Use of glacier river-fed estuary channels by juvenile Coho Salmon: transitional or rearing habitats?

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Abstract Estuaries are among the most productive ecosystems in the world and provide important rearing environments for a variety of fish species. Though generally considered important transitional habitats for smolting salmon, little is known about the role that estuaries serve for rearing and the environmental conditions important for salmon. We illustrate how juvenile coho salmon *Oncorhynchus kisutch* use a glacial river-fed estuary based on examination of spatial and seasonal variability in patterns of abundance, fish size, age structure, condition, and local habitat use. Fish abundance was greater in deeper channels with cooler and less variable temperatures, and these habitats were consistently occupied throughout the season. Variability in channel depth and water temperature was negatively associated with fish abundance. Fish size was negatively related to site distance from the upper extent of the tidal influence, while fish condition did not relate to channel location within the estuary ecotone. Our work demonstrates the potential this glacially-fed estuary serves as both transitional and rearing habitat for juvenile coho salmon during smolt emigration to the ocean, and patterns of fish distribution within the estuary correspond to environmental conditions.

Keywords Coho Salmon · Glacial estuaries · Early marine rearing · Smolting habitats

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Introduction

Pacific salmon exhibit a bet-hedging approach to survival, producing large numbers of offspring that incur high mortality, while expressing a range of life history traits (Holtby and Healey 1990; Healey 1994). Because salmon use dynamic habitats that vary in selection pressures over their life cycle, the bet-hedging life history strategy insures that a few individuals will possess the appropriate suite of traits to survive to maturity, thus permitting positive fitness for a subset of an individual's progeny and persistence at the population level in temporally stochastic environments. The range of life history traits that any one population

contains is a combination of genetic composition and a plastic phenotypic response to environmental conditions encountered during development (Stearns 1976; Schaffer 2004). Coho salmon (*Oncorhynchus kisutch*), in particular, can exhibit a wide range of life histories within a single population, including variability in age or size at which critical ontogenetic shifts take place (such as smolting), seasonal timing of these shifts, and duration of rearing in freshwater versus marine systems (Miller and Sadro 2003; Koski 2009). Spatial variability in trait expression among populations has been linked to inter-annual changes in both marine and freshwater environments and to resilience of an aggregated population under climatic shifts and a dynamic environment (Gargett 1997; Beamish and Mahnken 2001; Hilborn et al. 2003; Ebersole and Colvin 2009; Schindler et al. 2010).

Marine entry is considered a crucial period for salmon; conditions experienced during this transition can greatly impact survival (Gargett 1997; Beamish and Mahnken 2001; Beamish et al. 2004, 2008; Hillgruber and Zimmerman 2009). Prior to ocean entry, estuaries are thought to provide a gradual transition between fresh and saltwater during a stressful physiological shift (Healey 1982; McMahon and Holtby 1992; Beamish et al. 2004). Through provision of staging and possible rearing habitats, estuaries have the potential to influence plasticity in life history traits such as the timing and size of marine entry. Large estuarine ecotones, such as those described in Koski (2009), provide quality forage, and fish within estuary ecotones have higher survival rates over time than those abruptly transitioning to open ocean conditions (Beamish et al. 1997). Factors that are expected to impact individual marine survival include the duration of estuary occupancy, timing of early marine entry, environmental conditions, and body condition at outmigration (Healey 1982; Bohlin et al. 1993; Beamish et al. 2004).

Estuary ecosystems are complex and variable regarding the impacts of anthropogenic changes and interactions with seasonal and regime-level climate shifts. Estuaries are spatially defined by: 1) an upper, primarily freshwater region with limited tidal influence (generally very high tides); 2) a central, dynamic region of fresh and saltwater mixing and strong tidal influence; and 3) a lower mouth that is primarily saltwater, also strongly tidally influenced (Kaiser et al. 2005). Seasonal changes in river discharge, interacting with tidal regimes, will introduce variability in freshwater and allochthonous material (such as high

sediment loads or large wood debris) input that alter stream hydrology, thereby influencing salinity gradients and thermal regimes within these zones (Mann and Lazier 2006). Anthropogenic influences, such as water withdrawals for irrigation and hydroelectric projects, alter sediment, allochthonous inputs, nutrient content, and natural freshwater flow regimes. These practices can have a profound impact on estuary ecosystems and the composition of species sensitive to changing thermal and salinity gradients, and may be amplified by regional shifts in temperature and precipitation levels that also alter freshwater discharge regimes. Changes in environmental conditions may be especially pronounced in temperate latitudes where climate-related shifts are occurring at an amplified rate (Hinzman et al. 2005).

In this study, we examined juvenile coho salmon use of estuarine environments and relate fish characteristics to habitat use in a relatively undeveloped estuary in south central Alaska. We determined if variability in size, age, body condition, and patterns of abundance were linked to specific estuarine characteristics and habitat conditions along the tidal inundation gradient. This work provides insight into the roles environmental conditions play in driving estuary habitat use by juvenile coho salmon. This is relevant to management of both commercial salmon stocks and populations of conservation concern in other parts of their range where estuary function may be compromised by anthropogenic disturbances, as well as climate change and natural stochastic processes.

Methods

Study area

Work was conducted in tributary channels of the glacial melt-water fed Fox River estuary, located at the head of Kachemak Bay, approximately 27 km east of the Homer, Alaska (Fig. 1). The Fox River transitions through an approximately 6.0 km long delta into Kachemak Bay. Work conducted in a pilot study in 2009 determined that the Fox River estuary, particularly its tributary channels, provide migratory and possible nursery habitat for coho salmon (C.M. Walker, unpubl. data). Using these data as a basis for site selection, we chose four tributary channel habitats along the tidal inundation gradient within which we conducted a focused sampling effort. This tributary habitat type is characterized by square channels with soft, muddy substrate, steep banks with overhanging sedges
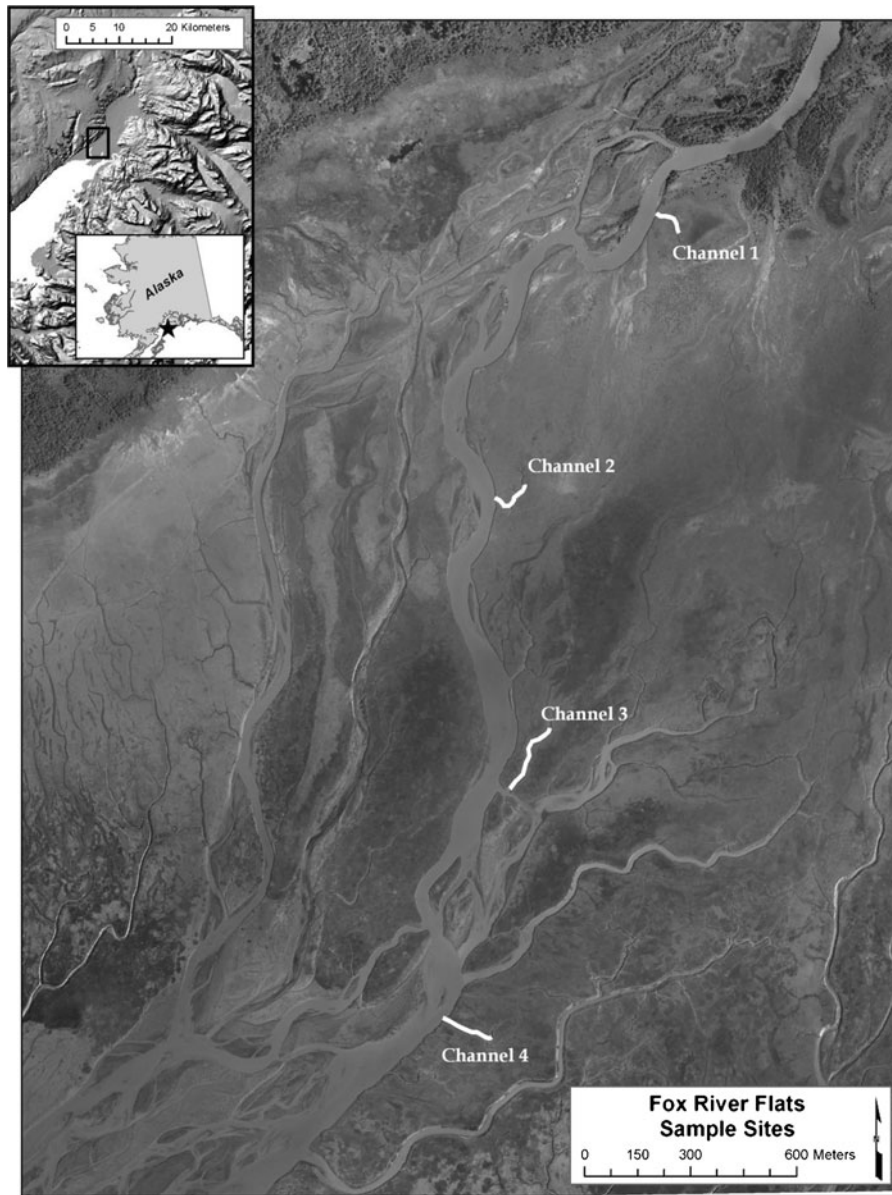
Fig. 1 The Fox River estuary sampling channels on the southern Kenai Peninsula, Alaska

and grasses, standing water, and slow water velocities within the intertidal zone. Water flow into these tributaries during mid-summer is largely from the increased glacial meltwater of the main river.

Surface salinities in tributary channel habitats sampled in 2009 ranged from 0–7‰. Water temperatures ranged from 5.6–13.8 °C, and turbidity, though not measured consistently, was high, with visibility less than 3.0 cm below the water surface from mid-May through mid-September (rain/snow-melt and glacial discharge related).

Habitat characteristics

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. Temperature and depth loggers were set at 15-min recording intervals, 5 m upstream from the channel mouth in each of the four channels. In addition, point measurements were collected before each sampling event at a cross-section located just downstream of the stationary loggers. Point measurements of data included

thalweg depth (m), conductivity (μS, standardized for temperature), salinity (‰), and temperature (°C, measured with a YSI model 30 probe held just below the surface, in mid-water column, and at the bottom).

Fish abundance and characteristics

A common site was sampled in each of the four channels over consecutive days, twice per month from early May to late September in 2011. The lower end of this site was located 5 m above the confluence of the each channel with the main river, just above the site of the temperature-depth logger. Fish abundance at each site was estimated using multiple-pass depletion methods (Hayes et al. 2007), validated to determine if they reflected actual fish abundances (see below). A 20 m length of channel was measured from the stationary logger location parallel to the channel upstream. The start and end points of each sampling unit were then obstructed with block nets (2.2 m×6.1 m, 0.31 cm mesh) secured along the sides and bottom with stakes to prevent fish escape. Pole seines (2.2 m×6.1 m, 0.31 cm mesh) were used to sample the site, pulled three times in the downstream direction. Fish from each haul were placed in separate, 19 L aerated tubs filled with water from the channel.

All fish captured were identified to species and counted. The first 50 juvenile salmon captured from each seine haul of each species were anesthetized in 70 mg/L tricane methane sulfonate, MS-222 (Bailey et al. 1998; Chittenden et al. 2008) and measured for fork length to the nearest 1.0 mm. To account for size selection in sampling, we gently mixed the fish in the container before drawing each sample (5–10 fish) with a small aquarium net. Up to three coho salmon (not to exceed 10 % of the total catch due to sampling permit restrictions), distributed among three size classes (small, medium, and large), were randomly selected and euthanized at each site using 140 mg/L MS-222 (maximum 24 individuals each month). These fish were labeled and frozen for laboratory analysis to determine condition, weights, and age.

To validate depletion methods, we generated mark-recapture estimates for a subset of our sampling events. Fish were captured using the same methods described for depletion (three hauls of the seine net). They were then batch dyed in one of the channels each month with Bismarck brown mixed in concentrations of 21 mg/L (Gaines and Martin 2004). All captured salmon were placed in containers of dye solution with portable aerators for 50 min. Water temperature was checked for increases

that could cause thermal stress to the fish at 20-min intervals during the dying procedure with the intent to add water if temperatures exceeded relative channel surface temperatures (temperatures changed little during dying in all events). Salmon were then released into the enclosed transect and allowed to acclimate and disperse randomly within the channel for 1 to 3 h. After recovery, the channel was resampled using the same effort (multiple pass seining), noting recapture of marked individuals.

We used water weight, wet weight, and Fulton's condition factor (K=W*L^{-3} *100,000, where W= laboratory weight [g] and L= laboratory length [mm]) for metrics of condition (Jonas et al. 1996; Pope and Kruse 2007). Coho salmon specimens were measured for fork length (±1 mm), then blotted and weighed to determine wet weight (± 0.01 g). Samples were placed in a 65–70 °C drying oven for 3 days, weighed, and returned to the oven for 24 h to be dried and re-weighed. Samples were considered dried when a minimal weight change was detected between consecutive daily weights (<0.001 g, Jonas et al. 1996). Water weight was determined by subtracting the oven dried sample weight from the wet weight (Jonas et al. 1996; Sutton et al. 2000).

Sagittal otoliths were removed from fish in the laboratory, rinsed, and stored in labeled plastic vials. Otoliths were aged after preparation for microstructure and microchemistry analysis (see Hoem Neher et al. 2013) by counting the winter annuli characterized by large, translucent rings composed of numerous, relatively small incremental growth bands (Campana and Neilson 1985). Ages generated from otolith analysis were used to validate size-at-age inferred from length frequency histograms.

Data analysis

Stationary logger data were summarized as 7-day maximum temperature, 7-day temperature variance, 7-day average depth, and 7-day depth variance. We also determined periods of exceedance of the Alaska Department of Environmental Conservation water temperature criteria for salmonid rearing (maximum daily for salmonid rearing 15 °C; ADEC 2011) and U.S. Environmental Protection Agency temperature criteria for migratory corridors (7-day average daily maximum <20 °C,USEPA 2012). Point measurements of salinity collected at each sampling event were combined and expressed as average, minimum, and maximum recordings for each sampling event. Data were compared spatially using the channel locations along the tidal inundation zone from

most upstream (channel 1) to most downstream sampling site (channel 4). We compared environmental conditions (temperature, depth, distance from low tide line, salinity) with patterns of coho salmon abundance for each channel to determine if environmental conditions related to patterns in fish abundance, body condition, and size.

Removal estimates of abundances with 95 % confidence intervals were generated for each species using depletion techniques for a closed population (Hayes et al. 2007). Removal estimates may be negatively biased due to declining sampling efficiency among depletion passes, and this bias can be affected by habitat conditions within channels (Rosenberger and Dunham 2005). To determine how well removal abundance estimates and total catch reflected actual fish numbers, we used mark-recapture sampling techniques as baseline measures of fish abundance once per sampling event within a single channel. Mark-recapture abundance estimates were calculated using single marking and single recapture estimates for a closed population following Hayes et al. (2007).

For fish retained for laboratory analyses, our protocol was to sample evenly across age classes; as a result, the composition of the laboratory fish sample did not correspond to catch composition. Age class composition of the total catch was inferred via length-frequency histograms and validated with otolith age for each sampling event. We examined the data for differences in means between the channels for fish size (fork length) and condition (laboratory fish only- Fulton's condition, dry weight, water weight) using one-way ANOVA. Abundance data were examined for relationships to environmental data using simple linear and multiple regression analyses. Catch data were tested for temporal autocorrelation using the Durbin-Watson test for autocorrelation (Durbin and Watson 1950, 1951). Based on those results, each sampling event was treated as an independent event. All environmental data were standardized and abundance data were transformed to meet homogeneity assumptions and assumptions of normality using R 2.14.1 statistical analysis software.

Results

Environmental data

Seasonal thermal characteristics (average water temperature and variance) differed among channels and were most likely related to water depth, surface run-off, and vertical stratification (Fig. 2a, b). The depth of the channel relative to the river depth/discharge levels and tides appears to be an important factor contributing to environmental conditions important for salmon, such as water temperature and cover from predation. The most upstream and downstream channels exhibited the warmest and greatest ranges in water temperature and the most shallow depths, being most similar to one another in depth relative to the river, particularly in the early season prior to the beginning of glacial melt-water run-off (Fig. 2). Water depths were low in May and early June, consistently increasing in depth with the glacial melt water until fall freeze and rain events (Fig. 2c, d). The most upstream and downstream channels also lacked the strong vertical stratification (variability from surface to bottom) in point measurements of salinity observed in channels 2 and 3; however, data is lacking from the most downstream channel during the high tides as it was completely inundated (Fig. 3). These two channels were most dissimilar to one another in tidal influence, with the most upstream channel inundated only at the highest spring tides and the most downstream channel inundated daily. When examined using standard water temperature criteria for salmonid rearing and migration, these two channels exceeded daily maximum temperatures of 15 °C in 12 and 34 of the 149 days measured and 20 °C in one and four of the 149 days measured, the most upstream and downstream channels, respectively (ADEC 2011, USEPA 2012, Table 1). The centrally located, deeper and less thermally variable channels (2 and 3) exhibited less extreme temperatures: channel 3 exceeded daily maximum temperatures of 15 °C in two of the 149 days measured, and neither channel exceeded maximum daily temperatures of 20 °C (Table 1).

Point measurements of salinity generally corresponded to the preceding tidal levels: higher salinity measurements followed the widest ranging spring tides, and lower salinity levels followed the moderate or low neap tides. Salinity levels were highest in the bottom strata of the centrally located channels (2 and 3), where water depth was sufficient to provide vertical stratification (Fig. 3). Channel 3 was consistently the most saline of the four channels, likely due to its location and orientation in the intertidal zone and water depth that allowed for increased water retention.

Fish data

Fish abundances for all channels were quantified using total catch and multiple pass depletion estimates (removal). For a subset of channels, these numbers were compared to mark-recapture (m-r) estimates (used as a baseline measure with
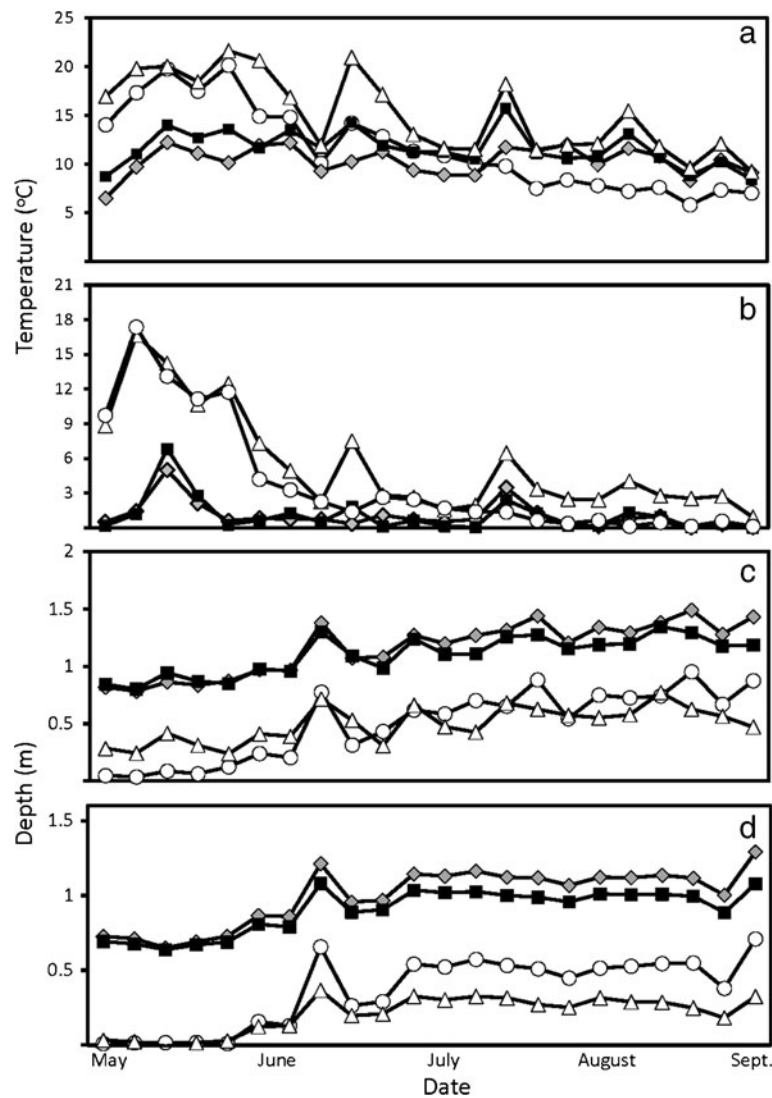
Fig. 2 Water temperature and depth plots from data loggers placed in tributary channels of the Fox River estuary, south-central Alaska: **a**) 7-day maximum temperature; **b**) 7-day temperature variance; **c**) 7-day average depth; **d**) 7-day minimum depth. *Symbols* and *colors* indicate most upstream Channel 1(○); Channel 2(◈); Channel 3 (■); to most downstream Channel 4 (△)

the exception of the July sampling event, during which one block net failed) to determine which technique (total catch or removal) most consistently corresponded to baseline measures of fish abundance. Both of these metrics had a high degree of correspondence to m-r estimates (R^2 values= 0.73, 0.85 for total catch and removal estimates respectively). Both estimates were lower than the baseline m-r value (73 % and 78 % of m-r estimate on average for total catch and removal estimates, respectively), but were consistently so. We did not have sufficient sample sizes to examine correlates of bias (such as differences in channel size, depth, and individual sampling technique). We therefore used the

uncorrected total catch for relative fish numbers with standardized effort for description and analysis. Using uncorrected total catch for relative fish numbers does not account for differences in catchability (q) related to changes in environmental conditions, however we used standardized methods of three pass removal in blocked channels at each event throughout the season yielding a relative catch per unit effort for each sampling event. Because our goal was not to estimate total abundance, but rather to compare catch with environmental conditions within each channel, we feel this measure allows for accurate comparisons across space and time.
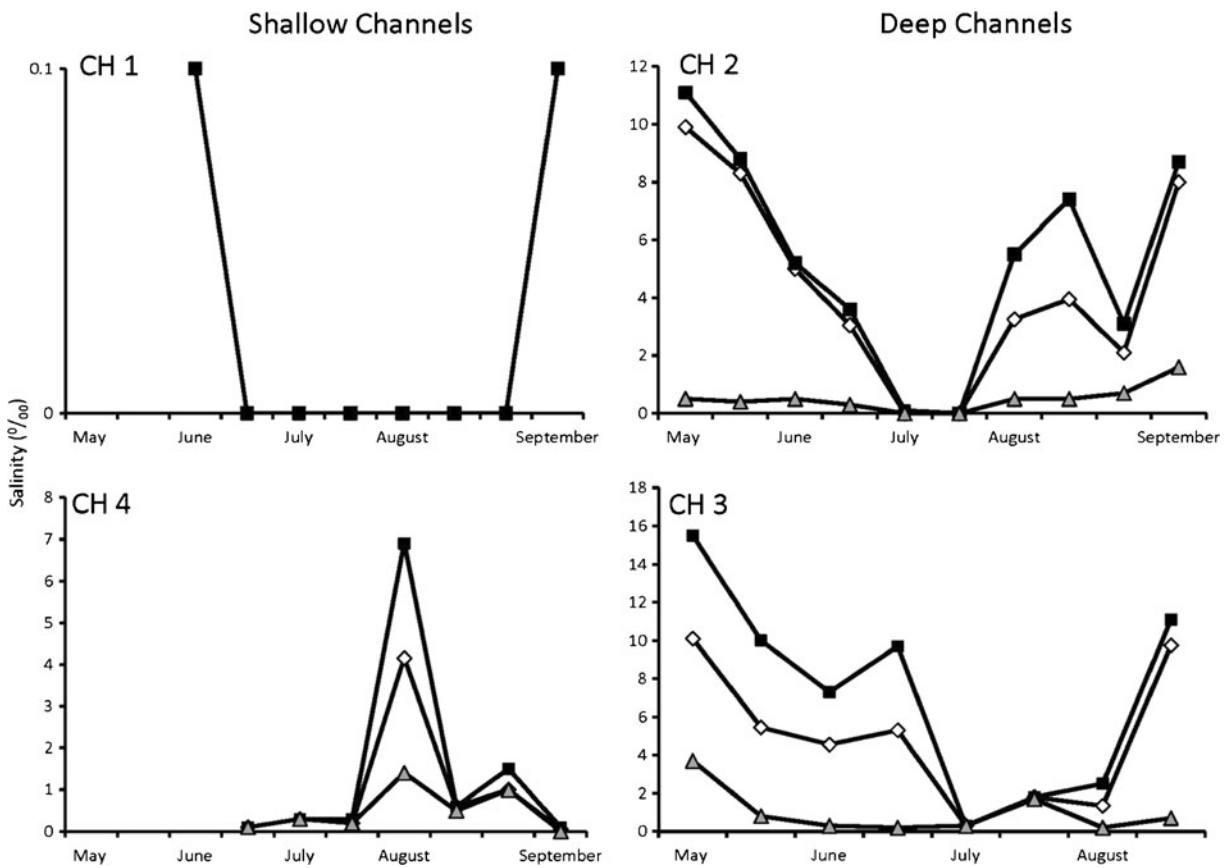
Fig. 3 Point measurements of salinity from the Fox River estuary channels in south-central Alaska, from most upstream channel (CH1) to most downstream channel (CH4) against sampling date. *Line colors* and *markers* delineate maximum (■); minimum (▲); and mean (◇)

We captured 4099 juvenile coho salmon, 1586 of which we measured, composed of three age classes (0, 1, and 2). Other fish species commonly captured with coho salmon included sockeye salmon *O. nerka*, starry flounder *Platichthys stellatus,* threespine stickleback *Gasterosteus aculeatus*, and several species of sculpin (family Cottidae).

Peak capture dates of coho salmon occurred in late July; however, the timing of peak capture differed for each age class, with most age-2 fish captured in May, June, and July and most age-0 and age-1 fish captured in July, August, and September (Fig. 4a). Few fish were captured during the May sampling events and those that were captured

Table 1 Seasonal, metrics for temperature (°C) from stationary logger data from the Fox River estuary, south-central Alaska. Data are from the most upstream channel 1 to most downstream channel 4

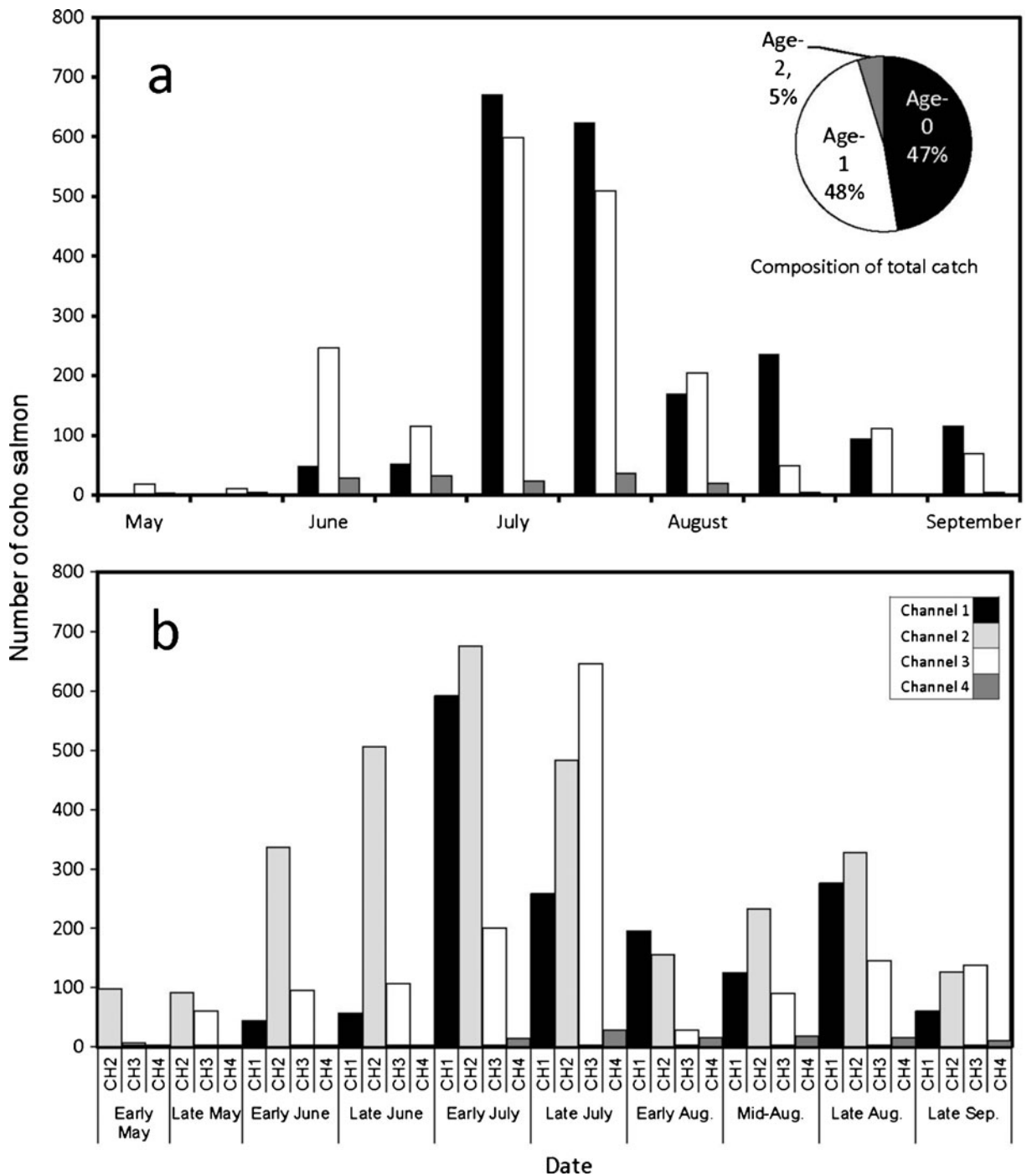| Temperature metric	Channel 1	Channel 2	Channel 3	Channel 4
Average (variance)	7.21 (6.19)	8.13 (2.82)	9.69 (2.39)	8.77 (7.39)
Maximum	20.14	12.21	15.72	21.61
Minimum	−2.23	3.64	4.42	0.89
Days maximum daily >15 °C	12	0	2	34
Days maximum daily >20 °C	1	0	0	4
Number of times 7 day maximum >15 °C	4	0	1	11
Number of times 7 day maximum >20 °C	1	0	0	4

Fig. 4 Coho salmon age composition and catch data shown by: a) date with all fish captured (age inferred to total catch from measured fish age compositions based on fish length for each date); and b) channel number from the Fox River estuary channels, south-central Alaska (measured fish only). Data are for all channels combined with age classes in panel a corresponding to colors: 0(■); 1(▨); and 2(□); and channel numbers in panel b corresponding to colors: 1(■); 2 (▨) 3 (□); and 4(▨);CH# indicates channel and number from most upstream (channel 1) to most downstream (channel 4)

were primarily age-1 and age-2 fish. Greater numbers of fish were captured in July consisting of a large proportion of age-0 fish in the total catch with the smallest fish captured measured to 23 mm FL (Fig. 4a).

We noted spatial variability in coho salmon total catch among channels with significant, though weak, relationships to variability in channel depth and temperature (F=6.57, P=0.01, adj. R^2=0.13; F=6.163, P=0.02, adj. R^2=0.13, depth and temperature respectively, 34 DF). ANOVA results (testing for differences in catch between channels) suggest that differences in catch are significant between channels, and that there is a significant interaction between the channel, depth, and temperature (F=4.65, P=0.02, 3 DF) and between the channel depth (F=4.07, P=0.04, 1 DF). This suggests that the environments of the channels are significantly different, but factors such as depth (and its correspondence with temperature) play a role in the numbers of salmon captured. The centrally located, deeper channels (2 and 3) had highest total combined catch throughout the season, with most salmon captured in the more upstream of these two channels (channel 2, Fig. 4b). The shallow, most upstream and most downstream channels (1 and 4) were seasonally available to salmon from mid-June to late August. Increases in glacial water inputs connected these shallow estuary channels from the main stem river consistently during mid-summer and for a brief period in early spring during Kachemak Bay's large (> 8 m) spring tides. When it was accessible to fish with deeper water levels, abundance was high for coho salmon in the most upstream channel, but coho salmon abundance in the most downstream channel was consistently low throughout the season, despite apparent accessibility.

We determined body condition for 69 coho salmon. Body condition, when compared by cohort between channels, was not significantly different; however, it is probably that we could not detect a difference given the sample size and distribution of fish between channels. The age-2 cohort was composed of a limited small sample size (n=5) and were missing entirely from one channel, and therefore we could not test for differences for this cohort (Table 2).

Discussion

A number of factors may play a role in how these estuary channels were used that we could not analyze with our study. These include the interaction of channel depth with the connectivity to the cold river channel, the amount of surface water run-off received by each channel in the tidal plain, and solar input (particularly to channels that receive substantial surface water run-off as this may alter water temperature significantly). In our study, we found that spatial and temporal variability in coho salmon abundance were related to temperature and water depth, constrained by accessibility of channel habitats to fish. These environmental conditions varied seasonally, prior to and following the glacial melt-water runoff, and spatially, particularly in the channels most influenced by connectivity to the river and daily tidal patterns. Deeper, cooler channels with less variability in both environmental measures were associated with consistent catches of coho salmon of older age classes (ages 1 and 2) throughout the season. Conversely, the abundances of coho salmon were lowest in shallow warm channels and/or channels with highly variable depth and water temperatures. Accessibility was also a factor contributing to seasonal patterns in catch. When water depth permitted access to the shallow upstream channel during the high glacial runoff period, abundances of salmon were high, particularly of young-of-year salmon potentially attracted to forage and/or warmer temperatures for growth. However, abundances declined dramatically when water levels decreased in September.

Water depth -though confounded with other environmental conditions, such as temperature and accessibility-

Table 2 Sample size and ANOVA test results for differences in Fulton's condition factor of fish captured in estuary channels, Fox River estuary, south-central Alaska

Age	Channel 1	Channel 2	Channel 3	Channel 4	F (P>F)	Power(groups)
All	14	29	20	6	1.19 (0.32)	–
0	5	12	4	2	2.98 (0.06)	0.73(4)
1	9	15	14	3	0.63 (0.60)	0.19 (4)
2*	0	2	2	1	*	0.25 (2)

*Sample size insufficient for statistical tests

was significantly related to fish catch, suggesting it is related to habitat features (such as refuge from predation or thermal strata), and may be particularly important for juvenile salmon in estuaries. Water depth is often altered or manipulated in watersheds for use by municipalities and agriculture through river flow alterations that provide power generation or crop production (Montgomery 2003; Mann and Lazier 2006). Additionally, changing climate regimes that alter precipitation events and sources of run-off will also impact water depth in rivers and side channels (Bryant 2009). These changes impact estuarine physical processes by altering the freshwater flow regime (Mann and Lazier 2006), including presence and distribution of deep water and thermally suitable habitat for juvenile salmon. Low abundances associated with shallow water depths support findings of Hering et al. (2010) that showed that little movement occurred in Chinook salmon using estuary channels when water depths were <0.4 m and that these shallow, tidal process dominated channels were often used intermittently through the tidal cycle (abandoned at low tides). Fish abundance was also more related to water depth than salinity; we observed the highest, most variable levels of salinity in the deep, centrally located downstream channel (channel 3) with intermediate seasonal patterns of fish abundance. These data also agree with the findings of Webster et al. (2007); water depths, rather than salinity, were more strongly related to the presence of Chinook salmon smolt. Salinity stratification in deeper channels may permit juvenile coho salmon to select microhabitats with optimal or consistent salinities.

Patterns of abundance, seasonal persistence, and distribution of cohorts among the channels within the estuary ecotone suggest that this glacial estuary serves as both rearing and transitional habitat. We observed a reverse relationship between the distance to low tide mark and the composition of fish captured; a larger proportion of age-2 fish were captured in the downstream deep channel and a greater proportion of age-0 fish were captured in the most upstream channel closest to freshwater habitats, showing differential use of habitats by different age-classes related to proximity to the marine environments. The high abundances of age-0 fish pose some curiosities regarding behavior patterns in this glacial estuary. Miller and Sadro (2003) found patterns of young of year coho salmon using the upper estuary ecotone for prolonged periods (up to 8 months) before returning to side channels and ponds within the lower river to overwinter. It is possible that young of year coho salmon in the Fox River estuary

also exhibit this pattern, taking advantage of the warmer water temperatures, abundant prey (C.M. Walker, unpubl. data), and turbid water within the estuary to optimize growth and reduce predation risk before returning to freshwater. Individuals in these habitats may represent a unique early life history tactic distinct from individuals that rear primarily in freshwater environments, or they may be using estuaries as supplemental or complementary habitats when freshwater habitats upstream are saturated or unavailable. We did not examine movement patterns between the estuary, lower-river, or marine environments during this study, which is an important topic for future study.

We observed patterns of increasing size within age cohorts throughout the season; fish are either using these estuary channels as rearing habitats, or freshwater growth continues throughout the summer as fish enter the estuary. Although we do not present direct evidence of estuary rearing, partner studies illustrate summer estuarine residency in the less variable environments for up to 82 days (Hoem Neher et al. 2013) and specific channel use of the estuary by coho salmon for periods up to 68 days (C.M. Walker, unpublished data). Partner studies also demonstrate evidence of feeding in the estuary channels, with differential diet composition corresponding to available prey surrounding each channel (C. Simenstad, Unpubl. data). In concert, these studies illustrate that the Fox River glacial estuary is an important rearing habitat for juvenile coho salmon; individuals may use these environments to not only make the physiological transition from freshwater to saltwater, but also attain body condition conducive to marine survival.

The Fox River watershed and estuary are located at the head of Kachemak Bay. Anthropogenic alterations in this area are limited to all terrain vehicle use and cattle grazing, with little influence from chemical pollutants, and no anthropogenic flow alterations. The relatively undisturbed and undeveloped upriver habitats above the estuary are a sharp contrast to those of many of the Northern Pacific watersheds that have lost habitat quality and complexity (Bottom et al. 2005; Shaffer et al. 2009). This study argues for a more detailed observation of habitat use by juvenile salmon outside of core areas of abundance and the importance of functioning estuary habitats to healthy salmon populations. Estuaries, though largely ignored in most juvenile salmon studies, may provide key rearing environments within which to explore alternative life history tactics such as movement timing and size during ontogenetic shifts, or they may

provide conditions that supplement against loss or saturation of rearing habitats in the upper watershed. We therefore argue that maintaining and restoring estuary habitats could facilitate resilience in salmon populations to both environmental changes and loss of upstream rearing habitat elsewhere.

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