

Nomads no more: early juvenile coho salmon migrants contribute to the adult return

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Abstract – The downstream movement of coho salmon fry and parr in the fall, as distinct from the spring migration of smolts, has been well documented across the range of the species. In many cases, these fish overwinter in freshwater, but they sometimes enter marine waters. It has long been assumed that these latter fish did not survive to return as adults and were ‘surplus’ to the stream’s carrying capacity. From 2004 to 2010, we passively integrated transponder tagged 25,981 juvenile coho salmon in three streams in Washington State to determine their movement, survival and the contribution of various juvenile life histories to the adult escapement. We detected 86 returning adults, of which 32 originated from fall/winter migrants. Half of these fall/winter migrants spent ~1 year in the marine environment, while the other half spent ~2 years. In addition, the median return date for fall/winter migrants was 16 days later than spring migrants. Our results indicated that traditional methods of spring-only smolt enumeration may underestimate juvenile survival and total smolt production, and also overestimate spring smolt-to-adult return (SAR). These are important considerations for coho salmon life cycle models that assume juvenile coho salmon have a fixed life history or use traditional parr-to-smolt and SAR rates.

Key words: coho salmon; smolt; survival; passive integrated transponder tag; life history

Introduction

Life history diversity is a critical component of long-term stability for salmonid populations and has been identified as a key component for the management and conservation of salmonids (Greene et al. 2010; Moore et al. 2010; Schindler et al. 2010). A decrease in life history diversity can lead to increased risk of population extirpation in the near and long term (Moore et al. 2010; Carlson & Satterthwaite 2011). All salmon species show diverse life history patterns, whether at the juvenile or adult stage; these include variation in freshwater residency, juvenile migration, time spent at sea and adult return timing (Groot & Margolis 1991; Quinn 2005). Some variations are more readily observable than others; nonetheless, it is difficult to quantify the contribution of any one particular life history pattern to the next generation and

to long-term population stability (Schindler et al. 2010).

Multiple life history strategies and multiple populations can dampen interannual variability in abundance and provide a measure of stability within a population complex. In salmonids, this ‘portfolio effect’ is best documented for large population complexes composed of several distinct spawning populations such as Bristol Bay sockeye *Oncorhynchus nerka* (Greene et al. 2010; Schindler et al. 2010) and California’s Central Valley Chinook salmon *Oncorhynchus tshawytscha* (Carlson & Satterthwaite 2011). However, the portfolio effect could also be used to describe multiple life history strategies exhibited by a single population in much smaller streams, such as the multiple Chinook salmon life history types reported in the Sixes River, Oregon (Reimers 1971). These multiple strategies may dampen the

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effects of environmental conditions such as highly dynamic stream flows or biological factors such as density dependence.

One species not typically known for its juvenile life history diversity is coho salmon *Oncorhynchus kisutch*. However, that perception is changing. At the southern end of its range, coho salmon are generally assumed to spend 1 year in freshwater and either 6 or 18 months in the ocean (Sandercock 1991; Quinn 2005), but other life history patterns have been identified (Chapman 1962; Miller & Sadro 2003; Roni et al. 2012). These range from downstream movement into the estuary within weeks after emergence to a more prevalent pattern of spending one winter in the stream and then migrating to sea as an age-1 smolt (Chapman 1962; Miller & Sadro 2003). At the other extreme, coho in northern latitudes may delay smolting until age-2 or age-3 (Meehan & Siniff 1962; Drucker 1972; Armstrong & Argue 1977).

Several studies have documented juvenile coho salmon migrating downstream in the spring, summer or fall of the first year of life (Crone & Bond 1976; Koski 2009). Chapman (1962) first termed fry migrants as 'nomads'. This early migration has generally been described as a movement down to the lower part of the watershed or estuary where juveniles then reside for a period of time before eventually either returning upstream or migrating into the open ocean (Miller & Sadro 2003; reviewed by Koski 2009). In addition, a late nomad strategy may exist in short systems with very limited estuary habitat where age-0 coho salmon migrate downstream in the fall or winter and find themselves in the marine environment whether by choice or accident (Bennett et al. 2011; Roni et al. 2012; Quinn et al. 2013). These recent studies suggest that five or more coho salmon juvenile life histories may exist simultaneously in some basins. These life history types include fry and parr migrants, fry and parr that enter salt water but return to overwinter in their natal stream or in a nearby stream, and smolts that migrate in spring after spending one or more years in freshwater (Roni et al. 2012).

This life history diversity in coho salmon has not been widely recognised, in part because little was known about the extent to which early migrating juveniles contribute to adult returns. Crone & Bond (1976) concluded that nomads did not contribute to the adult population in Sashin Creek, Alaska, but conceded that differentiating juvenile fresh and salt-water growth from adult scales was difficult. In the Salmon River, Oregon, Cornwell et al. (2001) used scale patterns to determine that between 3% and 18% of returning, adults had reared in the estuary as juveniles. Koski & Lorenz (1999) documented a smolt-to-adult survival rate of up to 6.5% for coho nomads

that left their natal stream early and reared for a time in a nearby stream. In the Taku River, Alaska, there was a large fall migration of age-0 coho salmon from the upper river down to near the estuary, where they were coded-wire tagged. Subsequent scale analysis of the coded-wire-tagged adults captured in the fishery revealed that rather than continuing to sea, the juveniles had remained in the river for 1–2 years before actually entering salt water (Murphy et al. 1997). These studies provide evidence that age-0 coho salmon will migrate to the lower reaches of rivers or estuaries to rear, then smolt and subsequently contribute to the adult populations. However, the fate of coho smolt fry or parr that migrate directly to sea without an intermediate period of estuary residence has not been well documented.

As part of a long-term study evaluating whole watershed restoration (Bilby et al. 2005), we have continually monitored the juvenile migration timing of individually passive integrated transponder (PIT) tagged coho salmon in three streams on the north Olympic Peninsula, Washington. Of the juvenile coho salmon migrating out of these streams from 2004 to 2010, nearly 75% migrated in fall/winter as age-0 migrants, while the remaining fish that survived over the winter migrated in spring as age-1 smolts (Roni et al. 2012). Using data from juvenile coho salmon tagged between 2004 and 2010, we (i) describe the contribution of fall/winter age-0 migrants and spring age-1 smolts to the adult return; (ii) describe the factors affecting smolt-to-adult return (SAR) rates; and (iii) discuss the management implications of a successful fall/winter migration life history pattern.

Methods

Study area

The East Twin River, West Twin River and Deep Creek watersheds are small (35, 32 and 45 km², respectively), forested watersheds on the north side of the Olympic Peninsula, Washington (Fig. 1). The elevations range from approximately 915 m in the headwaters to sea level where the streams empty directly into the Strait of Juan de Fuca. Yearly average discharge ranges from 0.57 m³·s⁻¹ in the West Twin River to 1.42 m³·s⁻¹ in Deep Creek (Washington Department of Ecology unpublished data). Precipitation averages 190 cm per year and occurs primarily between October and May as rain, with occasional brief snowfalls (Olympic National Forest 2002).

Geology of the upper watersheds is characterised by Crescent Formation volcanic rock and in the lower watersheds by marine sedimentary rock with terraces

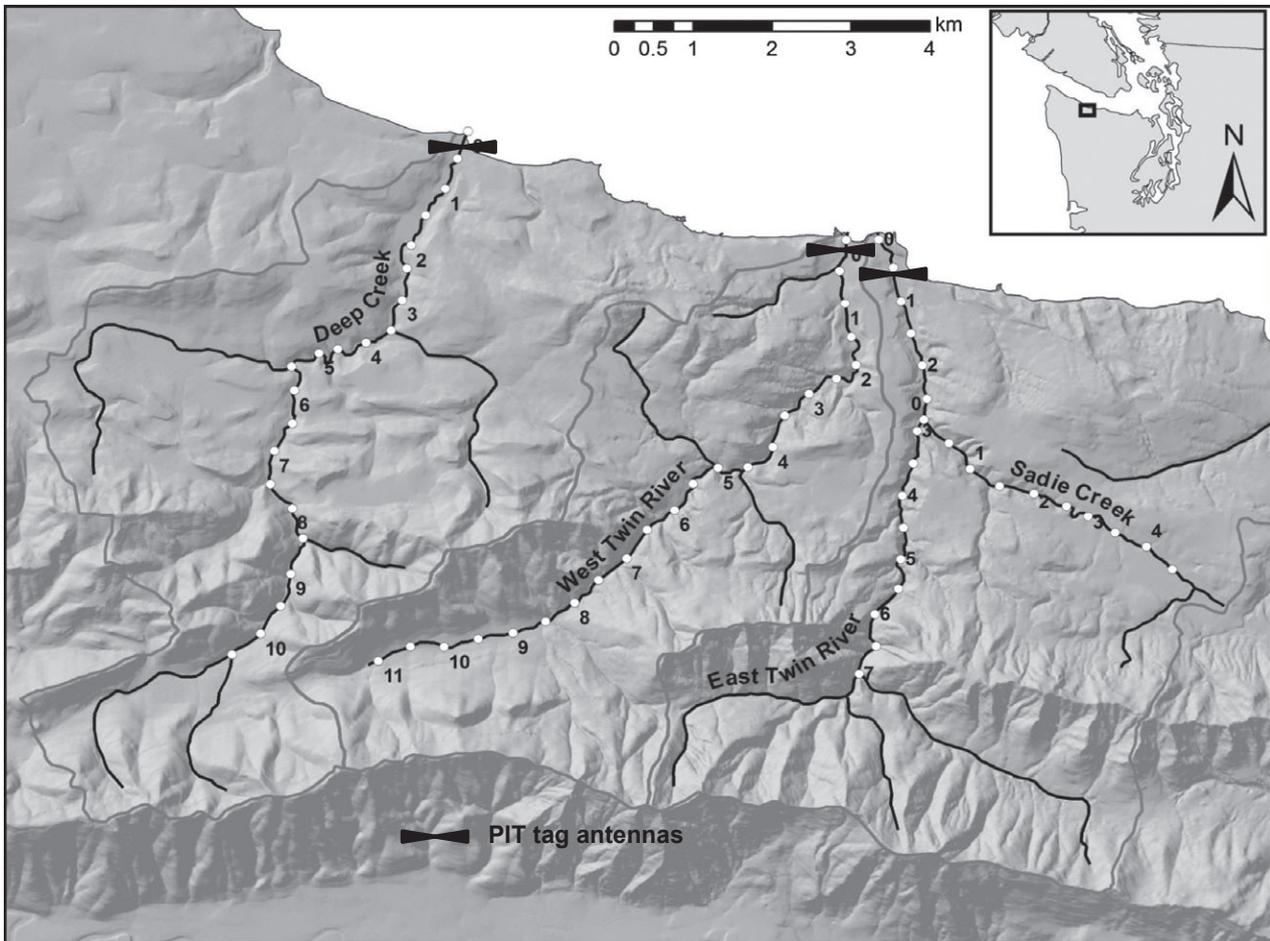


Fig. 1. Map of East Twin River, West Twin River and Deep Creek watersheds on the Olympic Peninsula of Washington ($48^{\circ}10'00\text{N}$, $123^{\circ}55'00\text{W}$). Numbers indicate kilometre from river mouth; white dots are 0.5 km increments.

of glacial deposits in the floodplains (Olympic National Forest 2002). There are three vegetation zones in these watersheds; the Sitka Spruce *Picea sitchensis* zone in the valley bottoms, the Western Hemlock *Tsuga heterophylla* zone in the low-to-mid elevations and the Silver Fir *Abies amabilis* zone in the headwaters (Olympic National Forest 2002). Land-use has historically been dominated by logging, which began in the early 20th century with railroad logging and transitioned to truck logging from the 1950's to present. Ownership is a mixture of federal, state and private industrial lands.

Fish species present in the three watersheds include coho salmon, steelhead/rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarki*), chum salmon (*Oncorhynchus keta*), Pacific lamprey (*Lampetra tridentata*), western brook lamprey (*Lampetra richardsoni*), torrent sculpin (*Cottus rhotheus*) and reticulate sculpin (*Cottus perplexus*). Coho salmon and other anadromous fishes are found below river kilometre (rkm) 5.8 on the East Twin mainstem and in Sadie Creek, which is a major tributary of the East Twin River at rkm 3.3 (M. McHenry, Lower Elwha

Klallam Tribe, unpublished data). The anadromous zone extends to barriers at approximately rkm 6.8 on West Twin and rkm 7.1 on Deep Creek (Olympic National Forest 2002).

The wetted and bank-full width of all reaches sampled average 3.76 and 7.6 m for East Twin River, 3.77 and 7.7 m for West Twin River, and 3.5 and 8.8 m for Deep Creek (Washington Department of Fish and Wildlife, Weyerhaeuser Co., unpublished data). However, bank-full width of all three streams near their confluence with the Strait of Juan de Fuca ranges from 20 to 25 m. Average per cent pool habitat from 2004 to 2012 was 32, 28 and 36 for East Twin River, West Twin River and Deep Creek, respectively (Washington Department of Fish and Wildlife, unpublished data). The gradients of the streams range from 0% to 6% and average 2.17%, 2.33% and 2.51% for East Twin River, West Twin River and Deep Creek, respectively (Weyerhaeuser Co., unpublished data). All of the streams are characterised by steep, narrow upper reaches leading to lower-gradient floodplains with limited off-channel habitat (Olympic National Forest 2002).

Tagging procedure, PIT tag antenna setup and antenna efficiency

A total of 25,981 juvenile coho salmon were tagged with PIT tags from 2004 to 2010 (Table 1). Juvenile coho salmon were captured using multiple-removal electrofishing at 10–15 sites throughout each watershed from mid-August to mid-September (see Roni et al. 2012). All coho salmon ≥ 55 mm were implanted with a 12.5 mm Destron-Fearing Model TX1411SST-1 PIT tag (Prentice et al. 1990). In a previous study, 80 tagged fish were held for 24 h to determine tag retention and mortality (Bennett et al. 2011). Tag retention was 100%, and there were no mortalities. Other researchers have described excellent retention and low mortality rates in similar-sized fish (Prentice et al. 1990); thus, we felt confident with our minimum fish size of 55 mm. Instream PIT-tag monitoring stations (Destron-Fearing 1001M, Destron-Fearing, South St. Paul, MN, USA) were installed 600 m from the mouth of the East Twin River in September 2004 and 300 m from the mouth of the West Twin River in early October 2004. In August 2009, a monitoring station was installed 100 m from the mouth of Deep Creek. The configuration for each site was two rows of three antennas separated by approximately 5 m. This configuration provided bank-to-bank coverage at all but the highest flows.

High flows and occasional equipment failure rendered our PIT tag stations either partially or fully inoperable for short periods of time. However, over the course of the study, the sites in the East Twin River and West Twin River were functioning 99.5% and 99.4% of the time, respectively. The site in Deep

Creek did not experience a failure during the study period. Fall and early winter flows (when age-0 fall/winter migrants are moving downstream and adults are moving upstream) are generally much higher than flows during the spring smolt migration. Under these conditions, PIT-tagged fish can pass high enough over the antennas to avoid detection. It is also possible that 10s of detections per day were missed during the equipment failures. Detection efficiency is often calculated as the probability of a tag being detected on a subsequent antenna or array after first being detected on one antenna or array (Zydlowski et al. 2006; Connolly et al. 2008). Based on juvenile migrants, detection efficiency at our readers ranged from 40% to 100%, but exceeded 90% in almost all months and years (Roni et al. 2012). However, the purpose of this study was to examine the life histories of the returning adults rather than to make estimates of juvenile out-migrant numbers or total escapement. Because we only used individual fish that were detected as adults and were also detected migrating out as juveniles, detection efficiency at either juvenile or adult stage is not applicable to our analyses.

Identification of juvenile and adult life histories

Juvenile coho salmon migrants detected between September 30 and February 28 were categorised as fall/winter migrants. Juvenile coho salmon detected migrating between March 1 and June 30 were categorised as spring smolts (Bennett et al. 2011). Adult coho salmon were classified using the European decimal system, where the numeral before the decimal indicates the number of winters in fresh water postemergence and the numeral after the decimal indicates the

Table 1. Individual fall/winter migrant and spring smolt passive integrated transponder tag detections and subsequent adult returns.

Tag year	2004	2005	2006	2007	2008	2009	2010	Total
Coho tagged	2391	6313	5007	2913	4566	912	3879	25,981
Coho detected								
F/W migrants	393	940	971	508	1331	290	1237	5670
Spring smolts	241	469	265	345	286	126	197	1929
Total migrants	634	1409	1236	853	1617	416	1434	7599
Adult return								
Age class of returning adults								
0.1	0	2	1	3	5	3	2	16
0.2	0	1	1	5	5	4	NA*	16
1.0	1	1	2	1	0	1	1	7
1.1	1	12	1	24	3	5	NA*	46
2.1				1				1
Total	2	16	5	34	13	13	3*	86
Smolt-to-adult return (%)								
F/W migrants	0	0.32	0.21	1.57	0.75	2.41	0.16*	
Spring smolts	0.83	2.77	1.13	7.54	1.05	4.76	0.51*	
Total	0.32	1.14	0.40	3.99	0.80	3.13	0.21*	

F/W migrant, Fall/Winter migrant.

*Not all adults from tag year 2010 have returned at time of writing.

number of winters at sea (Koo 1962; Fig. 2). For instance, 1.1 denotes an individual that spent one winter in fresh water and one winter at sea, a typical adult coho salmon. A fall/winter migrant that returned the following fall would be denoted as 0.1.

A step-wise procedure was used to filter the PIT tag detection data to determine the number of tagged juvenile coho salmon that returned as adults. This included the following:

1. Identifying tagged juvenile coho salmon detected migrating downstream between time of tagging and June 30th the following year.
2. Fall/winter migrants that were subsequently detected returning 1 or 2 years after emigration were classified as 0.1 or 0.2, respectively, and spring smolts that were detected returning 6 months or 1.5 years after emigration were classified as 1.0 or 1.1, respectively.
3. To confirm that the fish in step 2 were adults, the entire detection history of each individual was carefully reviewed. For each tag detected that could possibly be an adult, the antenna sequence was considered to make sure the individual was moving in an upstream direction during the adult migration period.

We excluded from analysis any purported returning adult that was only detected on one antenna, regardless of its juvenile detection history. With the thousands of tags placed in the streams over the course of the study, we experienced a number of ‘washdowns,’ where shed tags are mobilised during high flows and pass over the antennas. Because juvenile and adult salmon use higher flows to migrate, differentiating between live fish and loose tags can be difficult. If

we could not verify that a fish was moving in an upstream direction, it could not be considered an adult by our criteria. Using these criteria, we created a list of 86 confirmed adults. Our design was not to include every *possible* PIT-tagged returning adult, but rather to provide a conservative number of adults that had been verified migrating both as a juvenile and as an adult. However, it is entirely possible that more adults returned that were (i) detected neither leaving as juveniles nor returning as adults; (ii) were detected as juveniles but not adults or (iii) were detected as adults but not juveniles. Thus, the numbers reported here indicate minimum SAR rates.

Smolt-to-adult return

Because we had only 86 confirmed adults among the three streams over 7 years, we felt we did not have the statistical power to draw any conclusions about differences among watersheds. As more generations of fish return, this may change; however, at this point, all data were pooled across years and streams. Smolt-to-adult return (SAR) was calculated for fall/winter migrants and spring smolts, as well as in total.

1. $SAR_{Fall/Winter} = (\text{adults from fall/winter migrants}) / (\text{fall/winter migrants})$.
2. $SAR_{Spring} = \text{adults from spring smolts} / \text{spring smolts}$.
3. $SAR_{Total} = (\text{adults from fall/winter migrants} + \text{adults from spring smolts}) / (\text{fall/winter migrants} + \text{spring smolts})$.

We also compared the median return times of adults from fall/winter migrants and spring smolts using the normal approximation to the Mann–Whitney test.

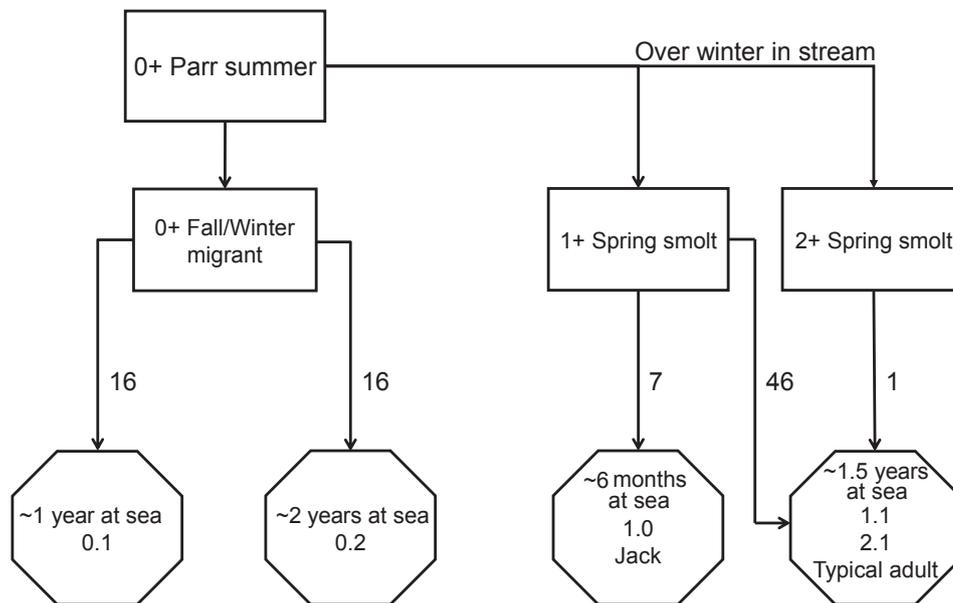


Fig. 2. Life history pathways exhibited by coho salmon in the East Twin River, West Twin River and Deep Creek. N = 86.

Size at tagging

Previous studies have shown that size at tagging can be an important determinant of both survival and the decision whether to migrate as smolts in spring or fall/winter (Bennett et al. 2011; Roni et al. 2012). We standardised fork length (FL) at tagging to September 15th of each year using an individually based annual von Bertalanffy growth curve (von Bertalanffy 1957). (Hereafter, standardised fork length is referred to as 'size at tagging.'). Study fish were classed by detection history into five groups: juveniles that were never detected again after tagging, juveniles detected as fall/winter migrants, juveniles detected as spring smolts, juveniles detected as fall/winter migrants that returned as adults and juveniles detected as spring smolts that returned as adults. Juveniles subsequently detected as adults are included in the juvenile out-migration categories. Size at tagging for the five groups was compared using notched box and whisker plots, where notches represent approximate 95% confidence intervals for the medians of the individual groups (McGill et al. 1978). Groups with nonoverlapping notches correspond to a conservative test for nonequal medians ($\alpha = 0.05$). This approach is robust to the very large differences in group sample size, and the moderate differences in variances, while providing sufficient power to illustrate the differences of interest.

Results

Contribution of fall/winter migrants and spring smolts to adult return

Based on our criteria, we identified 86 returning adults from the 7599 PIT-tagged fish detected migrating as juveniles (Table 1). These 86 adult coho salmon represented four life history patterns (Fig. 2). Of the confirmed adult coho salmon, 37% (32 of 86) were from fall/winter migrants (ages 0.1, 0.2; Fig. 2). Adults produced from the fall/winter migrants exhibited two life history types: those that spent approximately 1 year at sea (age 0.1, $n = 16$) and those that spent approximately 2 years at sea (age 0.2, $n = 16$). Adults produced from the spring smolts (ages 1.0, 1.1, 2.1; $n = 47$; Fig. 2) exhibited two marine life history types as well: jacks that spent approximately 6 months at sea (age 1.0, $n = 7$) and typical adults, which spent approximately 1.5 years at sea (age 1.1, $n = 46$; age 2.1, $n = 1$). While age 0.1 adults are technically the same age as the age 1.0 adults that are nearly exclusively small males (jacks; Sandercock 1991), without length or sex data of returning adults, we could not determine what effect an extra 6 months at sea had on the size and sex distribution of the age 0.1 adults (i.e., were they all male like

typical jacks, or a mix of male and female). Thus, they were considered different from age 1.0 jacks.

Factors affecting SAR rates and return timing for fall/winter migrants and spring smolts

Fall/winter migrants that returned as adults and spring smolts that returned as adults were similar in size at tagging, and both groups were larger at tagging than all other groups (Fig. 3). It is interesting to note that median length at tagging of the fall/winter migrant group (64 mm) was significantly smaller than that of the group that was never detected again (67 mm; Fig. 3). Comparison of median fork length at time of tagging indicates that fall/winter migrants that returned as adults (73.5 mm) were on average larger than those that did not (64 mm; Fig. 3).

Smolt-to-adult return of fall/winter migrants and spring smolts combined ranged from 0.32% to 3.99% with tag years 2007 and 2009 having much higher SARs than all other tag years (Table 1). SAR was influenced by juvenile length, in particular when the length at tagging was 70 mm or larger ($\chi^2 = 53.562$, $P < 0.001$; Fig. 4). SAR for coho salmon 70 mm or larger at tagging was nearly four times higher than that of coho salmon smaller than 70 mm at tagging. To explore this further, we related SAR to the proportion of coho salmon ≥ 70 mm for each tag year. The proportion of coho salmon ≥ 70 mm ranged from 0.18 to 0.76 across years, and SAR appeared to be highest when the proportion of fish larger than 70 mm was highest. For example, in tag year 2007, the proportion of coho salmon ≥ 70 mm was 0.57, and SAR was highest at nearly 4%. Tag year 2009 was similar, where the proportion of coho salmon ≥ 70 mm was 0.76 and SAR was 3.13% (Fig. 5, Table 1).

For tag years 2004–2009, SAR ranged from 0% to 2.41% for fall/winter migrants and 0.83% to 7.54% for spring smolts. Total SAR for fall/winter migrants and spring smolts combined ranged from 0.32% to 3.99% (Table 1). As of this writing, not all adults have returned from tag year 2010. While fall/winter migrants far outnumbered spring smolts during our study period, SAR was approximately 1.5 to 8.7 times higher for spring smolts than for fall/winter migrants (Table 1).

Fall/winter migrants were equally as likely to return after 1 year at sea as after 2 years at sea. A two-sample *t*-test determined that mean fork length at tagging of those coho salmon that spent 1 year at sea (76 mm, $n = 16$) was not significantly different than that of those that spent 2 years at sea (75 mm, $n = 16$; $P = 0.81$). We also compared fork length at tagging of spring smolts that returned as jacks (73 mm, $n = 7$) versus those that returned after spending one winter at sea (73 mm, $n = 47$) and found no significant difference ($P = 0.91$). The median

Fig. 3. Box and whisker plot showing fork length at tagging for juvenile coho that were subsequently undetected (UD), detected as fall/winter migrants (FWM), detected as adult returns from fall/winter migrants (FWMA), detected as spring smolts (SpS) and detected as adults returns from spring smolts (SpSA). For the adult groups, filled circles represent individuals. Notches represent individual 95% confidence intervals (McGill et al. 1978). Nonoverlapping notches for two groups correspond to a statistically significant difference in the medians ($\alpha \leq 0.05$).

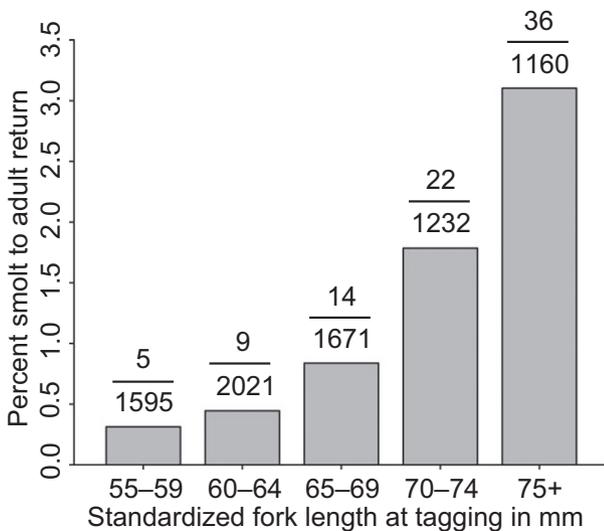
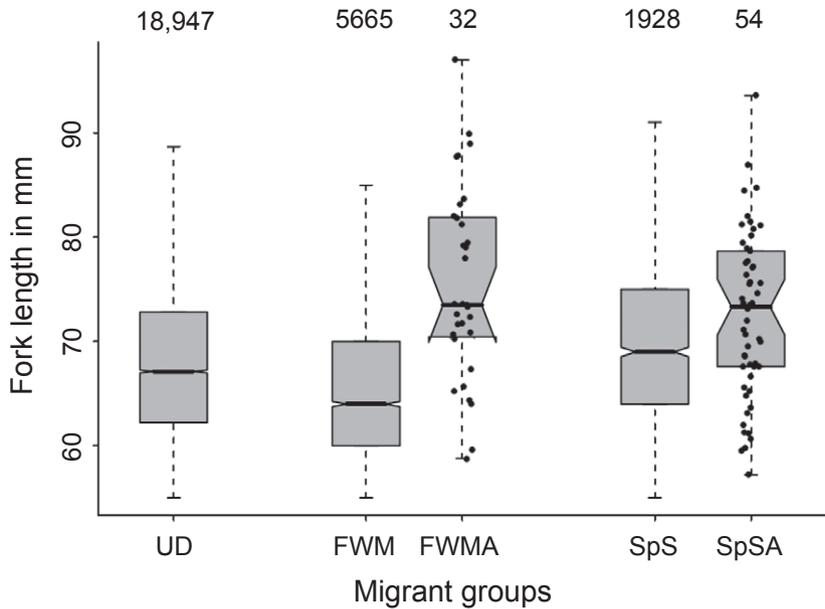


Fig. 4. Per cent smolt-to-adult return (including fall/winter migrants) relative to standardised size at tagging. Numerator is number of adult returns, and denominator is number of smolts (fall/winter migrants and spring smolts combined) in each size class.

return date of adults from fall/winter migrants (November 19) was 16 days later than that of adults from spring smolts (November 3) (Fig. 6). Normal approximation to the Mann-Whitney test; at $\alpha = 0.05$, $Z_{0.05(1)} = 1.6449$. As $Z = 3.506 > 1.6449$, return dates are significantly different.

Discussion

Contribution of fall/winter migrants and spring smolts to adult return

The contribution of age-0 fall migrants to the adult return has been documented for Chinook salmon

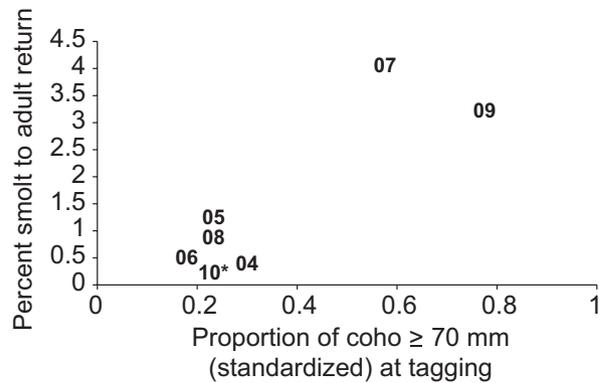


Fig. 5. Coho salmon smolt-to-adult return (including fall/winter migrants) relative to the proportion of coho ≥ 70 mm at tagging. Numbers indicate tag year. *Note not all adults from tag year 2010 have returned as of this writing.

(Achord et al. 2012) and is now being recognised in Atlantic salmon *Salmo salar* populations (Riley et al. 2009; Ibbotson et al. 2013). This study documents that life history pathway for coho salmon, that is, age-0 fall/winter migrants that produce returning adults. While the existence of age-0 fall/winter migrants has been documented in these systems and others (Koski 2009; Bennett et al. 2011; Pess et al. 2011; Roni et al. 2012 (described as ‘fall migrants’); Quinn et al. 2013), the discovery that they contributed 37% of the detected returning adults over an 8-year period is novel. Of this 37%, half spent two winters at sea; this is a novel discovery as well. In a review of 31 coho populations ranging from California to Alaska, Holtby & Healey (1990) reported no two-winter adult coho; however, it is possible that two-winter coho existed in these populations, but methods to determine timing of sea water entry, such as PIT tags or otolith analysis, were not available.

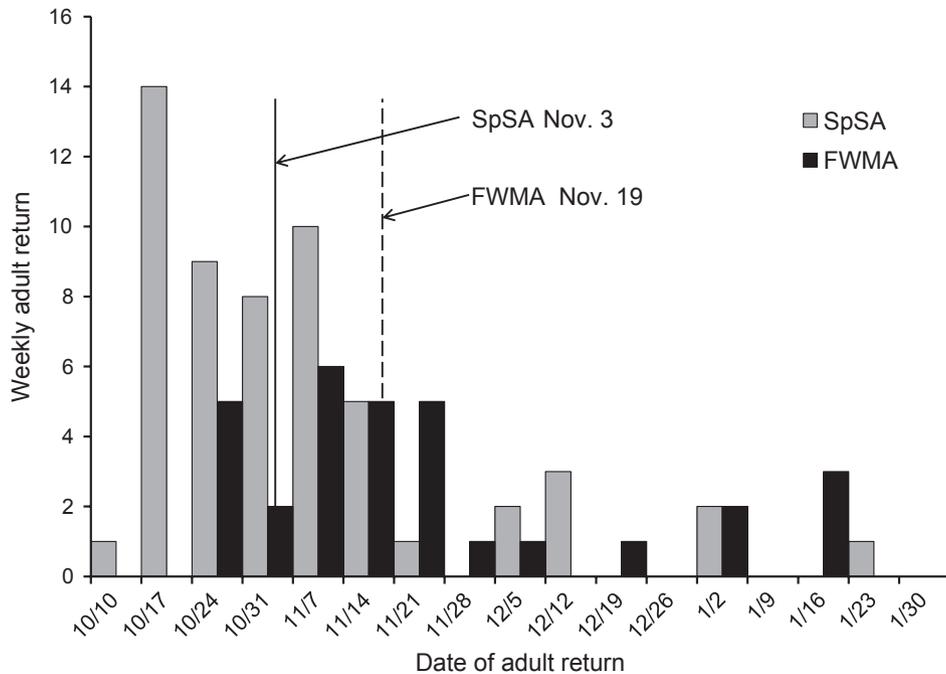


Fig. 6. Median adult return date from spring smolts (SpSA) = November 3 and median adult return date from fall/winter migrants (FWMA) = November 19.

Scale analysis alone may be unreliable to determine time of sea water entry (Crone & Bond 1976).

Migration from fresh water by age-0 fry and parr or ‘nomads’ (Chapman 1962) is widespread throughout the range of coho salmon (Koski 2009). Many of these nomads either use estuarine environments or return to natal (Miller & Sadro 2003) or non-natal streams to overwinter before moving out to salt water in the spring (Koski & Lorenz 1999). The East Twin River, West Twin River and Deep Creek have limited estuaries and discharge directly into the Strait of Juan de Fuca; thus, juveniles are likely subjected to full salt water immediately after leaving the stream. There is evidence that juveniles leaving our study streams will return to the stream or an adjacent stream, but typically <1% appear to do so (Roni et al. 2012). However, we did not have PIT tag monitoring systems on all nearby streams, so we could not determine the full extent to which juveniles returned to other streams either with or without an estuary. The nearest streams with an appreciable estuary are the Pysht River 17 km to the west, and Salt Creek [which also shows a fall emigration, albeit the peak is in September (Quinn et al. 2013)] 8.5 km to the east. Fall/winter migrants have been detected migrating out of our study streams and then detected again 1 or 2 years later returning as adults. While a spring smolt is three times more likely to return as an adult, a juvenile coho is 2.5 times more likely to migrate as a fall/winter migrant than a spring smolt. Thus, a trade-off occurs between migrating in the fall/winter when chances of entering salt water are higher, but

marine survival is lower, and overwintering in the stream where chances of entering salt water are lower, but marine survival is higher.

Factors affecting smolt-to-adult return rates and return timing for fall/winter and spring smolts

With any mark-recapture study, there are concerns about how fish size, fish collection techniques and the tagging process influence tag retention and the survival of the animals (Prentice et al. 1990; Brakensiek & Hankin 2007; Dieterman & Hoxmeier 2009). One method of determining this is multiple sampling events with short intervals between events (Brakensiek & Hankin 2007; Pess et al. 2011). These studies did find that larger fish survived at a higher rate. However, as with our study, it is difficult to determine whether the differential survival was due to the tagging process having a greater effect on the smaller fish, or merely that smaller fish (tagged or not) have a lower survival rate. Many studies have reported a tag retention of 97% or greater for fish ≥ 55 mm (Prentice et al. 1990; Gries & Letcher 2002; Dare 2003; Brakensiek & Hankin 2007; Bennett et al. 2011). Our analysis was based on the first detection of out-migration by juvenile coho salmon, which was typically greater than 2 months after tagging. We feel that it is safe to assume that any tag-related mortality or tag shedding across the range of fish sizes would have minimal effect on SAR rates for the different out-migrant groups.

Both saltwater tolerance and smolt-to-adult return rates have been linked to body size, where larger smolts tend to survive at a higher rate (Beckman et al. 1998; Quinn 2005), although that is not always the case (Holtby et al. 1990). Weisbart (1968) found a size threshold for coho survival in salt water of 70–80 mm, where smaller (50–60 mm) juveniles perished. Our data appear to align with these thresholds. Because we were unable to recapture fish in fall/winter, we did not know how large they were when they actually entered salt water; therefore, we used length at tagging for this analysis. The fall/winter migrants that returned as adults were larger at tagging than both spring smolts at tagging and spring smolts at tagging that returned as adults. However, the average size at tagging of all fall/winter migrants was significantly smaller than all of those three groups. That the fall/winter migrants were smaller on average, but only the largest of that group survived is an interesting phenomenon. Within the time frame of our study, small, early out-migrating fish have not been as successful as fish out-migrating at a larger size during either the fall/winter or spring. Nevertheless, this pattern was seen consistently across all years of tagging (Bennett et al. 2011; Roni et al. 2012). A possible explanation is that if smaller fish are not able to survive the high flows of winter as well as larger fish, it may behave them to leave prior to those high flows, even though they may not be as suited for marine survival as a larger fish. Given highly variable stream and ocean conditions these fish experience, these differing strategies may prove to even out if a long enough time series was examined.

The correlation between juvenile body size and SAR was far more apparent when comparing spring to fall/winter migrants. Mean survival across years was more than three times higher for spring smolts (3.01%) than fall/winter migrants (0.88%). Undoubtedly, fall/winter migrants experienced some growth between the time of tagging and migration, but they would most likely not be as large as spring smolts at sea water entry (~98 mm, Roni et al. 2012). Regardless of whether juvenile coho entered seawater in fall/winter or in spring, there seemed to be a size threshold at the time of tagging that affected the chances of survival. In these coastal streams, juveniles ≥ 70 mm at tagging had a much higher chance of returning as adults, as our data from 2007 and 2009 indicate. Holtby et al. (1990) found that smolt size provided an advantage for SAR only in years of low marine productivity. Moreover, there is evidence that relative size within a cohort rather than absolute size may be important in determining overwinter or marine survival rates (Quinn & Peterson 1996). While we saw large size differences between fall/winter migrants and spring smolts, we did not have

sufficient numbers of returning adults from each year to examine whether the size within a given cohort influences SAR. Size at sea water entry may not be the sole factor influencing survival, however. Juvenile coho that enter sea water in the fall/winter may encounter entirely different environmental conditions than those that enter in the spring: temperature, food availability and predator interactions may influence survival (Spence & Hall 2010). More research is needed to determine the differences in marine conditions during the fall/winter and spring migration periods.

Movement among streams by both juvenile and adult coho salmon may affect SAR rates; we observed both stream swapping by juveniles and straying by adults among our study streams. Twenty to 50 juveniles per year left the stream where they were tagged in the fall and for the most part moved westward, where they were detected moving into another stream [i.e., a tagged fish would leave the East Twin River and then be detected hours to weeks later in the West Twin River (Roni et al. 2012)]. In some years, up to half of these fish would then migrate back out in the fall, but in others, they overwintered in the stream and migrated as smolts in the spring. Four of the adults that returned had swapped streams as juveniles in the fall, left as smolts the following spring, and returned as adults to the stream where they had overwintered. Two adults were detected in a stream where they had not been tagged and subsequently were detected returning to the original stream where they had been tagged. Two adults, one that was a fall/winter migrant and one that was a spring smolt, were detected straying to a stream other than where they had been tagged and not detected leaving again; we can infer that they remained in those streams to spawn.

We found that the median time of adult return was 16 days later for fall/winter migrants than for spring smolts. Why this occurred and what role (if any) it may play in spawning success is yet to be determined. Even though the time of entry into the stream may differ, spawning time may not, as time of stream entry and time of spawning for many coho populations are not often correlated (Sandercock 1991). Late spawning may be an advantage for populations with high densities or those that compete with other species such as sockeye or chum, but at present, the coho populations in our study streams have neither high densities nor competition with other species.

Management implications

Traditional SAR estimates for coho salmon are calculated using spring smolt counts and some form of adult census, such as redd or carcass counts (Hilborn et al. 1999; Solazzi et al. 2000). Smolt trapping and

adult escapement estimates based on spawner surveys are done annually in our study streams by the Lower Elwha Klallam Tribe and Washington Department of Fish and Wildlife. During our study years, SAR estimates for all three streams based on these traditional methods ranged from 0.1% to 5.8% (M. McHenry, Lower Elwha Klallam Tribe, personal communication). However, traditional estimates include only spring smolts and do not account for any fish that migrate to sea prior to spring. Our PIT tag data indicate that autumn parr-to-out-migrant survival was 7.1% if only spring smolt numbers were used, but 28.0% when fall/winter migrants were included. Moreover, our data clearly demonstrated that using only spring smolts overestimated SAR, especially in years that had high returns from fall/winter migrants. For example, using tag year 2009 data, we observed that seven adults returned from fall/winter migrants and six from spring smolts. Using all adults and only spring smolt detections resulted in a SAR of 10.5% (13/124). However, only six of those were spring smolts, which resulted in a true spring SAR of 4.8% (6/124). Using both fall/winter and spring smolts, total SAR for tag year 2009 was 3.2% (13/408). Because the contribution of the adult return from fall/winter migrants was highly variable (0–77%), its impact on traditional SAR calculations was highly variable as well. This has management implications for both harvest and recovery of depressed populations. If harvest rates are based only on spring SAR, they could be set higher than is sustainable for many populations. Similarly, predicted increases in adult returns based on increased freshwater productivity may be overly optimistic if SAR rate is lower than expected. One way to refine these predictions may be to incorporate metrics other than just smolt numbers, such as size distribution of parr at tagging (e.g., proportion of coho ≥ 70 mm at tagging) and proportion of fall/winter migrants to spring smolts leaving the streams.

Conclusions

There has been considerable research documenting the early migration of juvenile coho salmon to salt water, but until now, there has been little evidence that these fish contribute to the spawning population. In our study streams, juvenile coho exhibited a strongly bimodal emigration pattern, with a large peak in the fall/winter that contributed to nearly 37% of the adult return from 2004 to 2010. Furthermore, adults from fall/winter migrants spent approximately 1 or 2 years in the ocean, compared to 6 months for a jack (age-1 smolt – fall return) and 18 months for a typical adult from an age-1 smolt. This diversity of life history patterns essentially provides a portfolio effect to spread the risk of mortality for coho in these

small streams. Coho populations may have developed these pathways in our small study streams to decrease variability due to limited overwinter habitat, high winter flows with the concomitant bedload movement, and limited estuary rearing habitat. Thus, they are able to create some balance between the risks of staying in the stream over winter or entering sea water at a suboptimal time. While answering Koski's (2009) question of whether other life history strategies or variants of the nomad strategy exist in coho populations, our study in turn raises others. For the juvenile life stage, are the drivers for fall/winter migration abiotic (e.g., photoperiod), biotic (e.g., genetic, size/growth-related) or some combination? For the adult stage, a basic understanding of the population structure is needed, including age and size at return, sex ratio, and breeding success of adults from different age classes. Because fall/winter migrants spend 6–12 months longer in the ocean than spring migrants of their cohort, they may be larger at the time of return. For males, this may provide a competitive advantage during spawning, and for females, this may translate to higher fecundity and deeper, more secure redds. More research using otolith microchemistry analysis and increased PIT tag coverage is needed to fully explore these life history variations, especially with regard to juveniles that swap streams in the fall and adults that stray to non-natal streams upon return. Determining the factors that drive fall migration and the characteristics of the adults produced by this life history will be instrumental in developing a restoration strategy to maximise recovery of these depressed coastal coho stocks.

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