The contribution of estuary-resident life histories to the return of adult *Oncorhynchus kisutch*

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This study evaluated estuarine habitat use, life-history composition, growth and survival of four successive broods of coho salmon *Oncoryhnchus kisutch* in Salmon River, Oregon, U.S.A. Subyearling and yearling *O. kisutch* used restored and natural estuarine wetlands, particularly in the spring and winter. Stream-reared yearling smolts spent an average of 2 weeks in the estuary growing rapidly before entering the ocean. Emergent fry also entered the estuary in the spring, and some resided in a tidal marsh throughout the summer, even as salinities increased to > 20. A significant portion of the summer stream-resident population of juvenile *O. kisutch* migrated out of the catchment in the autumn and winter and used estuary wetlands and adjacent streams as alternative winter-rearing habitats until the spring when they entered the ocean as yearling smolts. Passive integrated transponder (PIT) tag returns and juvenile life-history reconstructions from otoliths of returning adults revealed that four juvenile life-history types contributed to the adult population. Estuarine-associated life-history strategies accounted for 20–35% of the adults returning to spawn in the four brood years, indicating that a sizable proportion of the total *O. kisutch* production is ignored by conventional estimates based on stream habitat capacity. Juvenile *O. kisutch* responses to the reconnection of previously unavailable estuarine habitats have led to greater life-history diversity in the population and reflect greater phenotypic plasticity of the species in the U.S. Pacific Northwest than previously recognized.

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Key words: life-history diversity; Oregon; otolith microchemistry; Salmon River; survival; winter habitat.

INTRODUCTION

Conventional understanding of the life history of juvenile coho salmon *Oncorhynchus kisutch* (Walbaum 1792) in the U.S. Pacific Northwest has presumed a relatively fixed pattern of rearing and migration. This model presupposes that successful *O. kisutch* rear in natal streams and migrate to the ocean as age 1 year (*i.e.* yearling) smolts, returning as 3 year-old adults (Gilbert, 1913; Sandercock, 1991). Recent studies have found much greater variation in juvenile life history and habitat-use patterns than previously expected, including evidence that estuaries may play a significant role in the life histories of some *O. kisutch* populations (McMahon & Holtby, 1992; Miller & Sadro,

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2003; Koski, 2009; Bennett *et al.*, 2011). The extent of estuary rearing by *O. kisutch* and the contributions of estuary-resident life histories to adult returns are unclear. This research reconstructs freshwater and estuarine rearing and migration pathways of juvenile *O. kisutch* in the Salmon River basin on the central Oregon coast. It then quantifies the contribution of each juvenile life-history type to adult returns.

Many studies have documented movement or displacement of juvenile *O. kisutch* from natal streams soon after emergence or later during their first year of life (Chapman, 1962; Mason & Chapman, 1965) but the fate of these age 0 year (or subyearling) migrants is poorly understood. Competition for food or space has been cited as a reason that subyearlings may abandon stream territories and move downstream, presumably to less favourable habitats (Sandercock, 1991). High mortality of subyearling migrants is implied by adult scale patterns that rarely indicate marine growth prior to the first winter annulus (Gilbert, 1913; Crone & Bond, 1976). Although scale features often have been used to reconstruct the ages and migration pathways of Pacific salmon *Oncorhynchus* spp. (Gilbert, 1913; Rich, 1920; Shapovalov & Taft, 1954; Reimers, 1973), life-history interpretations from scales can be subjective and are not always validated. It is unclear, for example, whether structural features of adult scales can effectively distinguish individuals that may have spent time in estuarine habitat during their first year from those that had reared exclusively in streams (Oregon Department of Fish and Wildlife, unpubl. data).

Dispersal of *O. kisutch* fry soon after emergence has been interpreted as evidence of a carrying capacity limitation (Chapman, 1966; Hartman *et al.*, 1982). Fry migrant behaviour in *O. kisutch* (Quinn, 2005) and Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) (Healey, 1991) could represent alternative life-history patterns rather than merely excess production that is lost from the population. *Oncorhynchus tshawytscha* populations exhibit a diversity of juvenile life histories that spread mortality risks in time and space and may contribute to population resilience in variable environments (Healey, 1991; Bottom *et al.*, 2005). A number of studies have described variants from the typical yearling smolt life history in juvenile *O. kisutch* (Tschaplinski, 1987; Murphy *et al.*, 1997; Miller & Sadro, 2003; Koski, 2009), but the significance of alternative rearing strategies to the productivity or resilience of *O. kisutch* populations is not well established.

Nickelson *et al.* (1992), Nickelson & Lawson (1998) and Solazzi *et al.* (2000) have demonstrated that availability of high-quality stream habitats during the winter limits *O. kisutch* populations in Oregon and is a major influence on population viability. Yet few studies have examined *O. kisutch* use or performance in the large expanses of freshwater and estuarine habitat downstream of natal spawning and rearing areas (Koski, 2009). Prey species produced in estuarine marshes are important for foraging and growth of juvenile *O. tshawytscha*, chum *Oncorhynchus keta* (Walbaum 1792) and *O. kisutch* (Levy & Northcote, 1982; Healey, 1991; Gray *et al.*, 2002; Bieber, 2005; Eaton, 2010). In Oregon's Salmon River estuary, wetland restoration projects completed in the last 35 years have restored tidal inundation to greater than two thirds of the historical marshes that had been dyked for agricultural and other uses since the early 1960s (Gray *et al.*, 2002; Bottom *et al.*, 2005). Wetland restoration has enhanced prey production and foraging by juvenile *O. tshawytscha* throughout the spring and summer (Gray *et al.*, 2002; Bieber, 2005) and increased expression of estuary-resident life histories within the *O. tshawytscha* population (Bottom *et al.*, 2005; Volk *et al.*, 2010). Juvenile *O. kisutch* in Salmon River might similarly benefit from renewed access to

tidal marshes in the spring, although the potential productivity of marshes for *O. kisutch* during the winter months has not been explored.

Miller & Sadro (2003) reported that nearly half of each brood year of *O. kisutch* in Winchester Creek, South Slough, Oregon, moved downstream to the estuary to rear as subyearlings. Most stream habitat monitoring programmes continue to target small wadeable streams, where habitat features and juvenile abundances are most visible and readily measured (Johnson *et al.*, 2001). Current survey methods exclude large expanses of tidal freshwater or brackish estuarine habitats that could provide productive rearing areas for many populations. Moreover, intensively monitored watersheds for estimating *O. kisutch* survival rates in Pacific Northwest rivers are situated in freshwater tributaries of large basins and do not measure salmonid survival in main-stem and estuarine reaches downstream of each monitoring site.

The assumption that all *O. kisutch* conform to a yearling riverine smolt life history supported entirely by wadeable-stream habitats is inconsistent with recent survey results and may bias interpretations of their habitat needs, life histories and productivity. This study evaluates both stream and tidal habitats in the Salmon River basin to (1) identify juvenile life histories within the *O. kisutch* population as defined by migration time, size, age and estimated freshwater and estuary residency, (2) classify juvenile life-history types and estimate survival to adult and the proportional contribution of each type to adult returns and (3) evaluate the importance of estuarine habitat, including reconnected tidal marshes and their associated channels, to the growth, productivity and resilience of the Salmon River *O. kisutch* population. Tagging and otolith chemical methods were used to reconstruct juvenile *O. kisutch* rearing and migratory pathways and to test whether variants from the conventional yearling riverine smolt life history contribute to adult returns. The results depict *O. kisutch* population dynamics for four successive brood years.

MATERIALS AND METHODS

Field sampling in 2008–2011 was structured to describe and quantify abundance, distribution, migration patterns and performance of each life stage of *O. kisutch* in Salmon River catchment and estuary. Estimates were made of the abundance of adult *O. kisutch* during the autumn spawning period, age 0 year juveniles (parr) in freshwater streams during the summer and outmigrant age 0 year (fry) and age 1 year (yearling) life stages in the spring. Age 0 and 1 year juvenile *O. kisutch* were sampled in the estuary throughout the year. Fish were passive integrated transponder (PIT)-tagged and antennas were sited to determine migration timing, growth and behaviour of individual fish, and survival to adult. Otoliths were collected from juvenile and adult *O. kisutch* to independently assess migration and residence patterns and age at return.

STUDY AREA

The Salmon River catchment is located on the north-central Oregon coast (Fig. 1). The basin area is 195 km^2 with an 800 ha estuary that extends to river kilometre (rkm) 6·5. Eighty-one kilometres of stream are suitable for *O. kisutch* spawning, and up to 107 km of stream habitat are accessible for juvenile rearing. The upstream extent of spawning and rearing habitat is limited by geomorphic barriers and has not changed significantly during the period of published salmonid surveys (*i.e.* within the last 40 years). River flow varies from a seasonal low of 0·7–1·41 m s^{-1} in the summer and early autumn to freshets that may range from 25 to 150 m s^{-1} for a few days during winter and spring. Salinity in the estuary varies with river flow. During the winter and spring, fresh water extends to the ocean during low tide and high flow, and in the summer, salinities reach 32 at rkm 4.
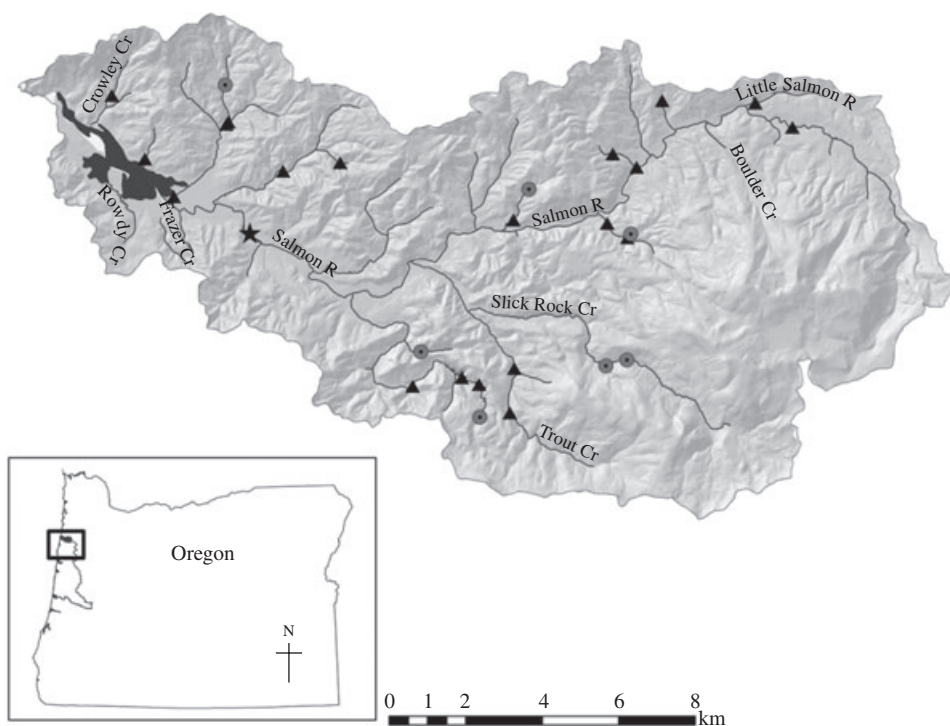
Fig. 1. Salmon River basin on the north-central Oregon coast, U.S.A., showing distribution of *Oncorhynchus kisutch* within the catchment and spawning and rearing sampling sites. A passive integrated transponder (PIT) antenna was deployed on the north side of the river at the site of the Salmon River hatchery. ⊙, rearing sites; ▲, spawning sites; ★, Salmon River hatchery; ⎯⎯, *O. kisutch* distribution; ▬, Salmon River estuary.

The Salmon River estuary was relatively undisturbed until the early 1960s when 254 ha of wetland and other nearshore habitats were dyked or filled to support cattle grazing and other uses. In 1978, the U.S. Forest Service, which manages the estuary and surrounding lands of the Cascade Head Scenic Research Area, initiated the first of five large wetland restoration projects. Today, a cumulative total of >175 ha of emergent marsh and tidal channels has been restored, re-establishing estuary connections to greater than two thirds of the original wetland habitat that previously had been dyked or filled (Fig. 2). The present array of natural and restored emergent marshes encompasses a salinity gradient from tidal fresh to marine zones (Bottom *et al.*, 2005) (Fig. 2). Additional information on the wetland restoration and vegetation can be found in Gray *et al.* (2002).

An Oregon Department of Fish and Wildlife hatchery on Salmon River at rkm 8 (Fig. 1) was established in 1978 to supplement *O. kisutch* and *O. tshawytscha* populations using local populations as broodstock. Prior to the initial release of hatchery fishes, information on the distribution and abundance of juvenile and adult salmonids in the Salmon River catchment and estuary was collected from 1975 to 1977 (Mullen, 1979). The 1976 *O. kisutch* spawning population was estimated at 1526 (594−3270; 95% c.i.) (Mullen, 1979). With recent changes in the hatchery programme, the final release of juvenile *O. kisutch* occurred in May 2007, and the last return of hatchery-origin adult *O. kisutch* spawned in autumn 2008. The hatchery fish in the spawning population were identified by the absence of an adipose fin (100% marked prior to release) and by scale patterns. This study excluded hatchery origin adults from the life-history analysis of the 2007 and 2008 populations. All adult *O. kisutch* that returned in autumn 2009, 2010 and 2011 were progeny of naturally produced fish. The hatchery continues annual releases of *c.*
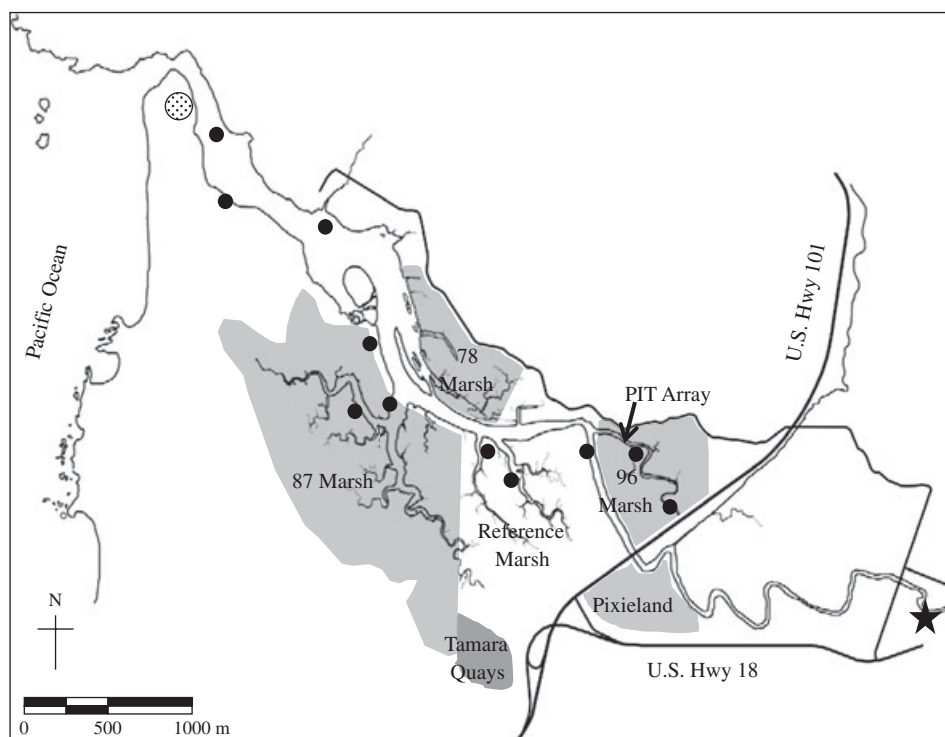
FIG. 2. Map of restored and natural wetlands in the Salmon River estuary. Three wetlands are designated by year of restoration (78, 87 and 96 Marshes). Tamara Quays along Rowdy Creek was restored in 2010 and Pixieland at the estuary confluence with Frazier Creek restored in 2011. Location of an unmodified reference wetland is also displayed. Beach seine sites (●), estuary mouth site (an index for ocean entry of salmon) (⊛), the location of a passive integrated transponder (PIT) antenna in the 96 Marsh (→) and the location of the screw trap and weir antenna (★) are shown. Hwy, highway.

200 000 subyearling autumn *O. tshawytscha* into the Salmon River during late August or early September.

Adult *O. kisutch* spawn from October to December (referred to as brood year) and into January and adults (recruits or progeny of the brood) return 3 years later (return year) (Nickelson & Lawson, 1998). In this paper, juvenile *O. kisutch* are considered age 0 year or subyearlings from time of emergence in late winter through the next 12 months. Subyearling *O. kisutch* are referred to as fry in the spring of their first year or parr in the summer through winter of their first year. Starting in March of the second year, the juvenile *O. kisutch* are referred to as yearlings or smolts as they enter the estuary and ocean.

ABUNDANCE, DISTRIBUTION AND TIMING OF ADULT *O. KISUTCH*

Spawning surveys to estimate adult *O. kisutch* distribution and abundance encompassed *c.* 15–20% of the 81 km of potential *O. kisutch* spawning habitat. Sites were selected within the distribution of spawning *O. kisutch* using the generalized random-tessellation stratified (GRTS) sampling methodology (Stevens & Olsen, 2004) to permit statistically rigorous representation of all streams and fish in the basin. The spawning surveys were conducted from 15 October to late January each year, and sites were visited every 10 or fewer days to estimate abundance (area-under-the-curve) for each site (Jacobs *et al.*, 2002). Population abundance

and variance was extrapolated to all rkm accessible to *O. kisutch* based on site weight and a local neighbourhood (LNB) estimator (Jacobs *et al.*, 2002, Stevens & Olsen, 2003). Scales and otoliths were collected from non-hatchery *O. kisutch* carcasses handled during spawning ground surveys. Migration time into freshwater in 2010 and 2011 was estimated at a PIT antenna at rkm 8, and spawn time was determined during the annual spawning surveys from 2007 to 2011.

A PIT antenna array, consisting of three antennas (each $3 \cdot 0 \text{ m} \times 1 \cdot 2 \text{ m}$) at the Salmon River hatchery weir (rkm 8) has operated continuously since 26 August 2010 to detect downstream and upstream movement of PIT-tagged juvenile and adult *O. kisutch*. The antenna array was placed on the north side of the 25 m wide river between the hatchery weir and shoreline. Adult fish are generally forced to the north side of the river to pass upstream until the river rises sufficiently to submerge the weir. The antenna operated even when the weir was overtopped at high flows, although fewer adult fish may have passed through the antenna than jumped over the centre or south side of the weir. The PIT-tagged fish are as likely to pass through the antenna as untagged fish, although it is not possible to directly estimate the proportion of the adult population that passed through the weir antenna because very few tagged adults are collected on the spawning grounds. Adult tag detections at the weir antenna array were used to estimate juvenile survival to adult and to assess freshwater return times and ages (based on known age at the time of tagging) to compare with spawning times and age interpretations from scales collected on the spawning grounds. The antennas were powered by a multiplexing transceiver (Destron Fearing, Inc. model FS1001M; www.destronfearing.com) connected to four 12 V deep cycle batteries that were recharged through a 110 AC power line from the hatchery. PIT-tag interrogation and transceiver diagnostic data were downloaded directly from the transceiver memory *via* a wireless modem.

JUVENILE *O. KISUTCH* ABUNDANCE AND DISTRIBUTION IN STREAMS

Juvenile (age 0 year) *O. kisutch* abundance was estimated in tributary and main-stem habitats in 107 km of stream in the basin from 2008 to 2011 (Fig. 1). Within this sampling frame, 25–30 GRTS survey sites were selected annually. Each site was considered target (accessible to juvenile *O. kisutch*) (Stevens & Olsen, 2004) and was equally weighted for expansion to unsurveyed habitat. Sites overlapped with the 2007–2010 adult survey sites but also included sites within the rearing-only distribution (*i.e.* stream reaches above the spawning distribution). Abundance was estimated in August and September each year by depletion method (Zippin, 1958) using backpack electroshockers. Each site was *c.* 20 active channel widths in length, with a minimum length of 50 m and a maximum length of 150 m. Blocknets were placed at the upstream and downstream end of each site, and multiple passes were made through the site until a 67% reduction in *O. kisutch* catch was achieved between subsequent passes. If < 10 fish were sampled at a site, a 50% reduction was required. *Oncorhynchus kisutch* were absent in some sites; these sites had an estimate of zero *O. kisutch* and were accounted for in the final population estimate. In some large sites where depletion reductions could not be met, mark-recapture techniques (Rodgers *et al.*, 1992) were used to estimate the number of *O. kisutch*. Depletion estimates of the number of fish at each site were derived from the programme CAPTURE (White *et al.*, 1982), and mark-recapture estimates were derived from NOREMARK (White, 1996). The abundance at each site was standardized to the number of fish m^{-1} or standardized to fish km^{-1}. Although variance is inherent in the precision of the field sampling, this source is small relative to the variations from site to site and from extrapolating a subsample (of size *n* units) to the entire stratum (of size *N* total units) (Dambacher *et al.*, 2009). The total number of *O. kisutch* parr rearing in the basin in the summer was estimated using the LNB estimator and expanded to all rkm (spawn and rear) in the basin. All juvenile *O. kisutch* sampled at each site were enumerated, measured and weighed. All *O. kisutch* >65 mm fork length (L_F) were PIT-tagged with full duplex 12·5 mm tags (Biomark TX1411SST 134·2 kHz, 0·1020 g; www.biomark.com). Fish of this size represented 71–79% of the *O. kisutch* handled in the catchment during the 4 years. PIT tags were placed in several hundred to more than a thousand subyearling *O. kisutch* during 2008–2011 catchment sampling (Table I).

TABLE I. Number of juvenile *Oncorhynchus kisutch* passive integrated transponder (PIT) tagged from 2008 to 2011 in the Salmon River

Area; method	*O. kisutch* yearling	*O. kisutch* subyearling
Upper watershed; electrofishing (August to September)		
2008	0	373
2009	0	1286
2010	0	658
2011	0	732
Lower river; rotary screw trap (March to June)		
2008	1053	40
2009	531	199
2010	568	61
2011	793	142
Estuary; beach seine (January to December)		
2008	291	433
2009	393	517
2010	1106	378
2011	471	509

CAPACITY OF FRESHWATER-REARING HABITAT

Habitat surveys were conducted in 2010 to model the potential rearing capacity of stream habitat during the summer and winter. Twenty-one GRTS-selected sites, each 1000 m in length, represented 20% of the stream habitat available to juvenile *O. kisutch*. The habitat-limiting factors model (HLFM: Nickelson *et al.*, 1992, 1993) was used to estimate the potential capacity and quality of stream habitat for juvenile *O. kisutch*. This model estimates the potential summer and winter habitat capacities (parr km^{-1}) at each site for *O. kisutch* by applying a density of juvenile *O. kisutch* to each habitat unit and multiplying by the surface area of the habitat unit. The capacity is therefore an integrated variable that emphasizes particular stream habitat features. Summer habitat capacity is primarily a function of the total amount of pool habitat, while winter habitat capacity is dependent on the amount of beaver ponds, off-channel pool habitats and scour pools with wood. The potential capacity is also related to the survival of fish because fish in higher capacity sites have higher overwinter survival rates (Nickelson, 1998). Sites considered low and high capacity supported < 900 or > 1850 parr km^{-1} (Nickelson, 1998; Rodgers *et al.*, 2005).

MIGRATION TO THE ESTUARY

The abundance, size and timing of downstream-migrating juvenile salmonids were quantified at a 1·5 m diameter rotary screw trap located *c.*100 m below the Salmon River hatchery weir at rkm 8 (Fig. 1). The upper PIT antenna array (adjacent to the hatchery weir) and the screw trap were *c.*1·5 km above the head of tide (Fig. 2) and therefore approximated *O. kisutch* migration times and sizes at estuary entry. From 2008 to 2011, the trap was operated continuously from mid-March to the end of June, and in 2011 to early August. Trap efficiency was calculated on a weekly basis, and abundance and confidence intervals were estimated following the techniques of Solazzi *et al.* (2000).

Juvenile salmonids that were >65 mm L_F and collected in the screw trap were marked individually with PIT tags to estimate estuary residency and migration times at recapture in the estuary, during detection at the hatchery weir, or from collections on the spawning grounds. Few of the subyearlings at the screw trap or in the estuary were >65 mm L_F in March and April, but by June, more than half were >65 mm L_F, and all were >65 mm L_F by July. More than 600 to > 1000

juvenile *O. kisutch* (subyearlings and yearlings combined) were PIT tagged at the rotary screw trap annually from 2008 to 2011 (Table I).

Additional autumn and winter outmigration information was gathered when juvenile fish tagged in the catchment were detected at the PIT antenna array near the hatchery weir at rkm 8 or at another PIT array deployed several km downstream in the 96 Marsh in the estuary (Fig. 2). Based on the ratio of tagged juveniles detected at both PIT antenna arrays ($n = 15$) relative to the total number of tagged fish detected in the 96 Marsh ($n = 96$), the weir antenna accounted for *c.* 15% of the downstream migrating juvenile fish in the winter and spring 2011. Fish tagged at the screw trap and released above the hatchery (214 of 914) yielded an average detection probability (per cent of fish passing through the antenna and being detected) for the weir antenna array of 23% for the period April to June 2011.

ESTUARY ABUNDANCE AND DISTRIBUTION

Relative habitat use by juvenile *O. kisutch* was determined in main-stem and wetland-channel habitats of the estuary. Beach seining is an effective method for capturing juvenile salmonids in the shallow Salmon River estuary (Mullen, 1979; Cornwell *et al.*, 2001; Bottom *et al.*, 2005), and catch per unit effort (CPUE) has been used to index salmonid abundance in this and other small Oregon estuaries (Reimers, 1973; Pearcy *et al.*, 1989). The main channel and wetland habitats in Salmon River estuary were sampled at least twice monthly from April 2008 to December 2011 using a 38 m beach seine. Site selection was representative of available main-stem and wetland habitats throughout the estuary from the 96 Marsh at rkm 3·7 to a site near the river mouth, where timing, sizes and abundance at ocean entry were estimated (Fig. 2). Beach seine sites consisted of sandy-mud or sandy substrata and were not obstructed by wood or other debris, allowing comparisons of relative abundance (CPUE) among sites and time periods.

In addition to the biweekly sampling throughout the estuary, juvenile *O. kisutch* were sampled weekly in the 96 Marsh through the summer and autumn, and at the estuary mouth year round to monitor ocean entry. The reference, 78 and 87 Marshes were used sparingly by juvenile *O. kisutch* except in the winter. Therefore, marsh sampling was concentrated in the 96 Marsh from April to November. In 2008 and 2009, abundance of juvenile *O. kisutch* within the 96 Marsh was estimated through short-term mark-recapture sampling (Reimers, 1973). All *O. kisutch* collected in the estuary were enumerated, measured and scanned for PIT tags. Estuary-captured juveniles >65 mm L_F that had not previously been tagged were implanted with 12·5 mm full duplex PIT tags (Table I).

From 22 April 2010 to 25 August 2010, a PIT antenna array was operated in the 96 Marsh channel, the first major off-channel habitat that juvenile salmonids encounter upon migrating to the estuary. The antenna was placed 200 m up the marsh channel from the confluence with the main estuary channel. The array consisted of five rectangular inductor coil antennas (three $3·0 \times 1·2$ m, two $2·4 \times 1·2$ m) arranged in a line stretching across the entire channel. Antennas were powered by a multiplexing transceiver (Destron Fearing, Inc. model FS1001M; www.destronfearing.com). The system was powered by four 12 V deep-cycle batteries that were recharged with two 85 W solar panels and a 10 A, 24 V charge controller. PIT-tag interrogation and transceiver diagnostic data were downloaded directly from the transceiver memory *via* a wireless modem.

RESIDENCE, GROWTH AND SURVIVAL

Minimum residence times, growth and survival were assessed through recapture or detection of previously tagged individuals. Residence time was determined from first to last recapture in a particular (*i.e.* freshwater or estuarine) environment. For example, minimum estuary residence was considered from the date of tagging at the screw trap just above the head of tide or in the estuary to the last detection or recapture in the estuary. Growth was determined as change in L_F or mass from one capture event to the next or averaged over multiple recaptures. Differences in L_F and growth among years and locations were assessed with ANOVA and Dunnett–Tukey–Kramer pairwise multiple comparison tests adjusted for unequal variances and unequal sample sizes.

Survival from juvenile to adult was estimated for two brood years of *O. kisutch* from the time of juvenile tagging to adult recovery. Tagged adults were detected at the weir antenna or

recovered on the spawning grounds. The 2007 and 2008 brood years, tagged as juveniles in 2008 and 2009, returned as adults in 2010 and 2011. Juvenile *O. kisutch* were stratified into five groups for estimating survivals: (1) subyearlings tagged at the screw trap or in the estuary during the spring and summer, (2) parr tagged in the catchment in late summer (August and September), (3) parr tagged in the estuary in the winter (October to February), (4) yearlings tagged at the screw trap in the spring (March to June) and (5) yearlings tagged in the estuary in the spring (March to June). Final captures or detections occurred 1·5 years later at the weir antenna or on the spawning ground. Survival of groups 1, 3, 4 and 5 were evaluated between groups and years across six recapture events using the Cormack–Jolly–Seber model in programme MARK 7.1 (White, 2013). A deviance information criteria (DIC) was used to select the best fitting model for survival and recapture probabilities. Survival estimates were calculated on a monthly interval to allow estimation of cumulative survival for each group. Too few of group 2 fish were recaptured to calculate their contributions to groups 3, 4 and 5.

OTOLITH ANALYSIS

The use of otoliths to reconstruct the environmental transitions of migrating juvenile salmonids has been validated in Salmon River through water sampling and otolith chemical analyses for juvenile *O. tshawytscha* (Volk *et al.*, 2010). Similar methods were applied in this study to interpret the juvenile life histories represented among returning adult *O. kisutch* collected on the Salmon River spawning grounds. Habitat transitions were inferred from changes in otolith strontium:calcium (Sr:Ca) ratios that occur when anadromous salmonids migrate between fresh and salt water (Volk *et al.*, 2000; Zimmerman & Reeves, 2002; Brenkman *et al.*, 2007). Relatively high Sr:Ca levels in the otolith core depict a typical marine signal from the female parent. This ratio drops after the egg develops and the fry emerges in fresh water. The ratio again increases immediately when an individual first encounters salt water in the estuary or ocean. After entering salt water, the Sr:Ca remains elevated throughout the early salmonid life history, unless an individual returns to fresh water to rear.

Otolith chemistry was analysed to reconstruct the juvenile life histories of adult *O. kisutch* sampled on the spawning grounds in 2008 ($n = 28$), 2009 ($n = 45$) and 2010 ($n = 49$). Sagittal otoliths were prepared for chemical analysis by thin sectioning in the sagittal plane, similar to methods used in Volk *et al.* (2010) and Campbell (2010). Otolith chemistry was analysed at the Keck Collaboratory for Plasma Mass Spectrometry at Oregon State University using a New Wave™ DUV 193 nm ArF laser coupled with a Thermal Elemental PQ Excell (www. esi.com) quadrupole inductively coupled plasma mass spectrometer (LA-ICP-MS; www.thermofisher.com). Ablated material was transported from the laser to the mass spectrometer using helium as the carrier gas. The LA-ICP-MS operating conditions were as follows: $13 \, l \, min^{-1}$ cooling gas, $0·95 \, l \, min^{-1}$ auxiliary gas and $0·75 \, l \, min^{-1}$ helium. The laser beam diameter was set at 30 μm, scanned at $5 \, \mu m \, s^{-1}$ at a pulse rate of 8 Hz. Laser transects were analysed from the otolith core to the otolith edge in the dorsal and posterior quadrant. Strontium levels in otoliths have been shown to respond quickly (1–2 days) to brackish and marine waters with higher salinities and Sr levels (Zimmerman, 2005; Volk *et al.*, 2010; Miller, 2011). Estuary and ocean entrance was determined using the point of strontium (Sr) inflection, defined as the point of rapid Sr increase from a freshwater signal. All reported Sr values are ratios of calcium (Ca) and reported as atomic ratios. Estuary and ocean entrance (E&OE) along the chemical transect was related to the physical location on the otolith by the equation (Brenkman *et al.*, 2007; Volk *et al.*, 2010; Campbell, 2010): $O_E \, (\mu m) = [T_E \, (ms) − T_S \, (ms)] \, (5 \, \mu m \, s^{-1}) \, (1000)^{-1}$, where T_S is the time at the beginning of the laser transect, T_E is the time at the point of Sr inflection along the laser transect and O_E is the corresponding otolith size at Sr inflection (estuary entrance). A fish size and otolith size relationship developed for *O. kisutch* in the Salmon River ($y = 0·1721x − 10·773$; $r^2 = 0·72$, $n = 80$) was used to backcalculate fish L_F at any given otolith size.

Otoliths were collected from juvenile *O. kisutch* at or near the estuary mouth (presumed ocean entry) and from adult *O. kisutch* on the spawning grounds. The otoliths from juvenile *O. kisutch* provided information on L_F, date of estuary entry and residence time. The L_F at entry was backcalculated based on size of otolith at the Sr increase and the date of entry was determined by counting daily increments back from time of capture. The first visible annulus (assumed to form during winter months) was used in conjunction with the Sr inflection point to estimate the season of ocean and estuary entry. If the point of Sr increase appeared prior to annulus formation,

the individual had migrated to the ocean in the summer or autumn. If the point of Sr increase occurred during or after annulus formation, the individual had left the Salmon River and entered the estuary sometime in the winter or spring. Adult fish that entered the estuary after the formation of the annulus were considered yearlings, although the exact date of entry was unknown. The juvenile otoliths provided additional perspective on fish that entered the estuary near the time of annulus formation.

Juvenile life histories of returning adult *O. kisutch* were classified based on L_F and times of entry into salt water as evidenced by the chemical signals on the otolith. Age at adult return was determined by scale analysis (Sandercock, 1991). Fish that returned at age 2 years were classified as either jacks or 2 year-old adults. Recoveries of six adult *O. kisutch* that were PIT tagged as juveniles at the rotary screw trap provided an independent measure of the approximate estuary entry time and size of each individual to validate interpretations from the otolith chemical analysis. If the otolith results are valid, the backcalculated L_F of each fish at the point of otolith Sr increase should approximate the measured L_F at tagging at the rotary screw trap, which was located within 1–2 km of detectable salinity.

RESULTS

The population surveys tracked abundance, performance (growth and survival) and migrations at each life stage of *O. kisutch* from spawning adult to freshwater and estuary-rearing juveniles.

ADULT POPULATION

The spawning populations of *O. kisutch* ranged from 753 to almost 4000 fish in 2007–2011 (Table II). The spawner populations in 2007–2008 comprised 6 and 17% of natural origin parents. The remaining hatchery fish in each spawning population had been released 1·5 years earlier from Salmon River hatchery as yearling smolts. Beginning in 2009, all adult *O. kisutch* were the progeny of natural spawners. Adults returned to fresh water from mid-September to early January, spawning peaked in early to mid-November, and spawner distribution was concentrated in the upper main-stem Salmon and Little Salmon Rivers and in Bear Creek.

JUVENILE *O. KISUTCH* POPULATIONS IN THE CATCHMENT

The juvenile *O. kisutch* (parr) sampled in the catchment were the progeny of the previous year's spawning population (Table III). Density and overall abundance in the summer increased as the spawning population increased. During each survey year,

TABLE II. Population estimates of ($\pm$95% C.I. as % of the value) of spawning population of *Oncorhynchus kisutch* in the Salmon River catchment, 2007–2011

Brood year	Abundance
2007	993 (54%)
2008	3853 (38%)
2009	753 (58%)
2010	1382 (42%)
2011	3636 (27%)

TABLE III. Population estimates of ($\pm 95\%$ c.i. as % of the value), mean density m^{-2}, mean density km^{-1} of juvenile *Oncorhynchus kisutch* in streams of the Salmon River catchment during August to September, 2008–2011

Brood	Year	Abundance	Density (m^{-2})	Density (km^{-1})
2007	2008	19 412 (43%)	0·04 (57%)	180 (43%)
2008	2009	67 794 (29%)	0·19 (36%)	630 (29%)
2009	2010	37 617 (34%)	0·11 (54%)	350 (34%)
2010	2011	44 344 (35%)	0·06 (37%)	414 (35%)

juvenile *O. kisutch* (parr) were present at 56–67% of the sites within the potential rearing distribution. High abundances occurred every year in the upper Salmon River and Bear Creek. Approximately 2·5% of the population was handled each year during the August and September sampling effort.

Juvenile *O. kisutch* in freshwater streams ranged from 42 to 109 mm L_F during all 4 years. Mean L_F was 76·7 mm in 2008 and 72·6, 72·7 and 70·6 mm in 2009 (Fig. 3), 2010 and 2011. The higher mean L_F in 2008 ($P < 0.05$) coincided with the lowest population estimate of the 3 years (Table II). No significant size difference was observed between years of very high (2009) and moderate (2010) abundance, although *O. kisutch* were significantly smaller in 2011 ($P < 0.05$).

STREAM HABITAT QUALITY FOR JUVENILE *O. KISUTCH*

Modelled habitat capacity for juvenile *O. kisutch* during the winter was generally low in the tributaries and the main-stem Salmon River. The exceptions included (1) two sites on the main-stem Salmon and Little Salmon Rivers, where habitat capacity for overwintering juvenile *O. kisutch* was rated high, (2) a site in lower Bear Creek of moderate rearing capacity and (3) a site in lower Little Salmon River of moderate capacity. The low habitat capacity in the tributaries reflects the lack of pools, large wood structure or beaver dams. The section of the upper main-stem Salmon River and Little Salmon River within the Van Duzer corridor had the highest habitat capacity, accounting for over half the modelled juvenile salmonid-rearing capacity.

MIGRATION OF AGE 0 AND 1 YEAR *O. KISUTCH* TO THE ESTUARY

Fish collections at the rotary screw trap just below the hatchery weir approximated the timing, abundance and L_F distribution of juvenile *O. kisutch* migrants at estuary entry (Figs 4 and 5). Subyearling and yearling juvenile *O. kisutch* migrated from the catchment to the estuary in the spring each year.

Age 0 year (subyearling fry) *O. kisutch* numbering from 11 000 to nearly 40 000 migrated past the screw trap from March (soon after emergence) to June (Table IV). Migration estimates were probably influenced by the timing of trap placement relative to peak migration. The fry already had begun actively migrating when the trap was installed such that the early peak may have skewed estimates of total abundance. After the peak movement of fry in late March, the number of migrants declined sharply. The age 0 year fish were usually too small (<65 mm L_F) to tag until late May (Fig. 5).
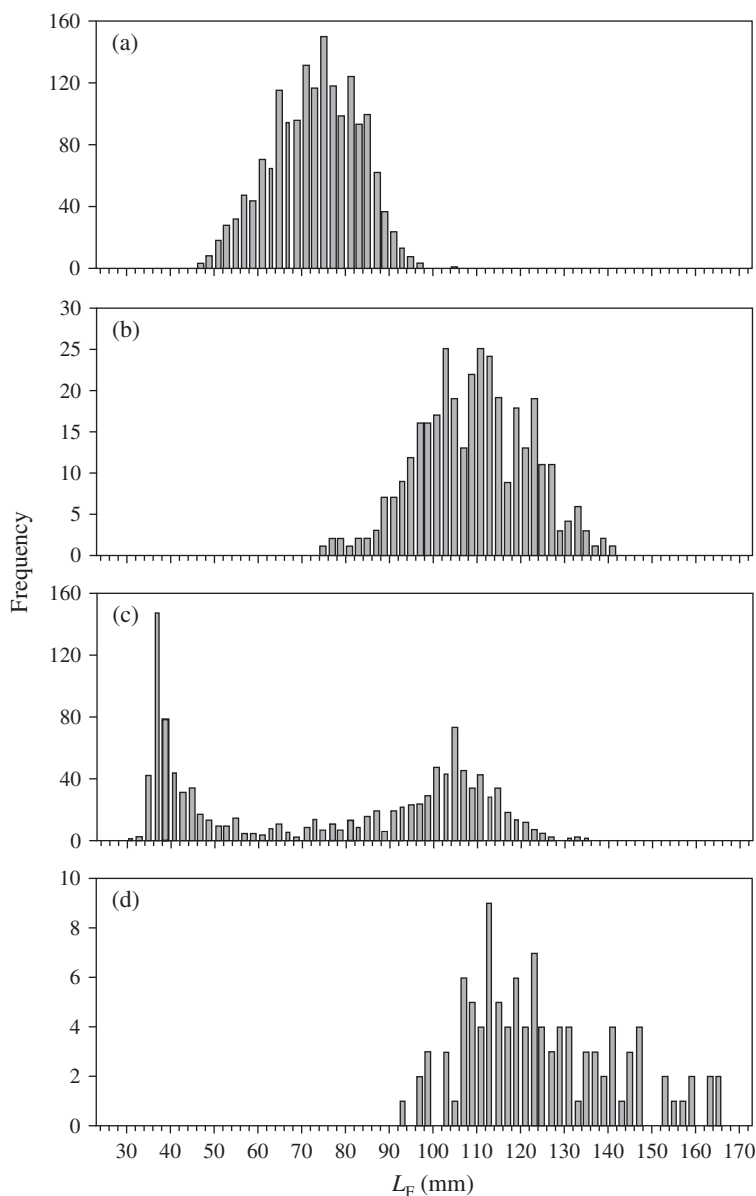
FIG. 3. Fork length (L_F) frequency of 2008 brood juvenile *Oncorhynchus kisutch* sampled in the (a) catchment (August to September 2009), in the (b) estuary (December to February 2009 to 2010), at the (c) screw trap (March to June 2010) and at the (d) ocean entry index site near the estuary mouth (April to June 2010).

Although the screw trap was operated to early August in 2011, subyearling *O. kisutch* (36 total) were only observed to mid-July.

Peak migration times for age 1 year (yearling) *O. kisutch* were late April in 2009 and mid-May in 2008 and 2010. A more protracted migration occurred in 2011. Approximately 15 000–21 000 yearling *O. kisutch* migrated annually from the Salmon River
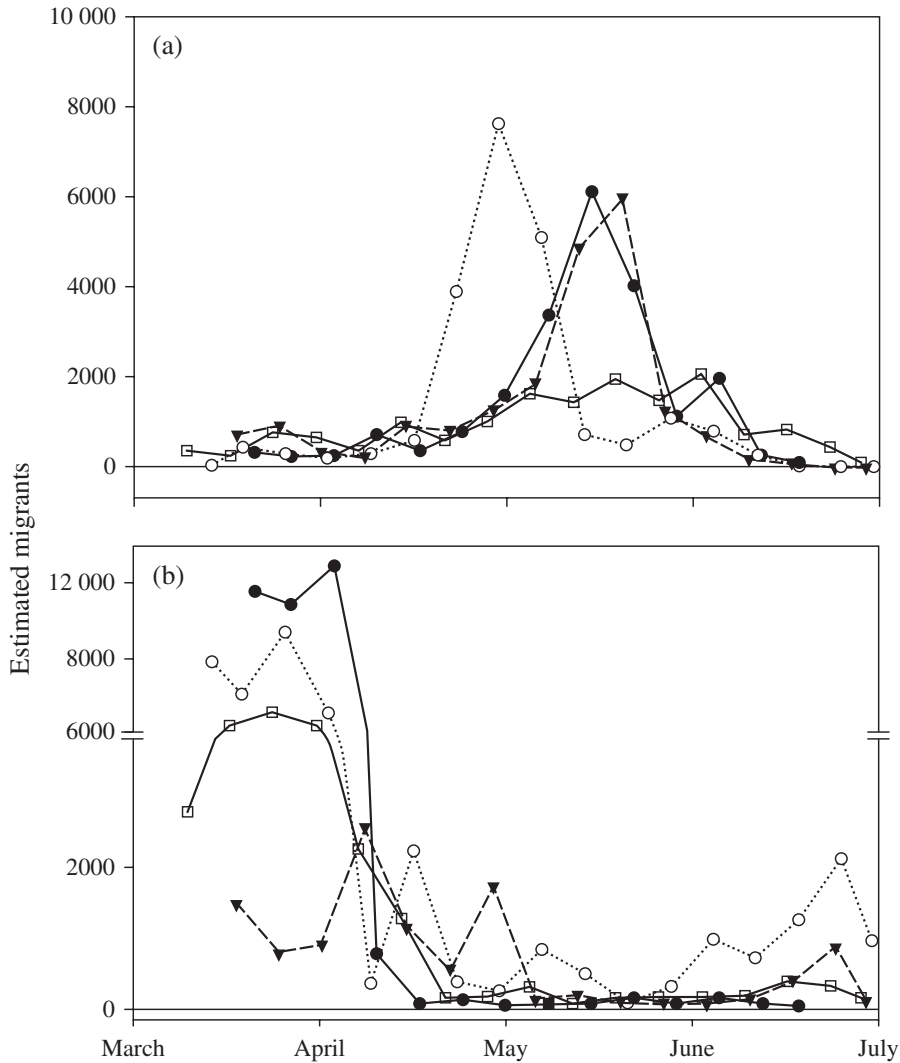
FIG. 4. Estimated migration of *Oncorhynchus kisutch* (a) yearlings and (b) subyearlings measured at the rotary screw trap from March to June 2008 (●), 2009 (○), 2010 (▼) and 2011(□).

in 2008–2011 (Table IV). Yearling smolts ranged from 63 to 151 mm L_F at migration from river to the estuary with an average size of 104 mm. The monthly L_F frequencies for juvenile *O. kisutch* exhibited a bimodal pattern from March to June corresponding to subyearling and yearling age classes (Fig. 5). L_F frequencies by month during 2008, 2010 and 2011 were very similar to the cumulative bimodal pattern shown for the screw trap in March to June 2009 (Fig. 3). Scale analysis indicated that little overlap occurred in L_F between yearling and subyearling *O. kisutch* in the late spring, although the L_F ranges separating the two age classes had decreased by June (Fig. 5).

A second movement of age 0 year *O. kisutch* from the catchment to the estuary coincided with the onset of autumn and winter rains. Although screw-trap operations were
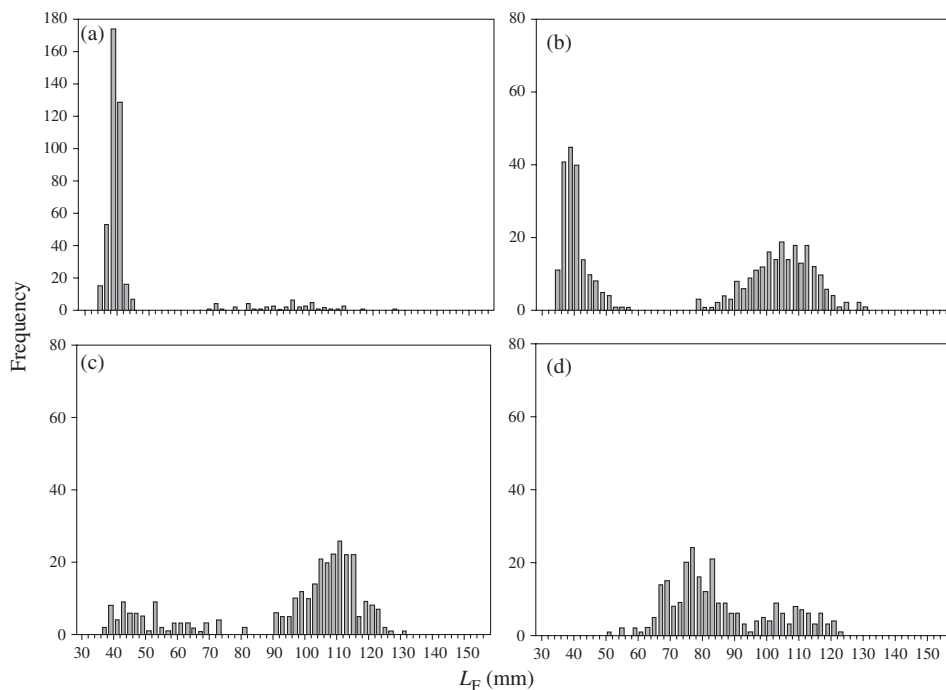
FIG. 5. Fork length (L_F) frequency of *Oncorhynchus kisutch* captured at the rotary screw trap in (a) March ($n=444$), (b) April ($n=391$), (c) May ($n=302$) and (d) June ($n=255$) 2009.

suspended after August, subyearling fish PIT-tagged in the catchment still could be monitored at the hatchery weir antenna at rkm 8 in the late autumn and winter (Fig. 6). No fish were observed to migrate between mid-July and late September (onset of autumn rains), separating the early spring and summer subyearling migrants from the autumn and winter migrants. Seven per cent (39 of 556) and 5·7% (42 of 664) of the fish tagged in the catchment above the weir were detected from mid-September to the end of February for the brood year 2009 and brood year 2010 juveniles; only 2·3% (13 of 556) and 1·7% (11 of 664) were detected at the antenna the following spring from March to June (spring yearling migrants). Considering the average detection probability of the PIT antenna (15–23%), up to 40% of the summer *O. kisutch* population may have migrated to the estuary during the autumn and winter. The L_F of the autumn and

TABLE IV. Annual abundance ($\pm$95% C.I. as % of the value) of juvenile *Oncorhynchus kisutch* collected in a rotary screw trap in March to June, 2008–2011. The *O. kisutch* are progeny of brood years 2006–2010

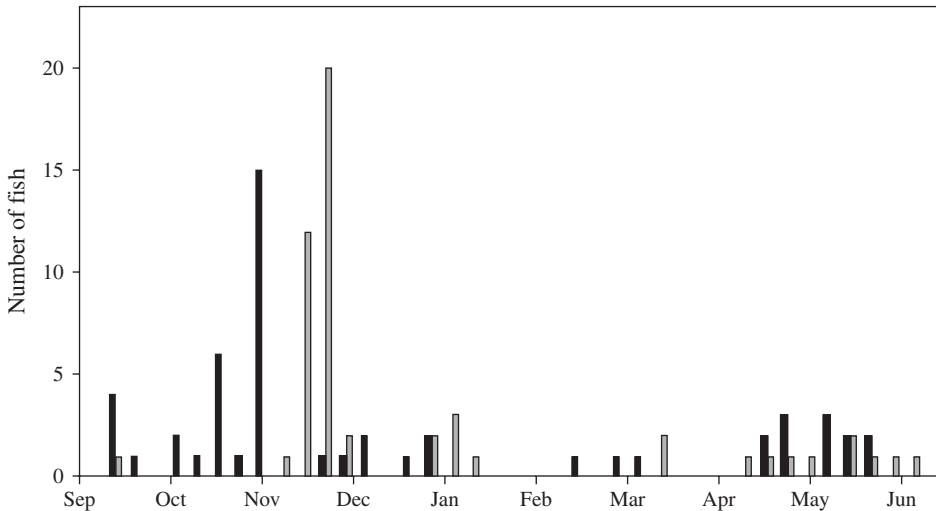| Age (years)	2008	2009	2010	2011
0	37 017 ± 72%	39 141 ± 42%	11 177 ± 44%	18 617 ± 55%
1	21 304 ± 29%	21 864 ± 85%	20 140 ± 58%	15 551 ± 34%

FIG. 6. Migration timing of juvenile *Oncorhynchus kisutch* tagged in the catchment and detected downstream at the passive integrated transponder antenna (rkm 8), just above the head of tide, in 2010–2011 (■, $n=52$) and 2011 and 2012 (▭, $n=53$).

winter migrants was not significantly different from that of the yearling spring migrants at the time of tagging in August and September in either 2010 or 2011 ($P < 0.05$).

JUVENILE-REARING PATTERNS AND GROWTH IN THE ESTUARY

Subyearling O. kisutch

The abundance of subyearling *O. kisutch* in the Salmon River estuary peaked in the spring and winter (Fig. 7). Similar to the patterns observed at the screw trap (Fig. 4) and the lower-river PIT antenna (Fig. 6), subyearling fry were observed in the estuary in the spring, and subyearling parr were observed primarily in the estuary in the late autumn and winter.

Subyearling fry that entered the estuary in the spring were observed exclusively in the upper estuary except in April 2008 when a few fry (35–50 mm L_F) were captured in the lower estuary on a single occasion (Fig. 7). Some of the subyearling fry survived and remained in the 96 Marsh during the summer as salinities increased. In October 2008, c. 243 subyearling *O. kisutch* (95% C.I., 201–311) were present in the 96 Marsh channel based on a 1 day mark-recapture experiment. Repeated population estimates in August and October 2009 were 326 (95% C.I. 170–482) and 35 (95% C.I. 18–171). Subyearling *O. kisutch* tagged and recaptured or detected in the 96 Marsh ($n = 180$) (PIT detections in Table V) were at large for a minimum of 31 days and a maximum of 147 days. Some subyearling fry may have remained in the estuary and entered the ocean as age 1 year smolts the following spring. Others may have moved into local streams to overwinter.

Subyearling *O. kisutch* also entered the estuary as parr during the autumn and winter. Large numbers of *O. kisutch* parr (CPUE ranged from 0 to 336) appeared in winter
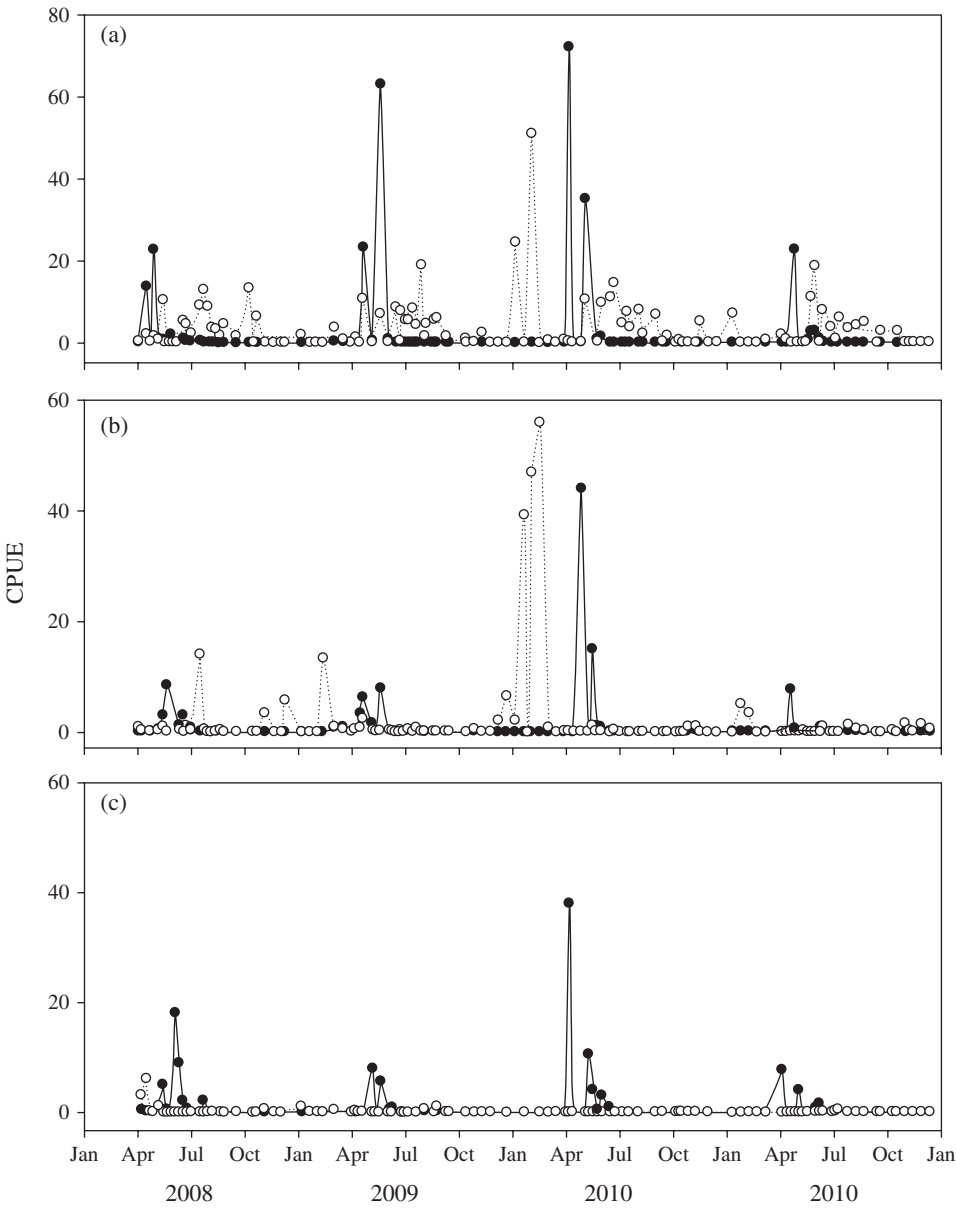
FIG. 7. Catch per unit effort (CPUE) of yearling (●) and subyearling (○) *Oncorhynchus kisutch* in the (a) upper, (b) mid and (c) lower zones of the Salmon River estuary. Juvenile parr were designated as yearlings on 1 March.

TABLE V. Backcalculated estimates of juvenile *Oncorhynchus kisutch* residence time and fork length (L_F) at estuary entry based on otolith chemistry and structure. All fish were captured near the site of ocean entry from April to June. No subyearling fry migrants (type 2) were sampled at the estuary mouth

Life-history type	N	Days of estuary residence Average (range)	L_F (mm) at estuary entrance Average (range)	L_F (mm) at capture Average (range)
Yearling	69	39*(0–85)	105 (76–160)	119 (81–175)
Fry migrant – nomad	4	150 (17–311)	68 (32–120)	125 (106–162)
Parr migrant	11	111 (49–195)	94 (56–122)	139 (115–172)

*The median number of days was 15.

beach seine catches in the upper and middle portions of the estuary (Fig. 7). The primary capture location in the upper estuary was in the 96 Marsh. The primary locations in the middle estuary were eelgrass-dominated channels, one inside the 87 Marsh channel and another in the main-stem channel along the north side of the estuary at rkm 1·6. Juvenile *O. kisutch* were regularly captured as far downstream as rkm 1·6, but rarely at the mouth. These *O. kisutch* included recaptures from the upper catchment (tagged in August and September), fish tagged in freshwater margins of the estuary (stream confluences) and fish tagged weeks to months earlier at other estuary locations. *Oncorhynchus kisutch* tagged in the winter in the middle and upper zones of the estuary were recaptured at the mouth in the late spring, suggesting that even fish distributed low in the estuary delayed their ocean migration until the following spring.

Seven subyearlings that were tagged at the screw trap and detected at the 96 Marsh PIT antennas had a median travel time of 3 days to the 96 Marsh channel (range 2–15 days). Although these fish were only detected for up to 6 days, additional evidence from subyearlings tagged in the 96 Marsh indicated longer residency. Eight (4%) of the subyearling *O. kisutch* (>65 mm L_F) PIT tagged at the smolt trap and four (2%) in the estuary in 2009 were detected in April and May 2010 on the marsh antennas, indicating that they may have spent an additional year rearing in the estuary or local tributaries after moving into brackish water. The PIT antenna array detected tagged *O. kisutch* using the marsh channel, even as salinity in the marsh increased through the summer. Although antenna efficiency presumably suffered as river flow dropped and salinity increased (Hering *et al.* 2010), juvenile *O. kisutch* were detected throughout the period of operation.

Growth rates of juvenile *O. kisutch* varied by rearing location. *Oncorhynchus kisutch* that were tagged in upper-basin streams during the August to September electrofishing and recaptured in the estuary 2–4 months later grew slowly at an average rate of 0·17 mm day^{-1} (0·54% body mass day^{-1}). *Oncorhynchus kisutch* tagged in the estuary in the summer grew at 0·29 mm day^{-1} (1·1% body mass day^{-1}). By contrast, *O. kisutch* tagged in the estuary in December and January and recaptured a month later in the estuary grew twice as fast, averaging 0·63 mm day^{-1} (1·91% body mass day^{-1}). Average growth was significantly higher for winter parr in the estuary compared to fish that reared in the catchment during the winter ($P < 0.05$). The fish sampled in the estuary in the winter were also significantly longer (average 102·5 mm L_F) than the fish that later arrived at the screw trap in April (average 99·5 mm L_F).

Yearling O. kisutch

Yearling *O. kisutch* that migrated from Salmon River in spring were detected at the PIT array in the 96 Marsh, captured in beach seines in the upper estuary and sampled in beach seines in the lower estuary and at the mouth. Twenty-seven per cent (160) of the yearling smolts marked with a PIT tag at the rotary screw trap in 2010 entered the 96 Marsh. An additional 7% ($n = 96$) of the *O. kisutch* tagged during the 2009 upper catchment population estimate were detected for the first time. The yearlings had a median travel time of 4 days to travel the 4·7 km from the screw trap to the 96 Marsh channel. Yearling *O. kisutch* tagged at the screw trap or in the estuary and recaptured in the estuary or detected on the 96 Marsh antenna had an average minimum residence time of 13 days and a range from 2 to 34 days. The yearling *O. kisutch* grew quickly in the estuary at an average rate of 0·7 mm day^{-1} and 2·0% of body mass day^{-1} and were significantly larger at ocean entry than fish collected in the estuary in the winter or the screw trap in the spring ($P < 0.05$). Ocean-bound juvenile *O. kisutch* ranged up to 165 mm L_F. Yearling *O. kisutch* were rarely sampled after June.

LIFE-HISTORY PATTERNS OF JUVENILE *O. KISUTCH*

Rearing and migration strategies by juvenile *O. kisutch* in the Salmon River basin were categorized by the migration size, timing and residency of individuals sampled at the screw trap and PIT array near the head of tide and at multiple estuary beach
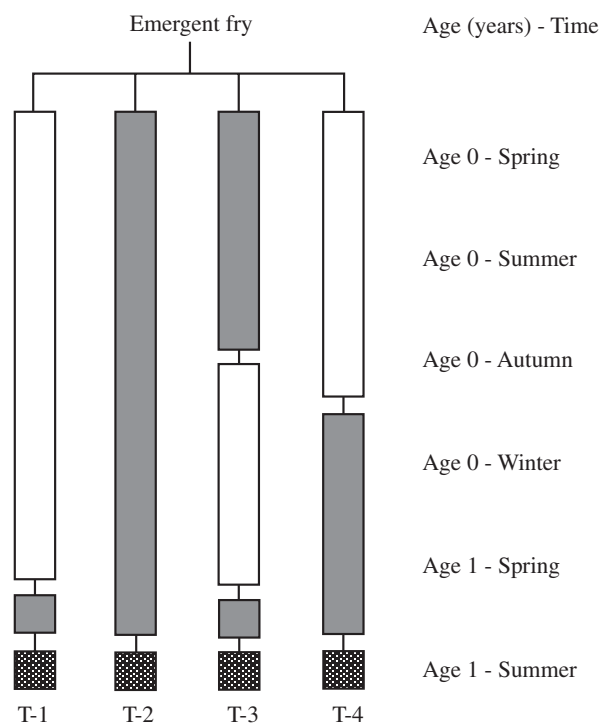

Fig. 8. Potential life-history pathways of juvenile *Oncorhynchus kisutch* in the Salmon River from emergence to ocean entrance. ☐, Stream and tidal fresh environments; ▨, estuary; ▨, ocean.
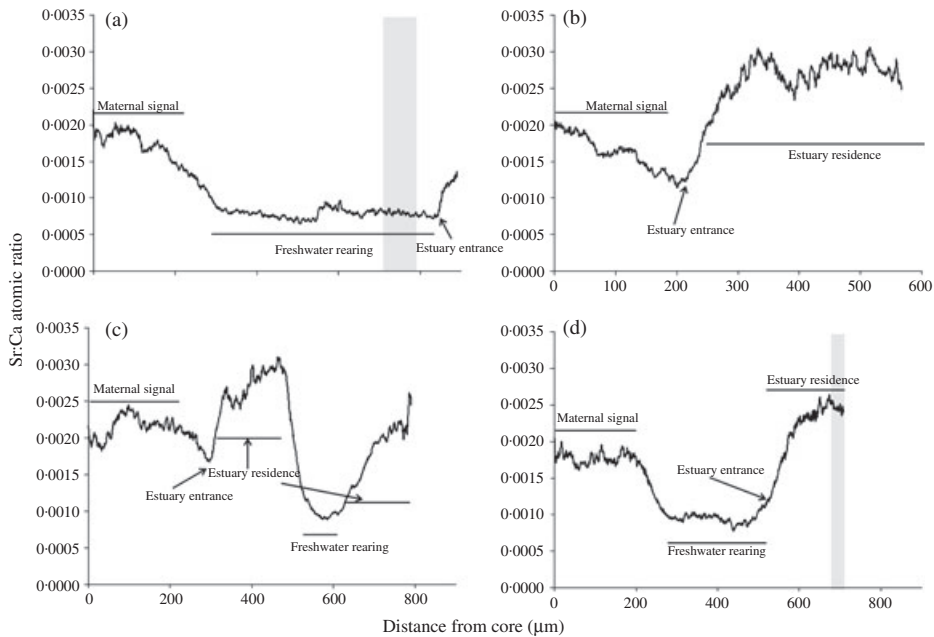
FIG. 9. Chemical transects of juvenile *Oncorhynchus kisutch* otoliths representing four life-history patterns: (a) yearling spring migrant (type 1), (b) fry migrant (type 2), (c) nomad (type 3) and (d) parr migrant (type 4). The *x*-axis is distance from the otolith core and the *y*-axis is Sr:Ca. The fry migrant was captured in the mid-estuary at a size smaller than the other three and prior to formation of the first annulus. The nomad was also captured prior to formation of the first annulus. ▮, First winter annulus.

seine sites (Fig. 8). The time elapsed between marking and recapture (or detection) of PIT-tagged fish (Table V) and the otolith chemical patterns of unmarked juveniles (Fig. 9) identified at least four juvenile life-history types within the Salmon River population: (1) yearling migrant, 1 year rearing in streams (non-tidal) before migrating to the estuary and ocean in the spring (>80 mm L_F at estuary entrance), (2) fry migrant, enter the estuary soon after emergence in the spring or early summer (35–50 mm L_F), reside in the estuary summer to winter and enter the ocean the following spring, (3) fry migrant nomad, enter the estuary in the spring or summer (<65 mm L_F), return to fresh water (streams) in the autumn and winter, and re-enter the estuary and ocean in the spring at age 1 years [defined by Koski (2009) as a nomad] and (4) parr migrant, enter the estuary in the autumn or winter (>75 mm L_F), remain in the estuary during the winter and enter the ocean in the spring at age 1 years.

The collection of otoliths at the mouth may not represent a statistical sample of the proportion of life-history types because the number of fish retained for microchemical analysis was necessarily limited. Nomad (type 3) and parr migrant (type 4) life histories were observed in 18% of the otoliths. Counts of daily increments on the juvenile otoliths also allowed greater precision in determining the residence times of each individual than recapture of tagged individuals (which only provides residence time between capture events). Nomads (type 3) generally arrived as subyearling fry at 60 mm L_F (median), then moved to fresh water during the winter, whereas parr migrants (type
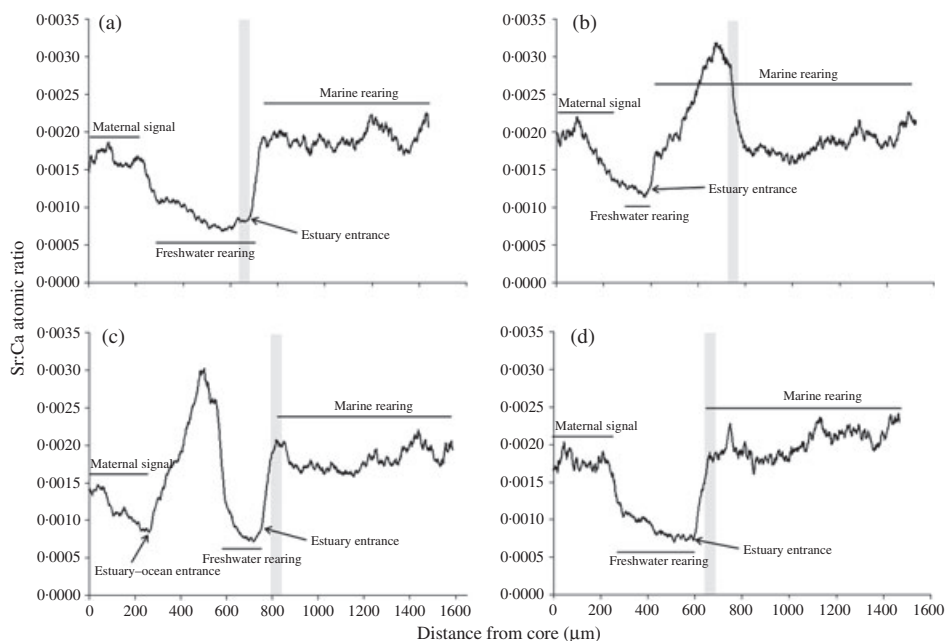
FIG. 10. Chemical transects of adult *Oncorhynchus kisutch* otoliths representing four juvenile life-history pat-
terns: (a) yearling spring migrant (type 1), (b) fry migrant (type 2), (c) nomad (type 3) and (d) parr migrant
(type 4). The *x*-axis is distance from the otolith core and the *y*-axis is Sr:Ca. ▮, First winter annulus.

4) arrived in the autumn or winter at a median size of 97 mm and remained in the estu-
ary for up to 101 days (Table V). Eight of the autumn and winter parr migrants entered
the estuary after the winter annulus was laid down. Based on backcalculating the date
of entry, the annulus may begin forming in November and December.

FRESHWATER AND ESTUARY-REARING PATTERNS OF RETURNING ADULT *O. KISUTCH*

The juvenile life histories represented in the spawning population at Salmon River
were similar to those classified from the juvenile sampling (Fig. 8). Juvenile life-history
patterns in the adult population were identified from the combined results of otolith
chemical analyses, scale analysis (age at return) and PIT detections (Fig. 8).

The strontium:calcium signals on adult otoliths indicated four principal patterns of
juvenile migration to the estuary, types 1, 2, 3 and 4 (Fig. 10). The Sr level of fry (fry
migrants and nomads) is elevated during the first year in salt water relative to the level
after the 1 year annulus. At age 1 year, the Sr levels of all migrant types are similar.
Backcalculation of L_F at saltwater entry indicated that yearling migrants entered the
estuary at an average 106 mm (range 82–142 mm), fry at 44 mm (range 35–66 mm)
and autumn and winter parr at 88 mm (range 73–101 mm), similar to the L_F frequency
of juvenile *O. kisutch* observed in the field sampling (Fig. 3) and to the L_F of the juvenile
fish at estuary entry interpreted from otoliths (Table V). The yearling migrant strat-
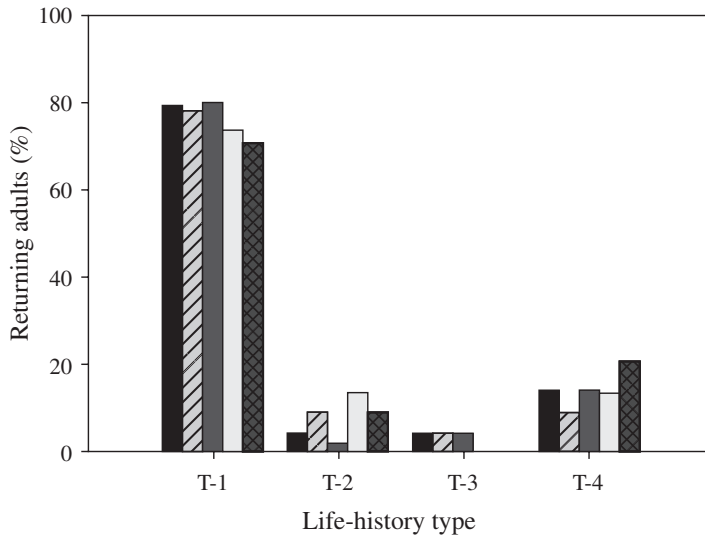egy (type 1) contributed 65–80% of the returns to the spawning grounds (Fig. 11).

FIG. 11. Estimated per cent contribution of each juvenile life-history type to adult *Oncorhynchus kisutch* returns in Salmon River, 2008–2011. Independent estimates are derived from results of otolith chemical analyses and passive integrated transponder tag detections. ■, Otolith 2008, $n=28$; ▨, otolith 2009, $n=45$; ■, otolith 2010, $n=49$; □, PIT 2010, $n=34$; ■, PIT 2011, $n=45$. Life-history types (T) 1–4. No type 3 *O. kisutch* were discerned at the PIT antenna in 2010 and 2011.

Cumulatively, subyearling strategies (Fig. 8) accounted for 20–35% of the total spawning population (Fig. 11) each year. The proportion of migrant parr life histories among returning adults may have been underestimated because yearling migrants (type 1) were defined as entering the estuary during or after the first annulus was formed. Data from the juvenile otolith analysis suggested that some parr migrants (type 4) already had formed an annulus on the otolith before entering the estuary in the winter. All spawners collected on the spawning grounds and used for the otolith analysis returned as 3 year-old adults.

   Returning adults detected at the PIT antenna at rkm 8 in 2010 and 2011 indicated similar juvenile rearing and migration patterns as those defined by juvenile field sampling and otolith chemistry (Figs 8 and 11). Insufficient recapture events may account for an absence of the nomad life history among tagged adults. Yearling migrants that were tagged at the screw trap or in the estuary in the spring and returned as 3 year olds represented the predominant life-history type (Fig. 11). Based on original tagging location and detection at the hatchery weir antenna, 35% of the returning adults showed evidence of some estuary rearing.

   Otolith analyses of six tagged adults that were recovered on the spawning grounds allowed cross-validation (otolith microchemistry and PIT detections) of several of the proposed life-history types. The classification based on otolith chemistry of four individuals tagged as yearling migrants (type 1) was consistent with the time, size and location of tagging and detections during juvenile outmigration. Otolith chemistry also identified a single nomad (type 2) that had entered the estuary as a fry (<50 mm L_F), migrated back into fresh water and later re-entered salt water at *c*. 95 mm L_F during winter and spring of the following year (Fig. 10). This individual was first captured

and tagged in the 96 Marsh at 68 mm L_F, consistent with the interpretation of early estuary entry and possible nomad life history. One tagged individual recovered on the spawning grounds was classified by otolith chemistry as a type 4 fish (subyearling autumn migrant). Estimated L_F at saltwater entry was *c.*79 mm during the late autumn or early winter. The same individual was captured and tagged in the mid-estuary (87 Marsh) in winter at 90 mm L_F.

SURVIVAL FROM JUVENILE TO ADULT

Survival of 2007 and 2008 brood *O. kisutch* varied by tag group as estimated from recapture history and final detections at the hatchery weir antenna or recovery on the spawning grounds in 2010 and 2011. The capture events allowed evaluation of survival rates of subyearling fry, subyearling parr tagged in the estuary and yearling *O. kisutch* tagged at the screw trap or in the estuary. Nomads (type 3) and early return fish (jacks) did not have enough recapture events or locations to assess survival of this type. Survival as estimated with Cormack–Jolly–Seber (CJS) model indicated that life-history types 1, 2 and 4 had enough recaptures and adult returns to calculate survival to adult.

The best model, selected by DIC, indicated that no significant difference in survival (delta DIC <1) was detected between 2010 and 2011, allowing the CJS model to draw on both years of data to estimate survival of each life-history type across brood years. Subyearling fry, tagged at the screw trap or in the estuary at sizes >65 mm L_F (type 2), survived to 3 year-old adult at a rate of 1·5%. Subyearling *O. kisutch* that overwintered in the estuary (type 4) survived at 3·2% and yearling *O. kisutch* tagged at the screw trap (type 1) survived at an average of 4·4%. Fish tagged as yearlings in the estuary had the highest survival at 6·8%. These fish could be a combination of types 1, 2, 3 and 4.

DISCUSSION

Juvenile *O. kisutch* in the Salmon River basin exhibited a greater diversity of rearing behaviours than the conventional yearling-smolt life-history model would indicate. Four juvenile life-history pathways contributed to the adult *O. kisutch* population in the Salmon River based on the field observations, otolith analyses and the PIT detection results. These results demonstrate that (1) juvenile *O. kisutch* can express a variety of alternative rearing and migration patterns to fully utilize all available habitat opportunities throughout a catchment, (2) juveniles that leave natal streams in their first year of life are not lost to the population but represent alternative life histories that may contribute significantly to adult returns and (3) a diversity of sizes and ages of juvenile *O. kisutch* occur in the estuary all months of the year, and some individuals may remain there for weeks or months before entering the ocean. These results further support the hypothesis that extensive tidal marsh restoration since 1978 has enhanced phenotypic variation in the Salmon River population by allowing *O. kisutch* to fully exploit the estuary and express subyearling-migrant life histories.

The life-history pathways of juvenile *O. kisutch* reflected the diversity of freshwater- and estuarine-rearing opportunities throughout the Salmon River basin. The typical yearling riverine life history, composed of juveniles that reside in the river year round, was most prominent during each of the 4 years of study. Other life histories

encompassed a wider range of habitats and seasons and demonstrated a larger role for estuary habitats in *O. kisutch* diversity and productivity than has been traditionally recognized, including: nomads that alternate between freshwater and estuary rearing; parr migrants that enter the estuary late in the year after the first autumn freshets: subyearlings that overwinter in the estuary and migrate to sea as yearlings the following spring. Minimum estuary residency estimates for subyearling *O. kisutch* during summer and winter ranged from weeks to months, comparable to the range of residence times reported for Salmon River *O. tshawytscha* (Volk *et al.*, 2010). In total, otolith results and PIT detections indicate that juveniles with estuary-resident life histories (types 2, 3 and 4) accounted for as much as one third of all *O. kisutch* spawners returning to the Salmon River.

Variations in the duration of ocean residency and the ages of *O. kisutch* adults returning to Salmon River could add further complexity to each juvenile life history. In addition to the typical 3 year-old adult pattern, 2 year-old precocious males (jacks) could return from any of the juvenile pathways. The jack life-history pattern has been well established in other *O. kisutch* populations (Sandercock, 1991; Nickelson & Lawson, 1998). Prior to this study, the contributions of the other three juvenile life histories to adult populations were unknown (Koski, 2009), but these types could produce jacks as well as 3 year-old adults. Four juvenile fish returned at 2 years of age. Two were tagged as yearlings and returned as jacks after one summer in the ocean. The other two were tagged as subyearling fry in the estuary. From the information analysed to date, it remains unclear whether the latter two emergent fry entered the ocean as subyearlings and returned as 2 year-old adults (*i.e.* an additional life-history type) or remained in the estuary for a year and migrated to the ocean as yearlings (type 2), returning as jacks following one summer in the ocean.

The drivers of the fry and parr migrations to the estuary are not well understood. The migration may have resulted from density-dependent interactions (Chapman, 1962), limited winter rearing capacity (Nickelson *et al.*, 1993) or high flows (Tschaplinski, 1987), or could represent an adaptive life-history strategy (Healey, 1991; Quinn, 2005). What is apparent is that the fry and parr that migrated and survived the transition to the estuarine environment had suitable habitat to rear until migrating to the ocean as yearling smolts.

Fry migrants are commonly observed in many river basins but adult survival of this life-history strategy has not been documented (Koski, 2009). In Salmon River, fry were able to reside in the 96 Marsh through the summer even as the salinity exceeded 20 in September and October. Subyearling *O. kisutch* grew in the 96 Marsh at rates comparable to those observed in freshwater streams and fry tagged at the screw trap or in the estuary during spring or summer returned as adults at an estimated rate of 1·5% in 2010 and 2011. This rate represents the survival of individuals that had already reached 65 mm L_F (*i.e.* the minimum threshold to allow tagging) and is a small proportion of all subyearling fish observed at the screw trap. Many of the fry that migrated past the screw trap in the spring probably perished prior to reaching 65 mm L_F, although some may have migrated to small freshwater tributaries that directly enter the estuary and others resided in the 96 Marsh.

The autumn and winter migrants originated from streams throughout the catchment, tagged in both high and low-quality habitats. No significant difference in size at tagging in August to September was apparent among the juveniles that entered the estuary later

that autumn or winter compared with yearling smolts that entered in the spring. The proportion of autumn and winter migrants was similar to that observed in East Twin River (Washington), although the size differential reported in that study between migrants and non-migrants was not evident in Salmon River (Bennett *et al.*, 2011; Roni *et al.*, 2012). The fate of autumn and winter migrant parr was uncertain in other river basins (Koski, 2009), but in Salmon River, many parr established residence in the estuary.

In Oregon coastal basins including the Salmon River, complex overwinter habitat is potentially limiting to *O. kisutch* populations (Nickelson *et al.*, 1992; Solazzi *et al.*, 2000; Rodgers *et al.*, 2005). The consistent outmigration of *c.*20000 smolts may represent the current rearing capacity of the occupied freshwater habitat in Salmon River. Survival from summer parr to migrant smolts the following spring requires complex, slow-water habitat, including pools with wood jams, beaver ponds and off-channel alcoves that provide refuge and promote survival during winter freshets. In the Salmon River basin, high-capacity freshwater habitat that benefits over-winter survival occurs primarily in the upper main stem and in the Little Salmon River. No estimates of summer parr populations are available for 2000–2002, but the number of *O. kisutch* yearlings migrating out of the system ranged from 7000 to 16 000 (Aquatic Inventories Program, ODFW, unpubl. data). It seems likely that the potential winter-rearing capacity of the occupied stream reaches in the Salmon River basin may be fully realized at *c.* 20 000 fish.

Winter-rearing habitat in the estuary may contribute significantly to the productivity of the *O. kisutch* population since the summer population (Table III) exceeds the apparent capacity of the winter stream habitat. Small numbers of juvenile *O. kisutch* now utilize the estuary's main channel during the winter but their primary habitats are off-channel areas of the 96 and 87 Marshes and the small tributary confluences at the margins of the estuary. Tagged juvenile *O. kisutch* actively migrated between the main estuary channel and the marshes. Rarely were *O. kisutch* captured at the estuary mouth except for yearling smolts that were present April to early July, suggesting that late autumn to winter migrants remained in the estuary until spring. High growth rates indicate that the estuary provided productive feeding conditions for winter residents, which may explain the relatively high rate of survival to adult (3·2%) among tagged autumn to winter migrants.

Until the largest tidal wetlands were restored in 1987 and 1996, the production of Salmon River *O. kisutch* would have depended primarily on winter-rearing opportunities in streams. During salmonid life-history studies in 1975–1977, all major expanses of estuarine wetland (except for the reference marsh) were blocked by dykes and tide-gates, and subyearling *O. kisutch* were rarely captured in the tidally influenced areas (Fig. 12) except in the main-stem river above the 96 Marsh (Mullen 1979). Mullen (1979) did not sample in the estuary from December to March, although recent survey results suggest that few juvenile *O. kisutch* likely reared in the main-stem estuary channel. The estuary now provides additional off-channel rearing opportunities for the population to express estuary-resident life histories (Fig. 12). A similar phenotypic response to wetland dyke removal has been shown for the Salmon River *O. tshawytscha* population. Fry and fingerling *O. tshawytscha* now migrate to the estuary to rear early in the spring and summer, life-history patterns that were not evident in the population when most of the wetlands were dyked and inaccessible to juvenile migrants
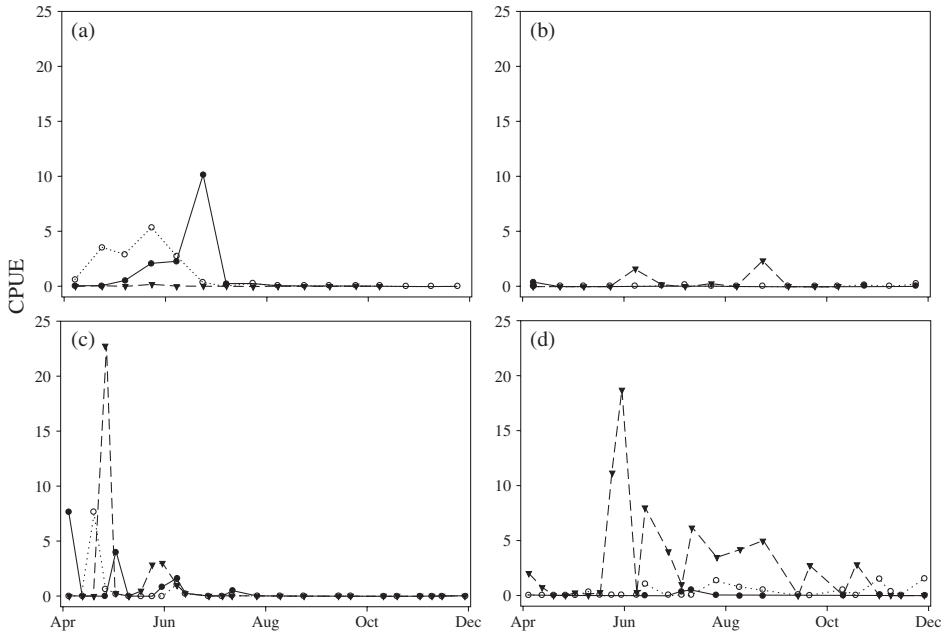
FIG. 12. Catch-per-unit-effort (CPUE) of (a) yearling and (b) subyearling *Oncorhynchus kisutch* in 1975–1977 and (c) yearling and (d) subyearling *O. kisutch* in 2011 in the upper (▼), mid (○) and lower (●) estuary during beach seine surveys. The 1975–1977 data were collected by Mullen (1979).

(Bottom *et al.*, 2005; Volk *et al.*, 2010). Juvenile *O. kisutch* at Salmon River now utilize restored tidal wetlands throughout much of the year, including late in the autumn and winter after juvenile *O. tshawytscha* have left the basin.

All life-history types observed in the juvenile *O. kisutch* population at Salmon River also were represented in the adult population. Yet, the additional production and diversity supported by estuary habitats is ignored by conventional *O. kisutch* production models, which assume a single life-history pathway (yearling riverine smolts) and estimate capacity from the wadeable-stream portion of the basin only (Sandercock, 1991; Nickelson & Lawson, 1998). The assumption that the early-migrant *O. kisutch* are insignificant population constituents that do not contribute to adult returns (Chapman, 1962; Crone & Bond, 1976; Sandercock, 1991) may not hold in catchments with productive and diverse estuaries.

This study reinforces other recent reports of phenotypic variation in *O. kisutch* populations (Koski, 2009; Bennett *et al.*, 2011; Roni *et al.*, 2012). As far as is known, this is the first research to quantify the contributions of diverse juvenile life histories to adult returns, including life histories and adult survivors that are directly linked to estuary habitats. These results underscore the importance of habitat connections that allow for the fullest possible phenotypic expression in salmonid populations. Access to off-channel habitats in the upper reaches of estuaries may be particularly important to sustain subyearling migrant life histories that require early transition and extended rearing in tidal or saline environments. At the same time, estuary connections to lower-basin tributaries are necessary to support the nomad life history, which involves re-entry of estuary migrants back into fresh water. In the Salmon River, full expression

of the nomad life history remains impeded by some historical alterations. For example, although dyke removal at the mouth of the 96 marsh has restored juvenile access to an important upper-estuary wetland habitat, highway construction that disconnected the 96 Marsh from its freshwater source (*i.e.* Salmon Creek) >50 years ago continues to block the upstream movement of any marsh-resident nomads.

Life-history diversity in *Oncorhynchus* spp. has been described as an example of response diversity in which variations in phenotypic behaviour confer resilience to populations under changing environmental conditions (Elmqvist *et al.*, 2003; Bottom *et al.*, 2009; Moore *et al.*, 2010). Spatial and life-history variations within and among populations have been shown to buffer fluctuations in sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) and *O. tshawytscha* (Hilborn *et al.*, 2003; Greene *et al.*, 2010; Moore *et al.*, 2010; Schindler *et al.*, 2010; Thorson *et al.*, 2013). The Salmon River results demonstrate that, even within a small watershed, *O. kisutch* can express considerable variation in their migratory pathways and rearing environments. Such variations constitute a high level of response diversity, spreading mortality risks in time and space. The results further suggest that the productive capacity of the basin for *O. kisutch* is also a function of phenotypic diversity. Estuary restoration has re-established a variety of habitats capable of rearing juveniles that were not supported by stream habitats in the upper basin. Under the environmental conditions experienced during this survey, estuarine wetlands accounted for as much as 30% of the adult *O. kisutch* that now return to spawn in Salmon River. These results suggest that life-history diversity and the habitat opportunities that sustain it are fundamental to the productivity as well as the resilience of Salmon River *O. kisutch*.

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