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ARTICLE

Residency and Movement of Juvenile Chinook Salmon at Multiple Spatial Scales in a Tidal Marsh of the Columbia River Estuary

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Abstract

Use of the Columbia River estuary by juvenile Pacific salmon *Oncorhynchus* spp. is garnering more attention as managers look to improve salmon survival through estuary restoration. Studies have shown that juvenile salmon are abundant in shallow-water habitats within the Columbia River estuary, but information on how juveniles exploit specific estuarine habitats is lacking. We used a combination of physical marks and PIT tag technology to record residence time, movement, and growth of juvenile Chinook Salmon *O. tshawytscha*, particularly subyearlings, within an emergent marsh of the Columbia River estuary during 2005, 2006, and 2008. We documented marsh-scale residency and movement within the marsh complex and channel-scale residency and movement within two small secondary channels. Many juvenile Chinook Salmon remained in the marsh for 2–4 weeks and increased in FL by 10–20 mm, with an average growth rate of 0.53 mm/d. Chinook Salmon entered secondary channels most frequently in late afternoon and occasionally did so against the tide. Our results indicate that subyearling Chinook Salmon take advantage of shallow estuarine habitat in the Columbia River to a greater extent than previously documented.

The widespread decline of Pacific salmonids *Oncorhynchus* spp. in the Columbia River basin, including the extinction of 54% of the historic Chinook Salmon *O. tshawytscha* populations (Gustafson et al. 2007), has led to extensive programs for the recovery of threatened and endangered stocks. Recent recovery efforts have focused on the lower Columbia River and estuary (NMFS 2011; Thom et al. 2013), where dike construction and other modifications over the last century have eliminated more than 65% of the tidal wetlands and swamps that provided salmon rearing opportunities (Thomas 1983; Bottom et al. 2005). Although more than 1,200 ha of shallow-water habitat have been restored in the Columbia River estuary since 2001 (Thom et al. 2013), the effectiveness of those actions for salmon recovery is unknown.

Recent studies have documented the presence of Columbia River salmonids in restored wetlands of estuarine tributaries as well as salmonid consumption of prey originating from those wetlands (Eaton 2010; Roegner et al. 2010). However, attributes that affect salmon residency and movement within

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estuarine wetland habitats, such as water depth, tidal stage, and time of day, are poorly understood. Likewise, the benefits of marsh residency for salmon growth or survival are not fully understood. The objectives of the present study were to (1) document the use of tidal wetlands by juvenile Chinook Salmon, especially subyearlings; and (2) describe the mechanisms by which juvenile Chinook Salmon exploit estuarine habitat for residency, movement, and growth at multiple spatial scales.

Estuaries and their associated wetlands are well-documented rearing grounds for juvenile Chinook Salmon and other anadromous salmonids (Levy and Northcote 1982; Healey 1991). The Chinook Salmon is often considered the most estuary-dependent salmonid species, as all life history types spend at least some time feeding and growing in estuarine habitats before migrating to the ocean (Healey 1982).

In many river systems of the Pacific Northwest, subyearling Chinook Salmon reside in estuaries for 25–60 d before entering the ocean (Healey 1980; Levy and Northcote 1982; Myers and Horton 1982; Levings et al. 1986; Volk et al. 2010). Scale analyses by Reimers (1973) indicated that the majority of returning fall Chinook Salmon in the Sixes River, Oregon, had resided in the estuary as juveniles for approximately 3 months. In a brackish emergent wetland of the Salmon River estuary, Oregon, Hering et al. (2010) observed maximum residency periods of 128 d (in 2004) and 48 d (in 2005) for subyearling Chinook Salmon.

In contrast, estuarine residency of subyearling Chinook Salmon in the Columbia River has mostly been inferred from the travel time of large subyearlings fitted with acoustic transmitters. Acoustic-tagged subyearlings moved quickly from Bonneville Dam (the upper limit of tidal influence at river kilometer [rkm] 234) to the river mouth, with a mean travel time of 4.1 d (McComas et al. 2008). In a study focusing on migration pathways through the estuary, Harnish et al. (2012) found that the travel times of acoustic-tagged subyearling Chinook Salmon through specific estuary reaches were on the scale of hours rather than days. More recently, Johnson et al. (2015) used acoustic tags to measure the residence time of subyearlings in main-stem and off-channel areas near the Sandy River delta (rkm 198 on the Columbia River); those authors reported median residence times of 2.5–3.4 h. However, measures of residency and travel time based on the larger individuals that are used for acoustic tag implantation likely do not apply to the smaller fry or fingerlings that reside in many estuaries for extended periods (Healey 1980, 1991; Levy and Northcote 1982; Hering et al. 2010; Volk et al. 2010; Harnish et al. 2012).

We know of only two Columbia River studies that have reported estuarine residence times for smaller subyearling Chinook Salmon. Dawley et al. (1986) described short estuarine residence times of 6 d or less for most hatchery fall-run subyearlings traveling from rkm 75 to rkm 11. However, Dawley et al. (1986) observed that one group of smaller (mean FL ~ 61 mm) juveniles remained in the estuary for up to 2.5 months. Using otolith microchemistry analysis, Campbell (2010) estimated a 50-d average residency for subyearling Chinook Salmon (61–90 mm FL) within the brackish portion of the Columbia River estuary.

Most Columbia River fish surveys have targeted open-water or nearshore sites that are adjacent to main-stem estuary channels (Bottom et al. 1984; Dawley et al. 1986; Roegner et al. 2012). Surveys of main-stem habitats and that focus on large, hatchery-produced salmon may select for active migrants, thus underrepresenting juveniles with estuarine resident life histories (Bottom et al. 2005). Shallow tidal wetlands in the Columbia River estuary afford off-channel rearing opportunities for many smaller, naturally produced juvenile salmon (McCabe et al. 1986; Bottom et al. 2011), and the availability of tidal wetlands could be an important factor influencing their estuarine residency or growth. However, salmon residency in tidal wetlands has not been quantified, and the overall effects of wetland restoration on the performance of salmon populations are unknown.

Previous studies have measured subyearling passage time through the entire Columbia River estuary (McComas 2008), sections of the estuary (Dawley 1986; Harnish et al. 2012; Johnson et al. 2015), or the salinity-influenced portion of the estuary (Campbell 2010). Such studies provide general information about estuarine travel times but do not depict salmon rearing behavior, habitat preferences, or growth at fine scales.

Passive integrated transponder (PIT) technology provides a useful tool for studying the behavior of small (≥55-mm FL) subyearling salmon at fine (i.e., habitat) scales. The tags are small (8–32-mm) radio frequency identification tags that are inserted into the body cavity and allow for the unique identification of individuals. Because PIT tags are passive, fish must swim within range of a transceiver antenna to be detected; PIT tag detection arrays can provide a continuous record of PIT-tagged fish presence that cannot be inferred from periodic beach seine recapture surveys. For example, fish can be detected during the night, on days when no sampling occurs, and after sampling surveys are discontinued. Passive integrated transponder antenna arrays have been deployed successfully in tidal marsh channels to monitor the movements of tagged individuals within a wetland complex (e.g., Hering et al. 2010).

We used tagging, remote detection, and recapture methods to determine the movements, residence times, and growth of subyearling Chinook Salmon in the lower Columbia River estuary. We assessed residence times and movement at two spatial scales within Russian Island, an emergent tidal freshwater marsh. At the marsh scale, we measured residency, movements, and growth rates in selected areas of the emergent marsh. At the channel scale, we monitored entry and exit movements and residence times within selected secondary channels for a given tidal cycle.

METHODS

Study area.—Russian Island is a relatively pristine freshwater emergent marsh located at rkm 36 on the Columbia River (Figure 1). Shoals and shallow water surround the island, and the main river channel is situated more than 6.5 km from the study site. Vegetation is dominated by Lyngbye's sedge *Carex lyngbyei* (Elliot 2004), and the marsh consists of an interconnected network of distributary, secondary, tertiary, and smaller side channels. The large distributary channels typically become dewatered during low tides except for a few areas that provide low-water refuge for fish. Secondary and smaller channels often are dewatered twice daily during low tides. However, elevated river flow (>11,327 m^3/s [>400,000 ft^3/s] at Bonneville Dam) in combination with neap low tides can cause secondary channels to retain up to 0.85 m of water. Russian Island is inundated during high tides, with water depth on the marsh surface occasionally reaching 1.2 m.

Scales of Chinook Salmon residency and movement.—During 2005, 2006, and 2008, we employed mark–recapture techniques in combination with PIT tag technology to track the residence time and movement of juvenile Chinook Salmon at two spatial scales. At the marsh scale, we measured (1) the residency of fish that spent any amount of time in the Russian Island marsh and (2) the movement of fish that potentially could have migrated anywhere throughout the marsh between repeated recaptures. At the channel scale (2008 only), measurements of movement and residency were limited to entry and exit activity and the amount of time spent within specific secondary channels during a particular tidal cycle.

In 2005 and 2006, marsh-scale residency (R_{MARSH}) was measured within each of two 23-ha regions (DC_{NW} and DC_{SE}) that encompassed a pair of distributary channels (Figure 1). Intramarsh movements were also recorded for any individuals that were tagged in one distributary region and recaptured in the other. In 2008, R_{MARSH} was measured within a 16-ha region of a single distributary channel on the north side of the marsh (DC_{PIT}; Figure 1). In this case, intramarsh movement was represented by individual excursions between the large distributary channel and either of two

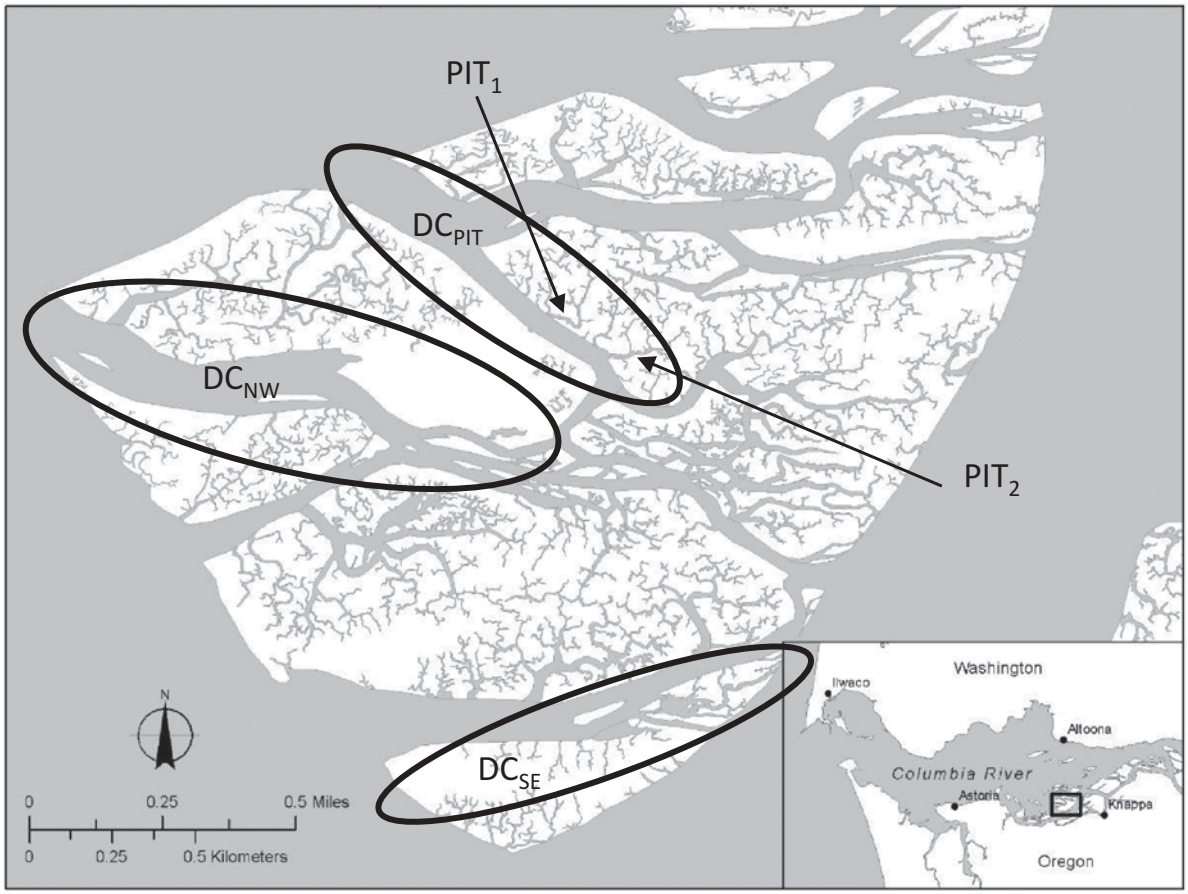

FIGURE 1. Sampling locations within Russian Island marsh in the Columbia River estuary. The approximate areal extent of sampling within each distributary channel (DC_{NW}, DC_{SE}, and DC_{PIT}; see Methods) is enclosed by an oval. Arrows point to the secondary channels (PIT_1 and PIT_2) where the PIT tag detection arrays were located.

small secondary channels (PIT_1 and PIT_2) draining from its northern shore. Secondary channel entry and exit and residence times ($R_{CHANNEL}$) were measured with a pair of autonomous PIT tag detection arrays—one located in PIT_1 and the other located in PIT_2 (Figure 1). The intramarsh movements depicted by the 2008 survey involved shorter travel distances than were examined in 2005 and 2006. However, the survey locations were chosen not to quantify travel distances but to determine whether marsh-resident juvenile Chinook Salmon typically remained within a single local channel or occupied a larger habitat network encompassing multiple channel locations over time.

Fish sampling.—Each year, the study began with a period of marking (either with acrylic paint or PIT tags, as described below) of juvenile Chinook Salmon, followed by a recapture period. A daily recapture effort was maintained for 4–6 d after the last day of marking; beyond that, the recapture effort became intermittent (i.e., every other day or every third day). We continued to sample until there were two consecutive sampling days in which no individuals were recaptured. Table 1 presents the dates of fish marking, daily recapture, and intermittent recapture efforts for each year of the study. Fish were collected with a 3- × 38-m, variable-mesh bag seine (10.0-mm and 6.3-mm mesh in the wings; 4.8-mm mesh in the bag) that was deployed from a small outboard skiff.

In 2005, we batch-marked juvenile salmon (≥40 mm FL) to test the feasibility of recapturing individuals within the marsh study area for the purpose of obtaining residency estimates. With a jet inoculator, acrylic paint diluted with distilled water was applied to the base of the caudal fin (Hart and Pitcher 1969; Thedinga and Johnson 1995). We used a distinct color that corresponded to the day of marking and release, but the marks did not differentiate individual fish within a given release group. As an additional external mark, a portion of the upper or lower lobe of the caudal fin was clipped.

After the successful recapture of batch-marked fish in 2005, we adjusted our methods in 2006 to include PIT-tagging, which permitted the measurement of individual growth rates and residence times. We injected 12-mm, full-duplex PIT tags (Destron Fearing Model TX1400ST) into the body cavity of each Chinook Salmon (≥55 mm FL) via the procedures outlined by the Columbia Basin Fish and Wildlife Authority (CBFWA 1999). We continued to apply dilute acrylic paint to the base of the caudal fin as a batch mark in Chinook Salmon fry (40–54 mm FL) that were too small to receive PIT tags. A combination of paint color and caudal fin clip (upper or lower lobe) was used to indicate the day of marking and release.

In 2008, we marked fish exclusively with PIT tags to (1) allow for the tagging and release of a greater number of individuals in the distributary channel near the two detection arrays and (2) increase the sample size for estimating individual growth rates. During that year, we PIT-tagged all 60-mm FL and larger Chinook Salmon by using 12-mm PIT tags inserted via the same procedures used in 2006. We increased the size threshold for tagging from 55 to 60 mm FL to minimize the risk of mortality and tag loss due to repeated (daily) recapture and handling of individual fish.

In all study years, fish were anesthetized with tricaine methanesulfonate (50 mg/L) and were inspected for prior marks or tags. Fish were then batch marked or PIT-tagged, measured, weighed, and held for a 1–4-h recovery period in a 190-L container with a constant source of fresh water. On the same day as marking or tagging, fish were released into the distributary channel from which they were collected. Tissue samples for genetic analysis were retained from a subsample of fish collected on each day of the fish marking period (data not presented).

To account for delayed handling mortality and tag loss, up to 10 fish/d were held for 24 h in a 0.2-m^3 net-pen consisting of a polyvinyl chloride (PVC) frame with 3.2-mm knotless mesh. However, the method failed because high water velocities precluded us from holding live fish throughout the tidal cycle. Another study reported delayed mortality rates of 0.1–0.3% and little or no tag loss from the PIT-tagging of similarly sized Chinook Salmon (Achord et al. 2007). If the mortality and tag loss rates in our study were similar to those previous measurements, then the principal impact would be a slight underestimate of R_{MARSH}.

If a PIT-tagged individual was recaptured during the fish marking period, the tag code was recorded, and the fish was measured, weighed, held for recovery, and released. If a batch-marked individual (i.e., marked with acrylic paint) was recaptured during the marking period, the batch code was recorded; the fish was then marked with a new batch code for the current day, measured, weighed, held for recovery, and released.

During the recapture period, juvenile Chinook Salmon were collected by seining in the same areas of Russian Island that

TABLE 1. Dates of juvenile Chinook Salmon marking and recapture within Russian Island marsh in the Columbia River estuary.

Year	Marking method	Marking period	Daily recapture period	Intermittent recapture period
2005	Batch marking	Apr 14–17	Apr 15–23	Apr 27–May 19
2006	Batch marking and PIT-tagging	Apr 3–7, Apr 9–11	Apr 4–7, Apr 9–15	Apr 17–May 25
2008	PIT-tagging	May 4–9	May 5–14	May 16–Jun 5

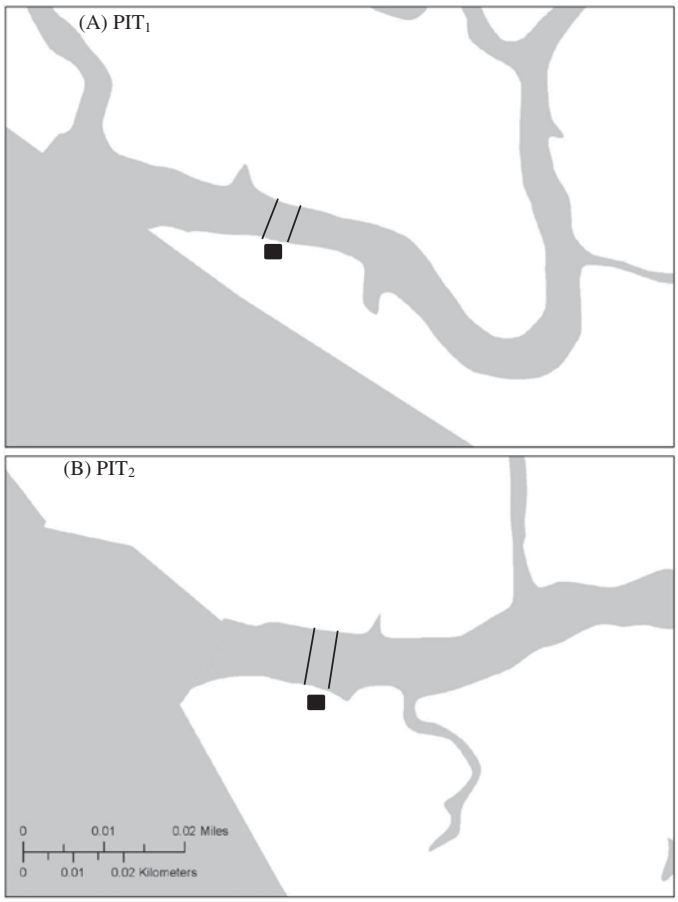

FIGURE 2. Close-up view of the secondary channels (PIT_1 and PIT_2) with PIT tag detection arrays in Russian Island marsh (see Figure 1). Each black line transecting a channel represents three PIT antennas; the black boxes indicate where the electrical equipment was housed.

were sampled during the marking period. Juveniles were anesthetized, inspected for marks and tags, measured, weighed, held for recovery, and released.

Passive integrated transponder detection arrays.—The PIT detection arrays deployed at PIT_1 and PIT_2 monitored fish use of secondary channels with surface areas of 0.40 and 0.37 ha, respectively (Figures 1, 2). Each PIT detection array consisted of six antennas that were configured into two parallel groups of three. Antennas measured either 3.1 × 1.2 m or 1.8 × 1.2 m and were constructed of 10.2-cm, schedule-80 PVC pipe. The larger (3.1-m) antennas housed six wraps of 10-AWG (American wire gauge) stranded tinned copper wire, while the smaller (1.8-m) antennas housed seven wraps. The PIT_1 array spanned the entire width of the 10.1-m channel, whereas the PIT_2 array was coupled with nets (3.2-mm, knotless, hexagonal mesh) to span the width of the 11.9-m channel (Figure 3). Each group of three antennas was suspended from a cable that was anchored to both sides of the secondary channel and spanned the width of the channel. Antennas were also individually anchored to the substrate with modified 1.27-cm rebar. Antenna numbers 1–3 made up the downstream line within an array, and antennas 4–6 composed the upstream line. This design enabled the directional movement of PIT-tagged individuals to be discerned. For example, a fish detected on antenna 3 followed by a detection on antenna 6 would be classified as exhibiting upstream movement, whereas a detection on antenna 3 followed by a detection on antenna 2 would be classified as representing lateral movement.

Each array was connected to a single multiplexing transceiver (Destron Fearing Model FS1001M). From May 4 to August 18, 2008, arrays continuously monitored PIT-tagged fish that entered or exited the channels. Onset Hobo U20 water level data loggers were deployed in both channels and recorded the water depth at 10-min intervals. An additional logger was deployed above the elevation of mean higher high water to record atmospheric pressure, which was used to normalize water depth readings. Each PIT tag detection was synchronized with water level by interpolating the water levels that were recorded immediately before and immediately after the detection.

During the fish marking period in 2008, detection efficiency of the antenna arrays was measured by releasing 20 PIT-tagged Chinook Salmon upstream from the arrays in each secondary channel on each of the 6 d of tagging. Fish that were used in the efficiency test were released in the late afternoon during an outgoing tide, when water levels had receded to below the marsh surface. This method provided a measure of detection efficiency for fish passing through each array but did not accurately measure the detection efficiency for the entire study. At other times during the study, tagged fish could have passed undetected above or around the antennas when the depth in each channel exceeded the bank-full level of about 1.7 m. Efficiency test fish were excluded from all analyses unless an individual clearly exited the channel and was subsequently detected in one of the two secondary channels or was recaptured with the seine.

Marsh-scale residence time and movement.—For all years, R_{MARSH} was determined based on seining recoveries and was calculated as the total number of days at large by subtracting the release date from the last date of recapture with the seine. The cumulative proportion of fish that were at large on each day of the recovery period was used to generate R_{MARSH} decay curves. We used a log-rank test of the Kaplan–Meier estimate (Pollock et al. 1989) to compare the decay curves of R_{MARSH} based on mark type (e.g., batch mark or PIT tag) and year.

For 2008 we also calculated a marsh-scale residence time based solely on detections at PIT_1 and PIT_2 (R_{DET}). For each detected fish, we combined all detections from the PIT_1 and PIT_2 arrays and subtracted the release date and time from the date and time of the last detection. A log-rank test of the Kaplan–Meier estimate was used to compare the decay curve of R_{DET} to that of R_{MARSH} (i.e., based on seine recoveries of

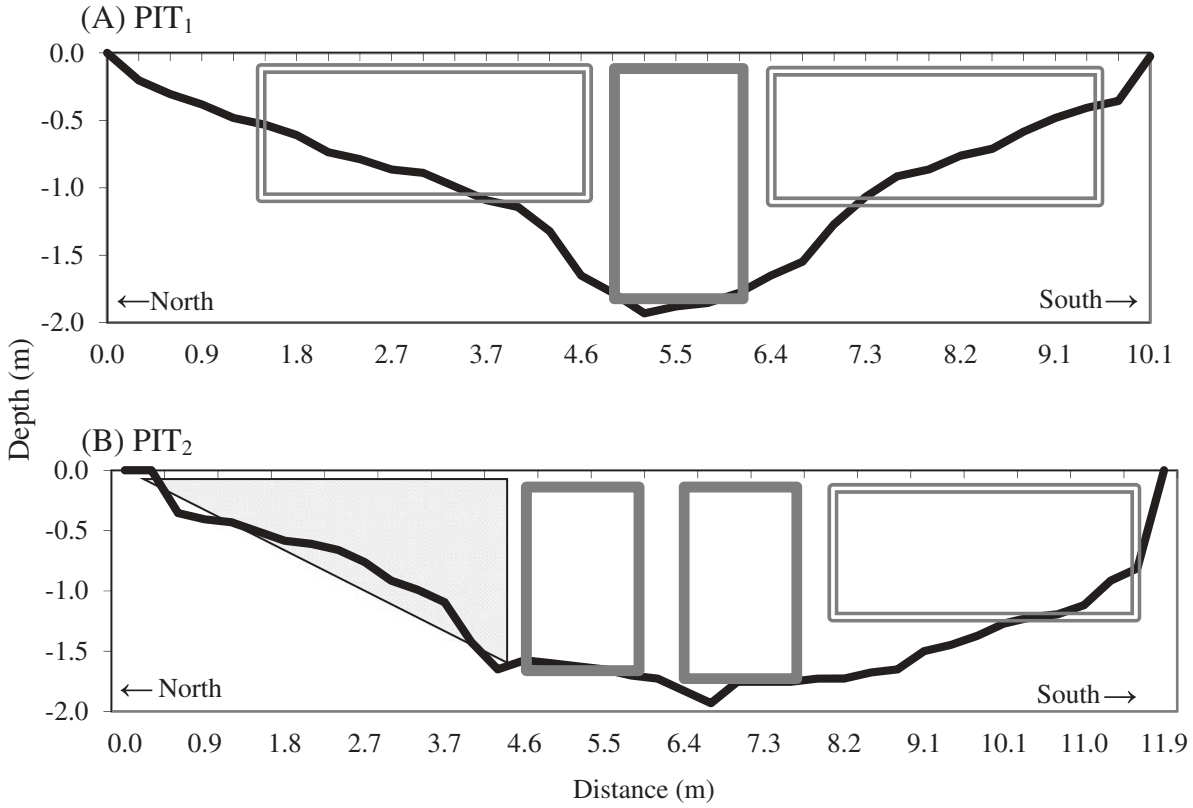

FIGURE 3. Cross-sectional schematics of the PIT tag detection arrays in two secondary channels within Russian Island marsh: **(A)** PIT_1 and **(B)** PIT_2. Antenna configurations were identical for the parallel detection lines within a given channel. The black lines represent the approximate channel profiles, the gray solid-lined rectangles represent the smaller (1.8-m) antennas, the gray double-lined rectangles represent the larger (3.1-m) antennas, and the gray triangle in panel (B) represents the block net. Portions of the antennas were dug into the substrate.

batch-marked and PIT-tagged fish) to determine whether residency measurements derived from PIT detection equipment were similar to those calculated from physical (seine) recaptures.

In 2005 and 2006, marsh-scale movement between DC_{NW} and DC_{SE} was determined by comparing the release location and the recapture location. However, our analysis was limited to fish movement from DC_{SE} to DC_{NW} because fish from the holding pen designed to estimate delayed mortality were released in deep water near the lower end of DC_{SE}, which may have confounded interpretations of fish movement from DC_{NW} to DC_{SE}. In 2008, detections of individual fish at the PIT_1 and PIT_2 arrays provided a measure of marsh-scale movement.

Channel-scale residence time and movement.—We defined $R_{CHANNEL}$ as the time spent upstream from a PIT tag detection array within a given tidal cycle. We calculated $R_{CHANNEL}$ by subtracting the entry date and time from the exit date and time for a given channel incursion past a PIT tag detection array. Therefore, fish that entered secondary channels more than once had an $R_{CHANNEL}$ value for each secondary channel use. Since the water level frequently rose above the PIT detection antennas, some fish may have entered or exited the channels undetected during high tides. Channel incursions in which clear ingress *and* egress were not observed were excluded from channel-scale analyses, likely resulting in the underestimation of $R_{CHANNEL}$.

In 2008, we examined channel-scale movements (ingress and egress) within both secondary channels. We normalized entry and exit detections around high tide and determined the tidal stage during which each entry and exit detection occurred. Chi-square tests were conducted to examine diel patterns of secondary channel use and to compare the frequency of daytime and nighttime tidal cycles during the study. The latter analysis was performed to ensure that the diel patterns of fish use were not biased by diel differences in channel accessibility due to the tidal cycle. Student's *t*-test was used to compare mean water depths during entry and exit.

Growth rate.—We calculated growth rates (G; mm/d) for PIT-tagged fish that were recaptured with the seine by using the following equation:

$$G = (FL_2 - FL_1)/(t_2 - t_1),$$

where t_1 is the time of release, t_2 is the time of final recapture; and FL_1 and FL_2 are the respective fork lengths at those times. To minimize the effect of precision errors in FL measurements, these calculations included only fish that were at large for more than 1 d between capture events.

RESULTS

We successfully recaptured juvenile Chinook Salmon within the Russian Island marsh during all 3 years of the study, despite the relatively small areas sampled and the wide availability of suitable wetland habitats throughout the lower estuary as a whole. As our methods shifted in 2006 and 2008 to emphasize juveniles that were large enough to be PIT-tagged, we marked and tagged fewer fish but generally improved the recapture rates (Table 2). Recovery rates of batch-marked fish were low in 2005 (5–7%), whereas recovery rates for fish marked in 2006 were three to four times greater (21–23%). In 2006, recovery rates were similar between batch-marked and PIT-tagged fish (>20%) except for PIT-tagged fish that were recovered at DC_{SE} (13%). Passive integrated transponder-tagged fish were recaptured from DC_{PIT} at a lower rate in 2008 (10%) than in 2006 (13–27%). However, fish that were tagged in 2008 were more than twice as likely (23%) to be detected by PIT arrays in the secondary channels, which each had an estimated detection efficiency of 94.1%. The overall recapture rate in 2008 was 29% (this was not an additive measure because 24 fish were recaptured by both methods; Table 2).

Marsh-Scale Residence Time and Movement

Over the course of the study, median R_{MARSH} for juvenile Chinook Salmon ranged from 1.8 to 5 d, and mean R_{MARSH} ranged from 3.7 to 7.4 d. Maximum R_{MARSH} ranged from 19 to 34 d. Median, mean, and maximum R_{DET} measurements in 2008 were similar: 2.3, 5.7, and 26.2 d, respectively. Table 3 provides a comparison of mean and maximum R_{MARSH} and R_{DET} for all years and marking methods.

No differences in R_{MARSH} were observed between Chinook Salmon that were recaptured in DC_{NW} and those that were recaptured in DC_{SE} during 2005 or 2006 (log-rank test: $P > 0.05$). Therefore, to simplify the analysis, we pooled results from DC_{NW} and DC_{SE} and compared R_{MARSH} by year and marking method.

TABLE 3. Comparison of median, mean (±SE), and maximum values for the marsh-scale residency (R_{MARSH}) of juvenile Chinook Salmon within Russian Island marsh.

Year	Mark or tag type	Recapture method	R_{MARSH} (d) Median	Mean ± SE	Maximum
2005	Batch mark	Seine	3	4.2 ± 0.4	19
2006	Batch mark	Seine	5	7.4 ± 0.8	34
	PIT tag	Seine	5	7.3 ± 0.6	27
2008	PIT tag	Seine	1.8	3.7 ± 0.5	25
	PIT tag	PIT array (R_{DET})	2.3	5.7 ± 0.5	26

In all years, recapture rates steadily declined from the time of release to the time of last recapture but started to level off at approximately 10 d (Figure 4). Marking method (batch marking or PIT tagging) had less of an effect on R_{MARSH} than did year. Decay curves for fish marked by the two different methods in 2006 were not significantly different (log-rank test: $\chi^2 = 0.06$, df = 1, $P = 0.800$); however, fish that were marked by the same method in different years showed statistically different decay curves. For example, the decay curves for fish that were batch-marked in 2005 and 2006 were significantly different (log-rank test: $\chi^2 = 15.13$, df = 1, $P < 0.001$). Likewise, the decay curve for fish that were PIT-tagged in 2006 significantly differed from the curve for fish that were PIT-tagged in 2008 (log-rank test: $\chi^2 = 32.52$, df = 1, $P < 0.001$). The strong effect of year on R_{MARSH} decay curves was likely a result of changes in recapture effort. In 2006, we had two crews available for beach seining, whereas only one crew was available in 2005 and 2008. The decay curves for R_{DET} and R_{MARSH} (all years and both marking methods combined) were not statistically different (log-rank test: $\chi^2 = 2.72$, df = 1, $P = 0.099$), thus

TABLE 2. Number, FL (mean ± SD), and recapture rate of juvenile Chinook Salmon that were batch marked or PIT-tagged in three distributary channels (DC; see Figure 1) within Russian Island marsh.

Year	Mark or tag type	Area	Number marked or tagged	FL (mm)	Recapture method	Number recaptured	Recovery (%)
2005	Batch mark	DC_{NW}	987	62 ± 20	Seine	65	7
		DC_{SE}	490	56 ± 16	Seine	23	5
2006	Batch mark	DC_{NW}	173	47 ± 4	Seine	36	21
		DC_{SE}	151	46 ± 5	Seine	35	23
2006	PIT tag	DC_{NW}	386	84 ± 27	Seine	103	27
		DC_{SE}	188	76 ± 18	Seine	25	13
2008	PIT tag	DC_{PIT}	704	92 ± 10	Seine	68	10
					PIT array	163	23

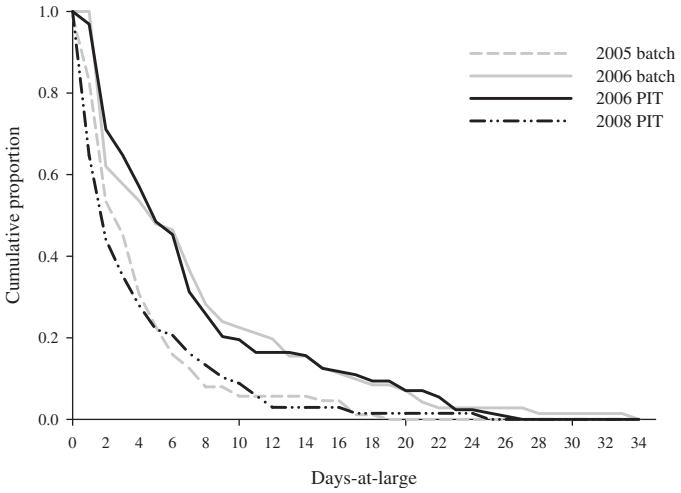

FIGURE 4. Comparison of marsh-scale residency (R_{MARSH}) decay curves based on the cumulative proportion of juvenile Chinook Salmon that were at large for each fish marking method (batch marking or PIT-tagging) during each study year within Russian Island marsh.

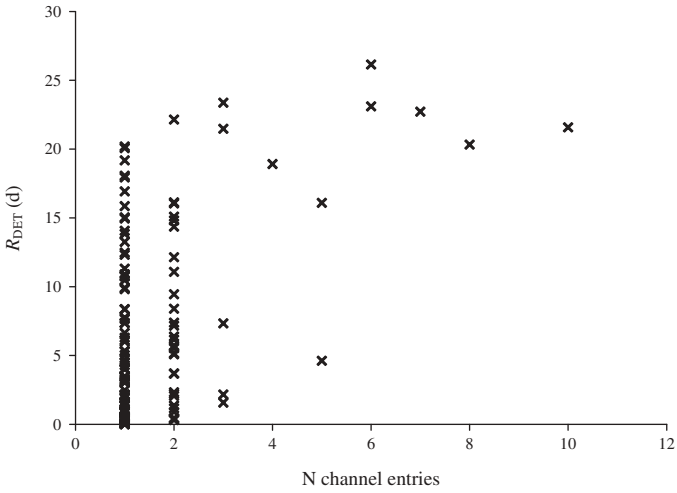

FIGURE 5. Comparison between marsh-scale residence time (R_{DET}; i.e., based solely on detections at PIT arrays in two secondary channels, PIT_1 and PIT_2) and the number entries into a secondary channel by juvenile Chinook Salmon within Russian Island marsh.

indicating that passive detection was as effective as active recapture methods in measuring residency and may be useful in normalizing effort across years.

Evidence of marsh-scale movement in 2005 was limited; only one fish that was released in DC_{SE} was recaptured in DC_{NW}. In contrast, during 2006, 15 fish from DC_{SE} were recaptured in DC_{NW}. Measurements of R_{MARSH} for fish that used multiple distributary channels were not significantly different from the R_{MARSH} for fish that remained in the channel of initial release (t = 0.89, df = 174, $P > 0.05$). In 2008, we monitored fish movement between the two secondary channels where the PIT detection arrays were deployed. Thirty-two individuals detected in both channels had significantly longer R_{DET} times than those of 131 fish that were detected in just one channel (t = 4.66, df = 161, $P < 0.0001$). Overall, fish that entered secondary channels multiple times tended to have a greater R_{DET} (r = 0.5242, df = 161, $P < 0.0001$; Figure 5), but the correlation was tenuous for fish that entered a secondary channel only once or twice. For those individuals, R_{DET} ranged widely from 6 min to 22 d.

Channel-Scale Residence Time and Movement

The PIT detection arrays recorded a total of 6,531 detections involving 246 incursions into the channels by 163 individual Chinook Salmon. Channel entry with subsequent exit was evident in 57% of the recorded channel incursions, and only data from those incursions were used in the channel-scale analyses below. Channel incursions where clear entry and exit behavior was not observed overwhelmingly (83%) coincided with higher high tides, during which fish likely passed undetected by swimming around or above the arrays or moved out of the channel via sheet flow rather than passing through the arrays undetected. Channel-scale residence time and movement results were similar between PIT_1 and PIT_2; therefore, data from the two channels were combined.

Channel-scale residency varied from a few minutes to several hours. The minimum observed $R_{CHANNEL}$ was 1.1 min, whereas the maximum $R_{CHANNEL}$ was 17.1 h. In 4% of channel incursions, $R_{CHANNEL}$ surpassed the duration of a tidal cycle. These instances always coincided with neap tides, when secondary channels retained enough water that fish were not forced to leave. The median and mean $R_{CHANNEL}$ values were 2.6 and 3.5 h, respectively.

The minimum depth required for subyearling Chinook Salmon to enter the secondary channels was 0.45 m; however, the median and mean water depths at channel entry were much higher—both 1.5 m. The mean and median water depths at the time of channel exit (both 1.4 m) were significantly lower than the depth at entry (t = 1.8, df = 139, P = 0.04), indicating that the water depth occurring when juvenile Chinook salmon exited the secondary channels was consistently lower than the water depth occurring at the time of entry.

Channel-scale entry and exit movements were more closely linked to tidal stage than to water depth. The majority of fish entered secondary channels on an incoming tide and exited the channels on an outgoing tide. However, 26% of channel entry events occurred against an outgoing tide, and 32% of exit events involved fish exiting against an incoming tide (Figure 6). Exit behavior seemed less discriminating with regard to tidal stage: fish exited during all four

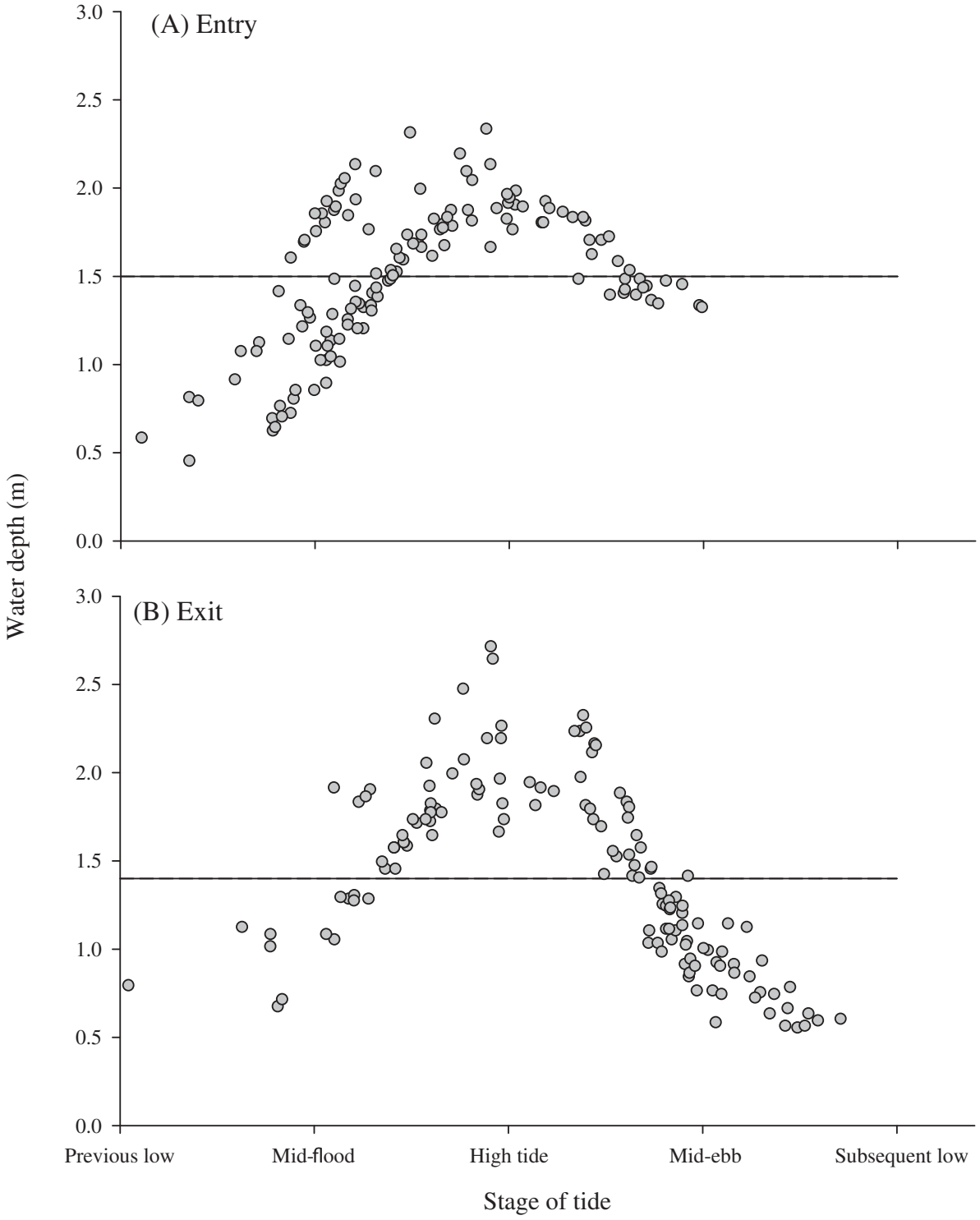

FIGURE 6. Tidal stage and water depth at which **(A)** entry and **(B)** exit movements of juvenile Chinook Salmon were recorded by two PIT tag detection arrays within Russian Island marsh. Horizontal lines represent the average depth of entry or exit.

quarters of the tidal cycle, but they entered during the first three quarters only.

Chinook Salmon entered secondary channels significantly more often during the daytime than during the night (chi-square test: $\chi^2 = 27.7$, df = 1, $P < 0.001$). Ingress most frequently took place during the afternoon to early evening (Figure 7). Egress followed a crepuscular pattern, with peak times of channel exit leading up to sunrise and sunset.

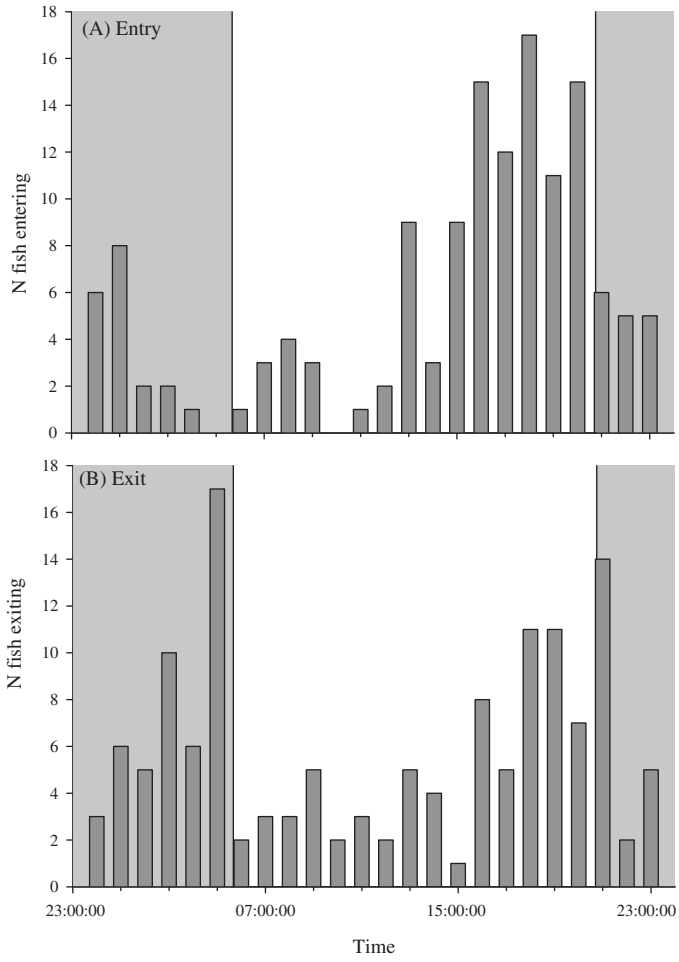

FIGURE 7. Frequency distribution of channel-scale **(A)** entry and **(B)** exit movements by juvenile Chinook Salmon within Russian Island marsh. Shaded areas indicate nighttime hours based on average sunrise and sunset for the study period.

The number of hours of incoming and outgoing tides throughout the study period was similar during daytime ($\chi^2 = 0.35$, df = 1, $P > 0.05$) and nighttime ($\chi^2 = 0.42$, df = 1, $P > 0.05$), indicating that increased fish entry into the channels during the daytime was not explained by a bias in tidal frequencies between daytime and nighttime hours.

Growth Rate

During both 2006 and 2008, the growth rate (mm/d) was highly variable for juvenile Chinook Salmon that resided in the marsh less than 5 d, but growth then approached an overall mean. The mean growth rate was not significantly different between years ($t = 0.82$, df = 166, $P > 0.05$). In the DC_{NW} and DC_{SE} areas combined, the mean growth rate was 0.49 mm/d during 2006 and 0.58 mm/d during 2008. The growth rate remained relatively constant over time. Size increased by 10–20 mm among individuals that resided in wetland areas longer than 15 d.

DISCUSSION

An understanding of habitat use by migratory species is important for identifying habitat corridors that most need protection. The reliance of subyearling Chinook Salmon on estuarine habitat has been established (Levy and Northcote 1982; Healey 1991), but the fine-scale habitat attributes that contribute to juvenile salmon performance had not been examined previously. In this study, we targeted shallow, peripheral wetlands with complex channel structure, where many small subyearling Chinook Salmon delay their seaward migrations for extended periods. Ours is the first study in the Columbia River estuary to (1) quantify the habitat-specific residence times and growth rates of subyearling Chinook Salmon and (2) assess the movements of these fish within and between tidal channel networks of an emergent marsh.

For all years and both fish marking methods, individuals varied widely in their wetland residency, consistent with research that has shown considerable phenotypic plasticity in the rearing behavior and life history characteristics of Chinook Salmon (Rich 1920; Reimers 1973; Healey 1991; Bottom 2005). Our measures of R_{MARSH} represent minimum values, as some individuals may have been tagged and released near the end of their wetland residency while others may have remained in or near the survey area for longer periods but went undetected by our sampling gear. Nevertheless, our observations of maximum R_{MARSH} were consistent with results from other studies in Pacific Northwest estuaries where subyearling Chinook Salmon residence times were measured on a similar spatial scale (Healey 1980; Levy and Northcote 1982; Hering et al. 2010).

Moreover, the present results indicate that the duration of wetland habitat use by Chinook Salmon changes vastly when analyzed at different scales. Channel-scale residency of some individuals may have been on the order of minutes or hours, whereas their R_{MARSH} extended 15–20 d. Likewise, many fish were not detected or recaptured until 1–2 weeks after release. The structural complexity of Russian Island likely provided a multitude of channel rearing and foraging opportunities, allowing fish to reside undetected outside of our immediate sampling areas. The importance of tidal marsh habitat is reinforced when one considers that subyearling Chinook Salmon must vacate the marsh with most of the outgoing tides, yet they return when the habitat is again accessible, redistributing themselves within the network of tidal channels. Similar movements and habitat use patterns have been observed in a resident marsh fish, the Mummichog *Fundulus heteroclitus* (Able et al. 2012). Such behaviors also highlight the importance of habitat connectivity with adjacent subtidal refuges. Indeed, highly intersected wetlands with numerous tidal channels may help to provide opportunities for longer residency than would be available from smaller marshes and sloughs with limited channel complexity.

Passive detection of PIT-tagged fish in secondary channels provided insight into channel-scale residency and movement

patterns and generally agreed with results from a similar study in the Salmon River estuary, Oregon. Subyearling Chinook Salmon spent a significant amount of the tidal cycle within secondary channels (4.9 h: Hering et al. 2010; 3.5 h: present study), and on average they remained in the channel until water depth was lower than the depth occurring at the time of entry (Hering et al. 2010; present study). We found that subyearlings accessed these channels preferentially in the afternoon and at times did so against prevailing currents. The afternoon to early evening time frame of secondary channel entry coincided with the daily peak emergence rates of the aquatic insects that are commonly found in the diets of juvenile Chinook Salmon at Russian Island (Ramirez 2008) and reinforces the finding of a high mean instantaneous ration based on the stomach contents of subyearling Chinook Salmon sampled at Russian Island just before nightfall (Bottom et al. 2011). In a study by Rozas et al. (1988), fishes that used intertidal habitat for foraging were three times more likely to be present in secondary channels than in distributary channels. Therefore, it is highly probable that extended residency of subyearling Chinook Salmon in tidal wetlands is related to foraging behavior. We observed that individuals with an extended R_{MARSH} (≥15 d) increased in FL by 10–20 mm.

Prior to this study, individual growth of juvenile Chinook Salmon had not been directly measured in the Columbia River estuary. Rich (1920) tracked monthly mean lengths of Chinook Salmon from the Columbia River mouth to approximately rkm 261 and estimated a 0.44-mm/d rate of change in length for fish that were collected in the lower estuary. Using similar methods, we estimated length changes of 0.25 and 0.31 mm/d based on subyearling data reported by McCabe et al. (1986) and Roegner et al. (2012), respectively. However, as the above authors noted, changes in mean FL over time likely do not accurately represent growth for an estuarine population that is influenced by continuous immigration and emigration of individuals. Campbell (2010) examined changes in otolith growth increments of individual Chinook Salmon to estimate a mean daily growth rate of 0.41 mm/d (range = 0.11–0.67 mm/d) for fish that were sampled in the saline portion of the lower Columbia River estuary. Recent otolith-derived growth estimates reported by Goertler et al. (2016) for subyearling Chinook Salmon in the upper 130 km of the tidal freshwater estuary were slightly lower on average (0.23 mm/d) but were within the same range (0.11–0.43 mm/d) as the estimates from Campbell (2010). The relatively high estimated growth rate in our study (grand mean = 0.53 mm/d) may reflect improved performance among marsh-resident subyearlings compared with similarly sized juveniles collected in other nearshore and main-stem areas. Similar growth rates were measured for subyearling Chinook Salmon residing in the brackish intertidal wetlands of the Salmon River estuary (Hering 2009).

The present study is the first to measure habitat-specific residence time, movement, and growth of juvenile Chinook Salmon in the Columbia River estuary. Although R_{MARSH} was variable, many subyearlings resided in the marsh for much longer time frames than were previously reported from Columbia River estuarywide studies, and those longer residency periods resulted in substantial size increases. Channel-scale residency and movement patterns suggested that subyearlings exploit the foraging opportunities in tidal channels rather than passively moving through the habitat. This idea was reinforced by the fact that juvenile Chinook Salmon returned to tidal channels despite being forced to vacate during low tides, and they even moved into secondary channels against the tide. Our results clearly demonstrate that tidal freshwater habitats in the Columbia River estuary are important rearing and foraging areas for subyearling Chinook Salmon.

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