

Interannual variability in life-stage specific survival and life history diversity of coho salmon in a coastal Oregon basin

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Abstract: We quantified the population dynamics and life history diversity of seven brood years of coho salmon (*Oncorhynchus kisutch*) using a life-cycle approach. Four life history patterns, composed of fry, fry–nomad, parr, and yearling migrants indicated the importance of connectivity and access to a full range of freshwater and estuarine rearing environments through the year. Survival of each life history type varied annually with the yearling migrants contributing an average of 70% to the spawners in all but one return year. Fifty-eight percent of the spawners of the 2013 return year had an estuarine rearing strategy, primarily parr migrants that overwintered in the estuary. Fry migrants, thought to be surplus production, were consistently observed in the estuary and represented in the returning spawners. The annual contribution of alternative rearing strategies to the spawners may support the resilience and viability of the population. We recommend that life cycle models of coho salmon account for the contribution of estuary migrants to the productivity and persistence of coho salmon in support of management and restoration of populations.

Résumé : Nous avons quantifié la dynamique de la population et la diversité des cycles biologiques de saumons cohos (*Oncorhynchus kisutch*) de sept années d'éclosion en utilisant une approche axée sur le cycle biologique. Quatre types de cycles biologiques composés d'alevins, d'alevins nomades, de tacons et de migrants d'un an, font ressortir l'importance de la connectivité et de l'accès à tout un éventail de milieux de croissance estuariens et d'eau douce au fil de l'année. Pour chacun des types de cycles biologiques, la survie varie annuellement, les migrants d'un an comptant en moyenne pour 70 % des géniteurs pour toutes les années de retour sauf une. Cinquante-huit pour cent des géniteurs de l'année de retour 2013 présentaient une stratégie de croissance estuarienne, principalement des tacons migrants qui passaient l'hiver dans l'estuaire. Des alevins migrants, qui constitueraient une production excédentaire, étaient uniformément observés dans l'estuaire et représentés au sein des géniteurs de retour. Les contributions annuelles de différentes stratégies de croissance au nombre des géniteurs pourraient appuyer la résilience et la variabilité de la population. Nous recommandons que des modèles de cycle biologique du saumon coho soient utilisés pour expliquer la contribution des individus à migration estuarienne à la productivité et à la persistance des saumons cohos afin d'appuyer la gestion et le rétablissement des populations. [Traduit par la Rédaction]

Introduction

Life history variations in juvenile coho salmon may represent alternative pathways that strengthen population resilience and viability in light of habitat loss and environmental change, as has been shown for Chinook salmon (*Oncorhynchus tshawytscha*) (Reimers 1973; Healey 1991), sockeye salmon (*Oncorhynchus nerka*) (Hilborn et al. 2003; Greene et al. 2010), and steelhead (*Oncorhynchus mykiss*) (Moore et al. 2014). Alternative juvenile life histories in many anadromous fish populations involve partial migration of population members (contingents; Kerr and Secor 2010) from fresh water into estuaries, spreading survival risks during vulnerable early life stages (Kerr and Secor 2012). For example, the majority contingents in populations of Chinook salmon (Reimers 1973; Healey 1991) disperse downstream to forage and grow in productive estuarine environments while minority contingents remain as freshwater residents; white perch (*Morone americana*) display partial migration although use of fresh and estuarine environments by majority and minority contingents varied by population (Kerr and Secor 2012); and striped bass (*Morone saxatilis*) exhibit diverse migratory patterns between and

within contingents (Gahagan et al. 2015). In contrast, partial migrations within coho salmon (*Oncorhynchus kisutch*) populations are exemplified by majority resident and minority migratory contingents in their first year, yet it is unclear how the migratory contingents contribute to the spawners. The contributions of divergent migration behaviors to the dynamics of coho salmon has not been explored in population models. Management and restoration of coho salmon populations are based solely on the estimated contribution of a single freshwater-resident recruitment pathway (e.g., Nickelson and Lawson 1998; Lawson et al. 2004; Falcy and Suring 2018; Ohlberger et al. 2019) ignoring other pathways that may contribute to the stability and persistence of coho salmon populations, including Oregon coastal coho salmon, presently listed as threatened under the Endangered Species Act (ESA).

Population and habitat models for coho salmon assume a fixed yearling smolt life history in which all juveniles that contribute to the adult recruits rear in fresh water for a full year and migrate rapidly to the ocean in their second spring (Sandercock 1992; Nickelson and Lawson 1998). Habitat models to estimate the rearing capacity of stream habitats for juvenile coho salmon during spring, summer

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and winter concluded that winter rearing habitat in streams was in most cases limiting freshwater production (Reeves et al. 1989; Nickelson et al. 1992, 1993) leading to habitat restoration recommendations focused on winter rearing habitat (Solazzi et al. 2000; ODFW 2007) and as a key component in life-cycle models to estimate extinction risks for coastal Oregon populations (Nickelson and Lawson 1998). Population models also reveal that mortality of juvenile coho salmon during the first months after ocean entry (Scarnecchia 1981; Nickelson 1986) may determine year class strength (Beamish et al. 2004; Lawson et al. 2004). Ocean survival and recruitment has been correlated with various physical factors, including upwelling and sea surface temperatures (Nickelson 1986; Cole 2000), and tied to broad-scale ocean environmental and climate indices (Lawson 2004). Population models based on the yearling smolt life history incorporate two primary limitations (bottlenecks) to the productivity of coho salmon populations: survival during winter rearing in streams and survival during the first few months following ocean entry. Although high mortality of juvenile steelhead and Chinook salmon has been observed in estuaries prior to ocean entry (Johnson et al. 2010; Harnish et al. 2012; Romer et al. 2013) and postulated for juvenile coho salmon (Nickelson 2003), the estuary environment has not been bracketed, but considered as part of ocean entry in population models.

Until recently, few studies have considered deviations from the yearling smolt life history strategy in coho salmon or investigated lower river and estuarine habitats that provide a transition between stream and ocean environments. Historically, coho salmon observed leaving their natal streams in large numbers soon after emergence were considered “surplus” to the population and were not expected to survive (Chapman 1962; Tschaplinski 1987). However, recent studies have reported juvenile coho salmon rearing in estuaries of the Northeastern Pacific Ocean and Salish Sea, from California (Rebenack et al. 2015; Wallace et al. 2015), Oregon and Washington (Miller and Sadro 2003; Craig et al. 2014; Jones et al. 2014; Nordholm 2014; Johnson et al. 2015; Weybright and Giannico 2018), to British Columbia and SE Alaska (Koski 2009; Hoem Neher et al. 2013). These authors suggested that estuary rearing is common, although uncertainty exists around relative performance and fate of these juvenile coho salmon after leaving the stream environment.

Juvenile coho salmon leave natal streams during three periods and have been observed in tidal environments in the first spring as fry, fall–winter as parr, and the following spring as yearling smolts (e.g., Miller and Sadro 2003; Koski 2009; Jones et al. 2014). This movement to the estuary may be a result of high flows, competition for space or food resources, or a directed movement as part of their life history. While many fry migrants remain in the estuary during the fall and winter, some move back into streams when fall rains arrive, referred to as “fry–nomad migrants” (Miller and Sadro 2003; Koski 2009). Three studies provide evidence that some subyearling (fry and parr) migrants do not perish and are not “surplus” production. Nordholm (2014) documented returns of coho salmon spawners with estuarine rearing life histories in a tide-gated tributary of Coos Bay in southern Oregon. Bennett et al. (2014) estimated the contribution of migrants to coho salmon spawners that had entered the Salish Sea directly from tributaries on the north side of the Olympic Peninsula during the fall and winter. Jones et al. (2014) identified three estuary migrant types (fry migrants, fry–nomad migrants, and parr migrants) that contributed to the spawners in Salmon River. These studies suggest that the potential production from estuarine rearing strategies may have a beneficial influence on population dynamics.

Salmon River on the central Oregon coast provides a novel opportunity to examine the contribution of multiple life history pathways across multiple generations. The basin supports a potentially self-sustaining or “independent” population of coho salmon (McElhany et al. 2000; Chilcote et al. 2005; Lawson et al. 2007) yet is small enough to allow robust sampling of fish in freshwater and tidal environments to quantify migratory patterns and

population dynamics. The initial four years of this study in Salmon River were published in Jones et al. (2014) and focused on size and time at migration, habitat use, growth, estuary residency, and life history diversity. Life history strategies (Fig. 1) were determined through structural and chemical analysis of otoliths from juveniles at ocean entry and spawners returning in 2008–2010, and through tagging of juveniles and recovery and detection of spawners in 2010 and 2011.

Here we evaluate annual variation in abundance and survival of each life history strategy across seven years to build a life cycle model inclusive of all migrant types of coho salmon. We build on earlier findings by extending the years of monitoring coupled with more extensive sampling, tagging and detection to describe population dynamics and life history contributions to the spawning population. We (1) estimate population abundance in each rearing environment during the juvenile life stages (fry, parr, yearling, smolt), (2) describe migration timing from fresh water to estuary to ocean, (3) calculate survival between life stages and cumulatively to spawner, and (4) estimate the contribution of each life history type to the spawners. The sampling and analyses across habitat types (stream, estuary, ocean) and life history strategies provide population and landscape scale perspectives.

Methods

Salmon River is a 195 km² basin on the central Oregon coast (USA) (Fig. 2) with 81 and 110 km of coho salmon spawning and freshwater rearing habitat, respectively. The basin is similar to other catchments on the Oregon coast; it has a mix of federal, state, and private land ownership with rural residential areas concentrated along the lower river. It differs, however, in that the estuary is managed and protected as part of the Cascade Head Scenic Research Area established in 1974, and the central 19.3 km of the Salmon River main stem has been protected in the H.B. Van Duzer Forest State Scenic Corridor since 1935. The 800 ha estuary has been extensively restored to a near natural condition through a series of large dike-removal projects that re-established estuary connections to ~175 ha (70%) of the historical tidal marsh habitat (~250 ha) from 1978–2014 (Flitcroft et al. 2016). The head of tide extends to river kilometre (rkm) 6.5, and a hatchery and weir are located at rkm 8 (Fig. 3). The weir does not impede downstream movement of juvenile fish. However, returning spawners are forced to the north side of the weir to pass upstream around the weir or enter the hatchery (for release back into the river) in the early fall but returning spawners can pass over the weir when river flows increase later in the fall. Of the 110 km of rearing habitat, 77% (85 km) are located above the weir. Other tributaries enter Salmon River below the weir or flow directly into the estuary. The estuary experiences high freshwater input October through April with peak flow events ranging from 25 to 150 m³·s⁻¹, reducing the salinity, except in the zone close to the ocean. Low flows range from 0.7 to 1.4 m³·s⁻¹ allowing highly saline water up to the 96 Marsh at rkm 5 during the summer (Cornwell et al. 2001). Tidal range is up to 3 m.

Most coho salmon in Oregon exhibit a 3-year life cycle (Nickelson and Lawson 1998). Coho salmon return to and spawn in Oregon coastal watersheds from early September through late January. The fry emerge from the gravel in spring and are generally less than 60 mm in length during March through May, but transition to parr by June. Parr are subyearling fish that range in size up to 90 mm in streams during the summer, and up to 140 mm in the estuary through February (Jones et al. 2014). We consider coho salmon as yearling fish beginning in March of their 2nd year and as smolts immediately prior to entering the ocean. Following the convention in Jones et al. (2014), the four life history types identified in Salmon River based on migration timing to the estuary include: fry migrants, fry–nomad migrants, parr migrants, and yearling migrants (Fig. 1). The fry migrants entered the estuary at age-0 in the spring and early summer and migrated to the ocean the following spring as yearlings.

Fig. 2. Salmon River basin and estuary. Juvenile rearing and spawning survey sites were distributed throughout the coho salmon distribution (OASIS 2019). The inset map of Oregon shows the location of the Salmon River basin. The map was created using ArcMap 10.8.1 (Esri, Redlands, California, USA). Credits: 10 m DEM base layer (USGS), hatchery site (ODFW), *O. kisutch* distribution (ODFW), boundaries (ODFW), PIT array (ODFW).

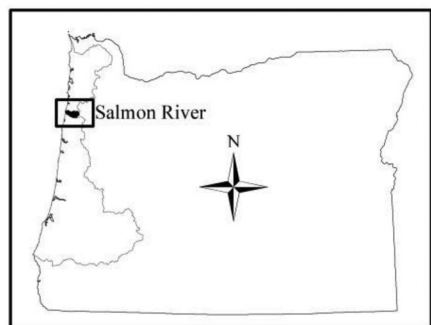
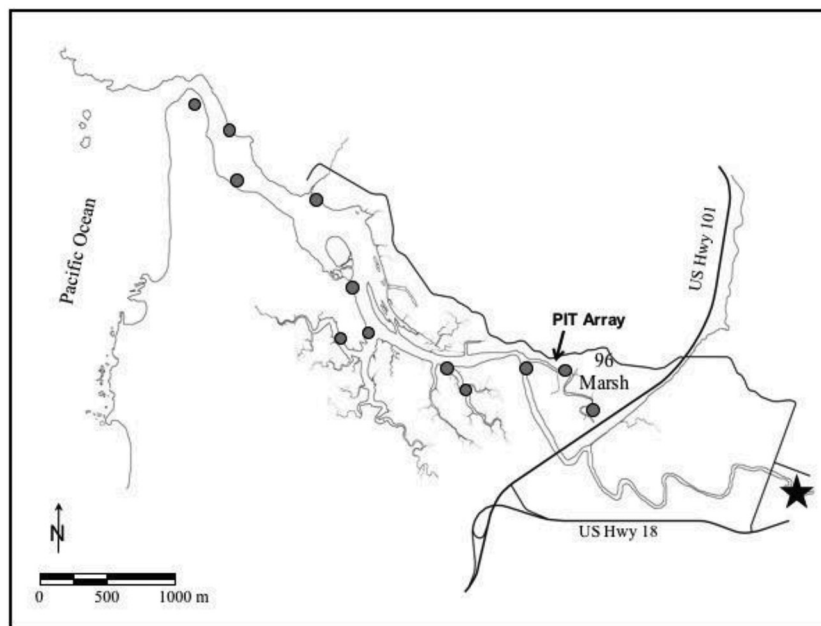


Fig. 3. Map of Salmon River estuary. The hatchery, screw trap, and a PIT array are located at rkm 8 (indicated by star), a PIT array is located in the 96 Marsh, and beach seine locations are indicated by filled circles. The head of tide extends to 1.5 km below the hatchery. The map was created using ArcMap 10.8.1 (Esri, Redlands, California, USA). Credits: 10 m DEM base layer (USGS), hatchery site (ODFW), beach seine sites (ODFW), boundaries (ODFW), PIT array (ODFW).



The fry-nomad migrants entered the estuary as fry migrants, re-entered estuary tributaries in the fall or winter, and returned to the estuary in the spring as yearlings. The parr migrants moved from the streams to the estuary at age-0 (>75 mm) with the first fall and winter rains. The yearling migrants remained in streams throughout the basin until age-1, entering the estuary in late spring. All juvenile life history types entered the ocean in the spring at age-1 and returned 18 months later at age-3.

The age-2 jacks (precocial males) were excluded from the analysis because very few tagged jacks were detected returning and jacks are rarely collected on the spawning grounds (Chilcote et al. 2005) to permit otolith analyses. However, jacks may represent up to 7.5% of the returning populations (Jones et al. 2018). No 2-year-old spawners were observed.

We refer to brood year (BY) as the year of spawning when eggs are deposited in the gravel and the return year (RY) as the year adults return to spawn. For example, a 3-year-old spawner that returned in fall of 2013 was produced in brood year 2010. The study began in 2008 with sampling of spawners in 2008 (2005 BY) and yearling juveniles produced in 2006 (2006 BY) that migrated to the estuary and ocean in 2008. We sampled all life stages produced in 2007 through 2011 (fry, parr, and yearling migrants), concluding with the return of spawners in 2014.

Spawner sampling and abundance

We obtained spawner abundance time series data for 2005–2014 for Salmon River from Oregon Department of Fish and Wildlife's Oregon Adult Salmonid Inventory and Sampling Program (OASIS 2019). Sites were selected using a generalized random tessellation stratified (GRTS) design within the spawning distribution of coho salmon to survey 15%–20% of the 81 km distribution annually (Fig. 2). Sites were visited from mid-October through January every 10 or fewer days to estimate abundance for each site using area under the curve method (Jacobs et al. 2002). During the surveys, carcasses were scanned for passive integrated transponder (PIT) tags. The GRTS design and analysis uses site weight and a local neighborhood (LNB) estimator to provide an unbiased estimate of the spawning population each year

(Jacobs et al. 2002; Stevens and Olsen 2003, 2004; OASIS 2019; Sounhein et al. 2019).

The hatchery program was terminated following the return of hatchery spawners (100% adipose fin clipped) in 2008 (Jones et al. 2018). The wild-origin spawners in 2008 were identified by the presence of an adipose fin. The juvenile coho salmon reported in this study were naturally produced although the spawners were a mix of hatchery-origin and wild spawners in 2005–2008 (Jones et al. 2018). All spawners in 2009–2011 were produced from natural-origin (wild) spawners.

Juvenile sampling and abundance

We empirically estimated the abundance of fish entering the estuary at two life stages, age-0 fry and age-1 smolts by capturing and enumerating migrants at a 1.5 m diameter screw trap placed in the lower river at rkm 7.9, 1.4 km above the head of tide (Fig. 2). The trap operated from mid-March through June (2008–2011) and through July (2012–2013). Trap deployment was limited by high flows until mid-March and by low flows in later June and July. Trap efficiency was estimated weekly by marking fish and placing them upstream of the trap. Abundance and variance of sub-yearling and yearling migrants were estimated for the migration period following protocols described in Solazzi et al. (2000).

The annual abundance of age-0 parr in streams was estimated by electrofishing depletion (Zippin 1958) or mark-recapture at some of the larger sites (Rodgers et al. 1992) during August and September in 2008–2012. Twenty-five to 30 sites were sampled annually within the 110 km rearing distribution (Fig. 2). Sites were selected using GRTS sampling methodology (Stevens and Olsen 2004), similar to that for spawners. Each site was approximately 20 bankfull channel widths in length (minimum 50 m and maximum 150 m), blocknets were placed at both upstream and downstream boundaries, and backpack electrofishers were used to collect fish. Multiple passes were made until a 67% reduction in catch was achieved, although a 50% reduction was sufficient when fewer than 10 fish were collected. The abundance estimate for each depletion and mark-recapture site was generated using programs CAPTURE (White et al. 1982) and NOREMARK (White 1996), respectively,

standardized to fish·km⁻¹ and expanded to estimate the population abundance and confidence intervals based on the number of kilometres available to juvenile coho salmon, site weight, and a local neighborhood estimator (Stevens and Olsen 2003).

To evaluate migration into and use of estuary habitats (0–5 rkm) through the year, we sampled juvenile coho salmon with a beach seine (38 m × 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 in channel and marsh habitats weekly to bi-weekly (Fig. 3) throughout the year, 2008–2013. The furthest downstream site was on a large sandbar three hundred metres from the ocean (Fig. 3) and was considered the point of ocean entry. Juvenile coho salmon were measured, weighed, and scanned for PIT tags.

Tagging, detection arrays, and migration timing

During all sampling activities in streams and estuary and at the screw trap, full duplex 12.5 mm PIT tags (Biomark TX1411SST 134.2 kHz, 0s*1020 g; www.biomark.com) were placed in coho salmon >65 mm fork length (FL) when captured (Table 1). Between 1765 and 5841 fish were tagged per year, including 200–2000 yearlings in the estuary from March through June prior to leaving for the ocean (Table 1). We documented movement and survival of fry, parr, and yearlings and estimated the contribution of each life history type to spawners using PIT antenna arrays and examining sampled fish. PIT antenna arrays were placed at the hatchery weir (rkm 8.0) and in the 96 Marsh (Fig. 2). The antenna array at the hatchery weir had three antennas each 3.0 m × 1.2 m placed side by side (9 m span) located on the north side of the 40 m wide river. Downstream migration was not impeded by the weir but in the early fall before river levels increased, spawners passed either through the hatchery ladder or passed the antennas on the north side of the weir. The weir PIT array operated continuously from 30 August 2010 through 25 June 2013 and 5 September 2013 through February 2015. Spawners that entered the hatchery were returned to the river and detected at a flat panel receiver (Biomark) in the raceway. The detection system in the 96 Marsh was placed 200 m from the confluence with Salmon River. The 96 Marsh was the first opportunity for downstream migrating fish to move out of the main channel as they entered the estuary. The system consisted of 4 antennas in a single array (12 m total width) that spanned the channel. The array operated from 23 April 2010 through 24 August 2010 and continuously from 19 March 2012 through 30 June 2013. The antennas were powered by a Destron Fearing multiplexing transceiver (Model FS1001M) that could be adjusted based on the salinity in the 96 Marsh. The two arrays detected juvenile coho salmon as they left fresh water, reared in the estuary, and returned as spawners.

Migration timing and survival of juveniles of brood years 2007–2011 tagged in the freshwater and estuarine environments were estimated using the detection history of PIT-tagged juveniles at the PIT arrays at the hatchery weir and the 96 Marsh, and from collections during seining in the estuary. Returning tagged spawners were detected at the PIT array at the hatchery weir (high detection rate during low river levels but unknown rates late in the fall or early winter when the river flowed over the weir), detected when passing through the hatchery ladder (at or close to 100% detection rate), or scanned (spawned out and dead) on the spawning grounds at survey sites.

Because the array at the hatchery weir only spanned a portion of the channel, we relied on repeat detections at the weir and 96 Marsh antennas from March 2012 through June 2013 to calculate an approximate detection rate (path efficiency) of downstream migrating juvenile fish at the weir antenna. Because both arrays were operating simultaneously and continuously for 16 months we could estimate path efficiency for the weir array for fry, parr, and yearling migrants during the year. Both arrays also operated concurrently in spring and summer 2010 to compare path efficiency for yearling migrants in springs 2012 and 2013. These rates were extrapolated to the periods when only the weir antenna was

Table 1. Number of juvenile coho salmon implanted with a PIT tag at each life stage and location.

Brood year	Age-0			Age-1	
	Screw trap	Watershed	Estuary	Screw trap	Estuary
2006	NS	NS	433	1053	291
2007	36	373	600	531	225
2008	199	1286	1155	568	468
2009	57	629	643	809	194
2010	147	742	969	624	872
2011	89	911	1554	1344	1943

Note: Age-0 estuary group includes subyearling fry tagged in the summer and subyearling parr tagged in the autumn–winter. Not sampled designated by “NS”.

operational to estimate the number of juvenile fish that migrated passed the weir into the estuary during the year. The path efficiency of the antenna array at the hatchery weir for downstream migrating juvenile salmon was calculated as 20.7% (Zydlewski et al. 2006):

$$E_{\text{in situ ARRAY1}} = (d_{\text{COMMON TO ARRAYS 1+2}}) \div (d_{\text{UNIQUE TO ARRAY 2}} + d_{\text{COMMON TO ARRAYS 1+2}})$$

The rate of detection (~20.7%) of downstream migrating juvenile fish at the weir antenna permitted a rough estimation of the number of parr migrants that left the watershed to enter the estuary during the fall and winter. Because only about one-fifth of the migrating parr were detected, we were unable to establish the migration timing or life history type of some of the parr tagged in streams during the summer, or for those fish entering the estuary directly from tributaries below the weir unless they were detected at the antenna in the 96 Marsh.

Survival

Survival from egg to fry was not possible to evaluate because the screw trap was not operated early enough in the spring, potentially missing a large influx of fry (Jones et al. 2014). However, assuming 2600 eggs per female (Jones et al. 2018) we estimated survival from egg to stream parr. A general linear model (glm) was used to relate juvenile coho salmon to spawners of the same brood (2007–2011). Total number of juveniles was used as the response variable and total number of spawners was the linear predictor. We also calculated the Pearson correlation matrix between the two variables. Both analyses were performed in R.

Survival of each tag group as defined by life stage and tagging location (fry migrants, stream parr, parr migrants, and yearling migrants) was estimated between life stages and for the cumulative survival from time of tagging of each group to returning spawner at the weir or on the spawning grounds using the Cormack–Jolly–Seber (C–J–S) model and Markov chain Monte Carlo methods (Sedinger et al. 2010) implemented in program MARK 8 (White and Burnham 1999; White 2016). The model incorporates the tagging and detection histories of each fish during the first year and again on return to estimate the survival between life stages and to spawners. With more detection arrays in place for juveniles produced in 2009–2011 with spawners returning in 2012–2014, the model was able to provide more precise estimates than for spawners returning in 2010 and 2011. Each life history type is discrete because of time and location of tagging (e.g., fry migrants tagged at the screw trap or estuary in the first spring) or multiple detections of a tag (parr migrants tagged during the summer in the streams and detected in the fall at the weir or 96 Marsh antennas). Yearling migrants were tagged in streams as parr and detected at the weir antenna or tagged at the screw trap in the spring. The final group was comprised of the estuary yearlings, tagged in the estuary from April through June and could be any of

Table 2. Population estimates ($\pm 95\%$ confidence intervals expressed as a percent) at locations in the watershed through the life cycle of coho salmon; at lower river screw trap (rkm 7.9) in the spring (age-0 and age-1), in watershed streams during the summer, and in the estuary during the fall–winter for brood years 2006–2011.

Brood year	Spawning	Lower River	Streams	Estuary	Lower River
	Adults	Age-0	Age-0	Age-0	Age-1
2006	1 160 (83%)	NS	NS	NA	21 304 (29%)
2007	993 (54%)	37 017 (72%)	19 412 (43%)	NA	21 864 (85%)
2008	2 664 (38%)	39 141 (42%)	67 794 (29%)	NA	20 140 (58%)
2009	753 (58%)	11 177 (44%)	37 617 (34%)	12 093	15 551 (34%)
2010	1 448 (42%)	18 617 (55%)	44 344 (35%)	13 550	6 866 (28%)
2011	3 636 (27%)	13 415 (23%)	55 515 (32%)	14 715	19 499 (19%)
2012	297 (134%)				
2013	1 165 (43%)				
2014	3 680 (24%)				

Note: The population in the estuary was estimated from the number of tagged fish detected at the PIT array at rkm 8.0 and expanded assuming a 20.7% path efficiency. NS = not sampled, NA = not available because detection array was not in place.

the life history types. We defined ocean entry in the C–J–S model as April–June of the second year. Because we did not have a PIT array at the mouth of the estuary, the model used the detection of tagged fish of each tag group at the antenna in the 96 Marsh or scanned during beach seine surveys. It is likely some of the fish spent another week or two prior to actual ocean entry. The model assumed that each life history type had equal detection probability from time of tagging to spawners. We ran full models and a few reduced models for every tag group and detections for every time period. The full models had the lowest DIC scores compared to the reduced models, following an initial run with a lower number of samples (10 000 – 100 000) to generate posterior distributions and compare models, and full models with 200 000 samples. The best fitting model for the survival and recapture probabilities was selected based on the lowest deviance information criteria (DIC). Survival estimates were generated for each brood year (BY) separately, except the 2007 and 2008 BYs were combined because they were not significantly different.

Life history diversity

Otoliths and scales were removed from juvenile coho salmon collected near the mouth in 2008–2010 ($n = 84$) and from spawners collected at the randomly selected (GRTS) spawning survey sites in 2008–2010 ($n = 122$). We estimated the contribution of each juvenile life history type to the returning spawners using otolith chemical analysis. Detailed descriptions of the methods, analyses, and graphic examples are provided in Jones et al. (2014). Scales were examined to determine age at return and otolith reconstruction provided a record of fish movements from fresh to brackish water (and marine) during the juvenile life stages as indicated by a sharp increase in strontium:calcium (Sr:Ca) ratio. The otoliths were prepared for structural and chemical analysis by thin sectioning in the sagittal plane, similar to methods used in Volk et al. (2010) and Campbell (2010). Laser transects were analyzed from the otolith core to the otolith edge in the dorsal–posterior quadrant 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 quadrupole inductively coupled plasma mass spectrometer (LA-ICP-MS). Coupled with fish size of time at entry into brackish water based on otolith width of juvenile coho salmon in Salmon River ($n = 80$) at time of Sr:Ca transition and the location of an annulus, we classified juvenile life histories of the returning spawners.

PIT tag detections of spawners returning in 2010–2014 (BYs 2007–2011) enabled life history reconstruction of all juvenile life history types except for the fry–nomad type. Life history reconstructions

from PIT tags require multiple detections (and multiple detection sites) to infer the movements of individual fish. For example, a parr tagged in a stream during the summer, detected passing the weir or in the 96 Marsh in the fall or winter at age-0, and detected again two years later indicated that the spawner was a parr migrant to the estuary as a juvenile. A fry–nomad enters the brackish estuary from its natal freshwater stream in the spring, migrates back into fresh water during winter and re-enters the estuary the following spring and migrates to the ocean (Miller and Sadro 2003; Koski 2009; Jones et al. 2014). Chemical analyses (Sr:Ca ratios) of the otolith can reveal repeated movements between fresh (indicated by low Sr:Ca) and brackish water (high Sr:Ca) environments (Jones et al. 2014). With only a single estuary detection site (in the 96 marsh) we were unable to track the seasonal movements of fry–nomad migrants entering or leaving small estuary tributaries, where we believe the nomads overwintered. Whereas the otolith collections on the spawning grounds (GRTS selected sites) provided an unbiased estimate of life history types in the spawners, the PIT detections of spawners were standardized based on the proportion tagged for each life history type or tagging location to adjust for the recovery rate of each tag group.

Results

Abundance and migration

Subyearling coho salmon began migrating downstream to the estuary soon after emergence and prior to the placement of the trap in early to mid-March. Annual estimates of fry migrants ranged from 11 000 to 39 000 (Table 2) but this underestimated actual population abundance as numbers of migrating fry migrants were well above 1000 per week at the time trap operations commenced. Most of the fry migrated by mid-April but some were observed moving downstream through late June with a few in July at >65 mm. Because fry generally did not reach this size until late May we were only able to tag a subset of the fry migrant life history representing less than 1% of the total number of outmigrants captured at the trap. It was difficult to establish a relationship between numbers of fry migrants and spawner abundance or river flow because fry were migrating prior to installation of the trap. Subsequent seining in the estuary indicated that few of the fry migrants survived but we consistently captured age-0 coho salmon through the summer, with the highest abundances as estimated by catch per unit effort (CPUE) in the 96 Marsh. We classified these as fry migrants that survived to the summer.

Approximately 19 000 to 68 000 subyearling parr reared annually in streams during the summer (Table 2). The number of parr was generally greater and survival from egg to parr lower in years

of larger spawning populations. Linear modeling indicated no difference from zero ($P = 0.15$ and 0.23 , respectively), likely because of small sample size ($n = 5$).

A large proportion of the stream-resident parr moved downstream after the onset of high flow events in the autumn (Fig. 4). Based on detections at the hatchery weir in fall 2010–winter 2013 (BYs 2009–2011) and the 20.7% path efficiency of the detection array, we estimated that approximately 25%–30% of the parr migrated out of the watershed to the estuary annually, 12 000–15 000 fish (Table 2). Between 5.4% and 6.7% of the fish tagged in the watershed above the hatchery weir were detected leaving the watershed annually between 15 September and 28 February of brood years 2009–2011. The initial pulse of migration coincided with the first high flow event of the autumn based on the Siletz River gage (USGS station 14305500): late September in 2010, late November in 2011, and mid-October in 2012 (Fig. 4). Salmon River flows are closely correlated with the Siletz River gage (Bottom et al. 2005). Winter migration to the estuary ceased by mid-January despite continued high flow events (Fig. 4). Flow patterns were similar across the three fall–winter periods (NRFC 2016).

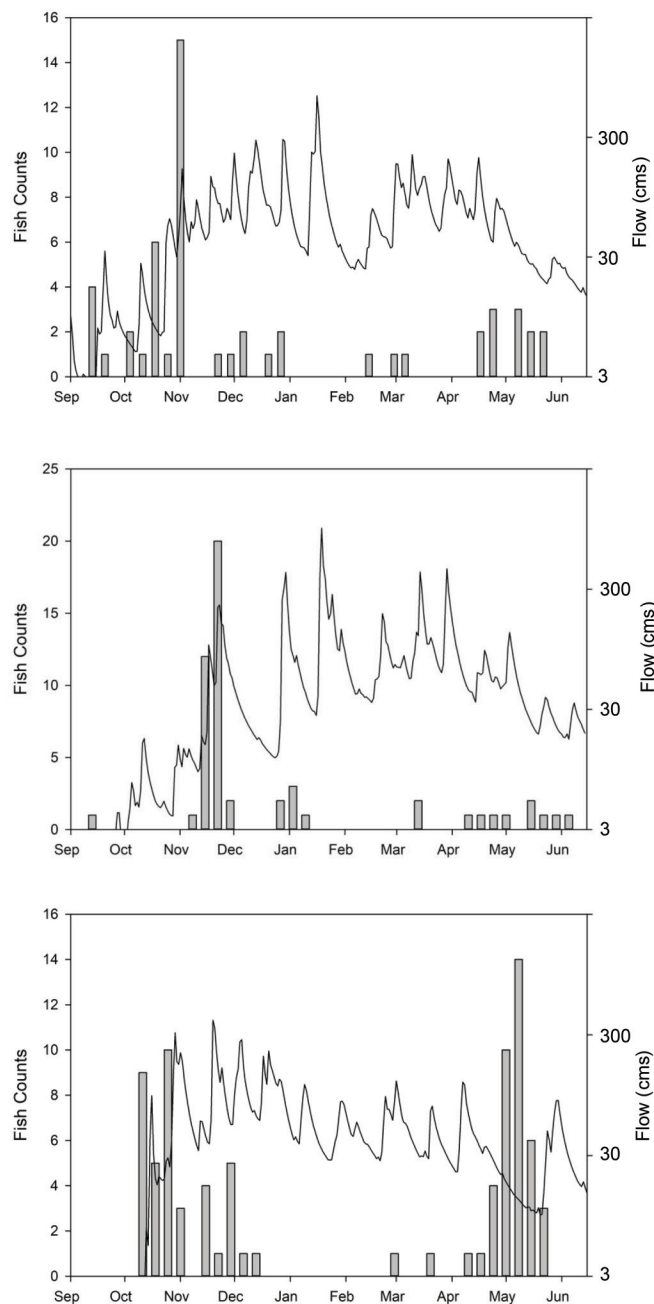
Beach seining in the estuary and operation of the PIT array in the 96 Marsh also confirmed that a large number of coho salmon parr were rearing in the estuary during the autumns and winters 2008–2013. Juvenile coho salmon were captured throughout the estuary in all months, particularly in the marsh channels. Salinity in all the marshes was quite low (<5 PSU) in the winter, even during high tide. During annual seining operations, in fall and winter, we tagged an average of 700 parr in each of six brood years (Table 1). An additional 90 of the parr tagged in streams during the summer were detected at the 96 Marsh during the 2012–2013 autumn–winter season. No juvenile coho salmon were captured at the mouth of the estuary from September through February despite sampling every 2–4 weeks.

The remaining stream rearing juveniles began migrating to the estuary in March as yearlings. Between 7000 and 22 000 yearling coho salmon migrated to the estuary from streams above the hatchery weir (Table 2). An additional 10%–30% may have entered the estuary from tributaries that directly enter the estuary below the weir, such as Deer, Salmon, and Crowley creeks (Fig. 2) based on the available stream km, fish density and population estimates each year. Most of the yearlings migrated past the hatchery weir and screw trap beginning in April, peaking in May and continuing through mid-June (Fig. 4; Jones et al. 2014). The spring migrations did not appear to be associated with changes in river flow (Fig. 4). We tagged an average of 820 yearling fish annually during operation of the screw trap (Table 1). The stream-resident summer parr estimate and screw trap estimate for the 2007 BY are incongruous (Table 2), but the confidence limits on the screw trap estimate were quite wide that year.

The yearling fish tagged at the screw trap spent one to four weeks in the estuary before entering the ocean. When the PIT array was operating in the 96 Marsh in the springs of 2010, 2012 and 2013, 25%–30% of the yearling migrants tagged at the screw trap were detected. Of the parr migrants tagged during the fall and winter in the estuary, 2.3%, 11.4%, and 9.1% were detected in the 96 Marsh PIT array in springs 2010, 2012, and 2013, respectively. In addition, some of the fry migrants tagged a year earlier at the screw trap or in the summer in the estuary were detected as yearlings at the PIT array in the 96 Marsh.

Analysis of otoliths collected from juvenile coho salmon near ocean entrance indicated the presence of the fry–nomad life history although PIT tag detections in the estuary did not corroborate the presence of the fry–nomad type. We hypothesize the fry–nomad life history types that reared in the estuary during the summer moved into small streams that directly enter the estuary during the winter rather than up the mainstem Salmon River past the weir, possibly a velocity barrier. No detection arrays were located on estuary tributaries such as Deer, Salmon or Crowley

Fig. 4. Migration timing of juvenile coho salmon relative to river flow (cms = cubic metres per second). The coho salmon were tagged in the basin and detected downstream at the passive integrated transponder antenna (rkm 8), just above the head of tide, in 2010–2011 ($n = 52$), 2011–2012 ($n = 53$), and 2012–2013 ($n = 80$). The antenna operated continuously from 30 August 2010 through 25 June 2013.



creeks although incidental observations support this contention because juvenile coho salmon were observed in a couple of small streams entering the estuary that had no spawning habitat.

We were unable to estimate the proportion of tagged spawners detected by the antenna array. Fish that entered earlier in the fall before river flows topped the weir were very likely to be detected as the spawners were forced to the north side of the weir or up the hatchery ladder to be released above the weir. However, some late returning spawners may have ascended undetected over the

weir after the river level rose. Of 11 tagged carcasses scanned on the spawning grounds, 6 were previously detected at the weir. The spawner population ranged an order of magnitude, from 297 to a high of 3680 (Table 2) based on the spawning ground surveys (Sounhein 2019).

Survival of life history types to ocean entry and to spawners

Detections of tagged juvenile produced in 2007–2011 allowed survival estimates of fry migrants, parr migrants, and yearling migrants to spawners returning in 2010–2014 (Table 3; Fig. 5). Yearling smolts from the 2007–2009 and 2011 BYs, tagged at the screw trap survived at the highest rate to spawner of the three life history types. However, the parr migrants of the 2010 BY detected entering the estuary or tagged in the estuary survived to spawner at the highest rate compared to yearling migrants despite a longer period from marking to recapture (i.e., parr migrants were detected or tagged ~2–5 months earlier than yearling migrants). Estimated survivals of the fry migrants (≥ 65 mm), which were tagged the earliest and reared in the estuary for almost a year, had the lowest survival from time of tagging to spawner of the three life history types, averaging ~0.4%.

We also estimated life-stage specific survivals from point of tagging to approximate ocean entry for the 2009–2011 BYs because we detected and recovered sufficient number of tags in the estuary during spring in these years. The fry migrants (>65 mm FL at time of tagging) that reared in the estuary for almost a year had a mean survival across 3 years of 10% (range 3%–15%) to ocean entry in May–June the following year. The parr migrants that overwintered in the estuary had a mean survival of 42% (range 16%–79%) from time of detection or tagging in the fall–winter to ocean entry (up to 7 months) and the stream-reared yearling migrants had a mean survival of 74% (range 60%–83%) from time of tagging at the screw trap in the spring to ocean entry (1–4 weeks). Applying the survival estimates to ocean entry for each brood year and life history type, we estimated that the spring population in the estuary prior to ocean migration numbered approximately 11 700, 20 000, and 23 500 for the 2009, 2010, and 2011 BYs, respectively (Table 2). Survival from ocean entry to spawner (marine survival) of fry migrants averaged 3% (range 1%–7%), parr migrants averaged 11% (range 2%–18%), and yearling migrants averaged 8% (range 3%–12%). The yearlings tagged in the estuary in the spring prior to ocean entry (a mix of life history types) indicated marine survival at 3.1%, 6.0%, and 11.2% for the 2009, 2010, and 2011 BYs, respectively.

We constructed a flow diagram of the life history pathways, abundance in each environment, movement, and survival of fish through the 3-year life cycle using the 2011 BY as an example (Fig. 6) to illustrate the connectivity between and importance of each environment to the overall survival and composition of the spawners. Lacking an empirical estimate, a density independent survival of 0.64 from spring fry to summer parr (Nickelson et al. 1993) suggested that approximately 87 500 fry were in the streams at the end of June. Estimates of freshwater and estuary survival from one life stage to the next, and marine survival from ocean entry to spawner for each life history strategy was estimated in the C–J–S model.

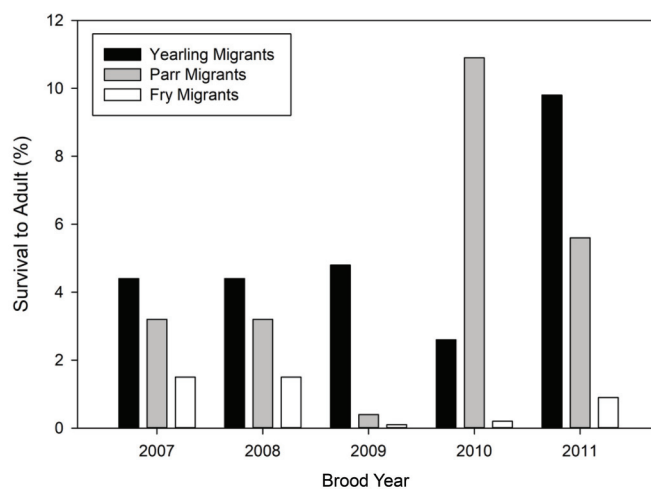
To validate our cumulative abundance and survival estimates by environment and life history pathway (i.e., Fig. 6), we compared our findings to independently collected estimates of spawning populations (Table 1; Sounhein 2019) for the 2012–2014 return years. Cumulative estimates of spawners by 3 life history types (fry migrants, parr migrants, and yearling migrants) were 790, 1703, and 2906. Using the population estimate of yearling fish of all life history types in the estuary immediately prior to ocean entry multiplied by estimated survival to spawner provided point estimates of 336, 964, and 2293, respectively. The actual mix of each type in the estuary may influence the later estimates. Independently derived estimates from surveys on the spawning grounds were 297 (95% CI: ± 397), 1165 (95% CI: ± 498), and 3680 (95% CI: ± 867) (RYs 2012–2014; Table 1).

Table 3. Estimated survivals of PIT-tagged juvenile coho salmon to spawner for 2007–2011 brood years.

Brood year	Estuary yearlings	Yearling migrants	Parr migrants	Fry migrants
2007	6.8%	4.4%	3.2%	1.5%
2008	6.8%	4.4%	3.2%	1.5%
2009	3.1%	4.8%	0.4%	0.1%
2010	6.0%	2.6%	10.9%	0.2%
2011	11.2%	9.8%	5.6%	0.9%

Note: The values reflect survival from initial point of tagging to adult detection at the weir or on the spawning grounds. Survival of 2007 and 2008 BYs was not significantly different within tag groups. Only fry larger than 65 mm were tagged. Estuary yearlings are comprised of all life history types.

Fig. 5. Cumulative survival by brood year from time of tagging to return in 2010–2014. Yearling migrants were tagged in spring at age-1, parr migrants in fall and winter at age-0, and fry migrants in late spring and early summer at age-0. Survival estimates of the 2007 and 2008 broods were not significantly different and were combined in the C–J–S model.



Annual variation in life history contributions to spawners

PIT tag detections at the weir and on the spawning grounds, coupled with otolith analysis (Jones et al. 2014), allowed us to estimate the contribution of different life history types to spawners for seven years. The life history types of the juveniles sampled at the mouth of the estuary (Jones et al. 2014) compared favorably to the life history types of the spawners across seven years (Fig. 7). The yearling migrant type was the most common juvenile life history in the estuary but varied widely from 43% to 79% of the returning spawners from 2005–2011 BYs (Table 4; Fig. 8). The parr migrant contribution varied from 9% to 50%, and the fry migrant type accounted for 0% to 10% of the spawners. Fry–nomad type contributed 2% to 4% of the returning spawners in 2008–2010 when we reconstructed life histories through otolith analysis. Fry–nomad migrants would have been mistakenly classified with fry migrants in the 2011–2014 return years because we relied on PIT detections and were not able to detect movement between the estuary and estuary tributaries. Fry migrants and fry–nomad migrants both entered the estuary as fry and exited to the ocean as yearlings.

Jacks were not collected during spawner surveys, and although detected on the PIT antenna at the weir, were not included in the survival estimates. In Salmon River, of 195 returning fish (2009–2011 BYs) detected at the weir, 12 were jacks, representing an average contribution of 6%. Of these only 5 were not tagged in the

Fig. 6. Life history pathways and survival of 2011 brood year based on estimates of abundance (in boxes) and survival (below arrows; as proportional survival between life stages). All life history types entered the ocean at age-1 in 2013 and returned as age-3 spawners in 2014. Spring fry in streams were backcalculated with survival estimate from [Nickelson et al. \(1993\)](#). Approximately 25% of the summer parr migrated in the fall–winter to the estuary. Of the remaining parr in streams, approximately 47% survived over the fall and winter to become yearling migrants.

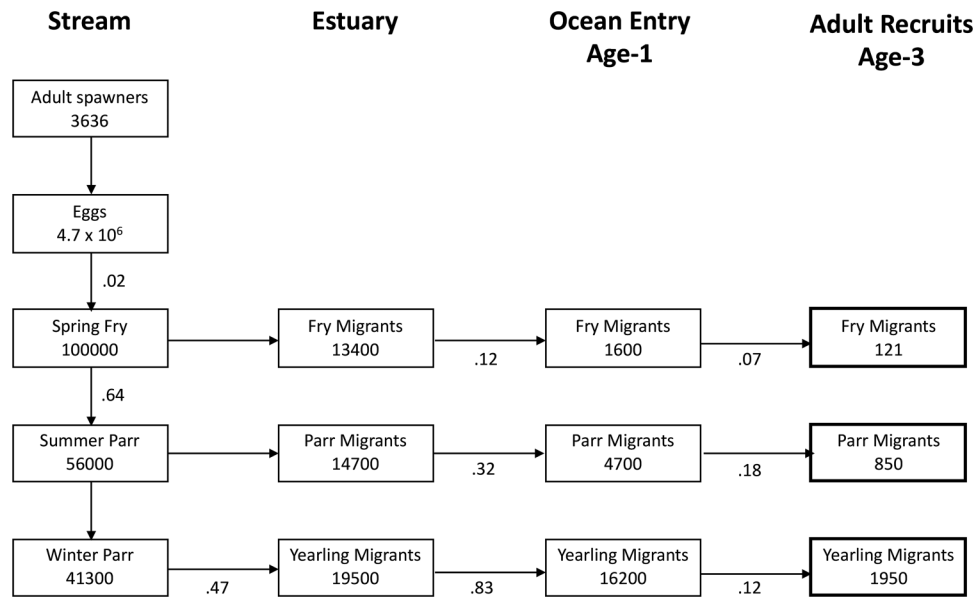
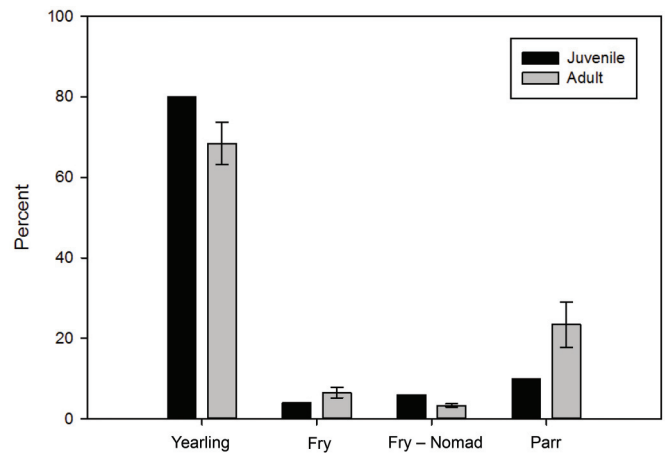


Fig. 7. Proportions of four juvenile life history migrant types represented among outmigrants in 2008–2010 and juvenile life history pattern of returning spawners in 2008–2014. The juvenile contribution is an average across the time period ($n = 84$). The spawner estimates include the standard error for the seven return years.



estuary as yearlings, preventing an analysis of the juvenile life history pathways of jacks. These jacks all emigrated to the ocean as yearlings.

Discussion

Four life history strategies of coho salmon contributed to the spawners across seven brood years in Salmon River. The additional production from juvenile coho salmon that rear for months in the estuary, while not accounted for in life cycle models and recovery plans of coho salmon, may improve population viability and buffer environmental fluctuations. Approximately 25%–30% of the stream-resident parr of the 2009–2011 broods migrated to the estuary

Table 4. Contribution of four juvenile life history types to the spawners based on otolith reconstruction (BY 2005–2007) and PIT detections at time of return (2007–2011).

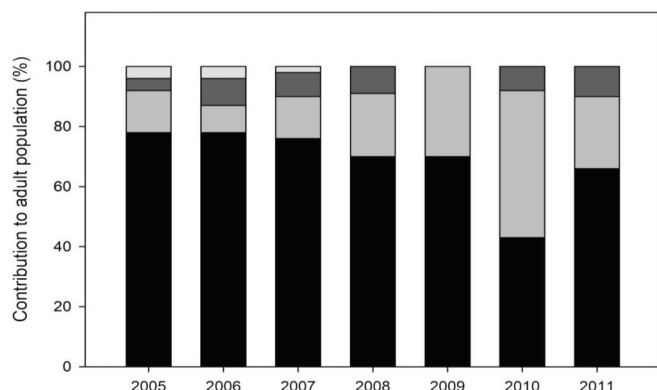
Brood year	Yearling	Fry–nomad	Parr migrants	Fry migrants
2005	79%	4%	14%	4%
2006	77%	4%	9%	9%
2007	78%	2%	14%	8%
2008	71%	NA	21%	9%
2009	70%	NA	30%	0%
2010	43%	NA	50%	8%
2011	66%	NA	24%	10%
Mean (SE)	69% (5%)	3% (0.7%)	23% (5%)	7% (1%)

Note: Fry–nomads are not detected effectively with PIT tags (NA = not available). Jacks are not included.

during the fall and winter and reared for 2–7 months before entering the ocean as yearlings. In addition, fry migrants and those that exhibited a fry–nomad life history strategy contributed to the spawners. Although the freshwater rearing strategy produced the majority of spawners in 6 of 7 years, the life history composition of the spawners varied among years. Without the additional estuarine rearing strategies, the spawners would have been reduced from 10%–60% in a given year, suggesting that life cycle models, restoration strategies, and monitoring programs should consider contributions from lower river and estuarine habitats. The comprehensive model accounts for what would otherwise be an egregious error with management consequences.

Divergent dispersal strategies within salmonid and other anadromous fish populations provide flexibility that may enable populations to persist in variable environments ([Kerr et al. 2010](#); [Gahagan et al. 2015](#)). Partial migration of the Salmon River coho salmon population was indicated by the dispersal of fry and parr migrant groups from natal freshwater streams into productive estuarine habitats. Such contingent behaviors (e.g., divergent resident and dispersal pathways during early life history) can promote resilience by distributing

Fig. 8. Contribution of four juvenile coho salmon life histories to subsequent adult recruits, summarized by brood year (2005–2011): fry–nomad migrants in light gray, fry migrants in dark gray, parr migrants in medium gray, and yearling migrants in black. Estimates are from otolith reconstruction (2005–2007) and PIT tag detection (2007–2011). Fry–nomad migrants were not detected with PIT arrays and were likely grouped with fry migrants.



population members spatially across habitats of varying survival conditions (Secor 2007; Kerr et al. 2010). Nursery habitats that support minority contingents in most years can become more important contributors over long periods (Hilborn et al. 2003; Kerr and Secor 2012; Schroeder et al. 2016). In the Salmon River estuary migrants were minority contributors to the spawners for most years but accounted for the majority of the spawners that survived to return in 2013.

Coho salmon management and population models that do not account for minority contributors may exclude critical habitats that allow populations to persist. Because most estuarine wetlands in the Pacific Northwest have been lost (Brophy et al. 2019), the lack of potential contributions of minority life histories (i.e., diverse estuarine migrants) to resilience of many coho salmon populations may be a fundamental conservation concern. Modeling the dynamics of white perch in Chesapeake Bay, Kerr et al. (2010) showed that both resident and migratory contingents contribute to long-term population stability, implying that conservation should consider larger combinations of nursery habitat rather than simply the most productive ones. For coho salmon, we have provided evidence that access to estuarine habitats supports fry and parr migrants and connectivity between tidal wetlands and tributaries support fry–nomad migrants. Restoration of ~70% of the estuary’s historical wetlands by removing tide gates and levees allowed unimpeded access to the channel networks, marsh surfaces and tributaries year-round (Flitcroft et al. 2016). Habitat complexity and connectivity within and between the freshwater and estuarine environments enabled young salmon to express a variety of alternative life histories (Bisson et al. 2009; Moore et al. 2015; Flitcroft et al. 2019).

The annual migration of fry to the estuary was part of a basin-wide dispersal, similar to that reported for Chinook salmon in the Fraser (Healey 1991) and Salmon (Bottom et al. 2005) rivers. The movement of emergent fry may be density independent as for Chinook salmon (Zimmerman et al. 2015). Fry migrants moved primarily in the early spring soon after emergence while flows were high and trickled down through late spring to early summer consistent with the observations from other coho salmon studies (Miller and Sadro 2003; Craig et al. 2014; Wallace et al. 2015). Despite the apparent low survival rate, the tagged fry migrants (>65 mm) survived to ocean entry at an average rate of 10% and have a recognizable signal (up to 10%) in the spawners in

Salmon River, and possibly in other systems. Fry migrants contributed relatively small proportions to the total spawners, but clearly are not “surplus” production (Chapman 1962).

We expect that fry–nomad migrants (Koski 2009) were present in the 2011–2014 return years, similar to that reported for the 2008–2010 return years when otolith reconstructions revealed their presence (Jones et al. 2014). We detected no tagged juveniles at the weir array that had migrated back upstream in the winter or spring. We posit that some of the migrant fry moved into small tributaries that directly enter the estuary during the winter similar to the pattern observed in a northern California estuary (Wallace et al. 2015) and in South Slough Oregon (Miller and Sadro 2003). Fry–nomad migrant contributions to the spawners would have been attributed to fry migrants for the 2011–2014 return years.

The initiation and duration of the coho salmon parr migration to estuaries in fall–winter may be driven by passive movement due to high flows, density dependent factors (Nickelson and Lawson 1998), or a reduction in stream carrying capacity due to lack of suitable winter habitat (Chapman 1966; Solazzi et al. 2000). The net effect of movement to the estuary was two-fold. The density of juvenile coho salmon was reduced by 25%–30% in streams and the migrating parr moved into an expansive and apparently productive habitat. The availability of both stream and estuary habitats likely improved the performance of both the stream-resident parr and the estuary parr by lowering fish densities, as parr survival is thought to be density dependent (Bradford et al. 1997; Zimmerman et al. 2015). Parr that migrated to the estuary in the fall–winter period survived at 41%, 86% and 36% to spring prior to approximate ocean entry (BYs 2009–2011). Accounting for the number of parr that overwintered in the streams above and below the weir (i.e., subtracting parr migrants to the estuary), the overwinter survival of yearling migrants to the screw trap was 71%, 25%, and 62% for the 2009, 2010, and 2011 broods, respectively. This compares with ~28% average overwinter survival of coho salmon in streams in the Siletz and Alsea basins for the same BYs (E. Suring, ODFW, personal communication, 2019), and 10%–25% in control streams and 30%–50% in restored stream reaches in the Alsea and Nestucca basins in 1987–1993 (Solazzi et al. 2000), and 70%–90% in a restored small Oregon watershed at low juvenile density (Johnson et al. 2005). For context, a density independent survival value of 0.70 is used in life cycle models (Nickelson 1998). Overwinter survival in the stream and estuary for the three brood years in Salmon River suggest that it is beneficial for the stream-resident fish to experience lower densities, and for the parr migrants to rear in the estuary. High salmon survival (this study) and growth (Jones et al. 2014) suggest an ample food supply and productive capacity in the estuary during winter. Furthermore, high growth in the estuary (parr migrants and yearling migrants) may improve ocean survival potential during the first year and influence year class strength (Nickelson 1986; Pearcy 1992; Beamish et al. 2004).

Typically, survival of juvenile coho salmon has been estimated in stream habitat and life cycle models at egg to fry, fry to parr, and parr to smolt (over winter) stages prior to estuary entry (Bradford 1995; Nickelson et al. 1993; Nickelson and Lawson 1998; Jensen et al. 2009). Here we estimated a separate mortality rate from river to ocean entry. Approximately 17%–40% of yearling migrants suffered mortality between the screw trap at rkm 7.9 and the ocean. Some of the mortality associated with the first couple months after “ocean entry”, generally estimated at time of release (hatchery fish) or at a screw trap in a river, may in fact, be occurring in the lower river or estuary.

Interannual variability in contribution to the spawners reflected differences in the freshwater and marine survival of each life history type. In particular, the survival of parr migrants of the 2009 BY was much lower than that of the 2010 BY, although the reasons for the survival differences are not readily apparent. Fall and winter river flows were similar (and normal) from fall 2010 – spring 2013

(NRF 2016) and indices of marine conditions were similar, in the intermediate to good range for coho salmon survival (Peterson et al. 2017). The El Niño and anomalous warm ocean temperatures in the NE Pacific Ocean dramatically changed marine conditions in the Northeastern Pacific Ocean in 2014, influencing spawners returning in 2015 and later (Bond et al. 2015; Peterson et al. 2017). Unfortunately, our study concluded in 2014 with the return of spawners from the 2011 brood. Nonetheless, our results illustrate a diverse life history portfolio as rearing conditions in the estuary become more or less beneficial to coho salmon survival relative to the stream environment.

Some of our conclusions are dependent on assumptions related to PIT tag implants and tag detections. Prentice et al. (1990) observed that PIT tags may not have affected survival or growth of Chinook salmon, sockeye salmon, or steelhead while Brakensiek and Hankin (2007) indicated that only very small (<55 mm) PIT-tagged coho salmon may experience higher initial mortality. However, Knudsen et al. (2009) observed loss of PIT tags and a reduction in smolt to adult recruits of Chinook salmon but stated that the loss did not bias comparisons between tagged groups. We tagged an average of 5% of the total population of juvenile fish of all groups, excluding subyearling fry (2009–2011 BYs) and subsequently detected just under 4% of the total estimated spawners returning 3 years later suggesting there was minimal impact of the tagging on survival. Additionally, we tested whether juvenile coho salmon length had an impact on detection rates. We tagged two groups of fish (65–71 vs 71–80 mm FL; 659 fish total) in the 96 Marsh and found no significant difference in detection rates between the two groups across 5 years (two-tailed paired *t* test, *p* = 0.88). Survival varied between years, but small fish had detection rates similar to larger fish each year. PIT tagging did not appear to unduly influence the overall survival of the population or bias individual life history types.

We questioned whether the placement and operation of the array at the weir influenced results because it covered a portion of the channel and experienced very high flows. The proportion of the summer parr population we detected migrating to the estuary in the fall–winter was consistent for the 2009–2011 broods (5%–7% annually). Because river flows and patterns were similar during fall 2010 through spring 2013 (NRF 2016), and detection rates of fish at the 96 Marsh array were similar in the springs of 2010, 2011, and 2012, we believe that the path efficiency (Zydlewski et al. 2006) of the weir PIT detection array was consistent, even though we were only able to directly estimate the path efficiency for 16 months in 2012–2013. The array remained operational even when flows overtopped the weir, detecting juveniles moving downstream and spawners upstream. Most spawners returned early in the fall to Salmon River compared to neighboring basins (Jones et al. 2018) allowing high rate of detection when passing through the hatchery or on the north side of the weir where the array was located. However, we certainly underestimated (only 6 of 11 recovered tagged carcasses were detected at the weir) spawners during high flow events although we did not observe a bias in life history type based on time at return. Also, we were not able to detect spawners returning to the 25 km of streams that directly enter the estuary. As a result, our cumulative estimate of returning spawners based on tag detection is likely low. However, our comparison of abundances and survivals of each migrant type to spawners compared favorably to the independent estimate from spawning surveys by OASIS (Sounhein et al. 2019).

The conventional perception of the coho salmon life cycle suggests little portfolio benefit from a single, fixed yearling–smolt life history that returns almost exclusively as 3-year-old spawners. Two important factors may have contributed to this perception. First, most historical estuarine wetlands along the Pacific coast that could have provided rearing opportunities for fry and parr migrants have been lost to diking, filling, and other development in the last century. One recent study estimated <20% of the historical tidal

wetland area remains along the West Coast of the United States (Brophy et al. 2019). Loss of estuarine rearing opportunities has likely reinforced the assumption that all juvenile coho salmon are freshwater residents. For example, subyearling coho salmon were not observed in abundance in Salmon River prior to restoration of estuary marshes (Jones et al. 2014). Second, for decades coho salmon hatcheries released large numbers of yearling smolts into coastal rivers, augmenting the dominant freshwater life history type and potentially placing smaller naturally produced juveniles at a competitive disadvantage (Nickelson et al. 1986). Recent studies in the Salmon River concluded that both historical wetland loss and hatchery production had adversely affected life history variation and productivity of the local coho salmon population (Jones et al. 2014, 2018).

Coho salmon hatchery releases have been eliminated in the Oregon coastal rivers north of the Rogue River, including the Salmon River, but progress restoring diked wetlands has been modest in most Pacific coastal basins (Brophy et al. 2019), except for the Salmon River. Comprehensive life cycle studies of Chinook salmon (Bottom et al. 2005) and coho salmon populations (this study) have demonstrated that migrant contingents can recover if access to productive estuary rearing habitats is restored, providing a case study for restoration activities in other estuaries.

Although all coho salmon in Salmon River enter the ocean as yearlings within the same late spring time frame and return as 3-year-old spawners, the population is supported by a steady input of different estuary rearing life history types (fry, fry–nomad, parr migrants), accounting for ~21%–44% of the spawners in most years but as much as ~58% of the spawners in the 2010 brood. These variations are another example of potential asynchrony (Moore et al. 2014) providing stability to the population. Similarly, for coho salmon in other systems, Bennett et al. (2014) reported 37% (32 of 86 spawners) contribution from fall migrants to the spawners in streams draining to the Salish Sea from 2004–2010 and Nordholm (2014) reported 32%–40% of the returning spawners in Palouse Creek Oregon in 2009 had an estuarine associated life history.

This study highlights the benefits of a population scale approach across multiple rearing environments and brood years to evaluate the variability and relationships between habitat, life history diversity, survival, and contribution to spawners. Habitat diversity within a watershed (Bisson et al. 2009; Moore et al. 2015) and ecological connectivity (Secor 2005; Bisson et al. 2009; Flitcroft et al. 2019) played key roles in sustaining life history diversity and population productivity in Salmon River. Studies in additional coho salmon populations (e.g., by collecting and reconstructing life histories from otoliths or tagging all migrant types) will likely identify the prevalence of alternative rearing strategies across different systems and underscore the importance of basin-wide restoration to restore system and life history diversity. Comprehensive life cycle modeling coupled with long-term monitoring (e.g., Hilborn et al. 2003; Greene et al. 2010; Moore et al. 2014), can be relevant to understanding population responses to short-term extreme events (e.g., El Niño) and to longer term systemic changes to freshwater and marine environments caused by climate change.

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