Reconstructing Juvenile Chinook Salmon Life History in the Salmon River Estuary, Oregon, Using Otolith Microchemistry and Microstructure

ERIC C. VOLK*

Alaska Department of Fish and Game, Commercial Fisheries Division,
333 Raspberry Road, Anchorage, Alaska 99518, USA

DANIEL L. BOTTOM

National Oceanic and Atmospheric Administration–Fisheries,
Northwest Fisheries Science Center, 2032 SE Marine Science Drive, Newport, Oregon 97365, USA

KIM K. JONES

Oregon Department of Fish and Wildlife, 28655 Highway 34, Corvallis, Oregon 97333, USA

CHARLES A. SIMENSTAD

School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington 98195-5020, USA

Abstract.—We quantified the juvenile rearing and migratory patterns of individuals from a population of fall-spawning Chinook salmon *Oncorhynchus tshawytscha* in Oregon's Salmon River estuary using otolith microchemistry and microstructure. The study confirmed the daily periodicity of otolith growth increments in a natural fish population under field conditions and validated fundamental assumptions about increased otolith strontium : calcium values during entry into saline waters. The otolith results indicated that more than 75% of the subyearling Chinook salmon captured near the mouth of the Salmon River had entered the estuary during the summer and that two-thirds of these fish had spent more than a month in the estuary before capture. Unlike in other Oregon coastal estuaries, in which the fingerling-migrant portion of their life histories is dominant, approximately two-thirds of Salmon River Chinook salmon in upper-estuary marshes were early fry (<50-mm) migrants. A much smaller proportion at the river mouth suggests that many fry migrants did not survive to the lower estuary or passed undetected during ocean emigration. Nonetheless, the otolith results reveal a substantially greater contribution of estuarine-rearing fry to the out-migrant population at the Salmon River than has been reported in other Oregon coastal basins. A small component of fall-migrating fish with long freshwater residence times also occurred at the river mouth. Most of these individuals had migrated quickly through the estuary. Rather than revealing a series of discrete "types" defined by the predominant rearing patterns in the population, the individual otolith results depict a continuum of freshwater and estuarine life histories that is consistent with reports of considerable phenotypic plasticity in Chinook salmon. Otolith analysis offers the potential to quantify the relative contributions of different juvenile rearing patterns to adult returns.

Juvenile Chinook salmon *Oncorhynchus tshawytscha* exhibit a wide array of rearing and migratory behaviors to complete their anadromous life cycles, including differences in the timing and age of freshwater emigration, duration of estuarine residency, and time and size at ocean entry (Rich 1920; Reimers 1973; Carl and Healey 1984; Healey 1991). Phenotypic variation in anadromous salmon has been linked to habitat and environmental opportunities for life history expression (Healey and Prince 1995; Bottom et al. 2005b) and is believed to promote population resilience by providing a hedge against stochastic environmental conditions in river, estuary, and ocean environments (Stearns 1976; Healey 1991; Thorpe 1994; Francis and Mantua 2003; Healey 2009). Because very few studies have quantified life history variations within Chinook salmon populations, the effects of habitat or environmental change on population resilience are poorly understood.

In small Pacific coastal drainages south of the Columbia River, large proportions of the populations are composed of individuals that migrate to sea in their first year of life (Nicholas and Hankin 1988; Healey 1991). Nonetheless, the sizes, ages, and timing of salmon smolting and out-migration can vary considerably even within small river basins (Reimers 1973;

Myers and Horton 1982). However, the few surveys that have interpreted juvenile life histories have relied on mean abundance patterns, size distributions, and mark-and-recapture results, which may not depict the full range of life history variation among individuals in a population (Reimers 1973; Nicholas and Hankin 1988; Bottom et al. 2005a).

For example, mark-and-recapture techniques in Oregon's Salmon River basin discerned four Chinook salmon life history types based on juvenile time and size of estuarine entry and exit, and relative duration of freshwater and estuarine residency (Bottom et al. 2005a), as follows: (1) fry migrants disperse to the estuary soon after emergence in early spring; (2) fingerling smolts reside in freshwater for a few weeks or (3) for several months before rearing in the estuary; and (4) larger juveniles leave the Salmon River late in the fall after an extended period of rearing upriver, in the estuary, or both. However, these general patterns may oversimplify the rearing and migration behaviors of the Salmon River population because the unique batch marks applied weekly to large groups of estuary entrants could not discriminate the life histories or growth of individual fish. Moreover, life history interpretations could have been biased by the relatively low rate of recapture of marked fish following their estuarine dispersal or by continued estuarine entry of salmon after July, when low seasonal flows halted upriver trapping and marking activities (Bottom et al. 2005a).

A very low recapture rate for marked fry at the mouth of Salmon River implies that few of the many fry migrants survived in the estuary (Bottom et al. 2005a). Estuarine dispersal of recently emerged fry is characteristic of many Chinook salmon populations but previously had not been identified as an important life history strategy in Oregon coastal rivers (Reimers 1973; Myers and Horton 1982; Nicholas and Hankin 1988; Bottom et al. 2005a). However, poor survival in the Salmon River estuary contradicts the conclusion that fry dispersal is an adaptive strategy for distributing juveniles among suitable rearing habitats rather than simply a passive displacement of surplus juveniles from their natal streams (Healey 1991). Methods for reconstructing the life histories of individual fish that do not depend on difficult mark–recapture techniques offer the best opportunity to resolve questions about juvenile life history variation, and in particular, the contribution of early fry migrants to Chinook salmon populations.

The primary objective of this study was to establish precise estimates of size and date of estuarine entry, residence time, and growth of juvenile Chinook salmon in the Salmon River using otolith attributes. We first test the assumption that patterns of otolith strontium abundance provide a reasonable indicator of salmon migrations through a salinity gradient that approximates estuary entry. Our approach compares water chemistry data in the Salmon River main stem and estuary with patterns of strontium abundance in otoliths from fish captured throughout the basin. We then validate otolith estimates of estuarine residence time and growth with results of concurrent mark-and-recapture experiments. Finally, we expand this approach to unmarked juvenile Chinook salmon captured throughout the estuary to describe variation in life history attributes and growth. By examining fish sampled at the estuary mouth, we estimate the contribution of various life histories to the out-migrant population and compare these results with the previous life history characterization for the Salmon River population using mark–recapture methods (Bottom et al. 2005a). We also examine whether early fry migration to the estuary constitutes a potentially viable life history strategy as indicated by the proportion of fry migrants among all juveniles leaving Salmon River for the ocean.

Methods

Study site.—Salmon River is a small drainage basin (194 km^2) on the central Oregon coast. Its 800-ha estuary is located immediately south of Cascade Head and a few kilometers north of Lincoln City (Figure 1). Tidal influence extends approximately 6.5 km upstream from the river mouth but salinity intrusion ranges between 0 and 5 km from the river mouth with variations in freshwater discharge. A population of Chinook salmon that typically ranges between 1,000 and 3,000 adults spawns naturally in the Salmon River. A state of Oregon salmon hatchery also rears and releases approximately 200,000 juvenile Chinook salmon annually. All hatchery Chinook salmon are identified by an excised adipose fin, marked with coded wire tags, and are released in August. Salt marsh vegetation accounts for almost half of the estuarine surface area, including approximately 145 ha of former marsh habitat that was returned to the estuary after a series of dike removal projects in 1978 (approximate river kilometer [rkm] 2.2, termed the "78 marsh"), 1987 (rkm 2.5; "87 marsh"), and 1996 (rkm 3.7; "96 marsh"). A fourth marsh not previously diked is referred to as the reference marsh (rkm 3.2). The physical characteristics of the drainage basin, estuary, and marsh habitats are described in greater detail in Gray et al. (2002) and Bottom et al. (2005a).

Otolith microchemistry.—We collected water samples throughout the watershed and otoliths from juvenile Chinook salmon in freshwater and estuarine
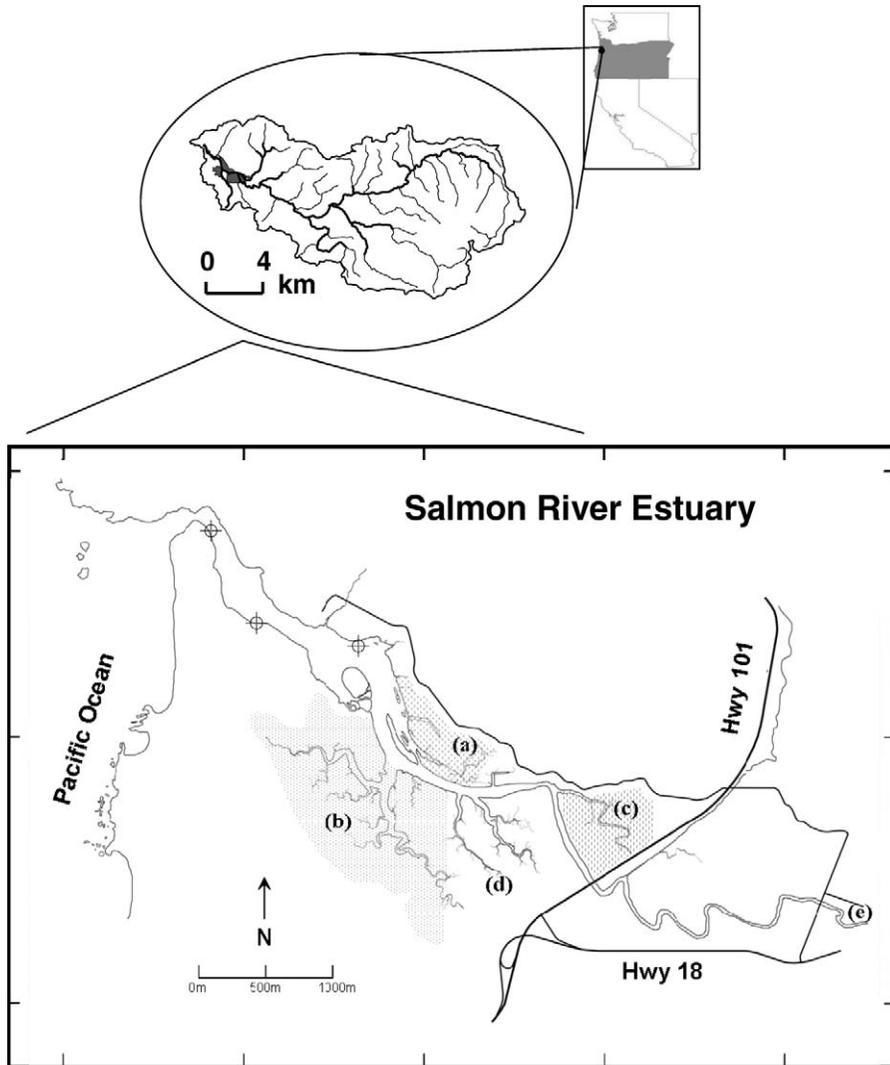
FIGURE 1.—Locations of the primary beach seine sites in the lower estuary (circles overlaid with plus signs); the trap net sites in the 78, 87, 96, and reference marshes in the upper estuary (a–d, respectively); and the downstream migrant trap (e) just above the head of tide.

locales to (1) characterize the chemical gradient in the river basin and (2) validate whether otolith chemistry can be used to distinguish freshwater from estuarine residency of juvenile salmon.

Water samples.—We sampled water from the confluence of the Little and Main Salmon rivers to the mouth of the Salmon River at Cascade Head on a single day in May 2002 using a 2-L Niskin bottle. Samples above the head of tide were taken from the Salmon River and the major tributaries to the river (Figure 1). Samples from near the head of tide and in the estuary were collected from a boat over a 2.5-h

period straddling both high and low tides. During low tide, we sampled only surface water samples from the main Salmon River channel because water depth was very shallow and thoroughly mixed, and marsh channels were essentially dry. During high tide, we sampled the 87, 96, and reference marshes and included samples near the bottom of two deep pools in the main stem.

Water samples were filtered through 0.45-µm membrane filters, then acidified to less than pH 2 with quartz-distilled nitric acid. Samples were diluted from 1 to 6 mL with 1% quartz-distilled nitric acid. We

TABLE 1.—Laser ablation inductively coupled plasma mass spectrometer operating conditions for analysis of Salmon River Chinook salmon otoliths.

Factor	Value
Gas flow rates (L/min)	
Cooling gas	13.00
Auxiliary gas	0.95
He carrier	0.75
Detector mode	Pulse counting and analog
Sweep mode	Peak hopping
Dwell time	10 ms
Points per peak	1
Analysis interval	360 s
Pulse rate	8 Hz
Number of analytes	10
Laser ablation diameter	30 μm

analyzed concentrations of Ca and Sr in water samples with a Varian Liberty 150 inductively coupled plasma optical emission spectrometer. Concentrations were calculated from the emission intensities and the intensities of standard solutions. Accuracy of the method was verified by running a National Institute of Standards and Technology (NIST) freshwater certified reference material (NIST 1643c).

Fish collections.—We collected 14 juvenile Chinook salmon from three freshwater sites above tidewater in 2002 to describe otolith chemical profiles in fish before estuary entry. Results of these analyses were used to assess the correspondence between otolith Sr:Ca patterns and the salinity regime in freshwater or estuarine habitats.

We retained for otolith analysis a subsample of five juvenile Chinook salmon collected monthly (March–July) to assess juvenile life histories in the upper Salmon River estuary in 2000–2002. All upper-estuary samples were collected in shallow marsh habitats above rkm 2 with a 0.6-cm-mesh fyke trap net and live box (Gray et al. 2002). In 2001, we sampled secondary channels of the three restored marshes and the reference marsh (Figure 1). During March–July 2002 we again sampled the upper-estuary sites, except for the 78 marsh, where limited access to the entry channel depressed monthly salmon catches (Bottom et al. 2005a).

We also retained for otolith analysis a subsample of Chinook salmon captured in the lower Salmon River estuary (below rkm 2) with a 38-m × 2.75-m beach seine, 1.3–1.9 cm in the wings, and a 1.0-cm (stretched) mesh in the bottom of the bag. Despite a slightly larger mesh size than the trap net, the beach seine effectively sampled emergent fry as small as 40 mm (Cornwell et al. 2001). We collected salmon from three lower-estuary sites during March through September or October 2001–2003 (Figure 1) (Bottom et al. 2005a).

A mark–recapture study from 2000 to 2002 estimated the number of downstream migrants entering the Salmon River estuary and described the variations in the times, sizes, and ages of migration among juvenile Chinook salmon in the Salmon River population (Bottom et al. 2005a). Located approximately 1 km above the head of tide, the trap and marking station was operated weekly from mid-March through mid or late July. Individuals were marked with a unique caudal-ray paint color applied for each marking week (Bottom et al. 2005a). We retained all marked individuals recaptured in the estuary to independently validate estuarine entry times and growth rates derived from otolith microchemistry and daily increment analyses (see Measures and Counts). Including both unmarked and marked salmon captured in the lower and upper estuaries, we reconstructed the freshwater and estuarine life histories of 268 individuals from otolith analyses.

Otolith preparation.—Dissected otoliths were cast sulcus (medial) side down into solid blocks of polyester resin. We ground mounted otoliths on a rotating lap wheel with 500 grit, then with 1,200-grit silicon carbide paper until a polished hemisection was created, exposing the surface of the otolith from core to edge. This surface was glued to a glass slide. After most of the resin block was removed with a diamond saw, the lateral otolith surface was again ground and polished by the same method to create a thin section (nominal thickness, 100 μm) exposing primordial core elements that were evident with reflected light. Sections were fine polished with a 1-μm alumina slurry.

Otolith analysis.—All sectioned specimens were analyzed at the Keck Collaboratory for Plasma Mass Spectrometry at Oregon State University. The laser ablation system consists of a New Wave DUV 193 nm ArF laser coupled to a Thermal Elemental PQ Excell quadropole inductively coupled plasma mass spectrometer (see Table 1 for analytical conditions). The sample chamber has a continuous flow of helium gas that carries the ablated material through Tygon tubing to the mass spectrometer. Analytical transects were initiated from a point near the otolith core and ended at a point beyond the margin of the otolith along a dorsal–posterior radius. Analyses were conducted with a 30-μm-diameter laser ablation at an 8-Hz pulse rate. The precise axis of analysis varied for some samples due to obvious cracks or pits in the otoliths obstructing our preferred transect. Each otolith analysis was paired with an analytical transect on a polished sample of NIST 612 glass standard.

Strontium profiles.—Time-resolved data were examined visually following each analysis and two regions were selected: one before the onset of ablation (background) and one after ablation began. Thermal Elemental Plasmalab software calculated integrated counts per second and SD values for all elements in both regions. These results and raw elemental count data were exported to Microsoft Excel spreadsheets for further analysis. Blank corrected count rates for each element were determined by subtracting their integrated background count rates from count rates at a particular location on the otolith transect. Element concentrations were calculated after Longerich et al. (1996) (as outlined by Russo 2001) with the equation

$$[x]_{sample} = (J_x)_{sample} \times [x]_{NIST}/(J_x)_{NIST}$$
$$\times (J_{Ca})_{NIST}/[Ca]_{NIST}$$
$$\times [Ca]_{sample}/(J_{Ca})_{sample},$$

where J is the blank corrected count rate for each element (x). In this calculation, we used otolith calcium concentrations as an internal standard to correct for different ablation rates in aragonite and NIST glass. These values were determined independently by electron microprobe analysis transects from the core to the otolith edge of 35 Salmon River Chinook salmon otoliths. This resulted in 568 individual spot analyses with a mean otolith calcium concentration of 38.05% (SD = 0.97%).

Raw data for each measured element were plotted in Microsoft Excel, allowing us to approximately locate inflection points or peaks in elemental raw count data. For strontium, we focused on the inflection point where count rates began increasing after their nadir, which we hypothesized indicated the fish's entry to waters with measurable salinity (see results). A z-test was used on running averages of 10 count rate values in the region to determine when count rates significantly increased. We determined the position of peak values visually and used the mean of 10 surrounding count rates for quantitative determinations. Once we recognized the location of any of these points of interest (POI) on raw count plots we noted the time in the analytical transect where they occurred and determined their position on the otolith using the following equation:

distance from edge (μm)
$$= \{[\text{time margin (ms)} - \text{time (POI)}]/1{,}000\}$$
$$\times 5 \text{ μm}.$$

We quantified otolith Sr:Ca values in 194 specimens at three specific locations in otolith chemical transects: (1) the core region of the otolith, (2) the count rate nadir immediately preceding the dramatic count-rate increase we presumed to represent estuary entry, and (3) at the otolith margins where strontium count rates were typically highest. These chemical transect regions respectively corresponded to the strontium signal passed on by the anadromous female parent (Volk et al. 2000), the presumptive freshwater residence period before estuary entry, and estuary residence immediately before capture.

Measures and counts.—We viewed each sectioned otolith with transmitted light microscopy to conduct radial measures and increment counts using Image Pro image analysis software. All otoliths were measured along a standard dorsal–posterior radius starting at the posterior most core element and ending at the otolith edge approximately 20° from vertical. The length of the laser scar also was measured from its beginning to the edge of the otolith. Since it was difficult to position the start of the laser transect precisely over the preferred core element, this measure provided a correction for accurately placing chemical transect data on the measured otolith radius from core to edge. We used the software to automatically enumerate otolith increments along the same radius, and a standard luminance peak-and-valley algorithm packaged with the program to identify the edges of otolith increments. All increment radials needed some editing and increments were enumerated as far back in the otolith as possible. When we could not reliably enumerate otolith increments along the preferred axis due to preparation difficulties, we enumerated increments along a general path from a landmark representing estuary entry. We could not reliably count increments on a few specimens.

We back-calculated fish size at any point of interest, such as estuary entry, based upon the relationship between otolith size and fish size for Chinook salmon in the Salmon River. Estuary entry date was determined by subtracting the number of estuary otolith increments from the capture date, assuming that otolith increments were produced with a daily periodicity. Estuary growth rates were determined by subtracting estimated estuary entry length from capture length and dividing by residence time in the estuary.

Results

Water Chemistry

Water samples from freshwater main-stem and tributary sites above the Salmon River estuary generally showed low Sr:Ca values (1.37–2.90 mmol/mol) associated with zero salinity (Figure 2a). For estuary sites sampled below the trap (rkm 7.9) during low tide, surface salinity values were typically <1‰ through the upper estuary (rkm 3–5), and Sr:Ca values gradually rose through the lower estuary, reaching a
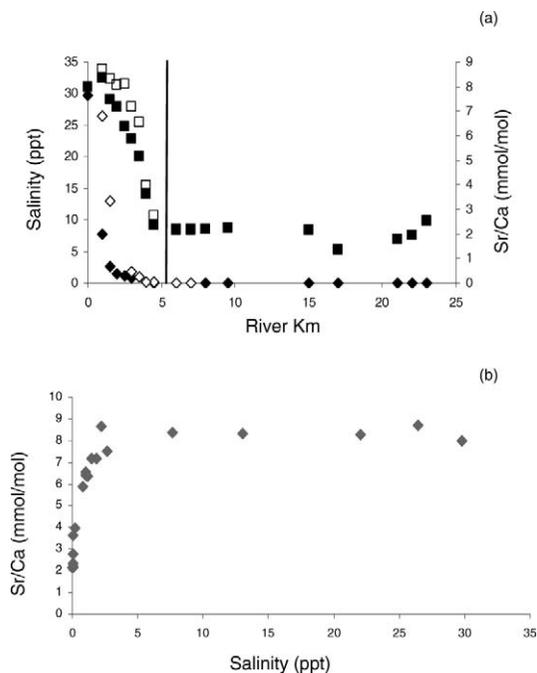
FIGURE 2.—Panel **(a)** shows the water salinity and Sr:Ca values of samples from the entire length of the Salmon River at high and low tide. The dark vertical line represents the position of the highway bridge, which roughly separates the river habitats from the estuarine habitats. The diamonds represent salinity values and the squares Sr:Ca values; open symbols denote values at high tide, closed symbols values at low tide. Panel **(b)** shows the relationship between water salinity and the Sr:Ca ratio for all Salmon River water samples.

FIGURE 3.—Plots of strontium count rates versus analytical times (otolith radial distances) in four Salmon River Chinook salmon otoliths **(A)**–**(D)**. The shaded boxes represent periods of estuary residence.

maximum of 8.7 mmol/mol near full strength seawater at the river mouth (Figure 2a). Water Sr:Ca values above the Highway 101 bridge (rkm 5–7) were similar to those from freshwater sites above the head of tide and increased significantly in the sample taken directly below the bridge (Figure 2a). At high tide, corresponding site values for salinity were higher, especially in the lower reaches of the estuary. However, high salinities on the incoming tide were also present higher in the estuary, including a 22‰ value at a 2.75-m depth near the mouth of the 96 marsh (rkm 3.7). Water salinity and Sr:Ca exhibited a nonlinear relationship; the elemental ratio rose sharply to approximately 8.0 at salinities less than 5‰ and reached an asymptote thereafter (Figure 2b).

Otolith Chemistry

Qualitatively, most otolith transects showed a consistent pattern of strontium abundance through early Chinook salmon life history. In all specimens,
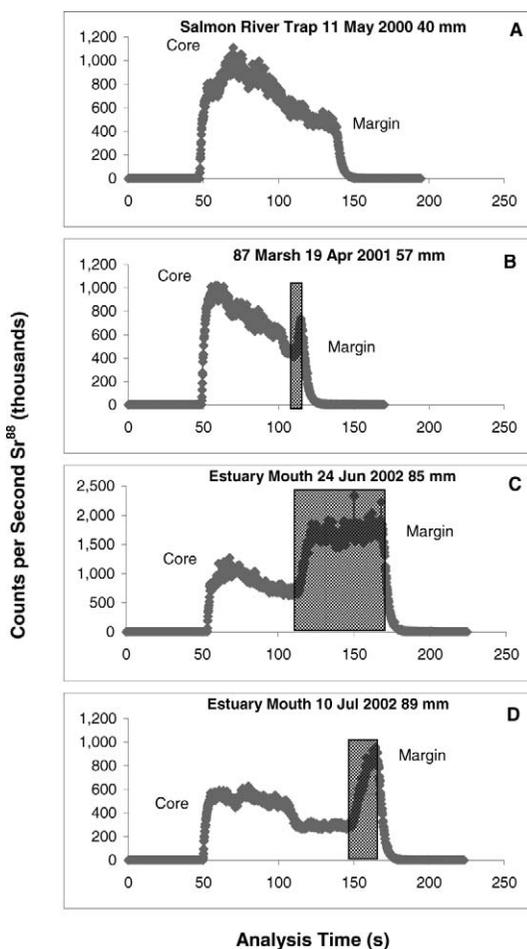
Sr counts were higher at the core of the otolith and gradually declined to a minimum at an otolith size roughly corresponding to the fry stage (Figure 3). For specimens collected as fry in freshwater habitats, after the Sr count rates reached a minimum beyond the otolith core, the values remained low to the margin (Figure 3A). In the vast majority of specimens captured in the estuary, the count rates of Sr^{88} increased dramatically at some point in otolith transects. In some specimens, this large increase occurred immediately after the initial decline in Sr counts (Figure 3B, C) while others exhibited count rate minima for a longer period after the initial decline (Figure 3D). Despite this variation in patterns, once otolith strontium peaked, the values fluctuated and rates of increase changed but never returned to their preinflection levels (Figure 3C).

TABLE 2.—Sr:Ca values (mmol/mol) of otoliths from Chinook salmon specimens captured in estuarine and freshwater zones. For some specimens, it was not possible to obtain core $(N = 2)$ or preentry values $(N = 4)$ owing to preparation problems. Within rows, different letters indicate significant differences between means $(P < 0.05)$.

Location and statistic	Estuary specimens	Freshwater specimens
Otolith core		
N	179	13
Range	0.75–3.81	1.42–2.35
Mean (SD)	1.73 (0.29) z	1.82 (0.06) z
Otolith edge[a]		
N	177	13
Range	0.41–1.50	0.68–0.92
Mean (SD)	0.85 (0.18) z	0.78 (0.06) z
Otolith edge		
N	181	13
Range	0.73–4.50	0.68–0.92
Mean (SD)	2.25 (0.70) z	0.78 (0.06) y

[a] Preentry for estuary specimens.

Based on water chemistry results, we hypothesize that the large sudden increases in Sr count rates represented the migration of juvenile Chinook salmon from freshwater habitats into the estuary (see Discussion).

Among all specimens, otolith core Sr:Ca values ranged between 0.75 and 3.81 mmol/mol, with 97% of values falling between 1.2 and 2.2 (Table 2). Otolith core Sr:Ca values for fish captured in the river did not differ significantly from those collected within the estuary (t-test: $P > 0.05$). For specimens captured in the estuary, presumed pre-entry otolith Sr:Ca values ranged between 0.41 and 1.50 mmol/mol, while those from the otolith margins ranged between 0.73 and 4.5 mmol/mol (Table 2). Fish captured in freshwater before estuary migration displayed Sr:Ca values at the otolith margins (freshwater residence) between 0.68 and 0.92 mmol/mol and were not significantly different from those measured in the pre-estuary region of otoliths from fish captured in the estuary (t-test: $P > 0.05$; Table 2). Fish length and the otolith radius used for chemical analyses were closely correlated among all specimens in the study, described as $y = 5.84x + 54.5$, where y is the otolith radius and x is fish length ($r^2 = 0.91$, $N = 263$).

Salmon Residency and Growth

Our estuarine residency estimates for Salmon River Chinook salmon support the common assumption that otolith increments are produced daily. Otolith increment counts after estuary entry compared favorably with the estimated time elapsed between the marking of individuals near the head of tide (rkm 7.9; Bottom et al. 2005a) and their subsequent recapture ($y = 1.01x − 0.33$, $r^2 = 0.97$, $N = 64$; Figure 4). Resolution of estuarine residency from the recapture of marked specimens was limited by our 1-week marking interval and by additional travel time to the estuary from the trapping site. We assumed that entry to the Salmon River estuary occurred within 1 d of marking, since the trap was located less than 1.0 km above the head of tide and 3.3 km above the highway bridge. For individual specimens, the mean difference between increment counts and time elapsed since marking was 5.1 (SD = 3.8), with a maximum difference of 18. Five outlying specimens were removed from this analysis, where
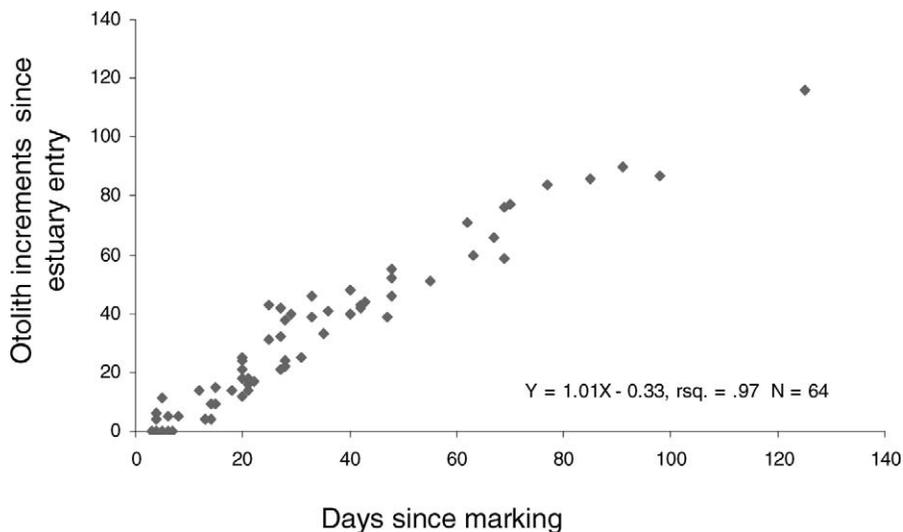

FIGURE 4.—Relationship between the number of Chinook salmon otolith increments counted from the point at which a chemical signal indicated estuary entry and residence time estimated from recoveries of marked fish.

TABLE 3.—Length distributions for Chinook salmon captured in the upper and lower estuary in all collection years (2000–2003) combined, by month. Numbers are proportions of N in each cell. Bold italics indicate the predominant length for each month; total $N = 159$ for upper estuary fish, 109 for lower estuary fish.

Month (mean length; N)	Fish length (mm)									
	<40	40–49	50–59	60–69	70–79	80–89	90–99	100–109	110–119	120+
Upper estuary										
Mar (35.2; 17)	*0.82*	0.18								
Apr (38.6; 18)	*0.56*	0.39	0.05							
May (42.3; 41)	*0.46*	0.34	0.20							
Jun (47.5; 32)	0.18	*0.50*	0.16	0.16						
Jul (58.6; 29)	0.07	0.17	*0.31*	0.28	0.17					
Aug (63.6; 18)	0.17	0.17	0.06	*0.22*	*0.22*	0.11	0.06			
Sep (77.0; 2)					1.00					
Oct (68.2; 1)			1.00							
Nov (129.8; 1)										1.00
Lower estuary										
Mar (0; 0)										
Apr (37.4; 1)	*1.00*									
May (48.9; 4)	0.25	0.25	*0.50*							
Jun (51.5; 16)	0.31	0.19	0.19	*0.25*	0.06					
Jul (70.7; 30)			0.13	*0.40*	0.30	0.13	0.03			
Aug (76.3; 22)		0.05	0.05	0.14	*0.41*	0.27	0.09			
Sep (74.8; 24)	0.04		0.04	0.25	*0.30*	0.25	0.12			
Oct (86.0; 11)				0.09	*0.27*	*0.27*	0.18	0.18		
Nov (120.6; 1)									1.00	

confusion in recapture colors (orange versus red, purple versus magenta, or burnt sienna versus tan) probably accounted for extremely divergent increment counts versus days since marking. Given the difficulties of recognizing some colors in the field, and the possibility that color marks may become less distinct over time, these proposed discrepancies in fin-mark color recognition seem plausible. The other two specimens were the only recaptures with a black fin color, which was later discontinued due to its similarity to natural pigments in juvenile fish.

Based upon the radial distance from the otolith core to the presumed chemical landmark representing entry to saline waters (see Discussion), we estimated fish size at this time using the relationship of otolith size to fish size developed among all specimens in the study. For fish captured in both the upper and lower estuary, fish size at estuary entry gradually increased as the sampling season progressed in all years (Table 3). For monthly upper-estuary captures, fry less than 50 mm dominated early collections, representing more than 80% of specimens collected through May. Proportions of fish that entered the estuary at sizes greater than 50 mm gradually increased through the summer, but freshwater emigrants greater than 80 mm were rare in upper-estuary collections, represented by only four fish captured between August and November. A single fish greater than 120 mm at estuary entry was captured in the upper estuary in November (Table 3). Among fish captured in the lower estuary, fry that had entered the upper estuary at less than 50 mm were far less common, representing only 12% of fish captured. Most were taken in spring collections; however, two fry immigrants were captured in the lower estuary in August and September beach seines. Nearly two-thirds of fish captured during July–October had entered the estuary at sizes greater than 70 mm, and entry sizes greater than 80 mm were common (Table 3). Back-calculations of estimated size at saline estuary entry for dye-marked fish using otoliths were similar to the mean lengths of fish marked each week at the lower Salmon River trap just above the estuary; although the otolith technique produced slight underestimates for the smallest size-classes (Table 4). This reflects a nonlinear relationship between otolith size and fish size at fish lengths less than 40 mm.

Assuming that increments were a reasonable reflection of time, we examined the distribution of estuary residence times to capture day for sampled fish. For fish taken in the upper-estuary and marsh habitats, residence time to capture ranged between 0 and 116 d, with a median value of 18 d and a mean of 26 d. Two-thirds of specimens had resided in the saline estuary for less than 1 month before capture (Figure 5). Fish captured in March and April were predominantly new recruits, having spent less than 1 month in the upper estuary, although one April-caught fish had resided there for nearly 2 months (Figure 5). May, June, and July collections remained dominated by fish with residence times of less than 1 month, but the proportion

TABLE 4.—Mean fish lengths (mm) and sample sizes (parentheses) of Chinook salmon, as measured at the lower Salmon River trap and estimated from otoliths at estuary entry each month. No fish were collected for length measurements after July because the downstream migrant trap was removed. Separate *t*-tests were used to compare means; within months and years, different letters indicate significant differences between means ($P < 0.05$).

Month	2000		2001		2002	
	Trap	Otolith	Trap	Otolith	Trap	Otolith
Mar	42 (45)	39 (1)	41 (39) z	37 (14) y	41 (25) z	37 (6) y
Apr	48 (69) z	43 (6) y	41 (200) z	38 (33) y	42 (125) z	38 (9) y
May	61 (112) z	56 (4) z	47 (160) z	48 (40) z	56 (100) z	57 (7) z
Jun			58 (160) y	63 (26) z	67 (100) z	68 (44) z
Jul			73 (159) z	73 (6) z	79 (75) z	81 (22) z

of fish resident for 1–2 months increased, and July collections showed an increased presence of fish with residence times exceeding 2 months. Numbers of fish collected from the upper estuary decreased in late summer and autumn, with a fairly even distribution of residence times for August collections, including some new recruits. A few fish captured in August and October had been in the upper estuary for more than 100 d (Figure 5).

Estuary residence times of fish captured in the lower estuary ranged from 0 to 113 d, with a median value of 41.5 d and a mean of 43.5 d. The few fish examined for April and May collections were exclusively new recruits to the estuary, with residence times of less than 20 d. Fish caught in June were evenly divided between those resident less than 1 month and those with residence times between 50 d and 3 months. July and August collections included fish typically resident for 20–50 d, although smaller proportions of shorter and longer residence times were apparent, including some fish that had entered the estuary less than 10 d before capture. In September and October, a wide range of residence times was represented. Most were in the estuary 2–3 months with a few recent immigrants resident less than 30 d (Figure 5).

Using data for residence time in the saline estuary, we reconstructed the distribution of estuary entry dates for combined monthly collections of fish (Figure 6). For fish captured in marsh habitats or other upper-estuary sites from all years combined, a small number arrived in the estuary during late February and the first 2 weeks in March. A much greater proportion entered over the next 3 months. Eighty percent of fish captured in the upper estuary entered by the middle of June (Figure 6). A small number of fish (<12%) captured in the lower estuary had entered before May 15, while 80% arrived during the next 10 weeks until mid-July (Figure 6). Of the fish captured in both upper- and lower-estuary sites, only a few emigrated from freshwater in August and September (Figure 6).

Among all fish captured in marsh habitats in 2001,

mean growth rates ranged between 0.35 and 0.65 mm/ d, with no significant difference among mean values from all marshes and months (analysis of variance [ANOVA]: $F = 0.86$, df = 69, $P = 0.59$; Table 5). In 2002, the few specimens collected from the 87 and 96 marshes showed growth rates similar to those recorded the previous year. However, mean growth rate estimates for fish captured from the reference marsh ranged between 0.19 and 0.29, less than half the value for the same period in 2001 (Table 5). Mean growth rates for specimens captured in the lower estuary in 2001, 2002, and 2003 ranged widely between 0 and 1.43 mm/d, all but three specimens falling in the range of 0.40–0.75 mm/d (Table 5).

To assess validity of otolith-based growth estimates, we compared them with estimates derived from the recapture of marked specimens. Among marked and unmarked juveniles that had entered the estuary in June or July during 2002, there was no significant difference in estimated monthly mean growth rates between unmarked fish (June: 0.44 mm/d, $N = 8$; July: 0.54 mm/d, $N = 7$) and marked fish (June: 0.49 mm/d, $N = 16$; July: 0.47 mm/d, $N = 12$) (*t*-test: $P > 0.05$). Growth rates estimated for 14 unmarked specimens in 2003 (0.57 mm/d, $N = 14$) were also not significantly different from the 2002 means (ANOVA: $P > 0.05$).

Salmon Life Histories

For specimens captured at the mouth of the river during 2002–2003, just before entry to the ocean, we classified fish into nominal life history types or categories defined by estimated date and size at estuary entry, and length of estuary residence before reaching the river mouth. For all years combined, these collections were dominated (~77%) by sum-mer-migrating fish that entered the estuary between June and August at sizes between 55 and 96 mm (Table 6). Approximately two-thirds of these fish had resided in the estuary for greater than 30 d. Spring-migrating fish, emigrating from freshwater at sizes up to 64 mm before June comprised 17% of captures at
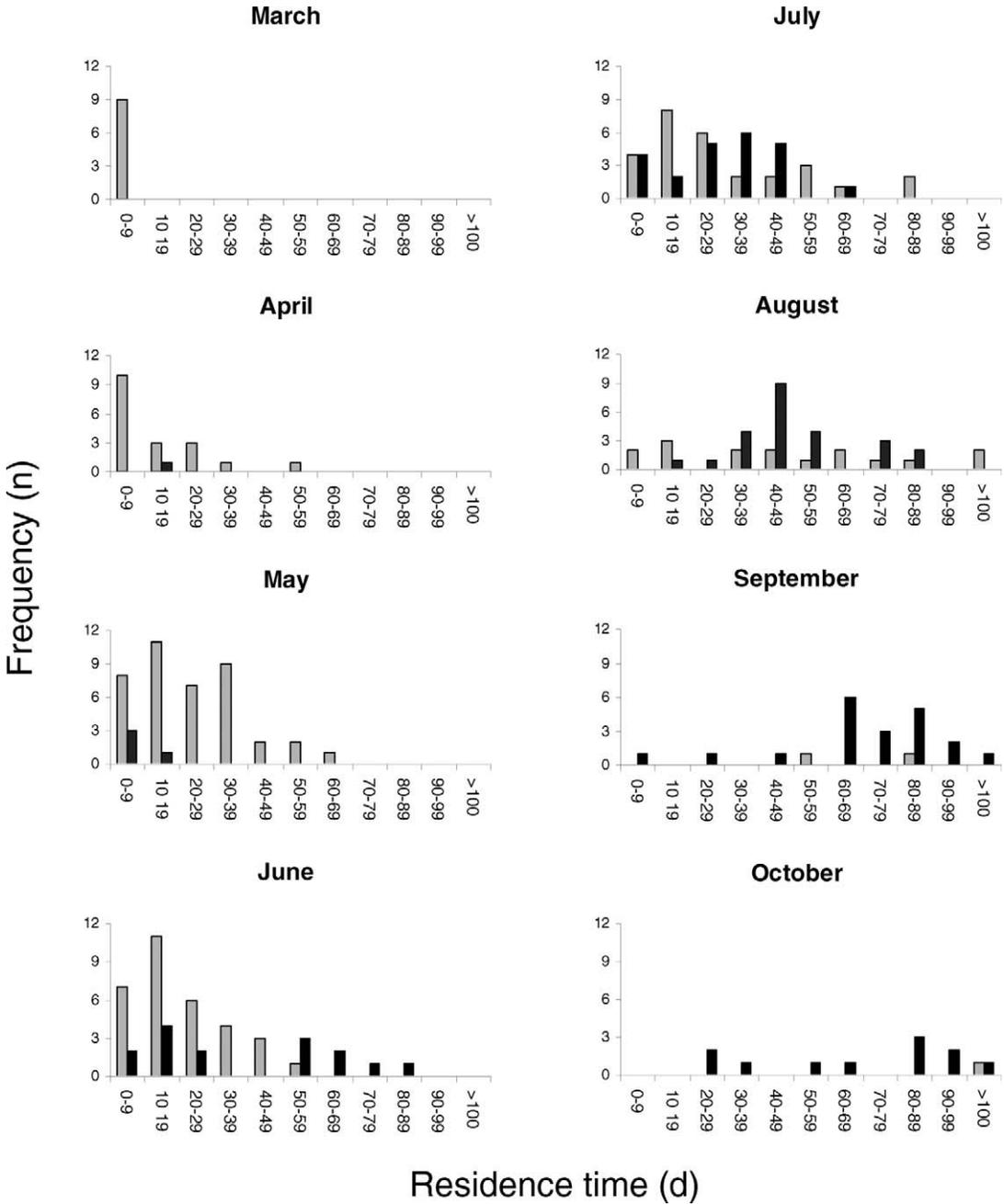
FIGURE 5.—Distributions of the estimated residence times of Chinook salmon specimens collected each month from upper-estuary (gray bars) and lower-estuary sites (black bars). Data are for all collection years combined (2000–2003). Only specimens for which the increments could be reliably enumerated were included.

the river mouth, and 43% of these fish had emigrated to the estuary as emergent fry less than 45 mm in length. All fish detected at the mouth that entered the estuary as emergent fry had spent at least 30 d in upper-estuary habitats before capture with no evi-dence of emergent fry having migrated directly to the river's mouth. A small fraction of mouth captures (6%) remained in freshwater through the summer and entered the estuary between September and November. Only a single individual in this category had
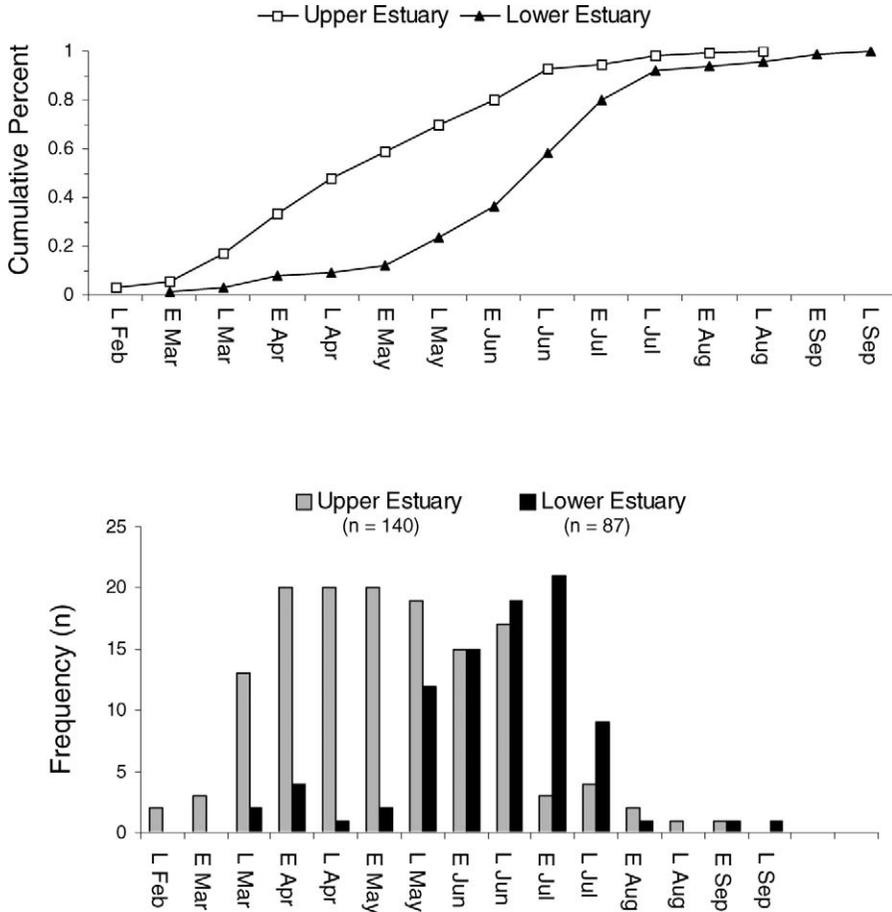
FIGURE 6.—The upper panel shows the cumulative percentages of Chinook salmon arriving in the Salmon River estuary during 2-week intervals for fish captured in the upper and lower portions of the estuary (early arrivals [E] arrived on days 1–15 of the month and late arrivals [L] on days 16–31). The lower panel shows the distribution of estuary entry dates for all fish captured in the upper and lower portions of the estuary.

spent more than 30 d in the estuary before capture at the mouth (Table 6).

Discussion

We used otolith strontium signals in tandem with daily increment counts to assess key life history metrics of individual juvenile Chinook salmon in Salmon River, including date and size at emigration from freshwater, residence time, and individual growth rates in the saline reaches of the estuary. With this method we were able to define specific attributes of the four general life history strategies previously described by Bottom et al. (2005a) and to resolve uncertainties associated with early fry migrant survival and length of estuary residence for late fall migrants. While most juveniles emigrated from freshwater in summer and spent 1–2 months in the estuary, individuals captured at

the river mouth before ocean entry comprised a broad continuum of migration strategies. Our results reinforce the reported variation in smolting characteristics at the center of the Chinook salmon range (i.e., in southern British Columbia, Washington, and Oregon) (Beckman et al. 2003) and quantify life history differences among individuals in a small river basin with extensive estuarine rearing habitat.

A cornerstone of our study is the correspondence between increased otolith strontium and fish migrations from freshwater to saline habitats. Water samples showed a close relationship between water Sr:Ca values and salinity, with elemental ratios rising quickly to maximum values at salinities less than about 5‰. Successive samples collected along the lower Salmon River demonstrated that dramatic changes in water salinity and Sr:Ca values occurred over a fairly limited

TABLE 5.—Mean growth rates (mm/d; SDs in parentheses) and total annual sample sizes (*N*) for fish captured in the upper and lower portions of the estuary from 2001 to 2003. Only specimens from which otolith increments could be reliably counted along the preferred measurement axis were used in these comparisons. Months represent estimated estuary entry dates.

Month and *N*	Upper estuary		Lower estuary		
	2001	2002	2001	2002	2003
Mar	0.60 (0.10)				
Apr	0.50 (0.17)	0.29 (0.22)		0.57 (0.16)	
May	0.55 (0.21)	0.34 (0.23)	0.49 (0.43)	0.68 (0.30)	
Jun	0.51 (0.30)	0.34 (0.23)	0.60 (0.40)	0.53 (0.34)	0.67 (0.26)
Jul		0.24[a]	0.40 (0.07)	0.55 (0.14)	0.52 (0.26)
Aug				0.31[a]	0.53 (0.07)
Sep					0.56 (0.01)
Oct					0.19[a]
N	70	18	10	54	17

[a] No SD value available.

geographic distance near the transition between river and estuary. Since numerous studies have demonstrated a correspondence between otolith and water Sr:Ca values (Secor and Piccoli 1996; Bath et al. 2000; Volk et al. 2000), we can reasonably conclude that rapidly rising Sr:Ca values in otoliths of migrating juvenile salmon generally reflect their entry into saline habitats. Zimmerman (2005) has experimentally demonstrated the connection between otolith Sr:Ca and salinity for several salmonid species, including Chinook salmon.

Most fish captured in estuarine habitats within the zone of salinity intrusion, had otolith microchemistry patterns with the dramatic increases in strontium count rates depicted in Figure 3. The few exceptions could be very recent migrants or may have entered during a period of high river flow when freshwater forces salinity intrusion further downstream into the estuary. All but one fish that failed to show large strontium spikes were captured during March–May, when river flows were highest during the period 2001–2003 (Bottom et al. 2005a). Among fish collected in freshwater habitats above the trap, we never observed the otolith strontium increases commonly seen in estuary samples below the trap. Furthermore, among estuary samples, otolith chemical values preceding the

TABLE 6.—Proportions of Chinook salmon captured at the Salmon River mouth (2001–2003; *N* = 81) by season of freshwater emigration and residence time in the estuary. Emergent fry are a subset of spring migrants. Fish sizes are actual ranges for the groups.

Migrant group (length)	Estuary residence times	
	<30 d	>30 d
Spring migrants (<64 mm)	0.05	0.12
Emergent fry (<45 mm)	0	0.43
Summer migrants (55–96 mm)	0.21	0.56
Fall migrants (97–109 mm)	0.05	0.01

dramatic rise in strontium count rates were similar to those calculated at the otolith margins for fish captured at two freshwater sites in the Salmon River. Taken together, these observations strongly support our conclusion that steep increases in otolith strontium observed in nearly all estuary specimens represent fish migrations from freshwater to saline estuarine habitats.

We recognize that higher river flows in spring will affect the position of the salinity gradient that fish experience, which may influence our estimated date of estuarine entry; e.g., particularly before the late winter high river flows decline and salinity intrudes far up into the estuary. However, in a small system such as the Salmon River, the salinity gradient is often compressed to a relatively short horizontal distance, and ocean and freshwater are well mixed. In larger systems with extensive stratification, the utility of the salinity gradient as a strict reflection of estuary entry may ignore considerable tidally influenced freshwater habitat above this chemical transition (Fairbridge 1980). The steeply rising, nonlinear relationship between salinity and water Sr:Ca in our study suggests that otolith strontium may not provide a sensitive indicator of fish associations with freshwater tidal habitats or those within narrow salinity ranges in the estuary.

Otolith increments following the dramatic Sr:Ca increases appear to be a valid proxy for estuarine residence time of Chinook salmon in the Salmon River. In validation experiments, the close correspondence of otolith increments with estimated time since marking fish at the trap (Figure 4) was compelling despite uncertainty about the exact date fish encountered the salinity gradient. While we assume that fish encounter a salinity gradient shortly after passing the trap in the Salmon River (about 1–3 km), changes in river flow could easily alter migration rates or the timing with which fish experience the gradient. These issues

undoubtedly account for some variability in the relationship, and could certainly have an influence on individual estimates of residence time. Agreement between back-calculated size at estuary entry for dye-marked specimens and monthly mean lengths of fish marked near the head of tide (Table 4) also supports the idea that otolith chemical indicators provide a valid indicator of fish migration into the saline estuary and that increment counts are a reasonable way to track time.

Data for time and size of estuarine entry and residency estimated from otolith analyses precisely describe seasonal migrations and habitat associations of individual fish in the Salmon River. Distributions of estimated freshwater emigration dates among all specimens showed some recruitment to upper-estuary marshes from early spring through August, with the largest proportion of new immigrants arriving between April and June. Collections in March–May were dominated by fish that had entered the estuary as fry (<50 mm), and resided in those habitats for less than 1 month before capture. Concurrent studies in the Salmon River showed that large numbers of fry dispersed into upper-estuary and marsh habitats before mid-May (Cornwell et al. 2001; Gray et al. 2002; Bottom et al. 2005a), a pattern observed in many Pacific Northwest estuaries (Healey 1991) but not in other Oregon coastal drainages where juveniles reportedly migrate to estuaries primarily as fingerlings (Reimers 1973; Healey 1982, 1991; Myers and Horton 1982).

Beach seining surveys at the Salmon River recaptured only a few individuals at the river mouth among the many thousands of fry that were marked just before estuary entry (Bottom et al. 2005a), suggesting either substantial mortality of fry migrants or poor mark retention or detection. Similarly, studies in British Columbia could not account for a large percentage of estuarine fry migrants (Healey 1982, 1991), leading researchers to conclude that many fry had perished soon after downstream migration. Despite the likelihood that fry also experienced high mortality in the Salmon River estuary, otolith analyses clarify that a significant proportion (17%) of all out-migrants from the basin consisted of individuals that had entered the estuary soon after emergence. These survivors had resided in the estuary for weeks or months, many in upper-estuary marshes, before migrating to the river mouth.

The availability of tidal wetland habitat could explain the importance of the fry-migrant strategy in the Salmon River. Fry migrants typically rear in tidal marshes and other shallow peripheral areas, gradually moving to deeper habitats and migrating seaward as their size increases (Levy and Northcote 1982; Healey 1982, 1991). Salt marsh, which covers nearly half of the surface area of the Salmon River estuary, may offer greater rearing opportunities for fry migrants than are available in the other Oregon estuaries where salmon life histories have been documented (Reimers 1973; Myers and Horton 1982). In the 1970s, before a series of dike-removal projects in the Salmon River had restored access to nearly 150 ha of salt-marsh habitat, few salmon entered the estuary until mid-summer after individuals had reached fingerling sizes (Bottom et al. 2005a).

Experimental studies in freshwater habitats have shown considerable variation in the propensity of juvenile Chinook salmon to migrate downstream after emergence (Bradford and Taylor 1997). Such variations, which lead some salmon to remain near natal spawning areas while others move considerable distances downstream, may promote dispersal of individuals among all available rearing habitats (Healey 1991; Bradford and Taylor 1997). Otolith results from the Salmon River similarly documented considerable variation in the age and time of migration of individuals from freshwater into the estuary. During early spring months, emergent fry appeared almost simultaneously in spawning tributaries, in the Salmon River main stem, and in upper-estuary marshes (Bottom et al. 2005a), while expansion into the more saline, lower-estuary habitats occurred more gradually in late spring and early summer. Considerable variation in the time and size of migration and in the periods of freshwater and estuarine residency allowed for continued turnover of all available rearing habitats among individuals, extending the period of estuarine arrival and use by juvenile Chinook salmon from early spring until fall.

The latest group of individuals to enter the Salmon River estuary had spent almost their entire juvenile life history in freshwater before capture. Lower-estuary collections in September through November showed some fish that had spent more than 3 months in freshwater, entering the estuary when they were greater than 90 mm and arriving near the river mouth after 10–30 d of estuary residence. Reimers (1973) recognized a fall out-migrating life history for Chinook salmon in the Sixes River, Oregon, that contributed to adult returns. Bottom et al. (2005a) similarly detected a group of fall out-migrants at the river mouth based on beach seine collections, but could not reconstruct length of estuary residence based on external marks because all fish-marking activities in the Salmon River had discontinued by July. Our results indicate that with a single exception, these fall migrants had moved quickly through the estuary. Unlike studies of other fall

Chinook salmon populations (Reimers 1973; Carl and Healey 1984), we found no evidence of individuals that had overwintered in freshwater and migrated through the estuary as yearlings.

Based on fish captured at the mouth of Salmon River during 2001–2003, our results suggest that juveniles emigrating from the river between June and August, and residing in the estuary for more than 30 d, were most prevalent, representing greater than 50% of all fish examined. Reimers (1973) concluded that the most successful juveniles in the Sixes River were those that emigrated from freshwater in early summer and reared in the estuary until ocean entry in the autumn. Future analysis of adult otoliths will allow us to determine the relative contribution of summer migrants with short estuary residence times (as well as the other juvenile life history patterns) to the adult survivors in the Salmon River.

By reconstructing the rearing histories of individual fish, our results reveal considerable variation in juvenile life history within a Chinook salmon population. Rather than a series of discrete life history "types" (e.g., Reimers 1973; Bottom et al. 2005a), the Salmon River population exhibits a continuum of juvenile rearing and migration behaviors, which are linked to the variety of freshwater and estuarine habitat opportunities and conditions that exist in the basin over the broad period of juvenile Chinook salmon out-migration. Most significantly, our otolith analyses reveal a diversity of estuarine entry times, sizes, and residency periods throughout the spring months (March–June) that were not evident in the population in the mid 1970s, when most of the tidal wetlands were diked and inaccessible to fish (Bottom et al. 2005a). By quantifying the finer details of life history expression, the otolith technique provides additional evidence that estuarine wetland restoration has increased biocomplexity of the Chinook salmon population in this small river basin (Bottom et al. 2005a). This technique should be applied beyond the juvenile life stage to quantify the contribution of various life history strategies to adult returns and to test directly the hypothesis that life history variation promotes population resilience in a fluctuating environment (Stearns 1976; Healey 1991; Thorpe 1994; Francis and Mantua 2003).

Acknowledgments

References

Bath, G. E., S. E. Thorrold, C. M. Jones, S. E. Campana, J. W. McLaren, and J. W. H. Lam. 2000. Strontium and barium uptake in aragonite otoliths of marine fish. Geochimica et Cosmochimica Acta 64:1705–1714.

Beckman, B. R., D. A. Larsen, and W. W. Dickoff. 2003. Life history plasticity in Chinook salmon: relation of size and growth rate to autumnal smolting. Aquaculture 222:149–165.

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., 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.

Bradford, M. J., and G. C. Taylor. 1997. Individual variation in dispersal behavior of newly emerged Chinook salmon (Oncorhynchus tshawytscha) from the upper Fraser River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 54:1585–1592.

Carl, C. M., and M. C. Healey. 1984. Differences in enzyme frequency and body morphology among three juvenile life history types of Chinook salmon (Oncorhynchus tshawytscha) in the Nanaimo River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 41:1070–1077.

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 Reports 2001–05, Portland.

Fairbridge, R. 1980. The estuary: its definition and geo-dynamic cycle. Pages 1–35 in E. Olausson and I. Cato,

editors. Chemistry and geochemistry of estuaries. Wiley, New York.

Francis, R. C., and N. J. Mantua. 2003. Climate and extinction risk for salmon populations of the Northeast Pacific. NOAA Technical Memorandum NMFS-NWFSC-56: 37–76.

Gray, A., C. A. Simenstad, D. L. Bottom, and T. J. Cornwell. 2002. Contrasting functional performance of juvenile salmon habitat in recovering wetlands of the Salmon River estuary, Oregon, U.S.A. Restoration Ecology 10:514–526.

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. 1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). Pages 311–391 in C. Groot and L. Margolis, editors. Pacific salmon life histories. UBC Press, Vancouver.

Healey, M. C. 2009. Resilient salmon, resilient fisheries for British Columbia, Canada. Ecology and Society [online serial] 14(1): article 2.

Healey, M. C., and A. Prince. 1995. Scales of variation in life history tactics of Pacific salmon and the conservation of phenotype and genotype. Pages 176–184 in J. L. Neilson and D. A. Powers, editors. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Levy, D. A., and T. G. Northcote. 1982. Juvenile salmon residency in a marsh area of the Fraser River estuary. Canadian Journal of Fisheries and Aquatic Sciences 39:270–276.

Longerich, H. P., S. E. Jackson, and D. Gunther. 1996. Laser ablation ICP mass spectrometric transient signal data acquisition and analyte concentration calculation. Journal of Analytical Atomic Spectrometry 11:899–904.

Myers, K. W., and H. F. Horton. 1982. Temporal use of an Oregon estuary by hatchery and wild juvenile salmon.

Pages 377–392 in V. S. Kennedy, editor. Estuarine comparisons. Academic Press, New York.

Nicholas, J. W., and D. G. Hankin. 1988. Chinook salmon populations in Oregon coastal basins: description of life histories and assessment of recent trends in run strengths. Oregon Department of Fish and Wildlife, Information Report 88-1, Portland.

Nielson, 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.

Rich, W. H. 1920. Early history and seaward migration of Chinook salmon in the Columbia and Sacramento rivers. U.S. Bureau of Fisheries Bulletin 37:2–73.

Reimers, P. E. 1973. The length of residence of juvenile fall Chinook salmon in Sixes River, Oregon. Research Reports of the Fish Commission of Oregon 4(2):1–42.

Russo, C. J. 2001. A trace element study of plagioclase and clinopyroxene phenocrysts in historical lavas from Mt. Etna, Sicily, by laser ablation ICP-MS. Masters thesis. Oregon State University, Corvallis.

Secor, D. H., and P. M. Piccoli. 1996. Age-and sex-dependent migrations of striped bass in the Hudson River as determined by chemical microanalysis of otoliths. Estuaries 19(4):778–793.

Stearns, S. C. 1976. Life history tactics: a review of the ideas. Quarterly Review of Biology 51:3–46.

Thorpe, J. C. 1994. Salmonid fishes and the estuarine environment. Estuaries 17(1A):76–93.

Volk, E. C., A. Blakley, S. L. Schroder, and S. M. Kuehner. 2000. Otolith chemistry reflects migratory characteristics of Pacific salmonids: using otolith core chemistry to distinguish maternal associations with sea and fresh waters. Fisheries Research 46:251–266.

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.