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Effect of Migration Pathway on Travel Time and Survival of Acoustic-Tagged Juvenile Salmonids in the Columbia River Estuary

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ARTICLE

Effect of Migration Pathway on Travel Time and Survival of Acoustic-Tagged Juvenile Salmonids in the Columbia River Estuary

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Abstract

We applied acoustic telemetry methods to characterize migration pathways and estimate associated travel times and survival probabilities for juvenile Chinook salmon *Oncorhynchus tshawytscha* and steelhead *O. mykiss* migrating downstream through the Columbia River estuary (from river kilometer [rkm] 86 to rkm 8). Acoustic-tagged fish were detected as migrating in the navigation channel and in off-channel areas at each of the estuarine reaches we examined during May–August 2010. However, the majority of fish traveled in the main navigation channel from rkm 86 to rkm 37, at which point most fish left the river-influenced navigation channel; crossed a broad, shallow tidal flat; and migrated the final 37 km in a secondary channel, which was characterized as having greater tidal transport than the navigation channel. The pathway used by acoustic-tagged smolts to migrate through the estuary affected their rate of travel. In most reaches, navigation channel migrants traveled significantly faster than fish that migrated through off-channel areas. Contrary to observations from previous studies, smolts that migrated through off-channel areas at a slower rate did not experience lower survival than their cohorts that used the navigation channel. Although no significant differences in survival probability were observed between navigation channel migrants and off-channel migrants, areas of high mortality were identified between rkm 37 and rkm 8. Dispersion of juvenile salmonids into multiple pathways during downstream migration can be beneficial in terms of increased expression of life history diversity and resiliency to environmental perturbations. Our results, which document juvenile salmon migration pathways and associated travel time and survival through a large estuary, can be used to focus future research and management activities in areas identified as having high mortality and therefore can be used to aid in the recovery of Endangered Species Act-listed salmon populations.

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Numerous stocks of anadromous salmonids from within the Columbia River basin have been listed as threatened or endangered under the Endangered Species Act (Nehlsen et al. 1991; Myers et al. 1998; Good et al. 2005). Survival and behavior of juvenile salmonids as they pass through reservoirs and dams within the Federal Columbia River Power System have been the focus of research and management aimed at the recovery of these stocks (e.g., Ferguson et al. 2005, 2007; NOAA Fisheries 2008). However, only limited research has focused on the survival and behavior of juvenile salmonids after they pass through the hydropower system and enter the lower Columbia River and estuary (Dawley et al. 1986; Schreck et al. 2006; Clemens et al. 2009; McMichael et al. 2010b).

Estuarine or early marine migration is commonly identified as a critical period in the life histories of many anadromous Pacific salmon *Oncorhynchus* spp. (Simenstad et al. 1982; Healey 1991; Thorpe 1994; Fresh et al. 2005). However, recent research has suggested that the Columbia River estuary (defined here as river kilometer [rkm] 86 to rkm 0, as measured from the mouth of the Columbia River) is a critically important environment in which emigrating salmonids experience relatively high rates of mortality (Ryan et al. 2003; Schreck et al. 2006; McMichael et al. 2010b). For example, McMichael et al. (2010a, 2010b) found that a significant proportion (0.22–0.47) of juvenile salmonids from the Columbia River basin failed to survive from Bonneville Dam (rkm 235) to ocean entry; the highest rates of mortality occurred in the downstream-most 50 km of the Columbia River estuary. A greater understanding of the magnitude, locations, and causes of juvenile salmonid mortality in the estuary is needed to develop recovery strategies that will improve survival of smolts during their estuarine migration. Consequently, determining the distribution of emigrating juvenile salmonids among available migration pathways and the associated survival is important to understanding population-level survival (Perry et al. 2010).

In most estuaries, emigrating juvenile fish encounter a complex series of channels, tidal flats, sand bars, and shallow bays, which create a continuum of habitat types that vary in water depth, water velocity, salinity, and substrate composition (Thomas 1983; Fox et al. 1984). The utilization of these habitats may vary by species, life history pattern, fish size, estuarine conditions, season, and time of day (Tyler et al. 1978; Dawley et al. 1986; McCabe et al. 1986; Thorpe 1994; Bottom et al. 2005, 2008; Schreck et al. 2005; Semmens 2008). Due to the complexity of estuarine environments and the diverse use of estuarine habitats by juvenile salmonids, seaward migrants use multiple migration pathways or routes to negotiate the estuary (Schreck et al. 2005; McMichael et al. 2010b; Melnychuk et al. 2010; Perry et al. 2010). The use of different migration pathways may expose juvenile salmonids to different environmental and biological conditions that influence their travel rates, foraging success, growth, and exposure to predators, resulting in differential survival among fish that use different pathways (Brandes

and McClain 2001; Schreck et al. 2005; McMichael et al. 2010b; Perry et al. 2010).

We used the Juvenile Salmon Acoustic Telemetry System (JSATS; McMichael et al. 2010a) during May–August 2010 to increase understanding of the influence of migration behaviors on travel time and survival of juvenile Chinook salmon *O. tshawytscha* and steelhead *O. mykiss* as they pass through the Columbia River estuary. The objectives of this study were to (1) provide resource managers with information regarding the estuarine migration pathways used by Chinook salmon and steelhead smolts and (2) identify areas of high use, mortality, and residence time. This information can be used to guide future management actions.

METHODS

Test fish and tagging procedures.—Fish used in these analyses were actively migrating juvenile salmonid smolts collected from the juvenile bypass facility (JBF) at John Day Dam (rkm 347) on the Columbia River. Yearling Chinook salmon and juvenile steelhead were obtained between 27 April and 31 May 2010, and subyearling Chinook salmon were obtained between 12 June and 16 July 2010.

Fish collected at the John Day Dam JBF received 2010-model JSATS transmitters (Advanced Telemetry Systems, Isanti, Minnesota), which were implanted by using methods similar to those described by McMichael et al. (2010a), Deters et al. (2010), and Brown et al. (2010). Transmitters averaged 5.21 mm (SE = 0.01) wide, 12.00 mm (SE = 0.01) long, and 3.77 mm (SE = 0.04) high; mean transmitter weight in air was 0.43 g, mean weight in water was 0.29 g, and mean volume was 0.14 mL (all SEs < 0.005). The pulse rate interval (PRI) was 3 s, and estimated tag life was 32 d. A randomly selected subsample of 50 transmitters was retained from both the spring and summer tagging sessions to quantify tag life. A passive integrated transponder tag (Model TX1411ST; 12.5 × 2 mm; weight in air = 0.06 g; Destron Fearling, South St. Paul, Minnesota) was also implanted into each fish to allow for possible detection in the JBFs and adult fish ladders of hydropower dams on the Snake and Columbia rivers. Acoustic-tagged fish were released at three different locations in the Columbia River to address the objectives of several studies. In total, 3,880 yearling Chinook salmon, 3,885 steelhead, and 4,449 subyearling Chinook salmon were collected, tagged, and released in 2010 (Table 1).

The size distribution of fish that received acoustic transmitters was generally similar to the size distribution of fish sampled randomly from the run-at-large as part of the Smolt Monitoring Program (Figure 1). We attempted to minimize tag burden (tag weight expressed as a percentage of fish weight) and any potential tag or tagging effects by only implanting tags into fish with fork lengths (FLs) of 95 mm or greater; therefore, the size distribution of subyearling Chinook salmon with transmitters differed slightly from the size distribution observed for the

TABLE 1. Number, fork length, tag burden (tag weight expressed as a percentage of fish body weight), and release dates for acoustic-tagged yearling Chinook salmon (CH1), steelhead (STH), and subyearling Chinook salmon (CH0) released into the Columbia River at Roosevelt, at The Dalles Dam tailrace (TDA TR), or near the mouth of the Hood River in 2010 (rkm = river kilometer; min = minimum; max = maximum).

Release location	Release rkm	Group	Release dates	N	Fork length (mm)			Tag burden (%)		
					Min	Max	Mean	Min	Max	Mean
Roosevelt	393	CH1	28 Apr–29 May	2,287	103	225	156	0.4	4.7	1.4
		STH	28 Apr–29 May	2,288	142	260	213	0.3	5.2	0.6
		CH0	13 Jun–14 Jul	2,849	95	250	111	1.1	5.7	3.5
TDA TR	307	CH1	30 Apr–1 Jun	796	99	221	154	0.3	5.4	1.5
		STH	30 Apr–1 Jun	799	148	260	212	0.3	3.4	0.6
		CH0	15 Jun–17 Jul	800	95	234	111	1.5	5.8	3.5
Hood River	275	CH1	1 May–1 Jun	797	104	227	154	0.4	4.2	1.5
		STH	1 May–1 Jun	798	140	260	209	0.2	1.9	0.6
		CH0	16 Jun–17 Jul	800	95	148	110	1.4	5.7	3.6

general population (Figure 1). Overall, mean tag burden was 1.4% for yearling Chinook salmon, 0.6% for steelhead, and 3.5% for subyearling Chinook salmon.

Acoustic telemetry receivers.—Acoustic transmissions from tagged fish were detected and decoded by stationary JSATS autonomous receivers (Model N201; Sonic Concepts, Inc., Bothell, Washington), which were deployed via the methods described by Titzler et al. (2010). In total, 82 acoustic telemetry receivers were deployed from 17 April to 9 August 2010 in multiple locations at and downstream of rkm 86 (Figure 2).

Receivers were deployed in lines (referred to as “arrays”) that ran approximately perpendicular to shore (Figure 2). Based on the effective detection range, receivers within an array were spaced about 100–200 m apart. However, at several of the array

locations, it was not possible to space receivers this closely across the entire width of the estuary. Specifically, in areas that consisted of broad, shallow tidal flats, receivers were deployed only in water that was deeper than about 4 m (during low tide) so as to keep receiver hydrophones submerged.

Six arrays were deployed (Figure 2). The arrays at rkm 86 and rkm 3 marked the upstream and downstream boundaries of the study site, respectively. Receivers within each of these arrays were deployed with overlapping detection range across the width of the channel. Detections on the rkm-3 array were used only to calculate the probabilities of detection and survival at the upstream arrays. Receiver arrays at rkm 50, 37, 22, and 8 were divided into navigation channel and off-channel subarrays to determine the pathways used by acoustic-tagged fish to migrate through the estuary. Subarrays were named as a concatenation of the channel and rkm at which they were located (Table 2; Figure 2).

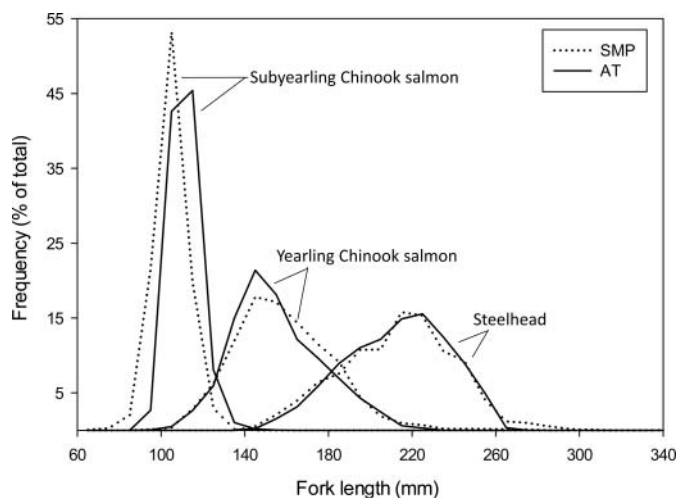


FIGURE 1. Size distributions of subyearling Chinook salmon, yearling Chinook salmon, and steelhead that were collected from the juvenile bypass facility (JBF) at John Day Dam on the Columbia River and tagged with acoustic transmitters (AT; solid line), presented in comparison with the size distributions of fish that were sampled randomly from the run-at-large at the John Day Dam JBF as part of the Smolt Monitoring Program (SMP; dotted line).

TABLE 2. Locations of and number of receivers in subarrays deployed in the Columbia River estuary to detect acoustic-tagged yearling Chinook salmon, subyearling Chinook salmon, and steelhead as they migrated through the estuary in 2010 (rkm = river kilometer; na = not applicable).

Array rkm	Subarray	Subarray location description	Number of receivers
86	Nav 86	Navigation channel	6
50	Nav 50	Navigation channel	3
	CC 50	Clifton Channel	1
37	Nav 37	Navigation channel	4
	CB 37	Cathlamet Bay	3
22	Nav 22	Navigation channel	5
	WA 22	Washington shoreline channel and midchannel	11
8	Nav 8	Navigation channel	11
	WA 8	Washington shoreline channel	11
3	na	Columbia River bar	27

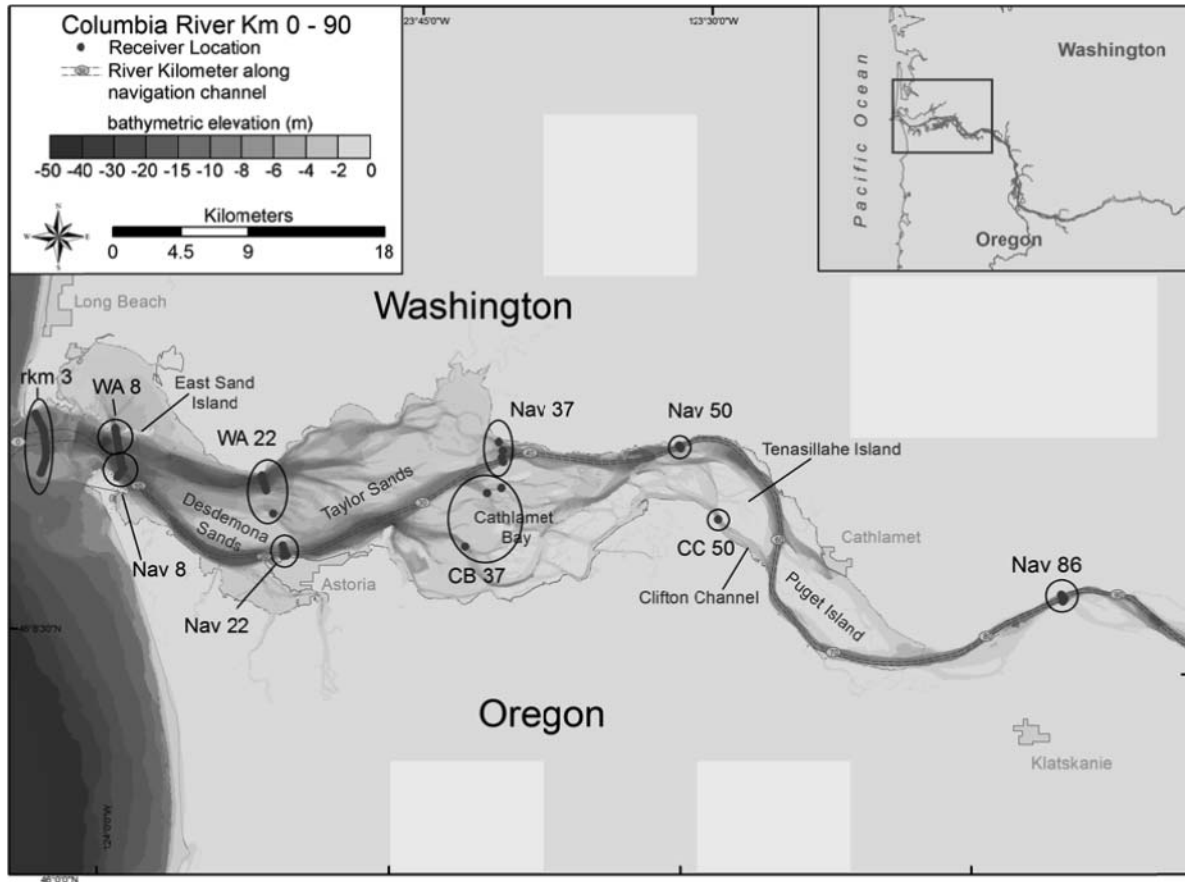


FIGURE 2. Locations of acoustic telemetry receiver arrays and subarrays (circled) that were deployed to detect acoustic-tagged yearling and subyearling Chinook salmon and steelhead as they migrated through various pathways of the Columbia River estuary between river kilometer (rkm) 86 and the river mouth. Subarrays are named with an abbreviation for their location (Nav = navigation channel; off-channel areas: CC = Clifton Channel; CB = Cathlamet Bay; WA = Washington shoreline channel) followed by the rkm at which they were deployed.

Data analyses.—Data files recovered from receivers were coded with the receiver location and stored in a database that we developed specifically for storing and processing JSATS telemetry data. False detections were filtered by using a post-processing program that (1) compared each detection with a list of tags that were released (i.e., only tags that were released were kept in the detection file); and (2) compared the detection date with the release date (only tags that were detected after release were kept in the detection file). Finally, for the detections to be included in the file of valid detections, we required a minimum of four detections from the same transmitter to occur within 36 s and the time spacing between these detections had to either match the tag's PRI or be a multiple of the PRI. These criteria provided a relatively conservative approach to accepting acoustic tag detections while optimizing the effective detection range.

Valid detections from each array were used to assign each fish to the subarray at which it was detected. However, some fish were detected by both subarrays. This occurrence was relatively rare at the rkm-50, rkm-37, and rkm-22 arrays; less than 3% of

detected fish were detected by both subarrays. Fish detected at the rkm-8 array were more commonly detected by both subarrays (12%) because there was no spatial separation between the WA 8 and Nav 8 subarrays (Table 2; Figure 2). In these situations, the date and time of detections were used to assign fish to a subarray. At the array that marked the upstream boundary of a reach, fish were assigned to the subarray at which the last valid detection occurred. This ensured that each fish was assigned to the subarray from which it migrated. At the array that marked the downstream boundary of a reach, fish were assigned to the subarray at which the first valid detection occurred. This ensured that each fish was assigned to the subarray to which it initially migrated.

All fish of the same salmonid group (i.e., subyearling Chinook salmon, yearling Chinook salmon, or steelhead) that were assigned to a common subarray at the upstream boundary of a reach were considered to be a “virtual release,” or a grouping based on fish detections at a specific subarray independent of when or where those fish were released (Buchanan et al. 2009; Skalski et al. 2009). The migration pathways, survival

probabilities (S), and travel times were estimated for each virtual release group from the upstream subarray to the next downstream array in four reaches of the Columbia River estuary. The study reaches, as delineated by the arrays (Table 2), were rkm 86–50, rkm 50–37, rkm 37–22, and rkm 22–8 (Figure 2).

The primary pathways used by fish to migrate through each study reach were identified by calculating the joint probability (λ) of fish migrating to a downstream subarray and being detected by that subarray. The λ at both downstream subarrays of each reach was calculated for each virtual release group by using the Cormack–Jolly–Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965).

Typically, for detection and survival probability estimation of mark–recapture data, detection data are summarized as the “detection history” for each marked fish. With only two opportunities for detection, the possible detection histories for tagged fish are

- 00 = never detected;
- 10 = detected by the upstream (primary) array but not by the downstream (secondary) array(s);
- 01 = detected by the downstream (secondary) array(s) but not by the upstream (primary) array; and
- 11 = detected by the upstream (primary) array and the downstream (secondary) array(s).

Probability of detection at the primary array is then estimated as the proportion of fish detected by the secondary array(s) that were also detected by the primary array (i.e., $n_{11}/[n_{11} + n_{01}]$).

To calculate λ , two separate detection histories (one for each downstream subarray) were constructed for each virtual release group; the subarray of interest was treated as the primary array, and all downstream arrays were treated as the secondary arrays. For example, the equation for estimating λ at the Nav 37 subarray for a Nav 50 virtual release group would be

$$\lambda_{\text{Nav50-Nav37}} = \frac{n_{11,\text{Nav37}}}{n_{11,\text{Nav37}} + n_{01,\text{Nav37}}},$$

where $n_{11,\text{Nav37}}$ is the number of acoustic-tagged fish from the Nav 50 virtual release group that were detected at the Nav 37 subarray and by at least one of the arrays located at rkm 22, 8, or 3; and $n_{01,\text{Nav37}}$ is the number of acoustic-tagged fish from the Nav 50 virtual release group that were not detected at the Nav 37 subarray but were detected by at least one of the arrays located at rkm 22, 8, or 3.

The equation for estimating λ at the CB 37 subarray for a Nav 50 virtual release group would be

$$\lambda_{\text{Nav50-CB37}} = \frac{n_{11,\text{CB37}}}{n_{11,\text{CB37}} + n_{01,\text{CB37}}},$$

where $n_{11,\text{CB37}}$ is the number of acoustic-tagged fish from the Nav 50 virtual release group that were detected at the CB 37 subarray and by at least one of the arrays located at rkm 22, 8,

or 3; and $n_{01,\text{CB37}}$ is the number of acoustic-tagged fish from the Nav 50 virtual release group that were not detected at the CB 37 subarray but were detected by at least one of the arrays located at rkm 22, 8, or 3.

Fish with a detection history of 01 at both subarrays either passed by one of the subarrays but went undetected or migrated through an area where receivers were not deployed. Because it was not possible to determine the subarray past which the undetected fish migrated, the probability of fish migrating through a subarray area cannot be estimated separately from the detection probability.

Detection histories were loaded into ATLAS version 1.1.4 (www.cbr.washington.edu/paramest/atlas/) to calculate tag-life-adjusted λ values. The program ATLAS uses the methods described by Townsend et al. (2006) to adjust CJS estimates for the probability of tag failure. The vitality model (Li and Anderson 2009) and the three-parameter Weibull distribution (Elandt-Johnson and Johnson 1980) were used to model the probability of tag failure for spring and summer migrants, respectively. Likelihood ratio tests were conducted in ATLAS to determine whether the λ values differed significantly ($\alpha = 0.05$) between fish that migrated from different upstream subarrays to the same downstream subarray. Fish that migrated from different upstream subarrays would be expected to have equal probabilities of being detected by a downstream subarray if (1) the fish were of similar size and origin and (2) the fish migrated through the reach at about the same time. For similar groups, significant differences in λ indicated that fish from one upstream subarray were more likely to migrate to the downstream subarray than fish that migrated from the other upstream subarray. These differences were used to determine the primary migration pathway utilized by fish that migrated from each subarray location.

Travel times were calculated and analyzed to determine the effect of migration pathway on the length of time taken by Chinook salmon and steelhead smolts to migrate through the Columbia River estuary. For each fish in each virtual release group that was detected at the downstream array, travel time was calculated by subtracting the date and time of last detection at the upstream subarray from the date and time of first detection at the downstream array. Because travel time data frequently were right-skewed and deviated from a normal distribution, median travel times were calculated for each virtual release group and nonparametric statistics were used. The Mann–Whitney rank-sum test ($\alpha = 0.05$) was used to determine whether there were differences in travel time between virtual release groups that migrated from different subarrays. Significant differences in travel time coupled with differences in λ would indicate that the pathway used by fish to migrate through the reach affected travel time.

The probability of survival through a reach was estimated for each virtual release group by using the CJS model (adjusted for tag life by ATLAS). Survival to a specific subarray could not be estimated because it was not possible to determine the subarray that fish with a 01 detection history migrated past undetected.

Therefore, S was estimated for each virtual release group from the upstream subarray to the next downstream array by using a single detection history, which combined detections from both downstream subarrays. Likelihood ratio tests were conducted with ATLAS to determine whether S differed significantly ($\alpha = 0.05$) between fish that migrated from different upstream subarrays to the next downstream array. Significant differences in S coupled with differences in λ would suggest that fish migrating through different pathways had different probabilities of surviving through the reach.

Differences in fish size, fish origin, and migration timing could cause differences in survival, travel time, and detection probability. Therefore, comparisons of mean fish size, median release date, median detection date, the proportion of fish that were unmarked (i.e., did not have an adipose fin clip), and the proportion of fish from each release location were made between navigation channel and off-channel virtual release groups to ensure that observed differences in λ , S , or travel time were a

product of the migration pathways used rather than some other factor. Proportions of unmarked subyearling Chinook salmon were not compared between virtual release groups because only about 56% of the hatchery subyearling Chinook salmon released upstream of John Day Dam were marked with an adipose fin clip in 2010 (FPC 2011).

RESULTS

More than 3,100 acoustic-tagged yearling and subyearling Chinook salmon and steelhead were detected by the receiver arrays in the Columbia River estuary during May–August 2010. Fish size, median dates of release and detection, proportions of unmarked fish, and proportions of fish from each release location were generally similar at each array for fish detected by the navigation channel and off-channel subarrays (Table 3).

Greater than 80% of the yearling and subyearling Chinook salmon and steelhead detected at the rkm-50 and rkm-37 arrays

TABLE 3. Numbers and proportions of acoustic-tagged yearling Chinook salmon, steelhead, and subyearling Chinook salmon that were detected at receiver subarrays (codes defined in Table 2) in the Columbia River estuary during 2010 (rkm = river kilometer; na = not applicable). Also shown are the mean fork length (FL, mm), median release and detection dates, the proportion of detected fish that were unmarked (i.e., did not have an adipose fin clip), and the proportion of detected fish that were from each release location (Roosevelt, The Dalles Dam tailrace, and Hood River).

Array rkm	Subarray	N detected	Proportion detected	FL (mm)	Release date	Detection date	Proportion unmarked	Proportion detected from each release site		
								Roosevelt	Dalles Dam	Hood River
Yearling Chinook salmon										
86	Nav 86	3,088	na	157	14 May	19 May	0.24	0.54	0.23	0.23
50	Nav 50	1,987	0.88	157	14 May	20 May	0.26	0.54	0.22	0.24
	CC 50	271	0.12	159	9 May	15 May	0.32	0.60	0.20	0.20
37	Nav 37	1,672	0.87	158	14 May	19 May	0.28	0.54	0.22	0.24
	CB 37	256	0.13	154	13 May	19 May	0.27	0.58	0.22	0.20
22	Nav 22	426	0.21	159	8 May	15 May	0.31	0.54	0.23	0.23
	WA 22	1,642	0.79	156	16 May	22 May	0.27	0.54	0.22	0.23
Steelhead										
86	Nav 86	3,047	na	213	14 May	19 May	0.28	0.54	0.23	0.23
50	Nav 50	1,529	0.84	213	14 May	19 May	0.28	0.54	0.23	0.22
	CC 50	299	0.16	214	14 May	19 May	0.24	0.58	0.23	0.19
37	Nav 37	1,326	0.82	214	13 May	18 May	0.29	0.53	0.24	0.23
	CB 37	294	0.18	210	16 May	22 May	0.30	0.55	0.23	0.21
22	Nav 22	654	0.41	215	10 May	16 May	0.28	0.50	0.26	0.24
	WA 22	953	0.59	213	15 May	21 May	0.29	0.53	0.22	0.25
Subyearling Chinook salmon										
86	Nav 86	3,197	na	111	29 Jun	3 Jul	na	0.57	0.21	0.22
50	Nav 50	1,916	0.84	111	28 Jun	3 Jul	na	0.58	0.21	0.21
	CC 50	362	0.16	112	5 Jul	9 Jul	na	0.54	0.24	0.22
37	Nav 37	1,659	0.88	111	29 Jun	3 Jul	na	0.57	0.22	0.21
	CB 37	226	0.12	111	2 Jul	8 Jul	na	0.50	0.20	0.29
22	Nav 22	317	0.13	111	1 Jul	8 Jul	na	0.57	0.20	0.23
	WA 22	2,172	0.87	111	26 Jun	2 Jul	na	0.58	0.21	0.21

were detected at subarrays located in the navigation channel (Nav 50 and Nav 37; Table 3). The remaining fish were detected at the off-channel subarrays in Clifton Channel (CC 50) and Cathlamet Bay (CB 37; Table 3). However, at rkm 22, most of the yearling Chinook salmon (79%), subyearling Chinook salmon (87%), and steelhead (59%) were detected by the off-channel subarray located in the Washington shoreline channel (WA 22; Table 3). In total, 779 yearling Chinook salmon, 381 steelhead, and 839 subyearling Chinook salmon were detected at all arrays. Of those fish, 11% of yearling Chinook salmon, 24% of steelhead, and 6% of subyearling Chinook salmon were only detected by navigation channel subarrays. The remaining fish were detected by at least one off-channel subarray.

River Kilometer 86 to River Kilometer 50

Yearling and subyearling Chinook salmon and steelhead that migrated from rkm 86 had higher λ values at the Nav 50 subarray ($\lambda = 0.51$ – 0.58) than at the off-channel subarray, CC 50 ($\lambda = 0.09$ – 0.11 ; Figure 3). Median travel times from rkm 86 to rkm 50 ranged from 11.8 h for steelhead to 12.4 h for yearling Chinook salmon (Figure 4). The probability of survival from rkm 86 to rkm 50 was high for all three salmonid groups, ranging from 0.97 (SE = 0.01) for steelhead to 1.01 (SE = 0.01) for yearling Chinook salmon (Figure 5).

River Kilometer 50 to River Kilometer 37

The pathway used by yearling and subyearling Chinook salmon and steelhead to migrate from rkm 50 to rkm 37 differed depending on the rkm-50 subarray at which they were detected. The values of λ at the Nav 37 subarray were significantly higher for fish that migrated from Nav 50 ($\lambda = 0.58$ – 0.64) than for fish that migrated from CC 50 ($\lambda = 0.10$ – 0.12 ; $P < 0.001$; Figure 3). Conversely, at the off-channel subarray, CB 37, the λ values were significantly higher for fish that migrated from CC 50 ($\lambda = 0.26$ – 0.32) than for those that migrated from Nav 50 ($\lambda = 0.01$ – 0.05 ; $P < 0.001$; Figure 3). The length of time taken to migrate from Nav 50 or CC 50 to rkm 37 differed significantly ($P < 0.001$) for all three salmonid groups. Median travel time to rkm 37 was 4.5 h for yearling Chinook salmon that migrated from Nav 50 and was 12.1 h for yearlings that migrated from CC 50 (Figure 4). Similarly, subyearling Chinook salmon and steelhead that migrated from Nav 50 had median travel times of 5.1 and 4.8 h, respectively, whereas subyearling Chinook salmon and steelhead that migrated from CC 50 had median travel times of 11.9 and 12.6 h, respectively (Figure 4). Yearling Chinook salmon and steelhead that migrated from CC 50 had higher probabilities of survival to rkm 37 than those that migrated from Nav 50 (Figure 5); however, the differences were not significant ($P > 0.054$). Estimated S was 1.01 (SE = 0.02) for yearling Chinook salmon that migrated from CC 50 and was 0.98 (SE = 0.01) for those that migrated from Nav 50 (Figure 5). Steelhead that migrated from CC 50 had an S -value of 0.99 (SE = 0.04) compared with 0.92 (SE = 0.01) for those that migrated from Nav 50 (Figure 5). Conversely, subyearling Chi-

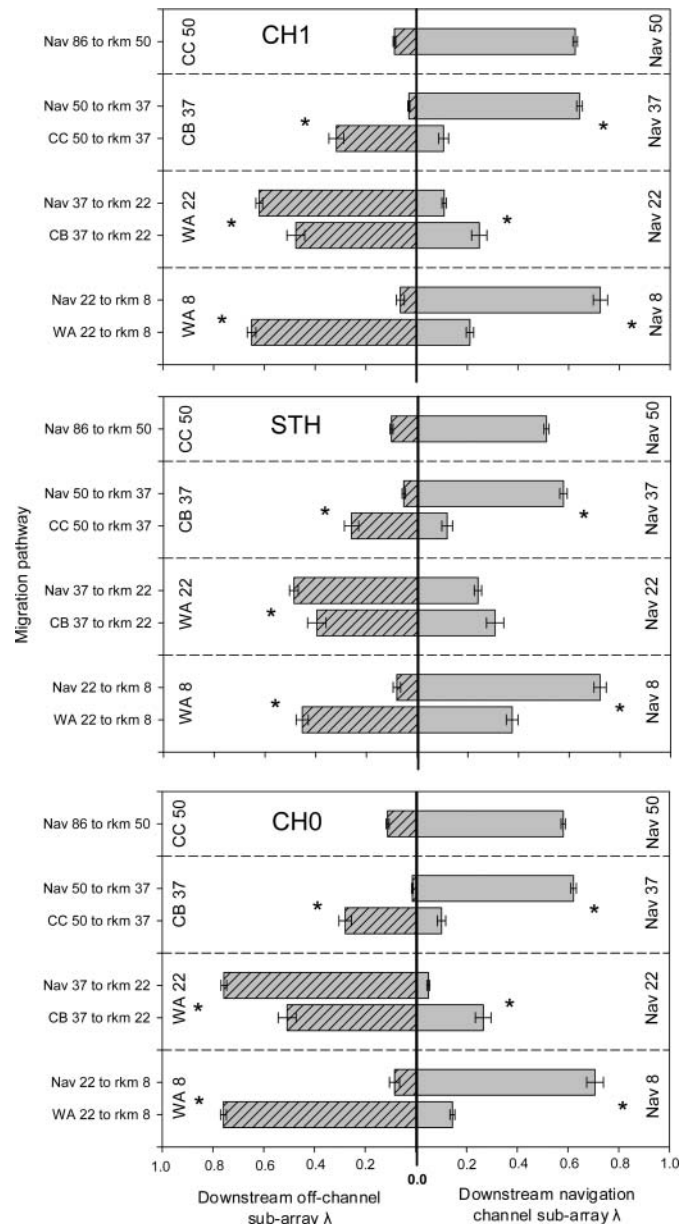


FIGURE 3. Joint probability (λ) of migrating to and being detected at subarrays in off-channel areas (CC 50, CB 37, WA 22, and WA 8; hatched bars) or in the navigation channel (Nav 50, Nav 37, Nav 22, and Nav 8; solid bars) at the downstream boundary of each Columbia River estuary reach for yearling Chinook salmon (CH1), steelhead (STH), and subyearling Chinook salmon (CH0) that were previously detected at subarrays (navigation channel or off-channel areas) at the upstream boundary of the reach. Subarray codes are defined in Figure 2 (rkm = river kilometer). Asterisks indicate significant differences in λ values between fish that migrated to the same downstream subarray from different upstream subarrays.

nook salmon that migrated from Nav 50 had a higher probability of survival to rkm 37 ($S = 0.99$; SE = 0.00) than subyearlings that migrated from the CC 50 subarray ($S = 0.95$; SE = 0.02; Figure 5); again, the difference was not significant ($P = 0.059$).

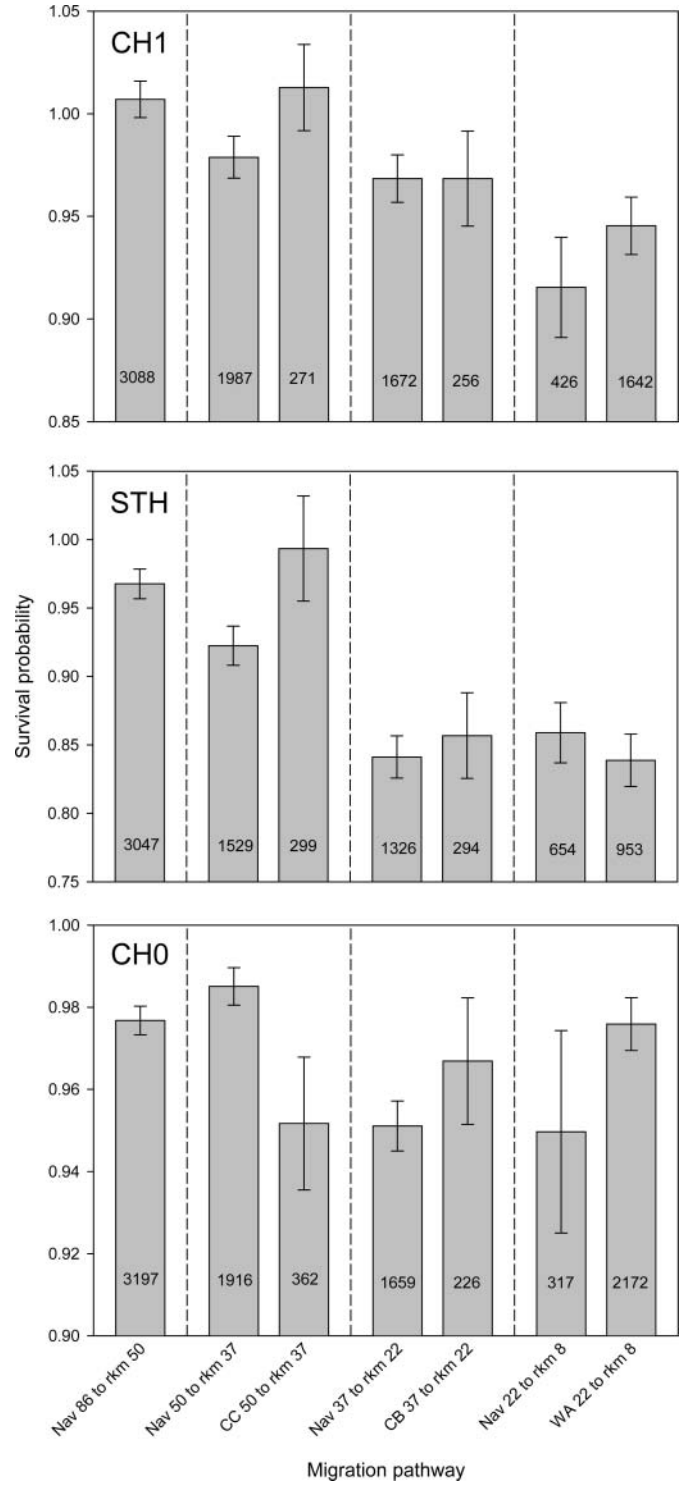
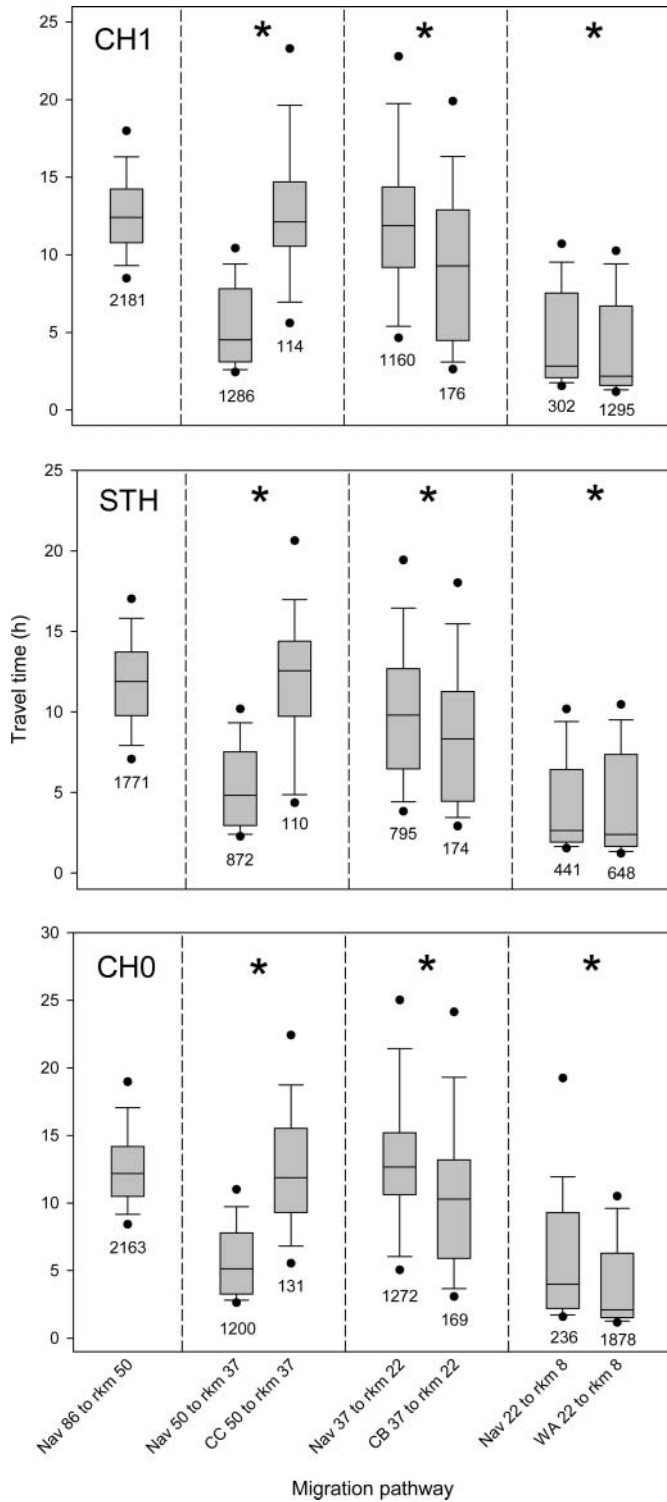


FIGURE 4. Box-and-whisker plot of travel time (h) through each Columbia River estuary reach for yearling Chinook salmon (CH1), steelhead (STH), and subyearling Chinook salmon (CH0) that migrated from each upstream subarray (solid horizontal line within each box = median; ends of box = 25th and 75th percentiles; ends of whiskers = 10th and 90th percentiles; dots = 5th and 95th percentiles). Sample sizes are shown below each box. Subarray codes are defined in Figure 2 (rkm = river kilometer). Asterisks indicate significant differences between fish that migrated through the same reach from different upstream subarrays.

FIGURE 5. Probability of survival through each Columbia River estuary reach for yearling Chinook salmon (CH1), steelhead (STH), and subyearling Chinook salmon (CH0) that migrated from each upstream subarray. Sample sizes are shown within each bar. Subarray codes are defined in Figure 2 (rkm = river kilometer).

River Kilometer 37 to River Kilometer 22

Between rkm 37 and rkm 22, most of the acoustic-tagged smolts appeared to cross over from the south side of the estuary and from the navigation channel to the Washington shoreline channel. Yearling and subyearling Chinook salmon and steelhead that migrated from either Nav 37 or CB 37 had higher λ values at WA 22 ($\lambda = 0.40\text{--}0.76$) than at Nav 22 ($\lambda = 0.05\text{--}0.31$; Figure 3). Furthermore, a comparison between fish that migrated from Nav 37 and those that migrated from CB 37 revealed that for all three tagged salmonid groups, fish that migrated from Nav 37 had significantly higher λ values at WA 22 ($\lambda = 0.49\text{--}0.76$) than fish that migrated from CB 37 ($\lambda = 0.40\text{--}0.51$; $P < 0.027$; Figure 3). Conversely, for yearling and subyearling Chinook salmon, λ values at Nav 22 were significantly higher for fish that migrated from CB 37 ($\lambda = 0.25\text{--}0.27$) than for fish that migrated from Nav 37 ($\lambda = 0.05\text{--}0.11$; $P < 0.001$; Figure 3). For steelhead, values of λ at Nav 22 ($\lambda = 0.24\text{--}0.31$) were similar ($P = 0.061$) regardless of whether the fish migrated from Nav 37 or CB 37 (Figure 3), and the values were relatively high in comparison with the λ values of yearling and subyearling Chinook salmon.

The length of time taken by yearling and subyearling Chinook salmon and steelhead to migrate from rkm 37 to rkm 22 differed depending on the rkm-37 subarray at which they were detected. Steelhead generally migrated through the reach in the least amount of time; steelhead that migrated from CB 37 took significantly less time (median = 8.3 h) than those that migrated from Nav 37 (median = 9.8 h; $P < 0.001$; Figure 4). Yearling Chinook salmon that migrated from CB 37 also took significantly less time (median = 9.3 h) than those that migrated from Nav 37 (median = 11.9 h; $P < 0.001$; Figure 4). Subyearling Chinook salmon took the most time to migrate from rkm 37 to rkm 22; again, subyearlings that migrated from CB 37 took significantly less time (median = 10.3 h) than those that migrated from Nav 37 (median = 12.7 h; $P < 0.001$; Figure 4).

Probabilities of survival between rkm 37 and rkm 22 for yearling and subyearling Chinook salmon were high ($S \geq 0.95$) and similar, regardless of whether the fish migrated from Nav 37 or CB 37 ($P > 0.362$; Figure 5). The probability of steelhead surviving from rkm 37 to rkm 22 (range of $S = 0.84\text{--}0.86$) was substantially lower than the S -values observed for Chinook salmon but was similar between steelhead that migrated from Nav 37 and those that migrated from CB 37 ($P = 0.639$; Figure 5).

River Kilometer 22 to River Kilometer 8

After passing rkm 22, yearling and subyearling Chinook salmon and steelhead remained primarily within their respective channels until they reached rkm 8. The λ values at the Nav 8 subarray were significantly higher for fish that migrated from Nav 22 ($\lambda = 0.71\text{--}0.73$) than for fish that migrated from WA 22 ($\lambda = 0.14\text{--}0.38$; $P < 0.001$; Figure 3). Conversely, λ values at the WA 8 subarray were significantly greater for fish that migrated from WA 22 ($\lambda = 0.45\text{--}0.76$) than for those that migrated from Nav 22

($\lambda = 0.06\text{--}0.08$; $P < 0.001$; Figure 3). The length of time taken to migrate from Nav 22 or WA 22 to rkm 8 differed significantly for all three salmonid groups. Median travel time to rkm 8 was significantly greater for yearling Chinook salmon that migrated from Nav 22 (2.8 h) than for yearlings that migrated from WA 22 (2.2 h; $P < 0.001$; Figure 4). Steelhead that migrated from Nav 22 had a median travel time of 2.6 h compared with 2.4 h for those that migrated from WA 22 (Figure 4). Although this was a difference of only about 15 min, it was significant ($P = 0.005$). The median travel time of subyearling Chinook salmon that migrated from Nav 22 was 4.0 h, which was almost twice the median for subyearlings that migrated from WA 22 (2.1 h; $P < 0.001$; Figure 4).

Survival from rkm 22 to rkm 8 was similar among pathways for yearling and subyearling Chinook salmon and steelhead. Yearling and subyearling Chinook salmon that migrated from WA 22 had higher probabilities of survival to rkm 8 (range of $S = 0.95\text{--}0.98$) than those that migrated from Nav 22 (range = $0.92\text{--}0.95$; Figure 5). However, the differences were not significant ($P > 0.240$). Steelhead had a substantially lower S than juvenile Chinook salmon, regardless of migration pathway. The probability of survival to rkm 8 was 0.86 (SE = 0.02) for steelhead that migrated from Nav 22 and was 0.84 (SE = 0.02) for those that migrated from WA 22 (Figure 5); the difference between pathways was not significant ($P = 0.462$).

DISCUSSION

Our study on the use of navigation channel versus off-channel pathways revealed new information regarding the influence of migration pathways on travel time and survival of emigrating juvenile salmonids in a large estuary. Yearling and subyearling Chinook salmon and steelhead exhibited generally similar migratory behaviors as they emigrated through the lower 86 km of the Columbia River estuary. The majority of fish appeared to travel in the vicinity of the main navigation channel from rkm 86 to rkm 37 before leaving the navigation channel to migrate through off-channel areas between rkm 37 and rkm 8. Additionally, we identified significant differences in travel time between groups that migrated in the navigation channel and those that moved through off-channel pathways. Differences in estimated survival, although not statistically significant, were noted between groups of navigation channel and off-channel migrants.

The complex migration pathways we observed for juvenile Chinook salmon and steelhead reflect the complex bathymetry, morphology, and hydrodynamics of the Columbia River estuary. From the upstream boundary of our study area (rkm 86) to the head of Cathlamet Bay (rkm 50), most of the flow is conveyed by the main navigation channel; this is due in part to the presence of channel training structures (e.g., pile dikes), which have been constructed to confine and scour the navigation channel (Fox et al. 1984). For example, near rkm 50, pile dikes direct river flow from the south side of Puget Island to the north side of Tenasillahe Island (Fox et al. 1984), which results in relatively

little flow into Clifton Channel. Similarly, between rkm 50 and rkm 37, pile dikes have been constructed to retain the majority of flow in the navigation channel by directing water away from Cathlamet Bay. Acoustic-tagged fish in our study generally appeared to follow these flow patterns. In studying juvenile fall Chinook salmon in the Sacramento River–San Joaquin River Delta, Perry et al. (2010) found a relationship between the probability of fish migrating through a pathway and the proportion of river flow in that pathway. It is possible that a similar relationship exists in the Columbia River estuary, particularly upstream of rkm 37. However, we did not perform this comparison because the fraction of river flowing through each of the pathways we examined was unknown.

The estuary downstream of rkm 37 has more variable flow patterns than upstream reaches and is composed of two primary channels. With aid from channel training structures, the main navigation channel flows from the north side of the estuary at rkm 37 to the south side at Tongue Point near rkm 28. The Washington shoreline channel, which drains much of the estuary north of the navigation channel between rkm 37 and rkm 8, has weaker river outflow, greater tidal transport, and a more salt-wedge-like salinity intrusion than the navigation channel (Chawla et al. 2008). Just upriver from the Astoria-Megler Bridge at rkm 22, small channels that cut through Taylor Sands convey tidal flows between the Washington shoreline channel and the navigation channel (Fox et al. 1984). The observed high values of λ at WA 22 for the Nav 37 and CB 37 virtual release groups indicate that the movements of acoustic-tagged fish were directed primarily by tidal flows between rkm 37 and rkm 22. Using mobile tracking of radio-tagged yearling Chinook salmon smolts, Schreck et al. (2005) found similar results; tagged fish moved from the main navigation channel and across Taylor Sands to enter the Washington shoreline channel between rkm 37 and rkm 22. It is possible that acoustic-tagged fish in our study migrated through this reach by allowing the current to direct their movement. Several studies have shown that juvenile salmon move downstream through estuaries primarily during ebbing tides (Fried et al. 1978; Moser et al. 1991; Miller and Sadro 2003). Because tidal currents flow from the navigation channel toward the Washington shoreline channel during ebbing tides (Fox et al. 1984), migrating fish would be drawn from the south side of the estuary and from the navigation channel toward the Washington shoreline channel. However, it is also possible that juvenile salmonids moving seaward in the navigation channel between rkm 37 and rkm 22 encountered increased levels of salinity in this more mixed environment and moved northward across Taylor Sands to the Washington shoreline channel, where the two-layer flow pattern (river water on top of marine water) was more well-developed (Chawla et al. 2008). The two-layer flow pattern would give emigrating salmonid smolts the opportunity to select salinity levels based on their readiness to adapt to seawater (Zaugg et al. 1985; Birtwell and Kruzynski 1989; Chernitskii et al. 1995). Once fish had selected either the navigation channel or the Washington shoreline channel, they tended to remain in that channel from rkm 22 to rkm 8.

The pathways used by fish to migrate through the estuary affected their travel time. Navigation channel migrants had shorter travel times than off-channel migrants between rkm 50 and rkm 22, which is consistent with the results obtained by Schreck et al. (2005). However, downstream of rkm 22, tagged fish that migrated in the Washington shoreline channel had shorter travel times than navigation channel migrants. Most of the flow is conveyed by the navigation channel upstream of rkm 22, whereas water flows are strongest in the Washington shoreline channel downstream of rkm 22 (Fox et al. 1984); thus, it appears that travel rate may be positively correlated with the amount of water flow in each pathway. Multiple studies have demonstrated this type of relationship between the travel rate of smolts and discharge in the Columbia River basin (Berggren and Filardo 1993; Tiffan et al. 2000).

Schreck et al. (2005) suggested that the slower travel time of off-channel migrants could potentially lower survival rates by increasing the period of exposure to avian predators, which have been shown to consume large numbers of juvenile salmonids in the Columbia River estuary (Collis et al. 2001, 2002; Ryan et al. 2001, 2003; Roby et al. 2003; Anderson et al. 2005, 2007). In our study, the greatest observed differences in travel time and survival between navigation channel and off-channel migrants occurred in the rkm-50–37 reach; off-channel migrants took two to three times longer to transit this reach than their cohorts in the navigation channel. Contrary to the hypothesis of Schreck et al. (2005), we found that survival through the rkm-50–37 reach was higher for the yearling Chinook salmon and steelhead smolts that migrated off-channel than for those that migrated through the navigation channel. Therefore, it appears that variables in addition to travel time affect the survival of navigation channel and off-channel migrants in this reach of the estuary.

Although differences in travel time were sometimes small, they were often statistically significant. However, dramatic changes that may affect juvenile salmonid behavior and survival can occur in the estuary within a short period of time. For example, as a result of the tidal exchange, water level changes of up to 20 cm can occur in as little as 15 min. Additionally, we recorded travel rates of nearly 16 km/h between rkm 22 and rkm 8. Fish moving at this rate could migrate almost 4 km within 15 min. Therefore, small differences in travel time may have biological significance.

If we had implanted transmitters into fish smaller than 95 mm FL, we likely would have observed longer travel times and a greater proportion of subyearling Chinook salmon using off-channel areas. Acoustic-tagged fish in our study were smaller than those in most previous telemetry studies that have been conducted to monitor the behavior and survival of juvenile salmon and steelhead in estuarine environments (Schreck et al. 2006; Melnychuk et al. 2007; Semmens 2008; Welch et al. 2008; Clemens et al. 2009; Rechisky et al. 2009). In addition, the lengths of our tagged fish corresponded well with the run-at-large at the upriver tagging site. Nevertheless, acoustic-tagged fish in our study were intended to represent actively emigrating smolts and did not reflect the relatively smaller

size distribution of juveniles originating from watersheds downstream of Bonneville Dam (McCabe et al. 1986; Bottom et al. 2008; Roegner et al. 2010). Most of the juvenile salmonids that spend considerable amounts of time (i.e., months) rearing in the estuary are fry or presmolts with FLs less than about 60–70 mm (Kjelson et al. 1982; Bottom et al. 1984, 2008, 2009; Healey 1991). Additionally, shallow off-channel areas are used primarily by subyearling Chinook salmon of smaller size-classes than those we tagged with acoustic transmitters (McCabe et al. 1986; Lott 2004; Bottom et al. 2008). Therefore, the results we report are not expected to be representative of the younger and smaller juvenile salmonids that rear in the Columbia River estuary for prolonged periods.

For the three salmonid groups we examined, the lowest survival rates were observed in the two downstream-most reaches (rkm 37–22 and rkm 22–8). Although potential mechanisms of mortality could be related to fish health (disease), physiology (stress), or bioenergetics (starvation), avian predation has been shown to account for a substantial amount of juvenile salmonid mortality in the Columbia River estuary (Collis et al. 2001, 2002; Ryan et al. 2001, 2003; Roby et al. 2003; Anderson et al. 2005, 2007). Thus, the lower survival we observed between rkm 37 and rkm 8 may be due to the proximity of large nesting colonies of piscivorous birds on East Sand Island. In our study, steelhead smolts suffered higher mortality rates than Chinook salmon yearlings or subyearlings. Juvenile steelhead may have a greater tendency to migrate closer to the water surface (Beeman et al. 1999; Antolos et al. 2005) and are, on average, larger than Chinook salmon smolts, thus making them more vulnerable to avian predation (Collis et al. 2001; Antolos et al. 2005).

It is possible that observed differences in smolt survival between estuarine reaches or pathways can be attributed to variations in avian predator habitat among the reaches or pathways. For example, high densities of Caspian terns *Hydroprogne caspia* have been observed to forage in tidal flats during ebbing tides (Lyons et al. 2007), when smolts would be most abundant in these areas. Therefore, smolts moving northward in the estuary between rkm 37 and rkm 22 may be exposed to greater avian predation risk if they pass through the shallow waters of Taylor Sands than if they remain in the deeper navigation channel. However, a more comprehensive study is needed to determine the relationship between the habitat use and foraging behavior of avian predators and the survival of salmonid smolts through particular migration pathways of the Columbia River estuary.

This study provides quantitative information about the pathways used by juvenile Chinook salmon and steelhead to migrate through the Columbia River estuary and the consequences—in terms of travel time and *S*—of migrating through each pathway. Our results show that multiple pathways are used and that travel times and survival differ among pathways. Understanding movement and survival rates among multiple pathways is critical because these parameters can have important implications for population viability (Perry et al. 2010). Variable and multiple migration pathway use by juvenile salmonids in the estuary

can be beneficial via greater expression of life history diversity, which confers an increased resiliency to environmental perturbations (Waples et al. 2009). Dispersion of juvenile salmonids into various pathways during downstream migration could buttress resiliency by decreasing the overall probability of encountering poor water quality, high predator concentrations, or other deleterious conditions (Koski 2009). Knowledge of migration pathways and movement patterns of targeted fish species along with the fraction of fish that use particular migration routes is also useful to managers for prioritizing management activities (Newman and Brandes 2010). This information, combined with survival data for fish using various pathways, could be applied to focus future research and management activities on areas where survival is low and where a likely mechanism for mortality has been identified.

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