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ARTICLE

Estuarine Environments as Rearing Habitats for Juvenile Coho Salmon in Contrasting South-Central Alaska Watersheds

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Abstract

For Pacific salmon, estuaries are typically considered transitional staging areas between freshwater and marine environments, but their potential as rearing habitat has only recently been recognized. The objectives of this study were two-fold: (1) to determine if Coho Salmon *Oncorhynchus kisutch* were rearing in estuarine habitats, and (2) to characterize and compare the body length, age, condition, and duration and timing of estuarine occupancy of juvenile Coho Salmon between the two contrasting estuaries. We examined use of estuary habitats with analysis of microchemistry and microstructure of sagittal otoliths in two watersheds of south-central Alaska. Juvenile Coho Salmon were classified as estuary residents or nonresidents (recent estuary immigrants) based on otolith Sr : Ca ratios and counts of daily growth increments on otoliths. The estuaries differed in water source (glacial versus snowmelt hydrographs) and in relative estuarine and watershed area. Juvenile Coho Salmon with evidence of estuary rearing were greater in body length and condition than individuals lacking evidence of estuarine rearing. Coho Salmon captured in the glacial estuary had greater variability in body length and condition, and younger age-classes predominated the catch compared with the nearby snowmelt-fed, smaller estuary. Estuary-rearing fish in the glacial estuary arrived later and remained longer (39 versus 24 d of summer growth) during the summer than did fish using the snowmelt estuary. Finally, we observed definitive patterns of overwintering in estuarine and near shore environments in both estuaries. Evidence of estuary rearing and overwintering with differences in fish traits among contrasting estuary types refute the notion that estuaries function as only staging or transitional habitats in the early life history of Coho Salmon.

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Pacific salmon exhibit multiple life histories in response to variability in selection pressures and habitat conditions (Healey 1994, Groot and Margolis 1991). Early marine entry and presmolt growth just prior to entry is a time of severe selective pressure due to the physiological and environmental changes experienced by salmon smolts (Williams 1996; Thorpe et al. 1998; Beamish et al. 2004). This life stage has been linked to an optimal out-migration survival period that corresponds to a period when ocean conditions provide suitable temperatures and abundant resources for growing and feeding (Gargett 1997; Johnsson et al. 1997; Beamish et al. 2008). The period and duration of optimal out-migration timing may change from year to year depending on precipitation levels, wind patterns, and solar energy inputs (Gargett 1997; Beamish et al. 2008). Fish size, body condition, and timing of marine entry are instrumental for optimal timing and to ensure coincidence with both the quantity and quality of available prey and the ability of the individual to use it (Beamish and Mahnken 2001; Hobday and Boehlert 2001).

Estuaries play an important role as transitional habitats prior to the ocean entry phase of salmon smolt. The mixing zone of freshwater and saltwater environments buffers against osmoregulatory and physiological stress in smolts (Healey 1982; McMahon and Holtby 1992; Miller and Sadro 2003; Beamish et al. 2004; Bottom et al. 2005a). Estuaries, however, also have potential to serve as important salmon rearing habitats; Chinook Salmon *Oncorhynchus tshawytscha*, in particular, have increased survival rates (Magnusson and Hilborn 2003) and life history variability (Bottom et al. 2005a; Campbell 2010; Volk et al. 2010) with estuarine habitat use. Factors expected to impact individual fish survival include the duration of estuary occupancy, timing of early marine entry, and environmental conditions that affect body condition (Healey 1982; Bohlin et al. 1993; Beamish et al. 2004). Given their importance for rearing, we anticipated that strong spatial and temporal variability in environmental conditions within estuaries may play a key role in trait expression of individuals subject to overall conditions within these habitats.

Estuaries fed by different freshwater hydrologic regimes may provide contrasting rearing environments for resident biota (Saltveit et al. 2001). Freshwater influx into northern estuaries is expected to be particularly high during snowmelt periods; however, within Alaska, many estuarine habitats are fed by glacial river systems. For these systems, peak freshwater discharge occurs in midsummer rather than early spring, yielding cold, sediment-laden discharge during the warmest months. Differences between glacial and snowmelt-fed estuaries may therefore contribute to variability in the timing and duration of estuarine use for juvenile salmon.

Previous investigations into estuary ecology of juvenile Coho Salmon *O. kisutch* are limited, but indicate that the transition from fresh to salt water life stages is complicated and may differ by age or life stage (McMahon and Holtby 1992). For example, young-of-year fish undertake seasonal migrations within the up-

per estuarine ecotone and freshwater river channels and sloughs, and residency between these areas is estimated to be as long as 8 months (Miller and Sadro 2003; Koski 2009). Fingerling (age-1 and -2) Coho Salmon were present in estuaries for only 2 months (McMahon and Holtby 1992), and individuals within these populations were reported to have short estuary residence times (up to 17 d; Chittenden et al. 2008). Understanding some of the environmental conditions that lead to the differences in use by young salmon may provide insight into critical rearing habitats for conservation and management.

Direct and unbiased documentation of estuarine habitat use by juvenile salmon is difficult, given a limited suite of tracking and marking techniques applicable to small fish. The use of otolith microchemistry in combination with examination of microstructure (incremental growth layers) can be used to determine ontogenetic patterns of habitat occupancy when water chemistry contrasts strongly between habitats (Neilson et al. 1985; Campana 1999; Kennedy et al. 2002; Réveillac et al. 2008). The salinity of the surrounding environment, in particular, has been linked to ratios of strontium to calcium (Sr : Ca) deposited in otoliths, a useful feature for measuring life history patterns in diadromous fishes (Zimmerman 2005). In tandem with microchemical analysis, microstructural analysis of incremental growth patterns and age of fish can allow discernment of habitat transitions through time (Campana and Neilson 1985; Neilson et al. 1985; Volk et al. 2010). It can be difficult, however, to determine and validate daily incremental growth patterns, particularly during periods of low growth (Campana and Neilson 1985). In that case, seasonal growth patterns may provide sufficient resolution to determine history, particularly in the case of estuarine or marine versus freshwater habitat use.

In this study, we investigated and compared the ecology and life history patterns of juvenile Coho Salmon captured within two contrasting estuary environments. Our first question was two-fold: (1) were juvenile Coho Salmon rearing within estuary systems, and (2) did fish rearing within estuaries show trait differences (condition, dates of entry, and weights) from those that did not? Using otolith microanalyses, we determined the timing and duration of use and correspondence with fish traits of different ages of juvenile salmon captured within estuary channels. We hypothesized that fish using estuaries, having a longer time for osmoregulatory adjustment and thereby benefiting from these environments, would exhibit greater lengths and body condition than those without evidence of estuary residence. The second question of our work was, did patterns of estuary use by juvenile Coho Salmon, including timing and duration of occupancy, differ between two estuaries with contrasting freshwater environments? We hypothesized that differences in freshwater discharge regimes (i.e., a glacial-fed versus snowmelt-fed estuary) that result in differences in thermal regimes and available habitats may be factors that drive use of differing estuary systems. This would suggest that physical processes are important drivers of ontogenetic variability in use of estuarine environments and therefore life history expression in juvenile salmon.

STUDY SITE

The large tidal range (>8 m depth) of Kachemak Bay and Cook Inlet (NOAA 2012) in south-central Alaska can create extensive estuarine ecotones with diverse habitat conditions, particularly in glacial rivers with heavy silt deposition zones. Our study compared environmental conditions and fish collected from similar channel habitat types sampled within two contrasting estuaries of the Anchor and the Fox rivers, located approximately 29 km apart, (Figure 1). Juvenile salmon were captured within channels located in the intertidal zone of each estuary, bordered by mud flats and vegetation. Channels were chosen to maximize habitat similarity between the estuaries (i.e., similar connectivity to the main-stem river, locations within the intertidal zones respective of the estuary size, channel shape, and channel length).

The Anchor River delta is a snowmelt and spring-fed, bar-built estuary that abruptly transitions into the marine environ-

ment of southern Cook Inlet; its estuary length is about 0.8 km (measured from the high-water tide line to its confluence with the Cook Inlet). The Fox River delta is a glacially fed estuary that transitions through a large delta, approximately 6 km long, into Kachemak Bay. The Fox River watershed is located in a smaller, more constrained valley and lacks freshwater back-channel areas in the lower river, whereas the Anchor River has numerous side-channel areas in the lower river. Compared with the Anchor River estuary, the Fox River estuary has more gradual, extended ecotones between the marine environments of Cook Inlet and freshwater environments of the Fox River.

METHODS

Habitat characteristics.—We sampled fish and recorded environmental data in tidal channels spaced within the intertidal zone of each estuary. Habitats upstream of these channels are

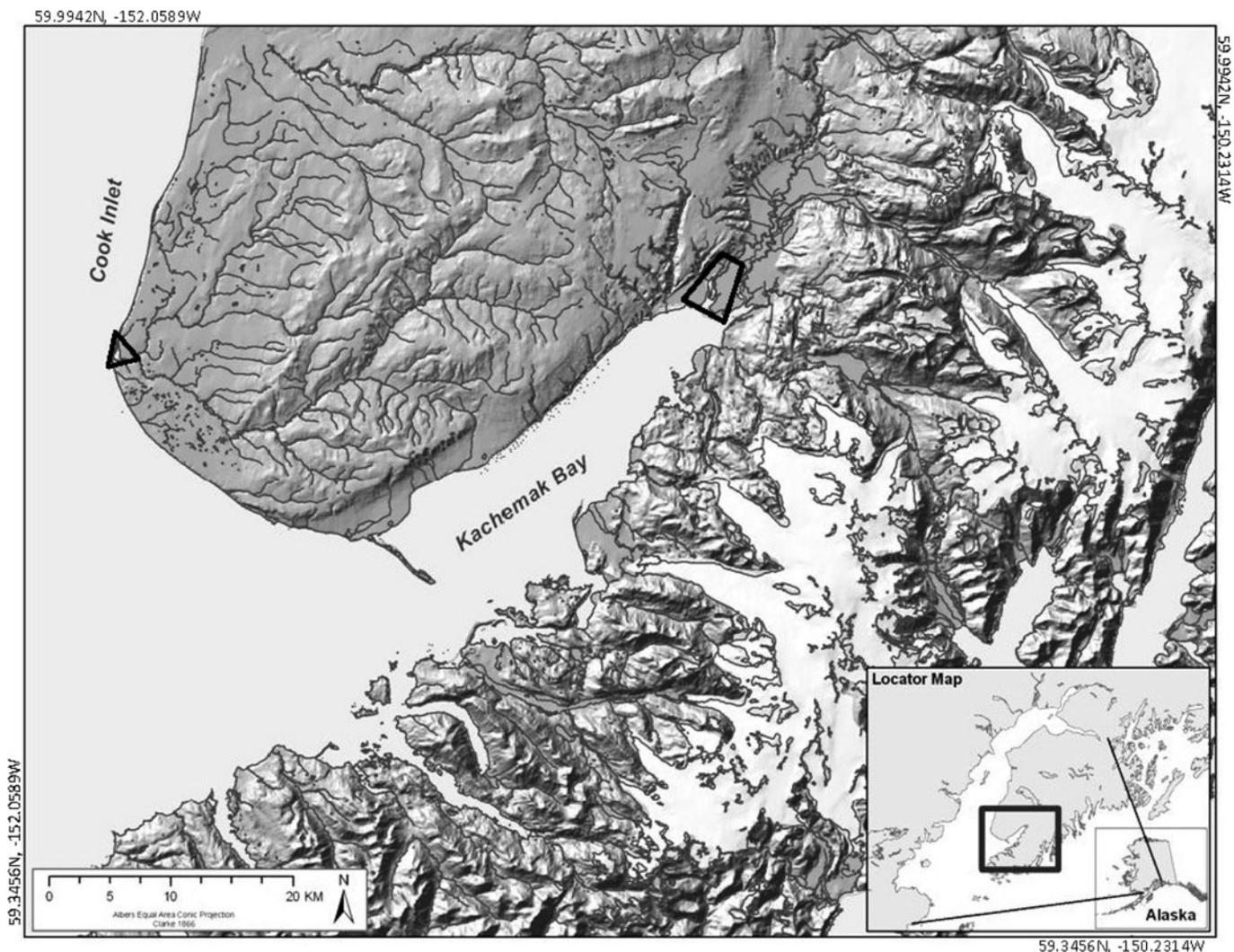


FIGURE 1. The study area on the lower Kenai Peninsula, Alaska, where age-0 to age-2 Coho Salmon were sampled from the Anchor River (triangle) and Fox River (trapezoid) estuaries.

not tidally influenced and therefore were not considered estuary habitats for this study. Four channels were sampled in the Fox River estuary and two channels were sampled in the Anchor River estuary, twice monthly from April through September for a total of 10 sampling events in the Anchor River and 11 sampling events in the Fox River. Sampling occurred during moderate tide levels in both estuaries because some channels could not be sampled at high tide. Sample events in each estuary usually occurred within 7 d of one another, often within the same week. Temperature and depth were measured and recorded using Solinst TM 3001 level loggers (Solinst Canada Ltd., Ontario, Canada) calibrated with a Solinst TM 3000 barologger set onsite. Level loggers were set at 15-min recording intervals and placed in 5 × 25 cm plastic PVC housings attached to steel fence posts driven approximately 25 cm into the substrate. Fence posts were located five meters upstream from the channel mouth in each of the six channels sampled, and one logger was placed along the margin of each river channel. In addition, measurements were taken for each sampling event at a cross-section downstream of the fence posts for each sampling event. Thalweg depth, conductivity (direct and standardized for temperature), salinity (measured as salt concentration), and temperature (with probe at the surface, mid water column, and channel bottom) were measured using a YSI model 30.

Habitat data were summarized for analyses as follows: continuous water level data as 7-d mean, minimum, and maximum depths for each estuary channel and the main-stem river. Continuous temperature data were summarized as daily averages summed for accumulated thermal units by week and month. Point measurements of salinity collected at each sampling event were combined and expressed as monthly mean, minimum, and maximum recordings.

Fish capture.—Juvenile Coho Salmon were captured in tidal channels of the intertidal zones of Fox and Anchor river estuaries within 25-m reaches using three depletion passes with a pole-seine (2.2 × 6.1 m, 0.31 cm mesh) twice per month from late April through September 2011. Prior to fish sampling, each unit was closed with blocking nets (2.2 × 6.1 m, 0.31 cm mesh) secured along the sides and bottom with stakes to prevent fish escape. Fish from each pass were placed in separate, 19-L aerated tubs filled with water from the channel. All fish captured were identified to species and counted. Fifty juvenile Coho Salmon captured from each of three passes of the seine (total, 150 fish/site per each event) were anesthetized in tricaine methanesulfonate (MS-222) at 70 mg/L of water (Bailey et al. 1998; Chittenden et al. 2008) and measured for FL (mm). If more than 150 Coho Salmon were captured at each site, samples were indiscriminately selected by gently stirring the incarcerated fish and removing samples with a hand dip net. Age-classes of Coho Salmon were apparent by length; therefore, three juvenile cohorts (≤10% of the catch) at each were indiscriminately collected at each site: small (age 0, <50 mm FL), medium (age 1, 50–85 mm FL), and large (age 2, >85 mm FL) and sacrificed via overdose of MS-222 at

140 mg/L, labeled, placed on ice, returned to the laboratory, and frozen.

Fish condition.—We used dry weight and Fulton's condition factor measured from the frozen specimens for metrics of condition (Jonas et al. 1996; Pope and Kruse 2007). Fulton's condition, $K = (W/L^3)100,000$, was calculated using laboratory measures of fish length (FL; mm) and whole fish weight (W; g). Dry weights were determined from dissected samples with all tissue other than stomachs and otoliths returned to the sample prior to drying. Coho Salmon samples were placed in a drying oven at 65–70°C for 3 d, weighed, and returned to the oven for 24 h, and then re-weighed. Samples were considered dried when minimal change was detected between consecutive daily weights (Jonas et al. 1996).

Estuary residence time.—We used analysis of otolith microchemistry combined with microstructural analysis to determine if juvenile Coho Salmon were rearing in the saline environments of estuaries. Sagittal otoliths were removed from both sides of the cranial cavity of fish prior to condition analyses, rinsed, and stored in plastic vials. Otoliths were mounted in thermoplastic cement on sections of cover slips and glued to standard microscope slides (Donohoe and Zimmerman 2010). Otoliths were mounted sulcus down, and the sagittal plane was ground with 2,000-grit sand paper to expose a clean, flat surface. The sample was reheated, turned over to expose the sulcus, and ground to expose the nucleus (Zimmerman 2005; Donohoe and Zimmerman 2010). The sample was labeled and aged via winter counts, and the cover slip was cut to remove the mounted sample. The sample was then glued in a 2.54-cm-diameter circle centered on a petrographic slide for analysis. Once the slide was filled, it was washed, rinsed with deionized water, and allowed to air dry prior to processing.

We used the Laser-ablation Inductively Couple Plasma Mass Spectrometer (Agilent mass spectrometer 7500ce fitted with a CS lens stack combined with a New Wave UP213 laser, LA-ICPMS) housed at the Advanced Instrumentation Laboratory of the University of Alaska Fairbanks to complete the microchemical analyses. Transects were ablated from the primordia perpendicular to the growth increments into the mounting medium beyond the distal edge of one otolith from each fish. Count data were collected for the elements strontium (^{88}Sr) and calcium (^{43}Ca). Calcium (^{43}Ca) was used as an internal standard and background-subtracted counts of Sr were adjusted to Ca and calibrated to glass standard reference material (NIST 610, National Institute of Standards and Testing). Calibration standards were run for 10 samples or less, depending on the number of samples on the slides, and one sample duplicate (both sagittal otoliths from one fish) was run for the entire batch. Laser speed was set at 5 $\mu\text{m/s}$ with a 25- μm spot diameter on a single pass transect set to 80% power. The elemental count/s output of the LA-ICPMS was then converted to concentration and sampling distance using the elemental weights for each constituent and the laser settings, respectively. Strontium : calcium (Sr : Ca) ratios were then calculated for each of the distance

measures. Otoliths were photographed under $4\times$, $10\times$, $20\times$, and $40\times$ magnification using a Leica DM1000 compound light microscope fitted with a Leica DFC425 digital camera housed at the Alaska Science Center (Anchorage, Alaska). Images were taken using a 1,000- μm stage standard at all magnifications to calibrate otolith measurements, and the images were digitally processed to enhance clarity of incremental growth patterns. ImageJ software (version 1.46 h, <http://imagej.nih.gov>) was used to process digital images and to overlay distance-ratio graphs on the image, calibrated to the laser distance.

Estuarine residence time was determined by counting incremental growth marks on otoliths from juvenile salmon captured in the estuary (Miller and Simenstad 1997; Neilson et al. 1985). We defined residence time as the daily growth within the saline reaches of the estuary. Residence time was calculated as the number of incremental growth bands following the point of estuarine entry determined by the Sr : Ca inflection point with the distance-matched ratio graph overlaid on the otolith digital image. The inflection point, or estuary signature, was defined as an abrupt increase in Sr : Ca, as visually determined as the consecutive ratio increase of >0.3 per reading; levels remaining at >1.0 followed the freshwater mean ratios (Figure 2). Inflection points often correspond with dark banding, identified by some researchers as an estuary growth check (Lind-Null and Larsen 2011). These growth checks, though not always easily identifiable or consistent among individuals, corresponded to inflection points and provided additional support in identifying the points of estuary entry. All fish were categorized according to the presence or absence of an estuarine salinity signature (inflection point followed by growth), and incremental growth counts were completed to determine duration of estuary use on those with estuary signatures. Duration of estuarine rearing was determined by using a digital image of the otolith taken at $20\times$ magnification overlaid with the distance-matched (μm) Sr : Ca graph. Inflection points were digitally marked on the image and were considered the point of estuarine entry. Growth increments were counted along two different radii from the distal edge of the otolith to the inflection point to determine days of residence (Figure 2). If counts differed between readings, a third count was made, and the median of the three counts was used. One group of salmon overwintered in estuarine/marine environments, therefore comparisons were made using summer season (April-September) residence times calculated as the date of capture less the incremental growth count (days) to the first discernible daily growth increment. The growth increment-time relationship was validated by marking a sample of four fish with alizarin complexone (Zimmerman 2005), holding them in a small net pen in an estuary channel for 6 d, sacrificing the fish, and counting the increments past the Alizarin mark on prepared otoliths. The results from this test verified that incremental growth rings indeed represented a 24-h period, all fish showing six increments corresponding to the 6 d held in captive nets in the estuary.

Statistical analyses.—Based on our study questions, we wanted to determine whether (1) estuaries were used by Coho Salmon for rearing purposes, (2) those salmon that used estuaries for rearing differed from those that showed no evidence of estuarine rearing, (3) salmon rearing in two different estuaries show differences in traits and residence times related to environmental conditions, and (4) factors that contribute most to the variability in fish traits (e.g., presence of estuarine rearing, estuary habitat conditions, or the age of the fish) could be identified. The otolith microchemistry and microstructural analysis described above addressed whether fish were using estuaries for rearing, and we used analyses of empirical data to address the remaining objectives. When possible, confounding sources of variability, such as timing of capture, were included in these analyses, along with several potential sources of error and bias.

Because samples were a subset of the total catch and collected over the summer season, potential sources of bias and error must be addressed. Our protocol sampled evenly across age-classes for fish retained for laboratory analyses; therefore, the composition of the laboratory fish sample did not correspond to catch composition. We therefore tested (chi-square goodness of fit) for differences in age-class composition of measured fish between estuaries and in the laboratory sample versus the measured group age structure. Finding significant differences on both accounts, we ran analyses to compare length, age-class composition, and capture date based on two subsamples of the total catch: those that were caught, measured, and released (hereafter, measured group) versus those sacrificed and analyzed in the laboratory (hereafter, laboratory group). For each sampling event we inferred age-class composition of the measured group via their length-frequency histograms from length groups validated via otolith-determined ages of the laboratory group. Analyses completed with all age-classes pooled were weighted to ensure that the laboratory sample results reflected the composition of the population relative to the total catch of fish; laboratory fish data were weighted by percent composition of each age-class from the measured group of fish for each estuary. We also examined the relationship between capture date and residence time using simple linear regression for each estuary; a strong linear relationship between residence time and date of capture would indicate bias.

For the second objective, we compared those juvenile Coho Salmon that had a marine signature in their otolith, indicating estuarine rearing, with those salmon that were captured in the estuary but lacking detectible marine signature in the otolith. Those comparisons were done to determine whether fish in these groups showed differences in trait patterns (time of entry, condition, length, and weight). Two separate analyses were used: ANCOVA for all age-classes pooled, and Student's *t*-tests for individual age-classes (due to small sample lengths and disproportionate distribution of age-classes between estuaries). We tested data from the laboratory fish group captured in each estuary via ANCOVA analyses. This analysis used the independent

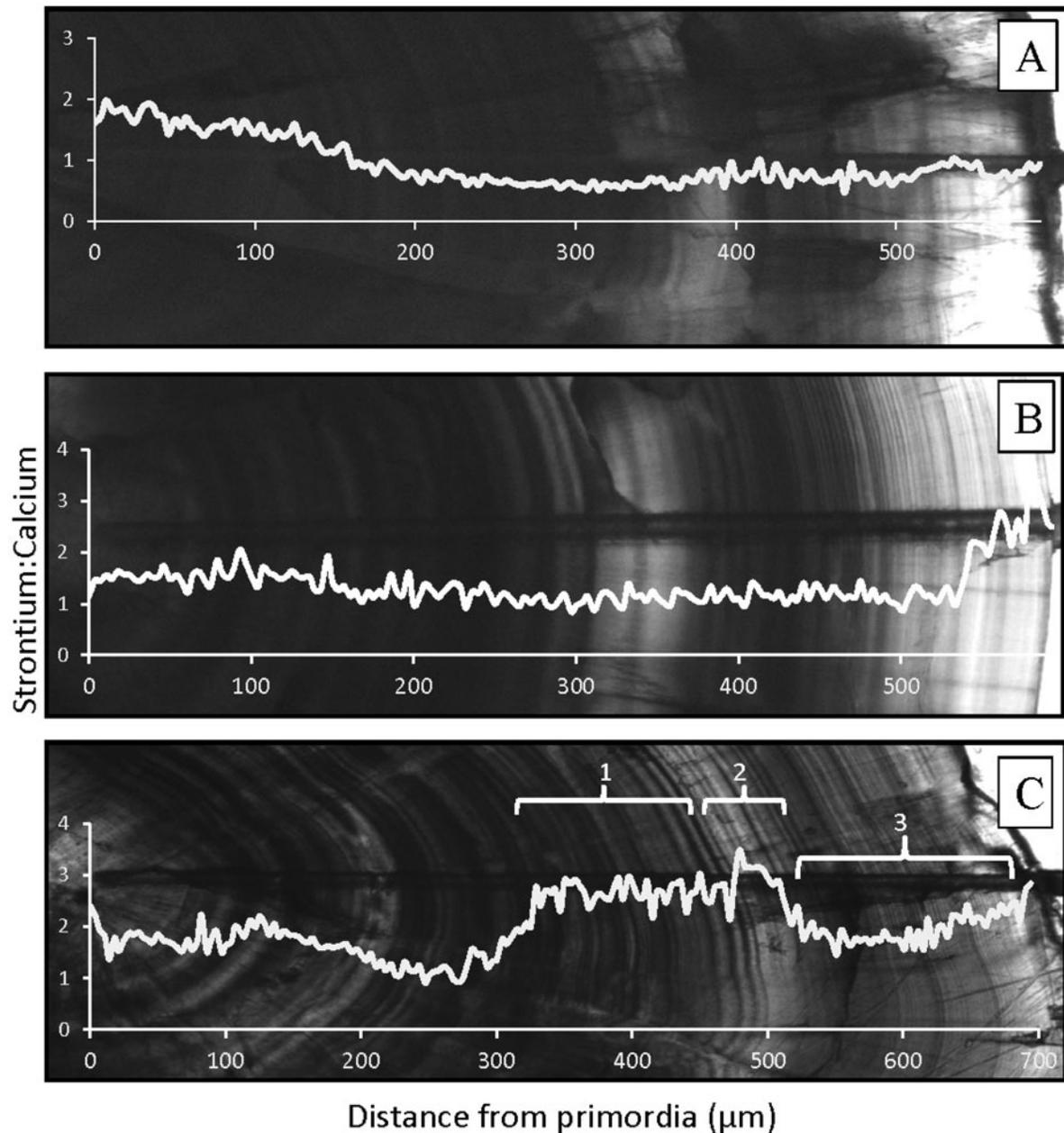


FIGURE 2. Images of otoliths of Coho Salmon from the Fox and Anchor River estuaries showing Sr : Ca ratio graphs overlaid with laser transect distances. Different estuary use patterns are depicted: (A) no estuary use, (B) summer season estuary use signature, and (C) age-2 fish with overwintering signature and variable use of salinities during the summer season, where (1) is the first summer estuary signature, (2) is the winter estuary signature, and (3) is the second summer estuary signature.

variable (condition) and dependent variable (date of capture) with estuary rearing as the covariate for fish comparison for all ages pooled (weighted bycatch). For the age-class comparisons, we compared traits (length, condition, dates of entry, and weights) between signature patterns using Student's unpaired two-sample *t*-tests for each age-class; estuaries were analyzed separately. Because, in this scenario, each variable was repeated a total of four times (for age-0 and age-1 classes by two es-

tuaries), we adjusted our alpha values accordingly (Dunn Sidak correction alpha level 0.013; Abdi 2007).

Our third objective focused on whether fish using the glacial Fox River estuary showed differential trait expression from those using the snowmelt, spring fed Anchor River estuary. Two separate analyses were performed as described above. For the between-age-class comparisons, traits were examined for differences between estuaries using Student's unpaired

two-sample *t*-tests for each age-class. To compare fish traits with all age-classes pooled, we used an ANCOVA analysis with each dependent variable (length, dry weight, condition) and capture date as the independent variable with estuary of capture as the covariate.

The final objective was to examine the influence of three potential factors (age, estuary type, and presence of an estuary signature) in explaining variability in Coho Salmon traits. We used a three-way catch-weighted ANOVA with the laboratory group data to address this question.

Data were standardized to the mean of each variable and fourth-root transformed (when necessary) to meet homogeneity assumptions for all linear tests. Data were checked for equal variance using *F*-tests for age-class comparisons. If samples had unequal variances and could not be transformed to meet this assumption, a Welch two-sample, unpaired *t*-test was used for comparison of age-class data.

RESULTS

Estuary Habitats

Temporal trends in habitat features followed trends and differences anticipated for snowmelt versus glacially fed estuaries. Minimum salinities were higher and more variable in the snowmelt-fed Anchor River estuary channels, particularly in midsummer (Student's two-sample unpaired *t*-test: $t = 1.32$, $P < 0.001$, $df = 18$; Figure 3; Table 1). Data from the stationary loggers placed in the sampling sites showed expected patterns in trends associated with each watershed type. The glacial Fox River showed seasonal increases in water depth and decreases in temperature associated with the glacial runoff, whereas the snowmelt and spring-fed Anchor River exhibited peak water depths and coolest temperatures in the early spring. The highest 7-d average estuarine water temperatures occurred in late May (13.3°C) for the Fox River and late July (15.3°C) for the Anchor River.

Fish

We captured a total of 1,743 Coho Salmon in the Anchor River and measured 532. In the Fox River we captured 4,232 individuals and measured 1,621. We sacrificed and retained 35

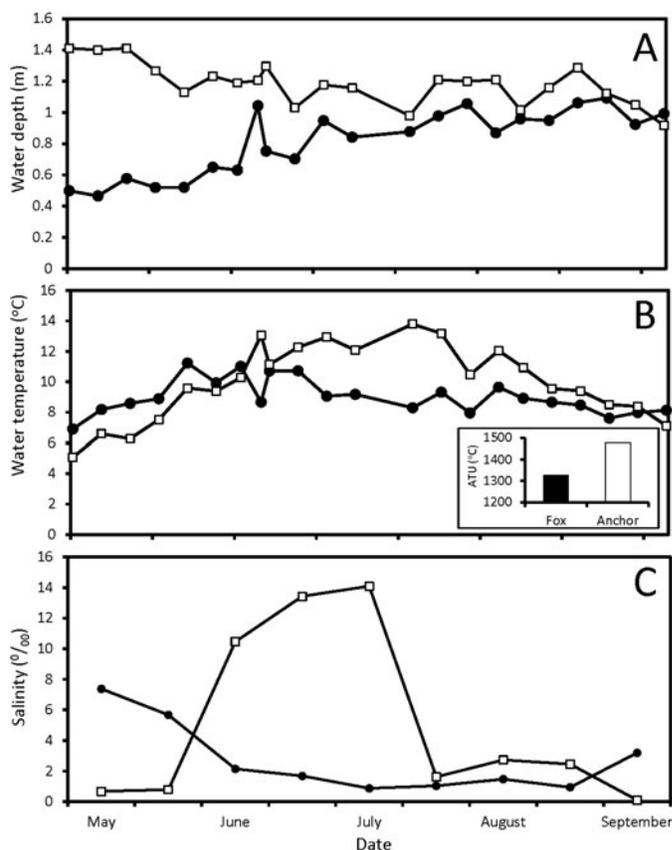


FIGURE 3. Continuous data logger results for the Fox River (black circles) and Anchor River (open squares) estuaries showing the summer-season 7-d average (A) water levels, and (B) water temperatures with an inset in accumulated thermal units (ATU). (C) Average weekly point measurements of salinity.

from the Anchor River estuary and 73 fish from the Fox River estuary for laboratory analysis.

Three age-classes of Coho Salmon were captured in both estuaries (0, 1, 2), though the relative dominance of age-classes within the measured group differed significantly between estuaries ($\chi^2 = 338.4$, $P < 0.001$, $df = 2$, Table 2; Figure 4). Fish captured in the Fox River estuary were primarily composed of younger age-classes (age-0 and age-1 fish), with less than 5% of the catch composed of age-2 fish. The Anchor River estuary

TABLE 1. Mean monthly measures of environmental conditions for the south-central Alaska's Fox and Anchor river estuary channels. Metrics were calculated for all channels combined within the Fox or Anchor estuaries. Water temperature is in accumulated thermal units (ATU).

Month	Fox River: mean (var)			Anchor River: mean (var)		
	Temperature ATU (°C)	Depth (m)	Salinity (mS/cm)	Temperature ATU (°C)	Depth m (var)	Salinity (mS/cm)
May	50.2 (17.3)	0.7 (0.1)	7.8 (4.5)	52.4 (11.4)	1.3 (0.3)	0.7 (1.2)
Jun	74.8 (5.0)	0.7 (0.4)	2.0 (2.5)	78.7 (13.2)	1.2 (0.2)	8.5 (11.1)
Jul	60.0 (10.3)	0.9 (0.4)	1.3 (2.3)	90.7 (9.3)	1.1 (0.2)	7.9 (10.8)
Aug	58.6 (4.0)	1.0 (0.3)	1.5 (1.5)	74.6 (10.6)	1.2 (0.2)	2.5 (1.1)

TABLE 2. Numbers of measured and laboratory Coho Salmon grouped by age for the Fox River and Anchor River estuaries. Counts of fish showing estuary use is denoted for the laboratory group in parentheses.

Estuary	Age 0	Age 1	Age 2	Total
Measured group composition: numbers of fish				
Fox	785	760	76	1,621
Anchor	291	133	108	532
Total	1,076	893	184	2,153
Laboratory group composition: numbers of fish				
Fox	24 (6)	45 (17)	4 (1)	73 (24)
Anchor	9 (3)	14 (11)	12 (10)	35 (24)
Total	33 (9)	59 (28)	16 (11)	108 (48)
Percent of total laboratory group with estuary signature				
Laboratory group	41	48	69	44

measured fish group was composed of over 20% age-2 fish and had a smaller proportion of age-1 fish than the Fox River (Table 2). We were restricted in retaining age-2 fish for individual analysis from the Fox River estuary due to low catch rates of this age-class in the system.

A substantial proportion of laboratory group fish displayed elevated Sr : Ca signatures, indicating growth within the saline reaches of the estuary (44%, 48 of 108 collected fish). Of these, 10 individuals overwintered in saline environments (either estuarine or near shore environments), 13 exhibited summer season use patterns of residence in saline environments followed by use of less saline environments (e.g., Figure 2A). Of the 35 Anchor River fish and 73 Fox River fish analyzed, 24 from each river exhibited evidence of estuary rearing. The Fox River fish showed a significantly lower proportion of fish with estuary signatures. Only two fish from the Fox River estuary showed estuary–marine overwintering signatures (one individual each from age-classes 1 and 2).

Disparity in patterns of capture, estuary use, and entry dates were apparent in comparisons of fish captured in the two estuaries (Table 3). The highest total capture of Coho Salmon occurred in the Anchor River estuary in late August and in late July in the Fox River (Figure 4). In both estuaries, most age-2 individuals were captured in April–June. Age-1 individuals predominated the June and early July catches, and age-0 individuals were not captured until later in June. Fish captured in the Anchor River estuary entered earlier during the sampling period and had shorter and less variable times of use than those captured in the Fox River estuary; however, these differences were not statistically significant (weighted 2-way linear model) for the pooled, catch-composition-weighted data for laboratory group with estuarine rearing: entry dates ($F = 1.71$, $P = 0.20$, $df = 46$) and residence ($F = 2.06$, $P = 0.16$, $df = 463.69$; Table 3). Only two variables were significant (Student's unpaired t -test) among comparisons made between estuaries by

TABLE 3. Mean residence times and capture dates for the laboratory group of Coho Salmon captured in the Fox and Anchor rivers in 2011.

Estuary	Age 0	Age 1	Age 2
Average summer season use (d)			
Fox	49.33	39.23	6.00
Anchor	36.33	29.72	14.80
Mean capture dates (estuary signature)			
Fox	Aug 21	Jul 31	May 28 ^a
Anchor	Aug 8	Jul 20	May 29
Mean capture date (no estuary signature)			
Fox	Jul 13	Jul 18	Jun 17
Anchor	Aug 23	Jul 13	Jul 4

^aSample size was 1.

age-class: laboratory group age-0 entry date ($t = -2.50$, $df = 30$, $P = 0.02$) and condition ($t = -1.92$, $df = 30$, $P = 0.06$).

Generally, fish captured and measured within the two estuaries differed in length, weight, and body condition; however this was only statistically significant when single age-classes were compared (Table 4). Compared with Fox River fish, the Anchor River mean FL at age was significantly (Student's unpaired t -tests) larger and less variable for each age-class in the measured group, i.e., age 0 ($t = -151.15$, $P < 0.01$, $df = 306$), age 1 ($t = -6.22$, $P < 0.01$, $df = 889$), and age 2 ($t = -3.35$, $P < 0.01$, $df = 108$; Table 5). Fish in the laboratory group followed a similar pattern as the measured group; however, these differences were statistically significant only in some comparisons made by separate age-classes (Table 5).

The age and presence or absence of an estuary signature significantly contributed to variability between traits (length, condition, dates of capture, and weights), whereas the estuary of capture did not. Fish that demonstrated more extended estuary use tended to be captured in the estuaries later than those that showed little to no estuary use (weighted 2-way linear model: $F = 5.14$, $P = 0.02$, $df = 103$; Table 5). Fish using the estuary were significantly (weighted 2-way linear models) greater in length and had higher condition when samples from both estuaries were pooled: length ($F = 5.75$, $P < 0.01$, $df = 103$) and condition ($F = 13.12$, $P < 0.01$, $df = 103$; Table 4). Finally, the evidence of estuarine rearing significantly (ANCOVA) accounted for variation in fish condition over time for both the Anchor ($F = 11.06$, $P < 0.01$) and Fox ($F = 6.42$, $P = 0.01$) river estuaries. Generally, fish in both estuaries increased in condition over time. However, fish lacking estuary signatures showed smaller sizes and lower condition when captured, and the condition increased at a greater rate over the summer season than it did among fish with an estuary signature (Figure 5).

In summary, juvenile Coho Salmon used estuaries for rearing, the greatest variability in fish traits (body condition, length, weight, capture date) being explained by the age-class and the presence or absence of estuary rearing. All fish exhibiting estuary use were significantly larger and had greater weights and

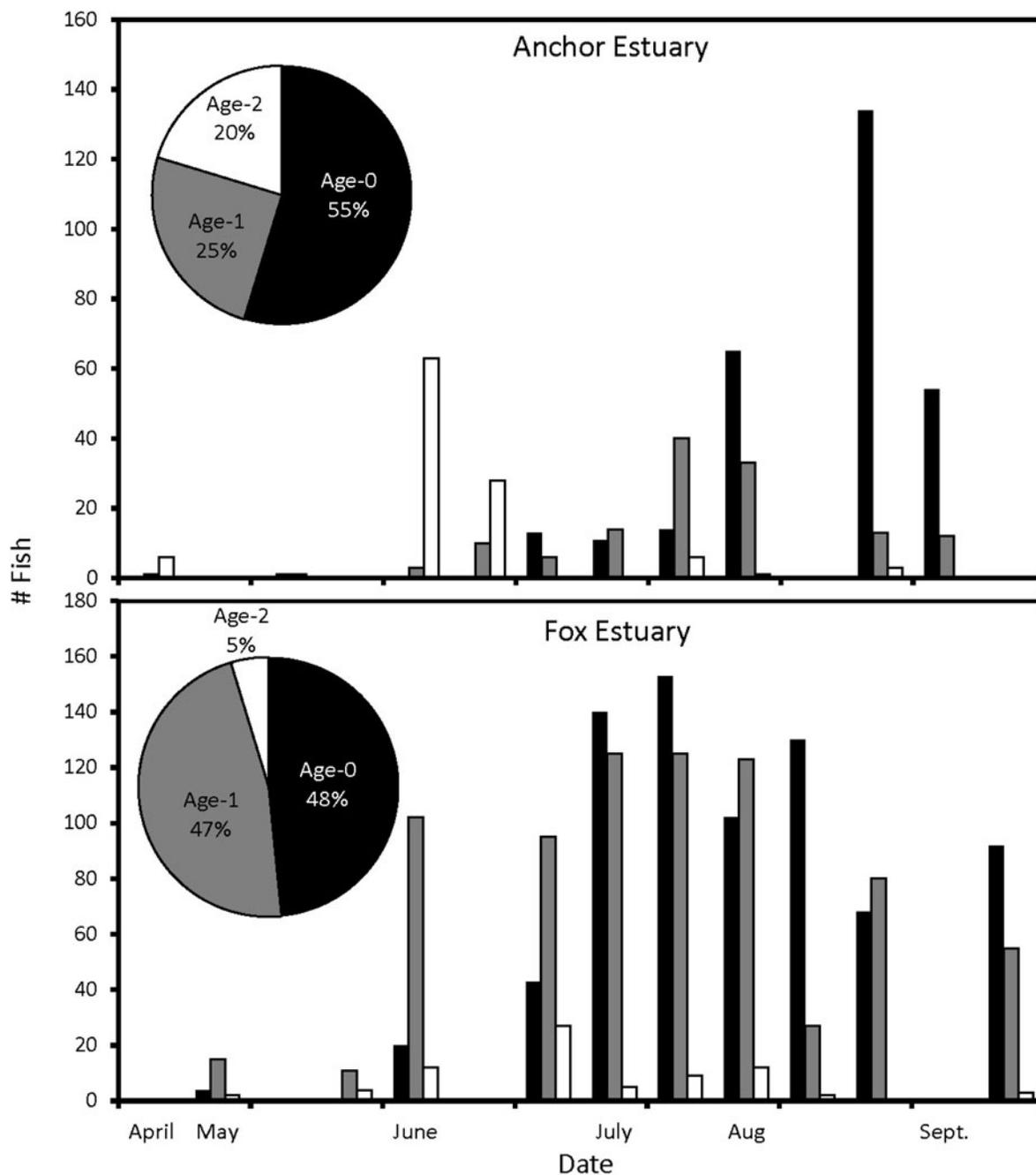


FIGURE 4. Comparison of total sample catch of Coho Salmon separated by age-class in the Fox and Anchor river estuaries. Inset pie charts illustrate age composition.

higher body condition than those lacking estuary-use signatures. Patterns of trait differences between estuaries were apparent, though not statistically significant given our limited sample sizes of estuary residents. Compared with fish in the Fox River estuary, those using the Anchor River estuary showed a higher proportion of overwintering use, and the summer composition of residents was higher in older individuals with greater body condition, length, earlier entry, and shorter times of use.

Finally, we addressed the potential for capture date to bias residence. We found a weak, though significant, positive relationship between capture date and residence days for fish from the Fox River estuary ($P < 0.01$, adjusted $r^2 = 0.18$) but not for fish from the Anchor River estuary ($P = 0.28$, adjusted $r^2 = 0.01$). This relationship could potentially be explained by the differences in behavior patterns of the fish from the two estuaries.

TABLE 4. Mean and variance of body size, weight, and condition for measured ($n = 2,153$) and laboratory ($n = 108$) groups of Coho Salmon captured in the Fox River and Anchor River estuaries.

Estuary	Age 0	Age 1	Age 2
Measured group mean size (variance)			
Fox	40.68 (73.16)	72.86 (176.75)	85.34 (166.70)
Laboratory group mean size (variance)			
Fox	41.91 (117.63)	76.11 (332.58)	90.75 (189.30)
Estuary signature	51.50 (96.30)	79.10 (214.74)	80.10 ^a
No signature	38.50 (85.01)	74.10 (411.18)	93.00 (207.33)
Anchor	48.22 (84.94)	77.90 (173.91)	99.75 (86.75)
Estuary signature	53.30 (114.33)	79.10 (137.69)	98.10 (76.98)
Laboratory group mean dry weight (variance)			
Fox	0.15 (0.02)	1.13 (0.80)	1.47 (0.42)
Estuary signature	0.30 (0.03)	1.22 (0.42)	0.96 ^a
No signature	0.09 (0.01)	1.08 (0.89)	1.60 (0.45)
Anchor	0.25 (0.02)	1.04 (0.40)	1.99 (1.05)
Estuary signature	0.32 (0.04)	1.11 (0.42)	1.91 (1.12)
No signature	0.18 (0.01)	0.70 (0.36)	2.40 (1.08)
Laboratory group Fulton's mean condition (variance)			
Fox	0.91 (0.04)	1.08 (0.02)	1.05 (0.01)
Estuary signature	1.12 (0.01)	1.12 (0.01)	1.14 ^a
No signature	0.84 (0.03)	1.06 (0.04)	1.03 (0.01)
Anchor	1.05 (0.02)	1.12 (0.01)	1.00 (0.02)
Estuary signature	1.12 (0.01)	1.15 (0.00)	1.00 (0.02)
No signature	1.02 (0.03)	0.99 (0.00)	1.02 (0.02)

^aSample size too small for variance calculations.

DISCUSSION

Fish using the estuaries in our study exhibited substantially greater estuary use times in the saline reaches of the estuary than previously reported for juvenile Coho Salmon, particularly older

cohorts (age-1 and age-2 juveniles; McMahon and Holtby 1992; Thorpe 1994; Magnusson and Hilborn 2003). Juvenile Coho Salmon in all age-classes used estuaries for extended periods of time, including overwintering in estuaries or nearshore areas,

TABLE 5. Trait comparisons between estuaries and signature groups for pooled, catch weighted data shown by age-class for Coho Salmon captured in the Fox River and Anchor River estuaries. Only tests with probability values <0.10 are reported.

Metric	Statistical significance	Pattern
Comparisons between estuaries		
Age 0		
Size	$t = 61.27, P < 0.01^a, df = 751$	Measured fish, Anchor fish larger
Entry date	$t = -2.50, P = 0.02, df = 30$	Laboratory fish, Anchor fish earlier entry date
Condition (Fulton's)	$t = -1.92, P = 0.06, df = 30$	Laboratory fish, Anchor fish higher condition
Age 1		
Size (FL)	$t = -5.95, P < 0.01^a, df = 889$	Measured fish, Anchor fish larger
Age 2		
Size (FL)	$t = -3.36, P < 0.01^a, df = 182$	Measured fish, Anchor fish larger
Comparisons between estuary signatures		
Condition (Fulton's)	$F = 13.12, P < 0.01^a, df = 103$	Fish with signature had higher, less variable condition
Dry weight	$F = 3.34, P = 0.07, df = 103$	Fish with signatures had higher, less variable dry weight
Capture date	$F = 5.14, P = 0.02, df = 103$	Fish with signatures showed later entry dates
Size (FL)	$F = 5.75, P = 0.02, df = 103$	Fish with signatures showed larger, less variable size

^aData are shown for all tests, Dunn-Sidak $\alpha = 0.013$ for significant tests.

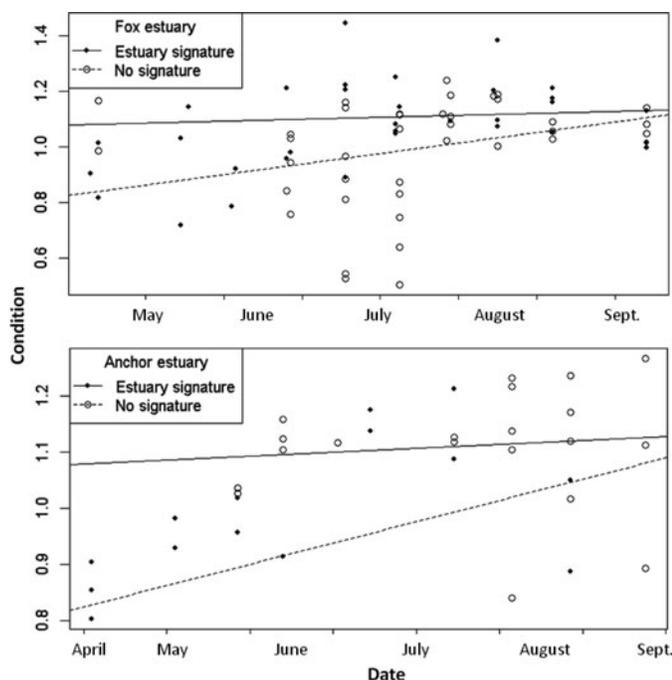


FIGURE 5. Fulton's condition factor for Coho Salmon shown by signature group and collection data from laboratory analyzed fish captured in the Fox River (upper panel) and Anchor River (lower panel) estuaries.

and these patterns of use differed between the two estuaries. The smaller, Anchor River estuary fed by snowmelt and spring water had larger, older fish that overwintered in the estuary or nearshore environments, and these fish used the estuary for shorter and earlier summer season periods prior to outmigration than did juveniles in the Fox River estuary. Fish in the larger, more complex, glacially fed Fox River estuary were composed of younger age-classes with longer summer residence times and few estuarine overwintering fish. Direct measurements of residence of older age-classes (ages 1–2) previously described were substantially shorter than those in our findings: up to 16 d (Chittenden et al. 2008) to 18 d (Miller and Sadro 2003).

Our observation of estuarine and nearshore overwintering juvenile Coho Salmon has theoretical implications regarding life history variability throughout the species range, though our observations are restricted to a central Alaska coastal population. This estuarine–marine overwintering life history pattern may be simply random movement or a response to a saturated or poor quality lower-river rearing habitat (Murphy et al. 1997) or, conversely, high estuarine habitat quality. Alternatively, it could represent exploitation of higher coastal productivity, forage, and nearshore habitat quality. All of these factors are expected to differ over the species range, even among adjacent systems within the same region. We note that incorporation of materials into the otolith matrix and our sampling regime do not allow us to distinguish between overwintering in the estuary channels themselves or the near shore environments of Kachemak Bay and Cook Inlet. The possibility exists that Coho Salmon enter nearshore

marine environments and rear by moving between a number of fjords and estuary habitats such as those that exist along the shoreline of Kachemak Bay and Cook Inlet. Further research is necessary for an understanding of the drivers and full range of overwintering areas used by these estuarine-resident juveniles.

Although we did not examine the mechanisms driving differential patterns of estuarine habitat use, we speculate that differences in timing of use among estuaries may be due to spatial variability in water turbidity, temperature regimes, and environmental factors that affect channel depths. Use of channels by juvenile salmon is often associated with water depth (Miller and Simenstad 1997; Webster et al. 2007; Hering et al. 2010), which in the glacially fed Fox River estuary increased gradually from mid-June to late August. The glacial run-off led to cooler and less variable water temperatures. Anchor River estuary channels are deepest in early spring during peak snowmelt and become most shallow and warm in mid-July and early August, cooling thereafter with fall rains. We captured most fish in late August in the Anchor River and in late July in the Fox River, suggesting a suitable combination of water temperature and channel depth to accommodate most estuary use.

Our findings also suggest variable use of estuaries by young-of-year and older age-classes of Coho Salmon. Miller and Sadro (2003) and Koski (2009) discuss the potentially important role of the “nomad” or young-of-year Coho Salmon that spend up to 8 months in the upper estuary ecotone and then return to freshwater to overwinter. Although a large proportion of young-of-year migrants exhibited summer season patterns of movement between freshwater and estuaries, we found no evidence of movement to freshwater environments to overwinter. The discrepancy here could be due to differences in the relative size and the definition of the estuary ecotones between our study and others or differences in methods. We defined the upper and middle estuary ecotones in which the sampling sites were located as the intertidal zone (point from highest to lowest tidal fluctuations) and may contain some channels with lower mean salinity levels at the upstream region of the intertidal zone. This may result in fewer fish from lower-salinity channels showing estuary use. We did examine the point measures of salinity across the tidal inundation zone and found that the most upstream channel of the Fox River estuary had generally low salinity (average, <2 mS/cm) with the exception of the spring tidal periods. However, we do not believe this biased our results because the sample size of fish was small and the relative proportion of fish with estuary signatures; i.e., fish lacking estuary signatures was similar to the overall sample (1:5 upper channel, 24:73 in the Fox River sample). Additional differences in our study may result from the variability of the tidal range (>8 m) because the Cook Inlet region is most likely very different from locations where other studies have been completed in lower latitudes. Finally, the methods we employed to determine estuarine residency were direct measures of Sr : Ca ratios (salinity of environment) and fish growth, as determined from the otoliths. Many other studies provide inference from mark–recapture work, which may be

biased to shorter periods and short-distance movements in areas where fish can be efficiently recaptured (Gowan et al. 1994).

Our study raises several interesting questions regarding the importance of the freshwater environment and watershed characteristics and their influence on exploitation of the estuarine environment—a point for future investigation. The influence of the watershed type and availability of suitable upstream rearing habitat may play a role in estuary use. Murphy et al. (1997) discuss the importance of lower-river freshwater areas in large glacial river systems for juvenile salmon rearing. We noted that the Fox River lacks the lower-river freshwater areas discussed by Murphy et al., whereas the Anchor River has ample lower-river habitats. The Anchor River estuary had a large proportion of older, larger resident fish with early entrance dates and shorter summer residence times, whereas the Fox River estuary had a smaller proportion of younger residents entering later and staying longer. This suggests that more suitable and extensive freshwater rearing habitat upstream may exist in the Anchor watershed (to allow for greater growth prior to estuary entry) and that temperature differences (cold glacier melt water versus warmer snowmelt and spring water) may contribute to patterns in growth and emergence timing. All but two of the Anchor River age-2 fish exhibited estuary overwintering during their second winter, implying an important role for the estuary, despite its small extent.

We did not determine the overall proportion of fish using the estuary during the juvenile phase in each population. It is possible that fish using the estuary for any amount of time may only contribute small numbers to the overall population within each river; it is probable that this varies from year to year. Simultaneous study of emigrating juvenile populations in the Anchor River (Gutsch 2012) noted a sudden drop in average length of Coho Salmon juveniles from approximately 100 mm to 80 mm toward mid-summer. These smaller individuals may overwinter within the estuary rather than move to the oceanic environment during a suboptimal period or body size—another possibility that warrants investigation. Regardless of the proportion of the reproductive population that these strategies compose, they contribute a unique suite of behaviors that increase trait diversity of each river's Coho Salmon population, diversity that represents adaptive potential that could contribute to population resilience to environmental change (Schindler et al. 2010).

Some interesting directions for future work include investigating the mechanisms for the differences in length, condition, residence times, and age composition found between fish using contrasting estuaries. We note that a possible nonlinear relationship between fish condition and time may exist in both estuaries (Figure 5). Though we are unable to address this question with our study sample, the possibility of influences of other estuarine environmental conditions on smolt condition (such as temperature and salinity) raises interesting questions for further investigation. A broader understanding of the importance of estuaries to different runs of salmon could be ascertained by determining the proportion of estuary residents in adult returns and how this

proportion varies over space, time, and estuarine complexity. Additionally, an understanding of the connections between the watershed, estuary, and near-shore environments during early marine rearing in Coho Salmon will facilitate strategic and knowledge-based management of these fragile and dynamic areas, thereby providing for resilient fisheries.

Prolonged use of estuary habitats (months during the summer and throughout the winter) may represent a distinct life history strategy that contributes to the overall population life history portfolio (Schindler et al. 2010). It follows, then, that pristine, functioning estuary habitats can contribute to resilience of salmon populations to environmental changes in two ways: (1) by providing a place for some individuals to increase in length and condition prior to ocean entry to improve survival, and (2) by providing for alternative life history strategies. Maximizing both the availability of supplemental habitats and life history diversity is particularly important given increasing human populations that stress land and water resource development and fishery resource use. Gaps in our understanding of environmental influences on life history expression arise from the fact that many of the highly studied salmon ecosystems in the Northeast Pacific are disturbed or substantially altered in some manner that has caused loss of variability in life history traits within populations (Miller and Simenstad 1997; Cornwell et al. 2001; Magnusson and Hilborn 2003; Bottom et al. 2005b; Healey 2009). Managers require a thorough understanding of the suite of environmental factors that influence the structure and survival of exploited fish populations to make decisions that provide the greatest benefit to all stakeholders (Bottom et al. 2009). This need stresses the importance of understanding functioning watersheds to inform management of endangered or threatened stocks.

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REFERENCES

- Abdi, H. 2007. The Bonferroni and Šidák corrections for multiple comparisons. Pages 103–107 in N. J. Salkind, editor. *Encyclopedia of measurement and statistics*. Sage Publications, Thousand Oaks, California. Available: www.utdallas.edu/~herve/Abdi-Bonferroni2007-pretty.pdf. (March 2013).
- Bailey, R. E., J. R. Irvine, F. C. Dalziel, and T. C. Nelson. 1998. Evaluations of visible implant fluorescent tags for marking Coho Salmon smolts. *North American Journal of Fisheries Management* 18:191–196.
- Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* 49:423–437.
- Beamish, R. J., C. Mahnken, and C. M. Neville. 2004. Evidence that reduced early marine growth is associated with lower marine survival of Coho Salmon. *Transactions of the American Fisheries Society* 133:26–33.
- Beamish, R. J., R. M. Sweeting, K. L. Lange, and C. M. Neville. 2008. Changes in the population ecology of hatchery and wild Coho Salmon in the Strait of Georgia. *Transactions of the American Fisheries Society* 137:503–520.
- Bohlin, T., C. Dellefors, and U. Faremo. 1993. Optimal time and size for smolt migration in wild Sea Trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* 50:224–232.
- Bottom, D. L., K. K. Jones, T. J. Cornwell, A. Gray, and C. A. Simenstad. 2005a. Patterns of Chinook Salmon migration and residency in the Salmon River estuary (Oregon). *Estuarine, Coastal and Shelf Science* 64:79–93.
- Bottom, D. L., K. K. Jones, C. A. Simenstad, and C. L. Smith. 2009. Reconnecting social and ecological resilience in salmon ecosystems. *Ecology and Society* [online serial] 14(1):article 5.
- Bottom, D. L., C. A. Simenstad, J. Burke, A. M. Baptista, D. A. Jay, K. K. Jones, E. Casillas, and M. H. Schiewe. 2005b. Salmon at river's end: the role of the estuary in the decline and recovery of Columbia River salmon. NOAA Technical Memorandum NMFS-NWFSC-68.
- Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Marine Ecology Progress Series* 188:263–297.
- Campana, S. E., and J. D. Neilson. 1985. Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1014–1032.
- Campbell, L. A. 2010. Life histories of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) in the Columbia River estuary as inferred from scale and otolith microchemistry. Master's thesis. Oregon State University, Corvallis.
- Chittenden, C. M., S. Sura, K. G. Butterworth, K. F. Cubitt, N. P. Manella, S. Balfry, F. Økland, and R. S. McKinley. 2008. Riverine, estuarine and marine migratory behaviour and physiology of wild and hatchery-reared Coho Salmon *Oncorhynchus kisutch* (Walbaum) smolts descending the Campbell River, BC, Canada. *Journal of Fish Biology* 72:614–628.
- Cornwell, T. J., D. L. Bottom, and K. K. Jones. 2001. Rearing of juvenile salmon in recovering wetlands of the Salmon River estuary. Oregon Department of Fish and Wildlife, Information Report 2001-05, Portland.
- Donohoe, C. J., and C. E. Zimmerman. 2010. A method of mounting multiple otoliths for beam-based microchemical analyses. *Environmental Biology of Fishes* 89:473–477.
- Gargett, A. E. 1997. The optimal stability 'window': a mechanism underlying decadal fluctuations in North Pacific salmon stocks? *Fisheries Oceanography* 6:109–117.
- Gowan, C., M. K. Young, K. D. Fausch, and S. C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? *Canadian Journal of Fisheries and Aquatic Sciences* 51:2626–2637.
- Groot, C., and L. Margolis. 1991. *Pacific salmon life histories*. University of British Columbia Press, Vancouver.
- Gutsch, M. K. 2012. Identification and characterization of juvenile Coho Salmon (*Oncorhynchus kisutch*) overwintering habitats and early spring outmigration in the Anchor River watershed, Alaska. Master's thesis. University of Alaska, Fairbanks.
- Healey, M. C. 1982. Juvenile Pacific salmon in estuaries: the life support system. Pages 315–341 in V. S. Kennedy, editor. *Estuarine comparisons*. Academic Press, New York.
- Healey, M. C. 1994. Variation in the life history characteristics of Chinook Salmon and its relevance to conservation of the Sacramento winter run of Chinook Salmon. *Conservation Biology* 8:876–877.
- Healey, M. C. 2009. Resilient salmon, resilient fisheries for British Columbia, Canada. *Ecology and Society* [online serial] 14(1):article 2.
- Hering, D. K., D. L. Bottom, E. F. Prentice, K. K. Jones, and I. A. Fleming. 2010. Tidal movements and residency of subyearling Chinook Salmon (*Oncorhynchus tshawytscha*) in an Oregon salt marsh channel. *Canadian Journal of Fisheries and Aquatic Sciences* 67:524–533.
- Hobday, A. J., and G. W. Boehlert. 2001. The role of coastal ocean variation in spatial and temporal patterns in survival and size of Coho Salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 58:2021–2036.
- Johnsson, J. I., J. Blackburn, W. C. Clarke, and R. E. Withler. 1997. Does presmolt growth rate in steelhead trout (*Oncorhynchus mykiss*) and Coho Salmon (*Oncorhynchus kisutch*) predict growth rate in seawater? *Canadian Journal of Fisheries and Aquatic Sciences* 54:430–433.
- Jonas, J. L., C. E. Kraft, and T. L. Margenau. 1996. Assessment of seasonal changes in energy density and condition in age-0 and age-1 Muskellunge. *Transactions of the American Fisheries Society* 125:203–210.
- Kennedy, B. P., A. Klaue, J. D. Blum, C. L. Folt, and K. H. Nislow. 2002. Reconstructing the lives of fish using Sr isotopes in otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* 59:925–929.
- Koski, K. V. 2009. The fate of Coho Salmon nomads: the story of an estuarine-rearing strategy promoting resilience. *Ecology and Society* [online serial] 14(1):article 4.
- Lind-Null, A., and K. Larsen. 2011. Otolith analysis of pre-restoration habitat use by Chinook Salmon in the Delta-Flats and nearshore regions of the Nisqually River estuary. U.S. Geological Survey, Open File Report 2010-1238 (version 1.1), Reston, Virginia.
- Magnusson, A., and R. Hilborn. 2003. Estuarine influence on survival rates of Coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific coast. *Estuaries* 26:1094–1103.
- McMahon, T. E., and L. B. Holtby. 1992. Behaviour, habitat use, and movements of Coho Salmon (*Oncorhynchus kisutch*) smolts during seaward migration. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1478–1485.
- Miller, B. A., and S. Sadro. 2003. Residence time and seasonal movements of juvenile Coho Salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. *Transactions of the American Fisheries Society* 132:546–559.
- Miller, J. A., and C. A. Simenstad. 1997. A comparative assessment of a natural and created estuarine slough as rearing habitat for juvenile Chinook and Coho salmon. *Estuaries* 20:792–806.
- Murphy, M. L., K. V. Koski, J. M. Lorenz, and J. F. Thedinga. 1997. Downstream migrations of juvenile Pacific salmon (*Oncorhynchus* spp.) in a glacial

- transboundary river. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2837–2846.
- Neilson, J. D., G. H. Geen, and D. Bottom. 1985. Estuarine growth of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) as inferred from otolith microstructure. *Canadian Journal of Fisheries and Aquatic Sciences* 42:899–908.
- NOAA (National Oceanic and Atmospheric Administration). 2012. Tides and currents: tidal station locations and ranges. NOAA, Silver Spring, Maryland. Available: tidesandcurrents.noaa.gov/tides07/tab2wc2b.html#154. (December 2012).
- Pope, K. L., and C. G. Kruse. 2007. Condition. Pages 423–471 in C. S. Guy and M. L. Brown, editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Réveillac, E., E. Feunteun, P. Berrebi, P. A. Gagnaire, R. Lecomte-Finiger, P. Bosc, and T. Robinet. 2008. *Anguilla marmorata* larval migration plasticity as revealed by otolith microstructural analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 65:2127–2137.
- Saltveit, S. J., I. Haug, and J. E. Brittain. 2001. Invertebrate drift in a glacial river and its non-glacial tributary. *Freshwater Biology* 46:1777–1789.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature (London)* 465:609–612.
- Sutton, S. G., T. P. Bult, and R. L. Haedrich. 2000. Relationships among fat weight, body weight, water weight, and condition factors in wild Atlantic Salmon parr. *Transactions of the American Fisheries Society* 129:527–538.
- Thorpe, J. E. 1994. Salmonid fishes and the estuarine environment. *Estuaries* 17:76–93.
- Thorpe, J. E., M. Mangel, N. B. Metcalfe, and F. A. Huntingford. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic Salmon, *Salmo salar* L. *Evolutionary Ecology* 12:581–599.
- Volk, E. C., D. L. Bottom, K. K. Jones, and C. A. Simenstad. 2010. Reconstructing juvenile Chinook Salmon life history in the Salmon River estuary, Oregon, using otolith microchemistry and microstructure. *Transactions of the American Fisheries Society* 139:535–549.
- Webster, S. J., L. M. Dill, and J. S. Korstrom. 2007. The effects of depth and salinity on juvenile Chinook Salmon *Oncorhynchus tshawytscha* (Walbaum) habitat choice in an artificial estuary. *Journal of Fish Biology* 71:842–851.
- Williams, G. C. 1996. *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton University Press, Princeton, New Jersey.
- Zimmerman, C. E. 2005. Relationship of otolith strontium-to-calcium ratios and salinity: experimental validation for juvenile salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 62:88–97.