

Juvenile life-history diversity and population stability of spring Chinook salmon in the Willamette River basin, Oregon

R. Kirk Schroeder, Luke D. Whitman, Brian Cannon, and Paul Olmsted

Abstract: Migratory and rearing pathways of juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*) were documented in the Willamette River basin to identify life histories and estimate their contribution to smolt production and population stability. We identified six primary life histories that included two phenotypes for early migratory tactics: fry that migrated up to 140–200 km shortly after emergence (movers) and fish that reared for 8–16 months in natal areas (stayers). Peak emigration of juvenile salmon from the Willamette River was in June–July (subyearling smolts), March–May (yearling smolts), and November–December (considered as “autumn smolts”). Alternative migratory behaviors of juvenile salmon were associated with extensive use of diverse habitats that eventually encompassed up to 400 rkm of the basin, including tributaries in natal areas and large rivers. Juvenile salmon that reared in natal reaches and migrated as yearlings were the most prevalent life history and had the lowest temporal variability. However, the total productivity of the basin was increased by the contribution of fish with dispersive life histories, which represented over 50% of the total smolt production. Life-history diversity reduced the variability in the total smolt population by 35% over the weighted mean of individual life histories, providing evidence of a considerable portfolio effect through the asynchronous contributions of life histories. Protecting and restoring a diverse suite of connected habitats in the Willamette River basin will promote the development and expression of juvenile life histories, thereby providing stability and resilience to native salmon populations.

Résumé : Les voies de migration et de croissance des saumons quinnats (*Oncorhynchus tshawytscha*) juvéniles dans le bassin de la rivière Willamette ont été documentées afin de cerner les différents cycles biologiques et d'estimer leur contribution à la production de saumoneaux et à la stabilité de la population. Nous avons relevé six principaux cycles biologiques qui comprennent deux phénotypes d'approche de migration précoce, soit des alevins qui migrent sur des distances pouvant atteindre de 140 à 200 km peu après leur émergence et des poissons qui demeurent de 8 à 16 mois dans leurs aires natales. Les pointes d'émigration des saumons juvéniles de la rivière Willamette étaient en juin-juillet (saumoneaux de moins d'un an), de mars à mai (saumoneaux d'un an) et en novembre-décembre (considérés comme étant des « saumoneaux automnaux »). D'autres comportements migratoires des saumons juvéniles étaient associés à l'usage répandu d'habitats variés qui englobent, à terme, jusqu'à 400 kmr du bassin, incluant des affluents dans des aires natales et de grandes rivières. Les saumons juvéniles qui demeuraient dans leurs tronçons nataux pour migrer en tant que saumoneaux d'un an représentaient le cycle biologique le plus prévalent et présentaient la plus faible variabilité temporelle. Cela dit, la contribution de poissons ayant des cycles biologiques dispersifs, qui représentaient plus de 50 % de la production totale de saumoneaux, accroissait la productivité totale du bassin. La diversité des cycles biologiques réduisait de 35 % la variabilité dans la population totale de saumoneaux par rapport à la moyenne pondérée des cycles biologiques individuels, indiquant un important effet de portefeuille découlant des contributions asynchrones des cycles biologiques. La protection et la restauration d'un ensemble varié d'habitats interconnectés dans le bassin de la rivière Willamette favoriseront le développement et l'expression des cycles biologiques de juvéniles, conférant ainsi stabilité et résilience aux populations de saumons indigènes. [Traduit par la Rédaction]

Introduction

Diversity in Pacific salmon (*Oncorhynchus* spp.) is a result of its evolutionary history in highly dynamic environments (Montgomery 2000; Waples et al. 2008) and confers species and populations with a capacity to adapt in variable and uncertain environments (Healey and Prince 1995; Waples et al. 2009). Life-history diversity, spatial structure, and differential responses to environmental fluctuations can provide stability to regional populations and stocks (Hilborn et al. 2003; Moore et al. 2010; Schindler et al. 2010). At the population level, alternate juvenile life histories may contribute differently to adult salmon returns over time and may buffer populations against environmental variability (Miller et al. 2010; Moore et al. 2014; Walsworth et al. 2015). Life-history strate-

gies of Pacific salmon evolved to maximize fitness in variable environments that occur over broad geographic ranges of species (Quinn et al. 2001; Waples et al. 2001; Brannon et al. 2004). Chinook salmon (*Oncorhynchus tshawytscha*) are widely distributed throughout the Pacific Northwest, occupy diverse habitats that span coastal rivers to streams >3000 km from the ocean, and display some of the highest levels of diversity in life histories observed among all Pacific salmon (Healey 1991; Waples et al. 2001; Brannon et al. 2004). In addition to variable age at maturity, two life-history strategies have been recognized: Chinook salmon that migrate to the ocean during the first year of life as subyearlings and those that migrate as yearling smolts during their second year of life (Taylor 1990; Healey 1991; Moran et al. 2013). Juvenile Chinook salmon can also undertake long-distance move-

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ments prior to smolting (Bradford and Taylor 1997; Connor et al. 2001; Shrimpton et al. 2014), resulting in multiple migratory and rearing pathways that can contribute to diversity in life histories. Given the widely documented loss of diversity within and among salmon populations that has occurred during the last century (Gustafson et al. 2007; Waples et al. 2009) and the potential for continued and increased loss in the near future from human-caused disturbances, it will be important to identify extant life history diversity and its contribution to population dynamics for the development of effective conservation and recovery measures (Ruckelshaus et al. 2002; Good et al. 2007).

Our study in the Willamette River basin, Oregon, was initiated to collect information on the life histories of juvenile Chinook salmon for developing and planning conservation and recovery measures for wild populations. Chinook salmon native to the Willamette River basin return from the ocean as adults in late winter and early spring (spring-run), the only season when passage was historically possible at Willamette Falls. Early run timing and isolation of the populations upstream of the falls resulted in a genetically divergent group among Columbia River Chinook salmon (Waples et al. 2004; Narum et al. 2011; Matala et al. 2011). Populations of wild spring Chinook salmon in the upper Willamette River basin have declined because of habitat degradation and simplification (e.g., dam construction and development in floodplains), large hatchery programs, and size- or age-selective harvest (Myers et al. 1998; Hulse et al. 2002). A key factor in the decline of wild salmon populations was the construction in the 1950s and 1960s of large dams for flood control that blocked access to 70%–95% of the historic spawning areas for three populations of spring Chinook salmon in the upper Willamette River basin and 25% of spawning habitat in the McKenzie River subbasin where some headwater spawning areas remain accessible (ODFW and NMFS 2011). Data collected in the 1940s indicated considerable variation in migration timing, size, and growth of wild juvenile salmon in the Willamette River, which included fry migrating from natal areas shortly after emergence and the presence of subyearling and yearling smolts (Craig and Townsend 1946; Mattson 1962). Diversity in life histories of juvenile Chinook salmon may have been lost or may be constrained because of direct habitat loss, habitat degradation, and decreases in the abundance of wild spawners. Populations of spring Chinook salmon in the Willamette River basin were classified as an evolutionarily significant unit (ESU) and listed as threatened under the United States Endangered Species Act in 1999 (NMFS 1999). A recovery plan was adopted in 2011 that identified actions including conservation and restoration of riverine habitats, modification of discharge from dams, and reintroduction of Chinook salmon upstream of dams (ODFW and NMFS 2011). Information about the migratory and rearing behavior of juvenile salmon will be critical for planning and implementing effective strategies. Previous studies on migration and rearing of juvenile spring Chinook salmon have been geographically restricted to a single tributary (Zakel and Reed 1984) or to the lower Willamette River (Friesen et al. 2007). Investigations have not been conducted on migratory and rearing behavior of wild juvenile Chinook salmon throughout the Willamette River basin or on the importance of diversity in salmon life histories to population dynamics during the freshwater life stages.

The primary objectives of our study on spring Chinook salmon in the upper Willamette River basin were to (i) identify the existing life-history diversity of wild juvenile salmon, (ii) identify general rearing areas for juvenile salmon in the basin, (iii) estimate the contribution of life histories to smolt production, and (iv) estimate the effect of life-history diversity on the stability of smolt numbers. Our results elucidate the importance of individual migratory behaviors for smolt production and will aid in the development of effective conservation and recovery strategies for spring Chinook salmon in the Willamette River basin. Our results

will also add to the growing knowledge of diversity in life histories of Chinook salmon within the Columbia River basin and elsewhere.

Methods

Study area and populations

The Willamette River basin (Fig. 1) is the fourth-largest catchment of the Columbia River and drains 29 728 km² (Baker et al. 2004). The basin encompasses diverse habitats and land uses between the Cascade and Coast Range mountains and joins with the Columbia River 163 km from the Pacific Ocean. The use of the Willamette River basin by anadromous fish has been influenced by Willamette Falls located 43 km upstream from the confluence with the Columbia River, which is formed by a 15 m high basalt ledge and was historically a barrier to most anadromous fish species except for spring-run Chinook salmon, winter-run steelhead (*Oncorhynchus mykiss*), and Pacific lamprey (*Entosphenus tridentatus*). Efforts to improve fish passage at the falls began in the late 1800s with excavation of “steps” in the basalt, but upstream passage remained difficult during late spring and summer until 1968–1975 when concrete fishways were constructed along the side of the falls (NOAA 1981).

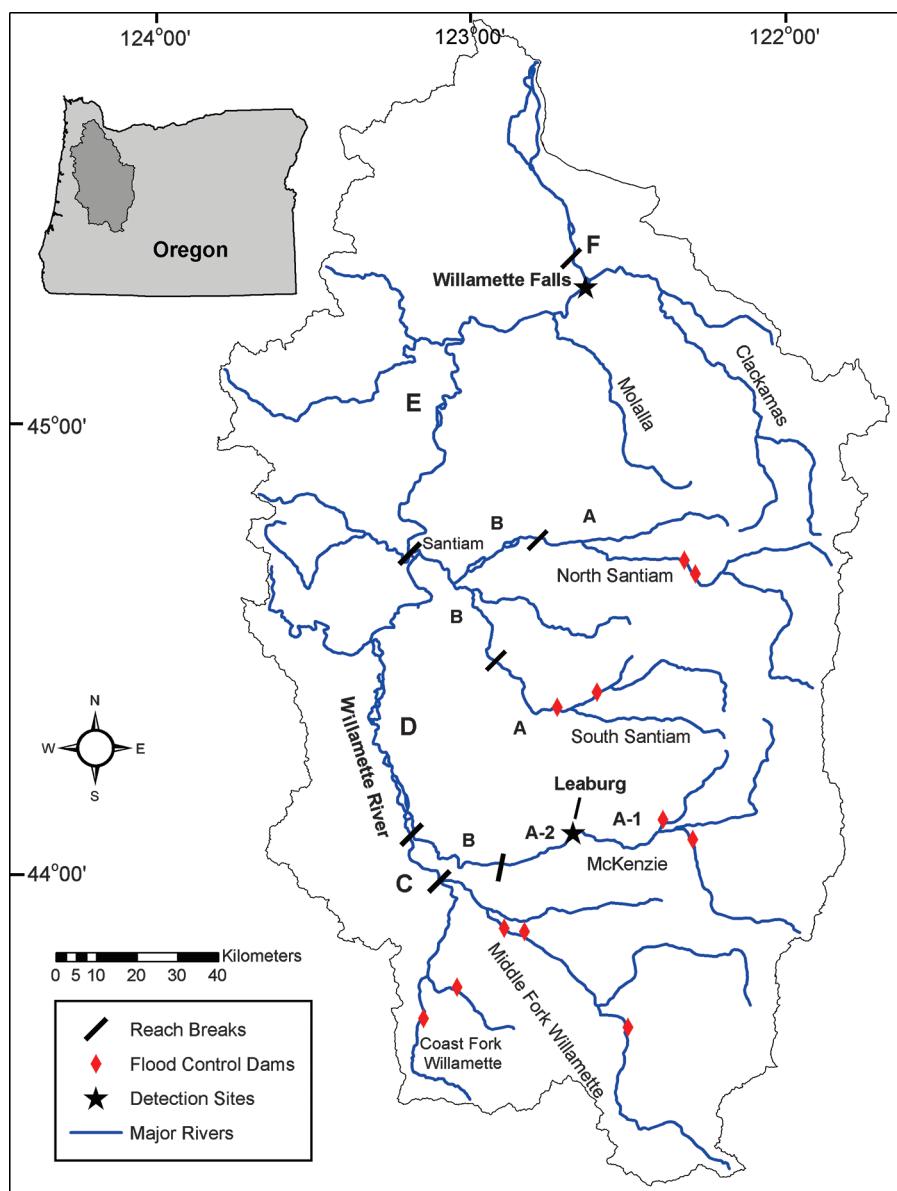
Chinook salmon in the Willamette River basin return from the ocean in late winter and early spring, and most migrate to spawning tributaries and hold through summer until they spawn in late August – late October. The primary spawning tributaries for spring Chinook salmon were historically the Clackamas, North and South Santiam, McKenzie, and Middle Fork Willamette rivers (Fig. 1). Spring Chinook salmon do not spawn in streams that flow east from the Coast Range Mountains because adult holding and spawning habitat is limited by low flow and high water temperatures during summer and autumn (Dimick and Merryfield 1945; Parkhurst et al. 1950; Willis et al. 1960). Genetic analyses of spring Chinook salmon in the Willamette River basin suggested weak but significant genetic structuring among subbasins (Johnson and Friesen 2014); therefore, juvenile fish sampled in this study represented several populations within the upper Willamette River ESU.

We studied the migratory and rearing behavior of juvenile Chinook salmon that were the progeny of adults spawning downstream of flood control dams or in accessible areas of the McKenzie River subbasin (hereinafter “wild”). The McKenzie River population was a primary focus of this study because it produces a majority of the wild fish in the upper Willamette River basin, and the McKenzie subbasin is the only one with accessible headwater spawning. The technical recovery team for the upper Willamette ESU designated Chinook salmon in the McKenzie River as a core population because of its historic abundance (McElhaney et al. 2003). The team also recognized the importance of life-history strategies to population viability. We therefore propose that migratory behaviors of the McKenzie Chinook salmon can provide a model of life-history diversity from which existing diversity in other populations can be evaluated and recovery strategies can be developed.

Juvenile fish collection and tagging

We organized our study around two migrant types of juvenile Chinook salmon based on the results of a study in the McKenzie River (Zakel and Reed 1984) that identified a large migration of fry shortly after emergence (hereinafter “movers”) and migrations of fish that remained in the spawning areas through at least their first summer of life (hereinafter “stayers”). We used a secondary classification for stayers based on their distinct seasonal migrations in October–December (fall migrants) and mid-February–May (spring migrants). We captured thousands of juvenile salmon throughout the Willamette River basin and used this dataset to identify migratory and rearing pathways and to estimate the con-

Fig. 1. Willamette River basin in Oregon, USA, showing flood control dams, sampling reaches, and PIT tag detection sites at Leaburg Dam on the McKenzie River and at Willamette Falls.



tribution of life histories to smolt production. We tagged fish with passive integrated transponders (PIT) and installed tag detection systems in existing fish bypass facilities to document passage. We sampled across multiple brood years (year in which parents spawned) to encompass a range of intra- and interannual variability in rearing and migratory conditions such as river discharge.

In 2005–2014, we captured movers with beach seines downstream of spawning areas and stayers in a trap at Leaburg Dam as they migrated downstream after rearing in natal areas. We supplemented our study of movers by capturing salmon fry from the 2011 and 2012 brood years with seines within and downstream of natal areas to document dispersal timing and distance. We also captured and tagged stayers within the natal reach of the McKenzie River subbasin in 2009–2014 to supplement information about the migration timing of stayers from natal areas and their subsequent emigration from the Willamette River.

We sampled juvenile salmon within (Reach A) and downstream (Reach B) of spawning areas and in four reaches of the Willamette River (Fig. 1). Primary spawning areas in the North and South

Santiam rivers are upstream of small diversion dams (river kilometre (rkm) 25 and 32, respectively) and downstream of spawning areas included 19 km of the Santiam River (Fig. 1). We used the 6 m high Leaburg Dam (rkm 55) as a break between primary (Reach A-1) and secondary (Reach A-2) spawning reaches in the McKenzie River because about 85% of the spawning occurred upstream of the dam (Sharpe et al. 2015). We sampled four reaches of the Willamette River: Reach C = Coast Fork and Middle Fork Willamette rivers (rkm 301) to McKenzie River (rkm 282), Reach D = McKenzie River to Santiam River (rkm 174), Reach E = Santiam River to Willamette Falls (rkm 43), and Reach F = Willamette Falls to rkm 34 downstream of the Clackamas River (Fig. 1). Other areas sampled were Middle Fork Willamette, Molalla, and Clackamas rivers to determine population sources of fry.

Movers

We documented the dispersal timing and distance of Chinook salmon fry (30–50 mm fork length, FL) by capturing fish within and downstream of spawning areas. Fry from the 2011 and 2012

brood years were captured with 6.1 m long \times 1.8 m deep pole seines (3.2 mm mesh). Our sampling coincided with emergence timing, which was estimated by accumulated temperature units (ATU; sum of the daily mean temperature that exceeded 0 °C) using water temperatures from US Geological Survey gauges or temperature data loggers placed in spawning reaches. We used spawning dates from redd surveys in each tributary to calculate ATUs, and we assessed emergence timing based on early spawning (first 5% of redds) and peak spawning. Fry emergence in the McKenzie River was estimated to be 1000 ATU in a previous study (Homolka and Downey 1995); therefore, we began sampling at 850–900 ATU (late November to early January) to document emergence. We seined in shallow water habitats along the margin of the river channels or in side channels at three to five sites within each reach, which were regularly sampled every 7–10 days. To sample across a range of flows, we generally selected sites with a gradual slope and road access to the river, but some sites were accessed by boat. We compared the dates we first captured fry in tributaries with the estimated dates of emergence for early and peak spawning. We then compared the dates fry were first caught in tributaries with the mean dates fry were first captured in the Willamette River. We assumed that salmon fry were widely distributed throughout the Willamette River when they were captured at $\geq 75\%$ of the sites. We estimated the distance fry dispersed as the difference between the farthest downstream site we caught fry and the nearest spawning location upstream. We assumed fry caught in the Willamette River were from the McKenzie or Santiam subbasins and tested our assumption by comparing catch rates of fry (fry-set^{-1}) among areas that included other potential population sources (Middle Fork Willamette, Molalla, and Clackamas rivers).

Because fry were too small to tag when they dispersed, we sampled approximately 20–125 km downstream of spawning areas in May–September 2005–2014 to capture and tag juvenile salmon that were representative of the mover life history. We started sampling in May (4–6 weeks after peak fry dispersal) to allow time for fry to reach tagging size and after most yearling smolts would have migrated from the Willamette River. We tagged subyearling Chinook salmon and differentiated subyearling and yearling fish by length; yearlings comprised <1% of the catch in the Willamette River and 0.1% of the catch in the Santiam and McKenzie subbasins. We captured juvenile salmon by deploying a beach seine (45.7 m long \times 2.4 m deep; ~6–10 mm square mesh) away from shore and retrieving it in an arc set (Hahn et al. 2007). Most sites were located on the inside bend of the main channel associated with submerged gravel bars, but we also sampled other habitats including side channels. We sampled an average of 60 days per year among all rivers and reaches, with a mean annual sampling effort of 217 seine sets at 37 sites in the McKenzie River subbasin, 256 seine sets at 58 sites in the Santiam River subbasin, and 390 seine sets at 58 sites in the Willamette River. We generally sampled each reach every 7–10 days and revisited two to five sites in each sampling cycle. Catch of subyearling salmon in Reach C of the Willamette River was low (<3 fish-set $^{-1}$ versus 20 fish-set $^{-1}$ in Reach D or 28 fish-set $^{-1}$ in the McKenzie River); therefore, we excluded these data in our analyses of migration timing from the Willamette River because of small sample sizes.

We counted and measured (FL, mm) all juvenile Chinook salmon and PIT-tagged fish ≥ 60 –65 mm FL if they were not injured and the adipose fin was present. During our study, all hatchery salmon released in the basin had an adipose fin clip to distinguish them from wild fish. Captured fish were held in a live well with circulating river water, then transferred to an anesthetic tub containing a buffered solution of tricaine methanesulfonate (MS-222, 60–80 mg·L $^{-1}$). We injected the fish with 134.2 kHz FDX-B PIT tags following recommended tagging procedures (PTSC 2014) and released the fish at or near the capture site after they had fully recovered.

Stayers

Our study of juvenile Chinook salmon rearing in natal areas focused on the McKenzie population because headwater spawning habitats remain accessible and a fish bypass at Leaburg Dam allowed us to tag fish as they migrated from natal areas or monitor the migration of fish tagged upstream of the dam. We classified stayers by their migration season: fall migrants in October–January or spring migrants in February–May. We captured fish in the bypass flume at Leaburg Dam in 2005–2014 with a modified rotary screw trap (1.2 m diameter) that funneled fish into a pipe attached to the live well and into an off-channel raceway. Juvenile salmon were transferred into holding tanks with circulating water and were handled and tagged by methods similar to those captured by beach seines. Fish were released into the bypass after they had fully recovered.

To collect additional information about the migration of fish from natal areas, we captured and tagged stayers in Reach A-1 of the McKenzie River subbasin in July–September 2009–2014. We started sampling in July when most fish began to reach tagging size and snorkeled throughout the reach to locate schools of fish. Two people positioned a pole seine (7 m long \times 3.8 m deep with 3.2 mm mesh) downstream of the school, and two snorkelers slowly crowded the fish toward the seine and helped pull the lead lines out of the water to trap fish in the bag. Captured fish remained submerged in the bag until they were transferred into a modified cooler with circulating stream water. Fish were handled and tagged in the same manner as fish captured by beach seines. After the fish had fully recovered, we released them at the location where they had been originally sighted.

Tag detection and expansion factors

We used detections of tagged fish to determine migration timing of juvenile Chinook salmon and identify migratory life histories. Tag detection systems were installed in the juvenile fish bypasses at Leaburg Dam and Willamette Falls to continuously monitor the migration of PIT-tagged juvenile Chinook salmon. We compared the migration timing of tagged fish past Leaburg Dam with the seasonal catch of juvenile salmon at the bypass trap to assess if the fish we tagged upstream of the dam were representative of the migrant population. We did not expand tag detections at Leaburg Dam because the mean flow was similar between October–January (136 m $^3\cdot\text{s}^{-1}$) and February–May (146 m $^3\cdot\text{s}^{-1}$) and subsequently was not a factor affecting the interpretation of seasonal migration. In contrast, the mean flow at Willamette Falls varied widely among seasons (400–1100 m $^3\cdot\text{s}^{-1}$), which affected the entrainment and subsequent detection of tagged fish. Because we used detections of tagged fish to estimate the relative abundance of migrants past Willamette Falls, we expanded detections to account for the effect of flow and efficiencies of the bypass system. Operation of the hydroelectric plant is run-of-river, and the plant operates continuously except for maintenance, construction, or extremely low river flow. A louver rack in front of turbine intakes guided fish into bypass routes where PIT tag detectors were located. We expanded tag detections at Willamette Falls by the efficiencies of PIT tag antennas and fish guidance to the bypass and by estimates of fish entrainment at different flow levels. Entrainment was estimated by the proportion of the total flow diverted through the plant and a measure of relative fish passage (P_r) from controlled studies of tagged fish at the falls to account for deviations from a 1:1 ratio between proportion of flow to the plant and entrainment (see Appendix A for detail).

The daily number of tagged salmon past Willamette Falls was estimated with the following equation:

$$ET = \frac{T}{[I/Q \cdot P_r \cdot E_G \cdot E_A]}$$

where ET = expanded daily tag detection, T = tags detected daily, I = intake at hydroelectric plant, Q = discharge at Willamette Falls, P_r = relative fish passage (ratio of entrained fish to discharge), E_G = efficiency of fish guidance to bypass routes (97%), and E_A = efficiency of PIT tag antenna (90%).

Data analyses

We defined life histories of juvenile Chinook salmon based on migratory and rearing pathways of tagged fish. We used passage timing of juvenile salmon at the falls to define smolt types and estimated the residence time of juvenile salmon within and downstream of natal areas to quantify the use of rearing areas within the basin. We considered the expanded number of tagged juvenile salmon migrating past Willamette Falls to be an index of smolt production and estimated the contribution of life histories to smolt production and population stability. Subyearling and yearling smolts emigrated in spring and early summer of their first or second year of life. Juvenile salmon that emigrated in fall and winter were considered to be “autumn smolts” (e.g., Beckman and Dickhoff 1998), although many of these fish likely overwintered in the Columbia River estuary and smolted the following spring.

Migration timing and rearing

We estimated passage timing at Willamette Falls from expanded detections of tagged juvenile salmon and summarized detections by brood year to facilitate comparison among all tag groups of different freshwater ages (i.e., tagged as subyearlings or yearlings). Detection dates were converted to day of year using fraction of the year between the detection date and the start of a year (1 January of the year following spawning) and multiplying by 365. Thus, for fish detected in their second year, the fraction of the year was >1.0. We calculated the median date of detection for each tag group and brood year from the frequency distribution of expanded detections. Groups with <25 unexpanded tag detections were excluded.

To determine if juvenile salmon passing Willamette Falls continued to migrate, we calculated migration rates of tagged fish to the Columbia River estuary using detection data from a National Marine Fisheries Service study that sampled fish with a midchannel trawl (Ledgerwood et al. 2004). We used rkm 75 (Jones Beach) as the detection point, which was the approximate midpoint of the reach sampled by the trawl. We compared migration rates ($\text{km} \cdot \text{day}^{-1}$) of juvenile salmon to Willamette Falls and to the estuary for fish that were detected at both locations and compared rates between subyearlings and yearlings from the McKenzie population. We analyzed differences in median migration rates with a Kruskal-Wallis test.

We estimated the residence time of juvenile Chinook salmon from the McKenzie River subbasin within or downstream of natal areas to quantify the use of rearing areas. For movers captured downstream of natal reaches and stayers captured at Leaburg Dam, residency was the number of days between release of tagged fish and subsequent detection at Willamette Falls. Because movers spent time downstream of natal areas as fry prior to tagging, we used the difference between tag date and date of peak fry catch in tributaries or full occupancy in the Willamette River to account for additional rearing. For salmon tagged in Reach A-1 of the McKenzie River, residency downstream of natal areas was the number of days between detections at Leaburg Dam and Willamette Falls. We estimated the residence time in natal areas for stayers as the number of days between the capture date at Leaburg Dam and the mean estimated date of peak emergence in 2004–2014 (18 February).

Life-history diversity and stability

We defined life histories of juvenile salmon by migration timing from natal reaches and passage at Willamette Falls and estimated the relative abundance of smolt types from expanded tag detections. Our analysis of migratory pathways was restricted to

the McKenzie River population because we could estimate migration from spawning areas for all juvenile life stages. Therefore, we used detections of fish tagged in the McKenzie and Willamette (Reach D) rivers and summed the expanded number of detections for each of three seasons: May–August of their first year of life, September–January, and February–May of their second year of life. To account for differences in the number of tagged fish released among sampling areas and years, we standardized the expanded number of detections per 1000 fish tagged. We estimated the relative percentage of stayers that migrated in fall or spring from the seasonal catch at Leaburg Dam and detections at the dam of fish tagged upstream.

We analyzed the effect of life-history diversity on the stability of smolt production over 8 brood years using the standardized number of expanded detections at Willamette Falls as an index of production. As a measure of population stability, we calculated the coefficient of variation (CV) of the annual estimated smolt abundance at the falls for six migratory life histories and the total indexed smolt population. Migratory life histories were defined as the combination of migration from natal reaches and smolt type at Willamette Falls: mover–subyearling smolt, mover–autumn smolt, mover–yearling smolt, stayer (fall migrant)–autumn smolt, stayer (fall migrant)–yearling smolt, and stayer (spring migrant)–yearling smolt. We used the weighted mean CV of life histories (sum of the products of the CV of life histories and their proportion) as an estimate of the predicted CV of smolt production in the basin if the life histories were synchronous (Moore et al. 2014). We compared the CV of each life history with the total CV and the predicted CV with that of the total (or observed) CV as a measure of a portfolio effect whereby diversity increases stability (Schindler et al. 2010; Moore et al. 2014). We assessed temporal correlation in the standardized number of expanded detections by calculating the Pearson product-moment correlation coefficients based on all pairwise comparisons among six migratory life histories over 8 brood years and evaluated the degree of asynchrony in the population of juvenile Chinook salmon migrating past Willamette Falls.

Results

We captured about 2300 fry in the McKenzie and Santiam subbasins and over 3700 fry in the Willamette River from the 2011 and 2012 brood years in December–April to identify timing and dispersal distance of newly emerged fry (movers). After fish that had migrated as fry had reached sufficient size for tagging (>60–65 mm FL), we seined downstream of spawning areas in spring and summer and tagged about 125 000 juvenile Chinook salmon (Table 1). We tagged juvenile Chinook salmon that remained in natal reaches (stayers) either in Reach A-1 (8741) or at Leaburg Dam in October–January (36 065) and February–May (10 374) as they migrated downstream (Table 1).

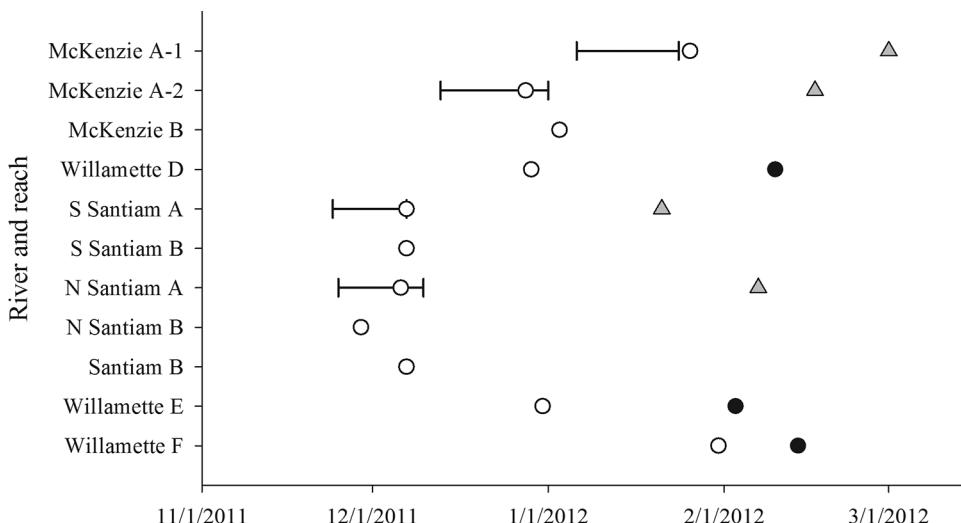
Migration in Willamette River basin

Chinook salmon fry migrated from spawning areas of the Santiam and McKenzie subbasins shortly after emergence and dispersed throughout the Willamette River within 4–6 weeks. We generally caught the first salmon fry in spawning tributaries near the predicted time of emergence at 1000 ATUs for early spawners (Fig. 2). The mean date when fry were caught in Reach D of the Willamette River was similar to the predicted date of emergence for early spawners in the McKenzie River and first catch of fry in the lower McKenzie River (Reaches A-2 and B), indicating rapid dispersal (Fig. 2). In Reach E of the Willamette River, the mean date of first catch was similar to that in Reach D and was 25–33 days later than the dates of early emergence or first fry catch in the Santiam River subbasin. These data suggest that McKenzie fry continued to disperse downstream or Santiam fry did not migrate to the Willamette River until more fish had emerged in the North and South Santiam rivers. Catch of fry in the Willamette River was

Table 1. Number of juvenile Chinook salmon given PIT tags and released in the Willamette River basin upstream of Willamette Falls, 2004–2013 brood years.

Brood year	Movers						Stayers		
	McKenzie Reach B	Willamette Reach D	S. Santiam Reach B	N. Santiam Reach B	Santiam Reach B	Willamette Reach E	Leaburg fall migrant	Leaburg spring migrant	McKenzie Reach A-1
2004	1967	2659	—	187	397	638	3268	626	—
2005	1592	1821	2503	1636	1488	578	3177	644	—
2006	1963	2039	1966	1419	1815	1956	4256	1663	—
2007	6600	7415	2498	1900	590	4390	4593	1301	—
2008	2829	2842	1762	1542	1577	2269	2211	1877	—
2009	1109	2457	1721	2178	948	3659	4027	813	—
2010	4713	5136	2825	1934	770	2648	3601	278	1970
2011	2968	7965	1212	734	—	3276	3517	2311	3023
2012	1177	3107	513	534	445	3410	5253	466	2906
2013	2054	2825	—	—	—	1773	2162	395	842

Note: Movers were subyearling Chinook salmon tagged and released in May–July; stayers in the McKenzie River were tagged and released at Leaburg Dam as they migrated downstream in October–January (fall migrant) and February–May (spring migrant) or upstream in Reach A-1 in July–September.

Fig. 2. Dates (month/day/year) of the first catch (open circles) of Chinook salmon fry by pole seines in three tributaries of the Willamette River basin upstream of Willamette Falls within spawning reaches (A) or downstream (B) and in three reaches of the Willamette River and dates when fry were caught in ≥75% of sites in the Willamette River (solid circles), 2011 brood year. Bracketed lines are dates for the range of accumulated temperature units at first fry sampling (850 ATU) through estimated emergence (1000 ATU) for early spawning (first 5% of redds), and triangles are estimated emergence dates for peak spawning. See Methods and Fig. 1 (map) for description and location of reaches.

about 4 weeks later downstream of the falls (Reach F) than upstream, and fry were widely distributed in the Willamette River by mid-February (Fig. 2). Results from the 2012 brood year were similar, although catch of fry in the tributaries was generally later than that of the 2011 brood year, likely because our sampling effectiveness was reduced by high flows in December that were two to six times higher in 2012 than in 2011.

By early January, we caught Chinook salmon fry in Reach D of the Willamette River at least 140 km from the nearest spawning areas and in Reaches E and F at least 190–200 km from spawning areas. To estimate dispersal distance, we assumed that most of the fry caught in the Willamette River were from the McKenzie or Santiam populations. The McKenzie River subbasin was the likely source of fry caught in Reach D of the Willamette River because the catch rate in Reach C and the Middle Fork Willamette River was much lower (0.9 fry-set^{-1}) than that in the McKenzie River (3.4 fry-set^{-1} , Reach B) or the Willamette River (4.6 fry-set^{-1} , Reach D). We caught no Chinook salmon fry in the Molalla River, indicating this spawning tributary was not a source for fry captured in Reach E of the Willamette River. The catch rate of fry in the lower Clackamas River (0.3 fry-set^{-1}) was much smaller than that in the Willamette River downstream of the Clackamas

(3.1 fry-set^{-1}), indicating most fry caught downstream of Willamette Falls originated from the Santiam or McKenzie subbasins.

Fry migrants that were tagged as subyearlings downstream of spawning areas exhibited a diversity of migration timing past Willamette Falls. Juvenile salmon tagged in the Willamette and Santiam rivers emigrated primarily as subyearlings (mean = 90.1% and 99.8%, respectively), and median dates of emigration were late May to mid-July (Fig. 3). Median dates of emigration for juvenile Chinook salmon tagged in the spawning tributaries (North Santiam, South Santiam, and McKenzie rivers) were more protracted than fish tagged in the Willamette and Santiam rivers (Fig. 3), and a higher percentage of the fish migrated as autumn or yearling smolts (mean = 34–50%).

Most of the juvenile Chinook salmon that remained in natal reaches through their first summer migrated to downstream areas in fall–winter. Of the tagged fish that passed Leaburg Dam, 72% were detected in October–January, which was comparable to the migration timing based on the catch rate at the dam (mean fall–winter catch = 77%; SD = 7.6%). The migration of stayers from natal reaches extended from October to June but generally peaked in the 6 weeks from November through mid-December (Fig. 4).

Fig. 3. Mean (and range) of the median day of passage at Willamette Falls from expanded detections of tagged juvenile Chinook salmon that were captured with seines in six areas of the Willamette River basin downstream of spawning areas (movers), captured with a trap at Leaburg Dam on the McKenzie River in October–January (stayers–fall migrant) or February–May (stayers–spring migrant), or captured with seines upstream of Leaburg Dam in Reach A-1, 2004–2013 brood years. Number of brood years for each release group is in parentheses and years with <25 unexpanded detections were excluded.

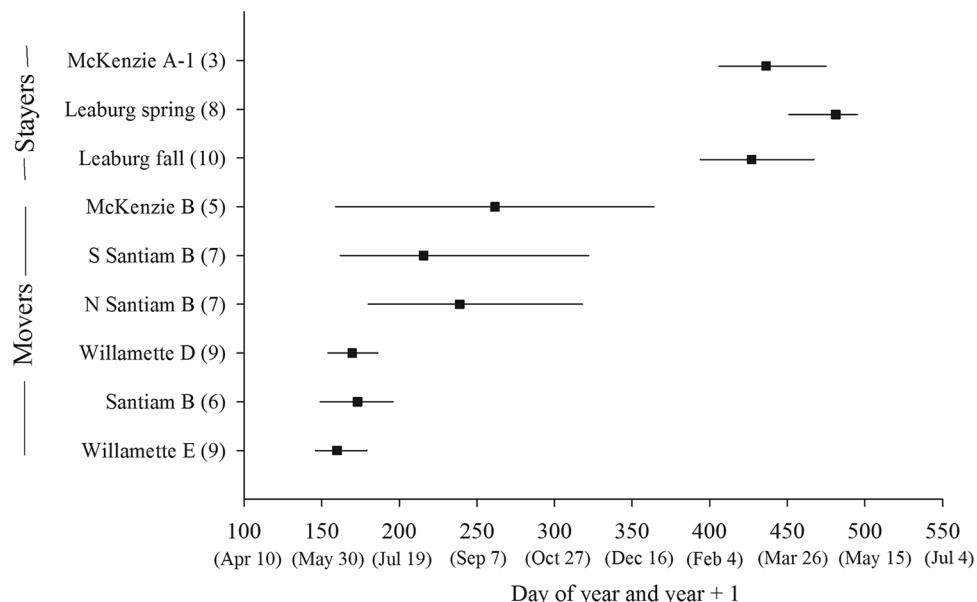
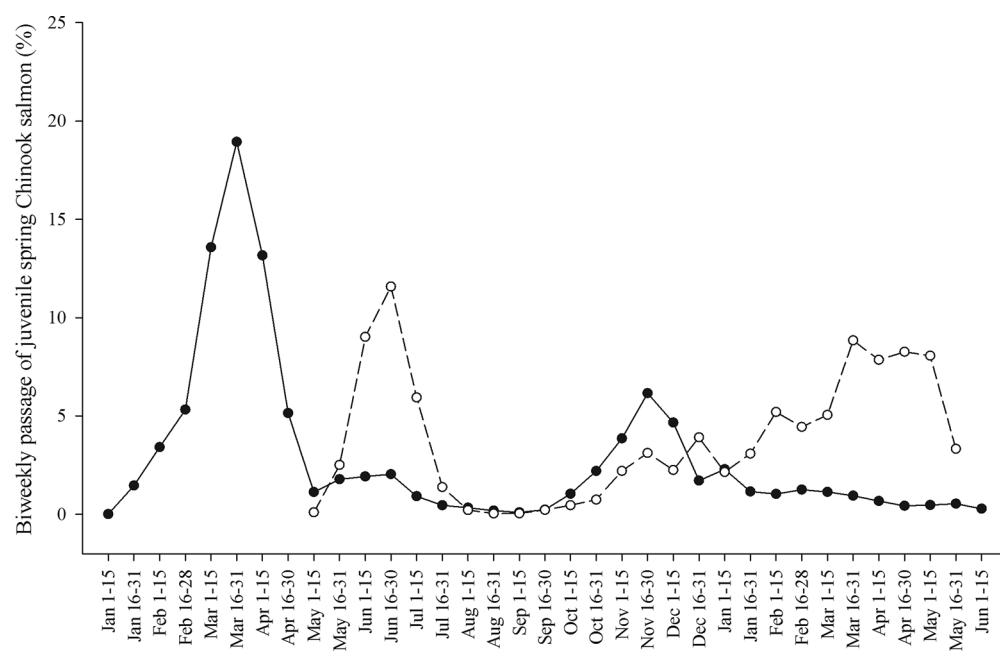


Fig. 4. Emigration timing of juvenile Chinook salmon from the upper McKenzie River subbasin based on the mean biweekly catch rate (fish·day⁻¹) at the Leaburg Dam bypass trap (solid circles, solid line) and emigration timing from the Willamette River based on the mean biweekly detections (expanded) of tagged McKenzie fish at Willamette Falls (open circles, dashed line), 2004–2013 brood years.



Juvenile Chinook salmon that migrated from the McKenzie River subbasin as stayers were detected at Willamette Falls in early spring for both fall and spring migrants (Fig. 3). The mean of the median dates of passage at the falls for fall migrants was over 7 weeks earlier than that for spring migrants (6 March versus 27 April), and median passage dates were more protracted for fall migrants (late January – early April) than spring migrants (late March – early May). Although some of the fall migrants continued past Willamette Falls as autumn smolts, their passage timing indicated many overwintered in the McKenzie and Willamette

rivers and migrated as yearling smolts the following spring. Because tagged juvenile salmon migrated from natal reaches of the McKenzie River primarily in fall–winter, their passage timing at Willamette Falls was similar to the fall migrants tagged at Leaburg Dam (Fig. 3).

Migration of juvenile Chinook salmon within the Willamette River basin continued throughout the year with seasonal peaks. Based on the biweekly catch of fish at Leaburg Dam, migration peaked in winter–spring (fry) and late fall (Fig. 4). Tagged juvenile salmon from the McKenzie population were detected at Willamette

Falls every month over the course of this study (Fig. 4), although fish migrated in August and September in only a couple of years when flow was above average and water temperature was below average. A migration peak of subyearling smolts at Willamette Falls in early summer followed fry dispersal from spawning areas of the McKenzie River, and a small peak of passage at the falls in early winter followed the fall-winter migration in the McKenzie River (Fig. 4). In contrast with the relatively small migration of yearlings in the McKenzie River, a larger migration of yearling smolts was observed at Willamette Falls, which reflects the contribution of fish rearing downstream of natal areas until their second year of life.

Migration to Columbia River

Juvenile Chinook salmon that we tagged in the Willamette River basin were detected in the lower Columbia River estuary during spring and early summer, indicating continued and directed migration to the estuary of the spring and summer migrants. Of the juvenile salmon detected at both Willamette Falls and in the estuary, fish migrated at a significantly higher rate from the falls to the estuary than from release sites to the falls (Kruskal-Wallis $H = 53.15$; $P < 0.001$), with a mean time of 5–6 days to travel 131 km from the falls to the estuary site. The median migration rate from the falls to the estuary was over twice as fast as that from release sites to the falls for subyearlings (25.2 versus $11.7 \text{ km} \cdot \text{day}^{-1}$) and was over nine times as fast to the estuary than to the falls for yearlings (31.1 versus $4.6 \text{ km} \cdot \text{day}^{-1}$).

Rearing

We estimated the residence time of juvenile Chinook salmon within or downstream of natal areas to evaluate the relative importance of rearing areas. The mean residence time downstream of natal areas for juvenile salmon of the mover life history was 125 days if they emigrated as subyearling smolts (the predominant life history for movers) and was three times longer for those that emigrated as yearling smolts (Table 2). We could not directly measure the residence time of fry migrants in natal areas, but the range was likely a few days for the early migrants we caught downstream up to about a month based on the difference between peak emergence (18 February) and peak catch of fry at Leaburg Dam in mid-March.

The mean residence time in natal areas for juvenile salmon with stayer life histories was 9–13 months (range = 8–16 months) before migrating to areas downstream (Table 2). For those that emigrated from the Willamette River in the same season they migrated from natal areas, 11% of their residency may have been in downstream areas (Table 2). By comparison, about 30% of the residence time for fall migrants was in downstream areas if they emigrated from the Willamette River as yearling smolts.

Life-history diversity and stability

We documented six primary life histories for McKenzie juvenile salmon based on migration from natal areas (movers and stayers) and smolt type at Willamette Falls (Fig. 5). Although over 70% of movers from the McKenzie River subbasin migrated as subyearling smolts (Fig. 5), we found that a higher percentage of movers tagged in Reach D of the Willamette River (McKenzie-source fish) migrated as subyearling smolts (89%) compared with those tagged in the lower McKenzie River (56%). The migration of stayers from natal areas was primarily in fall and early winter, but the majority of these fish overwintered and emigrated from the Willamette River as yearling smolts. We estimated that the yearling smolt life history represented about 69% of the smolts at Willamette Falls compared with much smaller contingents of subyearling and autumn smolts (Fig. 5). However, we found substantial variation in the contribution of six life histories to the total smolt production as measured by expanded detections of tagged fish at Willamette Falls (Table 3). For example, three migratory life histories contrib-

Table 2. Mean residence time of juvenile Chinook salmon within and downstream of natal areas in the Willamette River basin for movers (migrated as fry shortly after emergence) and stayers (remained in natal areas at least through their first summer of life).

Migrant type, smolt type (<i>n</i>)	Natal rearing		Downstream rearing	
	Mean	SD	Mean	SD
Mover				
Subyearling (2237)	—	—	125.5	15.2
Autumn (242)	—	—	245.3	25.2
Yearling (97)	—	—	384.4	23.4
Stayer-fall migrant				
Autumn (212)	267.8	14.9	33.3	24.1
Yearling (922)	283.7	25.8	119.7	31.2
Stayer-spring migrant				
Yearling (867)	394.8	26.0	47.8	22.9

uted to yearling smolts, and the largest contributor (stayers migrating in spring) varied from 31% to 72%. Two additional migrant types at Willamette Falls were fish that emigrated as fry and subyearlings that emigrated in late summer or early autumn (Fig. 5). Other minor life histories included male parr that resided and matured within the spawning areas (precocial) and fish that emigrated past Willamette Falls after their second summer, indicating the presence of a 2-year smolt life history.

We found evidence that temporal asynchrony in smolt numbers among life histories and stability of particular life histories conferred stability to the smolt population of Chinook salmon. In pairwise comparisons of the temporal variation in the number of detections for six life histories, 13 of 15 were not significant ($P > 0.05$), indicating substantial asynchrony among the contribution of life histories to the indexed smolt production (Table 4). However, life histories that shared the same early migratory phenotype when tagged (i.e., movers and stayers) were more correlated with each other than those with dissimilar phenotypes, suggesting asynchrony could be attributed to these phenotypic differences. Life histories were widely variable in their relative stability within the indexed smolt production (Fig. 6). The coefficient of variation was highest for movers that remained in the Willamette River through their first summer, although their relative proportion in total smolt production was low. Juvenile Chinook salmon migrating from natal reaches as yearlings were the most prevalent life history and had the lowest CV, thereby having the greatest influence on stability in the total smolt population. Although this life history represented 47% of the indexed smolt population, the cumulative contribution of other life histories increased the stability of the indexed smolt production. As evidence of a portfolio effect, we found the CV of the total population (0.34) was 35% lower than that of the predicted CV (0.52) calculated from the weighted mean CV of the six life histories (Fig. 6).

Discussion

This study identified six primary life histories of juvenile Chinook salmon based on migration from natal areas and rearing time in the basin before emigration past Willamette Falls. We documented the importance of habitats downstream of natal areas to all life histories and the importance of life-history diversity to smolt production and stability. We identified two phenotypes for early migratory tactics: fry that migrated shortly after emergence from redds (movers) and fish that migrated after rearing 8–16 months in spawning areas (stayers). Primary smolt life histories emigrating from the Willamette River included subyearling smolts from the mover phenotype and yearling smolts composed of mover and stayer phenotypes. Juvenile salmon emigrating in fall and early winter also contributed to smolt production, and although some may have been autumn smolts (e.g., Beckman and

Fig. 5. Migratory pathways of juvenile Chinook salmon from spawning areas to Willamette Falls for two phenotypes: fish that migrate from natal areas as emergent fry (movers = gray lines) and those that rear in spawning areas (stayers = black lines). Estimates of the percentage of fish expressing different migratory behaviors were from the detection of tagged juvenile Chinook salmon from the McKenzie River population. Primary migratory pathways are represented by thick lines and arrows, and smolt types are in boxes with thick borders and bold font; secondary pathways are narrow lines and arrows or dashed lines, and secondary migrant types are in boxes with dashed borders and italic font. Percentages for the pathways are additive, and percentages in boxes below the x axis are the mean contribution of three smolt types to the estimated smolt production, 2004–2013 brood years.

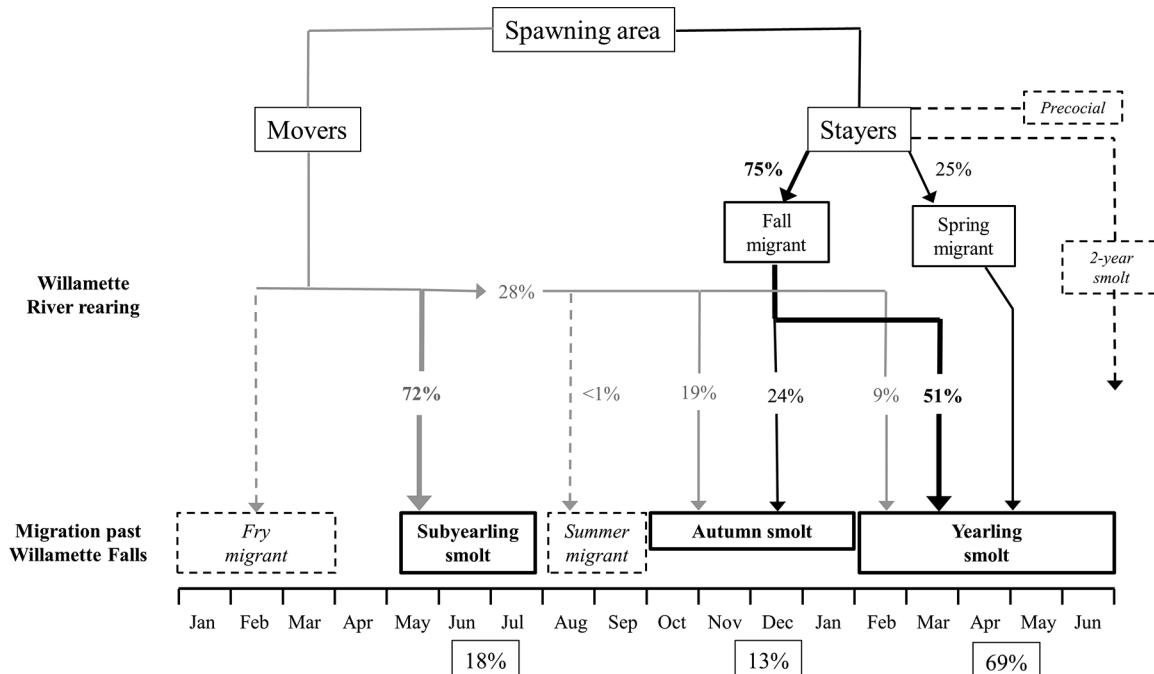


Table 3. Composition (%) by life history (tag group and smolt type) of juvenile Chinook salmon migrating past Willamette Falls based on the detection of tagged fish from the McKenzie River population.

Brood year	Mover			Stayer-fall			Stayer-spring		
	Subyearling	Autumn	Yearling	Autumn	Yearling	Yearling			
2004	11.0	3.3	0.7	15.0	12.3	57.7			
2006	6.7	0.8	1.6	7.3	12.0	71.6			
2007	13.0	10.1	4.7	8.0	14.5	49.7			
2008	15.3	3.5	0.4	6.3	22.9	51.6			
2009	34.2	7.9	2.4	5.1	11.7	38.7			
2011	29.0	1.3	0.7	3.2	24.8	41.0			
2012	11.4	0.4	0.4	8.8	26.9	52.1			
2013	23.7	1.1	1.0	18.2	24.5	31.5			

Note: Data excludes 2005 and 2010 brood years because shutdowns at Willamette Falls or Leaburg Dam resulted in incomplete data.

Dickhoff 1998), others likely migrated as yearling smolts from the Columbia River estuary.

Life-history diversity and stability

Studies have demonstrated that life-history diversity provides stability and resilience to salmon populations and fisheries (Hilborn et al. 2003; Schindler et al. 2010; Moore et al. 2014) and that juvenile life histories can contribute differentially to adult salmon populations (Miller et al. 2010; Copeland et al. 2014; Jones et al. 2014; Walsworth et al. 2015). Diverse juvenile life histories within and among populations can allow fish to respond to varying environmental conditions by following different migratory and rearing pathways ("response diversity"; Elmquist et al. 2003). Our study provides critical evidence that life-history diversity at juvenile life stages can provide a portfolio effect and confer stability

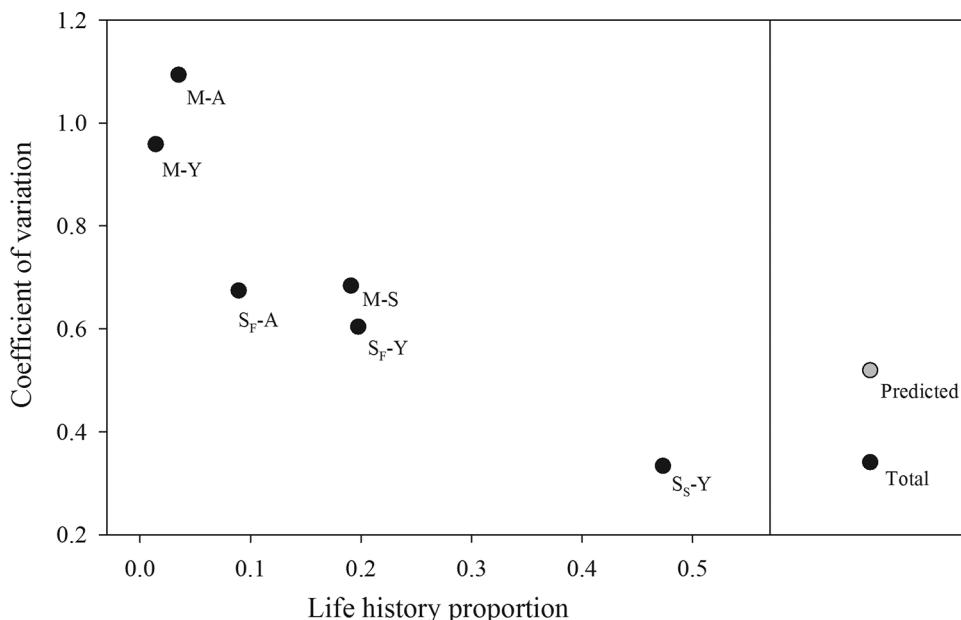
Table 4. Pearson's correlation coefficients of pairwise comparisons among the expanded number of six life histories of juvenile Chinook salmon detected at Willamette Falls over 8 brood years.

	M-A	M-Y	S _F -A	S _F -Y	S _S -Y
M-S	0.45	0.31	0.17	0.31	0.08
M-A		0.88**	-0.26	-0.32	-0.06
M-Y			-0.11	-0.28	-0.09
S _F -A				0.57	0.20
S _F -Y					0.73*

Note: Life histories are labeled as migration from natal areas (movers = M; stayers migrating from natal areas in fall or spring = S_F or S_S, respectively) and smolt type (subyearling = S; autumn = A; yearling = Y). Significant differences are denoted for P < 0.05 (*) and P < 0.01 (**).

within a population through variable contributions to smolt production. Copeland and Venditti (2009) found that three migratory life histories of Chinook salmon contributed to smolt production, but were unable to account for contributions from fry migrants that emigrated from the natal river shortly after emergence. Thorson et al. (2014) found evidence that spatial variation among populations buffered the temporal variability in the production of age-0 Chinook salmon in natal streams. We found that six life histories of Chinook salmon contributed differently to smolt production over 8 brood years. For example, contribution of the subyearling smolt life history to the estimated total was generally small (mean = 19%), but was 30% or more in some years. Fry migrants that reared through the summer also contributed to smolt production, sometimes representing over 50% of the fish emigrating from the Willamette River in fall and winter. Although certain life histories are a minor contributor to smolt production in some years, they may represent a critical component that contributes to

Fig. 6. Mean coefficient of variation (CV) and proportion of the contribution to smolts for six life histories of juvenile Chinook salmon (McKenzie River population) over 8 brood years based on the expanded number of detections at Willamette Falls standardized per 1000 fish tagged and released. Life histories are labeled as migration from natal reaches and smolt type: mover (M); stayer that migrated in fall (S_F); stayer that migrated in spring (S_S); subyearling smolt (S); autumn smolt (A); yearling smolt (Y). The right panel is the calculated CV for the total indexed smolt production (black circle) and the predicted CV of the migrant population (grey circle) estimated from the weighted mean CV of the six life histories (Moore et al. 2014).



the productivity of populations. In addition, productivity of certain life histories may be underestimated if their survival is constrained by the prevailing conditions of rearing and migratory habitats in the Willamette River basin or Columbia River estuary.

We found that the stability conferred to Chinook salmon at freshwater life stages resulted from asynchrony among life histories and the stability of specific life histories, similar to that reported for steelhead populations in British Columbia (Moore et al. 2014). In our study, the temporal variation among all life histories was more correlated within the life histories of the two migratory phenotypes (movers and stayers) than between them, indicating a degree of asynchrony attributed to diversity in early migratory behaviors. Juvenile Chinook salmon that reared in natal reaches and migrated as yearling smolts had the greatest influence on the overall stability of the indexed smolt population because their contribution to the total was high and their abundance was relatively stable ($CV = 0.33$) compared with that of the mover-subyearling smolt ($CV = 0.68$). However, because life histories contributed differently to smolt production over time, the combined contribution of all life histories provided stability to the smolt population and decreased the overall variability by 35%. Variability in the abundance of a steelhead population in a relatively pristine watershed was reduced by about 20% because of diverse life histories (Moore et al. 2014), which was smaller than we observed. However, their study was based on returning adults, and the effects of ocean mortality could reduce the asynchrony we observed in juvenile life stages.

Because mortality can be high in the early life of salmonids (Healey 1991; Bradford 1995; Quinn 2005), the asynchrony we observed in juvenile Chinook salmon could be attributed to differential survival between movers and stayers in their respective early rearing habitats. For example, the upper McKenzie River subbasin provides a relatively stable hydrologic and thermal environment for stayers because of its volcanic geology (Jefferson et al. 2006; Tague et al. 2007), which probably contributed to the stability of fish rearing in natal areas. In contrast, water temperature and flow were more variable in the Willamette River during

the early rearing period of January–April than in the natal reaches ($P < 0.001$). Therefore, the abundance of movers is likely to be more variable than that of stayers not only because of differences in survival in early rearing environments but also because of variability in the additional mortality experienced by dispersing fry.

Life-history diversity allows fish to exploit a full suite of environments and ecological niches (Murphy et al. 1997; Kraus and Secor 2004; Jones et al. 2014), and diversity of migratory behaviors such as dispersal of individuals can increase the productivity and resilience of fish populations (Kerr et al. 2010; Anderson et al. 2013; Copeland et al. 2014; Jones et al. 2014). Migration of juvenile Chinook salmon to rearing habitats downstream of natal reaches represents habitat shifts that entail trade-offs between costs such as predation and energetic demands and benefits such as increased growth opportunities. Juvenile salmon migrating to the Willamette River as fry in winter or as fall migrants starting in October would be rearing in winter habitat that is generally more productive than natal reaches. Mean water temperature is higher in the Willamette River than in the upper McKenzie River by 1–3 °C in November–February when fall migrants and fry would leave natal reaches and the temperature differential increases to 2–5 °C through the peak rearing period in spring and early summer. High winter flow in the Willamette River also provides a diverse suite of shallow water habitats for rearing, including flooded gravel bars, seasonal channels, and floodplains. Thus, juvenile salmon can exploit the spatial and temporal heterogeneity of habitats in the basin through alternative migratory behaviors, which can functionally increase carrying capacity and productivity (Bottom et al. 2005; Ruff et al. 2011; Armstrong and Schindler 2013). As a measure of increased productivity because of migratory diversity, the mean contribution to smolt production of the dispersive life histories was 53%.

We focused much of our tagging effort on fish that migrated as fry and reared downstream because we knew the least about this early migratory phenotype. We assumed the subyearling Chinook salmon we tagged downstream of natal reaches were representative of fry that migrated shortly after emergence. Although we

documented continued migration of fry past Willamette Falls, we believe many of the migrants took up residence in the lower spawning tributaries and in the Willamette River. Because stream residence behavior may take a number of days to develop (Reimers 1973), salmon fry could disperse far distances downstream before they settle. Dispersal of fry from natal reaches peaked in March; therefore, recruitment from upstream areas was limited when we captured thousands of subyearling salmon in May–July, indicating widespread residency of fry after dispersing.

We found that the average contribution of subyearling smolts to the total smolt production was relatively small, but we restricted our analysis to known McKenzie-source fish because we could not track all life histories in other subbasins (e.g., fall migrants in North and South Santiam rivers). Therefore, we likely underestimated the contribution of subyearling smolts because we excluded fish tagged in Reach E of the Willamette River, which was an unknown mix of Santiam and McKenzie populations, and these fish migrated almost exclusively as subyearling smolts (99.8%). The majority of fish tagged in the Santiam River subbasin also migrated as subyearling smolts (73%). These data indicate the contribution of the subyearling life history to total smolt production in the Willamette River basin is higher than we estimated based on the McKenzie population.

Although a small population of fall Chinook salmon is present in the upper Willamette River basin, we attributed the migratory behavior of juvenile salmon in this study to the spring run because they are more abundant with a greater spawning distribution than the fall-run salmon. Hatchery fall Chinook salmon were released upstream of Willamette Falls in 1971–1996 and a small naturalized population returns each year (2002–2014 mean = 1268 adults) to spawn in the lower Santiam River and limited areas downstream such as the lower Molalla River. By comparison, the mean annual return of wild and hatchery spring Chinook salmon to the upper Willamette River basin was about 33 300 adults in 2002–2014, excluding fin-clipped fish that returned to hatcheries. Genetic analyses of juvenile salmon in 2002–2004 indicated most were spring-run, including 67%–100% of the fish sampled at tagging sites in the Willamette and Santiam rivers and 97%–100% of emigrating juvenile salmon sampled at Willamette Falls in April–June and September–October (Schroeder et al. 2005).

Migration and rearing

The downstream migration from natal areas of juvenile Chinook salmon at various life stages in our study (fry, fall migrants, spring migrants) was similar to that described in other studies (Bjornn 1971; Murphy et al. 1997; Copeland and Venditti 2009; Daum and Flannery 2011). Areas downstream of natal reaches provided essential rearing habitat for juvenile salmon in the Willamette River basin, with mean residence times of 4–13 months for movers and up to 4 months for stayers. We documented extensive use of large river habitats for all life stages of juvenile Chinook salmon, including winter rearing, similar to that reported for the Fraser River in Canada (Levings and Lauzier 1991) and rivers in Idaho (Copeland et al. 2014). In contrast, Shrimpton et al. (2014) found that juvenile Chinook and coho salmon (*Oncorhynchus kisutch*) in British Columbia, Canada, used large rivers primarily as migration corridors based on otolith analysis of adult salmon.

We documented Chinook salmon fry migrating up to 140–200 km downstream from the nearest spawning areas within 3–6 weeks of emergence, which are among the longest migration distances reported for salmon fry. Studies in Canada reported dispersal of fry up to 100 km (unpublished data cited in Bradford and Taylor 1997), and the capture of juvenile Chinook salmon in nonnatal tributaries of the lower Fraser River suggested longer migration distances (Murray and Rosenau 1989). Long-distance dispersal of fry (100+ km) was inferred in a study of Chinook salmon in the Snake River (Idaho and Washington) based on the

genetic identification of relatively small fish (60 mm) from distant upstream watersheds (Connor et al. 2001). These studies, along with our data on rapid, long-distance dispersal from spawning areas, indicate fry can actively migrate as postulated by Healey (1991) rather than being passively swept downstream (Thomas et al. 1969; Irvine 1986).

Fry migrants and subyearling smolts were present in all populations we studied. Adult salmon in several tributaries of the upper Willamette River basin spawn downstream of barrier dams where water temperature is higher during incubation and a subyearling life history may be favored in these environments because of early fry emergence. However, a large fry migration was present in the McKenzie population where salmon have access to headwater areas, suggesting other factors influenced fry dispersal. Fry migrants and subyearling smolts were reported in Willamette spring Chinook salmon prior to construction of dams (Dimick and Merryfield 1945; Craig and Townsend 1946; Mattson 1962), indicating this migratory pathway is a natural component of the populations that has persisted despite widespread changes in habitat quantity and quality. Billman et al. (2014) found that body morphology of juvenile salmon in the Willamette River basin was correlated with life-history tactics expressed as migratory behavior, which suggested that fry dispersal was associated with differentiation in morphology.

We hypothesize that fry dispersal and emigration as subyearling smolts would be favored in the upper Willamette River basin because other salmon runs were absent and extensive areas of habitat were available downstream of natal reaches. Fry migrants would not be competing for food and space with juveniles of other species such as fall Chinook and coho salmon because they were historically absent upstream of Willamette Falls. Productive rearing habitat for dispersing fry would have been expansive in the historic Willamette River, which was a complex of braided channels connected to broad floodplains and side channels during frequent floods (Benner and Sedell 1997) and bordered by mature riparian forests that provided structure to the river (Sedell and Froggatt 1984; Gregory et al. 2002). Life histories of juvenile Chinook salmon in coastal rivers include the use of estuaries as nursery habitat by fry migrants prior to ocean entry as subyearlings (Reimers 1973; Healey 1991; Bottom et al. 2005). The Willamette River could function as an equivalent nursery area for fry migrants, thus providing the environmental template for the development of a successful life-history strategy whereby fry can attain the growth necessary to smolt as subyearlings.

Management implications

Large hatchery programs, age- or size-selective harvest, simplification or loss of habitat, and climate change can directly or indirectly reduce the diversity of life histories that results in a loss of stability and viability within and among populations (Moore et al. 2010; Carlson and Satterthwaite 2011; Anderson et al. 2015). Diverse habitats and spatial and temporal connectivity to habitats provides the ecological template that allows for local adaptation and the development and sustainability of diverse life histories (Rogers and Schindler 2008; Waples et al. 2009; Fraser et al. 2011; Schindler et al. 2015). Habitat for juvenile salmon in the Willamette River basin has been greatly reduced or simplified by direct loss (e.g., impassable dams) and decreases in water quality and quantity (e.g., reduced flooding and loss of connectivity). Measures to increase the diversity and connectivity of habitats and maintain the processes that produce habitat heterogeneity could therefore increase the expression of life histories, contribute to population productivity, and help increase the response diversity of populations to environmental fluctuations caused by anthropogenic disturbances such as habitat loss and climate change (Beechie et al. 2013; Jones et al. 2014; Walsworth et al. 2015; Schindler et al. 2015).

Our results showing the extensive use of the watershed by life histories of juvenile Chinook salmon and the varying contributions of life histories to smolt production illustrate the importance of integrating habitat conservation and restoration with the spatial and temporal scales at which life histories are expressed (Kocik and Ferreri 1998; Baguette et al. 2013). Conserving and restoring habitats for diverse life histories in the Willamette River basin should extend spatially from high elevation natal reaches to large river habitats and should provide longitudinal and lateral connectivity at the temporal scales of the migratory and rearing pathways (Beechie et al. 2010; Schindler et al. 2015). Conservation and recovery actions should include measures to restore a diverse suite of connected habitats to provide benefits for all life histories not just the most common ones observed under current conditions (Watters et al. 2003; Jorgensen et al. 2013; Copeland et al. 2014). For example, a larger number of juvenile salmon migrated in the fall than in the spring from natal reaches of the McKenzie River subbasin, but contribution of fall migrants to the estimated smolt production was about 40% lower than that of spring migrants, suggesting high winter mortality. Winter habitats could be lost or reduced because of anthropogenic changes to the Willamette River that include reduced frequency and magnitude of floods, increased duration of bank-full flows, and reduced channel complexity (Hulse et al. 2002; Wallick et al. 2007), resulting in loss of velocity refugia and connectivity to floodplains. Actions such as removing bank revetments and altering dam operations to more closely match historical hydrologic conditions could improve winter habitat and also help buffer populations against climate change (Beechie et al. 2013). Measures to reconnect adult and juvenile salmon to historic spawning and rearing areas upstream of dams would increase habitat diversity in the basin and could include effective upstream and downstream passage past dams and reservoirs, altered dam operations, or removal of dams.

Our results indicate life-history diversity provides population stability during freshwater life stages. Additional stability and resilience to populations should be conferred through adult life stages because of varying residence times in the ocean within a year class (e.g., Jones et al. 2014; Moore et al. 2014), and analyses are underway to identify and quantify the contribution of life histories within and among Willamette River basin populations over 10–12 brood years. The diversity observed in Willamette spring Chinook salmon should increase the likelihood that some individuals in the population will survive to reproduce under changing environmental conditions by spreading risks (bet-hedging strategy) across time and space (Stearns 1976). Maintaining this diversity and the habitats that support it will be critical considering the existing anthropogenic effects on salmon habitat within the basin such as impassable dams, the potential negative effects of future population growth in the Willamette Valley, and other uncertainties such as climate change.

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Appendix A. Effect of flow on expansion of tag detections

Because the volume of river flow diverted to the hydroelectric plant and fish bypass at Willamette Falls is relatively constant ($177 \text{ m}^3 \cdot \text{s}^{-1}$), we assumed the entrainment of migrating juvenile salmon would be inversely proportional to flow (i.e., decrease at increasing flow). We used the proportion of total river flow diverted into the plant to expand detections of tagged fish at the falls. We also developed a measure of relative fish passage (P_r) to account for changes in the relationship between flow and entrainment at different ranges of flow. Our estimates for P_r were derived from controlled releases of radio-tagged fish by Portland General Electric biologists and PIT-tagged fish by Oregon Department of Fish and Wildlife biologists. Tagged hatchery spring Chinook salmon were released upstream of the falls between ~ 280 and $1135 \text{ m}^3 \cdot \text{s}^{-1}$. The mean detection rates of tagged fish for multiple test releases at similar flows were used to develop three values of P_r : 1.0 ($<425 \text{ m}^3 \cdot \text{s}^{-1}$), 0.8 ($425\text{--}707 \text{ m}^3 \cdot \text{s}^{-1}$), and 0.5 ($708\text{--}1135 \text{ m}^3 \cdot \text{s}^{-1}$). Based on the shape of the curve fitted to the test data ($y = 4.67 + 0.019x^{-1}$), we assumed entrainment would continue decreasing at discharges $>1135 \text{ m}^3 \cdot \text{s}^{-1}$; therefore, we used P_r values of 0.3 at discharges $1136\text{--}1699 \text{ m}^3 \cdot \text{s}^{-1}$ and 0.2 at discharges $>1699 \text{ m}^3 \cdot \text{s}^{-1}$.

We tested our assumptions about the effect of flow on expansion of tag detections and subsequent estimates of migration timing by comparing the mean of median passage dates between years when the mean monthly flow in November–April was $\leq 1135 \text{ m}^3 \cdot \text{s}^{-1}$ (low-average flow) and years when flow was $>1135 \text{ m}^3 \cdot \text{s}^{-1}$ (high flow). We chose November–April for our tests because these are the months of highest flow in the Willamette River. We hypothesized that if our expansion factors underestimated detection of tagged fish at high flows, then the estimated median date of passage in high flow years would shift from that in low flow years (i.e., earlier median passage date for fish tagged as subyearlings because the later part of their migration occurs in fall-winter and later passage date for fish tagged in fall because the early part of their migration occurs in fall-winter). We compared the mean of median dates of detection with t tests between low and high flow years for fish tagged at Leaburg Dam as fall migrants and for two groups of subyearlings: (i) spawning tributaries (North and South Santiam and McKenzie rivers) and (ii) the Willamette and Santiam rivers.

The means of the median dates of detection at Willamette Falls were not significant between low-average and high flow years for fall migrants or subyearlings (Appendix A, Table A1), indicating our expansion factors were appropriate for estimating migration patterns at a seasonal scale. We summarized biweekly detections of tagged fish at Willamette Falls to estimate migration timing of juvenile salmon, and each 2-week period usually had some days of low to average flows, which would have provided opportunities for higher detection efficiency.

Table A1. Comparisons of passage timing at Willamette Falls between years when November–April flow was low-average ($\leq 1135 \text{ m}^3 \cdot \text{s}^{-1}$) and years when flow was high ($>1135 \text{ m}^3 \cdot \text{s}^{-1}$) for tagged juvenile Chinook salmon released in three areas of the Willamette River basin.

River (migrant type)	Low-average flow		High flow		<i>t</i>	<i>P</i>
	Mean (n)	SD	Mean (n)	SD		
McKenzie at Leaburg Dam (fall migrants)	425.7 (3)	6.4	428.2 (8)	27.3	0.16	0.44
North and South Santiam, McKenzie (subyearling)	233.8 (11)	73.6	239.6 (8)	72.4	0.17	0.43
Willamette and Santiam (subyearling)	169.7 (12)	16.1	162.8 (10)	11.6	1.13	0.14

Note: Passage timing is mean of the median date of detection expressed as day of the year starting 1 January of their first year of life.