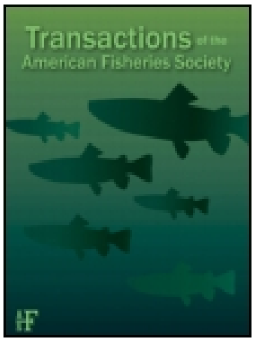

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ARTICLE

Life History Diversity of Steelhead in Two Coastal Washington Watersheds

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Abstract

We used PIT tags implanted in juvenile *Oncorhynchus mykiss* to monitor movement into and out of two coastal Washington State rivers, East Twin River and West Twin River. Movement patterns revealed at least 18 life histories of steelhead *O. mykiss* with variations in age and seasonal migration of juveniles, juvenile use of the ocean prior to migration, years spent in the ocean, season of adult return, and iteroparity. While most migrants left the river in their first fall or winter, we did not detect any returning adults from these age-0 migrants. Adults were only produced from age-1 and older migrants, of which most were age-2 spring migrants that returned after two summers in the ocean. Our results indicated a positive relationship between fish length at tagging and the probability of being detected as a migrant, while the probability of a migrant leaving at age 1 and older decreased with increasing length at tagging among fish that were detected as migrants. We hypothesize that fish attaining a large enough size early in life to survive over the winter but not big enough to trigger migration at age 0 were more likely to remain in the river to become age-1 migrants, which were more likely to produce a returning adult steelhead. We also found evidence that density-dependent growth may influence juvenile steelhead migration patterns and production of migrants as evidenced by increasing contributing-adult steelhead escapement being negatively related to average cohort body size, probabilities of fish being detected as migrants, and production of age-1 and older migrants. We anticipate that the findings of this study can be used to inform the development of steelhead recovery strategies for East Twin and West Twin rivers, which have experienced recent declines in adult returns much like other North Pacific Ocean stocks.

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Life history diversity and complexity among Pacific salmon *Oncorhynchus* spp. can increase population resilience and productivity by spreading risk over space and time (Stearns 1992; Greene et al. 2009; Moore et al. 2010). Life history diversity is increasingly being identified as a critical component to developing effective population management strategies for Pacific salmon (Waples 2002; Schindler et al. 2008, 2010; Greene et al. 2009; Kendall et al. 2014; Moore et al. 2014). Steelhead *Oncorhynchus mykiss* (anadromous Rainbow Trout) express the most diverse and complex life histories among Pacific salmon (Thorpe 1998; Kendall et al. 2014; Moore et al. 2014), and recent declines in steelhead abundance in the North Pacific Ocean highlights the need to develop recovery strategies that integrate life history diversity (Kendall et al. 2014; Moore et al. 2014; Thompson and Beauchamp 2014).

While all *O. mykiss* juveniles rear in freshwater, some migrate to mature in the ocean before returning to spawn as anadromous steelhead. Others may remain in freshwater throughout their entire life cycle as resident Rainbow Trout. Both anadromous and resident life histories express variations in age at maturity within and between sexes and in iteroparity (Behnke 2002; Kendall et al. 2014; Moore et al. 2014). Steelhead also express variations in age and timing of juvenile migrations to the ocean, years spent in the ocean, and seasonal timing of adult returns (Savvaitova et al. 2003; Kuzishchin et al. 2007; Moore et al. 2014). Life history expressions among *O. mykiss* are described as conditional strategies in which individuals have the capacity to express all life histories regardless of parentage or previous selective pressures (Thrower and Joyce 2004; McPhee et al. 2007; Kendall et al. 2014; Phillis et al. 2016). Expression of these strategies have been linked to interactions between genetically controlled thresholds and body size, growth rate, and lipid stores at particular times of the year (Beakes et al. 2010; McMillan et al. 2011; Tattam et al. 2013; Evans et al. 2014; Kendall et al. 2014; Thompson and Beauchamp 2014). Spatial and temporal variations in life history prevalence are also controlled by selective pressures balancing trade-offs of alternative strategies. For example, anadromy can produce larger individuals with higher fecundity but at the risk of higher ocean mortality (Gross 1987; McDowall 1997), while lower freshwater mortality and higher prevalence of iteroparity can offset smaller body size and lower fecundity among resident life histories (Kendall et al. 2014).

Characterizing life history diversity and identifying potential factors influencing the expression of steelhead life histories are logical first steps to integrate life history diversity with population management strategies. Life history characterizations have traditionally relied on sampling returning adults (Hodge et al. 2014; Moore et al. 2014), but this can bias conclusions given that only individuals surviving to adult return are sampled. Individual-based monitoring approaches from juvenile life stages can provide a more comprehensive characterization of life history diversity, which can include both successful and unsuccessful life histories. This is especially relevant when life history diversity is considered within a management context given that the relative frequency and success of different life histories can change over time within populations (Tattam et al. 2013).

A long-term monitoring program for two small coastal Washington State rivers provided an opportunity to evaluate life history diversity of steelhead using an individual-based approach. As part of the Washington State Intensively Monitored Watershed (IMW) Program (Bilby et al. 2005), long-term monitoring of the East Twin and West Twin rivers includes implantation of PIT tags into juvenile *O. mykiss*. This individual-based monitoring approach has been successfully used to characterize life history diversity of *O. mykiss* (e.g., Tattam et al. 2013; Evans et al. 2014) and other salmonids (e.g., Pess et al. 2011; Roni et al. 2012). We relied on this approach to characterize steelhead life history diversity, evaluate relative contributions of life histories to adult production, and explore potential factors related to the expression of life histories in the East Twin and West Twin rivers. Much like other *O. mykiss* populations in the North Pacific Ocean, recent declines in steelhead escapement have been observed in these two watersheds (Bilby et al. 2005). Therefore, we anticipate that the information presented here can be used to develop recovery strategies that integrate life history for these two coastal rivers, as well as inform development of recovery planning in other systems.

METHODS

Study site.—The East Twin and West Twin rivers flow into the Strait of Juan de Fuca along the north coast of Washington State (Figure 1). Drainage areas are 35 km^2 and 33 km^2 for the East Twin and West Twin rivers, respectively, and elevation in these basins reaches 915 m in the headwaters. Precipitation occurs primarily as rain between October and May and averages 190 cm/year (Olympic National Forest 2002). Mean daily water temperatures near the mouths of the East Twin and West Twin rivers range from a low of 0°C in winter to a high of 16.7°C in summer. Mean daily flows are 1.41 and 1.52 m^3/s in the East Twin and West Twin rivers, respectively, and range from 0.05 to 51.85 m^3/s in the East Twin River and from 0.01 to 40.99 m^3/s in the West Twin River (Washington Department of Ecology Stations 19D070 and 19C060).

Primary land use within both basins for the past 100 years has been industrial forestry (Olympic National Forest 2002; Bilby et al. 2005). Logging, removal of inchannel wood, and construction of logging roads on steep slopes have increased landslide frequency and created simplified and degraded channel habitat conditions (Bilby et al. 2005). Steelhead escapement estimates for both rivers indicate that steelhead stocks are depressed (McHenry et al. 1996) and that escapement has declined in recent years (Bilby et al. 2005). The Washington Department of Fish and Wildlife conducts annual spring steelhead redd counts from the mouths of both rivers to river kilometer (rkm) 4.7 in the West Twin River and rkm 4.2 in the East Twin River to estimate escapement in both rivers. Redd counts from approximately four surveys per year are expanded to adult escapement using area-under-the-curve estimates assuming 0.81 females per redd and an average sex ratio of 1:1.

All fish sampling was restricted to the lower 6.5 km of both the East Twin and West Twin rivers (Figure 1). Fish populations in the lower rivers include steelhead or Rainbow Trout, Coho Salmon *O. kisutch*, Cutthroat Trout *O. clarkii*, Chum Salmon *O. keta*, Pacific Lamprey *Entosphenus tridentatus* (also known as *Lampetra tridentata*), Western Brook Lamprey *L. richardsoni*, Torrent Sculpin *Cottus rhotheus*, and Reticulate Sculpin *C. perplexus* (Roni et al. 2012). The upriver extent of anadromy and headwater fish population composition above the sampling extent is not documented for both rivers. A canyon near rkm 6.5 on East Twin River is generally regarded as a barrier to anadromous fish passage, although there have been anecdotal observations of steelhead redds and Rainbow Trout above this canyon (M. McHenry, personal observation).

Fish collection and tagging.—Fish surveys have been conducted annually in the summer of each year (mid-August and mid-September) in the East Twin and West Twin rivers since 2005. Fish were captured using a combination of single-pass and three-pass electroshocking with block netting. Approximately 37 sites were sampled each year from 2005 to 2014 within the lower 6.5 km of both rivers (Figure 1). All captured *O. mykiss* were anesthetized with tricaine methanesulfonate (MS-222) and measured for FL, and fish larger than 60 mm were implanted with a PIT tag (12.5 mm long, 2.1 mm in diameter: Prentice et al. 1990). Fish were placed in an instream tub containing water for 15 min for recovery before being released into the habitat unit from which they were captured. Length-frequency distributions of all in-river captures and recaptures of *O. mykiss* from annual summer sampling of the East Twin and West Twin rivers from 2003 to 2014 were used to develop length-based age classifications. Fish scale samples were collected and archived to validate age structure, although these samples have not yet been processed.

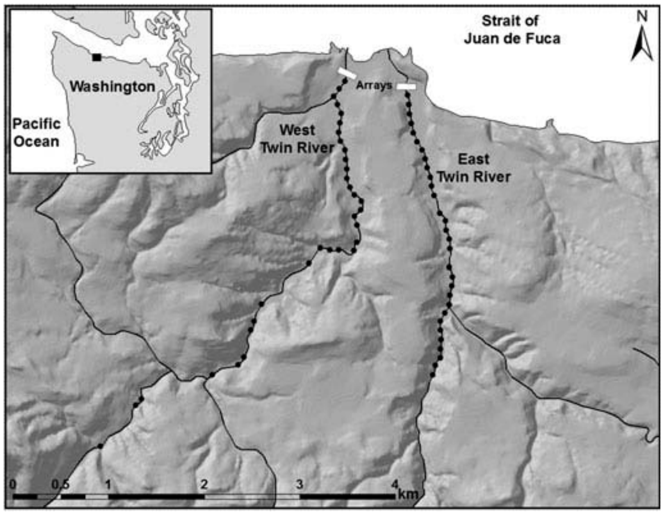

FIGURE 1. East Twin and West Twin rivers on the Olympic Peninsula, Washington, indicating sampling locations within each river (black circles) and stationary PIT tag reader arrays (white rectangles) near the mouths of both rivers.

Fish abundance within the lower 6.5 km of both rivers was estimated using S3 Infrastructure for Regular and Irregular Time Series package (Zeileis and Grothendieck 2005) in R statistical software (R Core Team 2015) to linearly interpolate between sampled reaches within each year. A weighted k-pass removal estimator (Carle and Strub 1978) implemented with the Fisheries Stock Analysis package (Ogle 2015) in R statistical software (R Core Team 2015) was used to estimate abundance at sites sampled with three-pass electroshocking. Regressions between estimated abundance from three-pass removals and captures from the first pass were used to expand single-pass captures to estimated abundance at sites that were only sampled with single-pass electrofishing. Migrant production estimates were derived from estimated summer abundances of age-0 juveniles that could be tagged (FL ≥ 60 mm) and proportions of tagged fish that were detected migrating within each age-at-migration group.

Fish detections and movement.—Tagged fish were detected at stationary multiplex PIT tag transceivers that were installed approximately 700 and 400 m from tidewater in the East Twin and West Twin rivers, respectively (Figure 1). These antenna arrays were maintained throughout the study, and detection data from August 2005 through February 2015 were used in this analysis. To maximize our probability of detecting PIT-tagged fish and to determine the direction of fish movements, each reader included two or three antenna arrays spaced approximately 3–5 m apart, and each array was composed of two or three antennas to span the stream under most flows (see Roni et al. 2012). High flows and occasional equipment failure rendered our PIT tag readers inoperable less than 0.6% of the study. This PIT tag reader configuration in streams with wetted widths of less than 15 m typically has an average detection efficiency greater than 95% (60–100%) over a range of flow conditions (Connolly et al. 2008; Pess et al. 2011; Roni et al. 2012). Detection efficiencies for our study were estimated by comparing detections at stationary arrays to captures of tagged fish at fence–weir smolt traps within 10 d of detection at the array. These smolt traps were located approximately 100 m downstream from the arrays and were operated by the Lower Elwha Klallam Tribe beginning in late April or early May through late May to mid-June of each year.

Fish that were not detected at the stationary arrays after being tagged were classified as undetected fish. For each tag that was detected at an array, we classified fish movement patterns based on age, seasonal timing, and direction of movement. Unpublished snorkel survey data from the lower river between the arrays and the mouth indicate juvenile fish detected moving downstream are migrating to the ocean and not residing in the river below the arrays (T. Bennett, unpublished data). Therefore, downstream movements through the array were classified as moving from the riverine to the marine environment, and upstream movements through the array were classified as movements from the marine to riverine environment. Juvenile ages at migration were based on estimated age at tagging, and ages were advanced by 1 year for each spring juveniles remained in the river. For example, a fish that was tagged in the summer at age 0 and moves downstream through the array in the fall would be classified as an age-0 fall migrant. A fish that was tagged at age 0 in the summer and remained in the river through the winter and was detected moving downstream in the spring would be classified as an age-1 spring migrant.

Returning adults were identified from individuals that were detected as juveniles moving downstream through the arrays, and the age of return to the river, season of return, repeat-spawning age, and seasonal timing were classified where clean detection histories provided directionality of movement through the arrays. Adult ages were based on age at tagging, age and seasonal timing of the migration to the ocean, number of summers spent in the ocean before returning to the river, and seasonal timing of return. For example, an age-2 spring migrant that was detected moving back into the river in the winter after two summers in the ocean would be classified as an age-2.2 adult having a total age of 4 years. This modified Koo aging system indicates the number of winters a juvenile spends in freshwater before the decimal and the number after the decimal indicating the number of summers spent in the ocean before returning as an adult (Koo 1962).

*Model development.—*We used logistic regression models to evaluate how a limited number of factors and continuous variables related to the probability of (1) a fish being detected as a migrant (migrated to the ocean verses undetected) and (2) migrants leaving at age 1 or older among fish that were detected as migrants (age-1 or older migrant versus age-0 migrant). We considered the river where fish were tagged (East Twin and West Twin rivers, as a factor), tagging year (2005–2011, as a factor), distance of tagging location from the river mouth (tenths of kilometers), fish length at tagging (mm), coefficient of variation for spring (February through May) river flow (m^3/s), and temperature (°C) for the year of emergence, and estimated adult steelhead escapement contributing to each cohort as predictors in the regression models. Model development was restricted to age-0 tagged fish from tagging years 2005–2011, as these represent complete cohorts given a maximum juvenile migrant age of 3 years and the temporal extent of our detection data.

We used the Multi-Model Inference package (Barton 2015) in R statistical software (R Core Team 2015) to develop all subsets modeling on standardized predictor variables and to select models using Akaike's information criterion adjusted for small sample sizes (AIC_c) (Burnham and Anderson 2002; Burnham et al. 2011). Models were selected with a $\Delta AIC_c < 7$ based on the premise that models within this range have some support and should rarely be dismissed (Burnham et al. 2011). Selected models were averaged based on calculated model weights, and standardized coefficient plots were produced from the averaged model to compare the effects of each parameter. Standardized coefficients with larger positive or negative values were considered to have a stronger relationship with the response, while those with smaller values were considered to have a weaker relationship. Standardized coefficients with 95% confidence intervals that spanned both negative and positive values were interpreted as factors for which we had low confidence in the estimated direction of the effect. We used the Companion to Applied Regression package (Fox and Weisberg 2011) in R statistical software (R Core Team 2015) to evaluate collinearity using dimension-adjusted generalized variable inflation factors. Pearson residual plots were used to graphically evaluate temporal and spatial autocorrelation in the residuals.

RESULTS

Fish Surveys

A total of 45,984 *O. mykiss* were captured from a combined total of 642 sampled habitat units in East Twin and West Twin rivers from 2005 to 2014. Approximately 44% of the habitat units were sampled using three-pass electrofishing, while the rest were sampled with single-pass electrofishing. Estimated probabilities of capture from three-pass sampled sites ranged from 0.26 to 0.90, with an average of 0.43 and SD of 0.10. Total captures from the first pass were significantly related to both the sum of captures from all three passes (linear regression: slope = 1.6; intercept = 4.5; F = 2,066; df = 1, 245; $P <$ 0.001; adjusted R^2 = 0.89) and the removal-estimated total abundance (linear regression: slope = 1.5; intercept = 2.5; F = 5,584; df = 1, 245; P < 0.001; adjusted R^2 = 0.96). Average FLs and average maximum FL by habitat unit were 81.9 ± 0.2 mm (mean ± SE) and 127.4 ± 1.6 mm, respectively, for the first pass, 80.2 ± 0.4 mm and 109.0 ± 2.0 mm, respectively, for the second pass, and 80.2 ± 0.5 mm and 95.8 ± 1.9 mm, respectively, for the third pass.

Three size-class modes were detected from length-frequency distributions of captured *O. mykiss*. The tails of the two primary length-frequency modes for all captured fish intersected at 86 mm (Figure 2), and this cutoff was used to classify juveniles with FLs of 86 mm and less as age 0. Recaptures of fish that were PIT-tagged in previous years were used to develop length-based classifications for age-1 and age-2 fish given that additional modes were not apparent in the length-frequency distribution of all captured fish above 86 mm (Figure 2). The intersection of length-frequency distributions for fish tagged at age 0 and age 1 and captured in the year after tagging was graphically estimated at 132 mm (Figure 2); this was used to

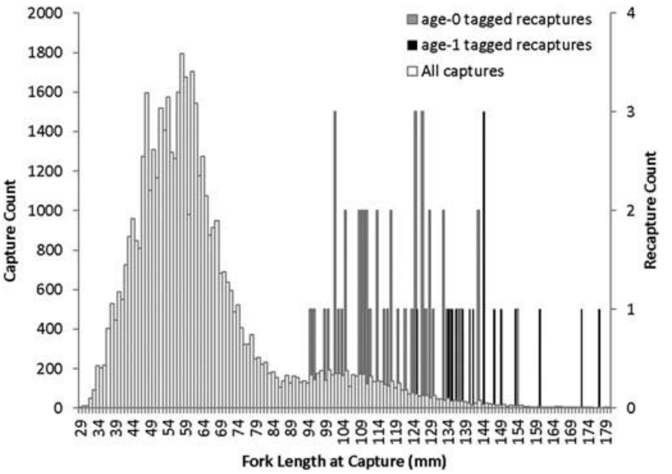

FIGURE 2. Length frequency distribution of *O. mykiss* captured during summer tagging surveys in East Twin and West Twin rivers. Counts by FL are shown for all fish that were captured during annual summer tagging surveys from 2005 to 2014 (all captures) and for fish that were tagged at age 0 or age 1 that were recaptured in the year after tagging (age-0 tagged recaptures and age-1 tagged recaptures, respectively). Fork lengths for recaptures are shown as the length at the time of recapture.

classify fish with FLs of 87–132 mm as age 1 and fish over 132 mm as age 2+. With these length-based age classifications, 86.5% (39,791 of 45,984) were age 0, 12.0% (5,533 of 45,984) were age 1, and 1.4% (660 of 45,984) were age 2+ from all captures pooled among years and rivers. Estimated summer abundance of age-0 *O. mykiss* in the lower 6.5 km of both rivers ranged from approximately 10,000 to 25,500 from 2005 to 2014 (Figure 3). Abundance of age-0 juveniles generally decreased from 2005 to 2008 in both rivers and then increased through 2014, with a spike in abundance in East Twin River from 2009 to 2010 (Figure 3). Average escapement from Washington Department of Fish and Wildlife surveys was 96 adults prior to our study period (1995–2004), while the average escapement was 51 adults during our study from 2005 to 2014 (Figure 3).

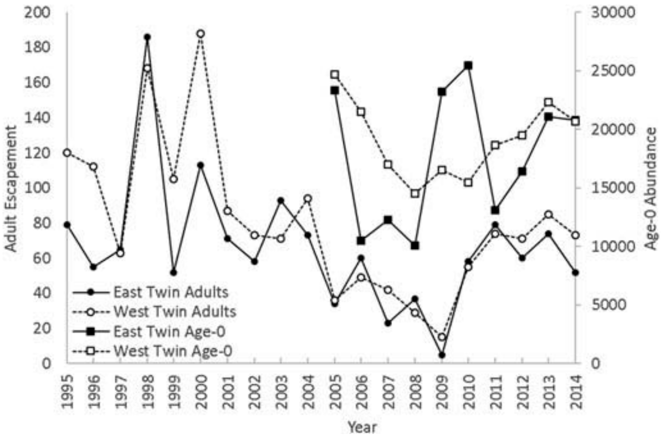

FIGURE 3. Estimated adult steelhead escapement from spring surveys of index reaches from river mouth to rkm 4.7 in West Twin River and rkm 4.2 in East Twin River provided by Washington Department of Fish and Wildlife, and estimated total age-0 juvenile *O. mykiss* summer abundance in the lower 6.5 km of East Twin and West Twin rivers by river and year.

Juvenile Detections

From all captured *O. mykiss*, a total of 20,259 were implanted with PIT tags in West Twin River (48%) and East Twin River (52%) from 2005 to 2014 (Table 1). Among these tagged fish, 69.6% were age 0, 27.0% were age 1, and 3.4% were age 2+ (Table 1). Detections of tagged fish captured at smolt traps within 10 d before capture indicated that array efficiency ranged from 52% to 82%, with an average of 75% and SD of 9%. River flows were 0.5 to 1.4 m^3/s, with an average of 1.0 m^3/s and SD of 0.3 m^3/s, from late April through mid-June when traps were deployed. The upper limit of flows for which efficiency could be estimated represented a flood exceedance probability of 0.34 based on analysis of daily river flows from 2005 to 2015 using Indicators of Hydrologic Alteration software (Nature Conservancy 2009). Detection efficiency outside of the period of time in which smolt traps were deployed could not be estimated.

Among fish that were detected, we observed seven juvenile steelhead life histories with migrations at age 0 to age 3 and distinct migration peaks occurring in the fall (October–December peak, August–February range) and spring (May–July peak, February–August range) among age-groups (Figure 4). Assuming a maximum migrant age of 3 years and a detection period spanning from the summer of 2005 through the winter of 2014, we could detect the full range of migrant ages for age-0 tagged fish from tagging years 2005 to 2011, age-1 tagged fish from tagging years 2005 to 2012, and age-2 tagged fish from tagging years 2005 to 2013. These complete cohorts were used to calculate percentages given that the full range of migrant ages could be accounted for from each cohort. From these complete cohorts, we detected 21.7% of age-0 tagged fish, 30.0% of age-1 tagged fish, and 37.3% of age-2 tagged fish as migrants (Table 2). Among complete cohorts of age-0 tagged fish, 58.9% left as age-0 fall migrants, 22.3% as age-1 spring migrants, 9.9% as age-1 fall migrants, 6.1% as age-2 spring migrants, 2.1% as age-2 fall migrants, 0.5% as age-3 spring migrants, and 0.1% as age-3 fall migrants (Table 2).

We detected two additional life histories in which juveniles moved into the ocean prior to their final migration to the ocean to mature. The first of these was revealed by detections of juveniles leaving the river in the summer at age 1, returning in the late fall, and then migrating back out to the ocean as an age-2 spring migrant the following spring after overwintering in the river. This was observed for 0.2% of age-0 tagged fish that were detected as migrants from 2005–2011 tagging years. The second was revealed through detections of juveniles moving between rivers, and this was observed for approximately 0.8% of detected migrants from age-0 tagged fish from 2005–2011 (Table 3). Significantly more juveniles moved from East

TABLE 1. Tagged *O. mykiss* counts by tagging year, river, age at tagging (age-0 fish 86 mm FL and smaller, age-1 fish from 87 to 132 mm FL, and age-2+ fish greater than 132 mm FL), and capture location in river kilometers from the mouths of East Twin and West Twin rivers.

		West Twin River (rkm from mouth)								East Twin River (rkm from mouth)							
Year	Age (years)	0–1	1–2	2–3	3–4	4–5	5–6	6–7	Total	0–1	1–2	2–3	3–4	4–5	5–6	6–7	Total
2005	0	286	497	88	78	33	22	9	1,013	190	230	342	17	36	0	1	816
	1	163	177	74	38	23	32	5	512	119	159	131	17	12	8	1	447
	2+	12	13	0	3	7	4	2	41	3	13	23	1	10	1	1	52
2006	0	336	402	32	41	39	92	35	977	40	337	149	242	71	1	0	840
	1	65	124	12	23	8	26	14	272	22	106	109	114	33	2	0	386
	2+	5	11	4	3	6	1	3	33	0	8	12	17	0	1	0	38
2007	0	167	792	131	52	41	78	55	1,316	406	728	463	33	25	0	0	1,655
	1	88	242	74	20	10	40	4	478	103	179	91	9	2	0	0	384
	2+	6	13	12	2	3	3	0	39	13	27	20	1	5	2	0	68
2008	0	230	253	51	52	28	21	0	635	51	321	413	32	0	1	0	818
	1	116	212	55	27	32	93	9	544	34	174	162	8	21	16	0	415
	2+	15	23	7	6	2	12	3	68	0	16	15	2	9	0	0	42
2009	0	191	348	47	81	76	141	32	916	572	435	61	5	24	0	0	1,097
	1	52	66	11	14	11	17	1	172	115	127	21	3	2	2	0	270
	2+	10	10	0	6	5	11	2	44	12	16	2	0	1	2	0	33
2010	0	231	39	98	29	68	89	12	566	150	186	181	24	18	5	0	564
	1	100	7	14	12	17	26	8	184	24	107	67	16	13	1	0	228
	2+	9	0	1	3	7	8	2	30	2	7	7	3	5	0	0	24
2011	0	104	77	47	30	58	44	13	373	89	146	151	46	0	17	2	451
	1	103	45	25	17	27	22	3	242	63	55	49	9	12	3	0	191
	2+	12	2	4	1	2	4	6	31	5	11	21	0	7	4	0	48
2012	0	124	52	50	76	34	31	1	368	128	202	98	36	0	0	1	465
	1	43	11	6	23	7	51	3	144	48	50	16	3	2	4	3	126
	2+	1	0	1	2	3	6	5	18	6	6	2	0	7	0	0	21
2013	0	42	43	44	53	50	65	15	312	51	123	90	10	28	6	0	308
	1	42	13	18	19	25	38	9	164	50	34	28	2	3	1	0	118
	2+	4	1	1	1	1	1	4	13	4	4	0	0	3	0	0	11
2014	0	40	7	18	62	36	86	21	270	131	132	68	0	7	3	1	342
	1	30	10	1	19	9	37	8	114	29	19	10	5	18	2	0	83
	2+	2	1	0	1	3	2	5	14	4	1	3	0	7	0	0	15

Twin River to West Twin River (75 of 6,241) compared with fish that moved from West Twin River to East Twin River (27 of 5,796) (two-sample chi-square = 18.503, df = 1, $P < 0.001$). Approximately 53% of these movements occurred in the fall while 22% occurred in the winter, 20% in the spring, and 5% in the summer. Juveniles moved between rivers at age 0 to age 2, with 48% moving at age 0, 44% at age 1, and 8% at age 2 (Table 3). We also observed fish moving back to the river in which they were tagged after moving into the adjacent river, and 14.8% (4 of 27) of the fish that left West Twin River returned to West Twin River after initially moving into East Twin River. In contrast, we only detected one fish out of the 75 moving back to East Twin River after entering West Twin River, and this fish subsequently moved back to West Twin River. The median time between detections at each river mouth was 65.8 h and the minimum was 1.9 h, which represent a median travel speed of 0.01 m/s and a maximum speed of 0.22 m/s assuming a least-distance travel path of approximately 500 m between arrays.

Adult Detections

We observed 13 life histories from 37 adult steelhead that were detected from all tagged fish when all years and rivers were pooled. Among these adults, we observed variations in age and season of juvenile migration, years spent in the ocean, season of return to the river, and repeat spawning (Figure 5). Adults were only detected with juveniles having migration ages of 1 year and older, with no adults having left the river as an age-0 migrant. The number of years spent in the ocean varied by age at juvenile migration, with age-1 migrants returning after 3 years in the ocean (age 1.3), age-2 migrants spending 1 to 3 years in the ocean (ages 2.1, 2.2, and 2.3), and

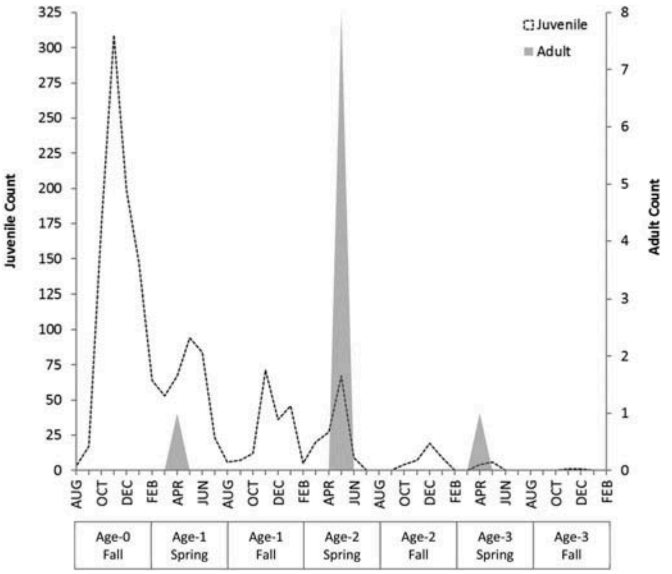

FIGURE 4. Counts of juvenile *O. mykiss* migrants by month of migration and counts of returning adults produced from each month and age-migrant group with river and tagging year pooled. Only age-0 tagged fish from tagging years 2005–2008 were included in this plot, as these are the only cohorts from which complete adult migration windows could be reconstructed assuming a maximum total adult age of 6 years. Juvenile migrant life history types, as determined from peaks in migrant timings, are labeled below the months showing age (age 0, 1, 2, or 3 years) and season (fall or spring) at juvenile migration. Adult counts are overlaid on the secondary axis showing the age and month at which the adult left the river as a juvenile.

age-3 migrants returning after 1 to 3 years in the ocean (ages 3.1, 3.2, and 3.3) (Figure 5). The maximum observed total adult age was 6 years, and adults returned from late fall to spring after 1 to 3 years in the ocean. Repeat spawning was observed among adults that left the river as age-2 spring migrants; the first return occurred after 1 or 2 years in the ocean and the second return occurred 1 year after the first return (Figure 5).

Assuming a maximum adult age of 6 years, we reconstructed complete cohorts for age-0 tagged steelhead from tagging years 2005–2008. Ten adults were detected from this subset, and these adults represented 8 of 13 life history variations observed among all detected adults (Figure 5). All 10 of the adults in this subset were spring migrants, of which seven left at age 2, one left at age 1, and one at age 3 (Figure 4). Among age-2 spring migrants, five spent two summers in the ocean before returning to the river while one returned after one summer and another returned after three summers (Figure 5). Age-1 and age-3 spring migrants spent 3 and 2 summers in the ocean, respectively, before returning to the river (Figure 5). Repeat spawning was observed in two age-2 spring migrants, of which one spent only one summer in the ocean and the other spent two summers in the ocean before the first return (Figure 5).

From the 10 adults that represented complete cohorts, smolt-to-adult return (SAR) rates increased with increasing age at juvenile migration. The SAR rates were 0 (0 of 848) for age-0 migrants, 0.0035 (2 of 564) for age-1 migrants, 0.0422 (7 of 166) for age-2 migrants, and 0.0833 (1 of 12) for age-3 migrants (Figure 4). Sample sizes of these proportions indicate that true SAR rates would be between 0 and 0.0043 for age-0 migrants, 0.0004 and 0.0127 for age-1 migrants, 0.0164 and 0.0816 for age-2 migrants, and 0.0019 and 0.3603 for age-3 migrants based on 95% Pearson–Klopper binomial CIs using the Binomial Confidence Intervals For Several Parameterizations package (Dorai-Raj 2014) in R statistical software (R Core Team 2015).

Factors Affecting Juvenile Migration

All considered factors were included in the selected suite of models to describe the probability of an individual fish being detected as migrant versus not being detected, and the probability of a migrant leaving the river at age 1 or older as opposed to leaving as an age-0 migrant (Table 4). Dimension-adjusted generalized variable inflation factors were less than 10 for all factors, indicating that inflation of estimated coefficients from collinearity was minimal (Fox and Weisberg 2011). Temporal autocorrelation was not apparent from graphical analysis of Pearson residuals from tagging year. However, spatial autocorrelation was apparent from Pearson residual plots of residuals and distance from the river mouth, with Pearson residuals increasing with increasing distance upriver. Tagging year, length at tagging, and distance from the river mouth were included in all selected models for both model sets (Table 4). With the exception of tagging year 2009, standardized coefficients from averaged models indicated that there was an increasing trend in the probability of an individual fish being detected as a migrant with increasing tagging year, while the probability of those migrants leaving as age-1 or older migrants decreased with increasing tagging year (Figure 6). Standardized coefficients from the averaged models also indicated that the probability of being detected as a migrant decreased with increasing distance from the river mouth (Figure 6). In contrast, fish that were detected as migrants had a higher probability of migrating at age 1 or older with increasing distance from the river mouth (Figure 6). Length at tagging also had an inverse effect on the probability of a fish being detected as a migrant and the probability of those that were detected as migrants leaving at age 1 or older (Figure 6). The probability of a fish being detected as a migrant increased with increasing length at tagging, while the probability of migrating at age 1 and older decreased with increasing size at tagging among those fish that were detected as migrants.

While the river in which fish were tagged was included in all selected models describing the probability of migrants leaving at age 1 and older, river was only included in a subset of models describing the probability of a tagged fish being detected as a migrant (Table 4). Migrants from West Twin River had a higher probability of leaving at age 1 and older than did migrants from East Twin River, while the effect of river on the probability of a

TABLE 2. Proportions of tagged *O. mykiss* in East Twin River and West Twin River, tagging year, and age at tagging that were classified as undetected (% not detected), age-0 migrants (% age 0), and age-1 and older (% age 1+) migrants relative to the total number of fish tagged at each age-class. NA denotes cohorts that could not be completely accounted for assuming a maximum migrant age of 3 years.

	Age-0 tagged fish				Age-1 tagged fish			Age-2 tagged fish		
Tag year	Number tagged	% not detected	% age-0 migrant	% age-1+ migrant	Number tagged	% not detected	% age-1+ migrant	Number tagged	% not detected	% age-1+ migrant
					East Twin River					
2005	816	83	7	9	447	70	30	52	65	35
2006	840	86	7	7	386	75	25	38	66	34
2007	1,655	73	16	11	384	64	36	68	57	43
2008	818	80	14	6	415	68	32	42	69	31
2009	1,097	65	24	11	270	57	43	33	64	36
2010	564	77	17	6	228	73	27	24	50	50
2011	451	78	16	5	191	85	15	48	79	21
2012	465	NA	NA	NA	126	69	31	21	67	33
2013	308	NA	NA	NA	118	NA	NA	11	82	18
					West Twin River					
2005	1,013	89	4	8	512	84	16	41	76	24
2006	977	81	8	12	272	68	32	33	58	42
2007	1,316	80	10	10	478	67	33	39	62	38
2008	635	74	19	7	544	72	28	68	57	43
2009	916	79	9	11	172	56	44	44	52	48
2010	566	75	18	7	184	57	43	30	60	40
2011	373	81	14	5	242	71	29	31	65	35
2012	368	NA	NA	NA	144	69	31	18	56	44
2013	312	NA	NA	NA	164	NA	NA	13	38	62

fish being detected as a migrant was unclear (Figure 6). The CVs (SD/mean) in spring river flow and temperature were included in a subset of selected models for both model sets (Table 4). Increasing variation in spring river temperatures increased the probability of a fish being detected as a migrant, while the effect on the probability of migrating at age 1 and older was unclear (Figure 6). Increasing variation in spring river flows decreased the probability of migrants leaving at age 1 and older, while the effect on the probability of fish being detected as a migrant was unclear (Figure 6).

TABLE 3. Numbers of *O. mykiss* detected moving between rivers from age-0 tagged fish in 2005 through 2011 tagging years by the age at which these migrations occurred. East to West Twin indicates movement of a fish tagged in East Twin River to West Twin River, and West to East Twin indicates movement of a fish tagged in West Twin River to East Twin River.

Age at migration (years)	East to West Twin count	West to East Twin count	Total count
0	39	10	49
1	33	12	45
2	3	5	8
Total	75	27	102

Contributing-adult steelhead escapement (i.e., the escapement of the contributing adults) was included in all selected models describing the probability of a fish being detected as a migrant but was only included in a subset of the selected models describing the probability of migrants leaving at age 1 and older (Table 4). Contributing-adult escapement in the spring before tagging was negatively related to the probability of an age-0 tagged fish being detected as a migrant (Figure 6), and the probability of an individual fish being detected as a migrant decreased with increasing escapement of contributing adults. Among the migrants, contributing-adult escapement was positively related to the probability of a migrant leaving at age 1 and older (Figure 6), and increasing adult escapement increased the probability that a migrant would leave at age 1 and older as opposed to age 0.

Contributing-adult escapement was not related to estimated abundance of age-0 juveniles in the summer in East Twin River (linear regression: slope = −33.6; intercept = 19,241; $F = 0.15$; df = 1, 8; $P = 0.71$; adjusted $R^2 \approx 0.0$) and West Twin River (linear regression: slope = 53.9; intercept = 16,235; $F = 1.31$; df = 1, 8; $P = 0.28$; adjusted $R^2 = 0.03$) (Figure 7A). However, the average length of age-0 juveniles in the summer was negatively related to contributing-adult escapement (Figure 7B) in East Twin River (linear regression: slope = −0.17; intercept = 64.5;

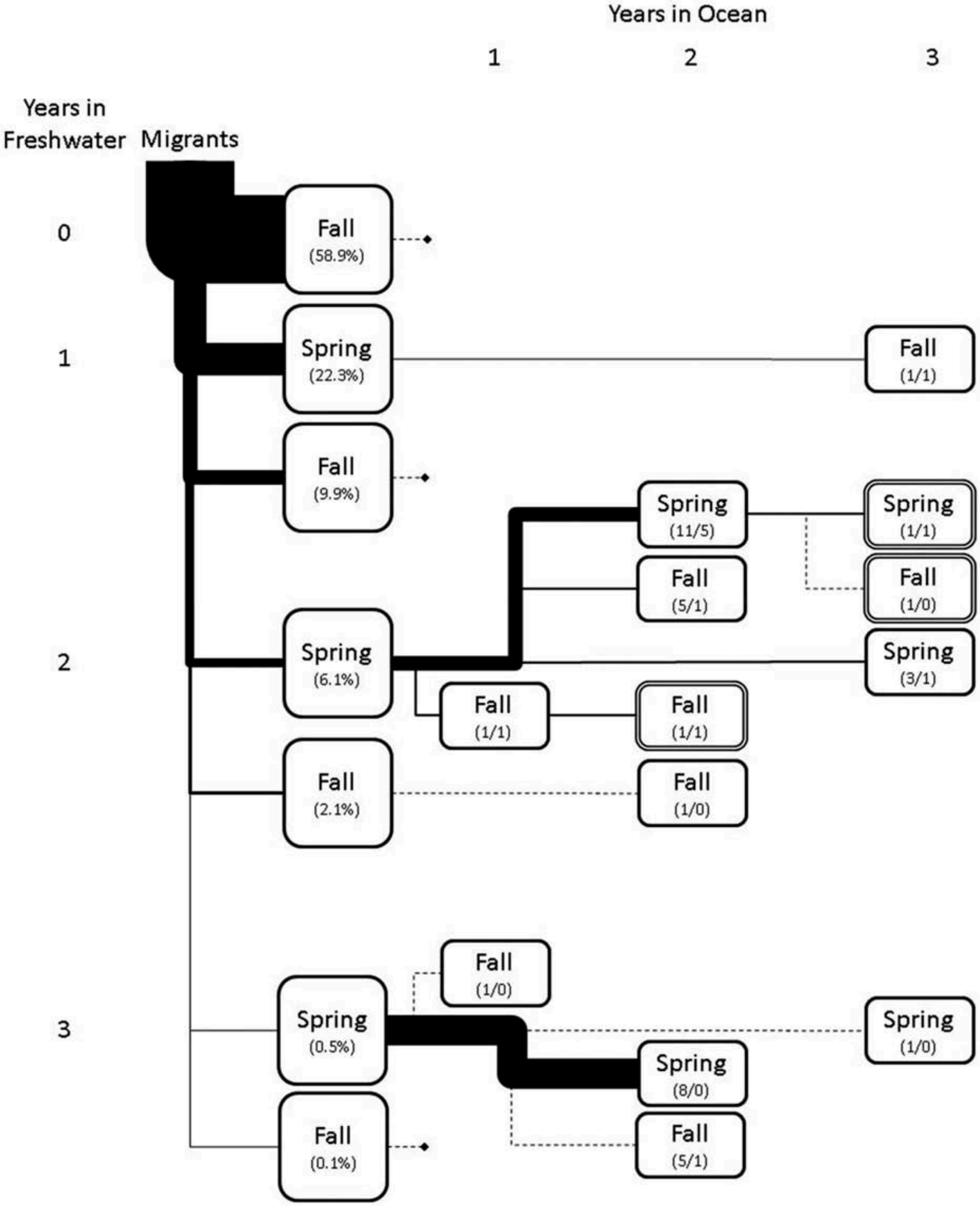

FIGURE 5. Flow chart of *O. mykiss* life history types observed in East Twin and West Twin rivers with years spent in freshwater (number of winters) along the *y*-axis and years spent in the ocean (number of summers) along the *x*-axis. The thickness of the solid lines for juvenile migrants is scaled to the percentage of migrants with that age and seasonal migration from age-0 tagged fish in tagging years 2005–2011, and the percentages are provided within each box of juvenile migrant type. Solid lines from juvenile migrant groups are scaled to calculated smolt-to-adult return (SAR) rates for adults observed from tagging years 2005 to 2008 for which complete cohorts could be reconstructed. Dashed lines indicate adult life histories that were observed but were not part of the complete cohorts. Dashed lines that end without an adult return timing represent juvenile migration timings for which we have not observed any returning adults. Repeat-spawning life histories are denoted with double borders. The counts of adults observed within each life history group are provided for the full data set (first number) and among the complete cohorts (second number) that were used to calculate SAR rates. Repeat spawners are included in the counts of the preceding life history type. “Half-pounder” and juvenile *O. mykiss* movements between rivers are not shown but represent two additional life histories expressed in these rivers.

TABLE 4. Selected logistic regression models with a $\Delta\text{AIC}_c < 7$ with standardized coefficients for the probability of an age-0 tagged *O. mykiss* from 2005–2011 tagging years being detected as a migrant, and the probability of those migrants migrating at age 1 or older. Coefficients for tagging river and year are relative to East Twin River and tagging year 2005, respectively. The CVs in river flow and temperatures for the spring of emergence (CV flow and CV temp, respectively), adult escapement contributing to the cohort of juveniles (Escapement), length of a fish at tagging (FL), and distance from the river mouth of the capture location (Distance) are presented as standardized coefficients for each model in which the parameters were included. No value present indicates that the parameter was not included in the model. The model df, log likelihood (LogLik), Akaike's information criterion adjusted for small sample sizes (AIC_c), change in AIC_c from the model with the lowest AIC_c score (Delta), and model weight based on the delta AIC_c score (Model weight) are also provided for each model.

River (West Twin)	Year (2006)	Year (2007)	Year (2008)	Year (2009)	Year (2010)	Year (2011)	CV flow	CV temp	Escapement	FL	Distance	df	logLik	AIC_c	Delta	Model weight
Probability of being detected as a migrant																
	0.495	0.627	0.906	0.076	1.831	1.941	0.188	0.477	–0.859	0.382	–1.205	12	–5,865.53	11,755.10	0.00	0.34
	0.509	0.710	0.835	0.195	1.595	1.591		0.427	–0.596	0.379	–1.221	11	–5,866.62	11,755.30	0.18	0.31
0.076	0.473	0.769	0.902	0.078	1.795	1.742		0.592	–0.646	0.380	–1.217	12	–5,866.15	11,756.30	1.25	0.18
0.024	0.485	0.655	0.920	0.051	1.870	1.953	0.169	0.525	–0.848	0.382	–1.206	13	–5,865.49	11,757.00	1.93	0.13
–0.137	0.640	0.421	0.730	0.327	1.377	1.729	0.255		–0.904	0.382	–1.202	12	–5,868.13	11,760.30	5.20	0.03
–0.086	0.655	0.560	0.663	0.430	1.154	1.345			–0.589	0.379	–1.219	11	–5,869.75	11,761.50	6.43	0.01
Probability of a migrant leaving at age 1 or older																
0.538	–0.436	–0.252	–1.680	–0.458	–2.316	–2.952	–0.668		1.106	–0.363	0.378	12	–1,658.24	3,340.60	0.00	0.47
0652	–0.543	–0.072	–1.525	–0.653	–1.938	–2.758	–0.723	0.411	1.143	–0.364	0.378	13	–1,657.85	3,341.80	1.24	0.25
0.435	–0.353	–0.620	–1.495	–0.856	–1.571	–1.668				–0.343	0.434	10	–1,661.99	3,344.10	3.47	0.08
0.515	–0.221	–0.541	–1.580	–0961	–1.628	–1.721	–0.219			–0.352	0.437	11	–1,661.13	3,344.40	3.75	0.07
0.411	–0.435	–0.599	–1.482	–0.732	–1.668	–1.865			0.189	–0.342	0.423	11	–1,661.80	3,345.70	5.10	0.04
0.598	–0.296	–0.415	–1.463	–1.120	–1.331	–1.534	–0.248	0.306		–0.352	0.439	12	–1,660.91	3,345.90	5.33	0.03
0.467	–0.393	–0.571	–1.440	–0.919	–1.438	–1.588		0.133		–0.343	0.434	11	–1,661.95	3,346.00	5.39	0.03

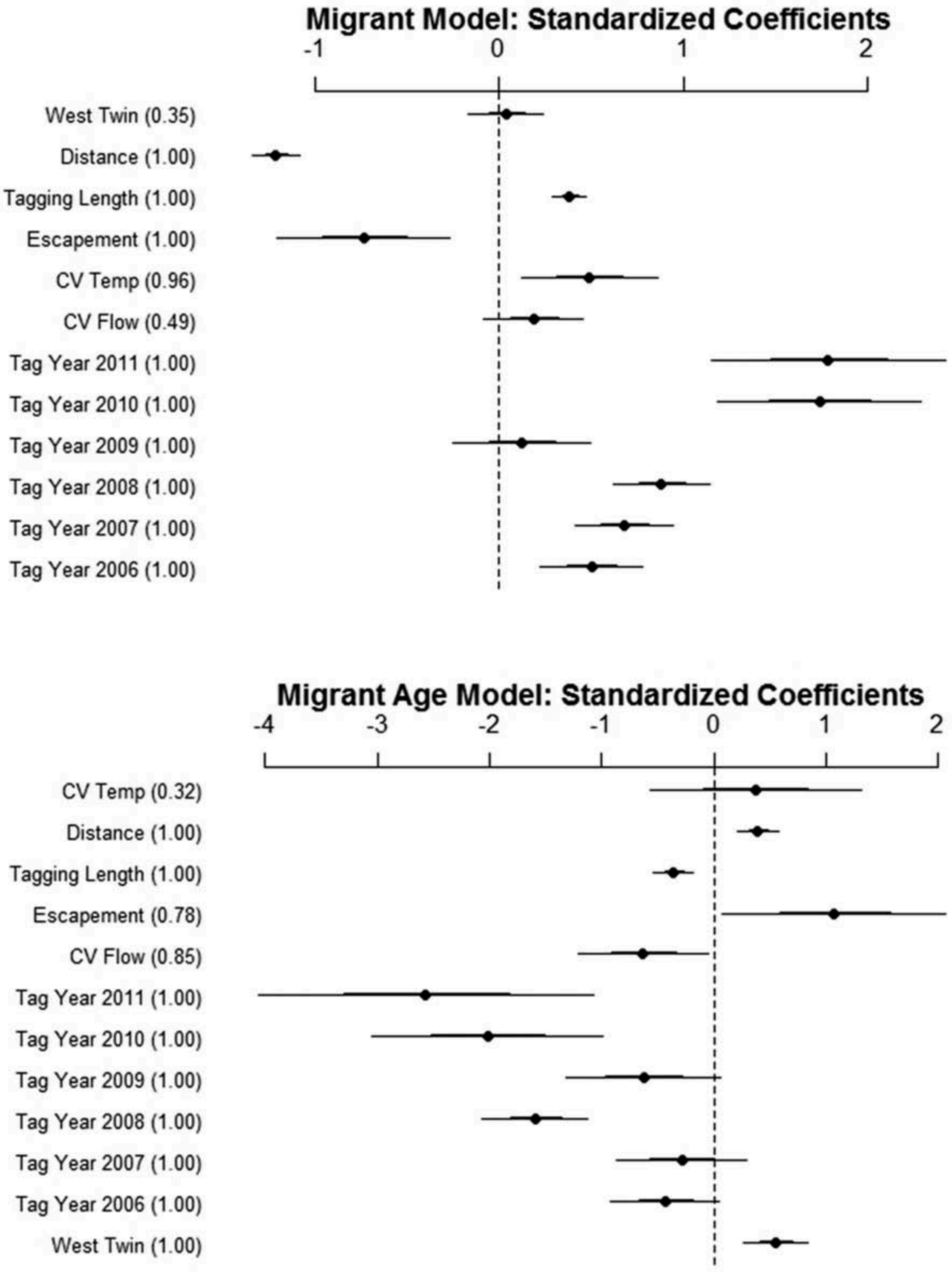

FIGURE 6. Standardized coefficients from model averaging of AIC$_c$-selected models for the probability of being detected as a migrant (top panel) and probability of migrating at age 1 or older (bottom panel) among fish that were detected as migrants. Juvenile *O. mykiss* tagged at age 0 during 2005–2011 summer tagging surveys were used to develop all models. Points represent the standardized coefficient estimate from the averaged model. Thick bars represent ±1 SD and a 68% CI while the thin bars represent ±2 SDs and a 95% CI. The importance for each factor is shown in parentheses after each factor, with a value of 1.00 indicating that the parameter was included in all selected models. Importance values for tagging year and river are reported for the categorical factor itself and not for each level of the factor. See Table 4 for models included within the averaged model.

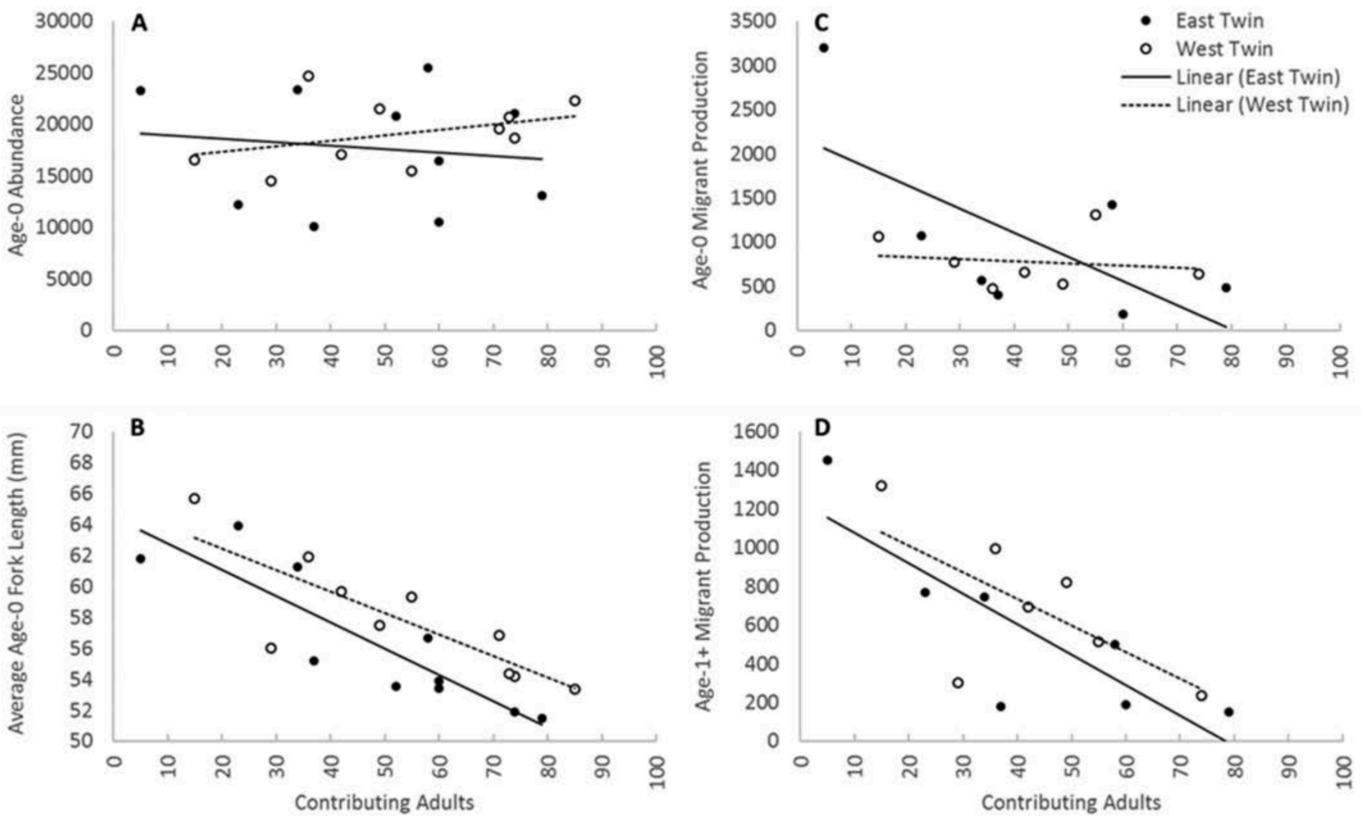

FIGURE 7. Estimated (**A**) summer abundance and (**B**) average FL of age-0 juvenile *O. mykiss* in the lower 6.5 km of both rivers relative to the estimated escapement of adult steelhead in the spring prior to the summer tagging survey. Estimated (**C**) age-0 migrant production and (**D**) the production of age-1 and older (age 1+) migrants are also shown relative to the adult steelhead escapement that contributed to each cohort. East Twin River is represented by filled circles with solid linear regression lines, and West Twin River is represented by open circles and dashed linear regression lines.

$F = 27.79$; df = 1, 8; $P = 0.001$; adjusted $R^2 = 0.75$) and West Twin River (linear regression: slope = −0.14; intercept = 65.3; $F = 16.5$; df = 1, 8; $P = 0.004$; adjusted $R^2 = 0.63$). Contributing-adult escapement was also related to estimated production of age-0 and age-1 and older migrants (Figure 7C, D, respectively), but the relationship strength was different among rivers. In East Twin River, the production of age-0 migrants was negatively related to contributing-adult escapement, but the relationship was not significant (linear regression: slope = −27.4; intercept = 2,204; $F = 3.88$; df = 1, 5; $P = 0.106$; adjusted $R^2 = 0.32$). Production of age-1 and older migrants had a significant negative relationship with contributing-adult escapement in East Twin River (linear regression: slope = −15.7; intercept = 1,234; $F = 11.89$; df = 1, 8; $P = 0.018$; adjusted $R^2 = 0.65$). In West Twin River, production of age-0 migrants was not related to contributing-adult escapement (linear regression: slope = −2.5; intercept = 884; $F = 0.12$; df = 1, 5; $P = 0.742$; adjusted $R^2 \approx 0$). Production of age-1 migrants in West Twin River was negatively related to contributing-adult escapement, but the relationship was not significant (linear regression: slope = −13.7; intercept = 1,284; $F = 4.16$; df = 1, 5; $P = 0.097$; adjusted $R^2 = 0.34$).

DISCUSSION

We detected at least 18 different steelhead life histories in East Twin and West Twin rivers, with variations in age and season of juvenile migrations, juvenile use of the ocean, years spent in the ocean, season of adult return, and iteroparity. More steelhead life history variations could be present among East Twin River and West Twin River steelhead given that adults were not detected from all juvenile migrant groups and our adult sample size was relatively low. In addition, other studies have documented more diversity among steelhead in other systems (e.g., Moore et al. 2014), and expression of life histories can change over time (e.g., Tattam et al. 2013). While continued monitoring may reveal other life histories, we observed several interesting patterns among East Twin River and West Twin River steelhead.

One unexpected finding was revealed through detections of juvenile use of the ocean as summer rearing habitat and as a corridor to move between rivers. Summer movements among a small minority of age-1 juveniles into the ocean were followed by a fall return to freshwater, overwintering in the river, and subsequent migration to the ocean as age-2 spring migrants. This pattern is consistent with the “half-pounder” life history described in coastal California and Oregon (Snyder 1925; Kesner and Barnhart 1972; Everest 1973), although few accounts of this life history have been documented in coastal Washington rivers and the benefits of this life history are not well understood (Hodge et al. 2014). We also observed juveniles moving between the two rivers at a range of ages and seasons, and the relatively short times between detections at each river suggest that the ocean was being used as a corridor to move between rivers as opposed to an intermediate rearing habitat like half-pounder steelhead (Hodge et al. 2014). Movements between rivers also suggest a directional preference, with significantly more juveniles moving from East Twin River to West Twin River and higher site fidelity among fish that moved to West Twin River. These movements are suggestive of individuals seeking alternative freshwater rearing habitat, and this behavior could contribute to range expansion and spread risk across spatial scales (Anderson and Quinn 2007; Koski 2009; Pess et al. 2012; Anderson et al. 2013), although our results do not reveal causes or benefits of this strategy.

We also observed interesting patterns within the more common array of juvenile steelhead life histories. While the majority of migrants left after their first summer as age-0 fall migrants, we only detected adults that had been age-1 and older migrants and most of those had been age-2 spring migrants. Smolt-to-adult return rates also increased with increasing age at migration, and this agrees with the premise that older and larger migrants have higher ocean survival rates (Ward and Slaney 1988; Evans et al. 2014). While our relatively low sample size of adults could account for the lack of adults from age-0 fall migrants, the lack of a relationship between the predominant and most productive juvenile migration strategies is particularly interesting. Expression of fall migration at age 0 may be related to previous selective pressures, and it is possible that maintenance of this migration strategy benefits population stability over time given that balances between ocean and freshwater survival can change (Copeland and Venditti 2009; Carlson and Satterthwaite 2011; Kendall et al. 2014; Moore et al. 2014). Continued monitoring and detection of more adults in East Twin and West Twin rivers could improve interpretations of how fall migrations of age-0 fish benefit steelhead in these systems.

Contributing-adult escapement and summer body size were strong factors influencing juvenile steelhead migration patterns in East Twin and West Twin rivers. Escapement was negatively related to average young of the year body size and estimated production of migrants from each cohort. Corresponding with these patterns, the probability of individuals being detected as migrants decreased with increasing escapement. Density-dependent growth could explain these patterns whereby increasing resource competition decreases early growth with increasing emergent fry densities corresponding with increasing adult escapement (Copeland and Venditti 2009; Myrvold and Kennedy 2015). Slower-growing individuals would require longer rearing times to attain sufficient body size to trigger migration, and this may increase exposure to freshwater mortality and size-selective mortality (Beakes et al. 2010; McMillan et al. 2011; Tattam et al. 2013; Evans et al. 2014; Kendall et al. 2014; Thompson and Beauchamp 2014). The negative relationship between production of age-1 and older migrants with adult escapement also suggests that poor overwinter survival and density-dependent growth may limit smolt productivity in East Twin and West Twin rivers (e.g., Connolly and Petersen 2003; Copeland and Venditti 2009). However, young of the year abundance was not related to contributing-adult escapement as might be expected if these patterns were driven by density-dependent processes. Given that late summer abundance could represent a thinned population (e.g., Dunham and Vinyard 1997), additional surveys to determine early summer emergent fry densities could improve our understanding of density-dependent processes in East Twin River and West Twin River steelhead.

Our results also suggest that there are strong spatial and temporal gradients influencing juvenile steelhead migration patterns. Spatially, the probability of migrants leaving at age 1 and older was greater in West Twin River than in East Twin River. In addition, the probability of fish being detected as migrants decreased with increasing capture distance upriver. These patterns could be the result of unmeasured differences in rearing habitat between rivers, spatial gradients in physical habitat or resources, decreasing fish abundance with increasing distance upriver observed in both rivers, or increased expression of residency with increasing distance upriver (e.g., McMillan et al. 2007). Temporally, the probability of migrants being detected generally increased with increasing tagging year, while these migrants were less likely to leave at age 1 and older with increasing tagging year. This suggests that the production of age-0 migrants relative to age-1 and older migrants is increasing over time, and this trend is particularly interesting within the context of recent declines in steelhead escapement and our observation that adults were only produced from age-1 and older migrants. Recent escapement estimates indicate that adult returns have generally been increasing since a low return in 2009, which appears to be inconsistent with conclusions that the production of age-1 and older migrants is declining over time given that the cohorts in our study would have at least partially contributed to adult returns after 2009. Adult straying from other systems, incomplete cohort representation, small adult sample sizes, or differences between tagged and untagged populations could account for this apparent inconsistency, although continued monitoring may be needed to reconcile these patterns.

Variability of river conditions during embryo incubation, as measured by spring river flow and temperature, were also considered as potential factors influencing steelhead life history patterns (e.g., Ward et al. 2015). While the effect of variability in spring river flow on juvenile steelhead migration patterns was unclear, variability in spring river temperatures was positively related to the probability of individuals being detected as migrants. The CVs in spring river temperatures were primarily driven by lower temperature extremes. Minimum spring river temperatures ranged from less than 1°C to over 4°C throughout our study period, and these temperatures fall below optimal steelhead incubation temperatures (McCullough et al. 2001). Given evidence for density-dependent growth, reduced survival to emergence with lower spring temperature ranges could ameliorate density-dependent effects by reducing resource competition early in life and thereby increase the probability that an individual would be detected as a migrant.

While our results reveal interesting patterns with potential management implications, we acknowledge that biases inherent with our study design may influence interpretation of the results. Uncertainty and bias associated with steelhead that were undetected are of particular concern given that undetected fish could be the result of natural mortality, tagging effects, tag expulsion, variable detection efficiency, and resident life history expression. While we assumed that tagging effects from implanting PIT tags were minimal, studies have shown some survival and physiological responses to tagging (Prentice et al. 1986, 1990, 1994). We also assumed that biases from tag expulsion were low although increased tag expulsion rates after spawning may bias detection of iteroparous adults (Prentice et al. 1986, 1994; Sandstrom et al. 2012). While our estimated detection efficiencies were similar to that of other studies with similar arrays (Connolly et al. 2008; Pess et al. 2011), we could only derive efficiency estimates during spring smolt trap deployments. River flows exceeded those observed during smolt trap deployments approximately 34% of the time, and higher flows occurred primarily in late fall and winter. Therefore, flow-dependent detection efficiency may have biased our results by reducing probabilities of detecting fish that move during fall migration peaks. While fish in small coastal rivers like East Twin and West Twin rivers are usually dominated by anadromous life histories (Pavlov et al. 2001; Kendall et al. 2014), resident life history expression could have been undetected within the river given that our arrays were positioned near the river mouths. Even though we encountered few large fish during late summer tagging surveys and capture methods did not appear to bias size-classes, fish expressing resident life histories could have emigrated to habitats outside of our survey extent or used the lower river at times other than our late summer tagging surveys.

With these limitations and potential biases in mind, we conclude that the results of our findings have potential relevance to the development of steelhead management and recovery strategies for East Twin and West Twin rivers. For example, our results indicated that density-dependent processes and overwinter survival may be limiting production of migrants that are more likely to produce returning adults. Density-dependent and overwinter survival limitations suggest that actions designed to increase the quantity or quality of rearing habitat will benefit recovery efforts. However, we recommend additional monitoring to confirm the presence of density-dependent growth and to better understand density-dependent effects on steelhead productivity. In addition, our findings also indicated that status and trend assessments should consider the full range of age and season at migration among juvenile steelhead. For example, we demonstrated that, while a majority of migrants leave after their first summer as age-0 fall migrants, adults were only detected from age-1 and older migrants. In addition, reliance on spring smolt traps to enumerate migrant production ignores fall migrant peaks, which do appear to produce returning adults among older migrants. Therefore, reliance on total smolt production without regard to age at migration and use of spring smolt traps have the potential to introduce substantial bias in status and trend assessments as opposed to the individual-based monitoring approach used in this study.

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