period. This index was used in this study rather than an estimate of the start or median migration date because smolt sampling began after the start of migration in some years, making accurate estimation of passage dates difficult. In addition, this index was assumed to be resistant to the biases associated with minnow trap catch data, indicating that daily variability in catch can be based on location, not on the actual number of fish outmigrating on a given day. This is because the index used in our study is based on a consistent decline in daily number of fish caught over the course of the migration period rather than on the number of fish caught on any single day. (He and Lodge, 1990).

Physical data: overwinter survival To determine the local factors influencing overwinter survival of Chinook salmon in the Chilkat River, environmental data for BYs during the fall and spring freshwater periods were examined. River discharge data were not available for the Chilkat River during 2000–2010 (BYs 1999–2009); therefore, the combined standardized mean monthly discharge from the Taku, Stikine, and Antler Rivers during 1998–2015 for fall (September–November) and spring (March–April) was used as a proxy for river discharge in SEAK. These rivers were chosen because they were the only glacial systems in the region with data for the entire study period. These rivers represent a range of drainage sizes, with mean annual discharges during 2014–2016 of 4 m^3/s for the Antler River, 401 m^3/s for the Taku River, and 1660 m^3/s for the Stikine River. Discharge data were obtained from the U. S. Geological Survey (USGS) National Water Information System (available from website, accessed February 2017) as follows: Taku River near Juneau (USGS gauging station no. 15041200), Stikine River near Wrangell (USGS gauging station no. 15024800), and Antler River near Auke Bay, Alaska (USGS gauging station no. 15055500). Although river discharge during winter may also affect overwinter survival (Lawson et al., 2004), the USGS rated discharge measurements from ice-covered rivers as poor, and rivers in SEAK are typically ice covered from December through early March (B. Elliott, personal commun.).

Long-term monthly temperature data were not available for the Chilkat River; however, air temperature data were available for a NOAA station close to the Chilkat River in Klukwan, Alaska (Haines 40 NW [station ID: USC00503504]; Global Summary of the Month data set based on the Global Historical Climatology Network daily data set available from website, accessed February 2017). Because stream temperatures are strongly correlated with air temperature above freezing (0°C), daily air temperatures from the Haines 40 NW station for September–November (fall) and March–April (spring) were used as proxies for stream water temperatures (Mohseni and Stefan, 1999). Although the relationship between air and water temperatures may be different for glacially fed streams, the air temperature indices used in these analyses likely captured the annual variation in water temperatures.

Physical data: marine survival To analyze how regional environmental factors that occur during the early marine period correlate to marine survival of Chinook salmon in the Chilkat River, SSTs from inshore marine waters of SEAK (in degrees Celsius) were collected by NOAA during the Southeast Alaska Coastal Monitoring survey in 1997–2015 (Orsi and Fergusson[9]). Sea-surface temperature was sampled monthly from May through August by using a conductivity, temperature, and depth sonde at a depth of 3 m at 3 different locations (Orsi and Fergusson[9]). These sampling locations represented inshore (Auke Bay Monitor) and strait (Upper Chatham Strait and Icy Strait) growing habitats (Orsi and Fergusson[9]) (Fig. 1). Because Chinook salmon in SEAK migrate to the marine environment from April through late May, an index of marine entry SSTs was developed by averaging the SSTs for all stations during June and July (Orsi and Fergusson[9]; Elliott and Peterson[2]). This index was lagged by 2 years (BY+2 years) to reflect conditions during ocean entry.

River conditions during smolt outmigration were also used in the analysis of marine survival. Average river temperature and river discharge at the time of outmigration (April–May) can affect run timing and early ocean conditions experienced by smolts. River temperature data were collected by the ADFG during smolt sampling of the CWT program for the period 2001–2011 (Elliott and Peterson[2]). Daily temperatures were averaged for each year to develop a variable for overall spring river water temperature. Using the previously described proxy for river discharge in SEAK, a spring migration period discharge index was developed by averaging monthly mean discharge (SEAK index on standardized scale) for April–May, the primary migration period for smolt Chinook salmon.

Data analysis The influence of biological and environmental factors on overwinter survival and smolt production of Chinook salmon in the Chilkat River was determined through principal component analysis and principal component regression. During preliminary examination of the data, the Pearson product-moment correlation coefficient (r) was used to make pairwise comparisons between explanatory variables. Results indicate significant positive correlation between parr length and fall discharge and early spring temperature and discharge (Table 1). Because of small sample sizes (n=11), 5 explanatory variables and multicollinearity between variables were most appropriate for principal component analysis and principal component regression. The environmental explanatory variables were lagged to represent conditions experienced by fish during their first fall prior to wintering in fresh water (BY+1) and during the following spring during outmigration (BY+2). Parr length, fall and spring discharge, and fall and spring air temperature were included in the analysis and new linear combinations of the standardized

[9] Orsi, J. A., and E. A. Fergusson. 2016. Annual survey of juvenile salmon, ecologically-related species, and biophysical factors in the marine waters of southeastern Alaska, May–August 2015. North Pac. Anadromous Fish Comm. Doc., 71 p. [Available from website.]

Table 1

Mean estimates of and Pearson product-moment correlation coefficients (r) from pairwise comparisons of explanatory variables used in analyses of freshwater survival and production (smolt abundance) and marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in the Chilkat River (with data for brood years 1999–2009) and in analyses of marine survival of Chinook salmon in the Stikine River (with data for brood years 1998–2009) in Southeast Alaska. Variables include mean parr mid-eye fork length, mean river discharge and air temperature in the fall (September–November), mean river discharge and air temperature in early spring (March–April), mean smolt length, migration timing, sea-surface temperature (SST), and mean river discharge and water temperature in the spring (April–May). A standardized index, based on monthly mean discharge averaged across rivers in Southeast Alaska for the primary migration period of smolts (April–May), was used for discharge in the Chilkat River. Data for river water temperature were not available for the Chilkat River. An asterisk (*) indicates a significant correlation between variables ($P<0.05$). SD=standard deviation.

	Estimate		r			
Variable	Mean	SD	Parr length	Fall discharge	Spring discharge	Fall temperature
Chilkat River: freshwater survival and production						
Parr length (mm)	68.85	2.67	–			
Fall discharge (index)	–0.06	0.76	0.71*	–		
Spring discharge (index)	–0.04	1.05	0.00	0.25	–	
Fall temperature (°C)	3.16	0.74	0.09	0.39	0.29	–
Spring temperature (°C)	–0.83	1.73	–0.54	–0.08	0.66*	0.11

	Estimate		r			
Variable	Mean	SD	Migration timing	SST	Smolt length	Spring discharge
Chilkat River: marine survival						
Migration timing (ordinal date)	136.09	4.16	–			
SST (°C)	12.03	0.79	–0.05	–		
Smolt length (mm)	73.42	3.37	0.73*	–0.10	–	
Spring discharge (index)	–0.02	1.03	–0.69*	0.53	–0.56	–
Spring temperature (°C)	4.34	0.76	0.44	–0.18	0.30	–0.32

	Estimate		r		
Variable	Mean	SD	SST	Smolt length	Spring discharge
Stikine River: marine survival					
SST (°C)	73.58	3.03	–		
Smolt length (mm)	12.07	0.77	–0.18	–	
Spring discharge (m^3/s)	40,499	11,381	–0.35	0.44	–

variables (mean: 0; standard deviation: 1) were created by using principal component analysis with varimax rotation (Jackson, 2005).

The number of rotated components (RCs) that contained interpretable information were chosen through a visual assessment of a scree plot. Principal component regression models were fit to test for significant relationships between response variables (log-transformed overwinter survival and smolt production) and RCs. In addition, to uncover potential density dependence during the pre-smolt freshwater period, a simple linear regression was fit to describe the relationship between parr abundance and parr length.

Principal component analysis in combination with principal component regression was used to estimate effects of biological and environmental factors on marine survival of Chinook salmon in the Chilkat River because of the low sample size, high number of explanatory variables, and multicollinearity. Results of pairwise comparisons of explanatory variables made by using the r indicate significant correlation between the timing of the end of the smolt migration and smolt length (positive) and late spring discharge (negative) (Table 1). For these analyses, log-transformed marine survival was used as the response variable, and principal component (PC) variables that combine spring river temperature and discharge, summer SST, ordinal date at the end of smolt outmigration, and smolt length were included as explanatory variables. Environmental and run timing variables were lagged (BY+2) to represent conditions and run timing experienced by a given BY. All statistical analyses were conducted in R, vers. 3.6.3 (R Core Team, 2020).

Stikine River

Biological data Marine survival, smolt abundance, and smolt fork length (in millimeters) of Chinook salmon returning to the Stikine River (BYs 1998–2009) were estimated with data collected by the ADFG, Fisheries and Oceans Canada, and Tahltan First Nation during the mark-recapture survey of adult Chinook salmon (we used data for the period 2001–2016) and during the CWT survey conducted in spring (we used data for the period 2000–2011) (Pahlke et al.[5]; Jaecks et al.[3]; Jaecks[10]). Data from the mark-recapture program were used to estimate in-river abundance of large Chinook salmon in the Stikine River, and those estimates, in turn, were used to calculate marine survival. The mark-recapture experiment was completed in 2 phases. During the first phase, Chinook salmon were captured during May–July with drift gill nets on the lower Stikine River; during the second phase, fish were captured from June through August with the same gear on the spawning grounds upriver (Jaecks et al.[11]). Captured Chinook salmon were measured for mid-eye fork length, externally examined to determine sex, sampled for scales, marked, and then released. Fish in both phases with missing adipose fins were processed similar to such Chinook salmon caught in the Chilkat River. The estimated abundance parameter was tabulated by using Chapman's modification of the Petersen estimator, as long as all assumptions were met (Seber, 1982). When assumptions were violated, a variety of stratification and modeling techniques were used on data to correct for bias as much as possible (Jaecks et al.[11]).

Data from the CWT study of juvenile Chinook salmon were used to estimate the number of smolts emigrating from the Stikine River. This study was designed as a modified Petersen 2-event mark-recapture effort, where the tagging of juveniles (>50 mm in fork length) in the spring was the first sampling event and the mark-recapture of adults (described previously) was the second sampling event. Juvenile Chinook salmon were sampled annually in mid-April in the lower reaches (U.S. side) of the Stikine River (Jaecks et al.[3]). Salmon were caught by using beach seines that were 18 by 2 m or 24 by 2 m (depending on the crew), all with 63.5-cm mesh, and by using Gee minnow traps baited with disinfected salmon roe. Smolt abundance was estimated, by using adult mark-recapture data, for the 5 years it takes for each brood of smolts to return to the river. The fraction of the population that had been originally marked was estimated each year. If those estimates were similar for all years, data were pooled and Chapman's modification of Petersen's estimator was used. If the estimates for the fraction of the population that had been marked were not consistent, the estimates were averaged over the years (Jaecks et al.[3]). Marked adult fish from the Stikine River were primarily recovered in marine, troll, and drift gill-net fisheries (Pahlke et al.[5]).

Physical data To assess the relationship between marine survival and regional environmental conditions during the early marine period for Chinook salmon from the Stikine River, SST and river discharge were included in the model. Sea-surface temperature, as described previously, was similarly used to represent conditions of the inshore marine waters of SEAK (in degrees Celsius) upon ocean entry of Chinook salmon (June–July). To represent river conditions during outmigration, data for monthly mean river discharge in the Stikine River was averaged for April–May (USGS gauging station no. 15024800). Data on river water temperatures were not available for the Stikine River and, therefore, not included in the model.

Data analysis For Chinook salmon in the Stikine River, multiple and simple linear regression analyses were used to test for significant relationships between log-transformed marine survival and spring discharge, summer SST, and smolt length. Environmental variables were lagged (BY+2) to represent experienced conditions of a given BY. The statistical approach used to examine factors for fish in the Stikine River was more simplistic than that used in analyses conducted for fish in the Chilkat River because there were fewer explanatory variables (n=3) and no correlation between those variables according to a pairwise comparison (Table 1). Results of the preliminary exploration of variables included in the analyses for salmon in the Stikine River indicate the presence of a possible outlier; therefore, robust linear regression analyses were used as implemented in the function lmRob of the robust package (vers. 0.5-0.0; Wang et al., 2020) in R. A backward-stepwise approach, which was based on the Akaike information criterion for small sample sizes and removed terms one at a time on the basis of the largest reduction in deviance, was used to select the top models. All statistical analyses were conducted in R.

Results

Chilkat River

Overwinter survival and smolt production Over the time series (BY 1999–2009), mean freshwater overwinter survival for Chinook salmon in the Chilkat River was 36% (standard error of the mean [SE] 10) and ranged from 21% (SE 5) for BY 2000 to 53% (SE 15) for BY 2005 (Fig. 2). Mean smolt abundance was 172,616 individuals and ranged from 105,300 individuals in 2000 to 282,700 individuals in 2003 (Fig. 2). There was no significant linear trend over time in annual estimates of overwinter survival

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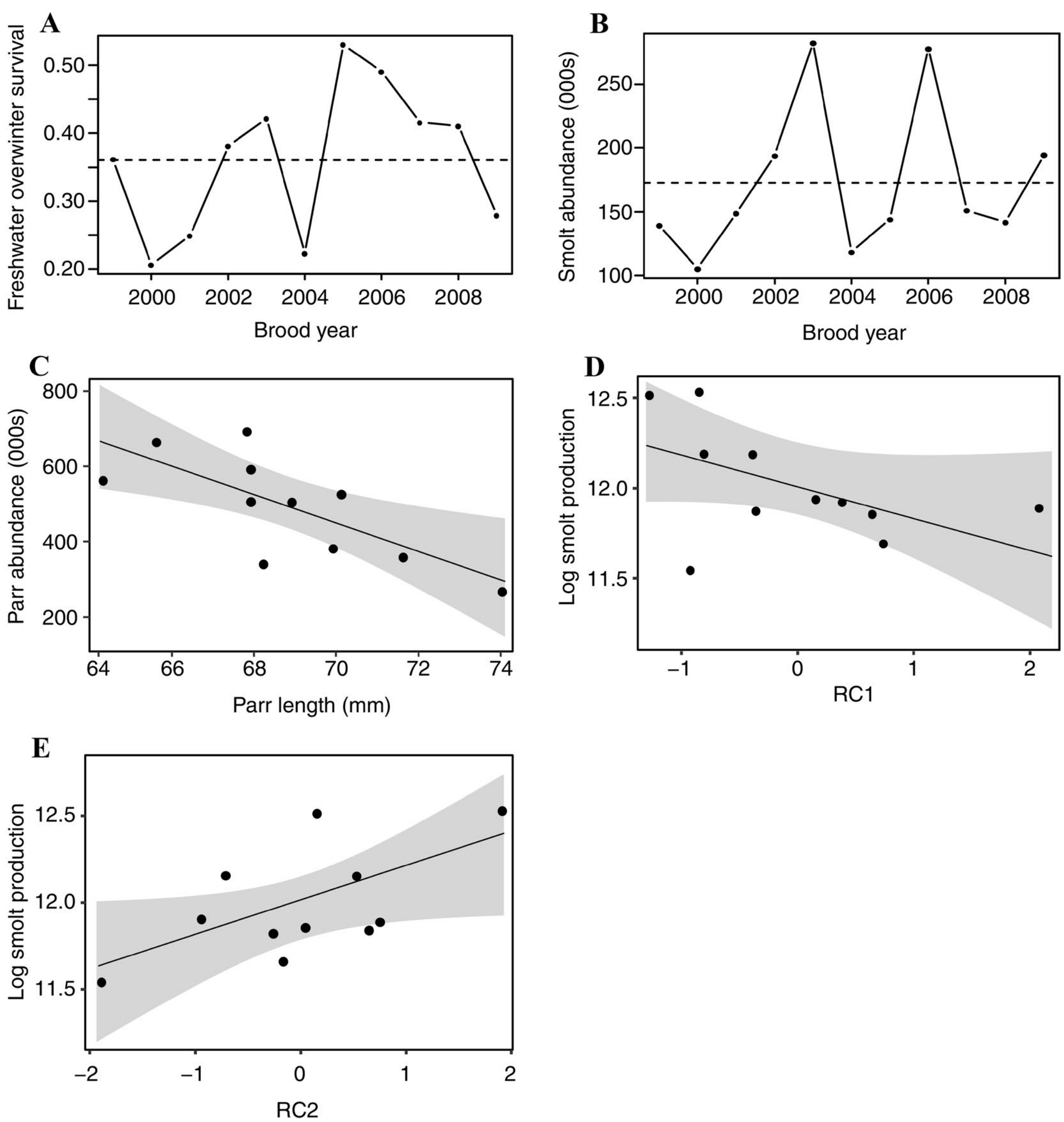

Figure 2

Time series of (**A**) overwinter survival and (**B**) smolt abundance by brood year (1999–2009), (**C**) the relationship between parr abundance and parr mid-eye fork length, and the relationships between log-transformed smolt production (estimated spring abundance) and the (**D**) first rotated component (RC1) and (**E**) second rotated component (RC2) for Chinook salmon (*Oncorhynchus tshawytscha*) during their freshwater period in the Chilkat River in Southeast Alaska. The horizontal dashed lines in panels A and B indicate mean freshwater overwinter survival and smolt abundance. The regression line and 95% confidence interval (gray areas) in panel C are based on a regression of parr length on parr abundance. The regression lines and 95% confidence intervals (gray areas) in panels D and E are based on the principal component regression of RC1 and RC2 on smolt production.

(coefficient of multiple determination [R^2]=0.12, P=0.29) or smolt abundance (R^2=0.05, P=0.49).

Overall mean parr mid-eye fork length was 69 mm, ranging from an annual mean of 64 mm in 2006 to 74 mm in 2005. Results from the simple linear regression indicate a significant negative relationship between parr length and parr abundance (R^2=0.54, P=0.01) (Fig. 2). Over the study period, river discharge was consistent in fall and was higher and more variable in spring. The mean temperature in fall was 3.2°C (range: 2.2–4.8°C), and the mean temperature in spring was −0.8°C (range: −3.8–2.5°C). There were no significant temporal trends in discharge (fall: P=0.45; spring: P=0.86) or temperature (fall: P=0.93; spring: P=0.74).

Two RCs were retained for analyses on the basis of a scree plot and accounted for 39% and 38% of the overall variability in the data set. The first RC (RC1) loaded most heavily on parr length and fall discharge, and the second one (RC2) loaded most heavily on early spring discharge and temperature (Table 2). Results from the principal component regression model indicate that the 2 RCs explained little of the variation in overwinter survival (adjusted R^2=0.14, F=1.78, P=0.23). There were no significant relationships between overwinter survival and RC1 (P=0.51) or RC2 (P=0.12) (Table 3). In contrast, smolt production was significantly related to both RC1 (standardized regression coefficient [β]=−0.10, P=0.05) and RC2 (β=0.19, P=0.03), indicating that smolt production was enhanced when parr were smaller and discharge was lower during the previous fall and when discharge was higher and temperatures were warmer in the spring (Table 3, Fig. 2).

Marine survival Over the time series (BY 1999–2009), mean marine survival of Chinook salmon in the Chilkat River was 2.8% (SE 0.7) and ranged from 1.3% (SE 0.4) for BY 2002 and 1.3% (SE 0.7) for BY 2008 to 4.7% (SE 1.0) for BY 2000 (Fig. 3). Although not significant at the 95% level, there was a negative temporal trend in marine survival for fish in the Chilkat River (R^2=0.34, P=0.06).

The annual mean mid-eye fork length for smolt Chinook salmon in the Chilkat River was 73 mm (range: 69–79 mm), and there was no significant trend in smolt length over the study period. Mean summer SST over the study period was 12.0°C, and summer SSTs ranged from 10.5°C to 13.0°C. Mean temperature in the Chilkat River during the spring migration period (April–May) was 4.3°C (range: 3.3–5.5°C). The index value for standardized mean spring discharge in SEAK was −0.02 (range: −1.5–2.3). There was no significant temporal trend over this period (temperature: P=0.16; discharge: P=0.57). On average across BYs, smolt outmigration in the Chilkat River ended on ordinal date 136 (15 or 16 May), and the end date ranged from ordinal date 129 (8 May) in 2004 (BY 2002) to ordinal date 143 (23 May) in 2001 (BY 1999). Outmigration timing (end date of outmigration) was positively related to smolt length (r=0.73) and negatively related to spring discharge (r=−0.69) (Table 1).

Three PCs were retained and used to explain variation in log-transformed marine survival of Chinook salmon in the Chilkat River. The first PC (PC1) loaded heaviest on migration timing, smolt length, and discharge, the second PC (PC2) loaded primarily on SST, and the third PC (PC3) loaded heaviest on average river temperature (Table 4). Log-transformed marine survival of Chinook salmon in the Chilkat River was significantly negatively related to PC1, indicating that marine survival was higher when outmigration ended later and smolt length was greater and that marine survival was lower when spring discharge was higher (R^2=0.5, P=0.01) (Table 5, Fig. 3).

Stikine River

For Chinook salmon in the Stikine River, mean marine survival was 1.7% (SE 0.3) and ranged from 0.6% (SE 0.1)

Table 2

Loadings of the first and second rotated components from principal component analysis of environmental and biological variables used to explain variation in overwinter survival and smolt production of Chinook salmon (*Oncorhynchus tshawytscha*) in the Chilkat River in Southeast Alaska. Data used in this analysis were for Chinook salmon from the brood years 1999–2009.

Component	RC1	RC2
Parr length	0.88	−0.31
Fall discharge	0.91	0.17
Spring discharge	0.18	0.87
Fall temperature	0.48	0.47
Spring temperature	−0.35	0.88
Proportion of variance explained	0.39	0.38
Cumulative proportion	0.39	0.77

Table 3

Results from the principal component regression model used to examine the relationships between the first and second rotated components and overwinter survival and smolt production of Chinook salmon (*Oncorhynchus tshawytscha*) in the Chilkat River in Southeast Alaska. Model statistics include the standardized regression coefficient (β), standard error of the coefficient (SE), coefficient divided by its standard error (t), and the coefficient of multiple determination (R^2). Data used in this model were for Chinook salmon from the brood years 1999–2009.

		Model statistic				
Explanatory variable	Response variable	β	SE	t	P	R^2
Freshwater overwinter survival	RC1	0.04	0.10	0.42	0.68	0.005
	RC2	0.14	0.10	1.37	0.21	
Smolt production	RC1	−0.16	0.07	−2.26	0.05	0.520
	RC2	0.19	0.07	2.75	0.03	

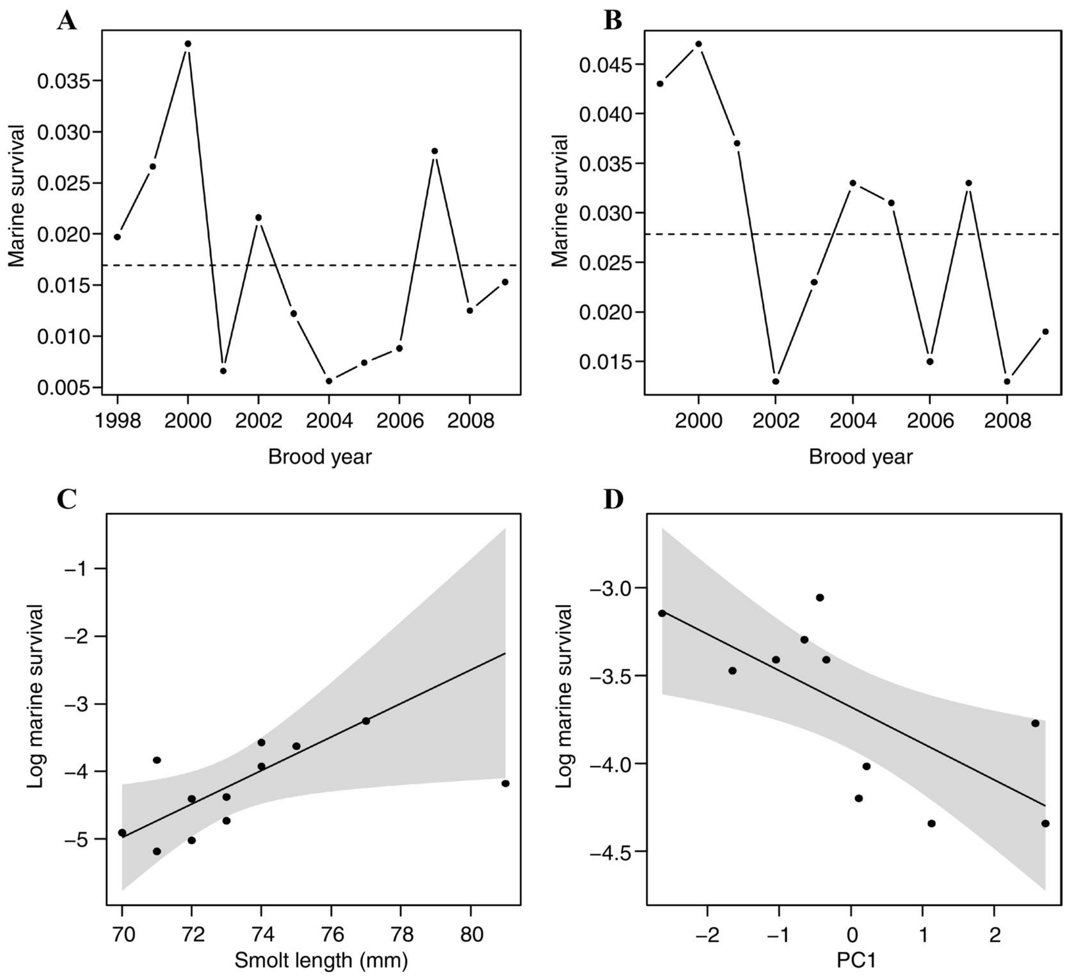

Figure 3

Time series of marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in the (**A**) Stikine River and (**B**) Chilkat River in Southeast Alaska. The horizontal dashed lines represent mean survival of Chinook salmon for all sample years, the brood years 1998–2009 for the Stikine River and the brood years 1999–2009 for the Chilkat River. The (**C**) relationship between log-transformed marine survival and smolt mid-eye fork length in the Stikine River and the (**D**) relationship between log-transformed marine survival and the first principal component (PC1) in the Chilkat River during the same sample periods are shown. Regression lines and 95% confidence intervals (gray areas) are presented in the bottom panels.

for BY 2004 to 3.9% (SE 0.6) for BY 2000. There was no significant temporal trend in marine survival of fish in the Stikine River (R^2=0.08, P=0.36) (Fig. 3).

Smolt Chinook salmon from the Stikine River were, on average, 74 mm in mid-eye fork length and ranged from 70 mm in 2005 to 81 mm in 2009. There was no significant trend in smolt length over the study period (BYs 1998–2009); however, mean smolt size in 2009 (81 mm) was substantially larger than in previous years and was considered an outlier in the data set. In summer (June–July) during the study period, mean SST was 12.1°C and SSTs ranged from 10.5°C to 13°C. Mean discharge in spring for the Stikine River was 1147 m^3/s (range: 679–1574 m^3/s), with no significant temporal trend (P=0.23).

Log-transformed marine survival of Chinook salmon in the Stikine River was significantly positively correlated to smolt length (R^2=0.26, P=0.05) (Table 5, Fig. 3). There were no significant relationships between marine survival and SST or between marine survival and spring discharge; therefore, neither relationship was included in the final model.

Discussion

Marine survival

Understanding factors influencing the survival and productivity of Chinook salmon during critical periods in their life history can enhance the accuracy of run forecasts of management agencies that are critical to efforts to sustain healthy populations well into the future. In this study, available data from 2 rivers in SEAK were used. Results of this research highlight variation in biological and environmental factors linked to marine survival of Chinook salmon from different BYs and stocks. Marine survival of Chinook salmon from the Chilkat River was correlated with the timing of the end of the smolt outmigration period, smolt length, and spring river conditions, and marine survival for Chinook salmon from the Stikine River was correlated to smolt body size. Previous research on marine survival of Pacific salmon has emphasized the importance of the early marine period in determining BY strength (Holtby et al., 1990; Graham et al., 2019). Although different factors influenced marine survival of Chinook salmon in the Stikine and Chilkat Rivers during the study period, these results reinforce the importance of the early marine period.

Table 4

Loadings of the first, second, and third principal components from a principal component analysis of environmental and biological variables used to explain variation in log-transformed marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in the Chilkat River in Southeast Alaska. Environmental variables include sea-surface temperature (SST), river discharge in spring, and river temperature in spring. Biological variables include migration timing and smolt length. Data used in this analysis were for Chinook salmon from the brood years 1999–2009.

Explanatory variable	PC1	PC2	PC3
Migration timing	–0.54	0.33	–0.10
SST	0.25	0.85	<0.01
Smolt length	–0.49	0.31	–0.29
Spring discharge	0.53	0.27	0.24
Spring river temperature	–0.36	0.06	0.92
Proportion of variance explained	0.54	0.22	0.15
Cumulative proportion	0.54	0.75	0.91

Marine survival was higher in the BYs when mean smolt length was longer, indicating that size-selective processes influence marine survival of Chinook salmon from both the Stikine and Chilkat Rivers. The movements of juvenile Chinook salmon from these rivers upon ocean entry are not well understood. However, the data on CWT recoveries in studies conducted by the ADFG indicate that adult fish from the Stikine River move offshore into the Gulf of Alaska and the Bering Sea and that fish from the Chilkat River inhabit the inside waters of northern SEAK (Pahlke et al.[5]; Elliott and Peterson[2]). Similarities in the relationship between smolt body size and marine survival in these 2 stocks further indicate the importance of freshwater growth and the early marine period, regardless of stock size or behavior.

Results of research on Chinook salmon in the Yukon River, sockeye salmon (*O. nerka*) across Alaska, and wild and hatchery-born chum salmon (*O. keta*) in SEAK also indicate that fish encounter increased size-selective pressures upon marine entry (Koenings et al., 1993; Murphy et al., 2013; Duncan and Beaudreau, 2019). Upon marine entry, smaller fish may encounter higher rates of predation from common nearshore species in SEAK, such as the Pacific staghorn sculpin (*Leptocottus armatus*) and Dolly Varden (*Salvelinus malma*), and larger fish may be more capable of emigrating farther from shore where pelagic zooplankton are more abundant (Koenings et al., 1993; Duncan and Beaudreau, 2019). Although the mechanisms that enhance the survival of larger (>74 mm in mid-eye fork length) juvenile fish in the Stikine and Chilkat Rivers are unclear, the results of our study and these other studies may indicate that size-selective pressures during the marine entry period are similar across stocks of Pacific salmon in the region.

The relationship between smolt size and marine survival also highlights the importance of the freshwater period

Table 5

Results from the final principal component regression and linear regression models used to examine the relationships between log-transformed marine survival and principal component 1 (PC1) and smolt length for Chinook salmon (*Oncorhynchus tshawytscha*) in the Chilkat and Stikine Rivers, respectively. The statistics used to evaluate the models include standardized regression coefficient (β), standard error of the coefficient (SE), coefficient divided by its standard error (t), and the coefficient of multiple determination (R^2). Data used in the models were for Chinook salmon from the brood years 1999–2009 for those from the Chilkat River and from the brood years 1998–2009 for those from the Stikine River.

Explanatory variable: marine survival	Response variable	Model statistic				
		β	SE	t	P	R^2
Chilkat River	PC1	–0.21	0.07	–3.03	0.01	0.5
Stikine River	Smolt length	0.25	0.11	2.18	0.05	0.26

and the conditions that allow for greater growth and larger smolt sizes. Smolt outmigration timing has been shown to be stock specific and to correlate with optimal local marine conditions (Hvidsten et al., 1998). Optimal conditions lead to fish experiencing favorable SSTs for growth, increased abundance of food resources, or reduced interactions with predators (Hvidsten et al., 1998; Mortensen et al., 2000). In our study, the end date of outmigration, which could only be tested for Chinook salmon in the Chilkat River, was positively related to marine survival, indicating that smolts of BYs that outmigrated later in the season had higher marine survival. Antonsson et al. (2010) similarly found that Atlantic salmon (*Salmo salar*) that migrated later had higher survival, but Mortensen et al. (2000) found that the earliest and latest emigrating smolt pink salmon (*O. gorbuscha*) had the lowest marine survival rates. Early outmigrants experienced colder water temperatures and lower prey densities, and that exposure likely resulted in lower survival (Mortensen et al., 2000). For Chinook salmon in the Chilkat River, migrations that ended later likely provided additional time for some smolts to attain a larger size before outmigration, given that mean smolt length was longer in years when migrations ended later. Alternatively, the later migration period may have distributed smolts over a wider range of conditions, increasing the chance that some individuals encountered favorable marine conditions.

Increased discharge in spring during outmigration can influence migration timing in some stocks and may also be linked to marine survival. For smolt Chinook salmon in the Nechako River, in British Columbia, high discharge and river temperatures resulted in shorter migration periods (Sykes et al., 2009). Lawson et al. (2004) found that high discharge in spring could facilitate outmigration by increasing swimming speed and allowing fish to be transported downstream more passively, potentially conserving energy reserves and improving survival. In our study, higher spring discharge resulted in earlier outmigrations and lower marine survival for Chinook salmon from the Chilkat River. In contrast, discharge was not significantly related to the survival of fish from the Stikine River. River conditions may be more indicative of the environment experienced by smolts that remain in coastal waters during the marine entry phase, when a large portion of marine mortality occurs. For example, smolt Chinook salmon from the Fraser River fared worse during years when discharge into the Strait of Georgia was high because it caused increased turbulence, reduced stability, and low production in estuarine areas (Gargett, 1997). High seasonal discharge may cause similar patterns in the inside waters of SEAK where Chinook salmon from the Chilkat River reside and, therefore, may limit survival. Alternatively, the lack of a relationship between discharge and marine survival of Chinook salmon from the Stikine River could be evidence of a rapid migration upon ocean entry to offshore waters that are less affected by freshwater discharge.

Local SSTs were not related to marine survival of Chinook salmon from the Stikine and Chilkat Rivers. Mortensen et al. (2000) found that higher SSTs in Auke Bay were related to higher growth and survival of pink salmon from Auke Creek, but Briscoe et al. (2005) found no correlation between local SST and marine survival of jack and adult coho salmon (*O. kisutch*) in the same system. Increases in survival related to SSTs stem from optimal growth conditions because temperature is the primary function that controls metabolic and growth rates for ectotherms (Brett et al., 1969; Groot et al., 1995). Sea-surface temperatures can also affect ocean conditions, such as upwelling, food availability, and predator assemblages, all of which may aid or hamper growth and survival of Pacific salmon (Cole, 2000; Mortensen et al., 2000; Mueter et al., 2002b). Mueter et al. (2005) found that warmer coastal SSTs were associated with increased survival for chum, sockeye, and pink salmon in Alaska. Similar results have been reported for Chinook salmon in the Unuk River, northeast of Ketchikan, Alaska, with higher marine survival occurring with higher coastal SSTs (Graham, 2016).

The lack of a relationship between nearshore SSTs and marine survival of Chinook salmon in the Stikine and Chilkat Rivers could be because the majority of individuals grew elsewhere. As mentioned previously, it is possible that most of the smolts from the Stikine River migrate directly and more rapidly to more open-ocean areas rather than occupying more nearshore waters upon marine entry as assumed in our study. Marine survival of Chinook salmon from the Chilkat River, a stock that is believed to grow in the inside waters of northern SEAK, was correlated to migration timing and river conditions but not to nearshore SSTs. Conducting trawl surveys during the summer in Icy Strait, a known migration corridor for salmon in northern SEAK, Orsi et al. (2013) found few ocean age-0 Chinook salmon in summer trawl hauls, indicating that these fish may be nonmigratory upon marine entry and remain in more local areas. Alternatively, average SST from June and July could have been too broad a range to detect a process that occurred over days or weeks, rather than over months, for Chinook salmon from the 2 rivers (Briscoe et al., 2005).

Overwinter survival and smolt production

Freshwater indices of survival and production were tested only for Chinook salmon from the Chilkat River because of constraints in data availability. We found that lower discharge in fall and higher discharge in early spring were associated with increased smolt production in the Chilkat River. Results from previous research indicate high variability and seasonality in the relationships between the freshwater life stage of salmon and river discharge. Low discharge levels in the fall and winter have been reported to limit survival and smolt production, likely reducing migratory pathways in the fall and overwintering habitat availability in some systems (Lawson et al., 2004; Crozier and Zabel, 2006). High discharge in summer has been linked to low production of stream-type juvenile Chinook salmon in the Yukon River, in Alaska, possibly because high discharge caused velocity barriers that limited habitat that was safe for drift foraging and increased risk-taking behaviors induced by foraging (Neuswanger et al., 2014). High spring flows have been determined to improve survival during smolt outmigration because higher discharge is associated with increased turbidity, which could protect fish visually from predators (Lawson et al., 2004). In our study, increased smolt production associated with low discharge in fall could indicate that these conditions enable increased fall foraging opportunities without limiting pre-winter migration corridors or habitat. Higher flows in early spring could increase habitat and drift-feeding opportunities while reducing competitive interactions between juvenile salmonids after the less productive winter period (Lawson et al., 2004).

Acclimation costs linked to changing water temperatures that occur in the fall and spring can result in the depletion of lipid reserves and lower body condition, possibly reducing salmonid survival during long winters (Cunjak et al., 1987). In our study, increased smolt production of Chinook salmon in the Chilkat River was correlated with warmer temperatures (>4°C) in early spring, potentially reflecting a survival advantage when winter periods are shorter and followed by warmer spring water temperatures. In contrast, Lawson et al. (2004) related air temperature to freshwater production of coho salmon in Oregon, near the southern end of their range, and found lower smolt production during years with higher annual temperatures. The variance in these results may be attributed to the lower range of temperatures in glacially fed streams, temperatures that do not reach the higher than optimal temperatures for streams, as they do in the streams in southern Oregon.

Body size of juveniles has also been proven to influence freshwater survival and production of salmonids. Larger body size has been linked to increased overwinter survival and production because higher lipid reserves enable larger individuals to tolerate harsh winter conditions, increase size-based predator avoidance abilities, and allow competitive advantages over smaller individuals for quality habitats (Quinn and Peterson, 1996; Meyer and Griffith, 1997; Zabel and Achord, 2004). In our study, higher smolt production was related to smaller parr body size for Chinook salmon, indicating density dependence in the freshwater environment because parr length was also negatively correlated with parr abundance. Armstrong and Griffiths (2001) found that the proportion of Atlantic salmon sheltering during the freshwater overwinter period decreased with abundance. In the Chilkat River, higher densities could have reduced the scope for growth because of competition for food or habitat refugia. Small body size may also be beneficial. For example, Carlson and Letcher (2003) observed that in 2 trout species, the brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*), older, larger individuals had lower survival rates than younger, smaller individuals and suggested that this relationship may be a result of larger fish being more habitat limited in winter and, therefore, more susceptible to predation. Density-dependent effects during the freshwater phase that limit parr body size may also affect marine survival, given that smolt size was an important indicator of BY success for Chinook salmon from the Chilkat River.

Conclusions

The results of our study indicate that environmental mechanisms influencing survival of Chinook salmon in SEAK were stock specific, as has been observed for other stocks of Pacific salmon in this region (Malick et al., 2009). River conditions in spring appear to have influenced marine survival of Chinook salmon in the Chilkat River but not in the Stikine River, possibly as a result of the differences between stocks in offshore foraging locations. Smolt length may influence survival in both rivers, and results from this study reinforced the importance of environmental and biological factors on freshwater production and early marine survival for determining brood strength of stocks of Pacific salmon. Warmer water temperatures and increased river discharge projected to occur as a result of climate change may affect these critical survival periods if mismatches between feeding and growth conditions are exaggerated in both freshwater and marine systems. Because reductions in the productivity and abundance of stocks of Chinook salmon throughout SEAK have led to increased effort for stock assessments and to reductions in allowable catch, understanding critical periods in the life history of these stocks was key (ADFG CSRT[1]).

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