Patterns of Chinook salmon migration and residency in the Salmon River estuary (Oregon)

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Abstract

We examined variations in the juvenile life history of fall-spawning Chinook salmon, *Oncorhynchus tshawytscha*, for evidence of change in estuarine residency and migration patterns following the removal of dikes from 145 ha of former salt-marsh habitat in the Salmon River estuary (Oregon). Mark-recapture studies and abundance patterns in the estuary during 2000–2002 describe the following life-history types among Chinook salmon: (1) fry disperse throughout the estuary, and many move into restored tidal-marsh habitats in the early spring soon after emergence; (2) juveniles reside in freshwater for several months, enter the estuary in June or July, and remain for (a) a few weeks or (b) several months before entering the ocean; and (3) juveniles enter the ocean later in the fall after an extended period of rearing upriver and/or in the estuary. The absence of fry migrants in the estuary during spring and early summer in 1975–1977 — a period that precedes restoration of any of the diked marshes — and the extensive use of marsh habitats by fry and fingerlings April–July, 2000–2002 indicate that wetland restoration has increased estuarine rearing opportunities for juvenile Chinook salmon. Year-to-year patterns of estuarine rearing and abundance by juvenile salmon may be influenced by flood and drought conditions that affected adult spawner distribution and over-winter survival of salmon eggs. However, persistent changes in spawner distribution since 1975–1977, including the concentration of hatchery strays in the lower river, may account for the large proportion of fry that now disperse into the estuary soon after emergence in the spring. Although few of these earliest migrants survived to the river mouth, many fry and fingerlings from mid- and upper-basin spawning areas distributed throughout a greater portion of the estuary during the spring and summer and migrated to the ocean over a broader range of sizes and time periods than thirty years ago. The results suggest that wetland recovery has expanded life history variation in the Salmon River population by allowing greater expression of estuarine-resident behaviors.
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1. Introduction

Widespread decline of salmon (*Oncorhynchus* spp.) populations throughout the Pacific Northwest (Nehlsen et al., 1991) and the importance of tidal marshes as salmon rearing habitat (Levy and Northcote, 1982)

have created considerable interest in estuarine wetland restoration as a means of salmon recovery. Historical loss of estuarine wetlands in the region has been substantial, ranging from 50% to 90% among Oregon's largest estuaries and even higher among some industrialized estuaries in Washington (Simenstad et al., 1982; SOER Science Panel, 2000). In 1997, we initiated studies in Salmon River estuary (Oregon) to evaluate the effects of salt-marsh restoration on juveniles of fall-spawning

Chinook salmon (*Oncorhynchus tshawytscha*). Initial results indicated that young Chinook salmon utilized restored marsh habitats even soon after dikes were removed and intertidal channels became accessible (Cornwell et al., 2001; Gray et al., 2002). In 2000–2002, we expanded this research to evaluate patterns of downstream migration and duration of estuarine residency among juvenile migrants throughout the Salmon River basin.

Agricultural activities during the past 40 years have greatly modified the Salmon River estuary. In the early 1960s, construction of a network of earthen dikes and tide gates converted more than 250 ha (approximately 65%) of the original salt-marsh habitat to pasture land, confining most of the estuary to a narrow ribbon of main-river channel. Subsequently, a cumulative total 145 ha of shallow wetland habitat was returned to the estuary after three successive dike-removal projects were completed in 1978, 1987, and 1996 (Gray et al., 2002).

The loss and subsequent recovery of most tidal wetlands in Salmon River estuary could readily influence the variety of juvenile life histories expressed by the Chinook salmon population. Within populations, Chinook salmon exhibit considerable variation in juvenile life history, including different ages of migration and duration of freshwater and estuarine residency (e.g. Reimers, 1973; Carl and Healey, 1984; Healey, 1991). These variations may be linked to diverse habitat opportunities throughout a river basin and its estuary (e.g. Healey and Prince, 1995; Unwin and Glova, 1997). Many Chinook salmon rear in estuaries for weeks or months before migrating to sea (Reimers, 1973; Healey, 1982), and the smallest size classes (i.e. fry and fingerlings) typically occupy shallow, near-shore habitats, including salt marshes, tidal creeks, and intertidal flats (Levy and Northcote, 1982; Myers and Horton, 1982; Simenstad et al., 1982; Levings et al., 1986). The availability of estuarine wetlands in Salmon River could affect size-dependent migrations of juvenile salmon, particularly the dispersal of fry into the estuary soon after emerging from the gravel — a life-history pattern documented in many other Chinook salmon populations but not widely reported in Oregon (e.g. Rich, 1920; Congleton et al., 1981; Kjelson et al., 1982; Levy and Northcote, 1982; Healey, 1991).

Use of Salmon River estuary and its restored marshes by juvenile Chinook salmon also may depend on other factors upriver that can affect the time, size, and age of downstream migrants. One potential influence is a state fish hatchery, which has artificially reared Chinook and coho (*Oncorhynchus kisutch*) salmon since 1977, releasing them just above tide water on the main-stem Salmon River. Since the 1980s, approximately 200,000 juvenile coho and 200,000 juvenile Chinook salmon have been released annually in May and August, respectively. Artificial propagation may account for an apparent increase in the total number of Chinook spawners in Salmon River from approximately 1100 or fewer adults in 1975–1977 (Mullen, 1979) to more than 3000 adults in all but two years since 1994 (Oregon Department of Fish and Wildlife, unpublished data). Today, approximately 50–60% of the Chinook salmon that return to spawn naturally in Salmon River are from juveniles that had been released from the hatchery (Oregon Department of Fish and Wildlife, unpublished data).

Relatively few empirical studies have examined effects of hatchery programs on wild salmon populations (Brannon et al., 2004), particularly effects on patterns of juvenile migration and estuarine habitat use (e.g. Myers and Horton, 1982; Unwin and Glova, 1997). Many salmon life-history traits are under some degree of genetic control (e.g. Taylor, 1990; Hankin et al., 1993), and hatchery programs can affect multiple traits, including age at maturity and juvenile age at migration (Unwin and Glova, 1997). Moreover, variations in salmon life history, including duration of juvenile residency in the river and estuary, have been linked to geographically and genetically discrete subpopulations within a river basin (Carl and Healey, 1984). Thus, changes in adult distribution or genetic structure from the many hatchery strays that now spawn in Salmon River could alter estuarine life history traits in the population (Carl and Healey, 1984; Unwin and Glova, 1997).

Juvenile migrations to the estuary each year may be further influenced by hydrographic conditions in the Salmon River basin. Pulses in river flow, particularly during the spring soon after salmon emerge from the gravel, can affect downstream movement of fry (Healey, 1980; Kjelson et al., 1981). Furthermore, extreme floods that scour eggs from the gravel or drought conditions that allow spawning beds to dewater can cause significant egg mortality (Gangmark and Bakkala, 1960; Becker et al., 1982; Healey, 1991). Thus, interannual and daily fluctuations in river flow during Chinook salmon spawning, incubation, or emergence could affect patterns of juvenile abundance, downstream migration, and estuarine residency by the Salmon River population.

Because the phenotypic behavior of estuarine-rearing Chinook salmon may be linked to factors upriver as well as habitat opportunities within the estuary, life-history variations in the population must be understood at a river-basin scale. Yet few studies have characterized juvenile life histories of Chinook salmon throughout a river basin (Reimers, 1973) or traced the upriver origin of individuals with known estuarine residency patterns (Carl and Healey, 1984). Here we use both survey and mark-recapture techniques to (1) examine variations in the juvenile life history of Chinook salmon in the Salmon River and estuary; and (2) assess potential effects of river flow, spawner distribution, and salt-marsh restoration on patterns of juvenile salmon migration and freshwater and estuarine residency.

To evaluate potential life-history changes associated with the recovery of estuarine wetlands, we compare results of recent juvenile surveys in 2000—2002 — four to six years after the last marsh restoration project was completed — with results of a wild salmon survey conducted in 1975—1977 (Mullen, 1978, 1979) — 12 years after the marshes had been diked but immediately before adults from the first hatchery brood began returning to Salmon River. For this analysis, we define variations in the life history of juvenile Chinook salmon based on their duration of freshwater and estuarine residency, size and time of estuarine entry, and size and time of ocean entry. We hypothesize that, barring significant effects of the hatchery program on the behavior of naturally produced Chinook salmon, recovery of salt-marsh habitat should allow expression of a greater diversity of juvenile life histories in the estuary. Specifically, wetland habitat opportunity should increase the proportion of fry (juveniles 40 mm fork length (FL) to 60 mm FL) and fingerlings (61—90 mm FL) that rear in the estuary during spring and early summer.

2. Materials and methods

2.1. Study area

Salmon River estuary is a small drowned river on the north central Oregon coast approximately 6 km north of Lincoln City, Oregon (45°01′ N, 123°58′ W) (Fig. 1a,b). The watershed drains approximately 194 km² and forms an 800 ha estuary that extends 6.5 km from the mouth. River flows are highly seasonal and can change rapidly. Sustained low flows from 700 to 1400 L s⁻¹ often occur throughout late summer and early fall. Flows are an order of magnitude higher November through January with occasional brief (several-day) flood events that typically range from 25,000 to 150,000 L s⁻¹. Estuarine salinities vary widely with river flow. At the surface, fresh water extends downstream near the river mouth during winter and early spring while full-strength sea water encroaches up to 4 km upriver in late summer before the onset of fall rains.

Extensive tidal marshes account for roughly half the area of Salmon River estuary (Fig. 1b). Dike removal projects in 1978, 1987, and 1996 restored 22, 63, and 60 ha of salt marsh habitat, respectively. Vegetative and physical characteristics of restored and previously undiked marshes of Salmon River estuary are described by Gray et al. (2002).

2.2. Juvenile migration and residency

We established a mark and recapture program during 2000—2002 to monitor the downstream migration of juvenile salmon and the upriver origin of individuals in the estuary. Fish traps were placed immediately downstream of three principal Chinook salmon spawning areas to capture and mark juveniles (Fig. 1a). These include the upper main-stem Salmon River near Rkm 21.1 (Upper Salmon trap), lower Bear Creek just above its confluence with Salmon River at Rkm 11.6 (Bear Creek trap), and the lower main-stem Salmon River near the Salmon River Hatchery just above the head of tide at Rkm 7.9 (Lower Salmon trap).

We sampled salmonids at the Upper Salmon and Bear Creek sites with a 1 m and a 0.65 m inclined plane trap, respectively (McLemore et al., 1989). In 2000 we operated the upper two traps four days per week between mid-March and early (Upper Salmon) or late (Bear Cr.) June. Except during a few peak flood events, the upper two traps operated continuously (7 days per week) in 2001 and 2002 from mid- or late March until mid-June. By late June stream flows dropped, the traps could no longer operate effectively, and most juveniles had migrated out of the upper watershed and tributaries and into the main-stem Salmon River.

At the Lower Salmon site, we collected fish with a 1.5 m rotary screw trap (Thedinga et al., 1994). Beginning in mid-March the Lower Salmon trap was operated on average four days per week in 2000 and continuously (seven days per week) during 2001 and 2002, except during a few high-flow episodes that required trapping activity to be temporarily suspended. The trapping period for the lower trap extended until mid- or late July (end of June only in 2000) when main-stem river flows dropped to base levels.

Whereas the Upper Salmon and Bear Creek traps monitored downstream migrants from discrete spawning areas, the Lower Salmon trap collected juveniles from the lower main-stem spawning area as well as those from all other spawning areas in the basin, including Upper Salmon and Bear Creek. Because the Lower Salmon trap is located just above the head of tide, individuals captured at this site provide an indicator of the time and size of salmon entry into the estuary. Although a few small streams, including Deer Creek #1 and Salmon Creek, enter the main-stem Salmon River below this lowermost trap, these are not major spawning tributaries for Chinook salmon. We therefore assume production of juvenile Chinook salmon below the Lower Salmon trap is minimal.

We marked fish collected at each trapsite with acrylic paint (Liquitex® Concentrated Artist Color) using a Panjet™ needleless injector (Hart and Pitcher, 1969; Thedinga and Johnson, 1995). We injected the paint into one of three fin rays (anal, dorsal, or caudal) to represent the location (Upper Salmon, Bear Creek, Lower Salmon, respectively) of capture and marking for each individual. To indicate the approximate date of marking, we changed paint color weekly. We tested the
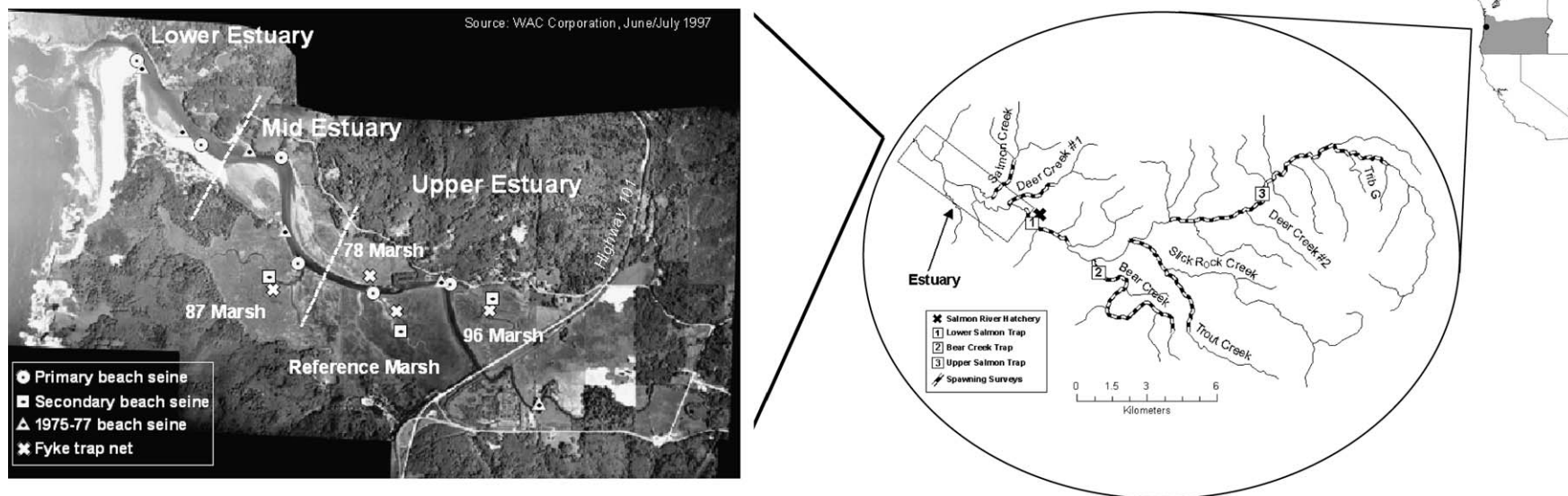
Fig. 1. Salmon River basin and estuary with locations of (a) downstream migrant traps and spawning survey areas; and (b) reference and restored estuarine marshes, 2000—2003 trap-net and beach-seine sites, and 1975—1977 beach-seine stations. Restored marshes are designated by the year of dike removal: 78 marsh (1978), 87 marsh (1987), and 96 marsh (1996).

longevity of the marking technique in the laboratory for 14 colors of acrylic paint. Although all paint colors faded with time throughout the test period, faint marks were discernible for most colors for 3 months after marking. During the field studies, we excluded the most poorly performing colors from the marking program.

We estimated weekly trap efficiencies of salmon by measuring the rate of recapture of at least 25 individuals of each age class marked daily and released above each trap. We calculated the total number of downstream migrants each week as the total catch for the week divided by the estimated trap efficiency. Total annual population size (N) and variance at each trap were estimated following procedures in Thedinga et al. (1994). To compare migration patterns and abundances with the 2001 and 2002 results, population estimates for 2000 were extrapolated by applying an average weekly catch and efficiency to days when the traps did not operate.

In the estuary, we monitored salmon abundance and size distribution and recaptured individuals that were marked upriver using a 38×2.75 m beach seine, 1.3 to 1.9 cm in the wings, and a 1.0 cm (stretched) mesh in the bottom of the bag. Primary beach-seining sites along the main channel of the estuary were sampled approximately biweekly during 2000 and 2001 from March through October or November (Fig. 1b). Secondary beach-seining sites within the Salmon River marshes were sampled approximately biweekly or as tides permitted access to shallow marsh channels. In 2002, we increased sampling frequency at the primary beach-seining sites to once per week in an effort to increase the number of marked fish recaptured in the estuary.

To further monitor salmon abundance in shallow tidal marshes, we also established trapping sites on selected secondary channels of the restored and previously undiked marshes (Fig. 1b). From March or April through August, these sites were sampled monthly with a 0.6 cm fyke trap net and live box (Gray et al., 2002) that was set across each channel at high slack tide. Fish were collected until the channel drained at low tide. Trap efficiency was determined by placing marked juvenile Chinook above the fyke net site. Abundance was expressed as the total catch adjusted for trap efficiency at each marsh site.

From 1975 through 1977, the Oregon Department of Fish and Wildlife (ODFW) surveyed abundance and distribution of wild salmonids throughout the Salmon River basin to provide population and life-history information needed to operate the new hatchery (Mullen, 1978, 1979). ODFW sampled biweekly at two sites each in the Lower and Middle Estuary zones (Fig. 1b) using a beach seine of identical length (38 m) and similar mesh size (1.3 cm) as that used during our 2000–2002 survey. During 1977 two additional seining sites also were sampled in the Upper Estuary zone with a smaller beach seine (23×1.2 m, 1 cm mesh) from April through June and with the standard 38 m beach seine, July through October. To compare abundance patterns during the 1975–1977 and 2000–2002 surveys, we calculated biweekly catch per seine haul from the total catch at all stations sampled within each of the three estuary zones (Fig. 1b).

2.3. Spawner surveys

Since 1986, the Oregon Department of Fish and Wildlife (ODFW) has estimated annual escapement to Salmon River by collecting and tagging adult Chinook salmon at the hatchery fish ladder, releasing them above the hatchery, and surveying upriver spawning grounds for tagged and untagged fish. We analyzed the ODFW survey data to compare abundance, distribution, timing, and relative proportions of hatchery and wild Chinook salmon on the spawning grounds for the 1999, 2000, and 2001 return years. These broods correspond to all juveniles subsequently sampled in 2000, 2001, and 2002, respectively.

ODFW surveyed 24.9 km of the primary main-stem and tributary spawning habitat weekly in Salmon River from October through January, 1999–2001 (Fig. 1a). An additional 14.0 km was surveyed less frequently as time allowed. Surveyors noted the total number of live and dead adults, the presence or absence of tags (for population estimates), and the wild or hatchery origin of each fish as determined by the presence or absence of an adipose-fin clip. Analyses of spawning distribution and timing presented herein are based on carcass counts only (i.e. no counts of live fish included). ODFW used the Chapman version of the Peterson mark-recapture formula (Ricker, 1975) to estimate the population size of Chinook salmon that migrated upstream from the Salmon River Hatchery. Details of adult surveys and population estimates at Salmon River were described by Boechler and Jacobs (1987).

We compared spawning survey results from 1999 to 2001 with those reported by Mullen (1979) for 1975–1977. Mullen (1979) estimated the abundance of adult Chinook in 1976, and mapped spawning distribution in 1975–1977. Survey methods and areas were similar to those used since 1986.

3. Results

3.1. Historical and contemporary river flow

Flows in Salmon River in 1975–1977 and during the 2000–2002 salmon studies reveal similar seasonal and interannual patterns. From October 1974 through September 1976, flows followed a typical pattern (Fig. 2) for coastal Oregon watersheds with several high flow
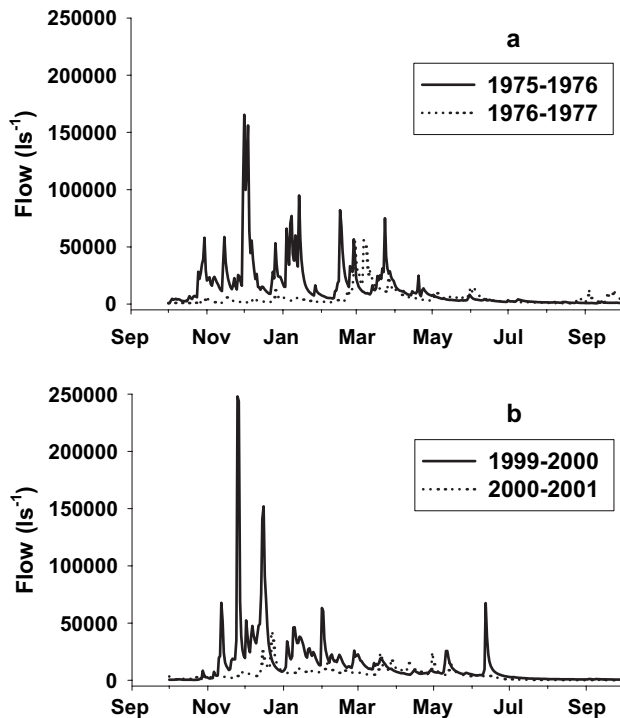
Fig. 2. Estimated river flows (L s^{-1}) for: (a) Salmon River near Otis, Oregon, October 1975–September 1977, and (b) October 1999–September 2001. Actual flows in Salmon River were used for 1 April 2001–21 June 2001. For other periods in 1999–2001 flows were estimated from measurements in the Siletz River.

events beginning in the late fall, a brief maximum spike each December between 165,000 and 180,000 L s^{-1}, and a gradual decline to minimum levels during the summer and fall following decreasing rainfall in the spring. A sustained drought occurred during the 1976–1977 water year following the failure of winter rains and only a few brief increases in March to approximately 55,000 L s^{-1} (Fig. 2).

Operation of the flow gauge in Salmon River was discontinued in 1994 except for additional measurements for the period 1 April–21 June in 2001 and in 2002. Although absolute flows were higher, the seasonal patterns for the nearby Siletz River were almost identical to Salmon River throughout the 1974–1977 water years ($R^2 = 0.91$), and 1990–1993 ($R^2 = 0.95$), indicating that measurements at the Siletz River gauging station provided a valid index of seasonal and daily flows in Salmon River for the periods not measured during 1999–2002. Siletz River flows indicate that Salmon River probably experienced seasonal patterns during the 1999–2000 and 2001–2002 water years similar to those of 1974–1975 and 1975–1976 (Fig. 2). One exception was the substantial flood in western Oregon on 25 November, 1999, which produced estimated Salmon River flows (based on the correlation with the Siletz River gauge) of nearly 248,000 L s^{-1}, much higher than the maximum flow (165,439 L s^{-1})

recorded during the 1974–1976 period on 7 December, 1975. During this event, high water inundated rearing ponds at the Salmon River Hatchery and allowed the escape of thousands of steelhead (*Oncorhynchus mykiss*) held at the hatchery. In contrast to the 1999 water year, the Salmon River basin experienced a severe drought during 2000–2001, similar to the 1976–1977 drought, except flow increases were negligible even during the spring 2001. The flow conditions represented during the two survey periods depict surprisingly similar examples of seasonal and annual variation for comparing fish responses before and after marsh restoration (Fig. 2).

3.2. Downstream migration

An estimated 750,686 and 486,372 juvenile Chinook salmon migrated past the Lower Salmon trap and entered Salmon River estuary in 2001 and 2002, respectively (Table 1). During these years, estimated abundance was greatest at the Lower Salmon site, which provided an integrated sample of migrants from all tributary and main-stem reaches above RKm 8 (Fig. 3). In 2000, however, estimated abundance at the Lower Salmon trap was only 83,780, less than a quarter of the population estimate for the Upper Salmon trap (362,617) and not much greater than estimates for the Bear Creek site (74,985). The 2000 estimates are extrapolated from four days of trapping each week. Nonetheless, daily catches at the Lower Salmon site in 2000 were much less than in 2001 and 2002. Furthermore, 2000 estimates probably represent maximum values because marked individuals used for weekly efficiency tests could have migrated downstream when the traps were not operating, causing us to underestimate efficiencies and inflate population estimates.

Peak migrations at the three tributary and main-stem trap locations occurred during early spring in all three years and consisted of newly emerged fry (average size ~40 mm FL) (Fig. 3). However, only a slight increase

Table 1
Population estimates for juvenile Chinook salmon sampled at three migrant traps in the Salmon River basin, 2000–2002

Migrant year	Trap location	Average trap efficiency (%)	Population estimate (±95% CI)
2000[a]	Upper Salmon R.	1.6	362,617 ± 33,517
	Bear Cr.	7.7	74,985 ± 3321
	Lower Salmon	3.5	83,780 ± 6482
2001	Upper Salmon R.	4.0	268,967 ± 8271
	Bear Cr.	17.0	103,253 ± 1282
	Lower Salmon R.	5.4	750,686 ± 12,821
2002	Upper Salmon R.	9.0	231,318 ± 6151
	Bear Cr.	12.5	240,176 ± 5112
	Lower Salmon R.	6.5	486,372 ± 10,075

[a] Traps operated only 4 days wk^{-1} in 2000. Population estimates were extrapolated from weekly mean catch and trap efficiencies applied to days when the traps were not operating.
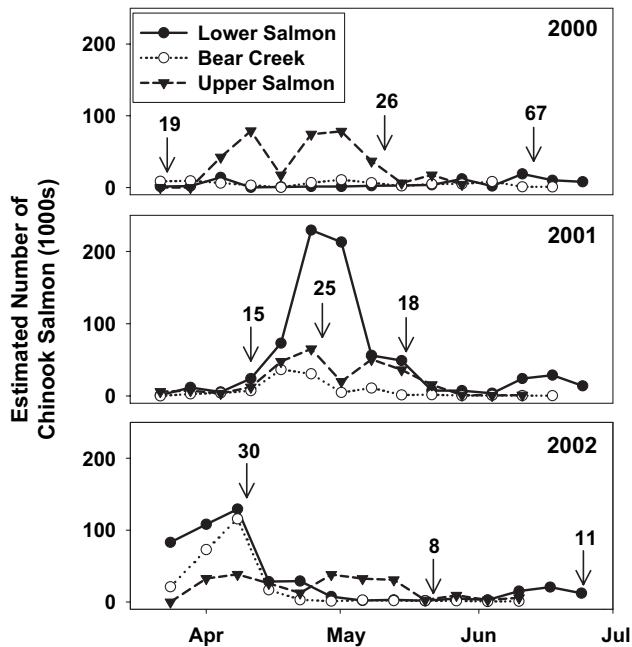
Fig. 3. Downstream migration of juvenile Chinook salmon at Lower Salmon, Bear Creek, and Upper Salmon trap sites in Salmon River during 2000, 2001, and 2002. In 2000, the traps were operated for an average of 4 days wk^{-1}. Estimates for 2000 are extrapolated by applying mean trap efficiencies and catches each week for days when the traps were not operating. Peak flow periods during downstream migration are designated by arrows with numerals indicating thousands of L s^{-1}.

was evident at the Lower Salmon trap during spring 2000. The initial fry migration occurred between late March and early April in 2000 and 2002 but was delayed by several weeks (late April to early May) in 2001. The timing of peak fry migration in the spring 2001 and 2002 coincided with peak flow events in Salmon River > 25,000 L s^{-1} (Fig. 3).

During early or mid-May in all three sampling years, a second downstream-migration peak occurred at the Upper Salmon trap that was unrelated to peak flow events. Smaller and later migration peaks also subsequently occurred downstream at the Lower Salmon trap in June and/or July (Fig. 3). These later migrations consisted of large fry and fingerling (∼ 55 mm FL or greater) Chinook salmon that had reared in the main river for several months before passing the Lower Salmon trap and entering tidewater. Increased beach-seine catches in the Upper Estuary zone during each summer or early fall indicate that some juvenile Chinook salmon continued to enter the estuary after the Lower Salmon trap was removed in late July (Fig. 4).

3.3. Historical and contemporary use of the estuary

Beach seining results in 2000, 2001, and 2002 indicate that Chinook fry (∼ 40 mm FL) moved past the Lower

Salmon trap into tidal freshwater and were observed in the Upper and Mid-Estuary zones by early April (Fig. 4). At about the same time, many fry also appeared in small secondary marsh channels, where trap-net catches peaked in April 2001 or May 2002 but showed no spring peak in 2000 (Fig. 5). Abundance of juvenile Chinook salmon in the marsh channels averaged 400 to 600 fish on a tidal cycle in spring 2001 and 2002, higher than the 100 fish in 2000 (Fig. 5). Although our monthly sampling frequency could have missed the timing of peak marsh abundance, this seems unlikely: the average abundance trends for marshes in the Upper and Mid-estuary zone are consistent with observed patterns of fish movement past the Lower Salmon trap and into upper tidewater (Fig. 3). Moreover, despite the late start of sampling in 2002, the abundance peak in late April is also consistent with the abundance pattern observed at bi-weekly beach seining sites in the Upper and Mid-estuary zones (Fig. 4). Calibrated by area of unvegetated marsh channel, peak spring abundance was less than 0.02 fish m^{-2} in 2000 compared with 0.07 m^{-2} in 2001 and 0.11 m^{-2} in 2002. Juvenile Chinook were observed in marsh habitats from April through August and in the main channel habitats from April through October.

Juvenile Chinook arrived in the Mid-estuary zone within two weeks of their arrival in the upper estuary (Fig. 4). Chinook were present in the Mid-estuary from May through October, peaking at a CPUE of 40–60 fish in July 2001 and August 2000 and 2002. Juveniles began appearing in the Lower Estuary zone near the river mouth by early June 2000–2002 (Fig. 4), and were observed through the end of sampling in November. Peak catch per unit effort (CPUE) occurred in the Lower Estuary zone during July and August in 2000 and 2002 with sustained peak levels near 40 CPUE and a relatively brief but higher peak near 100 CPUE in August 2002. An extended period of high abundance was evident in the lower estuary in 2001 from June through October, at 20–40 CPUE.

Mean lengths of juvenile salmon during 2000–2002 generally increased through time and with distance downstream from the head of tide (Lower Salmon trap) to the estuary mouth (Fig. 6). One exception to this trend was a rapid increase in the average length of migrants at the Lower Salmon trap in late June to early July, which exceeded the mean length of juvenile Chinook in the Upper Estuary zone. This pattern generally coincided with small, late outmigration peaks of large fry and fingerlings (> 55 mm FL) at the Lower Salmon trap in June and July each year (Fig. 3).

In 2001, recently emerged fry (approx. 40 mm FL) continued to migrate past the Lower Salmon trap through mid-May, and mean lengths remained slightly smaller throughout the spring than during 2000 or 2002 (Fig. 6). For example, mean length of juvenile Chinook reached 60mm FL at the Lower Salmon trap by late
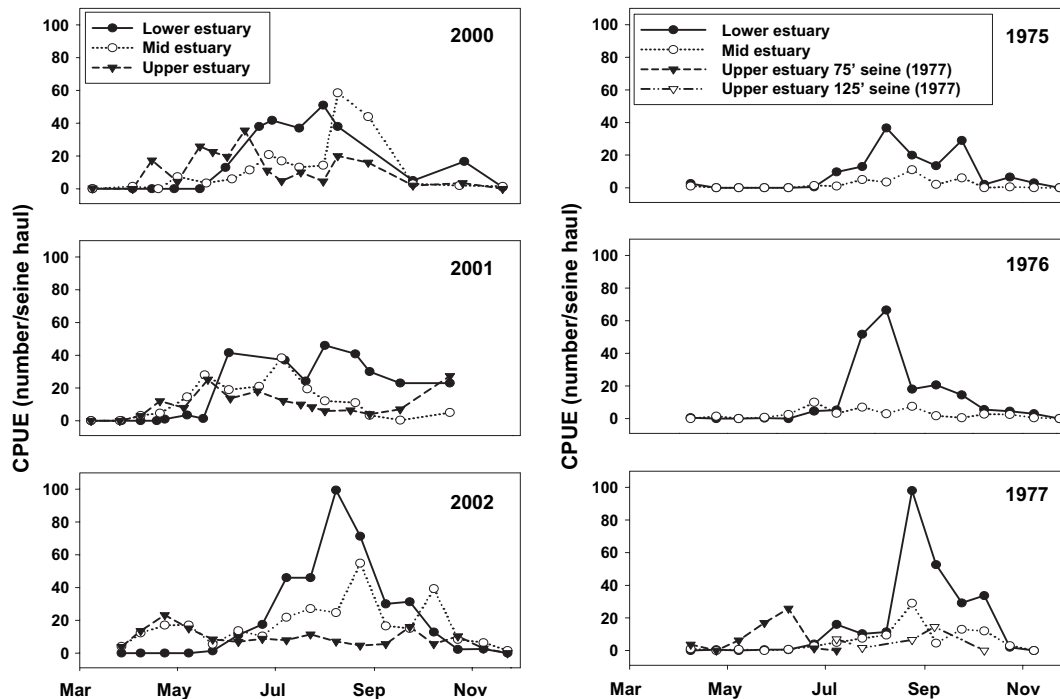
Fig. 4. CPUE for Chinook salmon at beach-seining sites in the Upper, Mid-, and Lower Estuary zones during 2000–2002 and 1975–1977.

May in 2000 and 2002 but not until a month later in 2001. Fish were on average slightly smaller in the estuary throughout 2001. Mean lengths near the end of the estuarine rearing period (mid-October) in 2001 were 15 mm and 9 mm smaller than in 2000 and 2002, respectively ($P < 0.05$).

During the 1975–1977 juvenile surveys, Chinook salmon abundance in the estuary increased later in the summer and for a shorter duration than in 2000–2002 (Fig. 4). A brief pulse of fry (< 50 mm FL) occurred in the Upper Estuary in June 1977, the only year Mullen (1979) sampled fish in this estuary zone (Figs. 4 and 5). Yet very few juvenile Chinook salmon were caught in the Mid- or Lower Estuary zones before July during any of the 1975–1977 surveys. Catches in the Mid-Estuary zone remained low most months except for brief pulses
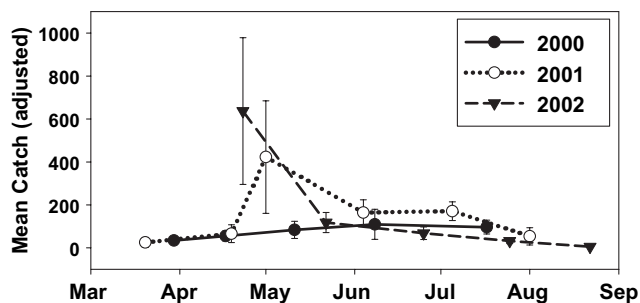

Fig. 5. Mean total catch and standard error of juvenile chinook salmon (adjusted for trap efficiency) in Salmon River marsh habitats (96 marsh, reference marsh, and 87 marsh) during each of three years, 2000–2002.

(less than 25 CPUE) in August and October 1977. As in 2000–2002, CPUE was greater in the Lower Estuary than in the other zones. Annual peak CPUE in the Lower Estuary occurred in early August and ranged from 37 to 98 during the three years. Smaller secondary peaks also were evident in the Lower Estuary zone each fall during September or October, a pattern similar to the fall peaks observed in 2000–2002 (Fig. 4). As in 2000 and 2002, the average length of Chinook at ocean entry in September and October of 1975–1977 was greater than 110 mm FL (Fig. 6).

3.4. Travel times, residency, and growth

Although a few individuals arrived within a week or two after marking regardless of marking location, travel times to Salmon River estuary in 2001–2002 generally increased with distance upriver (Fig. 7a,b). Median travel time from Upper Salmon was approximately eight weeks, compared with four weeks from Bear Creek and two to three weeks from the Lower Salmon trap.

We recaptured at the Lower Salmon trap 12 individuals in 2001 and 15 individuals in 2002 that were previously marked at the Upper Salmon trap. These recaptures yield mean travel rates from the upper river to the head of tide of approximately 0.26 ± 0.81 (95% CI) km day^{-1} in 2001 and 0.36 ± 0.59 (95% CI) km day^{-1} in 2002. Whereas recaptured individuals at the Lower Salmon trap in 2001 had been marked throughout an extended period from April 2 to June 4, recaptures from Upper Salmon in 2002 were from late migrating groups
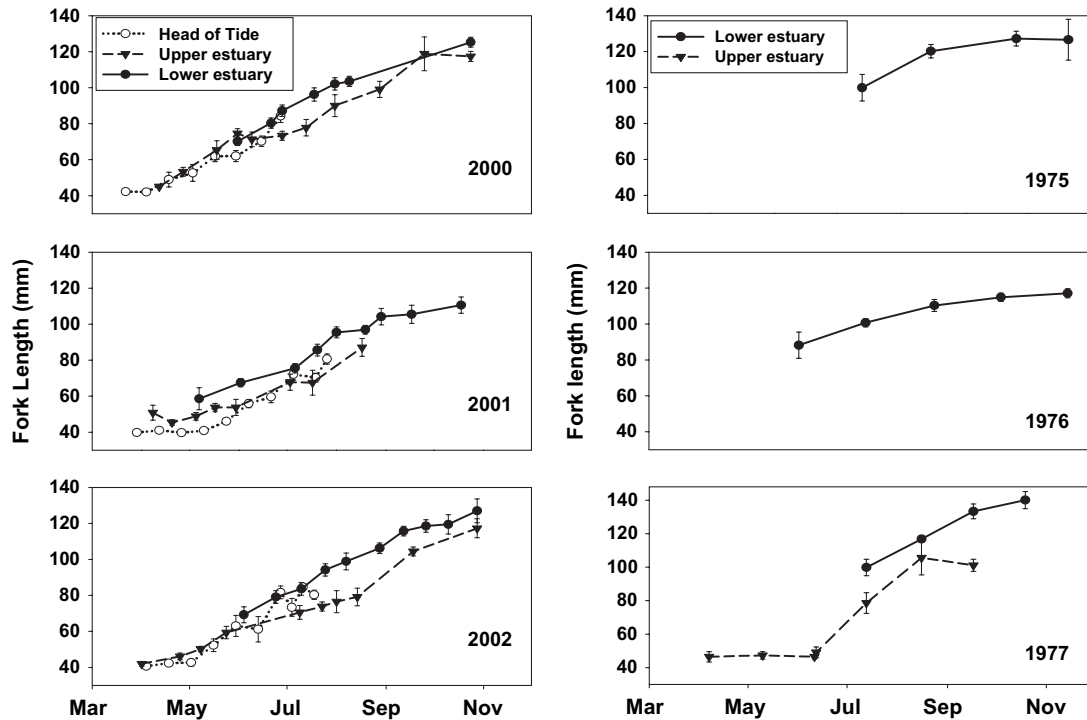
Fig. 6. Mean fork length (and 95% CI) of juvenile Chinook salmon captured at the Lower Salmon trap and in Upper Estuary and Lower Estuary zones during 2000–2002 and 1975–1977.

marked primarily during late May through June 10. The median travel time during 2001 and 2002 from the upper Salmon River trap was just over five weeks to the lower Salmon River trap although 25% of the fish spent 7–12 weeks traveling downstream (Fig. 7a). The majority of fish (83%) migrating past the Bear Creek trap took less than two weeks to reach the lower Salmon River trap (Fig. 7a).

Juvenile migration from the Lower Salmon trap to the Upper and Mid-estuary zones was relatively rapid, averaging about two weeks (Fig. 7b). Fish lingered for somewhat longer periods before moving into the Lower Estuary zone. Median estuarine residence time for individuals recaptured in the Lower Estuary zone was approximately five weeks. However, as many as 20% of the fish marked at Lower Salmon had resided in the estuary for nine weeks or more at the time of recapture in the Lower Estuary zone. A single individual marked the first week of May 2002 was recaptured 17 weeks later (28 August) in the Lower Estuary zone.

Total length of estuarine residence was independent of the date of marking (Fig. 8). We recaptured only a few individuals <60 mm fork length at the mouth of the estuary, and with one exception, none that had been marked before early June (Fig. 8). The largest marked individuals were recaptured in the Lower Estuary zone in late summer and early fall and had resided in the estuary for several months.

3.5. Spawner abundance and distribution

Estimated adult escapement to Salmon River increased during recent spawning surveys from 1973 ± 397 (95% CI) in 1999 to 2688 ± 431 (95% CI) in 2000 and 3134 ± 445 (95% CI) in 2001. Smaller adult population estimates are reflected in lower average carcass counts for most spawning survey reaches in 1999 compared with those in 2000 and 2001 (Fig. 9). Primary spawning areas in all three years were in the main-stem Salmon River above the hatchery, in tributaries in the central part of the watershed (Bear, Slick Rock, and Trout Creeks), and in the upper watershed above Deer Creek #2 (Fig. 1). In all three years, carcass counts were highest in reaches near or just above the Salmon River Hatchery from RKm 8 to 12. Relatively high counts were also consistently found in the upper Salmon River from RKm 24 to 26 (Fig. 9).

A consistent geographic gradient in the ratio of hatchery spawners to wild fish was evident in all three years (Fig. 9). In river reaches just above the Salmon River Hatchery, the total number of hatchery spawners was four to five times greater than that of wild fish; in mid-basin tributaries near RKm 13 and 14 (Slick Rock Creek/Trout Creek) the ratio was approximately equal; and in the upper Salmon River, wild fish were two to four times more abundant than hatchery spawners. For all years combined, the upper Salmon River had
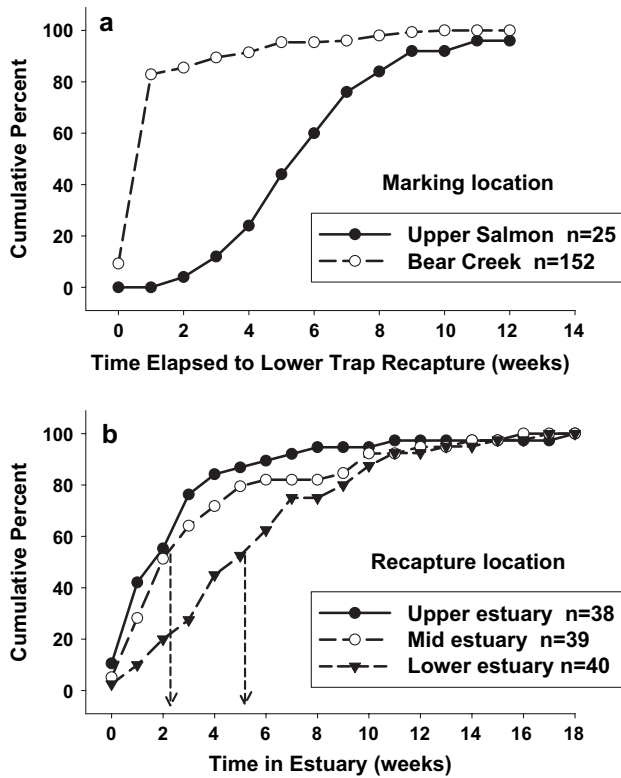
Fig. 7. Cumulative percent curves for travel rates/residence times of juvenile Chinook salmon (a) from Upper Salmon and Bear Creek traps to the Lower Salmon trap near head of tide, and (b) from Lower Salmon trap to Upper, Mid-, and Lower Estuary zones in 2001 and 2002. Travel rates/residence times are approximated by the weeks elapsed from marking to recapture within each estuary zone. Median residence time is estimated by the time required to account for 50% of all recaptures from each marking location.

significantly fewer hatchery spawners than the lower Salmon River and mid-basin tributaries ($P < 0.05$).

While most salmon spawned from late October through November in 1999 and 2001, a protracted
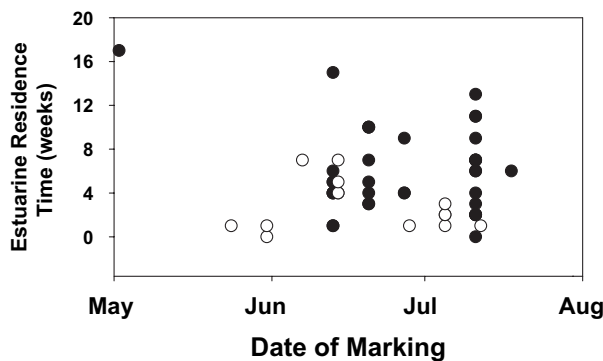

Fig. 8. Comparison of estuarine residence times (weeks) in 2001 (open circles) and 2002 (filled circles) with date of marking. Because no fish were marked upriver after July, we have no measure of residence times for later entrants to the estuary. Residence times are estimated as the time elapsed between the week of marking at Lower Salmon trap and the week of recapture at the lowermost seining site near the estuary mouth.
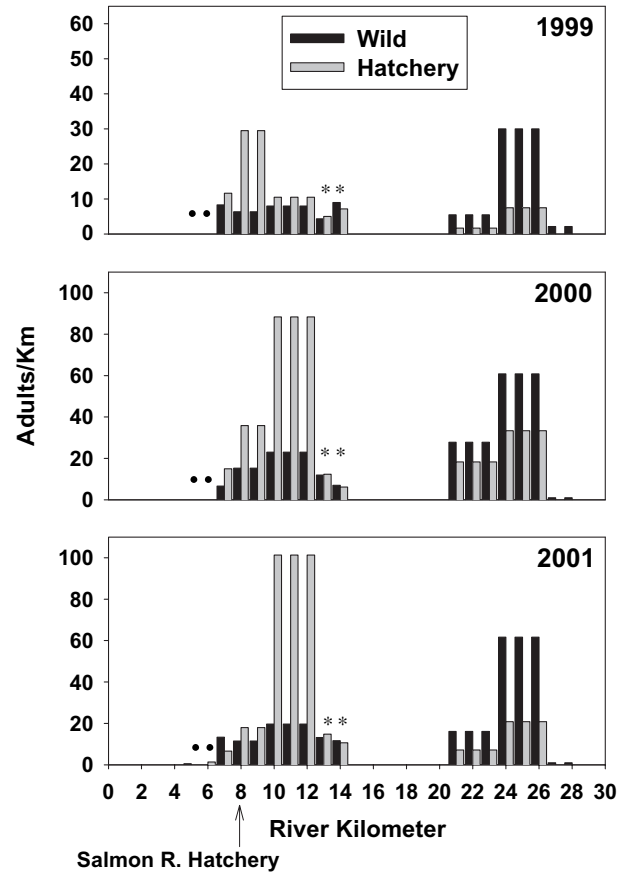

Fig. 9. Density of hatchery and wild Chinook salmon carcasses on the Salmon River spawning grounds during the 1999, 2000, and 2001 return years. The distribution of spawner densities along the main-stem Salmon River are depicted as mean carcass counts plotted for every 1 km surveyed in each reach. Results for tributary surveys are depicted for the river mile where each stream intersects the main-stem Salmon River. A single average spawner density is applied to each of two tributaries below RKm 7 (●), Salmon Creek (4 km survey reach) and Deer Creek #1 (3.8 km reach). A single average is also applied to each of two mid-basin tributaries (*), Bear Creek (5.3 km reach), and Slick Rock/Trout Creeks (6.7 km reach).

spawning period during the 2000 drought extended throughout December and into January (Fig. 10). Time of spawning generally delayed with distance upstream, beginning in lower Salmon River, extending into the mid-basin tributaries, and, finally, into the upper main stem. Despite greater overlap in spawning times among regions in 1999 and 2001 than in 2000, the distribution for all three years was skewed toward the earliest spawners, which were concentrated in the lower river near Salmon River Hatchery.

Composition, abundance, and distribution of the spawning adults in 1975–1977 had a different pattern from that in 1999–2001 (Mullen, 1979). All spawning fish were wild origin as adults from the first hatchery brood had not yet returned to Salmon River. The population estimate for 1976 was 1127 fish, but the number of tagged and recaptured adults on the spawning
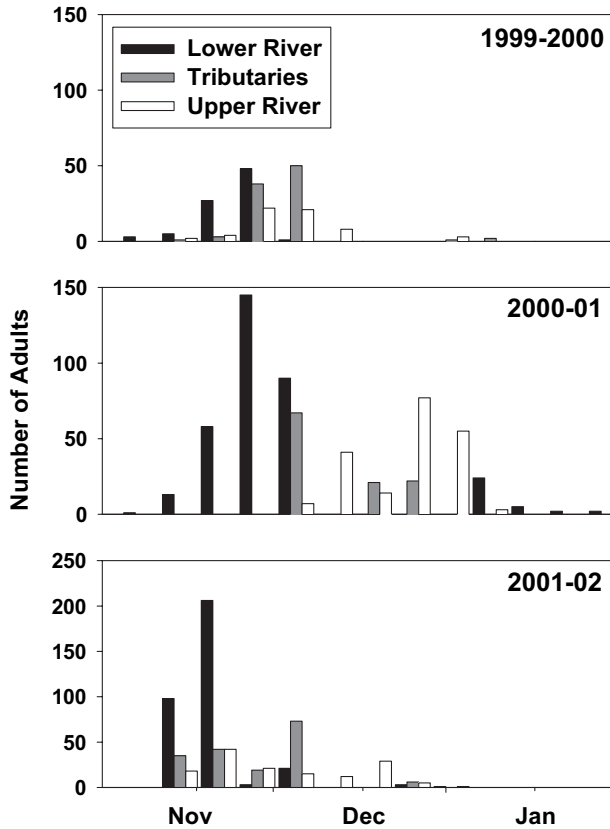
Fig. 10. Time of spawning of Chinook salmon in Salmon River in 1999, 2000, and 2001. Spawning times depicted as total carcass counts during each survey date in each of three major areas: lower main stem (Salmon River Hatchery at RKm 8 to RKm 13), upper main stem (above Rkm 20), and tributary streams (between RKm 6 and RKm14).

grounds was too low to estimate absolute abundances in 1975 and 1977. Mullen (1979) reported that spawning was concentrated in the mid-basin tributaries and upper basin. However, survey data do not allow analysis of spawning distribution by survey reach as shown for 1999–2001 (Fig. 9). In 1976 spawning also was observed near the hatchery site and in the main-stem river, when

drought conditions and low water levels prevented adult Chinook from moving upstream into the smaller tributaries until late fall (Mullen, 1979). Spawning during 1976–1977 extended from mid-October through mid-January, but peaked in November.

4. Discussion

Our results are consistent with the hypothesis that restored access to tidal wetlands has increased estuarine rearing opportunity and life-history variation of juvenile Chinook salmon in the Salmon River basin. While in the mid-1970s, fry rarely entered the estuary and did not extend below its uppermost zone (Mullen, 1979), fry and fingerling migrants were abundant throughout the Upper and Mid-Estuary zones from April through June 2000–2002. Many of these fish dispersed into formerly inaccessible marsh habitats within days or weeks of emergence. The relative absence of Chinook salmon in the Mid-Estuary zone of any size throughout the spring and early summer 1975–1977 and their appearance in this region during the same periods in 2000–2002 likely reflect expanded estuarine rearing opportunity following the removal of dikes from 82 ha and 63 ha of tidal wetland in the upper and mid estuary zones, respectively. Today, juvenile salmon occupy all estuary zones for a longer duration and appear at the river mouth earlier in the summer at smaller average sizes than 30 years ago, when the potential rearing area of the estuary was much smaller.

Since the dikes were removed from estuarine marshes, estuarine-resident life histories have become more prominent and resemble patterns observed in a number of other Northwest rivers, including the small Sixes River watershed and estuary on the southern Oregon coast (Table 2) (Reimers, 1973). The most prevalent life histories in 2000–2002 consisted of juveniles that emigrated from riverine habitats by early summer to rear in the estuary for several weeks or months (Types 2

Table 2
Juvenile life histories and relative abundances of Chinook salmon in Salmon River basin compared with five types identified in Sixes River, Oregon (Reimers, 1973)

Life history type	Description	Rank abundance Sixes River estuary	Relative abundance Salmon River estuary
1	Emergent fry to ocean within weeks (Fry migrant)	5	Absent
1a	Emergent fry to estuary for extended rearing (Early subyearling estuarine smolt)	Absent	Fry abundant but survival uncertain
2	Freshwater rearing until early summer, brief estuarine rearing before ocean entry (Early subyearling riverine smolt)	1	Abundant July/August
3	Freshwater rearing until early summer, estuary rearing through late summer (Late subyearling estuarine smolt)	2	Abundant August/September
4	Freshwater rearing until autumn then immediate ocean entry (Late subyearling riverine smolt)	3	Common in September/October?
5	Freshwater rearing for full year, then ocean entry second spring (Yearling riverine smolt)	4	Rare or absent

and 3, Table 2). This differs from the predominant riverine pattern observed during the 1970s, when most Salmon River juveniles remained in fresh water until July or August and emigrated from the estuary after a relatively brief period of late-summer rearing (Mullen, 1979). In 1975–1977 and 2000–2002, we also found evidence of a group of late (fall) outmigrants from the estuary, similar to the pattern of late riverine migrants (Type 4, Table 2) described in Sixes River (Reimers, 1973). Since we did not track downstream movements at the Lower Salmon trap after July, however, we cannot be certain whether these individuals had previously reared in the river, the estuary, or both environments. Rare or absent from Salmon River estuary were yearling migrants (Type 5, Table 2), which reside in many other Northwest rivers until their second spring (Rich, 1920; Reimers, 1973; Carl and Healey, 1984). This result is not surprising because, in the region south of 56°N, the yearling life-history pattern occurs primarily in large rivers (Healey, 1991).

The greatest proportion of the Salmon River migrants in 2001-02 entered the upper estuary as fry before mid-May. Simultaneous abundance peaks at all three Salmon River traps in early and late April of 2002 and 2001, respectively (Fig. 3) indicate that estuarine entry early in the spring coincided with a basin-wide dispersal soon after fry emergence (i.e. at sizes near 40 mm). A similar dispersal has been reported among many Chinook salmon populations, and may be a mechanism to distribute fry among available rearing habitats (Reimers, 1973; Healey, 1980, 1991). Although not widely reported in Oregon south of the Columbia River (Rich, 1920; Reimers, 1973; Myers and Horton, 1982), emergent fry are among the most abundant migrants to many Pacific Coast estuaries (Healey, 1991), where they often reside in shallow, nearshore habitats, including salt marshes and tidal creeks (Levy and Northcote, 1982; Simenstad et al., 1982; Levings et al., 1986). Although it has been suggested that early fry swept into estuaries represent those that are surplus to the carrying capacity of riverine rearing habitats (Lister and Genoe, 1970), Healey (1991) concludes that the fry-migrant pattern characteristic of many river basins is likely an adaptive response to productive estuarine nursery areas.

The factors determining whether fry migrate to the estuary or remain upriver are uncertain (Healey, 1991). Both pulses in river flow (Healey, 1980; Kjelson et al., 1981) and social interactions or density-dependent mechanisms (Reimers, 1968) have been suggested as potential causes for downstream displacement of fry. We found little evidence that changes in river flow explain the appearance of Chinook fry in Salmon River estuary in recent years. Although peak fry dispersal in Salmon River in 2001 and 2002 coincided with spring freshets between 25,000 and 30,000 L s^{-1}, few fry entered the estuary in 1975–1977 during similar or higher spring flow events. Moreover, a second migration peak past the Upper Salmon trap each May in 2000–2002 was not associated with flow pulses.

It is possible that increased concentrations of hatchery adults in the lower river may have increased density-dependent interactions since the 1970s and contributed to the arrival of emergent fry in the estuary in April 2001 and 2002. Studies in stream tanks suggest that agnostic behavior by a few dominant individuals can stimulate downstream movement by subordinate Chinook salmon fry (Reimers, 1968). Even modest movement from the lower Salmon River spawning area would have placed fry in the estuary due to its close proximity to tidewater.

Extreme winter-flow conditions in the Salmon River basin may influence interannual patterns of downstream migration and estuarine habitat use by juvenile salmon. For example, the 2000–2001 drought delayed upstream movement of adults and created a bimodal spawning distribution of early (October–November) lower-river and late (November–January) upper-river spawners (Fig. 10). This distribution, in turn, may explain the relatively late migration (through early May) of recently emerged fry past the lower Salmon River trap in 2001 (Figs. 3 and 6). On the other hand, the 25 November, 1999 flood probably caused considerable mortality of salmon eggs deposited during October and November in the lower river and may account for the failure of emergent fry to appear at the Bear Creek and Lower Salmon traps during April 2000. The relatively few adults that spawned after the November flood were distributed in middle tributaries and in the upper main stem (Fig. 10), which may explain why an early (April) migration peak was still evident at the Upper Salmon trap (Fig. 3).

Downstream movement and time of estuarine entry by juvenile Chinook salmon may not simply result from physical or biological displacement but, in part, could be genetically determined. Many life-history variations in salmon populations have been demonstrated experimentally to be under some degree of genetic control, including time of spawning and rate of egg and larval development (Beacham and Murray, 1987), juvenile growth rate, and age of seaward migration (Carl and Healey, 1984; Taylor, 1990). Moreover, genetic variation in Chinook salmon within some river basins has been linked to the geographic structure of spawning subpopulations. In the Nanaimo River estuary, for example, juveniles from different spawning subpopulations in geographically distinct areas of the basin exhibited differences in age of migration, body morphology, and genetic characteristics (Carl and Healey, 1984). We observed some life history variation among the major spawning areas in Salmon River that may or may not reflect genetic differences, including the later

spawning period for adults in the upper than the lower river (Fig. 10), and the extended fingerling migration from upper Salmon River weeks after the initial (April) fry dispersal, a pattern which was rare or absent at the Bear Creek site (Fig. 3).

Whether or not the juvenile life history patterns in Salmon River are genetically programmed, the timing of migrant peaks at each Salmon River trap (Fig. 3) and travel rate estimates from various river locations (Fig. 7a,b) suggest that distinct patterns of freshwater and estuarine residency may be associated with different spawning subareas of the basin. For example, salmon from middle tributary and lower main-stem spawning areas most likely accounted for the early build up of recently emerged fry in the Salmon River marshes during April 2001 and 2002 (Fig. 5). Average travel time from Bear Creek to the Lower Salmon trap was only a week or two, and most fry migrants from the lower main-stem spawning area (just above the trap) could have entered tidewater within days of emergence (Fig. 7a,b). In addition, the failure of emergent fry to pass the Bear Creek and Lower Salmon traps in April 2000 (Fig. 3) and their low abundance in the estuarine marshes during the same period (Fig. 5) offers further evidence that lower main-stem and tributary spawners may be the primary sources of early fry migrants to the estuary.

Because estimated travel times from the Upper Salmon trap to the Upper Estuary zone averaged six to eight weeks, it is unlikely that upper river spawners contributed many newly emerged fry to the estuary population. On the other hand, upriver spawning grounds may be the primary source of larger fry and fingerling Chinook salmon that rear in the main-stem river for several months before entering the upper estuary and marsh habitats in June or later. A small increase in abundance at the Lower Salmon trap near the end of each sampling season (mid- or late June) is consistent with the average travel time expected for the second wave of fingerling migrants that left the upriver spawning area in late April or May 2000–2002 (Fig. 3). A distinct migrant group from upper basin rearing areas also might account for the increased mean length of juveniles at the Lower Salmon trap each June or early July, which exceeded the average length of individuals downstream in the Upper Estuary zone (Fig. 6).

The apparent linkage between juvenile life history and spawner distribution implies that the Salmon River hatchery could account for some recent changes in the age and timing of estuarine migration by juvenile Chinook salmon. In 1975, just before the start of hatchery operations, most Chinook salmon spawned in the upper main stem above Deer Creek #2 (Rkm 21) and in the lower portions of two mid-basin tributaries (Bear Creek and Slick Rock Creek) (Fig. 1a) (Mullen, 1979). While Chinook salmon still use these spawning areas, the center of adult abundance has shifted downstream to the lower main-stem river, where a large number of hatchery strays now spawn just above the Salmon River Hatchery. Because spawning occurs earliest and travel time to the estuary is shortest in this lowermost spawning area, the hatchery program could be a key factor in the early arrival of emergent fry to the Upper and Mid-Estuary zones and the restored marshes.

Even though the largest proportion of fry migrants from Salmon River now enter tidewater during April and early May, mark-recapture results indicate that few of these fish survived to the river mouth (Fig. 8). The low survival of emergent-fry migrants may not be unusual. Studies in the Fraser (Levy and Northcote, 1981) and Nanaimo River estuaries (Healey, 1980, 1982) similarly could not account for a large proportion of the downstream migrants to each estuary and suggested a high mortality may have occurred soon after migration was completed. Most marked individuals that we later recaptured near the mouth of Salmon River (and presumably, were about to exit the estuary) had not entered the estuary before June. This pattern is further supported by the results of beach seining surveys, which collected few individuals, marked or unmarked, within the Lower Estuary Zone before June. We also found evidence of high in-river mortality among emergent fry migrants from the Upper Salmon spawning area as indicated by a recapture of only 2–3% (adjusted for trap efficiency) of the marked fish at the Lower Salmon trap. The causes of poor survival of emergent fry in the river and estuary are not known.

The diverse life histories of juvenile salmon have been described as alternative survival strategies that insure successful reproduction in uncertain environments (Healey, 1991; Thorpe, 1994). In the Salmon River, we observed considerable variation in juvenile life history among the survivors that reached the river mouth: for any particular entry date during June and July, some individuals migrated directly to the mouth while many others lingered in the estuary for weeks to months before migrating seaward (Fig. 8). Moreover, since the Salmon River marshes were restored, life-history variation among juvenile Chinook salmon has increased as evidenced by expanded periods of estuarine residency and outmigration during late spring and early summer (Fig. 4).

Greater variation in migration characteristics and time of ocean entry for the Salmon River Chinook population may increase the likelihood that some individuals will survive in an unpredictable ocean environment. Marine production processes linked to salmon survival (e.g. wind-driven upwelling, time of spring transition, and the Pacific Decadal Oscillation) are quite variable along the Oregon coast (e.g. Huyer, 1983; Landry et al., 1989; Mantua et al., 1997); and marine mortality of juvenile salmon may be greatest

soon after ocean entry (Nickelson, 1986; Pearcy, 1992; Logerwell et al., 2003). Magnusson and Hillborn (2003) concluded that Chinook salmon from relatively unaltered estuaries — as indicated by the proportion of intact salt marsh, eelgrass, and other shallow rearing habitat — have higher average survival rates than those from severely altered estuaries.

We conclude that juvenile Chinook salmon have responded to increased habitat opportunities in the Salmon River estuary resulting from wetland restoration. Relative to patterns observed in the 1970s, fry and fingerling migrants now enter the estuary over a longer period throughout the spring and summer, extend their distribution further downstream throughout the Mid- and Lower Estuary zones, and occupy restored wetland habitats, April through August. The large proportion of fry that now enters the estuary soon after emergence may reflect changes in spawner distribution and abundance resulting from the large concentration of stray hatchery adults that spawn just above tide water. Nonetheless, we documented salmon survivors at the river mouth (i.e. ready to enter the ocean) for a wider range of time periods and sizes than in the 1970s. Most of these individuals had remained upriver to rear until June or later before entering the estuary and may have originated primarily from historical spawning areas in the upper basin, where relatively fewer hatchery strays occur. These results describe important linkages between the geographic structure of spawning populations and the patterns of estuarine habitat use by juveniles, underscoring the need for whole-basin approaches to salmon conservation and recovery (Nehlsen et al., 1991).

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