

Role of estuarine rearing for sockeye salmon in Alaska (USA)

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ABSTRACT: A suite of adaptive traits allows Pacific salmon to exploit diverse habitats during their lives, facilitating their persistence in highly variable and heterogeneous environments. We investigated how juvenile sockeye salmon *Oncorhynchus nerka*, which typically rear in lakes before migrating rapidly to sea, make use of riverine and estuarine habitats in the Chignik Lake system (Alaska, USA) where lacustrine rearing capacity limits sockeye salmon productivity. Their distribution, growth, and genetic stock composition were examined during June to August, 2007 to 2009. Sockeye salmon inhabited the estuary for up to 3 mo each summer, representing 2 distinct age classes: Age-0 fry and parr, and Age 1+ smolts. The fry and parr grew rapidly in the estuary, attaining sizes comparable to the lake-reared smolts. Smolts also grew in the estuary in all years, although they occupied the estuary for a briefer period in years when they entered at a larger size. Using genetic mixture analyses, fry and parr in the estuary were assigned to a population that spawns in Chignik River immediately upstream of the estuary, whereas the smolts were assigned to 2 genetically distinct population groups associated with separate nursery lakes farther up in the basin. Our findings highlight the role of estuaries for juvenile sockeye salmon in systems with limited freshwater rearing capacity and high salmon density. The persistence of such populations depends in part on preserving a continuum of habitat types, especially in the southern range of the species where a shifting climate and human activities are expected to most greatly impact populations.

KEY WORDS: *Oncorhynchus nerka* · Life history variation · Estuary · Rearing habitat · Juvenile growth · Genetic stock composition · Single nucleotide polymorphism · Climate

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INTRODUCTION

The life history diversity which contributes to the persistence of Pacific salmon *Oncorhynchus* spp. populations is largely shaped by phenotypic plasticity and evolutionary responses to environmental variation (Waples et al. 2008, Quinn et al. 2009). Anthropogenic disturbances to freshwater systems threaten salmon resilience, especially for populations whose juveniles depend on periods of extended freshwater development, such as sockeye *O. nerka*, Chinook *O. tshawytscha*, and coho *O. kisutch* salmon

and steelhead trout *O. mykiss*. Degraded freshwater habitats and a warmer climate have led to higher extinction rates for such populations in the western continental USA (Gustafson et al. 2007) compared to species with short freshwater residence periods such as pink *O. gorbuscha* and chum salmon *O. keta*. Where freshwater habitats are under pressure, salmon populations that depend on freshwater growth may persist through the use of alternative habitats such as estuaries (Healey 2009, Koski 2009).

Estuaries provide a number of functions for Pacific salmon, including an osmoregulatory gradient and

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migration corridor for smolts (Thorpe 1994). Estuarine productivity supports rapid growth in juvenile salmon (Neilson et al. 1985) which has been associated with higher early marine survival for both wild (Reimers 1973) and hatchery-reared Chinook salmon (Magnusson & Hilborn 2003). Additionally, salmonid populations can augment their juvenile freshwater development through the use of brackish habitats in systems where freshwater rearing is limited by overall productivity or density-dependent processes (Hayes et al. 2008). For steelhead in Scott Creek (California, USA), the estuary supports higher growth and survival rates compared to stream-reared counterparts in other coastal California systems (Bond et al. 2008). In this way, estuaries can support growth and development for populations that are affected by freshwater habitat degradation, contributing to the diversity of life history patterns supported by a system.

Three life history variants, or ecotypes, of anadromous sockeye salmon are recognized (Wood et al. 2008). The most common variant is the lake-type, which rears in nursery lakes for up to 3 yr (typically 1 or 2 yr) prior to seaward migration. In addition, there are 2 non-lake rearing forms. Sea-type sockeye salmon migrate to sea within their first year, whereas the river-type migrates after growing for 1 yr in a river (Gilbert 1913, Burgner 1991). For the sea-type, Age-0 fry and older Age-0 parr remain in off-channel river and estuary habitats for up to 4 mo prior to seaward migration (Birtwell et al. 1987, Heifetz et al. 1989). In contrast, the river-type may migrate downstream shortly after emergence but delay entry to the estuary, using off-channel river habitats and sloughs for up to 1 yr (Murphy et al. 1988, Powers et al. 2007). Non-lake-rearing ecotypes typically occur in coastal systems in the northern range of the species (Wood et al. 1987), from the Stikine River in northern British Columbia (Canada) to the Bolshaya (Semko 1954) and Kamchatka rivers in Russia (Krogus 1958), but there are also small populations in rivers towards the southern end of the species' range (Gustafson & Winans 1999). These systems are often characterized by low freshwater productivity that is unable to support juvenile sockeye salmon metabolic demands (Kaeriyama 1996).

Most cases of sea- and river-type life history variants represent small, persistent populations whose early life history and ecology are less understood than the more abundant lake ecotype (Foerster 1968). However, in systems where lake habitat is limited or absent (Wood et al. 1987), these non-lake life histories can contribute significantly to the overall productivity of sockeye salmon. For example, sea-

type and river-type sockeye salmon contribute a combined 39 to 48% of the overall sockeye salmon production in the Stikine River (Wood et al. 1987). The neighboring glacial transboundary rivers also support large populations of non-lake ecotypes (Pahlke & Riffe 1988). Presumably, the high proportions of sea-type and river-type sockeye salmon returning to the Ilnik system on the Alaska Peninsula (36 to 45% in 2006 to 2009; Foster 2011) is in part due to its lack of lake rearing habitat.

While estuarine use by sockeye salmon is most often attributed to the sea-type life history variant (Birtwell et al. 1987, Heifetz et al. 1989), subtle estuarine associations with non-sea-type life history variants may also occur but remain undocumented due to the difficulty of separating population groups within the mixed stock complex in estuaries. Documenting the range of habitats used by each life history type could provide valuable information about how sockeye salmon may compensate for the loss of commonly used habitats such as lakes. More broadly, such information is necessary to inform management measures that conserve the full range of available habitats that support early development and population persistence (Healey & Prince 1995). During 2007 to 2009, we used field and genetic techniques to identify patterns of summer habitat use by juvenile sockeye salmon populations and ecotypes in the Chignik Lake system in southwestern Alaska. The objective of this study was to increase understanding of estuarine use by sockeye salmon by characterizing the range of non-lake habitats used by multiple sockeye salmon ecotypes in a system with available lake habitat. Previous studies in Chignik have documented the occurrence of juvenile sockeye salmon in both the river and estuary habitats (Iverson 1966, Phinney 1968), although the stock compositions of these sockeye salmon were never determined.

MATERIALS AND METHODS

Study area

The Chignik Lake system on the Alaska Peninsula is composed of 2 interconnected lakes, associated tributary rivers, and a large brackish estuary. Black Lake sits in a shallow topographic depression in the upper watershed, and is connected downstream to Chignik Lake via a 15 km stretch of braided river (Fig. 1). This study focused on components of the lower system, including (1) the Chignik River, (2) the interface between the Chignik River and Chignik

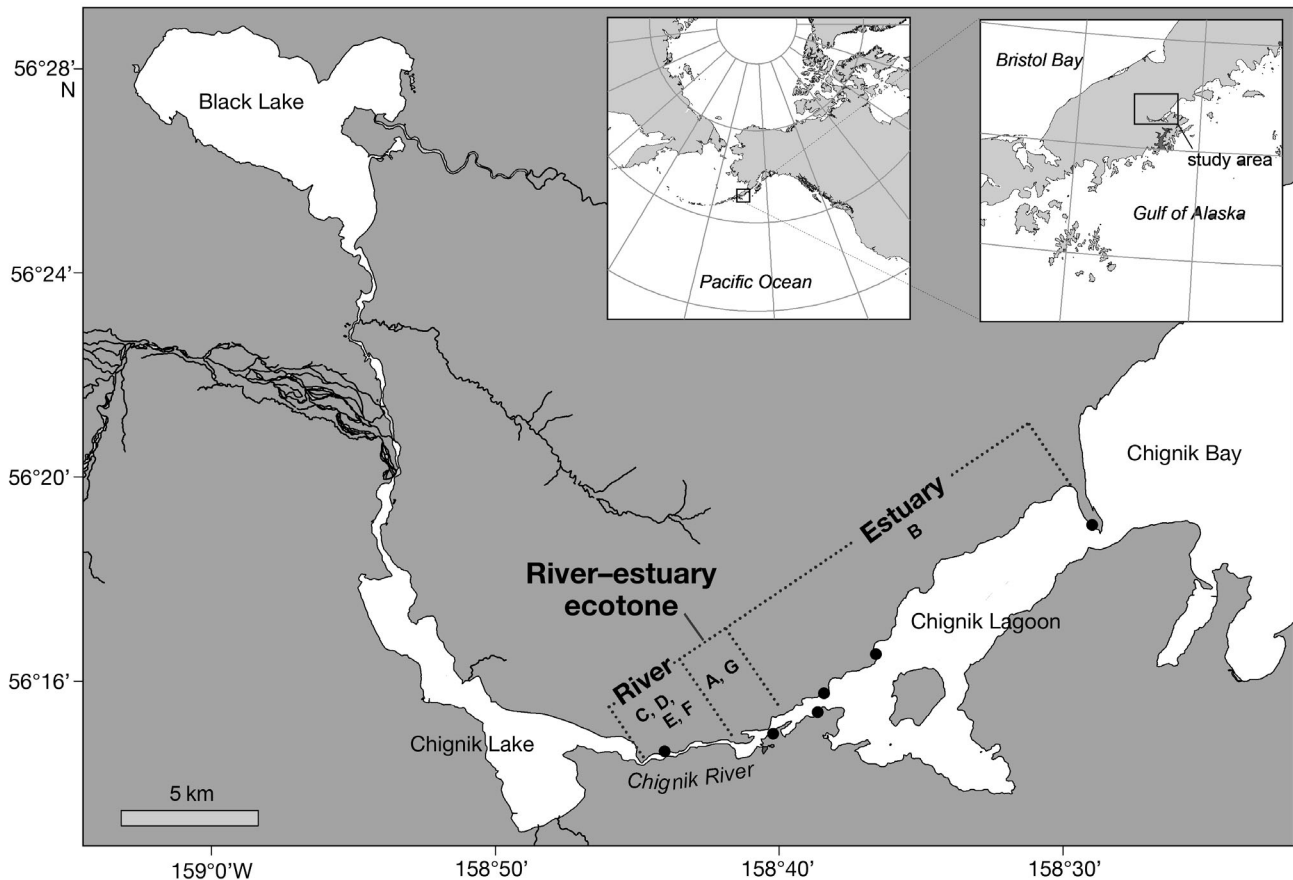


Fig. 1. Chignik watershed, Alaska, USA, including sample sites (●). Sampling location(s) of each group of fish tested in genetic mixture analyses are denoted by letters A through G

Lagoon (hereafter called the river–estuary ecotone; Odum 1971), and (3) Chignik Lagoon itself (the estuary; Fig. 1). The Chignik River is a short (4 km) and moderate-velocity outflow from Chignik Lake. It is the principal freshwater input into Chignik Lagoon and the only river connected to the lagoon that supports sockeye salmon. Chignik River flows into the estuary through a transitional river–estuary environment, characterized by low salinities (0–6‰) and strong tidal flushing (Fig. 1). This ecotone transitions into Chignik Lagoon, a 9 km² semi-enclosed shallow estuary that is protected from the Gulf of Alaska by a sand spit. Tidal amplitudes exceeding 3 m can expose half of the estuarine substrate, largely covered by eel grass *Zostera* spp., at low tides (Phinney 1968). A strong salinity gradient exists across the estuary, reflecting the influence of full marine seawater (>30‰) flowing into the estuary near the outer sand spit and the influx of freshwater from the Chignik River outflow. The inner estuary, where much of the sampling occurred during this study, is characterized by relatively low salinities (<15‰).

Sockeye capture, scale pattern analysis, and apparent growth

Juvenile sockeye salmon were sampled from the estuary (4 sites) and river–estuary ecotone (1 site) using a beach seine (30 × 3 m with 3 mm mesh). Sampling at each site occurred every 2 wk during high tide from June to August, 2007 to 2009. Catch per unit effort (CPUE) was calculated as the number of sockeye salmon caught per beach seine haul. The period of estuarine residence by a subset of the smolt outmigrants (rather than individual residence) was inferred based on the CPUE of smolts in estuarine sampling each year paired with downstream migration CPUE data in 2008. Additional sampling occurred in Chignik River in mid-June through August 2008 to characterize downstream and upstream movements of juvenile sockeye salmon after the peak of the smolt outmigration (mid-June; Finkle & Ruhl 2009). Downstream movement was assessed using 2 fyke nets (one with a 1 m² opening with 3 × 1 m wings; one with a 1.22 m² opening with 5 ×

1.22 m wings) that were deployed overnight near the river thalweg every 7 to 10 d. Fyke net CPUE was calculated as the number of sockeye salmon captured per hour of deployment for each sampling event and net. Upstream movement of juvenile sockeye salmon was assessed near the outlet of Chignik Lake using a 10 m block net (4 mm stretch mesh). The net was angled downstream from the shoreline toward the river thalweg, where water velocities surpassed the maximum swimming speed of juvenile sockeye salmon (Brett 1964). This effectively guided upstream-moving individuals into the shallows where they were collected and enumerated after each 10 min deployment. Chignik River was also sampled using the beach seine on 26 July 2008 for DNA samples.

Sockeye salmon captured by the 3 sampling methods were enumerated, and a subsample of individuals (target $n = 200$ for beach seine; target $n = 100$ for fyke net and block net) was measured (fork length, FL, in mm) and weighed (nearest 0.1 g, wet weight). Subsample targets were not always achieved. Caudal fin tissue was removed from subsampled individuals and preserved in 2.0 ml of 95% ethanol for DNA extraction during 2007 and 2008 sampling. Scale samples were removed from sockeye salmon (>45 mm, approximately the size at which scales are formed) captured in the estuary and ecotone during July ($n = 123$) and August ($n = 118$) in 2007. Scales were scraped from above the lateral line as described by Koo (1962) and mounted onto glass microscope slides. Scales were magnified using a microfiche reader to determine the age at capture by counting annuli along the anterior portion of the scale's longest axis. Scale annuli were identified as areas of narrowing between circuli and transition to irregular banding which may include broken or crossover circuli patterns.

Apparent growth rates were estimated for sockeye salmon life stages in the estuary when these life stages could be clearly separated by dividing the difference in mean length between 2 sample dates by the number of days between the sample dates. All juvenile sockeye salmon captured in this study were categorized by their most likely life stage to better characterize the life histories present in the ecotone and the estuary. Due to the continuous nature of fish lengths encountered, and the interannual variation in size patterns, life stage groups in the ecotone and estuary were determined using a combination of age, length, and date of capture information. Three life stages were identified during the course of the study, including Age-0 fry, Age-0 parr, and smolts. Because

the parr and smolt length frequencies commonly overlapped in the ecotone and estuary, the first quartile of all smolt lengths measured annually in the Chignik River (Finkle & Ruhl 2009) was used to separate these 2 life stages to estimate the relative catch of smolts by month. The first quartile was preferred over other metrics to best characterize the lower size range of smolts because it placed less weight upon the highly variable sizes (usually much shorter FL) and low abundances of late-season smolts recorded in the Chignik River smolt trap (Finkle & Ruhl 2009).

DNA extraction and single nucleotide polymorphism (SNP) genotyping

Seven collections of juvenile sockeye salmon were screened for genetic variation and assigned a corresponding letter (A through G; Table 1). Each collection consisted of a group of individuals captured at a specific location either during a single sampling event or over a period of time; collection sizes ranged from 196 to 230 individuals. Genomic DNA extraction was performed using Qiagen DNeasy 96 tissue kits. Individuals were genotyped using the protocol developed by Seeb et al. (2009), using Fluidigm 96.96 Dynamic Arrays. Each 96-well plate was loaded with sample DNA from 95 individuals (the 96th well used as a no-template control using TE buffer), and the TaqMan assays for the 45 sockeye salmon SNPs described by Creelman et al. (2011) and Habicht et al. (2010) using an automated workstation. Plates were then pressurized using a Fluidigm Integrated Fluidic Circuit Controller HX to load the mixtures into the plate array. DNA amplification followed Seeb et al. (2009), using a polymerase chain reaction (PCR) in thermal cyclers programmed for 50 cycles of 92°C for 15 s and 60°C for 1 min. A Fluidigm Biomark was used for end-point reads of each plate array. Each plate array was subsequently scored independently by 2 researchers using genotyping software provided by Fluidigm. To control for potential genotyping discrepancies, 8 individuals from each plate were reanalyzed for all 45 SNP assays.

Mixed stock analysis

A basin-wide genetic baseline was developed previously by Creelman et al. (2011), based on SNP markers representing 2013 sockeye salmon individuals from the major spawning populations within the

Table 1. *Oncorhynchus nerka*. Metadata and genetic mixture analysis results for sample collections (A through G) of juvenile sockeye salmon collected in the lower Chignik watershed (Alaska, USA) during 2007 and 2008. Sample location, sample date, the directional movement of fish (m) targeted by each sampling (i.e. upstream: u/s, downstream: d/s, or no movement: -), and sample size (n) are reported for each collection. Stock group proportion estimates include the mean posterior proportion (in **bold**) and the 2.5 and 97.5 credibility intervals. Shaded posterior proportions indicate mean values of 10 to 50% (light grey) and 50 to 100% (dark grey). Sample collections with multiple dates represent the span of time in which tissues were collected. Mean posterior proportions may not add to 1.0 due to rounding

		Collection						
		A	B	C	D	E	F	G
Location		Ecotone	Estuary	River	River	River	River	Ecotone
Year		2007	2007	2008	2008	2008	2008	2008
Date (m/dd)		6/13–7/23	7/5–7/23	7/14	7/26	7/30	8/19–8/20	8/9
m		–	–	u/s	–	d/s	u/s	–
n		230	201	199	202	196	199	196
Black Lake	2.5 %	0.00	0.17	0.17	0.08	0.00	0.00	0.11
	Mean	0.00	0.25	0.32	0.25	0.12	0.04	0.26
	97.5 %	0.02	0.33	0.47	0.43	0.25	0.15	0.41
Chignik Lake	2.5 %	0.00	0.00	0.53	0.51	0.75	0.85	0.37
	Mean	0.01	0.02	0.68	0.71	0.88	0.96	0.54
	97.5 %	0.05	0.07	0.83	0.90	1.00	1.00	0.97
Chignik River	2.5 %	0.94	0.65	0.00	0.00	0.00	0.00	0.13
	Mean	0.98	0.73	0.00	0.04	0.00	0.00	0.21
	97.5 %	1.00	0.81	0.21	0.14	0.03	0.01	0.30

system. Based on levels of genetic differentiation, these populations fell into 3 reporting groups that reflected unique geographic regions where spawning and rearing of those populations occur, including (1) a Black Lake group; (2) a Chignik Lake group; and (3) a single population spawning in the Chignik River near the estuary. The baseline and reporting groups developed by Creelman et al. (2011) were used in the mixed stock analysis portion of this study. The development and structure of this genetic baseline and the reporting groups are fully described by Creelman et al. (2011).

The stock composition of each of the 7 mixtures of genotyped individuals was estimated using the program BAYES (Pella & Masuda 2001), which uses Bayesian methods to estimate the relative contribution of each of the 3 baseline reporting groups (Black Lake, Chignik Lake, and Chignik River) in each mixture. Treatment of the 45 original loci in each of the 7 mixtures followed Creelman et al. (2011), resulting in the combining of 5 loci into 2 and the removal of 3 others for a final total of 39 unique loci. The 14 pooled and unpooled baseline collections from across the watershed were each assigned a flat prior to give them equal weight in the BAYES analyses. Flat priors were assigned because we had no *a priori* information regarding the genetic composition of the collections. Three Monte Carlo Markov chains (MCMC) of

20 000 iterations were used for testing each sample mixture (burn-in samples = 10 000). Each of the 3 chains started with a different set of majority contributions by baseline collection, using a combination of 0.90, 0.05, and 0.05. Estimates of the stock-group compositions from each MCMC sample chain were then summarized by combining the 3 chains for the mean estimate 95% probability intervals for each reporting group. The univariate shrink factor described by Gelman & Rubin (1992) was used to test for convergence of each estimate to the posterior probability density.

RESULTS

Sockeye size, age, and distribution in the ecotone and estuary

Sockeye salmon fry and smolts were abundant in both the river–estuary ecotone and Chignik Lagoon during all 3 summers, but the size distributions varied markedly between years. These size differences were driven by interannual variation in both the relative abundance of sockeye salmon fry (<40 mm) and the mean size of smolts entering these habitats (Fig. 2). Sockeye salmon fry were present in great numbers during the early summer only in 2007, pri-

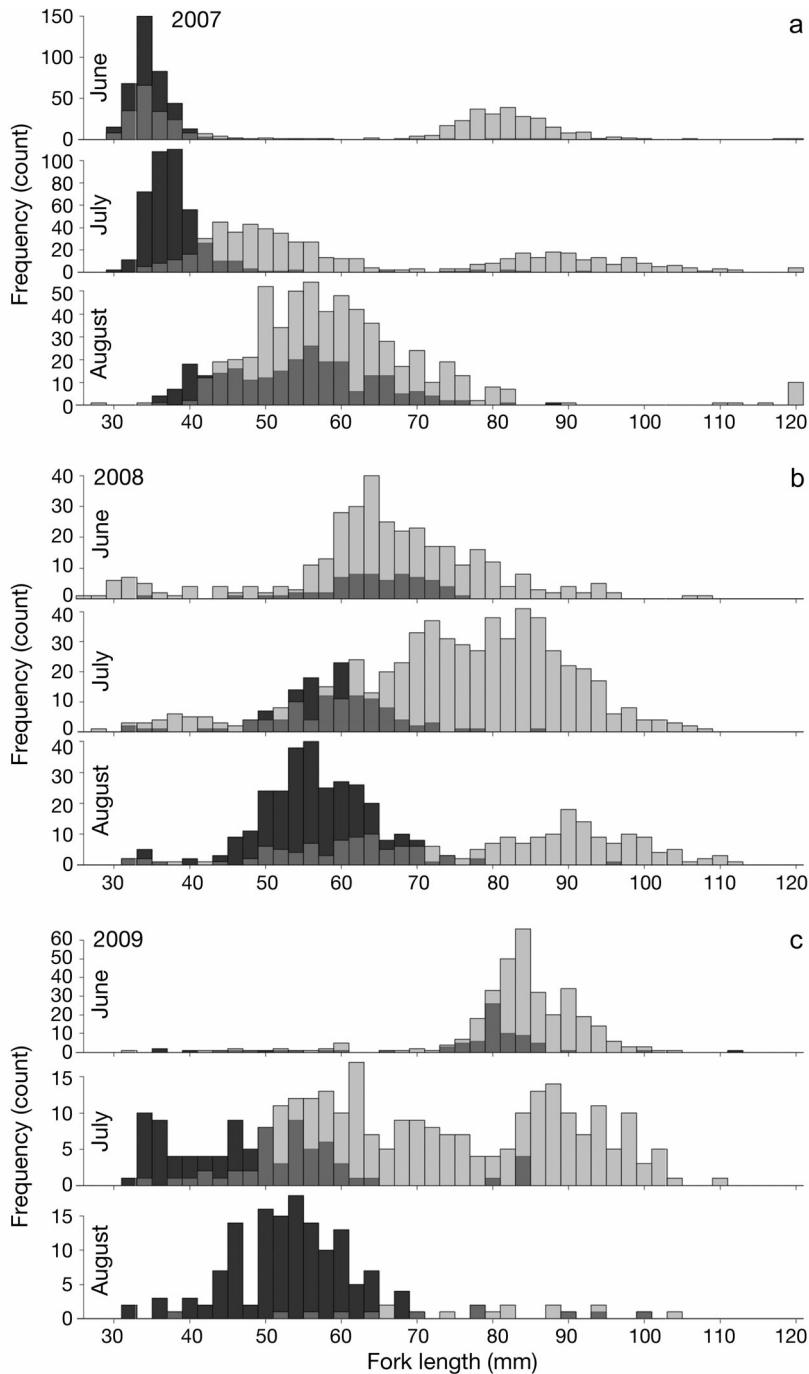


Fig. 2. *Oncorhynchus nerka*. Combined length–frequency distribution of sockeye salmon captured by beach seine during June, July, and August of (a) 2007, (b) 2008, and (c) 2009 in the river–estuary ecotone (dark grey bars) and estuary (light grey bars). Histogram bars are semi-transparent, leading to an intermediate shade of grey where the length frequencies from the ecotone and estuary overlap. A plus group was included for fish >120 mm for (a)

marily in the river–estuary ecotone where salinities were lowest. This preponderance of fry in the river–estuary ecotone lasted until 23 July in 2007, when the modal length increased abruptly by 15 mm by

7 August to mirror the length frequency in the estuary itself (Fig. 2). Sub-yearling parr (fish ≤ 70 mm in July; ≤ 80 mm in August) were most abundant in July and August during all 3 years, and were captured in both the ecotone and estuary (Fig. 2). Smolts were mainly caught in the estuary itself, where they were a common component of the catch until late July in 2007 and 2009, and late August in 2008 based on CPUE (Fig. 3). CPUE was higher in salinities $\leq 9\text{‰}$ versus $>9\text{‰}$ in 2007 (mean \pm SE: 161 ± 29 versus 30 ± 9) and 2008 (88 ± 24 versus 69 ± 17), but not 2009 (73 ± 31 versus 89 ± 33). Small sockeye salmon (<60 mm) were most common in salinities $\leq 9\text{‰}$, and were limited almost exclusively to these low salinities in 2008 and 2009 (Fig. 4). In 2007, however, small sockeye salmon were abundant across the entire salinity gradient (Fig. 4).

Age analysis from scales in 2007 indicated that a portion of Age-0 fry/parr attained sizes comparable to smolts that were at least 1 yr older (Fig. 5). Apparent growth rates of both the Age-0 fry/parr complex and smolts were estimated in 2007 due to the clear separation of length frequencies during that year (Fig. 2). During their summer residence in the estuary, smolts grew an average of 0.39 mm d^{-1} , increasing in average size by 12 mm between 8 June (mean \pm SE: 79.4 ± 0.85 mm) and 9 July (91.5 ± 1.3 mm). Age-0 fry/parr grew at a similar rate (0.33 mm d^{-1} , from 34.5 ± 0.57 mm on 8 June to 61.9 ± 0.64 mm on 27 August). Overlap in size frequency between life stages in 2008 and 2009 precluded similar estimates of growth rates in these years. However, inspection of smolt length frequencies suggested that similar rates of growth occurred during these years (Fig. 2). A dramatic shift in age composition signaled the departure of the majority of smolts in the estuary between July and August in 2007, with the relative proportion of Age-1 sockeye salmon dropping from 89 to 36% between months (Fig. 6).

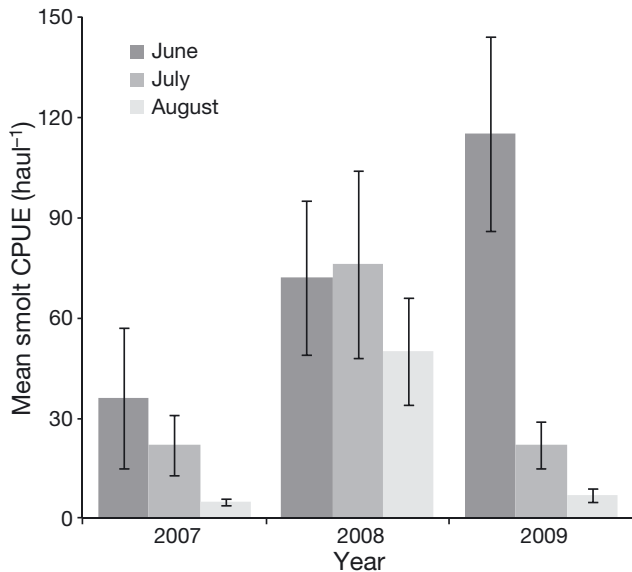


Fig. 3. *Oncorhynchus nerka*. Mean \pm SE catch per unit effort (CPUE, fish haul⁻¹) by beach seine of sockeye salmon smolts in the estuary during June to August, 2007 to 2009

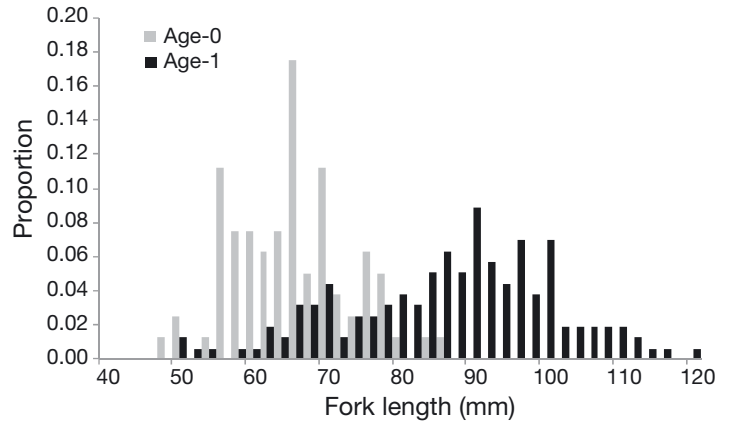


Fig. 5. *Oncorhynchus nerka*. Length-frequency distribution by age class of sockeye salmon that were captured and aged during 2007 in the river–estuary ecotone and estuary, including Age-0 (n = 80) and Age-1 (n = 158) individuals. Age-2 sockeye salmon are not included (n = 6)

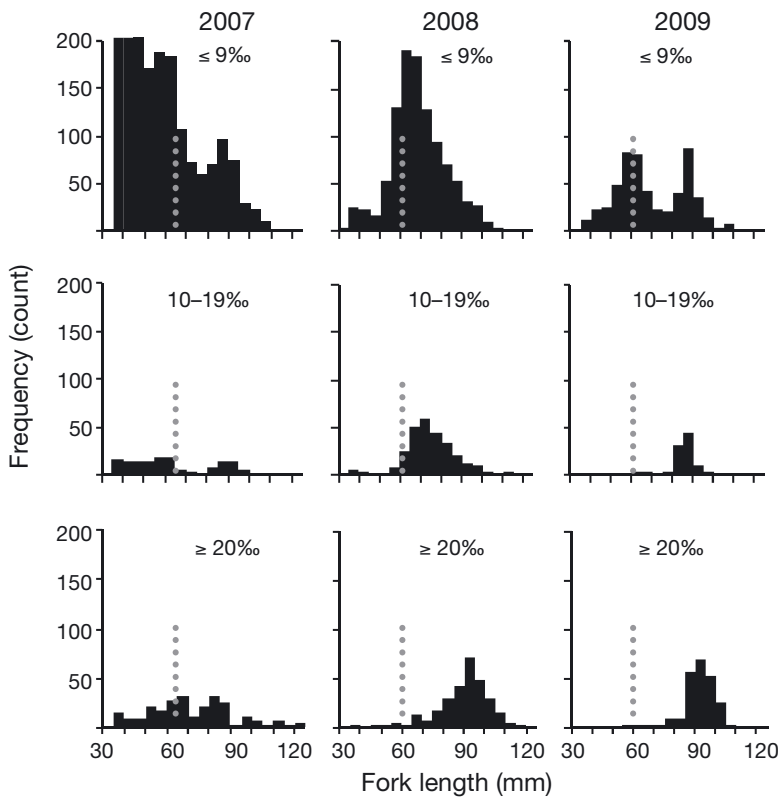


Fig. 4. *Oncorhynchus nerka*. Length-frequency distribution of sockeye salmon grouped by the salinity (≤ 9 , 10–19, ≥ 20 ‰) at which fish were captured in the river–estuary ecotone and the estuary during June to August, 2007 to 2009. Vertical dotted lines indicate the 60 mm fork length cutoff, below which fish display different preferences for the mid- and high-range salinities between years

Seasonal movements of sockeye in Chignik River

Sockeye salmon displayed differing patterns of downstream and upstream movement throughout the summer of 2008. The smaller fyke net was not effective in capturing sockeye salmon, so CPUE and length comparisons were drawn from fish captured in the larger fyke net. Downstream movement of sockeye salmon peaked in June and decreased steadily through the summer (Fig. 7). The mean FL of downstream migrants also peaked in June and decreased through the period of sampling (Fig. 8), dropping below the mean FL of smolts captured in the Chignik River smolt trap operated by the Alaska Department of Fish and Game (ADF&G) by late June (FL = 63 mm; Finkle & Ruhl 2009). In contrast, the mean size of upstream migrants remained relatively unchanged during the same period (Fig. 8) and was larger than downstream migrant mean size in both July and August ($p < 0.001$ and < 0.05 , respectively, 2-sample t -tests for samples with unequal variance). Sockeye salmon fry were only captured moving downstream towards the river–estuary ecotone and estuary, never upstream.

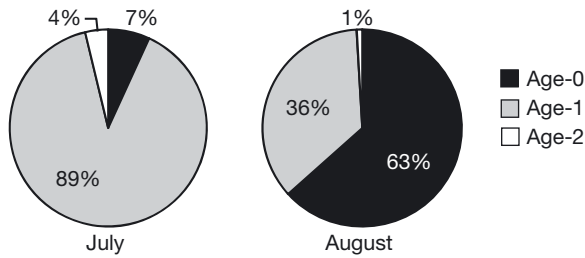


Fig. 6. *Oncorhynchus nerka*. Age class proportions (Age-0 through Age-2) of sockeye salmon aged during 2007 in the the river–estuary ecotone and estuary

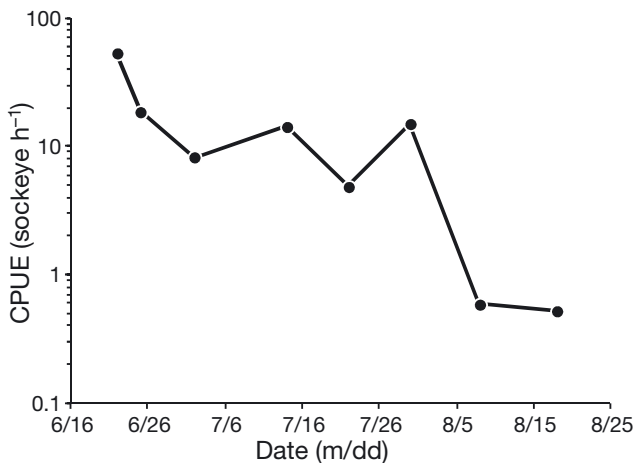


Fig. 7. *Oncorhynchus nerka*. Catch per unit effort (CPUE, fish h⁻¹) by the large fyke net of sockeye salmon moving downstream in Chignik River during June to August 2008

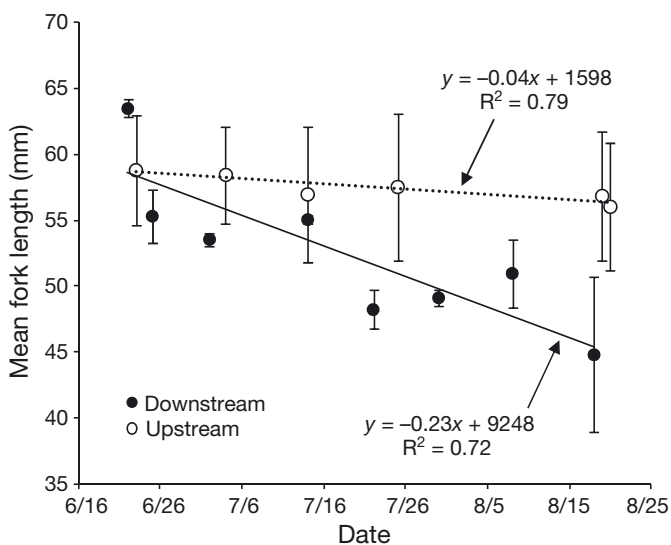


Fig. 8. *Oncorhynchus nerka*. Mean fork length (\pm SE) of sockeye salmon moving both downstream (●) and upstream (○) in Chignik River during June to August 2008

Stock proportions by habitat

Convergence was achieved for all MCMC chains performed in BAYES, with shrink factor values between 1.00 and 1.03. While the 2007 and 2008 datasets were not entirely comparable, differences in genetic composition between years were driven in part by the interannual variation in the relative abundance of fry in beach seine catches between 2007 and 2008 (Table 1, Fig. 2). During 2007, the Chignik River population dominated both the river–estuary ecotone (98%) and the estuary itself (73%). By contrast, in 2008, the Chignik River population accounted for only 21% of the fish sampled in the river–estuary ecotone (Table 1), although collections from the ecotone were sampled in different months in 2007 and 2008. The Chignik River population only accounted for 4% of the 796 sockeye salmon sampled from the Chignik River for genetic analysis, and upstream movements in the Chignik River were composed entirely of lake-reared individuals. Chignik Lake was consistently dominant (54 to 96%) in both the river and river–estuary ecotone in 2008. Black Lake was the next largest component, with the greatest proportions in-river in July (12 to 32%) and in the river–estuary ecotone in August (26%; Table 1).

DISCUSSION

Juvenile sockeye salmon in estuary and river habitats

The estuary was used extensively by 2 distinct groups of juvenile sockeye salmon: Age-1 lake-reared smolts and Age-0 fry and parr. Downstream migrant sampling in 2008 indicated that the influx of smolts into the estuary through the Chignik River was largely over by late June, consistent with smolt sampling conducted by ADF&G in the Chignik River (Finkle & Ruhl 2009). Thus smolts captured in the estuary during July and August likely exhibited some period of residence within the estuary after leaving the Chignik River. Size at entry in the estuary affected the duration of estuarine residence for at least a subset of lake-reared sockeye smolts, with larger average smolts in 2007 and 2009 (mean FL: 83 and 75 mm, respectively) spending less time in the estuary than smolts in 2008 (mean FL: 63 mm; Figs. 2 & 3). Age-2 smolts used the estuary primarily as a migration corridor, likely remaining offshore as they moved through the habitat, as indicated by their scarcity in beach seine catches. In contrast, Age-1

smolt residence was likely more variable, with a subset still available to the sampling gear for up to 2 mo in 2007 and 2009 and 3 mo in 2008. Age-1 smolts may balance the tradeoff of leaving at a younger age and smaller size with growth opportunity in the estuary to offset size-selective mortality in their early life at sea (Koenings et al. 1993, Farley et al. 2007b).

The origin of sockeye salmon fry and parr in the estuary was of great interest due to their highly variable interannual abundances and their rapid growth in the estuary. Genetic mixture analyses indicated that the Chignik River population, spawning adjacent to the ecotone and lagoon, was the main source of these fry and parr in both habitats during 2007. This was corroborated by 2008 sampling, when a drop in relative fry abundance in the ecotone matched a drop in the estimated proportion of the Chignik River population at this site, although these are not entirely comparable datasets, since the ecotone collections were sampled in different months in 2007 and 2008. Still, interannual variation in adult returns and spawning production of the Chignik River population may in part determine the relative availability of juveniles from this population for capture and subsequent genetic analysis. Moreover, an unusually large flood in December 2007 likely reduced embryo survival in the Chignik River population incubating in the river bed.

The Chignik River population was previously believed to migrate upstream after emergence to rear in the adjacent nursery lake (Narver 1966). A genetically-based positive rheotaxis or upstream orientation is commonly observed in sockeye salmon populations that emerge below nursery lakes, guiding migration into the lake (e.g. Babine Lake: McCart 1967, Clarke & Smith 1972; Karluk Lake: Raleigh 1967; Chilko Lake: Brannon 1972). Often, fry emerging in these rivers move downstream immediately after emerging from the gravel but within a few days or weeks migrate upstream during the day into their nursery lake. While we found extended residence in downstream brackish habitats for up to 3 mo, we still anticipated that the Chignik River population would be detected in mixture analyses of upstream migrants moving into Chignik Lake via the Chignik River. However, we found no evidence of movement toward Chignik Lake by this population either as emergent fry or larger parr during 2008. Instead, upstream movements were composed entirely of lake-reared populations from Chignik Lake and Black Lake. Presumably, these individuals volitionally moved down the river or were displaced there, and subsequently moved back upstream to the lake

(Iverson 1966). Chignik River juveniles appeared to vacate their natal river shortly after emergence; only 4% of the 796 sockeye salmon sampled in the river were assigned to this population in 2008.

Habitats and life history variants

A broad suite of habitats was used by each life history variant, emphasizing the spectrum of habitats used by these generalists (Quinn 2005). While it is common to separate sockeye salmon life history variants by the environmental niches they fill early in life, it is worth considering how the species may opportunistically exploit available habitats. The lake-reared stocks, for example, made use of non-lake environments both early in their development and later, prior to ocean entry. Much of the inner estuary in Chignik (including the ecotone site and 2 inner estuary sites) is characterized by relatively low salinity water (<15‰), making it accessible for young salmon from both lake- and non-lake ecotypes and reducing the metabolic demand of osmoregulatory processes (Boeuf & Payan 2001). While salinity affects the growth and survival of small (<50 mm length) sockeye salmon (Heifetz et al. 1989, Rice et al. 1994), the range of salinities tested in those studies was relatively high (≥ 22 ‰), and such salinities only occurred in the outer 2 estuary sampling sites during this study.

Differences in the patterns of fish size across the estuarine salinity gradient during 2007 to 2009 revealed perhaps the greatest insight into the nature of estuarine use for the non-lake ecotype. Of the sockeye captured in 2008 and 2009, the smallest individuals mainly held to the lowest salinity habitats, while larger fish and smolts were caught across a greater range of salinities (Fig. 4), reflecting a size-related salinity tolerance (Heifetz et al. 1989). However, this pattern was largely absent for fry/parr in 2007 (mainly composed of the non-lake ecotype based on genetic analyses), with small fish (<50 mm) caught in habitats across all salinities (Fig. 4). This may indicate that the non-lake ecotype has a higher affinity for saline waters which allows them to use a greater portion of the estuarine environment at relatively small sizes, although we did not test the genetic composition of sockeye salmon in the estuary in 2008 or 2009 to provide a comparison between years. Our study supports findings by Rice et al. (1994), who concluded that while sea-type sockeye salmon may fare the best in the estuarine environment, freshwater-reared ecotypes may also rear in

saltwater if they reach a critical size (50 mm). Thus, habitat remains an important determinant of the early life histories present in a system (Rice et al. 1994).

The Chignik River population likely represents a sea ecotype, extensively using the river–estuary ecotone and the estuary (for genetic-based evidence, see also Creelman et al. 2011). Other studies have noted similar patterns of Age-0 sockeye salmon in estuaries (e.g. Birtwell et al. 1987, Heifetz et al. 1989), but the Chignik system is different because of the close proximity of a suitable nursery lake available to the fry. Non-lake ecotypes typically occur in sockeye salmon systems where lakes are either unproductive, inaccessible, or absent. This unexpected pairing of a sea ecotype so close to accessible lake habitat may reflect rearing pressures in the Chignik nursery lakes, causing the circumvention of lake residence altogether. Rearing in Chignik Lagoon enabled Age-0 Chignik River sockeye salmon to attain sizes of lake-reared fish 1 yr older (Age-1 smolts), reflecting the superior growth environment that the estuary provided. Fry in Chignik Lagoon grew at rates similar to sea-type sockeye salmon in the Situk River estuary (Heifetz et al. 1989), but little is known about whether the fry in Chignik Lagoon migrate to sea like those in the Situk River estuary or whether they remain to overwinter.

Role of estuaries in changing landscapes

Buffering freshwater environmental variability through additional growth in estuaries may be critical for young salmon due to their high mortality early in life (Beamish et al. 2000, Greene et al. 2005), and especially in early marine life (Hartt 1980, Van Doornik et al. 2007). For sockeye salmon, growth can be rapid during their first summer at sea (Farley et al. 2005), and their size at the end of this first summer influences their survival (Farley et al. 2007b). While the effects of climate and oceanographic conditions on early ocean survival cannot be ignored (e.g. Farley et al. 2007a), sockeye salmon size at marine entry strongly influences marine survival for individuals within a cohort (Henderson & Cass 1991).

Sockeye salmon smolts from the Chignik Lake system are small in comparison to other Alaskan populations, yet their marine survival is relatively high. In a review of 26 Alaskan systems where average Age-1 sockeye salmon smolt size was surveyed, those from Chignik were in the 15th percentile (Burgner 1987). Despite their small size, Chignik smolts have a

higher average marine survival rate (22%; St. Saviour & Hunt 2012) than the Alaska biostandards for marine survival (12%) described by Koenings et al. (1993). While sockeye salmon enter the estuary at a small size compared to other systems, at least a portion of them exit the lagoon much larger, suggesting that smolt size as measured at the traps in Chignik River does not necessarily correspond to size at ocean entry (and subsequent marine survival). Our data suggest that smolts growing in the estuary were 90 to 100 mm before exiting for the ocean, which would place them in the 65th percentile of sockeye salmon smolt size from Alaskan systems. In a previous study, between 1/3 and 2/3 of adult sockeye salmon returning to Chignik included a unique scale pattern attributed to estuarine growth (Phinney 1968).

Productivity of sockeye salmon in Chignik has historically been limited by rearing capacity, although both lakes have high rates of primary productivity (Narver 1966, Ruggerone 2003). Recent natural shifts in the hydrology and morphology of Black Lake have caused further rearing pressures in the upper lake, which has in turn caused a marked shift in the community structure in the lower lake and has led to increased competition for prey resources (Ruggerone 2003, Elhakeem & Papanicolaou 2008, Westley et al. 2010, Simmons et al. 2013). Currently, top-down pressures on the zooplankton community are evident in Chignik Lake due to the size regulation of cladocerans, likely caused by intense predation from rearing sockeye salmon (St. Saviour & Hunt 2012). In a system where sockeye salmon rearing habitat is rapidly changing, Chignik Lagoon may provide stability through its role as an additional growth environment for lake-reared smolts faced with highly variable freshwater conditions and bottlenecks in freshwater rearing capacity.

Productive estuaries may augment growth and survival for sockeye salmon populations that are limited to a fraction of their historic freshwater ranges, such as those within the Columbia River basin which have lost 96% of their habitat (Northwest Power Planning Council 1986) as well as the Baker River population of Puget Sound (Nehlsen et al. 1991). Recent modeling of factors affecting Chinook salmon runs in the Skagit River by Greene et al. (2005) identified the period of juvenile residence in the bay adjacent to the associated tidal delta as an indicator of subsequent adult returns. This residency in the adjacent bay may be especially important because about 80% of the adjacent Skagit River intertidal delta habitat has been lost (Greene et al. 2005). Even so, the Skagit River remains relatively intact compared to more

industrialized rivers of the US Pacific Northwest, which have lost a far greater portion of their respective estuaries. Armoring, channelization, and reclamation of agricultural land have drastically reduced the natural habitat available in major estuaries throughout the Pacific Northwest (Simenstad et al. 1982), and the loss of these habitats may play a part in the declines of Pacific Northwest salmon populations (Nehlsen et al. 1991). Still, recent estuary restoration efforts have shown that the loss of overall habitat diversity is reversible (Bottom et al. 2005), and the relative size of the estuary can be a small fraction of a watershed yet remain important for the growth of individuals and survival of populations (Bond et al. 2008).

Adapting to environmental variability remains essential for the persistence of Pacific salmon populations. Here we have shown evidence suggesting the important role an intact estuary can play in supporting additional growth for sockeye salmon of multiple life stages faced with limited growth potential in freshwater habitats. The finer life history patterns revealed in this study highlight how local adaptations may support the persistence of regional salmon stock complexes (Hilborn et al. 2003, Schindler et al. 2010). Such information can help identify factors that contribute to the resilience of Pacific salmon populations, which will be increasingly important as climatic (McCarty 2001, Mote 2003) and anthropogenic (NRC 1996) pressures threaten the freshwater systems used by Pacific salmon.

Acknowledgements. We dedicate this work to the memory of Duane Earl Phinney (1940–2012) whose pioneering research in Chignik Lagoon helped shape this study. We thank D. Narver, M. Dahlberg, R. Iverson, and B. Parr among others for their early research in the Chignik watershed. The residents of Chignik were instrumental in supporting this project, especially J. and E. Slaton, J. Lind, R. Lind, and W. Lind. M. Stichert and T. Dann of the Alaska Department of Fish and Game provided logistic support in the field. We greatly appreciate all who assisted in the collection of field data, especially P. Westley, J. Griffiths, B. Williamson, C. Gowell, and M. Bond. Laboratory support was graciously provided by C. Pascal, E. Grau, N. Davis, and L. Creelman. This is a contribution of the University of Washington Alaska Salmon Program, and was supported by the US National Science Foundation, the Gordon and Betty Moore Foundation, the Chignik Regional Aquaculture Association, and the National Marine Fisheries Service.

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*Editorial responsibility: Jana Davis,
Annapolis, Maryland, USA*

*Submitted: January 13, 2012; Accepted: November 21, 2012
Proofs received from author(s): March 26, 2013*