

Iteroparity in Columbia River summer-run steelhead (*Oncorhynchus mykiss*): implications for conservation

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Abstract: We used ultrasound imaging and passive integrated transponder (PIT)-tagging programs to assess maturation status and iteroparity patterns in summer-run steelhead (anadromous rainbow trout, *Oncorhynchus mykiss*) of the interior Columbia River Basin (Pacific Northwest, USA). Postspawn kelts examined in downstream fish bypass systems at Columbia River and Snake River dams were disproportionately female (>80%) and majorities were of wild origin, unlike pre-spawn steelhead at these sites. Annual repeat migration estimates varied from 2.9% to 9.0% for kelts tagged at lower Columbia River dams ($n = 2542$) and from 0.5% to 1.2% for Snake River kelts ($n = 3762$). Among-site differences reflected greater outmigration distance and additional dam passage hazards for Snake River kelts. There was also strong evidence for condition-dependent mortality, with returns an order of magnitude higher for good- versus poor-condition kelts. Disproportionately more females and wild fish also returned, providing potentially valuable genetic and demographic benefits for the Columbia River's threatened steelhead populations. Results overall provide baseline data for evaluating kelt mortality mitigation efforts and basic life history information for steelhead conservation planning.

Résumé : L'imagerie ultrasonique et les programmes de marquage transpondeurs intégrés passifs (PIT) nous servent à évaluer le statut de maturation et les patrons d'itéroparité chez les truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) à montaison estivale du bassin intérieur du Columbia (nord-ouest pacifique, É.-U.). Les charognards d'après la fraie examinés dans les systèmes de passes migratoires de dérivation vers l'aval aux barrages des rivières Columbia et Snake sont de façon disproportionnée de sexe féminin (>80 %) et la plupart des individus sont d'origine sauvage, contrairement aux truites arc-en-ciel anadromes à ces mêmes sites avant la fraie. Les estimations de l'importance des migrations annuelles répétées varient de 2,9–9,0 % chez les charognards marqués aux barrages du Columbia inférieur ($n = 2542$) et de 0,5–1,2 % chez les charognards de la Snake ($n = 3762$). Les différences entre les sites reflètent la plus grande distance de migration vers la mer et les risques additionnels du passage des barrages pour les charognards de la Snake. Il y a aussi de fortes indications de l'existence d'une mortalité reliée à la condition; en effet, les retours sont dix fois plus abondants chez les charognards en bonne condition que chez ceux en mauvaise condition. De façon disproportionnée, il y a aussi plus de retours de femelles et de poissons sauvages, ce qui apporte potentiellement des bénéfices génétiques et démographiques précieux aux populations menacées de truites arc-en-ciel anadromes du Columbia. Globalement, nos résultats fournissent les données de base nécessaires pour évaluer les efforts de mitigation de la mortalité des charognards, ainsi que des informations démographiques fondamentales pour planifier la conservation de la truite arc-en-ciel anadrome.

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Introduction

Postspawning survival rates vary widely among the diadromous Salmoninae, from relatively high survival for *Salvelinus* and some *Salmo* species to complete semelparity (death following first spawning) in most but not all *Oncorhynchus* species (Rounsefell 1958; Fleming 1998). Semelparous and iteroparous (repeat spawning) life history strategies share a common evolutionary lineage, with semel-

parity believed to have developed last in response to several interrelated selective pressures (Stearley 1992). These include increased energetic costs associated with anadromy, long-distance migration, and breeding competition and also greater reproductive investments in secondary sexual characteristics, body size, and egg size (Willson 1997; Crespi and Teo 2002). In contrast, iteroparous life history types allocate relatively less energy to each reproductive episode and relatively more to postspawning survival (Dodson 1997). This

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strategy spreads the risk associated with catastrophic reproductive failure by allowing multiple spawning events by individual fish (Fleming and Reynolds 2004; Wilbur and Rudolf 2006).

Iteroparity, like variable age at maturity (Groot and Margolis 1991), may offer several population-level advantages. Both strategies maintain genetic diversity and reduce demographic risks by increasing the number of unique adult pairings across years (Crespi and Teo 2002; Niemelä et al. 2006). Iteroparous individuals may also be more productive than semelparous conspecifics because of higher cumulative fecundity and lifetime fitness (Fleming and Reynolds 2004). This may be especially important for females, given their strong influence on nest site selection, spawn timing, and early juvenile survival (Fleming 1996; Quinn 2005). Iteroparity within populations is typically dominated by females (Withler 1966; Fleming 1998), improving sex ratios that are often strongly skewed towards males (Mills 1989; Burgner et al. 1992; Willson 1997).

The benefits of iteroparity are unrealized in many anadromous populations because human activities typically select against repeat spawning by increasing adult and kelt (post-spawned adult) mortality (Altukhov et al. 2000; Crespi and Teo 2002). For example, harvest rates often differ among maiden and repeat spawners because of size-selective fisheries, migration timing differences, and (or) ocean distribution patterns (e.g., Dempson et al. 2004). Additionally, hydroelectric dams and other fish passage barriers present a variety of direct and indirect mortality hazards for outmigrating kelts (Wertheimer and Evans 2005; Arnekleiv et al. 2007; Scruton et al. 2007) that differ from those for upstream migrants. Kelts are often emaciated, with limited somatic energy reserves and reduced swimming abilities (Booth et al. 1997; Scruton et al. 2007), and consequently they are especially vulnerable to entrainment in hydroelectric turbines or other hazardous passage routes. Further, dams and reservoirs can slow kelt outmigrations by reducing water velocities and increasing time spent searching for passage routes (e.g., Wertheimer and Evans 2005; Wertheimer 2007). These delays have direct energetic costs and postpone the critical resumption of ocean feeding and gonadal recrudescence.

The outmigration environment for steelhead (anadromous rainbow trout, *Oncorhynchus mykiss*) kelts in the Columbia River Basin is one of the more difficult among iteroparous populations. In addition to long downstream migration distances (up to ~1500 km), summer-run (freshwater maturing) kelts must pass as many as nine hydroelectric dams and reservoirs to reach the Pacific Ocean. Kelt migration mortality in the impounded portion of this system can be very high (>95% in some years, Wertheimer and Evans 2005), suggesting strong selection against iteroparous forms. Recent documentation of this mortality has focused attention on improving kelt survival in the Columbia system, where broad-based population declines have resulted in US Endangered Species Act listing of most interior steelhead stocks (National Marine Fisheries Service 1997; Good et al. 2005). Current steelhead recovery efforts include increasing iteroparity to take advantage of genetic and demographic benefits of repeat spawners (National Marine Fisheries Service 2000).

Although the Columbia River historically supported some of the largest and most diverse steelhead runs in North America (Brannon et al. 2004; Augerot 2005), little is known about historic or current iteroparity patterns. A single predam publication reported repeat spawner rates of 2%, 4%, and 12% for summer, fall (freshwater maturing), and winter (ocean maturing) runs, respectively (Long and Griffin 1937). These estimates were based on scale samples collected at multiple but unspecified sites. More recent estimates have mostly been $\leq 5\%$ for a small number of interior summer steelhead stocks and up to 17% for some winter-run populations returning to sites downstream from all dams (Whitt 1954; Leider et al. 1986; Meehan and Bjornn 1991).

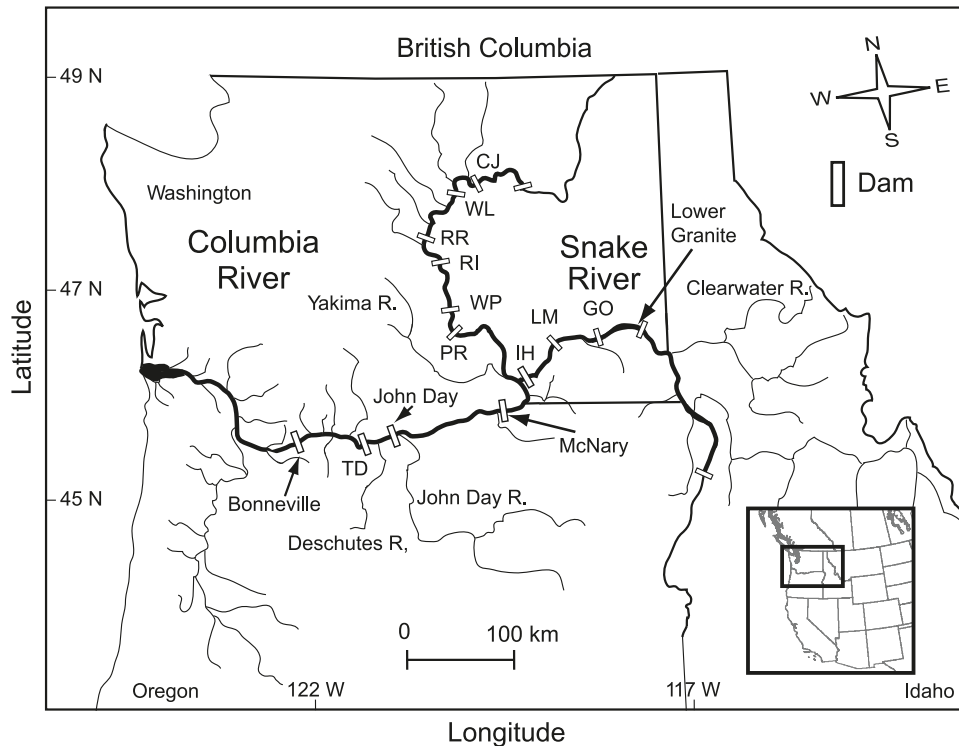
In this study, we addressed some of the basic iteroparity information gaps in the aggregated summer-run steelhead population of the interior Columbia River Basin. There were three interrelated study objectives. First, we collected kelt demographic and condition data at collection sites along the outmigration corridor, including fish sex, size, origin (hatchery versus wild), and coloration. Second, we examined associations among repeat spawner return rates and kelt demographics, outmigration timing, collection location, and year. We used an information-theoretic approach to assess the relative roles of these factors in predicting repeat spawner returns because the collected data were observational. Third, we examined life history characteristics of returning fish, including breeding interval, migration timing, and distribution within the Columbia River Basin. The combined objectives tested the following hypotheses: (i) repeat spawner return rates would be affected by outmigration distance, with lower returns expected for kelts collected at sites more distant from the ocean; (ii) return rates would differ among demographic groups, with higher returns expected for females, wild fish, and kelts in good physical condition; (iii) return rates would differ with outmigration timing, with higher returns expected for fish outmigrating during the peak of the kelt runs when rapidly increasing snowmelt runoff would presumably increase migration speed; and (iv) breeding interval would differ with outmigration timing and distance given their potential effects on ocean entry timing. We expected that some late-timed kelts and those with the longest migrations would enter the ocean with insufficient time to restore lost energy reserves and remature within a single season.

Materials and methods

Fish collection and tagging

Adult steelhead (both kelts and prespawners that were falling back downstream; Boggs et al. 2004) were collected from juvenile bypass systems at John Day and McNary dams on the Columbia River and at Lower Granite Dam on the Snake River (Fig. 1). These sites were 347, 470, and 695 river kilometres (rkm) from the Pacific Ocean, respectively. Sampling occurred from mid-March or early April through late May or mid-June in 4 years at John Day Dam (2001–2004) and 3 years each at McNary (2001–2002, 2004) and Lower Granite (2002–2004) dams (Fig. 2). In total, maturation status was evaluated for 13 193 adult steelhead: 4394 at John Day, 1390 at McNary, and 7409 at Lower Granite. Fish were directly diverted (John Day) or transferred via

Fig. 1. Map of the Columbia and Snake rivers showing mainstem dams and major tributaries mentioned in the text; inset shows locations in the Pacific Northwest, USA. Steelhead (*Oncorhynchus mykiss*) kelts were collected at John Day, McNary, and Lower Granite dams in 2001–2004. Repeat spawners were detected at passive integrated transponder (PIT) tag interrogators at Bonneville, McNary, Ice Harbor (IH), Lower Granite, Priest Rapids (PR), Rock Island (RI), and (or) Wells (WL) dams in 2001–2005. Other dams include Wanapum (WP), Rocky Reach (RR), Chief Joseph (CJ), Lower Monumental (LM), and Little Goose (GO).



dip net or flumes (McNary, Lower Granite) to nearby tanks containing aerated river water and anesthetic (60 ppm tricaine methanesulfonate (MS-222) or 30 mg·L⁻¹ of clove oil) (Prince and Powell 2000; Pirhonen and Schreck 2003). While fish were anesthetized, we recorded fork length (cm), overall physical condition (rated as good, fair, poor), coloration (rated as bright, intermediate, dark), origin (hatchery, wild), and sex. Condition was based on the degree of visible external damage (e.g., abrasions, lesions, fungal infections; see Evans 2003), while coloration (an indicator of physiological state) was based on the degree of the fish's silvery, ocean-like external appearance. Clipped adipose fins indicated hatchery origin and fish with adipose fins were presumed wild unless other hatchery marks were evident (e.g., blunt dorsal fins). Ultrasound imaging of gonads was used to identify sex and distinguish prespawn steelhead from post-spawn kelts using the technique described in Evans et al. (2004b).

Uniquely coded passive integrated transponder (PIT) tags were injected into the pelvic girdle of 52%–55% of the kelts sampled at each dam ($n = 1946$ at John Day; 596 at McNary; 3762 at Lower Granite). PIT tags were used because retention rates are high, tag life is unrestricted, and negative tag effects are minimal (Gibbons and Andrews 2004). PIT-tagging percentages varied across weeks and years and among dams (Fig. 2) as a result of personnel availability and evolving study objectives. At all sites, kelts selected for PIT tagging were more likely than the full kelt samples to be in good or fair condition (Table 1), resulting in higher

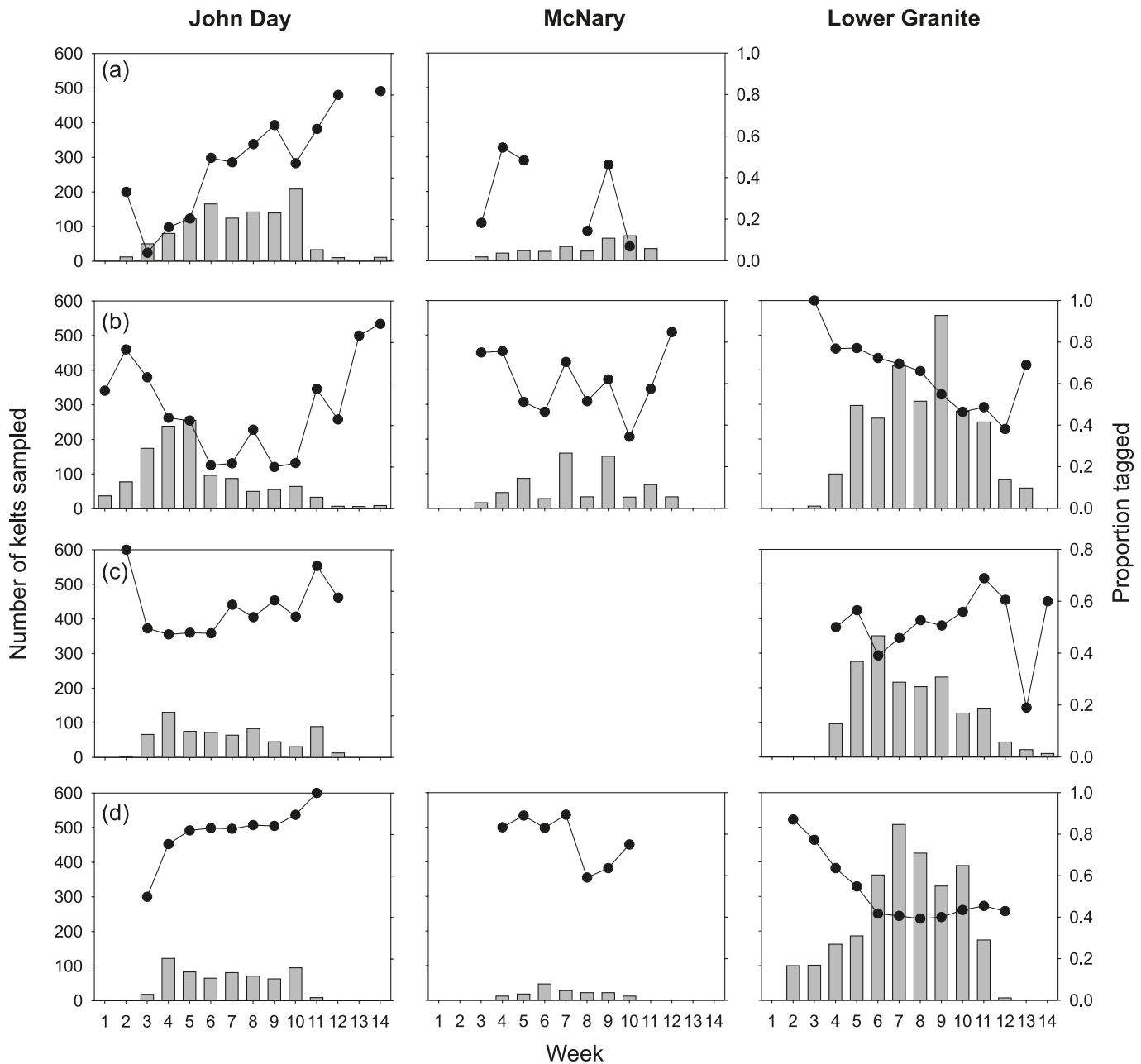
percentages of tagged wild and female kelts compared with the full samples. These tagging patterns added some potential bias to return evaluations in that brighter, good-condition kelts were disproportionately tagged. However, kelts of all condition types, sexes, and origins were tagged at all sites in all years.

Many PIT-tagged kelts (6%–38%) were also externally radio-tagged (see Wertheimer and Evans 2005 for summary data). Telemetry studies were in 2001, 2002, and 2004 at John Day and McNary dams and in 2002 and 2003 at Lower Granite Dam. Following tagging, all kelts recovered in temporary holding tanks until equilibrium was regained; fish then volitionally exited or were transferred directly into the dam's tailrace to continue downstream migration.

Repeat spawner monitoring

Steelhead returning on repeat spawning migrations could be enumerated at a series of PIT tag interrogation systems in dam fish ladders (e.g., Keefer et al. 2008b). PIT detection systems were in place at Bonneville and Lower Granite dams in 2001 and were added at McNary and Wells dams in 2002 and at Priest Rapids, Rock Island, and Ice Harbor dams in 2003. Detection efficiency estimates for the PIT tag systems were >90% for adult steelhead in independent evaluations at Bonneville and McNary dams in 2001 and 2002 (Downing and Prentice 2003), and efficiencies improved as a result of system refinements and interrogator redundancy in subsequent years. The probability of a repeat-spawn steelhead passing upstream undetected was therefore

Fig. 2. Numbers of steelhead (*Oncorhynchus mykiss*) kelts sampled at John Day, McNary, and Lower Granite dams (bars) in 2001–2004, with the proportions that were passive integrated transponder (PIT)-tagged (●): rows (a) = 2001; (b) = 2002; (c) = 2003; (d) = 2004. Week 1 = 18–24 March; week 14 = 17–23 June.



both low and increasingly unlikely as the kelt studies progressed. In addition, steelhead from upriver spawning populations were less likely to pass undetected, as their route included multiple interrogator sites. Repeat spawner rates presented here, however, are still minimums, as PIT tag retention rates (i.e., proportion of tagged fish that retained tags) and the effects of kelt handling or tagging on survival were not quantified; these effects were considered to be minimal sources of bias.

Statistical analyses

The likelihood of steelhead returning on repeat spawning migrations was examined using a combination of univariate

analyses (e.g., Pearson χ^2 and Fisher’s exact tests) and multiple logistic regression models. Predictor variables included kelt characteristics (condition, coloration, length, sex, origin) and (or) outmigration metrics (year, release week, release site). These terms were not strictly independent (e.g., kelts in good condition were more likely to be brightly colored and female). A preliminary logistic regression model included all PIT-tagged kelts from all sites and years to assess differences among release locations and gross differences related to fish characteristics. A series of additional logistic models were run separately for each release site and were limited to fish in good condition in an effort to minimize the possible effects of tagging bias due to dispro-

Table 1. Origin, sex, and condition summaries for all steelhead (*Oncorhynchus mykiss*) kelts sampled annually from 2001 to 2004, including the total subsamples of passive integrated transponder (PIT)-tagged fish.

Dam	Year	n	Origin (%)		Sex (%)*			Condition (%)			
			Wild	Hatchery	F	M	U	Dead	Poor	Fair	Good
John Day	2001	1096	76	24	57	5	39	2	26	24	48
	2002	1188	58	42	64	12	24	4	47	23	27
	2003	669	73	27	69	9	22	5	45	22	28
	2004	607	73	27	61	17	23	4	34	24	39
	Total	3560	69	31	62	10	28	3	38	23	36
	PIT	1946	71	29	63	11	27	—	25	27	47
McNary	2001	330	63	37	53	5	42	1	32	14	53
	2002	650	66	34	74	11	15	2	40	15	43
	2004	161	70	30	70	15	15	2	27	24	47
	Total	1141	66	34	67	10	23	2	36	16	46
	PIT	596	71	29	73	11	17	—	11	23	66
Lower Granite	2002	2610	51	50	83	17	—	—	24	28	48
	2003	1714	50	50	83	17	—	—	27	26	46
	2004	2744	56	45	84	16	—	—	18	42	40
	Total	7068	52	48	83	17	—	—	22	33	44
	PIT	3762	53	47	84	16	—	—	11	38	51

*F, female; M, male, U, unknown.

portionate sampling. We compared these models using information-theoretic techniques (Burnham and Anderson 2002). The candidate models included univariate terms, several a priori subsets of the predictor variables (i.e., fish characteristics), and the most parsimonious subsets identified using backward stepwise regression (Hosmer and Lemeshow 2000). All of the main effects models were ranked using Akaike's information criterion (AIC) and evaluated with respect to Δ AIC, the change in AIC relative to the best or most parsimonious model (Buckland et al. 1997; Burnham and Anderson 2002). Interaction terms were not included in the AIC model selection procedure. However, associations between all first-order interactions and kelt return rates were evaluated in separate models to assess their influence relative to individual predictor variables.

Varying proportions of repeat spawners returned in the same calendar year as their outmigration (hereafter referred to as consecutive repeat spawners) or returned the calendar year after their outmigration (hereafter referred to as skip repeat spawners because of the additional winter at sea). Consecutive and skip return percentages were compared among kelt release sites and among years using χ^2 tests. Outmigration and return migration timing distributions for these groups were compared using Kruskal–Wallis tests, and analysis of variance was used to assess fork length differences among groups.

Results

Maturation status

Across years, 81%–82% of John Day and McNary samples and 95% of the Lower Granite sample were determined to be kelts, 17%–18% were considered prespawners, and maturation status was undetermined for 1% of all fish. Prespawners were more numerous in late March to early April, when they made up 30%–60% of samples at all sites. There-

after, percentages of kelts rapidly increased and made up >90% of almost all mean weekly samples in May and June. Prespawners were more likely than kelts to be of hatchery origin at John Day (58% of 828 prespawners versus 31% of 3560 kelts) and Lower Granite (61% of 317 prespawners versus 48% of 7068 kelts) dams, but not at McNary Dam (31% of 248 prespawners versus 34% of 1141 kelts).

Kelt samples

Kelt characteristics (i.e., origin, sex, condition, length, and coloration) varied across sites and years and within year. Overall, 66%–69% of all kelts sampled at John Day and McNary dams and 52% at Lower Granite Dam were wild origin (Table 1). Percent wild differed significantly among dams each year ($\chi^2 \geq 24.6$, $P < 0.001$). Of those kelts that could be confidently sexed, far more were female (83%–87%) than male (13%–17%) at all sites in all years. Sex assignment was unknown for about a quarter of the kelts evaluated at John Day and McNary dams, primarily because gonads had been completely evacuated or absorbed following spawning, leaving no discernable eggs or testes (Table 1). At John Day Dam, unknown sex fish were morphologically more similar to females than males on average (e.g., tended to be larger, brighter, and in better condition); patterns were equivocal for unsexed fish at McNary Dam. With all years combined and unknown sex fish excluded, sex ratios did not differ by kelt origin (hatchery, wild) at John Day or Lower Granite dams ($P \geq 0.13$), while at McNary Dam, 66% of females were wild versus 79% of males ($\chi^2 = 7.0$, $P = 0.008$). In individual years, significantly ($P < 0.05$) more males than females were wild at Lower Granite and McNary dams in 2002; the opposite was true at Lower Granite Dam in 2003.

Kelt condition (good, fair, poor) was better overall for fish at Lower Granite (44% good condition) and McNary

Table 2. Results of multiple logistic regression model to predict repeat spawner returns of steelhead (*Oncorhynchus mykiss*) kelts using all fish passive integrated transponder (PIT)-tagged in all years.

Effect	df	χ^2	<i>P</i>	Effect	Odds ratio	95% CI
Tag site	2	48.79	<0.001	John Day vs. Lower Granite	5.88	3.73–9.67
				McNary vs. Lower Granite	3.94	2.23–6.97
Condition	2	31.95	<0.001	Good vs. poor	25.36	6.10–105.43
				Fair vs. poor	10.27	2.40–43.84
Week	1	20.30	<0.001	—	0.85	0.79–0.91
Coloration	2	9.85	0.007	Dark vs. bright	0.22	0.05–0.97
				Intermediate vs. bright	0.60	0.42–0.87
Origin	1	8.19	0.004	Hatchery vs. wild	0.56	0.37–0.83
Year	3	7.73	0.052	2001 vs. 2004	1.10	0.69–1.76
				2002 vs. 2004	1.14	0.75–1.74
				2003 vs. 2004	0.51	0.22–1.13
Sex	2	3.27	0.195	Male vs. female	0.65	0.30–1.39
				Unknown vs. female	1.29	0.87–1.90
Length	1	1.75	0.186	—	0.98	0.96–1.01

Note: Predictor variables included collection location, year, and week and kelt condition, color, origin, sex, and fork length. River discharge and dam spill terms were excluded because these variables varied across sites. No fish were PIT-tagged at Lower Granite Dam in 2001 or McNary Dam in 2003, but a reduced model that included data from 2002 and 2004 only produced qualitatively similar results. CI, confidence interval.

(46% good condition) dams than at John Day Dam (36% good condition) (Table 1). Condition differed among sites in each year and with all years combined ($\chi^2 \geq 15.4$, $P < 0.001$). Wild kelts were in better overall condition than hatchery kelts at each site ($\chi^2 \geq 21.1$, $P < 0.001$, all years combined), and more females than males were in good condition at each site ($\chi^2 \geq 16.0$, $P < 0.001$). These sex- and origin-related condition differences were also significant ($P < 0.05$) in most individual site \times year samples. Kelt fork length also differed ($P \leq 0.05$, *t* tests) among sites and by origin and sex. On average, the largest kelts were at Lower Granite Dam, females were larger than males, and wild fish were larger than hatchery fish. Although significant, differences in means were generally ≤ 4 cm.

Kelt origin varied within season in several ways. Percentages of wild kelts increased with increasing migration date at John Day and McNary dams, from $\sim 60\%$ early in the migrations to $\sim 80\%$ during the last sampling weeks. At Lower Granite Dam, the mean wild kelt percentage decreased from $\sim 60\%$ early in the migration to $\sim 30\%$ in midseason and then rapidly increased to nearly 100% by late migration in all years. Sex ratios were relatively constant through time at all sites, with females outnumbering males. Percentages of kelts in good condition and with bright coloration tended to increase within season, while dark kelts and kelts in poor condition decreased at all sites.

Return rates

Across release sites and years, 164 of 6304 (2.60%) PIT-tagged kelts were detected on repeat spawning migrations, and two of these (0.03%) were recorded returning twice (i.e., on a third migration). A full-sample multiple logistic regression model that included release site, migration timing, and kelt characteristic variables indicated that release site, kelt condition, and release week were the most influential predictors of returns (Table 2). Odds ratios showed kelts tagged at John Day Dam and McNary Dam were 5.9 and 3.9 times more likely to return than those tagged at Lower

Granite Dam, respectively. Kelts in good or fair condition were respectively >25 and >10 times more likely to return than those in poor condition. Early-timed, bright colored, and wild origin kelts were also significantly ($P < 0.05$) more likely to return. There was also evidence for year effects ($P = 0.052$, Table 2), while fish length and sex were nonsignificant terms in the full model.

Although sex was not included in the full logistic regression model, proportionately more females than males returned from all release sites (2.30% versus 1.22%), and females returned at higher rates than males at all sites in all years (Table 3). These differences were not significant in univariate tests with all years combined or for any individual site \times year sample ($P \geq 0.10$; male versus female only, Table 3). The presence of unsexed fish at two of three study sites, however, may have affected this nonsignificant finding, especially given that unsexed fish returned at the highest rates. When sex data was limited to kelts tagged at Lower Granite Dam (where 100% of kelts were classified as male or female), a higher percentage of females returned as repeat spawners (0.79%, 25 fish) relative to males (0.17%, 1 fish). The small numbers of returning fish from both sexes, however, limited statistical comparisons.

Other univariate evaluations were also informative. Across years, return percentages were 5.45% (106/1946) for John Day releases, 5.37% (32/596) for McNary releases, and 0.69% (26/3762) for Lower Granite releases (Table 3). Among-site differences were significant with all years combined ($\chi^2 = 134.39$, $P < 0.001$) and in each year that fish were tagged at Lower Granite Dam ($\chi^2 \geq 15.94$, $P < 0.001$). Among-year return differences were significant for John Day ($\chi^2 = 11.14$, $P = 0.011$) and Lower Granite ($\chi^2 = 6.77$, $P = 0.034$) releases, with the lowest returns in 2003 for both sites (Table 3). Kelts in good condition returned at higher rates (9.22%, John Day; 7.16%, McNary; 1.19%, Lower Granite) than those in poor condition (0.20%, John Day; 1.54%, McNary; 0.00%, Lower Granite) for all release sites ($P \leq 0.027$, all years combined) (Table 3). Condition effects

Table 3. Summary of steelhead (*Oncorhynchus mykiss*) return rates (%) by kelt passive integrated transponder (PIT)-tagging site, outmigration year, sex, origin, and condition.

Dam	Variable	Year				Total
		2001	2002	2003	2004	
John Day	Female	7.72 (298)	5.59 (322)	2.32 (302)	4.00 (300)*	4.91 (1222)* [†]
	Male	0.00 (15)	4.11 (73)	0.00 (43)	2.63 (76)*	2.42 (207)*
	Unknown	8.72 (172)	5.60 (125)	5.66 (106)	11.40 (114)*	7.93 (517)*
	Wild	9.07 (386)*	5.37 (298)	3.57 (336)	5.43 (368)	5.98 (1388) [†]
	Hatchery	3.03 (99)*	5.41 (222)	0.87 (115)	5.74 (122)	4.12 (558)
	Poor	0.00 (10)	0.42 (240)*	0.00 (124)*	0.00 (115)*	0.20 (489)*
	Fair	5.94 (101)	6.04 (149)*	1.42 (141)*	2.08 (144)*	3.74 (535)*
	Good	8.56 (374)	13.74 (131)*	5.91 (186)*	10.39 (231)*	9.22 (922)*
	Total	7.84 (485)	5.38 (520)	2.88 (451)	5.51 (490)	5.45 (1946) [†]
McNary	Female	5.56 (36)	6.13 (310)	—	5.75 (87)	6.00 (433)
	Male	0.00 (2)	4.88 (41)	—	0.00 (20)	3.17 (63)
	Unknown	13.79 (29)	0.00 (52)	—	0.00 (19)	4.00 (100) [†]
	Wild	7.55 (53)	6.47 (278)	—	5.43 (92)	6.38 (423)
	Hatchery	14.29 (14)	2.40 (125)	—	0.00 (34)	2.89 (173) [†]
	Poor	0.00 (2)	2.00 (50)*	—	0.00 (13)	1.54 (65)*
	Fair	7.69 (13)	1.11 (90)*	—	2.70 (37)	2.14 (140)*
	Good	9.62 (52)	7.22 (263)*	—	5.26 (76)	7.16 (391)*
	Total	8.96 (67)	5.21 (403)	—	3.97 (126)	5.37 (596)
Lower Granite	Female	—	0.59 (1350)	0.41 (740)	1.29 (1083)	0.79 (3173)
	Male	—	0.00 (267)	0.00 (128)	0.52 (194)	0.17 (589)
	Wild	—	0.51 (780)	0.62 (483)	1.64 (732)	0.95 (1995)*
	Hatchery	—	0.48 (837)	0.00 (385)	0.55 (545)	0.40 (1767)*
	Poor	—	0.00 (402)*	0.00 (4)	0.00 (5)	0.00 (411)*
	Fair	—	0.00 (446)*	0.00 (336)	0.47 (637)	0.21 (1419)*
	Good	—	1.04 (769)*	0.57 (528)	1.89 (635)	1.19 (1932)*
	Total	—	0.49 (1617)	0.35 (868)	1.17 (1277)	0.69 (3762) [†]

*Varied ($P < 0.05$) across category (i.e., sex, origin, condition).[†]Varied ($P < 0.05$) across years.

were consistent for individual site \times year samples (Table 3) and across most combinations of sex and origin. Wild kelts returned at higher rates than hatchery kelts from all release sites (5.98% versus 4.12%, John Day; 6.38% versus 2.89%, McNary; 0.95% versus 0.40%, Lower Granite; Table 3). This pattern was significant for the Lower Granite sample with all years combined ($\chi^2 = 4.22$, $P = 0.040$) and the John Day sample in 2001 ($\chi^2 = 3.98$, $P = 0.046$).

In comparisons of models using kelt characteristics, migration year, and migration timing variables, outmigration week was the most informative univariate predictor for good-condition fish at all release sites (Table 4). Later migrants were less likely to return in all cases, with odds ratios of 0.89 (95% CI = 0.81–0.97; $\chi^2 = 7.03$, $P = 0.008$) for John Day, 0.84 (95% CI = 0.70–0.99; $\chi^2 = 3.88$, $P = 0.049$) for McNary, and 0.75 (95% CI = 0.63–0.90; $\chi^2 = 9.93$, $P = 0.002$) for Lower Granite releases.

Among the a priori models, the model with all six terms was the most parsimonious for John Day releases (Table 4). The year + week model was best for McNary and Lower Granite kelts. The model identified using backward stepwise selection was different for each release site (Table 4). The stepwise model for the John Day sample (week + length + color) indicated the kelts most likely to return were early migrating ($\chi^2 = 8.97$, $P = 0.003$), bright colored ($\chi^2 = 8.76$,

$P = 0.013$), and relatively smaller ($\chi^2 = 3.72$, $P = 0.054$). The McNary model (week) indicated returns were highest for early outmigrants ($\chi^2 = 3.88$, $P = 0.049$), and the Lower Granite model (week + origin) indicated wild ($\chi^2 = 3.88$, $P = 0.049$), early migrants ($\chi^2 = 10.94$, $P < 0.001$) were most likely to return (Table 4).

Generally, the 15 first-order interaction terms explained little additional variation than the main effects models or the stepwise regression results. For all three release sites, the lowest AIC values were for interaction terms that included week (e.g., week \times length, week \times color), suggesting an overall outmigration timing effect. AIC values for these terms were similar to or slightly higher than those for the univariate and a priori models in Table 4.

There was no evidence that radio tagging negatively affected returns relative to PIT tagging. Return percentage comparisons based on the two tagging procedures showed no significant ($P > 0.05$) differences at any site or in pairwise tests based on site and either condition, origin, or sex. We note that none of 347 radio-tagged kelts from Lower Granite returned (versus 0.69% for the full sample).

Breeding interval, migration timing, and distribution of repeat spawners

Of 164 PIT-tagged kelts that returned as repeat spawners,

Table 4. Logistic regression model selection and comparison statistics used to predict if steelhead (*Oncorhynchus mykiss*) kelts in good condition returned to spawn, by collection site.

Model	df	John Day		McNary		Lower Granite	
		AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC
Univariate							
Year	2–3	569.0	11.2	206.7	5.2	251.0	10.2
Week	1	564.0	6.1	201.5	0.0	243.1	2.3
Origin	1	570.2	12.4	203.2	1.7	250.2	9.4
Sex	1–2	570.1	12.2	205.7	4.2	251.4	10.6
Length	1	569.6	11.7	204.3	2.8	253.4	12.6
Color	1–2	566.0	8.1	NA*	NA*	253.7	12.9
A priori							
Year + week	3–4	565.9	8.1	204.4	2.9	244.5	3.7
Origin + sex	2–3	571.0	13.2	205.3	3.8	250.0	9.2
Sex + length	2–3	570.4	12.6	206.8	5.3	253.0	12.2
Origin + sex + length + color	5–6	567.3	9.5	NA*	NA*	253.7	12.9
Year + week + origin + sex + length + color	8–10	561.5	3.7	NA*	NA*	246.1	5.3
Backward stepwise selection							
Week + length + color	4	557.8	0.0	—	—	—	—
Week	1	—	—	201.5	0.0	—	—
Week + origin	2	—	—	—	—	240.8	0.0

Note: Models include each univariate predictor, several a priori models, and models identified using backward stepwise selection ($P < 0.1$ as the cutoff for variable retention).

*No “dark” kelts returned from McNary Dam releases.

57% ($n = 94$) were consecutive repeat spawners, 43% ($n = 70$) were skip repeat spawners, and at least one fish exhibited both return strategies (i.e., returned twice). Kelts tagged at John Day Dam were more likely to be consecutive spawners (65%) than those tagged at McNary (47%) or Lower Granite (38%) ($\chi^2 = 7.83$, $P = 0.020$) dams. Generally, breeding interval (consecutive, skip) did not differ by kelt origin or condition within release site ($P > 0.05$). For McNary fish, consecutive return percentages differed by year (2001 > 2004 > 2002; $\chi^2 = 9.97$; $P = 0.007$). Consecutive spawners tended to have longer fork length than skip spawners (2.1–2.7 cm, on average across years), but differences were significant ($P < 0.05$, analysis of variance (ANOVA)) only for the 2002 John Day and 2004 McNary samples. Twelve skip spawners were recaptured at Bonneville Dam on return migrations in 2003; mean fork lengths for these fish were 57 cm (range = 52–62 cm) when they were PIT-tagged as kelts and 69 cm (range = 63–77) upon recapture.

Consecutive spawners outmigrated earlier as kelts than skip spawners (Fig. 3), with median outmigration dates earlier by 11 days (John Day releases), 7 days (McNary releases), and 16 days (Lower Granite releases) with all years combined ($P \leq 0.037$, Kruskal–Wallis tests). This pattern was consistent in all years for all release sites but was generally not significant ($P > 0.05$). When evaluated within a given return year, return migration timing also differed between consecutive and skip spawners (Fig. 4). Median return dates at Bonneville Dam for consecutive returns were 33 days (John Day releases), 45 days (McNary releases), and 28 days (Lower Granite releases) later than for skip returns. With all years combined, these differences were significant ($P < 0.001$, Kruskal–Wallis tests) for fish tagged at John Day and McNary dams but not at Lower Granite Dam

($P = 0.079$). Patterns were similar for the majority of individual site \times year samples, but were generally not significant ($P > 0.05$).

Overall, 97% of known returning steelhead were detected at Bonneville Dam PIT tag interrogators, and percentages were consistently high across kelt release sites and years. On average, 36% of returning fish from the John Day tagging group were detected at McNary Dam, 8%–11% were detected at Snake River dams, and 4%–7% were detected at mid-Columbia River dams. Means for the McNary release group were 97% at McNary Dam, 20%–23% at Snake River dams, and 5%–26% at mid-Columbia River dams. These patterns suggest that many kelts tagged at John Day Dam originated in the John Day River, while many kelts tagged at both John Day and McNary dams were from sites other than the Snake River. In all cases, additional fish almost certainly returned to mid-Columbia sites, where PIT monitoring did not begin until 2002 (Wells Dam) or 2003 (Priest Rapids and Rock Island dams).

Discussion

Iteroparity patterns

Steelhead return rates in the Columbia River Basin varied along several gradients that mostly supported our hypotheses. First, there was a clear negative relationship between kelt outmigration distance and repeat spawner return rates, with kelts tagged at John Day Dam (third mainstem dam, rkm 347) about six times more likely to return than those tagged at Lower Granite Dam (eighth mainstem dam, rkm 695). This likely reflects a combination of life history differences among populations and some level of distance- and (or) dam-related migration mortality for upriver kelts. Second, there was persuasive evidence for condition-dependent

Fig. 3. Outmigration timing distributions of steelhead (*Oncorhynchus mykiss*) kelts that were consecutive spawners (shaded boxes) or skip spawners (open boxes) by kelt collection site. Boxes show median, quartile, and 5th and 95th percentiles.

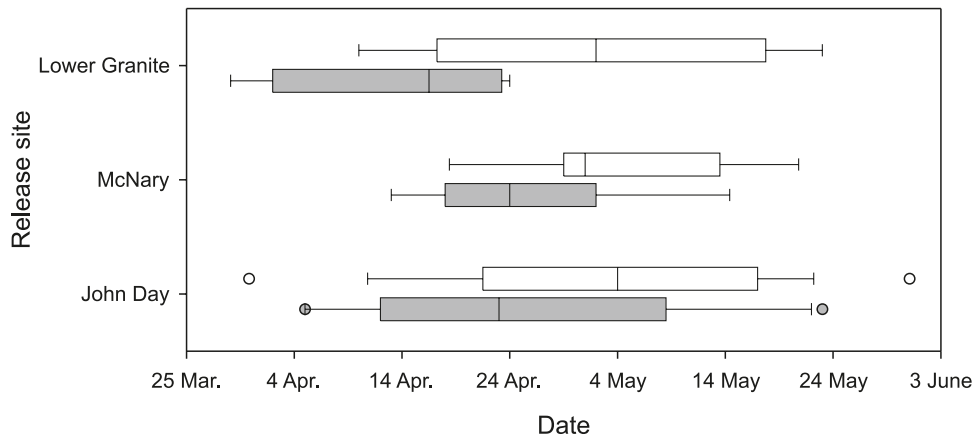
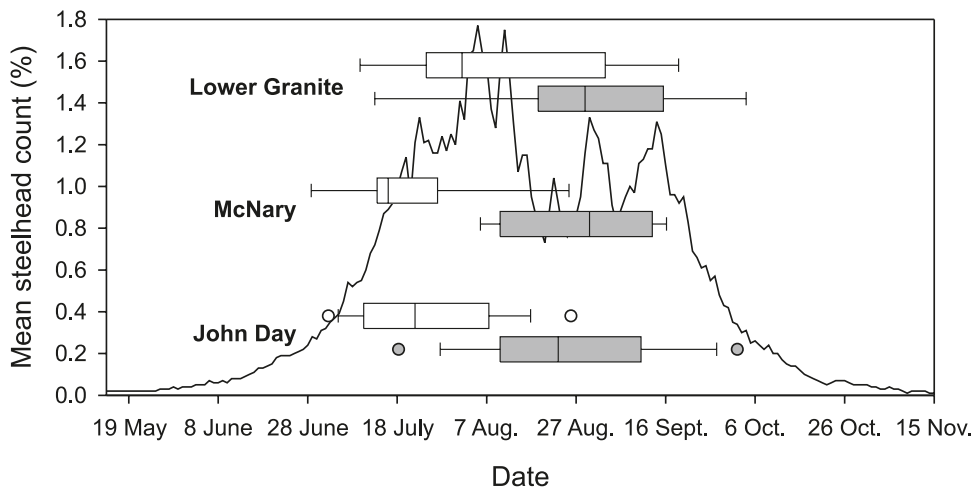


Fig. 4. Return timing distributions at Bonneville Dam for steelhead (*Oncorhynchus mykiss*) that were consecutive spawners (shaded boxes) or skip spawners (open boxes) by kelt collection site. Boxes show median, quartile, and 5th and 95th percentiles. Line shows the mean steelhead count (expressed as %) at Bonneville Dam from 2001 to 2005.



mortality, as kelts in good external condition returned at rates more than an order of magnitude higher than poor-condition fish from all collection sites. Third, known females were both far more abundant than males and were at least two to four times more likely to return as repeat spawners. Fourth, proportionately more wild than hatchery fish and more small than large fish returned, particularly from upstream release groups. Finally, both outmigration year and timing appeared to influence return rates for all groups, with relatively higher returns for earlier outmigrants, and rates differing among years by a factor of two to three at each site.

At the individual fish level, almost all of the kelt characteristics associated with repeat spawning migrations in the Columbia system have parallels in other populations and regions. The tendency for female-dominated iteroparity, for example, is widespread among iteroparous salmonids. This has been attributed to greater reproductive competition among males and subsequently higher postspawn male mortality (e.g., Jonsson et al. 1991; Fleming and Gross 1994). Typical iteroparous females also have fewer individual spawning bouts than males and relatively limited investment

in postspawn nest defense, behaviors that result in shorter residency times and higher postspawn survival (Burgner et al. 1992; Fleming 1996; Lohr and Bryant 1999). The tendency for higher returns by smaller steelhead kelts is a trait shared with many Atlantic salmon (*Salmo salar*, Jonsson et al. 1991), brown trout (*Salmo trutta*, Jonsson and L'Abèe-Lund 1993), and Arctic char (*Salvelinus alpinus*, Dutil 1986) populations. Size-related survival may signal some of the same selective pressures that favor large body size in semelparous species (e.g., large body size evolved as migration difficulty increased) as well as a reduced ability for larger fish to restore energy lost during spawning (Crespi and Teo 2002; Kinnison et al. 2003). On average, the largest kelts we examined were from the Snake River, where the life history of many Clearwater and Salmon river steelhead includes an additional ocean year (Busby et al. 1996). Apparent size-related kelt mortality may therefore also be a function of spawner age. Notably, Clearwater and Salmon river steelhead are relatively abundant among Snake River stocks, but were grossly under-represented in kelt genetic samples at Lower Granite Dam (Narum et al. 2008). This suggests initially high postspawn mortality

(i.e., on or near spawning grounds) for these large-bodied steelhead, consistent with a more semelparous strategy.

In preparation for ocean reentry, kelts must undergo a series of physiological, behavioral, and morphological changes akin to those for juvenile salmonids (“smoltification,” reviewed in McCormick et al. 1998). The most visible manifestation of this process is a coloration shift towards the cryptic, silvered appearance typical of pelagic ocean fishes. Smoltification is energetically demanding (Wedemeyer et al. 1980), which may explain why steelhead kelts in poor physical condition were disproportionately darkly pigmented (also see Evans 2003). Not surprisingly, bright kelts in good condition were far more likely to return on repeat migrations. Kelt condition and color metrics may therefore be reasonably good surrogates for kelt energetic reserves and overall physiological readiness for seaward migration and survival. The relative effects of physical condition and physiology on kelt survival and iteroparity could be directly tested by nonlethally measuring kelt energetic reserves (e.g., using a microwave lipid meter), osmoregulatory capability (e.g., Na^+/K^+ ATPase activity), and (or) stress hormones levels (e.g., plasma cortisol) (Congleton et al. 2000; Wagner and Congleton 2004; Cooke et al. 2005).

In smolts, the highest outmigration survival typically occurs when physiological changes coincide with optimum environmental conditions (i.e., temperature, photoperiod, and flow) and upon ocean entry (McCormick et al. 1998). A lack of synchrony during these optimal windows reduces smolt survival and subsequent adult return rates. We expect a similar set of optimal conditions exists for kelts, and outmigration timing and river and ocean conditions may be critical components affecting kelt survival and subsequent repeat spawning events. However, the influence of outmigration river environment on subsequent iteroparity remains unclear. In this study, returns by good condition kelts were much more variable across years (differing by a factor of >2) than were river flow and temperature conditions during outmigration. Wertheimer and Evans (2005) provided evidence for lower kelt outmigration survival in low-flow years, but relationships between river conditions and return rates were inconsistent in our exploratory analyses. This may have been because kelts encounter a wide range of conditions during outmigration — making it difficult to select appropriate metrics — or because river environment or dam operations affect iteroparity at finer scales than we considered. It is also possible that other factors, like ocean conditions, mask the effects of outmigration river conditions. For example, Wertheimer and Evans (2005) reported relatively high downstream survival of 15.6% for Snake River kelts in 2002, yet only $\sim 1\%$ of good-condition fish returned from that sample.

We did find that early-migrating kelts returned at relatively higher rates, a somewhat unexpected result given that bright kelts were increasingly abundant as migrations progressed and peak kelt passage was not observed until mid-season (i.e., late April and May). Assuming past selection for migration timing (e.g., Quinn et al. 2000), we expected kelt survival to be highest during peak passage, particularly as this time period is closer to the spring flood. However, the benefits of migrating during historically optimal times may be offset by greatly reduced kelt migration speeds in

this impounded system. If there are strong selection pressures for rapid outmigration and ocean reentry timing, the substantial reductions in Columbia River runoff volume and velocity (e.g., Quinn and Adams 1996; Robards and Quinn 2002) could explain the apparent asynchrony between the kelt migration peak and higher iteroparity for early migrants. Alternately, early migrants may have had greater energetic reserves, may have originated from populations more likely to repeat spawn, or may have encountered more favorable river or ocean conditions. A combination of factors likely influenced the reported return rates, and we emphasize that environmental hypotheses remain largely untested.

Our fourth hypothesis, that breeding interval of repeat migrants would differ with kelt outmigration timing and distance, was supported by the data. Compared with kelts that spent a winter at sea (or in the estuary) before returning (i.e., skip repeat spawners), consecutive spawners outmigrated earlier as kelts, were larger, were disproportionately collected at the downstream sites, and returned relatively later in the fall. These patterns likely reflect the time kelts require to restore lost somatic and gonadal energy reserves (Niemelä et al. 2006). Early Columbia River outmigrants may have adequate time to complete this process in a single season, whereas late outmigrants that miss productive ocean conditions in spring may require additional residency. Recovery times may also differ as a function of freshwater migration distance or difficulty (Schaffer and Elson 1975; Willson 1997), perhaps explaining why Snake River kelts overwintered at substantially higher rates than kelts collected at lower Columbia River sites. On average, about 4 months elapsed between hydrosystem detections for consecutive repeat spawners compared with ~ 15 months for skip repeat spawners. The latter breeding interval is somewhat more typical among anadromous, iteroparous species (Dutil 1986; Jonsson et al. 1991; Behnke 1992).

The general iteroparity and migration timing patterns described above were interrelated in complex ways. For example, kelt coloration and condition varied seasonally and differed between sexes and between wild and hatchery fish (also see Evans et al. 2004a). River conditions and dam operations also varied within season, potentially affecting kelt passage routes and survival probabilities (e.g., Wertheimer and Evans 2005). The observational nature of this study made these layers of complexity particularly challenging to untangle, as there were no control groups and potentially important, unmeasured explanatory variables (e.g., ocean effects). The statistical results were therefore useful for identifying broad patterns (i.e., the importance of kelt condition and sex and also migration timing and distance), but these models oversimplify the processes affecting iteroparity and should not be used to infer causality.

We also reiterate that our estimates apply to a broad amalgam of Columbia and Snake river steelhead, potentially representing 30 or more distinct spawning populations upstream from John Day Dam (Brannon et al. 2004; Keefer et al. 2008a). Inferences drawn from the aggregate should not be applied to individual stocks given probable among-population variability in spawner age, sex ratios, initial post-spawn survival, and (or) iteroparity. As an example, genetic analyses of kelts collected at Lower Granite Dam showed Snake River populations did not contribute to kelt outmigra-

tions in proportion to population size or distance to spawning grounds (Narum et al. 2008). This implies that repeat spawning rates for individual stocks may be much higher or lower than aggregate estimates, particularly for kelts passing lower Columbia River dams, where the mix of Snake, mid-Columbia, and upper Columbia river fish is most diverse.

Conservation and management implications

Iteroparity estimates for the aggregate Columbia River samples (5%–6%, across years) were comparable with rates for British Columbia steelhead (Withler 1966), but were generally lower than those reported across a variety of life history types in Washington (7%–11%), Oregon (11%–21%), California (17%–23%), and Alaska (21%–51%) (Shapovalov and Taft 1954; Busby et al. 1996; Lohr and Bryant 1999). Four or more spawning events have been noted in some of these populations, whereas only two steelhead were recorded on a third spawning migration in our study. The iteroparity estimate for Snake River fish (~1%) was among the lowest recorded for any steelhead population and places this group at the low end of the iteroparity continuum for anadromous salmonids (i.e., Fleming 1998). The low rates may be attributable to energetically demanding migrations that favor high single-episode reproductive investment (Crespi and Teo 2002; Fleming and Reynolds 2004) and may have been the norm historically given that interior Columbia River populations have among the longest freshwater migrations recorded for the species (Busby et al. 1996).

An essential management challenge for Columbia River Basin kelts is to reduce the direct and indirect mortality risks associated with dams and reservoirs. In many respects, these risks parallel those for salmonid smolts, with direct mortality hazards including contact with turbine blades, rapid pressure changes in powerhouses, and trauma from passage over spillways (e.g., Čada 2001; Ferguson et al. 2005). A partial list of indirect effects includes energetically costly migration delays, accumulated physiological stress, and possible asynchrony between migration timing and readiness for ocean entry (Venditti et al. 2000; Budy et al. 2002; Schaller and Petrosky 2007). Bypass systems and operational changes designed for smolts (e.g., increased spill during outmigration) may benefit kelts, but these assumptions have rarely been directly tested. The large numbers of kelts collected in juvenile bypass systems and kelt use of a surface-flow bypass structure at Bonneville Dam (Wertheimer 2007) indicate that these facilities can be effective kelt passage routes. Similarly, kelts and prespawn adults pass downstream via spillways when adequate flow is available (Boggs et al. 2004; Wertheimer and Evans 2005). However, understanding route-specific mortality risks, relative use among routes, and effects of route on respawning success will require further investigation.

Broader changes in river environment, such as reduced peak flows during outmigration, are difficult to evaluate without historic data. However, downstream kelt migration rates in the impounded Columbia River system of 13–16 km-day⁻¹ in Snake and upper Columbia river reaches and 38 km-day⁻¹ in lower Columbia River reaches (Wertheimer and Evans 2005; English et al. 2006) are well below the mean rates these authors report in the Skeena River (42–

54 km-day⁻¹), Fraser River (100 km-day⁻¹), and in unimpounded Columbia River reaches (99–111 km-day⁻¹). These data were all collected in low-gradient mainstem reaches, suggesting passage barriers or reduced water velocity in reservoirs delayed outmigration. Directly testing the relationship between outmigration delay and the likelihood of repeat spawning would require large sample sizes but may offer important guidance on flow augmentation or operations-related mitigation.

Two additional strategies to increase iteroparity in Columbia River summer-run steelhead are currently being evaluated. First, a kelt transportation program seeks to circumvent mortality risks associated with dam and reservoir passage by collecting and then transporting kelts downstream in barges or trucks. This effort is modeled after the smolt transportation program, a long-standing Snake River salmonid recovery effort (Ruckelshaus et al. 2002; Buchanan et al. 2006). In a transportation evaluation run concurrently with this project, transport benefits were highest for kelts with the longest migrations (i.e., those collected at Lower Granite Dam) and for wild-origin females (Evans et al. 2008). A second mitigation strategy, kelt reconditioning, involves culturing captive postspawned fish as they reinitiate feeding and redevelop mature gonads. Reconditioning has been successful with Arctic char (Boyer and Van Toever 1993), Atlantic salmon (Johnston et al. 1990; Crim et al. 1992; Moffett et al. 1996), and steelhead (Hatch et al. 2004). Our results suggest targeting females and (or) wild fish in these efforts may provide cost-effective recovery benefits.

In summary, the expression of iteroparity among interior Columbia River steelhead has persisted despite decades of impoundment-related selection pressures against this life history type. This is perhaps unsurprising given the broad phenotypic and reproductive plasticity of *O. mykiss* (e.g., Behnke 1992). The presented data suggest that hundreds to thousands of repeat spawners return to the Columbia River each year, with dispersal throughout the interior basin. Allocations of these fish among the basin's threatened populations and their relative reproductive contributions are currently unknown. However, the results show that repeat spawners are disproportionately female and of wild origin. These are desirable traits given greater reproductive success in wild steelhead (e.g., Chilcote 2003; Araki et al. 2007a, 2007b) and the tendency for females to be limiting in male-skewed populations (Fleming and Reynolds 2004). Efforts to recover protected populations in the basin should include provisions to promote the demographic, genetic, and stabilizing effects of iteroparity and, more generally, to encourage the full expression of steelhead life history diversity.

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References

- Altukhov, Y.P., Salmenkova, E.A., and Omelchenko, V.T. 2000. Salmonid fishes: population biology, genetics and management. Blackwell Science, Oxford, UK.
- Araki, H., Cooper, B., and Blouin, M.S. 2007a. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science* (Washington, D.C.), **318**: 100–103. doi:10.1126/science.1145621. PMID:17916734.
- Araki, H., Waples, R.S., Ardren, W.R., Cooper, B., and Blouin, M.S. 2007b. Effective population size of steelhead trout: influence of variance in reproductive success, hatchery programs, and genetic compensation between life-history forms. *Mol. Ecol.* **16**: 953–966. doi:10.1111/j.1365-294X.2006.03206.x. PMID:17305853.
- Arnekleiv, J.V., Kraabøl, M., and Museth, J. 2007. Efforts to aid downstream migrating brown trout (*Salmo trutta* L.) kelts and smolts passing a hydroelectric dam and a spillway. *Hydrobiologia*, **582**: 5–15. doi:10.1007/s10750-006-0547-8.
- Augerot, X. 2005. Atlas of Pacific salmon: the first map-based assessment of salmon in the north Pacific. University of California Press, Berkeley, Calif.
- Behnke, R.J. 1992. Native trout of western North America. *Am. Fish. Soc. Monogr.* **6**. Bethesda, Md.
- Boggs, C.T., Keefer, M.L., Peery, C.A., Bjornn, T.C., and Stuehrenberg, L.C. 2004. Fallback, reascension and adjusted fishway escapement estimates for adult chinook salmon and steelhead at Columbia and Snake River dams. *Trans. Am. Fish. Soc.* **133**: 932–949. doi:10.1577/T03-133.1.
- Booth, R.K., Bombadier, E.B., Mckinley, R.S., Scruton, D.A., and Gossney, R.F. 1997. Swimming performance of post spawning adult (kelts) and juvenile (smolts) Atlantic salmon, *Salmo salar*. *Can. Manuscr. Report Fish. Aquat. Sci.* 2406.
- Boyer, J.N., and Van Toever, W. 1993. Reconditioning of Arctic char (*Salvelinus alpinus*) after spawning. *Aquaculture*, **110**: 279–284. doi:10.1016/0044-8486(93)90376-A.
- Brannon, E.L., Powell, M.S., Quinn, T.P., and Talbot, A. 2004. Population structure of Columbia River Basin chinook salmon and steelhead trout. *Rev. Fish. Sci.* **12**: 99–232. doi:10.1080/10641260490280313.
- Buchanan, R.A., Skalski, J.R., and Smith, S.G. 2006. Estimating the effects of smolt transportation from different vantage points and management perspectives. *N. Am. J. Fish. Manage.* **26**: 460–472. doi:10.1577/M05-080.1.
- Buckland, S.T., Burnham, K.P., and Augustin, N.H. 1997. Model selection: an integral part of inference. *Biometrics*, **53**: 603–618. doi:10.2307/2533961.
- Budy, P., Thiede, G.P., Bouwes, N., Petrosky, C.E., and Schaller, H. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. *N. Am. J. Fish. Manage.* **22**: 35–51. doi:10.1577/1548-8675(2002)022<0035:ELDMOS>2.0.CO;2.
- Burgner, R.L., Light, J.T., Margolis, L., Okazaki, T., Tautz, A., and Ito, S. 1992. Distributions and origins of steelhead trout (*Oncorhynchus mykiss*) in offshore waters of the North Pacific Ocean. *Int. North Pac. Fish. Comm. Bull.* **51**.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- Busby, P.J., Wainwright, T.C., Bryant, E.J., Lierheimer, L.J., Waples, R.S., Waknitz, F.W., and Lagomarsino, I.V. 1996. Status review of west coast steelhead from Washington, Idaho, Oregon, and California. NOAA Tech. Memo. NMFS-NWFSC-27.
- Čada, G. 2001. The development of advanced hydroelectric turbines to improve fish passage survival. *Fisheries*, **26**: 14–23.
- Chilcote, M.W. 2003. Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (*Oncorhynchus mykiss*). *Can. J. Fish. Aquat. Sci.* **60**: 1057–1067. doi:10.1139/f03-092.
- Congleton, J.L., LaVoie, W.J., Schreck, C.B., and Davis, L.E. 2000. Stress indices in migrating juvenile Chinook salmon and steelhead of wild and hatchery origin before and after barge transportation. *Trans. Am. Fish. Soc.* **129**: 946–961. doi:10.1577/1548-8659(2000)129<0946:SIIMJC>2.3.CO;2.
- Cooke, S.J., Crossin, G.T., Patterson, D.A., English, K.K., Hinch, S.G., Young, J.L., Alexander, R.F., Healey, M.C., Van Der Kraak, G., and Farrell, A.P. 2005. Coupling non-invasive physiological assessments with telemetry to understand inter-individual variation in behaviour and survivorship of sockeye salmon: development and validation of a technique. *J. Fish Biol.* **67**: 1342–1358. doi:10.1111/j.1095-8649.2005.00830.x.
- Crespi, B.J., and Teo, R. 2002. Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. *Evolution*, **56**: 1008–1020. PMID:12093015.
- Crim, L.W., Wilson, C.E., So, Y.P., Idler, D.R., and Johnston, C.E. 1992. Feeding, reconditioning, and rematuration responses of captive Atlantic salmon (*Salmo salar*) kelt. *Can. J. Fish. Aquat. Sci.* **49**: 1835–1842. doi:10.1139/f92-203.
- Dempson, J.B., O'Connell, M.F., and Schwarz, C.J. 2004. Spatial and temporal trends in abundance of Atlantic salmon, *Salmo salar*, in Newfoundland with emphasis on impacts of the 1992 closure of the commercial fishery. *Fish. Manag. Ecol.* **11**: 387–402. doi:10.1111/j.1365-2400.2004.00407.x.
- Dodson, J.J. 1997. Fish migration: an evolutionary perspective. *In* Behavioural ecology of teleost fishes. Edited by J.-G.J. Godin. Oxford University Press, Oxford, UK. pp. 10–36.
- Downing, S., and Prentice, E. 2003. Overview of the performance of PIT-tag interrogation systems for adult salmonids at Bonneville and McNary Dams. Bonneville Power Administration, Portland, Ore. BPA Rep. DOE/BP-00013411-1.
- Dutil, J.-D. 1986. Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). *Copeia*, 1986(4): 945–955. doi:10.2307/1445291.
- English, K.K., Robichaud, D., Sliwinski, C., Alexander, R.F., Koski, W.R., Nelson, T.C., Nass, B.L., Bickford, S.A., Hammond, S., and Mosey, T.R. 2006. Comparison of adult steelhead migrations in the mid-Columbia hydrosystem and in large naturally flowing British Columbia rivers. *Trans. Am. Fish. Soc.* **135**: 739–754. doi:10.1577/T05-043.1.
- Evans, A.F. 2003. Development and application of steelhead (*Oncorhynchus mykiss*) kelt identification techniques. M.S. thesis, Oregon State University, Corvallis, Ore.
- Evans, A.F., Beaty, R.E., Fitzpatrick, M.S., and Collis, K. 2004a. Identification and enumeration of steelhead kelts at a Snake River hydroelectric dam. *Trans. Am. Fish. Soc.* **133**: 1089–1099. doi:10.1577/T03-121.1.
- Evans, A.F., Fitzpatrick, M.S., and Siddens, L.K. 2004b. Use of ultrasound imaging and steroid concentrations to identify maturational status in adult steelhead. *N. Am. J. Fish. Manage.* **24**: 967–978. doi:10.1577/M03-112.1.
- Evans, A.F., Wertheimer, R.H., Keefer, M.L., Boggs, C.T., Peery, C.A., and Collis, K. 2008. Transportation of steelhead kelts to increase iteroparity in the Columbia and Snake rivers. *N. Am. J. Fish. Manage.* In press.
- Ferguson, J.W., Matthews, G.M., McComas, R.L., Absolon, R.F., Brege, D.A., Gessel, M.H., and Gilbreath, L.G. 2005. Passage of adult and juvenile salmonids through federal Columbia River Power System dams. Northwest Fisheries Science Center, NOAA–Fisheries, Seattle, Wash. Rep. NMFS-NWFSC-64.

- Fleming, I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. *Rev. Fish Biol. Fish.* **6**: 379–416. doi:10.1007/BF00164323.
- Fleming, I.A. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. *Can. J. Fish. Aquat. Sci.* **55**(Suppl. 1): 59–76. doi:10.1139/cjfas-55-S1-59.
- Fleming, I.A., and Gross, M.R. 1994. Breeding competition in a Pacific salmon (coho: *Onchorhynchus kisutch*): measures of natural and sexual selection. *Evolution*, **48**: 637–657. doi:10.2307/2410475.
- Fleming, I.A., and Reynolds, J.D. 2004. Salmon breeding systems. *In Evolution illuminated: salmon and their relatives. Edited by A.P. Hendry and S.C. Stearns.* Oxford University Press, Oxford, UK. pp. 264–294.
- Gibbons, J.W., and Andrews, K.M. 2004. PIT tagging: simple technology at its best. *Bioscience*, **54**: 447–454. doi:10.1641/0006-3568(2004)054[0447:PTSTAI]2.0.CO;2.
- Good, T.P., Waples, R.S., and Adams, P. 2005. Updated status of federally listed ESUs of west coast salmon and steelhead. NOAA Tech. Memo. NMFS-NWFSC-66.
- Groot, C., and Margolis, L. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver, B.C.
- Hatch, D., Branstetter, R., Whiteaker, J., Blodgett, J., Bosch, B., Fast, D., and Newsome, T. 2004. Kelt reconditioning: a research project to enhance iteroparity in Columbia basin steelhead (*Oncorhynchus mykiss*). Bonneville Power Administration, Portland, Ore. Rep. DOE/BP-00004185-5.
- Hosmer, D.W., and Lemeshow, S. 2000. Applied logistic regression. 2nd ed. Wiley-InterScience, Hoboken, N.J.
- Johnston, C.E., Farmer, S.R., Gray, R.W., and Hambrook, M. 1990. Reconditioning and reproductive responses of Atlantic salmon kelts (*Salmo salar*) to photoperiod and temperature manipulation. *Can. J. Fish. Aquat. Sci.* **47**: 701–710. doi:10.1139/f90-079.
- Jonsson, B., and L'Abée-Lund, J.H. 1993. Latitudinal clines in life-history variables of anadromous brown trout in Europe. *J. Fish Biol.* **43**: 1–16.
- Jonsson, N., Hansen, L.P., and Jonsson, B. 1991. Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. *J. Anim. Ecol.* **60**: 937–947. doi:10.2307/5423.
- Keefer, M.L., Boggs, C.T., Peery, C.A., and Caudill, C.C. 2008a. Overwintering distribution, behavior, and survival of adult summer steelhead: variability among Columbia River populations. *N. Am. J. Fish. Manage.* **28**: 81–96. doi:10.1577/M07-011.1.
- Keefer, M.L., Peery, C.A., and Caudill, C.C. 2008b. Migration timing of Columbia River spring Chinook salmon: effects of temperature, river discharge, and ocean environment. *Trans. Am. Fish. Soc.* **137**: 1120–1133. doi:10.1577/T07-008.1.
- Kinnison, M.T., Unwin, M.J., and Quinn, T.P. 2003. Migratory costs and contemporary evolution of reproductive allocation in male chinook salmon. *J. Evol. Biol.* **16**: 1257–1269. doi:10.1046/j.1420-9101.2003.00631.x. PMID:14640417.
- Leider, S.A., Chilcote, M.W., and Loch, J.J. 1986. Comparative life history characteristics of hatchery and wild steelhead trout (*Salmo gairdneri*) of summer and winter races in the Kalama River, Washington. *Can. J. Fish. Aquat. Sci.* **43**: 1398–1409. doi:10.1139/f86-173.
- Lohr, S.C., and Bryant, M.D. 1999. Biological characteristics and population status of steelhead (*Oncorhynchus mykiss*) in Southeast Alaska. US Forest Service, Pacific Northwest Research Station, Portland, Ore. Gen. Tech. Rep. PNW-GTR-407.
- Long, J.B., and Griffin, L.E. 1937. Spawning and migratory habits of the Columbia River steelhead trout as determined by scale studies. *Copeia*, 1937(1): 62. doi:10.2307/1437376.
- McCormick, S.D., Hansen, L.P., Quinn, T.P., and Saunders, R.L. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **55**(Suppl. 1): 77–92. doi:10.1139/cjfas-55-S1-77.
- Meehan, W.R., and Bjornn, T.C. 1991. Salmonid distributions and life histories. *In Influences of forest and rangeland on salmonid fishes and their habitats. Edited by W.R. Meehan.* American Fisheries Society, Bethesda, Md. pp. 47–82.
- Mills, D. 1989. Ecology and management of Atlantic salmon. Chapman and Hall, New York.
- Moffett, I.J.J., Kennedy, G.J.A., and Crozier, W.W. 1996. Freshwater reconditioning and ranching of Atlantic salmon, *Salmo salar* L., kelts: growth and reproductive performance. *Fish. Manag. Ecol.* **3**: 35–44.
- Narum, S.R., Hatch, D., Talbot, A.J., Moran, P., and Powell, M.S. 2008. Iteroparity in complex mating systems of steelhead trout. *J. Fish Biol.* **72**: 45–60.
- National Marine Fisheries Service. 1997. Endangered and threatened species: listing of several evolutionarily significant units (ESUs) of west coast steelhead. *Fed. Regist.* **62**: 43937–43954.
- National Marine Fisheries Service. 2000. Endangered Species Act — Section 7 consultation. Biological opinion. Reinitiation of consultation on operation of the Federal Columbia River Power System, including the juvenile fish transportation program, and 19 Bureau of Reclamation projects in the Columbia Basin. National Marine Fisheries Service, Northwest Region, Seattle, Wash.
- Niemelä, E., Erkinaro, J., Julkunen, M., Hassinen, E., Lämsman, M., and Brørs, S. 2006. Temporal variation in abundance, return rate and life histories of previously spawned Atlantic salmon in a large subarctic river. *J. Fish Biol.* **68**: 1222–1240. doi:10.1111/j.0022-1112.2006.001012.x.
- Pirhonen, J., and Schreck, C.B. 2003. Effects of anaesthesia with MS-222, clove oil and CO₂ on feed intake and plasma cortisol in steelhead trout (*Oncorhynchus mykiss*). *Aquaculture*, **220**: 507–514. doi:10.1016/S0044-8486(02)00624-5.
- Prince, A., and Powell, C. 2000. Clove oil as an anesthetic for invasive field procedures on adult rainbow trout. *N. Am. J. Fish. Manage.* **20**: 1029–1032. doi:10.1577/1548-8675(2000)020<1029:COAAAF>2.0.CO;2.
- Quinn, T.P., and Adams, D.J. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. *Ecology*, **77**: 1151–1162. doi:10.2307/2265584.
- Quinn, T.P., Unwin, M.J., and Kinnison, M.T. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced chinook salmon populations. *Evolution*, **54**: 1372–1385. PMID:11005303.
- Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. American Fisheries Society, Bethesda, Md.
- Robards, M.D., and Quinn, T.P. 2002. The migratory timing of adult summer-run steelhead in the Columbia River over six decades of environmental change. *Trans. Am. Fish. Soc.* **131**: 523–536. doi:10.1577/1548-8659(2002)131<0523:TMTOAS>2.0.CO;2.
- Rounsefell, G.A. 1958. Anadromy in North American *Salmonidae*. *Fish. Bull. (Washington, D.C.)*, **131**: 171–185.
- Ruckelshaus, M.H., Levin, P., Johnson, J.B., and Kareiva, P.M. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. *Annu. Rev. Ecol. Syst.* **33**: 665–706. doi:10.1146/annurev.ecolsys.33.010802.150504.
- Schaffer, W.M., and Elson, P.F. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. *Ecology*, **56**: 577–590. doi:10.2307/1935492.

- Schaller, H.A., and Petrosky, C.E. 2007. Assessing hydrosystem influence on delayed mortality of Snake River stream-type Chinook salmon. *N. Am. J. Fish. Manage.* **27**: 810–824. doi:10.1577/M06-083.1.
- Scruton, D.A., Pennell, C.J., Bourgeois, C.E., Goosney, R.F., Porter, T.R., and Clarke, K.D. 2007. Assessment of a retrofitted downstream fish bypass system for wild Atlantic salmon (*Salmo salar*) smolts and kelts at a hydroelectric facility on the Exploits River, Newfoundland, Canada. *Hydrobiologia*, **582**: 155–169. doi:10.1007/s10750-006-0557-6.
- Shapovalov, L. and Taft, A.C. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. *Calif. Dep. Fish Game Fish. Bull.* 98.
- Stearley, R.F. 1992. Historical ecology of Salmoninae, with special reference to *Oncorhynchus*. In *Systematics, historical ecology, and North American freshwater fishes*. Edited by R.L. Mayden. Stanford University Press, Stanford, Calif. pp. 622–658.
- Venditti, V.A., Rondorf, D.W., and Kraut, J.M. 2000. Migratory behavior and forebay delay of radio-tagged juvenile fall Chinook salmon in a lower Snake River impoundment. *N. Am. J. Fish. Manage.* **20**: 41–52. doi:10.1577/1548-8675(2000)020<0041:MBAFDO>2.0.CO;2.
- Wagner, T., and Congleton, J.L. 2004. Blood chemistry correlates of nutritional condition, tissue damage, and stress in migrating juvenile chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* **61**: 1066–1074. doi:10.1139/f04-050.
- Wedemeyer, G.A., Saunders, R.L., and Clarke, W.C. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. *Mar. Fish. Rev.* **42**: 1–14.
- Wertheimer, R.H. 2007. Evaluation of a surface flow bypass system for steelhead kelt passage at Bonneville Dam, Washington. *N. Am. J. Fish. Manage.* **27**: 21–29. doi:10.1577/M05-216.1.
- Wertheimer, R.H., and Evans, A.F. 2005. Downstream passage of steelhead kelts through hydroelectric dams on the lower Snake and Columbia rivers. *Trans. Am. Fish. Soc.* **134**: 853–865. doi:10.1577/T04-219.1.
- Whitt, C.R. 1954. The age, growth, and migration of steelhead trout in the Clearwater River, Idaho. M.S. thesis, University of Idaho, Moscow, Idaho.
- Wilbur, H.M., and Rudolf, H.W. 2006. Life-history evolution in uncertain environments: bet hedging in time. *Am. Nat.* **168**: 398–411. doi:10.1086/506258. PMID:16947114.
- Willson, M.F. 1997. Variation in salmonid life histories: patterns and perspectives. US Forest Service, Pacific Northwest Research Station, Portland, Ore. Res. Pap. PNW-RP-498.
- Withler, I.L. 1966. Variability in life history characteristics of steelhead trout (*Salmon gairdneri*) along the Pacific coast of North America. *J. Fish. Res. Board Can.* **23**: 365–393.