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Juvenile coho salmon movement, growth and survival in a coastal basin of southern Oregon

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Abstract

Juvenile salmonids display highly variable spatial and temporal patterns of early dispersal that are influenced by density-dependent and density-independent factors. Although juvenile coho salmon (*Oncorhynchus kisutch*) movement patterns in streams and their relationship with body mass and growth have been examined in previous studies, most observations were limited to one season or one stream section. In this study, we monitored the movement of juvenile coho salmon throughout their period of residence in a coastal basin to identify prevalent dispersal strategies and their relationships with body mass, growth rates and survival. Our results revealed seasonally and spatially variable movement patterns. Juvenile coho salmon that dispersed to tidally affected reaches soon after emergence remained more mobile and expressed lower site fidelity than those individuals that remained in upper riverine reaches. We did not detect significantly different growth rates between sedentary and mobile individuals. Although a greater proportion of sedentary than mobile fish survived winter to emigrate from the creek in the spring, reach of residence at the onset of winter influenced these survival estimates. Hence, apparent summer-to-smolt survival for mobile individuals was greater than for sedentary fish in tidally influenced reaches, whereas in riverine reaches the sedentary strategy seemed to be favoured. Our research identified complex movement patterns that reflect phenotypic and life history variation, and underscores the importance of maintaining diverse freshwater and estuarine habitats that support juvenile coho salmon before marine migration.

KEYWORDS
coho salmon, condition dependence, life history, movement, tide gate

1 | INTRODUCTION

Anadromous salmonids exhibit diverse dispersal patterns following emergence from the gravel, as they occupy different summer and winter habitats before smolting for their marine migration (McCormick, Hansen, Quinn, & Saunders, 1998; Nickelson, Rodgers, Johnson, & Solazzi, 1992; Shrimpton et al., 2014). For juvenile salmonids, both timing and range of dispersal from natal stream reaches can vary greatly among individuals and populations (Bradford & Taylor, 1997; Fausch & Young, 1995) in response to stream discharge (Hartman, Anderson, & Scrivener, 1982), availability of resources (Fausch & Young, 1995) and social interactions (Chapman, 1962; Metcalfe, Huntingford, Graham, & Thorpe, 1989).

Metabolic rates and social dominance are strongly linked in juvenile salmonids because individuals that grow quickly and become relatively larger than others in their cohort are most likely to occupy dominant positions within feeding hierarchies (Metcalfe, Taylor, & Thorpe, 1995; Nielsen, 1992). Coho salmon (*Oncorhynchus kisutch*) is a territorial species for which the *competitive exclusion* of subordinate individuals by dominant fish has been used to explain the early dispersal of large

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numbers of fry (Chapman, 1962; Hartman et al., 1982). However, more recently, the idea of *early condition-dependent movement* began to receive more attention after some studies found that large individuals are more likely to disperse greater distances than small ones (Anderson et al., 2013; Bowler & Benton, 2005; Einum, Sundt-Hansen, & Nislow, 2006). These different mechanisms describing coho salmon early fry dispersal to downstream reaches are not mutually exclusive and likely influence each population and cohort uniquely depending on fish abundance and habitat quality and availability (Anderson et al., 2013).

As one might expect, foraging resources are some of the most important factors influencing young coho salmon early movements. After dispersing from the spawning reaches in early spring, which tends to coincide with the migration of yearling smolts to estuaries, most subyearling coho salmon that remain in the stream during summer were commonly thought to move little until the onset of fall conditions (Hartman & Brown, 1987). The dominant individuals that establish foraging territories tend to defend them aggressively, and this forces many subordinate individuals to seek food and other resources elsewhere (Chapman, 1966; Nielsen, 1992). However, this hierarchical model cannot explain all subyearling coho salmon movements. For example, Armstrong and Schindler (2013) reported that diel movements by subyearling coho salmon in an Alaskan stream appeared to serve a thermoregulatory purpose, as these fish moved more than 1,000 m to forage on sockeye salmon eggs in coldwater areas and returned to relatively warmer groundwater-fed tributaries to better assimilate those nutrient-rich food resources. In three Western Washington streams, Kahler, Roni, and Quinn (2001) observed that 28% to 60% of juvenile coho salmon moved from shallow poor-quality habitats with low fish densities into deeper habitats that supported higher densities of competitors. The fish that moved did not differ in size and grew at a faster rate than more sedentary individuals, which suggests that these were not subordinate individuals displaced by competitive interactions. Anderson et al. (2013) similarly found that movement of subyearling coho salmon occurred independently of fish density and that the distance moved was positively correlated with body size. These studies indicate that bigger fish are more capable than smaller fish to take advantage of dispersal opportunities and are consistent with the condition-dependent hypothesis. Hence, it becomes apparent that the traditional understanding of subyearling coho salmon being mostly sedentary and highly territorial during the summer months is an oversimplification of a much more complex reality.

By the same token, juvenile coho salmon seasonal movement patterns among habitats and stream reaches are likely to be more diverse than we think. Most evidence indicates a large-scale habitat shift occurs among subyearling coho salmon during fall and early winter, which coincides with the increased frequency and magnitude of freshets (Ebersole et al., 2006; Giannico & Healey, 1998). The inhospitable winter conditions of main channel habitats seem to force the young fish into wetlands, side ponds, small tributaries and different types of off-channel habitats (Bell, Duffy, & Roelofs, 2001; Nickelson et al., 1992; Peterson, 1982a). In many basins, groundwater-fed ponds and channels provide thermal refuge, and coho salmon continue feeding and growing during the winter months (Giannico & Hinch, 2003; Peterson, 1982b), but in less favourable winter habitats, the fish hide and are largely inactive, particularly during the day (Roni & Fayram, 2000). Access to off-channel habitats and instream structures is essential for juvenile coho salmon, particularly during winter when high-discharge events displace many fish and adversely affect survival in mainstem habitats (Bell et al., 2001; Nickelson & Lawson, 1998; Solazzi, Nickelson, Johnson, & Rodgers, 2000).

Spatial and temporal variability in stream habitat conditions (e.g., water temperature, discharge), prey abundance, fish density and the interaction between these factors can cause large differences in the growth rates of subyearling coho salmon (Armstrong et al., 2013; Scrivener & Andersen, 1984). In turn, such differences in growth and body size engender disparities in competitive ability. Juvenile coho salmon that experience high growth rates and attain larger than average size often have an advantage over smaller individuals in terms of competing for the limited food resources and maintaining position within favourable habitats (Bell et al., 2001; Nielsen, 1992). Several studies reported that body size of subyearling coho salmon in late summer or early fall is positively associated with winter survival rate (Brakensiek & Hankin, 2007; Ebersole et al., 2006; Pess et al., 2011; Quinn & Peterson, 1996). Additionally, there is evidence that larger coho salmon smolts experience greater ocean survival, particularly during periods in which overall survival is low (Holtby, Andersen, & Kadowaki, 1990). Thus, it seems that growth rate and body size may positively affect condition and overall fitness of juvenile coho salmon throughout the freshwater and early marine life history phases.

In coastal streams, the early downstream migration of large numbers of coho salmon fry into estuarine habitats has been well documented for over five decades (Chapman, 1962; Hartman et al., 1982; Jones, Cornwell, Bottom, Campbell, & Stein, 2014; Miller & Sadro, 2003; Murphy, Koski, Lorenz, & Thedinga, 1997). Although these estuarine migrants were initially considered to be “surplus” fish unable to maintain territory among larger and more aggressive individuals, large-scale migration of coho salmon fry has been observed even at low fry densities (Tschaplinski, 1982). This suggests that this early system-wide movement from the upper stream reaches to the tidally influenced low reaches and the brackish waters of the upper estuary is likely to occur in response to density-independent factors (e.g., discharge, temperature) as well as competitive interactions (Hartman et al., 1982). The fate of these early estuarine migrant fry remained unknown for decades, and analyses of scales (Crone & Bond, 1976) and salt water challenge tests (Kennedy, Shoop, Griffioen, & Solmie, 1976) indicated that most did not survive to adulthood. Only recently, using passive integrated transponder (PIT) tag technology and the microchemical composition of otoliths, Jones et al. (2014) were able to confirm that approximately 1.5% of subyearling estuary migrating coho salmon fry returned to their natal streams to spawn and that they represent an alternative life history.

Although several studies have examined the relationship between juvenile coho salmon freshwater movements and body mass and growth rate, it remains unclear whether in all circumstances the more mobile individuals are the relatively small fish that are displaced from high-density rearing habitats (Chapman, 1962; Rhodes & Quinn, 1998) or the large fish that can better exploit resource-rich heterogeneous habitats (Anderson et al., 2013; Kahler et al., 2001). Unlike those studies that focused on fish size or growth rate and were limited to one season or one section of a stream, our study examined the movement strategies of individually marked juvenile coho salmon during their entire residence period within the freshwater and brackish reaches of a small coastal stream and the implications of those movements on fish body mass, growth and apparent survival. Specific objectives were to (i) describe juvenile coho salmon movement strategies and patterns during their residence period in Palouse Creek; (ii) determine the relative proportions of juvenile coho salmon likely to exhibit each movement strategy; (iii) establish whether coho salmon body mass or growth rates are related to movement strategy; and (iv) evaluate whether apparent winter survival of juvenile coho salmon is associated with movement strategy.

2 | METHODS

2.1 | Study area

Palouse Creek is a third-order coastal stream within the Coos River basin, Oregon, USA (Figure 1). Palouse Creek is approximately 15 km long, with a 3-m waterfall at river kilometre (RKm) 12.1 and a total catchment area of 28.2 km^2. Lower portions of Palouse Creek and lowland tributaries were dredged, straightened, diked and tide gated in the early 1900s, and periodic dredging and dike construction since that time have maintained the initial modifications. Palouse Creek is tide gated at the confluence with Haynes Inlet (RKm 0.0), a northern arm of Coos Bay, to reduce tidal influx in the lower reaches of the basin. The tide gates consist of two rectangular wooden, top-hinged flap-doors (4.1 m high, 2.6 m wide) that function based on hydraulic head differential between upstream (stream) and downstream (bay) areas. The tide gates reduce inflow of saline tidal surges by closing during rising tides that increase hydrostatic pressure on the bay side of the gates relative to the stream side. The gates open during ebbing tides when bay side hydrostatic pressure decreases, which allows freshwater discharge into the estuary. Impoundment of stream flow during the periods when the gates are closed creates a reservoir immediately upstream of the tide gates that fluctuate up to 1.8 km in length daily and seasonally in response to changes in stream discharge and tidal cycles. The Palouse tide gates were last refurbished in 1985, and since then, large scour holes have developed under the tide gate box, thus allowing the upstream intrusion of estuarine waters into the reservoir. The magnitude of this brackish water lens is such that salinity greater than 20 ppt has been recorded as far as 1.4 km upstream of the tide gates and measurable salinity up to 2.7 km from the tide gate.

Habitat in the Palouse basin ranges from estuarine lowlands to moderate-gradient upland reaches. Study reaches in the Palouse basin (see Figure 1) were classified as follows: tide gate reservoir (Reach 1), tidally affected stream reaches upstream of the reservoir (Reach 2 and Tributary A), low-gradient (0%–1%) riverine reaches (Reaches 3 and 4 and Tributary B) and moderate-gradient (1%–5%) upland reaches in which most adult coho salmon spawn (Reaches 5 and 6, Bear Creek and Tributary C). Tidally affected reaches generally feature wide, low-gradient (<1%) channels with dune-ripple channel morphology and low structural complexity relative to reaches upstream of tidal influence (Montgomery & Buffington, 1997). Palouse Creek is a perennial stream, although surface flows in several tributaries, including Tributary C, are seasonal. Discharge in Palouse Creek typically ranges from <0.1 m^3 s^{-1} in summer to approximately 5 m^3 s^{-1} during peak winter freshets.

Water temperature was monitored at 15 mainstem and tributary locations during the study period with loggers (Hobo Water Temp ProV2) that recorded ambient temperature at 30-min intervals. Salinity

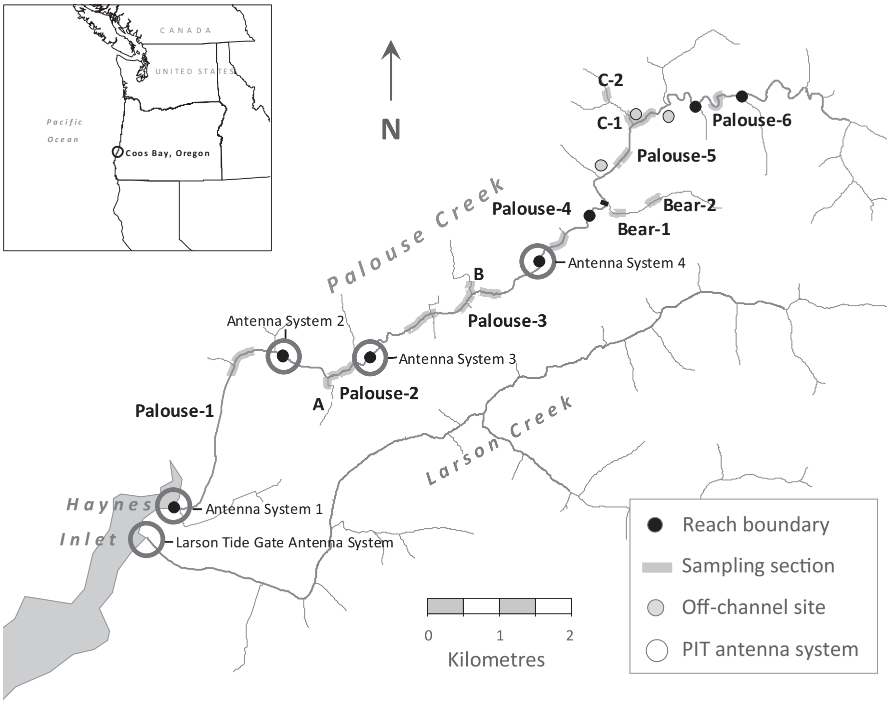

FIGURE 1 Map of Palouse and Larson basins with locations of study reaches, sampling sections, off-channel sites and passive integrated transponder (PIT) antenna systems in each basin. Mainstem reaches are numbered, while those labelled with letters are tributary channels. Palouse Creek drains into Haynes Inlet on the northern end of Coos Bay. Inset map shows regional location of Coos Bay

in Haynes Inlet and the Palouse tide gate reservoir was recorded at a depth of 1 m and at 5-min intervals from May to October 2009 at three locations (Haynes Inlet, RKm 0.0, RKm 0.45) and from July to December 2010 at five locations (Haynes Inlet, RKm 0.0, RKm 0.45, RKm 0.9, RKm 1.35) using loggers (Star-Oddi DST CT). Temperature was summarised as the highest seven-day running average maximum temperature (maximum weekly maximum temperature [MWMT]), while salinity was reported as maximum values.

2.2 | Juvenile salmon sampling and tracking

Juvenile coho salmon of brood years 2008 and 2009 were used in this study. During 2003–2009, annual adult coho salmon escapement in the Palouse basin ranged from 43 to 1,763 and the estimated escapements for 2008 and 2009 were 422 and 491 coho salmon respectively. Adult coho salmon return to Palouse Creek in the late fall and spawn in winter (November through January). Age-0 juvenile coho fry emerge and disperse from spawning gravels in late winter and early spring (February through April), which is concurrent with the typical period of age-1 coho smolt emigration (January through May) from the basin to marine areas. In addition to coho salmon, fish species found in Palouse Creek include the following: Chinook salmon (*Oncorhynchus tshawytscha*), steelhead (*O. mykiss*), resident and sea-run cutthroat trout (*O. clarkii*), sculpin (*Cottus* spp.), three-spined stickleback (*Gasterosteus aculeatus*), Pacific lamprey (*Entosphenus tridentatus*) and Western brook lamprey (*Lampetra richardsoni*).

Tagging of each coho salmon brood was initiated following dispersal of age-0 fry from redds. Tagging and recapture of 2008 brood year juvenile coho was conducted during six sampling periods: (i) 4 April–4 May 2009, (ii) 19 May–2 June 2009, (iii) 16 June–7 July 2009, (iv) 11 August–2 September 2009, (v) 29 September–2 November 2009 and (vi) 4 January–12 February 2010. Coho salmon from the 2009 brood year were captured and tagged during three periods during the summer period: (i) 1 April–18 June 2010, (ii) 30 June–16 July 2010 and (iii) 19 September–2 October 2010. Coho salmon of each brood year were tracked from the date of tagging through emigration from Palouse Creek as age-1 smolts in spring. Juvenile coho salmon tagging and monitoring was conducted in Palouse Creek, four tributaries and three off-channel ponds and on the downstream side of the Palouse tide gate in Haynes Inlet (Figure 1).

Three sampling methods (beach seining, pole seining and electrofishing) were used due to differences in stream channel size and complexity among study reaches. In the relatively wide (>20 m) partially confined tidal channels of the lower half of Reach 1, fish were captured using single-pass removal with a small-mesh beach seine (1.8 × 21.3 m, 3.2 mm mesh bag). Three fixed and three rotating beach seine sites were randomly selected in Reach 1 and seined at low and high tides during each season based on a rotating panel sampling design. Fixed sites were sampled during each visit, while rotating sites were sampled on only two consecutive visits (two low tides and two high tides) before replacing them at random with other locations ($N = 20$ sites).

In narrow channels (<20 m), located at the upper extent of tidal influence (upper Reach 1 and Reach 2), and in riverine reaches (Reaches 3–6), fish were captured using pole seine nets or backpack electrofishing equipment in randomly chosen sampling sections that were nested within each reach (Figure 1). Sampling sections were approximately 300 m long in mainstem reaches and 150 m long in tributary reaches. In each sampling section, one fixed and one rotating pool and/or glide site was randomly selected and sampled for the duration of the study using a rotating panel design. Pole seining was used in riverine and tidally affected channels with small substrate and minimal amount of instream wood ($N = 64$ sites), while electrofishing was performed in stream sites with complex physical habitat (large substrate and wood accumulations) where the use of a net was less effective ($N = 34$ sites).

Captured fish were enumerated by species for each removal. A subsample of captured juvenile coho salmon was implanted with full-duplex PIT tags and measured for fork length (FL) to the nearest millimetre (mm) and for weight to the nearest 0.1 gram (g). Two sizes of PIT tags were used to mark juvenile coho salmon; fish with FL of 48 to 60 mm were marked with PIT tags 8.5 mm in length (hereafter "8.5-mm tag"; width: 2.12 mm; weight: 0.067 g), whereas fish longer than 60 mm were marked with PIT tags 12.5 mm in length (hereafter "12.5-mm tag"; width: 2.07 mm; weight: 0.102 g). Tag weight was not considered to affect behaviour of each size class (Acolas, Roussel, Lebel, & Bagliniere, 2007; Brown, Cooke, Anderson, & McKinley, 1999).

Capture and sampling of fish was performed during winter 2009. Capture of juvenile salmonids during winter may be affected by diel shifts in behaviour induced by low-water temperature (Heggenes, Krog, Lindas, Dokk, & Bremnes, 1993), although the extent to which salmonids exhibit this behaviour may depend on regional climate (Reeves, Grunbaum, & Lang, 2010). To evaluate whether coho salmon diel behaviour patterns may have potentially biased winter fish capture efforts, fish abundance was compared between day and night snorkelling surveys. Snorkel surveys were conducted in 17 habitat units distributed among Reaches 3, 4 and 5 during successive day and night periods on 9 February 2010. Mean day and night snorkel counts were compared with paired two-sample *t* test using R software (v2.12.1; R Development Core Team 2005).

Movements of tagged juvenile coho salmon were tracked in two ways: direct fish recaptures during visits to sampling sites and at stationary instream antennas. Juvenile coho salmon captured at sampling sites were scanned for PIT tag presence with a portable PIT antenna and transceiver (Destron Fearing Model FS2001), which recorded each tag code, date and time. Stationary instream PIT antennas and transceivers were installed at four sites in the mainstem Palouse Creek and at the Larson Creek tide gate opening (RKm 0.0; Figure 1). At each site, multiple antenna arrays (channel-spanning antenna/s that intersect the stream channel at a single cross section; sensu Zydlewski et al., 2006) were installed within 4 m to one another to improve tag detection efficiency and ascertain direction of fish movement. Each array consisted of one or two antennas based on channel dimensions to maximise coverage of wetted cross-sectional area. The assemblage of transceiver and arrays at each site was termed an antenna system. Palouse antenna systems 1 (RKm 0.0) and 2 (RKm 3.2) and the Larson Creek antenna system were operated for the duration of the study period, whereas antenna system 3 (RKm 4.1) operated from December

2009 to October 2010 and antenna system 4 (RKm 7.2) recorded data from October 2009 to July 2011.

Multiplexing transceivers (Destron Fearing Model FS1001M) at Palouse antenna systems 1, 2 and 4 and at the Larson tide gate recorded the date, time and tag code of each tag detection. Two Allflex series panel readers (Model 840029-001, Allflex USA, Inc.) were used to record tag detections at antenna system 3 (December 2009–September 2010) and at antenna system 4 (October–December 2009). Allflex readers recorded the tag code but did not record date or time of detections; consequently, tag detections were assigned to the date of download, which was performed at least three times per week. Antennas at tide gate array systems were constructed using litz wire to enhance tag detection range and efficiency in the saline environment (Bass, Giannico, & Brooks, 2012), while antennas installed in freshwater locations were of standard copper wire construction. Detection efficiency at each antenna system was calculated as the percentage of fish detected at the antenna system among the total number known to pass the antenna system (Zydlewski et al., 2006). A tagged coho was known to have passed an antenna system if the fish was detected both upstream and downstream of the antenna system by direct capture in association with stream sampling or at an antenna system. In this manner, Palouse tide gate efficiency was based in part on detections at the Larson tide gate.

2.3 | Juvenile salmon movement

Coho salmon locations were summarised by spring, summer and fall-winter seasonal periods that were distinguished based on juvenile coho salmon life history patterns and environmental factors (i.e., rainfall, stream discharge and water temperature). The spring season represented the approximately concurrent periods of age-0 coho salmon fry dispersal from redds and age-1 coho salmon smolt emigration, which was estimated based on the total daily number of tagged age-1 coho detected at each antenna system. The summer period began following smolt emigration and was typified by low stream discharge and warm stream temperatures. The onset of the fall-winter conditions (hereafter "winter") was defined by the timing of the first freshet in the fall of each year. Winter conditions were generally characterised by high and variable stream discharge and low stream temperatures. The seasonal periods for both brood years were defined as follows: (i) spring (21 January–17 June); (ii) summer (18 June–12 October) and (iii) winter (13 October 2009–20 January 2010).

Movement of tagged juvenile coho was described in summer and winter based on recapture of tagged fish during revisits to sampling sites and on PIT tag detections recorded at antenna systems. Juvenile coho salmon not recaptured or detected after tagging were not included in movement analyses. The term "recovered" is used to refer to a tagged fish whose location was known as a result of either recapture during stream sampling or detection at an antenna system. Fish were classified as sedentary or mobile based on observed residency at a sampling unit or recorded movement between stream reaches. Coho salmon recaptured at the site of tagging but not detected at an antenna system during an entire season were considered "sedentary." Juvenile coho salmon that moved between stream reaches were labelled "mobile." The recovery of a tagged fish in a different reach from the one where it was tagged or previously recovered in was considered evidence of movement. Our sampling design was structured to detect seasonal fish movement among reaches after age-0 fry dispersed from redds following emergence from the gravel; movements that occurred in association with this early dispersal or within a study reach are not reported. It was assumed that sedentary individuals did not move between recapture events and that the last known location of a tagged fish during summer was its location at the beginning of winter. We also assumed that fish movement occurred on the date of recovery.

Comparisons of juvenile coho salmon sedentary and mobile strategies were completed at two temporal scales: (i) Palouse Creek residence period, representing the combined summer and winter seasons, and (ii) individual season (summer, winter). Movement pattern during the Palouse Creek residence period was described for brood 2008 coho salmon tagged in spring or summer that were recovered at least once during each summer and winter season (i.e., at least two recovery events after initial capture and tagging) such that movement could be evaluated across seasons. Palouse Creek residence movement patterns were defined in terms of the four possible combinations of sedentary and mobile behaviours between the two seasons: Type 1: sedentary in summer and winter, Type 2: sedentary in summer and mobile in winter, Type 3: mobile in summer and sedentary in winter and Type 4: mobile in summer and winter. Movement during individual seasons was based on tagged fish that were recovered at least once within a summer or winter season. Movement comparisons were not completed for winter 2010 (brood year 2009) because stream site capture was not performed during this period. Movement strategies were not characterised for tagged age-1 coho salmon during each spring as nearly all age-1 individuals emigrated from the Palouse basin and were thus mobile during this time. Seasonal comparisons of sedentary and mobile strategies were performed using data from coho salmon marked with 12.5-mm tags only. Fish marked with 8.5-mm tags were not used for the comparative analysis of due to the low detection rates of 8.5-mm tags among PIT antenna systems.

Movement timing, direction and maximum observed distance moved were summarised for mobile juvenile coho salmon in stream reaches with PIT antenna systems at the upstream and downstream extents of the reach. Movement timing was based on recovery date, while movement direction was inferred by fish recovery location relative to the previous known location and tag detection sequence within an antenna system. Maximum observed distance moved (RKm) was the difference between the furthest downstream and upstream locations at which a fish was either tagged or recovered within a season.

Discontinuous operation of antenna systems during the study was a potential source of bias associated with movement detection. In particular, abbreviated operation at antenna systems 3 and 4 during summer 2009 may have represented a bias to sedentary behaviour in Reaches 3–6 as fish that were mobile in these riverine reaches during antenna system inactivity may not have been detected at operational antenna systems 1 and 2. To approximate the portion of mobility that may have been undetected at antenna systems 3 and 4 in summer

2009, we calculated the proportion of tagged coho that were classified as mobile during summer 2010 based on detections at each antenna system independent of detections at other antenna systems. This analysis assumes that movement patterns were similar between years.

2.4 | Juvenile salmon body mass and growth

Among PIT-tagged coho recaptured at least once, instantaneous growth rates were calculated using the following equation: Growth rate = $100 \times (\log_e W_t - \log_e W_0) \times (t_t - t_0)^{-1}$, where W is fish mass (g) recorded at the initial (t_0) and final (t_t) capture and measurement dates. Growth was also calculated using coho salmon length measurements with the above equation to validate results. Growth rates of fish marked with either tag type (i.e., 8.5 mm or 12.5 mm) were summarised by seasonal period based on the visual assessment of growth curves and timing of recapture events. Only growth periods greater than 29 days were used for growth analyses to limit tagging effects on calculated growth rates.

To evaluate whether body size was a predictor of summer movement, the early summer body mass of juvenile coho salmon was compared between those that exhibited sedentary or mobile behaviour during each summer using two-sample *t* tests. To test whether growth of sedentary and mobile coho salmon differed, summer and winter growth rates of sedentary and mobile juvenile coho salmon were similarly compared. Size and growth comparisons were made within tag type (i.e., 8.5 mm or 12.5 mm) and reach; growth of mobile coho was ascribed to the reach of residence at the onset of each season. Assumptions of normality and equal variance were evaluated visually based on histogram plots and *F*-tests for equal variance respectively.

2.5 | Juvenile salmon survival

Apparent winter survival was estimated for tagged coho salmon known to be alive near the onset of each winter period and was estimated for each brood year using the following equation: Survival = $100 \times D \times (T)^{-1}$, where D is the number of tagged fish detected at antenna system 1 (RKm 0.0) during the spring period of smolt outmigration (January–June), corrected for detection efficiency at antenna system 1, and T is the total number of coho salmon that were either tagged or recovered near the start of each winter during October 2009 and September 2010. Coho salmon detected at antenna system 1 during spring were labelled as survivors, while PIT-tagged fish not detected at antenna system 1 were treated as mortalities. Survivorship was apparent because the number of detected fish was not an absolute measure of survival; the true fate of undetected fish is unknown, but was assumed to be mortality for this analysis. Tagged coho that emigrated early from Palouse Creek (i.e., prior to January 2010) or passed undetected by the antenna would be incorrectly identified as mortalities. Observed detections and estimated detection efficiency at antenna system 1 indicated that both of these situations were uncommon. Only juvenile coho marked with 12.5-mm PIT tags were used for the apparent survival analysis.

3 | RESULTS

3.1 | Juvenile salmon sampling and tracking

A total of 1,421 brood year 2008 juvenile coho salmon fry were tagged with 12.5-mm PIT tags following dispersal in May (*n* = 69), June and July (*n* = 280), August (*n* = 517) and October 2009 (*n* = 555), while 1,425 were marked with 8.5-mm tags during April (*n* = 10), May (*n* = 464), June and July (*n* = 742) and August 2009 (*n* = 209). A total of 248 coho salmon marked with 12.5-mm tags were recovered during summer 2009, and 409 were recovered during winter 2009. A total of 380 fish with 8.5-mm tags were recovered during summer 2009. In 2010, a total of 667 brood year 2009 coho salmon were tagged with 12.5-mm tags during April–June (*n* = 181) and July 2010 (*n* = 486) and 301 were marked with 8.5-mm tags primarily during April–June 2010 (*n* = 299). Of these, 259 were recovered with 12.5-mm tags and 118 with 8.5-mm tags during summer 2010. Movement strategies were evaluated for 589 coho salmon of brood year 2008 and 259 coho salmon of brood year 2009 that were marked with 12.5-mm tags.

Detection efficiencies at PIT antenna systems were consistently higher for 12.5-mm PIT tags than 8.5-mm tags, and antenna systems operated by Destron Fearing (DF) multiplexing transceivers (Larson and Palouse 1, 2 and 4 [brood 2009 only]) detected higher proportions of tagged fish compared to Allflex readers (Palouse 3). Efficiency estimates for brood year 2008 coho salmon marked with 12.5-mm tags were 89% (*n* = 37) at Palouse 1, 96% (*n* = 466) at Palouse 2, 64% (*n* = 441) at Palouse 3, 58% (*n* = 416) at Palouse 4 and 75% (*n* = 12) at the Larson tide gate antenna system. Detection efficiency estimates for brood year 2009 fish with 12.5-mm tags were 78% (*n* = 9) at Palouse 1, 72% (*n* = 92) at Palouse 2, 8% (*n* = 257) at Palouse 3, 74% (*n* = 42) at Palouse 4 and 25% (*n* = 4) at Larson. Low detection efficiencies (<60%) for 8.5-mm tags precluded the use of this tag type for movement analyses.

Coho salmon marked with 12.5-mm tags detected at antenna arrays during the study were commonly detected on multiple dates. The proportion of fish detected at antenna arrays on two or more dates was 52% (*n* = 33) during summer 2009, 68% (*n* = 194) during winter 2009 and 61% (*n* = 46) during summer 2010. Most brood year 2008 coho salmon marked with 12.5-mm tags were recaptured once at sampling sites within each summer and winter season, while a small portion (5% or less) were recaptured on two separate sampling events in each season.

Among mobile coho salmon in summer 2010 (*n* = 75), most (96%) were classified as such based on detection at an antenna system rather than recapture (4%), and most (56%) were detected at one antenna system only compared to multiple antenna systems. Of the 259 tagged coho recovered during summer 2010, the proportion determined to be mobile based on detections at individual antenna systems (i.e., independent of detections at other antenna systems) was less than 1% at antenna system 1, 5% at antenna system 2, 7% at antenna system 3 and 5% at antenna system 4. A total of 12 brood year 2008 and 6 brood year 2009 were detected at the Larson antenna system, although these fish were not determined to be mobile based on detection at the Larson tide gate.

We observed no difference in coho salmon diel abundance during winter in Palouse Creek, which validated daytime sampling as an appropriate winter capture method. Mean winter abundance of coho salmon in snorkelled units was similar ($p = .4$; $df = 32$) during daytime (mean = 27.0, 95% CI: 15.7, 38.3) and nighttime (mean = 20.4, 95% CI: 9.1, 38.6). Moving seven-day average minimum daily water temperature in Palouse Creek ranged from 7.3°C to 8.2°C during the period of winter fish capture efforts.

Water temperature among Palouse Creek study reaches was highest in Reach 1 during each summer of 2009 and 2010 and was warmest near the tide gate. In summer 2009, MWMT ranged between 25.5°C and 21.2°C at three monitoring locations in Reach 1, while MWMT values elsewhere in Palouse Creek were 19.4°C in Reach 3, 20.7°C in Reach 4, 19.7°C in Reach 5 and 20.2°C in Reach 6. In summer 2010, MWMT values in Reach 1 (23.5°C), Reach 2 (18.1°C), Reach 3 (18.8°C), Reach 5 (17.2°C) and Reach 6 (18.1°C) reflected comparatively cooler water temperatures than observed in 2009. Maximum daily salinity conditions at continuous monitoring locations in Reach 1 were nearly 30 ppt at RKm 0.0 throughout July–October 2010 and peaked at over 22 ppt at RKm 1.35 in early October 2010. Salinity at this upstream monitoring site (RKm 1.35) appeared to vary seasonally with the stream hydrograph such that maximum daily values increased in July 2010 as stream discharge declined and fell to nearly zero as discharge levels rose in winter.

3.2 | Juvenile salmon movement

A total of 64 juvenile coho salmon marked with 12.5-mm tags were recovered at least once during both summer and winter 2009 (i.e., tracked across seasons), and their Palouse Creek movement patterns matched one of four possible types (Table 1). Most juvenile coho salmon were sedentary during summer (78%; Types 1 and 2), and subsequently relatively similar proportions of them exhibited either sedentary (Type 1) or mobile strategies (Type 2) during winter (Table 1). However, among the individuals who adopted the less common summer strategy, which was the mobile type (Types 3 and 4), the majority became sedentary in winter (Type 3). Only a small proportion of tagged fish were mobile during both seasons (Type 4). The movement strategies adopted by the larger number of juvenile coho salmon that were only tracked within single seasons were also predominantly sedentary for summer (75% in 2009 and 70% in 2010) and mobile for winter (70%; Figure 2).

TABLE 1 The percentage of juvenile coho salmon marked with 12.5-mm passive integrated transponder tags recovered at least once during both summer and winter 2009 that exhibited each of four Palouse Creek residence movement patterns

	Seasonal behaviour		
Movement pattern	Summer	Winter	Percentage ($n = 64$)
Type 1	Sedentary	Sedentary	37
Type 2	Sedentary	Mobile	41
Type 3	Mobile	Sedentary	16
Type 4	Mobile	Mobile	6

During both summers of this study, nearly all fish who displayed a mobile pattern were found in the lower and tidally affected reaches of the creek (Reaches 1 and 2). Nearly all juvenile coho salmon tracked in Reach 1 were mobile during summer (Figure 3). Among coho detected in Reach 2, 26% and 47% exhibited mobility during summers 2009 and 2010 respectively. Mean maximum distances covered by mobile individuals during summer were 4.7 km ($SD = 2.3$, $n = 60$) for fish in Reach 1, 0.7 km ($SD = 0.9$, $n = 28$) for those in Reach 2 and 1.2 km ($SD = 0.9$, $n = 15$) for those from Reach 3. Emigration from Reaches 1 and 2 was mostly in an upstream direction and occurred in early summer (June and July; Figure 4). Among mobile coho in Reach 1, most (57%) moved

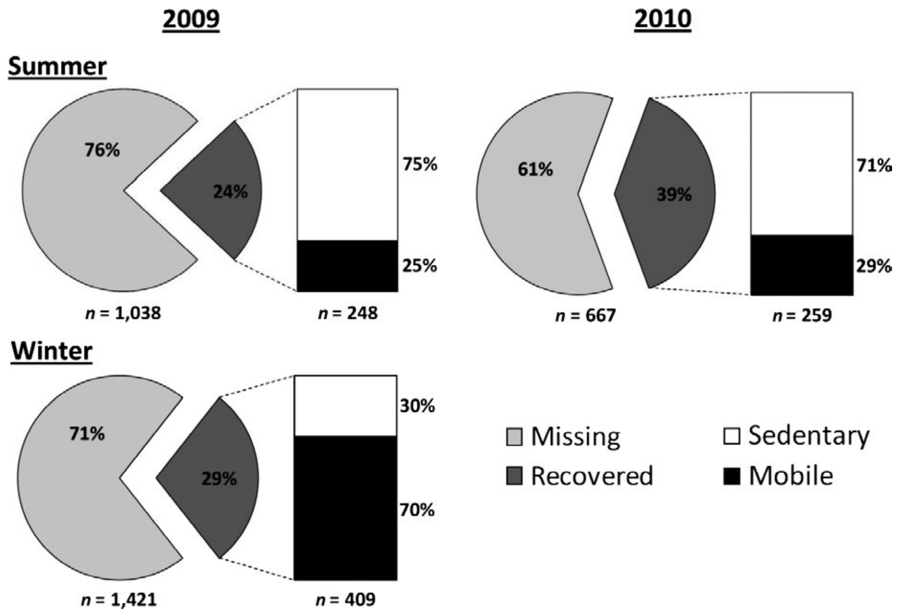

FIGURE 2 Percentages of recovered juvenile coho salmon marked with 12.5-mm tags that exhibited sedentary and mobile behaviours within each summer and winter season. Missing (not recovered) coho salmon were not included in the movement analyses

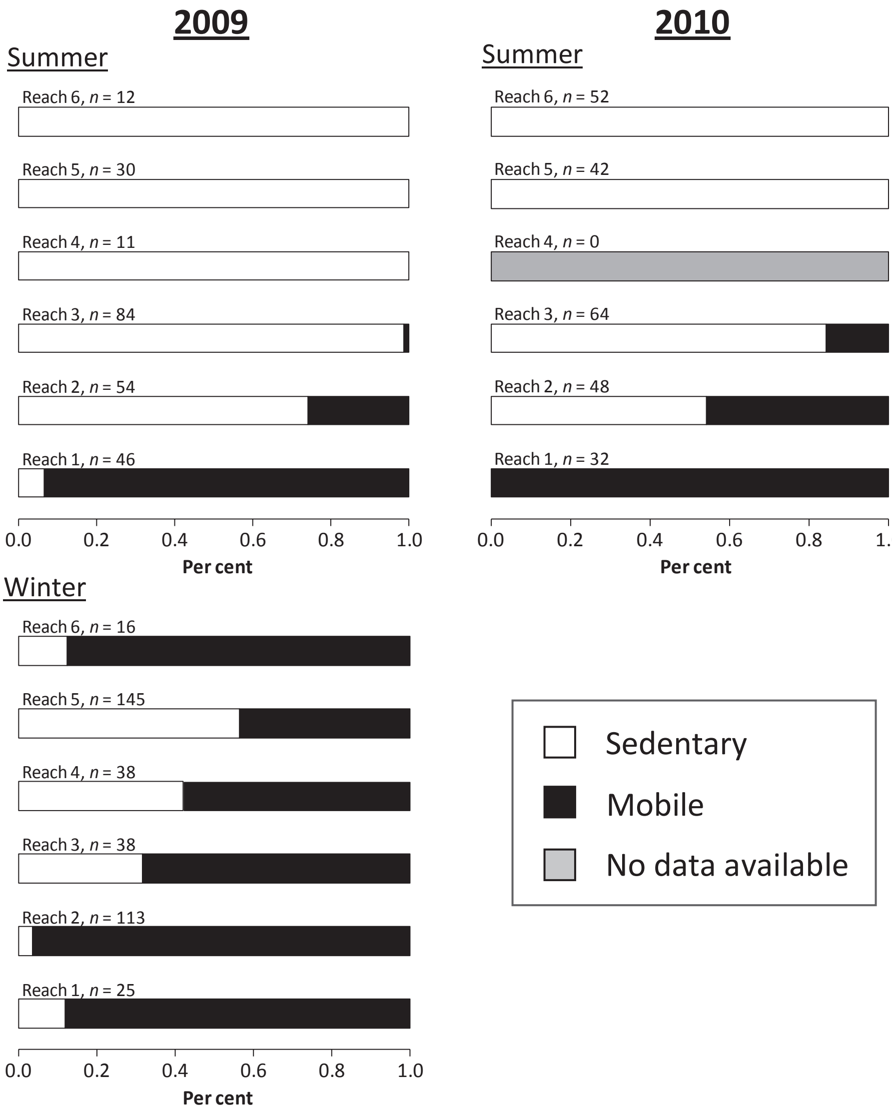

FIGURE 3 Percentages of recovered juvenile coho salmon with 12.5-mm passive integrated transponder tags that exhibited sedentary and mobile strategies during the summers of 2009 and 2010, and the winter of 2009 by mainstem reach. No tagged coho salmon were recovered in 2010 from Reach 4

upstream at least as far as antenna system 4 (5.1 km) during summer 2010 and similar movement was observed during summer 2009. Fish that left Reach 3 travelled primarily downstream during early summer, although movement occurred in both directions. No fish moved from Reaches 4, 5 or 6 before the end of either summer (Figure 3).

During winter 2009 (October 2009–January 2010), large proportions of juvenile coho salmon displayed highly mobile behaviour in all mainstem reaches (Figure 3). The greatest percentages of mobile fish were detected in Reaches 1, 2 and 6. Coho salmon movement from Reach 1 was predominantly in an upstream direction, while most mobile coho in other reaches moved downstream (Figure 4). Approximately half of mobile juvenile coho in mainstem Reaches 2–6 moved to Reach 1 in winter (55% in 2009, 57% in 2010). Although upstream and downstream winter movement typically occurred during rain events, movement by many coho preceded them or occurred in the absence of measurable precipitation. Average maximum distance moved in winter 2009 by mobile coho salmon was 1.3 km (*SD* = 1.2, *n* = 30) from Reach 1, 0.7 km (*SD* = 0.8, *n* = 118) from Reach 2, 2.9 km (*SD* = 1.9, *n* = 29) from Reach 3 and 5.7 km (*SD* = 2.8, *n* = 15) from Reach 6.

3.3 | Juvenile salmon body mass and growth

Body mass and individual growth rates were summarised for 784 brood year 2008 and 252 brood year 2009 coho salmon tagged following dispersal from natal redds and recaptured at least once. Early summer body mass of sedentary and mobile juvenile coho was compared in Reaches 1, 2 and 3 in 2009 and 2010. Mobile coho salmon were larger than sedentary fish in Reach 1 during July 2009 and in Reach 2 during July 2010 ($p < 0.05$; Table 2), while mean body mass did not differ ($p > .05$) between sedentary and mobile coho salmon in Reach 2 in 2009 or in Reach 3 in 2010. This suggests that early summer body mass has an interaction term between reach and year.

Mean growth rates of mobile and sedentary coho salmon were compared in Reaches 1 and 2 during summer 2009 and in Reach 5 during winter 2009. Mobile juvenile coho salmon in Reach 2 exhibited higher mean growth than sedentary fish during early summer (May to August), while sedentary coho grew at a higher rate in late summer (August–October; Table 3). Mean growth rates throughout the summer (June to August) were not different between mobile and sedentary

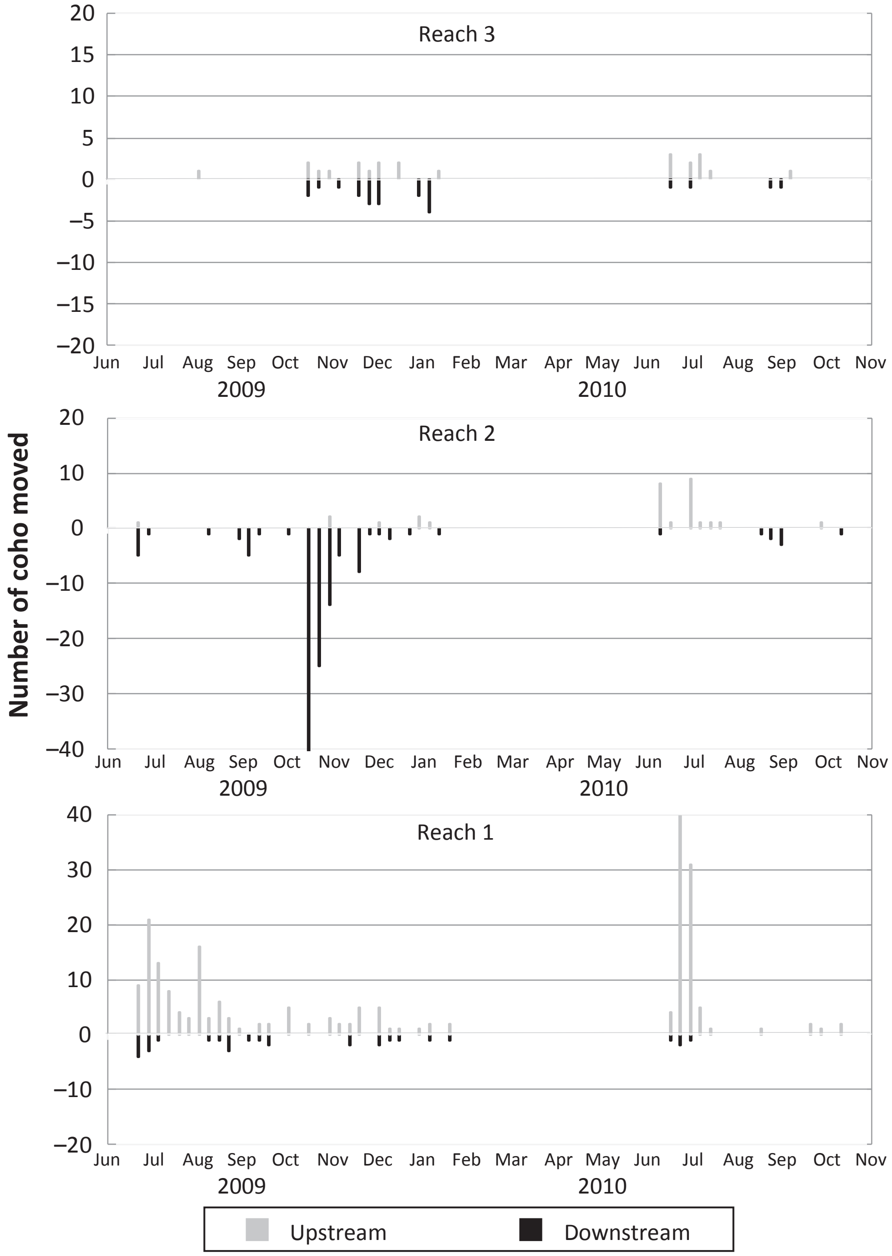

FIGURE 4 Weekly counts of recovered mobile juvenile coho salmon with 12.5-mm passive integrated transponder tags that moved upstream and downstream from Palouse Reach 1, Reach 2 and Reach 3 during summer 2009 (18 June–12 October), winter 2009 (13 October 2009–20 January 2010) and summer 2010 (18 June–12 October)

TABLE 2 Comparisons of mean body mass in early summer among juvenile coho salmon that exhibited sedentary and mobile movement during summer, with associated 95% confidence intervals (in parentheses), sample sizes (in brackets) and *p*-values corresponding to two-sample *t* tests. Asterisks indicate significance ($p < .05$)

Movement type	Reach	Capture timing	Size, g	*p*-value
Sedentary	1	July 2009	2.7 (1.7–3.5) [3]	.05*
Mobile			3.6 (3.3–3.8) [27]	
Sedentary	2	June 2009	3.9 (2.5, 5.2) [4]	.10
Mobile			3.9 (2.7, 5.0) [6]	
Sedentary	2[a]	July 2010	3.6 (3.2, 3.9) [22]	.05*
Mobile			4.7 (3.7, 5.7) [10]	
Sedentary	3	July 2010	4.3 (3.8, 4.8) [41]	.12
Mobile			5.6 (4.1, 7.0) [5]	

[a] Comparison made using Welch's two-sample *t* test due to unequal variances.

TABLE 3 Comparisons of mean growth rates among juvenile coho salmon that exhibited sedentary and mobile movement during summer and winter 2009, with associated 95% confidence intervals (in parentheses), sample sizes (in brackets) and *p*-values corresponding to two-sample *t* tests. Asterisks indicate significance ($p < .05$)

Movement type	Reach	Growth period	Growth, $\text{g g}^{-1}\text{ day}^{-1}$	*p*-value
Sedentary	1	Early Summer	1.04 (0.87, 1.22) [10]	.60
Mobile			0.96 (0.64, 1.28) [3]	
Sedentary	2	Early Summer	0.89 (0.66, 1.13) [3]	.03*
Mobile			1.29 (1.06, 1.53) [3]	
Sedentary	2[a]	Late Summer	0.14 (0.02, 0.25) [17]	.01*
Mobile			0.01 (−0.04, 0.06) [4]	
Sedentary	2	All Summer	0.58 (0.46, 0.70) [10]	.10
Mobile			0.78 (0.56, 1.01) [3]	
Sedentary	5[a]	Winter	0.38 (0.36, 0.40) [25]	.40
Mobile			0.45 (0.38, 0.52) [8]	

[a] Comparison made using Welch's two-sample *t* test due to unequal variances.

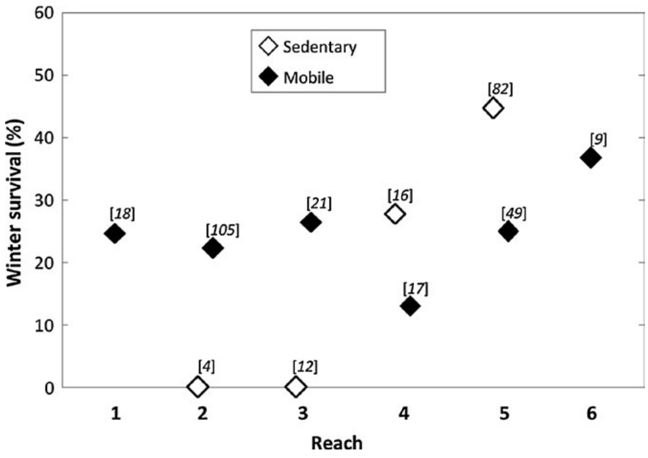

FIGURE 5 Apparent winter survival rates for brood year 2008 juvenile coho salmon that exhibited sedentary and mobile behaviour during winter. Estimates are summarised by stream reach of residence at the start of winter. Sample sizes are in brackets.

individuals in Reach 2 (p = .10). Mean growth rates of mobile and sedentary coho salmon in Reach 1 during early summer (p = .60) and in Reach 5 during winter (p = .40) also did not differ. The use of fish fork length for comparisons of early summer fish size as well as summer and winter growth between sedentary and mobile types did produce the same results.

3.4 | Juvenile salmon survival

Apparent winter survival was estimated for 602 brood year 2008 juvenile coho salmon and 191 brood year 2009 fish that were marked with 12.5-mm tags and known to be alive in late summer. For brood year 2008, apparent winter survival was 27% (n = 127) for juvenile coho salmon that had been sedentary in the summer and 17% (n = 20) for those who had been mobile during that season. Juvenile coho salmon that were sedentary in winter, regardless of summer behaviour, similarly experienced higher apparent winter survival (35%, n = 119) than those that were mobile (23%, n = 235), although survival varied with late summer reach of residence. For example, sedentary coho in Reach 5 experienced high apparent survival (45%) compared to mobile individuals that left this reach (26%), while mobile fish in Reach 2 and Reach 3 survived at a greater rate than sedentary coho in these reaches (Figure 5). Apparent winter survival of brood year 2009 coho salmon was 19% (n = 171) and 24% (n = 20) among fish that were sedentary and mobile during summer respectively and 16% (n = 62) for fish that were mobile during winter 2010.

4 | DISCUSSION

Juvenile coho salmon movement has been described previously within single seasons at the stream reach (Bell et al., 2001; Kahler et al., 2001) or sub-basin spatial scales (Anderson et al., 2013; Ebersole et al., 2006). This study provides closer insight into juvenile coho salmon movements by tracking tagged individuals throughout their entire residence period in the freshwater and brackish reaches of a small coastal basin. Our results show that juvenile coho salmon in the Palouse basin exhibited a diverse repertoire of movement patterns, which were derived from various combinations of two main strategies (i.e., mobile and sedentary behaviours) throughout seasons and space. Most juvenile coho salmon we tracked exhibited movement strategies that differed between summer and winter. The majority of tagged individuals were sedentary during summer and mobile in winter; however, a substantial proportion of fish displayed alternative behaviours to these common movement patterns. We also observed a clear spatial trend during the summer months, with the lowermost reaches (i.e., those tidally affected) occupied by juvenile coho salmon that were predominantly mobile and the higher upstream reaches dominated by individuals with tendency to be sedentary. By contrast, mobility during winter was a common strategy in nearly all mainstem reaches. Mean body mass of mobile coho salmon was greater than sedentary coho in early summer, although summer and winter growth rates of sedentary and mobile fish were not consistently different across reaches and years. Apparent winter survival, however, was higher for juvenile coho salmon with an entirely sedentary movement pattern (i.e., sedentary in both summer and winter) than for highly mobile individuals, but reach of residence in early winter also appeared to affect survival.

Juvenile coho salmon that emerged from redds in Reaches 5 and 6 during the springs of 2009 and 2010 dispersed throughout the study area, including tidally affected reaches. Similar coho salmon fry migration to estuarine habitats has been reported by studies in Oregon, Washington, British Columbia and Alaska (Hartman et al., 1982; Miller & Sadro, 2003; Koski, 2009; Craig et al. 2014). The cause of such early estuarine entry has been attributed to either competitive exclusion (Chapman, 1962) or abiotic factors (e.g., high stream discharge; Hartman et al., 1982), but it is likely that various mechanisms influence this behaviour. Studies by Chapman (1962) suggested that downstream dispersal by coho salmon fry soon after emergence was due primarily to competitive exclusion, which forces small individuals to move downstream. However, small size among downstream migrants is not universal, as some mobile fish can be larger than resident individuals (Chapman, 1962; Hartman et al., 1982). The dispersal of larger-than-average fish may be described by the concept of early condition-dependent movement, which maintains that large fish may be more capable of dispersing than smaller individuals (Anderson et al., 2013; Bowler & Benton, 2005). Observations of coho salmon fry dispersal during our study did not support hypotheses suggesting that early estuarine migration is a result of competitive exclusion or displacement by high stream discharge. Despite the fact that we did not measure early rearing densities or stream discharge, our observations indicate that early estuary migration by coho salmon fry in the spring of 2010 occurred before many rearing riverine habitats became occupied and often was independent of fluctuations in stream discharge.

Brood year 2008 coho salmon tracked through summer and winter exhibited four different movement patterns during these seasons (Table 1). This illustrates the flexible nature of juvenile coho salmon movement behaviour, which is an important aspect of phenotypic diversity within a population (Fox, 2005). Although previous work had described the movement strategies of coho salmon within summer or winter (e.g., Bell et al., 2001; Ebersole et al., 2006; Kahler et al., 2001), the movement of marked individuals during their entire stream residence period had not been well documented. The patterns we observed reflect the coho salmon life history diversity described by Jones et al. (2014), and the movement of juvenile salmonids that occurs among adjacent basins (i.e., juvenile coho salmon from Palouse Creek detected at the Larson Creek antennas) typifies a primary means by which populations may colonise unoccupied habitats (Anderson et al., 2013; Koski, 2009; Milner et al., 2000) and interact with each other (Rieman & Dunham, 2000). By allowing genetic exchange between neighbouring populations, the observed behavioural diversity increases the resiliency of the entire metapopulation in the face of environmental and demographic stochasticity (Gaggiotti & Hanski, 2004).

Most juvenile coho salmon in Palouse Creek were sedentary during summer, but 25% (2009) to 29% (2010) of them were mobile. Large-scale movement was particularly common among coho salmon in tidally influenced habitats (Reaches 1 and 2). Movement in tidally affected areas of Palouse Creek is similar to the nomadic life history strategy reviewed by Koski (2009), although the timing of upstream movements from Reach 1 in June and July is earlier than upstream movements in fall reported among most nomadic populations. The upstream movements of coho salmon from tidally affected habitats in Palouse Creek may have been hastened by high water temperatures in Reach 1, which exceeded 23°C in each year. Long-distance (>1 km) summer movement documented in other populations was in response to seasonally pulsed food subsidies and as part of colonisation of new habitat (Anderson et al., 2013; Armstrong & Schindler, 2013). Kahler et al. (2001) documented summer movement at small spatial scales (i.e., between habitat units) among substantial portions (28%–60%) of juvenile coho in three stream basins, typically from shallow to deeper habitats. Coho salmon movement documented by Kahler et al. (2001), Anderson et al. (2013) and Armstrong and Schindler (2013) occurred independently of fish density, which suggests that movement in some circumstances is likely condition dependent and not dictated by agonistic interactions.

During fall and winter 2009, 70% of juvenile coho salmon in the Palouse basin exhibited highly mobile behaviour and more than half of these fish moved into the tide gate reservoir of Reach 1. Among Palouse stream reaches, coho salmon residing in Reach 5 at the onset of winter exhibited the highest proportion of sedentary behaviour (Figure 3), which may be a consequence of the abundant off-channel habitats (i.e., ponds and tributaries) present in this reach (Figure 1). Similar coho salmon fall habitat relocations have been reported in other settings (Bramblett, Bryant, Wright, & White, 2002; Jones et al., 2014; Peterson, 1982a), although movement patterns often vary among populations. In a coastal stream in California, approximately 50% of juvenile coho salmon tagged in early winter moved from their original locations of capture to other habitat units during winter; those individuals who occupied alcove habitats exhibited the highest site fidelity relative to backwater and mainstem pool units (Bell et al., 2001). In South Slough, on the southernmost coast of Coos Bay, approximately 30% of juvenile coho dispersed from riverine areas to tidal habitats during fall and early winter (Miller & Sadro, 2003), while most coho that exhibited movement during winter in a separate Oregon basin relocated from mainstem to tributary habitats (Ebersole et al., 2006). Such differences in movement patterns among populations likely reflect the variability in suitable winter habitat and underline the importance of habitat connectivity to maximise coho salmon carrying capacity of coastal streams. Accessibility to good habitat patches combined with the ability of individual fish to discern gradients in environmental quality and patch profitability ultimately affect the extent to which movement occurs (Anderson et al., 2013; Fausch & Young, 1995; Giannico & Healey, 1999; Kahler et al., 2001).

Juvenile coho salmon movement into the tide gate reservoir was common in winter, although relatively few individuals were detected leaving for the open estuary. Less than 3% of tagged coho salmon were detected at antennas located in the Palouse tide gate or via recapture in association with sampling in Haynes Inlet during winter 2009, and 17% were detected during winter 2010. These observations agree with those of other studies in Oregon estuaries (Jones et al., 2014; Miller & Sadro, 2003), but differ from what was reported for other coastal streams in Washington and British Columbia, where most juvenile coho salmon emigrated from the estuary during winter (Bennett, Roni, Denton, McHenry, & Moses, 2015; Quinn, Harris, Shaffer, Byrnes, & Crain, 2013; Tschaplinski, 1982). Although the tide gate restricted juvenile coho movement in and out of the Palouse estuary, the reservoir that formed upstream seemed to have provided the young fish with suitable winter habitat and opportunities for estuarine acclimation because of its rather extensive brackish water lens.

An independent analysis to evaluate potential bias associated with inconsistent operation of antenna systems 3 and 4 indicated that most (56%) juvenile coho salmon classified as mobile during summer 2010 were detected at one antenna system only compared to multiple antenna systems. Of fish tracked in summer 2010 ($n = 259$), the proportion determined to be mobile based on detections at only one antenna system ranged from 1% at antenna system 1 to 7% at antenna system 4. Assuming that movement patterns in Palouse Creek were similar between summer 2009 and summer 2010, these results suggest that the proportion of mobile coho in 2009 was underestimated in reaches proximal to antenna systems 3 and 4, but that the degree to which mobility was underestimated was small (<10%). These results, in conjunction with the overall similarity in movement patterns between years, indicate that inconsistent functionality of antenna systems 3 and 4 did not greatly affect the observed spatial trends in movement.

Our results showed that mean body mass of mobile coho salmon in early summer was larger than sedentary fish, while differences in mean growth rates during summer between sedentary and mobile were not consistent. The conventional wisdom on juvenile coho salmon movement, based on early studies of their ecology and behaviour (Chapman, 1962; Hartman et al., 1982), was that mobile fish are generally small, subordinate individuals that are prevented from establishing territories in optimum habitats through intraspecific competition; however, more recent studies have shown that this is not always the case. Juvenile coho salmon that disperse widely after gravel emergence and through the first summer of life can be similar in size to sedentary individuals (Ebersole et al., 2006; Kahler et al., 2001; Tschaplinski, 1982), and when movement is likely condition-dependent (e.g., upstream migration or long-distance movement), the young movers may even be larger than average (Anderson et al., 2013). In cases in which movement occurred in response to differences in habitat quality, mobile coho salmon may even exhibit higher growth rates than more sedentary members of their cohort (Armstrong & Schindler, 2013; Kahler et al., 2001). Although juvenile coho salmon body size appears to impart some advantages in defending territories (Fausch, 1984; Nielsen, 1992; Rhodes & Quinn, 1998), a smaller than average body size is not always a good predictor of early downstream movement (Gowan, Young, Fausch, & Riley, 1994). The ability of these fish to exploit the diverse mosaic of stream habitat patches available during both summer and winter, and consequently attain high growth and survival rates, may be best explained by a rich behavioural repertoire than by body size alone (Armstrong & Schindler, 2013).

Coho salmon that were sedentary in summer and winter 2009 experienced greater apparent winter survival rates than fish that were mobile during those seasons; however, our results suggest that the reach of residence in early winter also influenced survival. Mobile fish in the tidally affected areas and Reach 3 survived well compared to sedentary individuals, while sedentary fish in the upper reaches survived at a higher rate than those that moved from these areas, which may be attributed to the abundance of off-channel habitats in Reach 5. Although Bell et al. (2001) did not find differences in winter survival rates between sedentary and mobile coho salmon in a coastal Californian stream, they also reported that survival rates were higher among fish who occupied alcove and backwater habitats during winter compared to those in mainstem pools. Similar associations were observed between coho salmon winter survival rates with channel complexity and off-channel habitat at large spatial scales (i.e., stream reach and sub-basin; Quinn & Peterson, 1996; Solazzi et al., 2000; Ebersole et al., 2006), which suggests that mobility during winter may confer survival benefits in terms of locating refuge from extreme conditions.

Although coho salmon fry disperse from redds shortly after their emergence from gravel, their range of movement is highly variable. Whereas some individuals remain in the proximity of their redds during their first summer, other fry disperse up to several kilometres in either an upstream or an downstream direction (Anderson et al., 2013; Kahler et al., 2001). In fact, the downstream migrants may travel as far as the estuary during spring when coho salmon smolt emigration is underway (Koski, 2009). This early mobile behaviour can represent a sizeable proportion of each cohort, and those that migrate into estuarine habitats as age-0 fry (i.e., in spring or summer) have been estimated to constitute approximately 10% of the adult spawning runs (Jones et al., 2014). However, among the young coho salmon that remain in freshwater, there seems to be two main types of movement strategies: mobile and sedentary. Although both types explore their surroundings and select habitat patches balancing their foraging with their risk avoidance needs (Giannico, 2000; Grand, 1997), their scouting behaviour occurs at rather different spatial scales and changes between seasons. Our results did not reveal clear benefits of either the sedentary or the mobile strategies in terms of body mass or growth rates. Although sedentary individuals seemed to experience greater apparent survival rates in the basin, this varied among reaches. Sedentary behaviour provided a survival advantage for fish that occupied the middle and upper reaches in the creek, but a mobile strategy appeared to grant greater survival benefits to individuals in the low and tidally influenced reaches.

Our study complements the findings of other researchers who documented the variety of coho salmon early movement patterns and habitat utilisation, and emphasises the importance of maintaining a mosaic of seasonally accessible nursery habitats for sustaining viable populations. We documented coho salmon use of tide-gated creeks, which has received little attention in the past, and found that habitats influenced by tide gate operation, such as the tide gate reservoir (i.e., Reach 1), may provide habitats that are suitable for coho salmon from fall to spring, but likely limit coho salmon distribution and may be potentially lethal during summer. The partial impoundment created by the tide gates in Palouse Creek creates a relatively deep reservoir of brackish water most of the time except for the summer when water quality conditions (e.g., high water temperature) can be detrimental to salmonids among other fish (Giannico & Souder, 2005). Future research may consider focusing on a potential genetic basis for the two main types of early movement strategies observed in coho salmon, particularly among individuals that remain in freshwater during an entire year and those that enter estuarine habitats during their first summer of life. This would constitute an important piece in the puzzle of coastal coho salmon population life histories, which is critical to the conservation and management of these populations.

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