TECHNICAL REPORT 2008-13

IDAHO COOPERATIVE FISH AND WILDLIFE RESEARCH UNIT

A MULTI-YEAR SUMMARY OF STEELHEAD KELT STUDIES IN THE COLUMBIA AND SNAKE RIVERS

C. T. Boggs, M. L. Keefer, C. A. Peery
Idaho Cooperative Fish and Wildlife Research Unit
Department of Fish and Wildlife Resources
University of Idaho, Moscow, Idaho 83844-1141, USA

J. T. Dalen, P. L. Madson, R. H. Wertheimer
U.S. Army Corps of Engineers
PO Box 2946
Portland, Oregon, 97208, USA

K. Collis, A. F. Evans
Real Time Research, Inc.
52 SW Roosevelt Ave
Bend, Oregon, 97702, USA

For

U.S. Army Corps of Engineers
Portland and Walla Walla Districts

2008

A MULTI-YEAR SUMMARY OF STEELHEAD KELT STUDIES IN THE COLUMBIA AND SNAKE RIVERS

Prepared by:

R. H. Wertheimer
U.S. Army Corps of Engineers
PO Box 2946
Portland, Oregon, 97208, USA

and

C. T. Boggs, M. L. Keefer, C. A. Peery
Idaho Cooperative Fish and Wildlife Research Unit
Department of Fish and Wildlife Resources
University of Idaho, Moscow, Idaho 83844-1141, USA

and

K. Collis, A. F. Evans
Real Time Research, Inc.
52 SW Roosevelt Ave
Bend, Oregon, 97702, USA

Prepared for:

U.S. Army Corps of Engineers
Portland and Walla Walla Districts

December 2008

Table of Contents

Table of Contents (cont.)

Executive Summary

This report summarizes results of research activities conducted from 2000-2004 and subsequent years o repeat spawner returns. The collaborative projects were undertaken to aid in the management and recovery of steelhead kelts (*Oncoryhnchus mykiss*) in the Columbia River basin. For additional project details, we refer the reader to the annual reports.

Peer-reviewed publication is an important priority for the staff at our respective organizations because publication provides our results to a wide audience and ensures that the work meets high scientific standards. Therefore, this report was prepared with the intention that two manuscripts would eventually be submitted to fisheries journals. Since this writing, both chapters have been accepted at journals and we refer the reader to those papers for the definitive references. The report includes supplementary material that was not included in the peer-reviewed versions.

Keefer, M. L., R. H. Wertheimer, A. F. Evans, C. T. Boggs, and C. A. Peery. 2008. Iteroparity in Columbia River summer-run steelhead (*Oncorhynchus mykiss*): implications for conservation. Canadian Journal of Fisheries and Aquatic Sciences 65:2592-2605.

Evans, A. F., R. H. Wertheimer, M. L. Keefer, C. T. Boggs, C. A. Peery, and K. Collis. 2008. Transportation of steelhead kelts to increase iteroparity in the Columbia and Snake rivers. North American Journal of Fisheries Management 28:1818-1827.

Acknowledgements

Many people provided time and assistance during the course of this study. The project was funded by the U.S. Army Corps of Engineers. We would like to thank T. Wik, M. Shutters, R. Baxter, and R. Kalamacz for their assistance, as well as M. Halter, J. Harmon and the staff at Lower Granite Dam and R. Cordie, M. Zyndol and the staff at John Day Dam. We are grateful to M. Jonas, B. Winans, E. O'Brien, C. Naumann and J. Sandquist for their field work, G. Nardacci (Normandeau Associates) for project oversight, and R. Beaty (Bonneville Power Administration) for his innovative ideas regarding this research. We also thank the staff of the Columbia River Inter-Tribal Fish Commission. B. Burke and S. McCarthy (NOAA-Fisheries) and M. Jepson and K. Tolotti (University of Idaho) helped manage the telemetry database.

CHAPTER 1

ITEROPARITY IN COLUMBIA RIVER SUMMER-RUN STEELHEAD (*ONCORHYNCHUS MYKISS*): SUMMARY OF 2001-2004 KELT STUDIES

Abstract

We used ultrasound imaging and tagging programs to assess maturation status, postspawn migration behaviors, and iteroparity patterns in summer-run steelhead (*Oncorhynchus mykiss*) of the interior Columbia River basin. Over four years, 13,193 adult steelhead were examined in fish bypass systems (collected while moving downstream) at three Columbia and Snake River dams. Of these, 89% were postspawn kelts. Kelts were disproportionately female (>80%) and majorities were of wild origin, unlike prespawn steelhead we inspected at these sites. Annual iteroparity estimates varied from 2.9–9.0% for kelts PIT-tagged at lower Columbia River dams (n = 2,542) and from 0.5–1.2% for Snake River kelts (n =3,762). Among-site differences correlated with greater outmigration distance and additional dam passage hazards for Snake River kelts. There was strong evidence for condition-dependent mortality, with iteroparity rates an order of magnitude higher for good- versus poor-condition kelts. Proportionately more females and wild fish also returned, providing potentially valuable genetic and demographic benefits for the Columbia's threatened steelhead populations. Results overall provide baseline data for evaluating kelt mortality mitigation efforts and basic life history information for steelhead conservation planning.

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 semelparity believed to have developed last in response to several inter-related selective pressures (Stearley 1992). These include increased energetic costs associated with anadromy, long-distance migration, and breeding competition, and 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 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; Niemalä et al. 2006). Iteroparous individuals may also be more productive than semelparous conspecifics due to 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; Fleming 1998).

The benefits of iteroparity are unrealized in many anadromous populations because human activities typically select against repeat spawning by increasing adult and kelt (postspawned adult) mortality (Altukhov et al. 2000; Crespi and Teo 2002). For example, harvest rates often differ among maiden and repeat spawners due to 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; Arnekliev 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, *O. 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 ~1,500 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 rates 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 pre-dam 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 ≤ 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; Busby et al. 1996).

In this paper, we address some of the basic iteroparity information gaps in the aggregated summer-run steelhead population of the interior Columbia River basin. The data were collected in a series of research projects evaluating kelt abundance, outmigration timing and survival, and repeat spawner abundance. Specific objectives included describing: (1) kelt abundance and outmigration timing in the main stems of the Columbia and Snake rivers; (2) kelt outmigration survival, behaviors, passage times, and passage routes at dams; (3) variability in return rates, breeding interval, and return timing of repeat spawners; and (4) associations between return rates, kelt characteristics (i.e., condition, coloration, length, sex, hatchery versus wild origin, migration timing), and collection location and year. Our emphasis here is on return rates (objectives 3 and 4), as kelt abundance and survival data were described by Evans et al. (2004a), Wertheimer and Evans (2005), and Wertheimer (2007).

Methods

Fish collection and tagging

Adult steelhead (both kelts and prespawners) 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 (Figure 1). These sites were 347, 470, and 695 kilometers from the Pacific Ocean, respectively. Sampling occurred from mid-March or early April through late May or mid-June in four years at John Day Dam (2001-2004) and three years each at McNary (2001-2002, 2004) and Lower Granite (2002-2004) dams (Figure 2). Fish were directly diverted (John Day) or transferred via dip net or flumes (McNary, Lower Granite) to nearby tanks containing aerated river water and anesthetic (60 ppm tricaine methanesulfonate [MS-222] or 30 $mg \bullet L^{-1}$ 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 et al. 2003), while coloration was based on the degree of the fish's silvery, ocean-like external appearance (Evans et al. 2003). 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 postspawn 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. PIT tags were used because retention rates are high, tag life is unrestricted, and negative tag effects are minimal (Gibbons and Andrews 2004). In addition to PIT-tagging, 6-38% of sampled kelts were radio-tagged using the external harness and suture methods of Wertheimer and Evans (2005). Transmitters weighed 1.5-2.1 g in water and were 20-29 mm long (Lotek Wireless, Inc., Newmarket, Ontario). Kelts selected for radio-tagging were disproportionately in good or fair condition in an effort to maximize data collection (see Results). Kelts were radio-tagged in 2001, 2002, and 2004 at John Day and McNary dams and in 2002 and 2003 at Lower Granite Dam (Figure 2). 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.

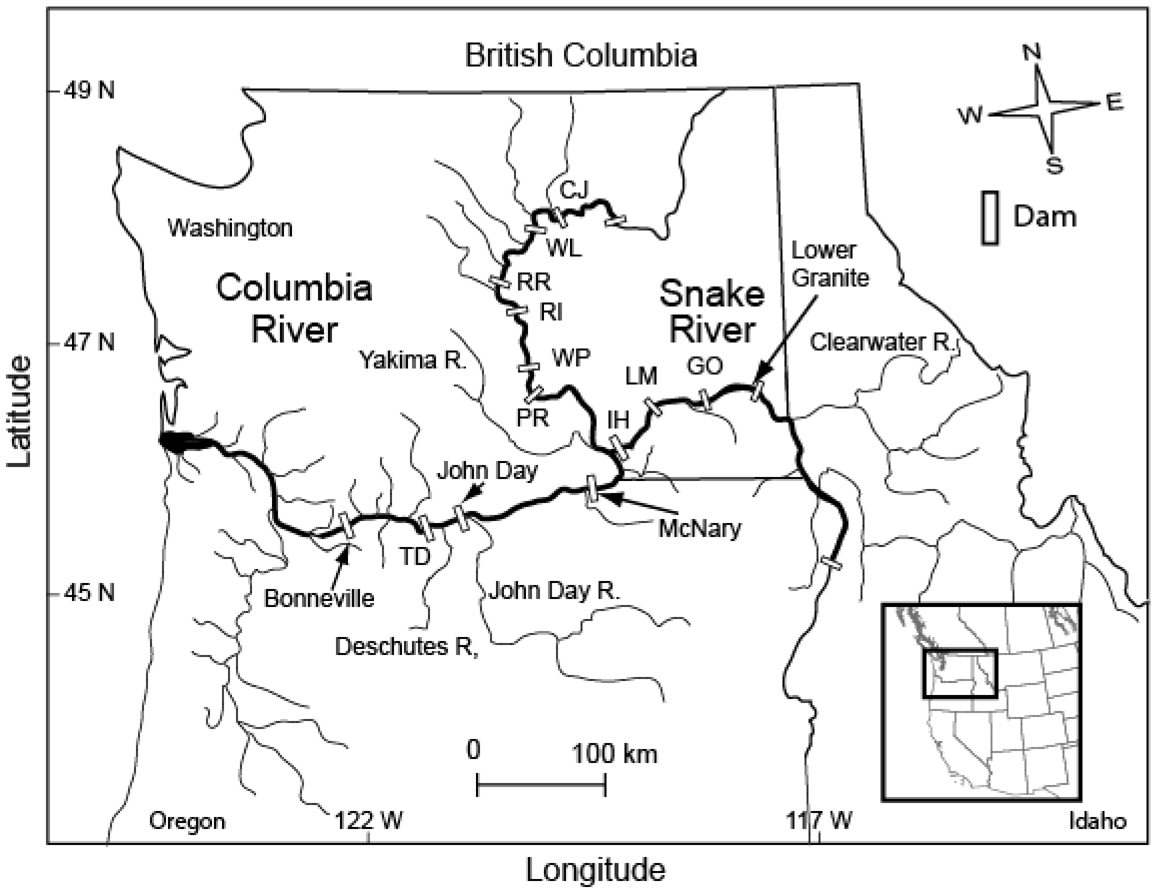

Figure 1. Map of the Columbia and Snake rivers showing main stem dams and major tributaries mentioned in the text. Steelhead (*Oncorhynchus mykiss*) kelts were collected at John Day, McNary, and Lower Granite dams in 2001-2004. Repeat spawners were detected at PIT-tag interrogators at Bonneville, McNary, Ice Harbor (IH), Lower Granite, Priest Rapids (PR), Rock Island (RI), and/or Wells (WL) dams in 2001-2005. Other dams: WP = Wanapum; RR = Rocky Reach; CJ = Chief Joseph; LM = Lower Monumental; GO = Little Goose.

Kelt and repeat spawner monitoring

Radio-tagged kelts were monitored during outmigration using a series of fixed-site antennas in the forebays and tailraces of Columbia and Snake River dams, with the most complete coverage at Bonneville, The Dalles, and John Day dams (Figure 1). Telemetry sites were used to assess downstream passage routes, kelt migration times past and between dams, and survival rates (largely described in Wertheimer and Evans 2005 and Wertheimer 2007). Here we used kelt downstream passage information from telemetered kelts to investigate potential associations between kelt passage routes and return rates.

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. 2008). 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 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 affects of kelt handling/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 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 disproportionate 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 ΔAIC, 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.

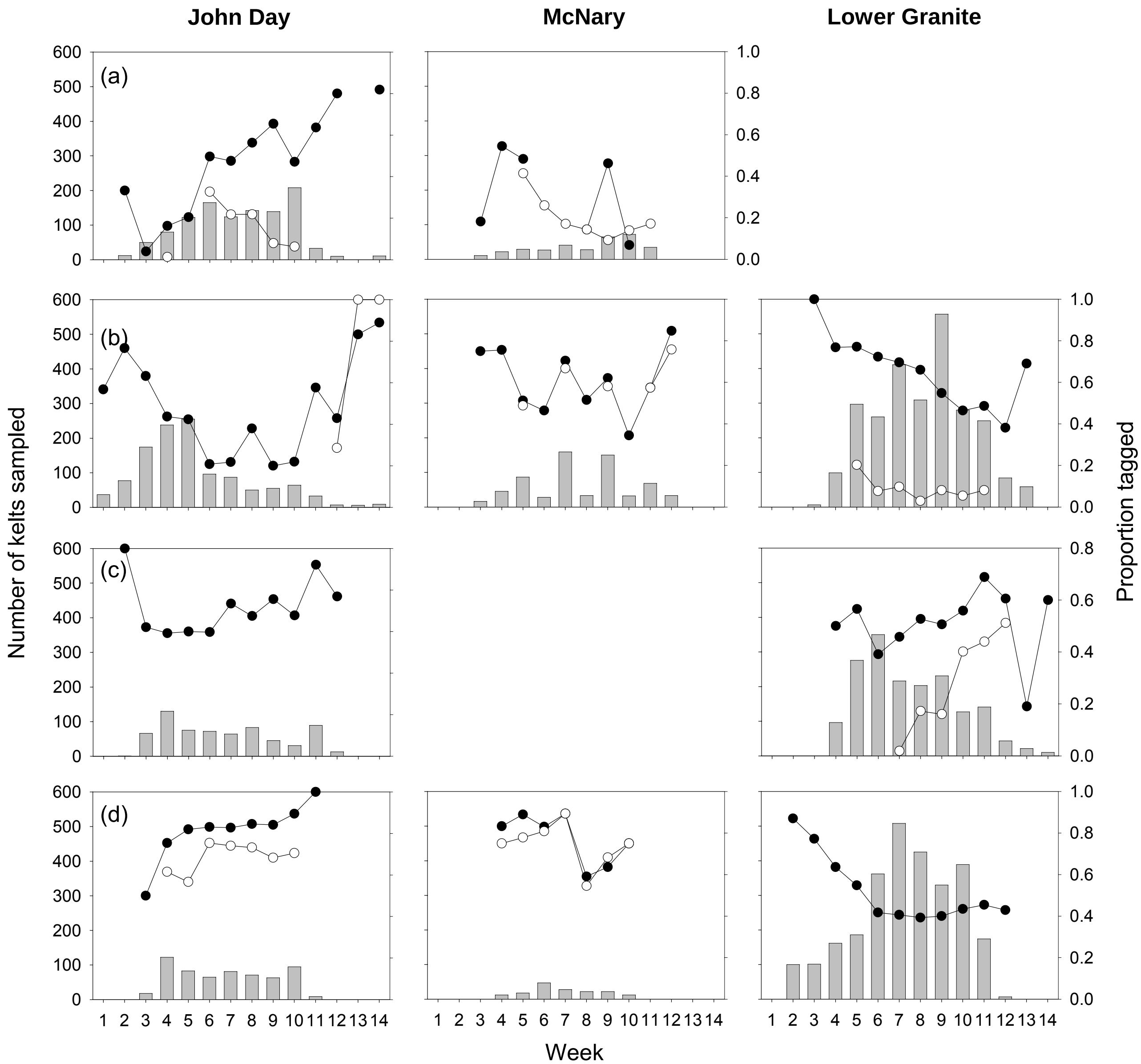

Figure 2. Numbers of steelhead (*Oncorhynchus mykiss*) kelts sampled at John Day, McNary and Lower Granite dams (bars) in 2001-2004, with the proportions that were PIT-tagged (●) and/or radio-tagged (○). Rows (a) = 2001; (b) = 2002; (c) = 2003; (d) = 2004. (Week 1 = 18-24 March. Week 14 = 17-23 June.)

Pearson chi-square tests and logistic regression were used to compare return migration percentages for radio-tagged kelts that used different downstream passage routes at John Day, The Dalles, and Bonneville dams. These analyses were restricted by small sample sizes of returning steelhead for some kelt outmigration routes and strong seasonal differences in route use. Fisher's exact tests were used in cases with small samples, and test results were reported when they differed from the Pearson tests.

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 due to the fish’s additional winter at sea). Consecutive- and skip return percentages were compared among kelt release sites and among years using chi-square tests. Outmigration and return migration timing distributions for these groups were compared using Kruskall-Wallis tests.

Results

Maturation status

We evaluated the maturation status of 13,193 adult steelhead collected at John Day (n = 4,394, four years), McNary (n = 1,390, three years) and Lower Granite (n = 7,409, three years). A maturation status determination (prespawner vs. kelt) was made for 99% of the total sample. Across years, 81-82% of John Day and McNary samples and 95% of the Lower Granite sample were determined to be kelts; 1% of all fish were undetermined. Prespawners were more numerous in late March to early April, when they made up 30-60% of samples at all sites (Figure 3). Thereafter, 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 vs. 31% of 3,560 kelts) and Lower Granite (61% of 317 prespawners vs. 48% of 7,068 kelts) dams, but not at McNary Dam (31% of 248 prespawners vs. 34% of 1,141 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 to indicate sex (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, 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 (Table 1).

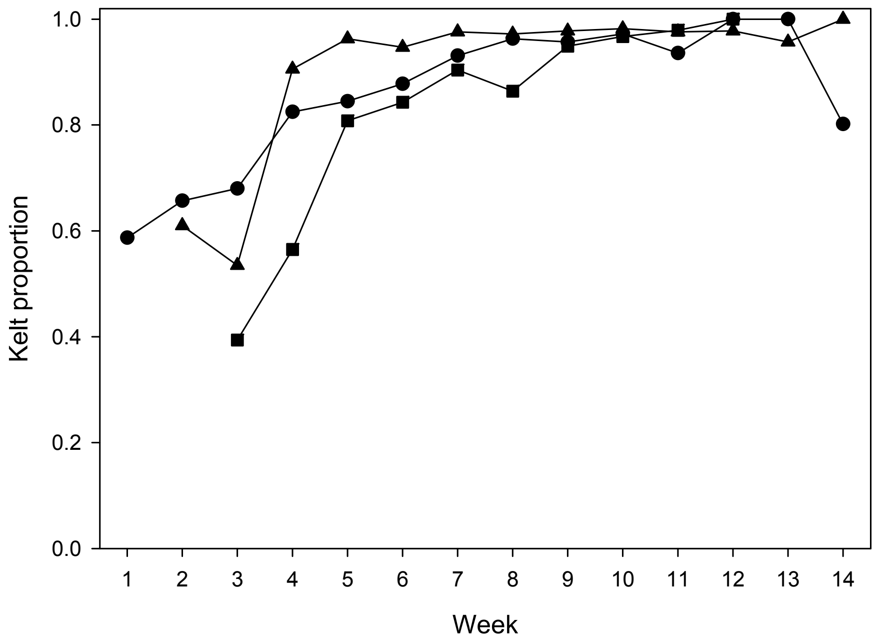

Figure 3. Mean weekly proportions of all steelhead (*Oncorhynchus mykiss*) sampled in juvenile bypass systems that were considered kelts at John Day (●), McNary (■) and Lower Granite (▲) dams by sampling week. All years combined. (Week 1 = 18-24 March. Week 14 = 17-23 June.)

Kelt condition (good, fair, poor) was better overall for fish at Lower Granite (44% good condition) and McNary (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×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 (Table 2).

Kelt origin varied within season in several ways. Percentages of wild kelts increased with increasing migration date at John Day and McNary dams, from ~60% early in the migrations to ~80% during the last sampling weeks (Figure 4). At Lower Granite Dam, the mean wild kelt percentage decreased from ~60% early in the migration to ~30% in mid-season 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 (Appendix 1). 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 (Appendix 1).

Table 1. Origin, sex, and condition summaries for all steelhead (*Oncorhynchus mykiss*) kelts sampled annually from 2001-2004, including the total sub-samples of PIT- and radio-tagged fish.

			Origin (%)		Sex (%)			Condition (%)			
Dam	Year	*n*	Wild	Hatchery	F	M	U	Dead	Poor	Fair	Good
John Day	2001	1,096	76	24	57	5	39	2	26	24	48
	2002	1,188	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	**3,560**	**69**	**31**	**62**	**10**	**28**	**3**	**38**	**23**	**36**
	PIT	***1,946***	***71***	***29***	***63***	***11***	***27***	***-***	***25***	***27***	***47***
	Radio	***516***	***80***	***20***	***66***	***10***	***25***	***-***	***9***	***31***	***60***
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	**1,141**	**66**	**34**	**67**	**10**	**23**	**2**	**36**	**16**	**46**
	PIT	***596***	***71***	***29***	***73***	***11***	***17***	***-***	***11***	***23***	***66***
	Radio	***437***	***68***	***32***	***78***	***8***	***14***	***-***	***8***	***24***	***68***
L. Granite	2002	2,610	51	50	83	17	-	-	24	28	48
	2003	1,714	50	50	83	17	-	-	27	26	46
	2004	2,744	56	45	84	16	-	-	18	42	40
	Total	**7,068**	**52**	**48**	**83**	**17**	**-**	**-**	**22**	**33**	**44**
	PIT	***3,762***	***53***	***47***	***84***	***16***	***-***	***-***	***11***	***38***	***51***
	Radio	***424***	***57***	***43***	***82***	***18***	***-***	***-***	***10***	***30***	***59***

Table 2. Kelt fork length summary, by collection site, year, sex, and origin. Unknown-sex fish not included.

		Wild				Hatchery			
		Male		Female		Male		Female	
Site	Year	*n*	*Mean*	*n*	*Mean*	*n*	*Mean*	*n*	*Mean*
John Day	2001	37	56.8	477	62.4	14	58.4	137	61.7
	2002	79	58.3	427	60.5	62	61.7	328	60.1
	2003	47	60.9	328	66.6	14	57.3	130	62.3
	2004	67	57.7	272	60.1	33	58.1	96	60.7
	Total	**330**	**58.4**	**691**	**60.9**	**123**	**59.9**	**1504**	**62.4**
McNary	2001	9	57.7	118	62.3	7	57.6	55	64.4
	2002	57	59.4	315	60.9	14	62.4	167	58.6
	2004	21	57.2	77	61.1	3	65.0	36	58.4
	Total	**87**	**58.7**	**510**	**61.2**	**24**	**61.3**	**258**	**59.8**
L. Granite	2002	273	62.7	1044	65.1	167	60.6	1126	62.3
	2003	131	62.9	723	69.8	165	59.7	695	62.4
	2004	236	61.8	1286	69.1	208	58.6	1014	61.5
	Total	**640**	**62.4**	**3053**	**67.9**	**540**	**59.6**	**2835**	**62.0**

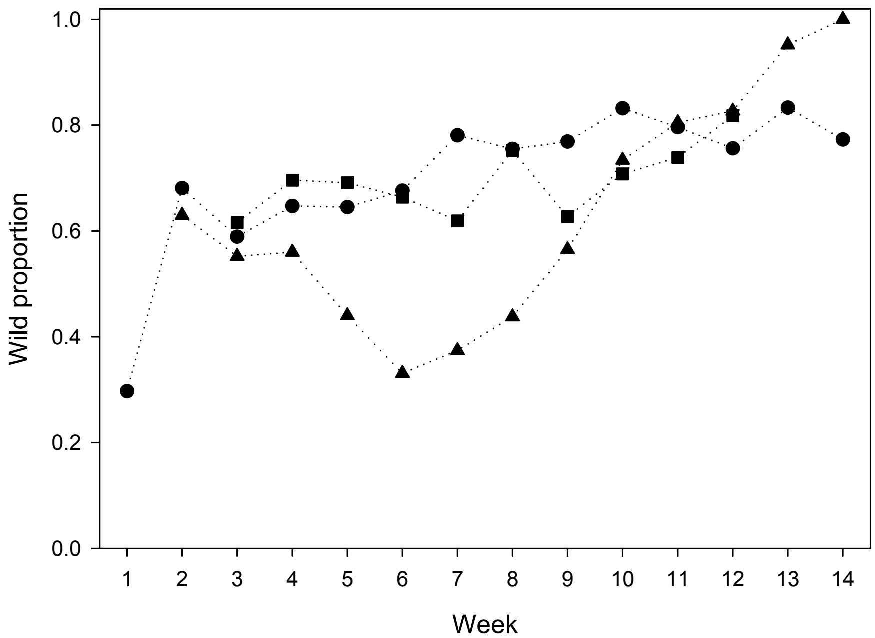

Figure 4. Mean weekly proportions of all sampled kelts that were of presumed wild origin at John Day (●), McNary (■) and Lower Granite (▲) dams by sampling week.

Kelt tagging

At each site, 52-55% of all sampled kelts were PIT-tagged (*n* = 1,946 at John Day; 596 at McNary; 3,762 at Lower Granite) and 6-38% were radio-tagged (*n* = 516, John Day; 437, McNary; 424, Lower Granite) (Table 1). Tagging percentages for both tag types (i.e., telemetry and PIT) varied across weeks and years and among dams (Figure 2) as a result of personnel availability and evolving study objectives, including a kelt transportation evaluation for which additional kelts were tagged (see Chapter 2). Across years, PIT-tagging effort was most consistent at Lower Granite Dam, was most variable at McNary Dam, and was relatively high early and late in the migrations at John Day Dam. At all sites, kelts selected for PIT tagging were more likely than the full kelt samples to be in good or fair condition; those selected for radio-tagging were in the best overall condition (Table 1). Selection for kelts in good/fair condition resulted in higher percentages of tagged wild and female kelts compared to 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.

Return rates for PIT-tagged kelts

Across release sites and years, 164 of 6,304 (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 capture site, kelt condition, and release week were the most influential predictors of returns (Table 3). Odds ratios showed kelts tagged at John Day Dam were 5.9 and 3.9 times more likely to return than those tagged at

Lower Granite or McNary dams, respectively. Kelts in good or fair condition were > 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 3), while fish length and sex were non-significant terms in the full model.

Table 3. Results of multiple logistic regression model to predict repeat spawner returns of steelhead (*Oncorhynchus mykiss*) kelts using all fish PIT-tagged in all years. Predictor variables included collection location, year, week, and kelt condition, color, origin, sex, and fork length. River discharge and dam spill terms were excluded because these variables varied across sites. (Note: 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.)

Effect	*df*	χ^2	*P*	Effect	Odds ratio	95% CI
Tagsite	2	48.79	<0.001	John Day vs. L. Granite	5.88	3.73-9.67
				McNary vs. L. 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

Although sex was not included in the full logistic regression model, proportionately more females than males returned from all release sites (2.30% vs. 1.22%), and females returned at higher rates than males at all sites in all years (Table 4). These differences, however, were not significant in univariate tests with all years combined or for any individual site×year sample ($P \geq 0.10$; male vs. female only, Table 4). The presence of unknown sexed fish at two of three study sites, however, may have affected this non-significant finding, especially given evidence that unsexed fish were disproportionately female (based on external characteristics) and unsexed fish returned at the highest rates. When sex data was limited to kelts tagged at Lower Granite (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% (106/1,946) for John Day releases, 5.37% (32/596) for McNary releases and 0.69% (26/3,762) for Lower Granite releases (Table 4). 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 4). 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 4). Condition effects were consistent for individual site×year samples (Table 4) and across most combinations of sex and origin (Table 5). Wild kelts returned at higher rates than hatchery kelts from all release sites (5.98% vs. 4.12%, John Day; 6.38% vs. 2.89%, McNary; 0.95% vs. 0.40%, Lower Granite; Table 5). This pattern was significant for the Lower Granite sample with all years combined (χ^2 = 4.22, *P* = 0.040) and the John Day sample in 2001 (χ^2 = 3.98, *P* = 0.046).

Table 4. Summary of steelhead (*Oncorhynchus mykiss*) return rates, by kelt PIT-tagging site, outmigration year, sex, origin, and condition.

		Year				
Dam	Variable	2001	2002	2003	2004	**Total**
John Day	Female	7.72 (298)	5.59 (322)	2.32 (302)	4.00 (300)*	**4.91 (1,222)***†
	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 (1,388)**†
	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 (1,946)**†
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)**
L. Granite	Female	-	0.59 (1,350)	0.41 (740)	1.29 (1,083)	**0.79 (3,173)**
	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 (1,995)***
	Hatchery	-	0.48 (837)	0.00 (385)	0.55 (545)	**0.40 (1,767)***
	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 (1,419)***
	Good	-	1.04 (769)*	0.57 (528)	1.89 (635)	**1.19 (1,932)***
	Total	-	**0.49 (1,617)**	**0.35 (868)**	**1.17 (1,277)**	**0.69 (3,762)**†

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

To evaluate the relative effects of kelt characteristics, migration year, and migration timing, we compared site-specific univariate and multiple logistic regression models using AIC. Only fish in good condition (83% of all returning fish) were included to minimize the effects of sampling bias. Among univariate predictors, outmigration week was the most informative for all release sites (Table 6). Earlier migrants were more likely to return in all cases, with odds ratios of 0.89 (95% CI = 0.81-0.97; χ^2 = 7.03; P = 0.008) for John Day, 0.84; (0.70-0.99; χ^2 = 3.88; P = 0.049) for McNary and 0.75 (0.63-0.90; χ^2 = 9.93; P = 0.002) for Lower Granite releases.

Table 5. Percentages of PIT-tagged steelhead (*Oncorhynchus mykiss*) that returned by kelt PIT-tagging site, sex, origin, and condition pooled across years.

			Percent that returned (*n*)			Among-group	
Dam	Origin	Sex	Poor	Fair	Good	χ^2	*P*
John Day	Wild	M	0.00 (49)	0.00 (46)	11.90 (42)	11.74	0.003
		F	0.50 (201)	3.64 (220)	8.97 (446)	20.89	< 0.001
		U	0.00 (66)	5.56 (108)	10.95 (210)	9.49	0.009
	Hatchery	M	0.00 (34)	0.00 (16)	0.00 (20)	-	-
		F	0.00 (112)	3.70 (108)	5.19 (135)	5.67	0.059
		U	0.00 (27)	5.41 (37)	14.49 (69)	5.78	0.056
McNary	Wild	M	25.00 (4)	0.00 (22)	3.85 (26)	5.72	0.057
		F	0.00 (34)	3.64 (55)	9.55 (220)	5.30	0.071
		U	0.00 (6)	0.00 (12)	4.55 (44)	0.85	0.655
	Hatchery	M	0.00 (2)	0.00 (5)	0.00 (4)	-	-
		F	0.00 (14)	0.00 (33)	3.90 (77)	1.88	0.391
		U	0.00 (5)	7.69 (13)	5.00 (20)	0.43	0.805
Lower Granite	Wild	M	0.00 (62)	0.00 (130)	0.65 (153)	1.26	0.533
		F	0.00 (102)	0.32 (625)	1.73 (923)	8.10	0.017
	Hatchery	M	0.00 (33)	0.00 (105)	0.00 (106)	-	-
		F	0.00 (214)	0.18 (559)	0.80 (750)	3.85	0.146

Among the a priori models, the model with all six terms was the most parsimonious for John Day releases (Table 6). 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 6). The model for the John Day sample (Week + Length + Color) indicated the kelts most likely to return were early migrating (χ^2 = 8.97; P = 0.003), bright colored (χ^2 = 8.76; P = 0.013), and relatively smaller (χ^2 = 3.72; P = 0.054). The McNary model (Week) indicated returns were highest for early outmigrants (χ^2 = 3.88; P = 0.049), and the Lower Granite model (Week + Origin) indicated wild (χ^2 = 3.88; P = 0.049), early migrants (χ^2 = 10.94; P < 0.001) were most likely to return (Table 6).

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×length, week×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 6.

Return rates for radio-tagged kelts

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. However, none of 347 radio-tagged kelts from Lower Granite returned, though this result might be expected given returns for all tagged fish were just 0.69%.

Downstream passage routes for radio-tagged kelts were estimated at John Day, The Dalles, and Bonneville dams. In general, routes were not significantly associated with differing return rates, but analyses were confounded by small route-specific sample sizes, within-season differences in route use, and limitations in telemetry coverage. For example, early migrants were more likely to encounter no-spill conditions, to pass via turbines, and also to return. With all years combined, the highest returns by route at John Day Dam were for the juvenile bypass facility (6.7%, n = 10) and via unknown routes (9.1%, n = 22); none of 14 fish that passed through turbines returned. The route associated with the highest return rate at The Dalles Dam was unknown (22.2%, n = 45) followed by the spillway (6.5%, n = 572); none of 25 fish that passed via turbines returned. At Bonneville Dam, kelts that used the juvenile bypass had the highest return (14.5%, n = 76), followed by those that passed via turbines (7.5%, n = 93). An estimated 191 fish used the surface-flow corner collector at Bonneville Dam (2004 only) and 6.3% returned (Table 7).

Table 6. Logistic regression model selection and comparison statistics used to predict if steelhead (*Oncorhynchus mykiss*) kelts in ‘good’ condition returned to spawn, by collection site. 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).

		John Day		McNary		Lower Granite	
Model	*df*	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC
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	n/a[a]	n/a[a]	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	n/a[a]	n/a[a]	253.7	12.9
Year + Week + Origin + Sex + Length + Color	8-10	561.5	3.7	n/a[a]	n/a[a]	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

[a] No ‘dark’ kelts returned to McNary

Migration timing and distribution of repeat spawners

Of 164 PIT-tagged kelts that returned as repeat spawners, 57% (n = 94) were consecutive repeat spawners and 43% (n = 70) were skip repeat spawners. Kelts tagged at John Day Dam were more likely be consecutive spawners (65%) than those tagged at McNary (47%) or Lower Granite (38%) (χ^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; χ^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, 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.

Table 7. Percentages of steelhead (*Oncorhynchus mykiss*) kelts radio-tagged at John Day, McNary or Lower Granite dams (2001, 2002, 2004[1]) that returned to spawn, based on their estimated downstream passage routes. (Note: bias for fish in fair/good condition.)

	Percent that returned (*n*)			
Estimated route	2001	2002	2004	Total
John Day Dam				
Juvenile bypass		6.7 (15)		6.7 (15)
Spillway		6.4 (188)	4.6 (88)	5.8 (276)
Turbine		0.0 (13)	0.0 (1)	0.0 (14)
Unknown/Other		11.1 (9)	7.7 (13)	9.1 (22)
χ^2		*1.2*	*0.3*	*1.3*
P		*0.742*	*0.864*	*0.725*
The Dalles Dam				
Sluiceway	0.0 (14)	0.0 (14)	4.0 (25)	1.9 (53)
Spillway	5.3 (38)	8.3 (192)	5.6 (342)	6.5 (572)
Turbine	0.0 (11)	0.0 (12)	0.0 (2)	0.0 (25)
Unknown/Other	22.2 (45)			22.2 (45)
χ^2	*10.1*	*2.3*	*0.2*	*20.5*
P	*0.018*	*0.311*	*0.894*	*< 0.001*
Bonneville Dam				
Juvenile bypass	23.3 (30)	12.9 (31)	0.0 (15)	14.5 (76)
Corner collector[2]	-	-	6.3 (191)	6.3 (191)
Sluiceway	18.2 (11)	0.0 (15)	0.0 (15)	4.9 (41)
Spillway	8.3 (24)	5.6 (144)	5.2 (97)	5.7 (265)
Turbine	2.6 (38)	13.0 (23)	9.4 (32)	7.5 (93)
Navigation lock			0.0 (1)	0.0 (1)
χ^2	*7.7*	*4.5*	*2.9*	*7.8*
P	*0.053*	*0.211*	*0.723*	*0.171*

[1] Downstream passage routes were not monitored in 2003
[2] Bonneville corner collector route available in 2004 only

Consecutive spawners outmigrated earlier as kelts than skip spawners (Figure 5), with median outmigration dates earlier by 11 d (John Day releases), 7 d (McNary releases) and 16 d (Lower Granite releases) with all years combined (*P* ≤ 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 (Figure 6). Median return dates at Bonneville Dam for consecutive returns were 33 d (John Day releases), 45 d (McNary releases), and 28 d (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 Lower Granite Dam (*P* = 0.079). Patterns were similar for the majority of individual site×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 (except that 1 of 2 returns from the 2002 Lower Granite release were detected) (Figure 7). Mean annual detections at McNary Dam ranged from 36% for John Day releases to 97% for McNary releases. Detections at Snake River dams were 8-23% for John Day and McNary releases versus 63-80% for Lower Granite releases, suggesting many kelts tagged at the lower Columbia River dams originated from sites other than the Snake River. Detections at mid-Columbia River dams ranged from 2-7% of John Day and McNary releases on average, except 26% of McNary-released fish were detected at Priest Rapids Dam in 2003-2005.

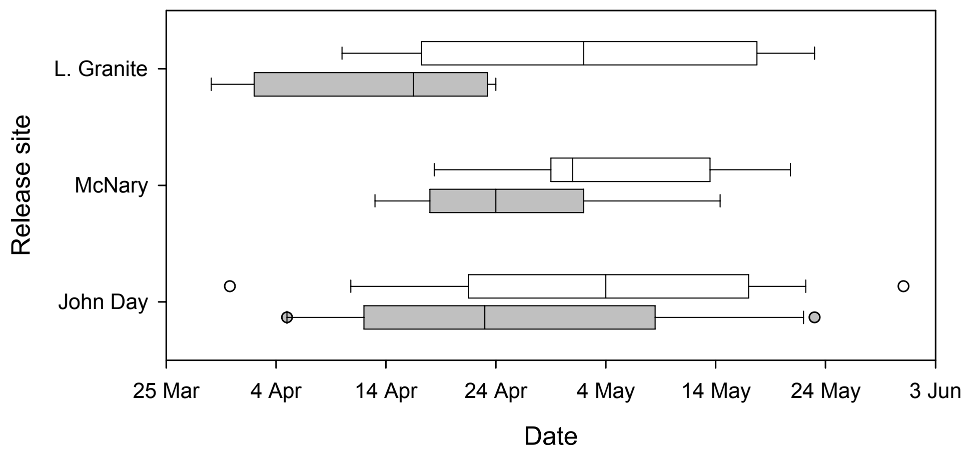

Figure 5. Outmigration timing distributions of steelhead (*Oncorhynchus mykiss*) kelts that were consecutive spawners (gray boxes) or skip spawners (white boxes) by kelt collection site. Boxes show median, quartile, 5th and 95th percentiles.

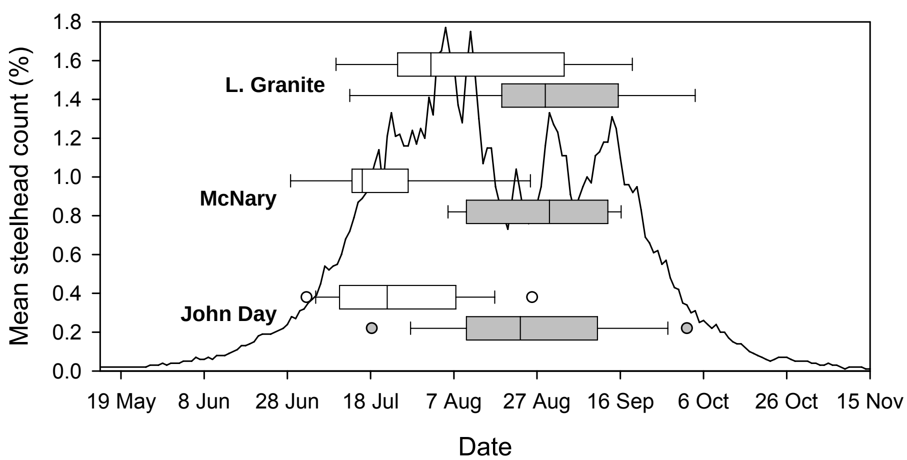

Figure 6. Return timing distributions at Bonneville Dam for steelhead (*Oncorhynchus mykiss*) that were consecutive spawners (gray boxes) or skip spawners (white boxes) by kelt collection site. Boxes show median, quartile, 5th and 95th percentiles. Line shows the mean steelhead count (expressed as %) at Bonneville Dam from 2001-2005.

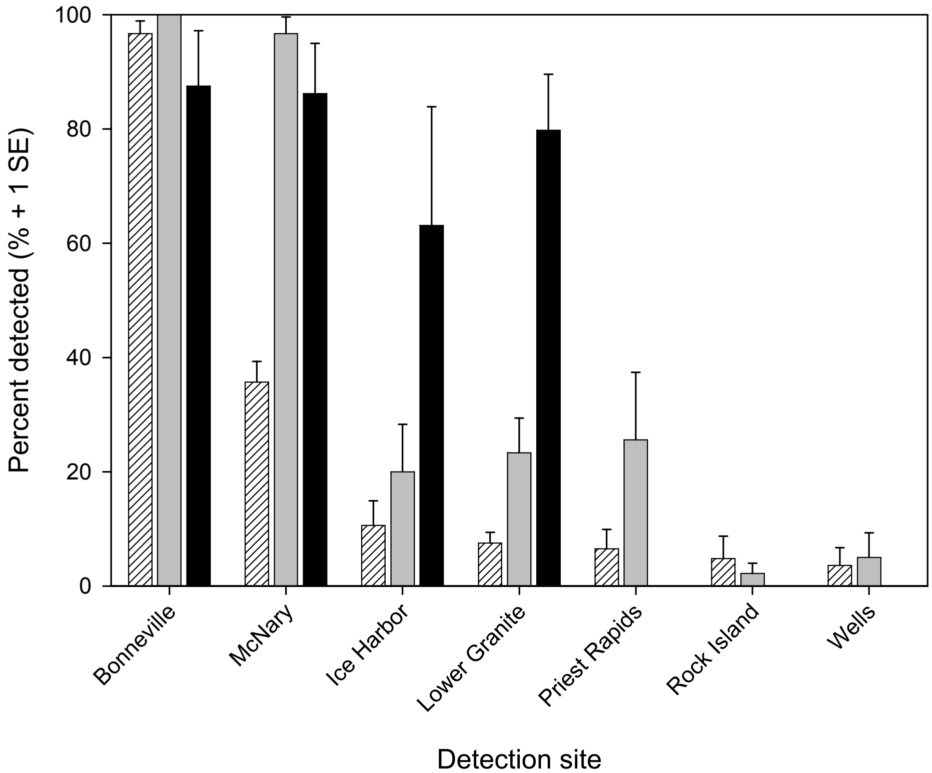

Figure 7. Mean (+ 1 se) annual percentage of returning steelhead (*Oncorhynchus mykiss*) detected at dam PIT-tag interrogation sites, by kelt release site (hatched bar = John Day Dam; gray bar = McNary Dam; black bar = Lower Granite Dam). Means were based on the number of return years each interrogation site was in operation: 2001-2005 (Bonneville, Lower Granite dams), 2002-2005 (McNary, Wells dams), 2003-2005 (Priest Rapids, Rock Island, Ice Harbor dams).

Discussion

Iteroparity patterns

The iteroparity data in this study are the most comprehensive collected for summer-run steelhead in the Columbia River Basin. Results both advance our understanding of iteroparous populations with long freshwater migration distances, and demonstrate the potential contribution of repeat spawners to the aggregate of threatened interior steelhead populations in the Columbia River. Across study years, 5.45% (John Day), 5.37% (McNary), and 0.69% (Lower Granite) of kelts returned as repeat spawners. Selection bias for kelts in good or fair condition likely inflated these estimates to a degree but this may have been offset by kelt handling and PIT tag retention effects. As a whole, we are confident that the iteroparity estimates presented here are the best data available given the large demographic scope of the study. We emphasize, however, that these estimates apply to a broad amalgam of Columbia and Snake River steelhead, potentially representing thirty or more distinct spawning populations upstream from John Day Dam (Brannon et al. 2004; Keefer et al. 2008). Inferences drawn from the aggregate populations should not be applied to individual stocks given probable among-population variability in spawner age, sex ratios, initial post-spawn survival, and/or iteroparity. For example, genetic analyses of kelts collected at Lower Granite Dam indicate that Snake River steelhead populations do not contribute to kelt outmigrations in proportion to population size or distance to spawning grounds (Narum et al. 2008). This implies repeat spawning rates for individual populations may be much higher or lower than the reported aggregate estimates. We expect unmeasured among-population variability may be highest among kelts passing lower Columbia River dams, where the mix of Snake, mid-Columbia, and upper Columbia River fish is most diverse.

Despite uncertainty regarding stock-specific effects, results for the aggregate Columbia and Snake River kelt runs suggest that iteroparity in the basin varies along several gradients. First, there was a clear negative relationship between kelt outmigration distance and repeat spawner return rates, with kelts tagged at John Day dam (third main stem dam, rkm 347) about six times more likely to return than those tagged at Lower Granite Dam (eighth main stem dam, rkm 695). This likely reflects a combination of life history differences among populations and distance travelled, including some level of “extra” dam-related migration mortality for upriver kelts. That is, poor condition or dying kelts present at Lower Granite Dam were already lost to the system prior to sampling at McNary and John Day dams. Second, there was persuasive evidence for condition-dependent 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 (~82% of all kelts with known sex) than males and were at least two to four times more likely to return as repeat spawners. The survival bias for females was probably even higher given evidence that unsexed kelts with relatively high return rates were mostly female. Fourth, proportionately more wild than hatchery fish and more small than large fish returned, particularly from upstream release groups, suggesting possible life history or genetic differences among groups. Differences between wild and hatchery fish, however, may also be influenced by harvest rates because fin-clipped steelhead can be harvested while most wild fish (those with adipose fins) must be released unharmed. Finally, both outmigration year and timing appeared to influence return rates for all groups, with among-year rates differing by a factor of two to three at each site and relatively higher returns for earlier outmigrants.

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 pattern 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 relative to males and invest little or nothing 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). We also found smaller steelhead kelts were more likely to return than larger kelts, a trait shared with many Atlantic salmon (*S. salar*, Jonsson et al. 1991), brown trout (*S. trutta*, Jonsson and L’Abee-Lund 1993), and arctic char (*S. 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 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 re-entry, 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 non-lethally 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 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 therefore outmigration timing and river and ocean conditions may be critical components affecting kelt survival and subsequent iteroparity rates. In this study, there was some evidence for lower outmigration survival in low-flow years (e.g., Wertheimer and Evans 2005). However, the influence of river environment on subsequent iteroparity rates was unclear. For example, there was no obvious relationship between river discharge and return rates among good condition kelts tagged at John Day Dam. The highest return rate for this group was in 2002 (13.74%), when discharge during outmigration was 91% of average (15 March to 15 June at Bonneville Dam). Return rates were 5.91% in 2003 (also 91% of average flow), 8.56% in 2001 (52% of average), and 10.39% in 2004 (85% of average). Similarly, returns for good condition kelts tagged at Lower Granite Dam were much more variable across years (1.04% in 2002, 0.57% in 2003, and 1.89% in 2004) than were flow conditions during outmigration. The lack of clear patterns suggests that river discharge may affect iteroparity at finer scales than we considered or that other factors like spill rates at dams or ocean conditions have a greater impact on annual return rates than river discharge alone. Kelt mortality in the estuary or ocean may mask the effects of river environment, particularly as kelt mortality after passing through the dammed portion of the Columbia system can apparently be quite high. Wertheimer and Evans (2005), for example, reported downstream survival of 15.6% for kelts radio tagged at Lower Granite Dam in 2002, yet only ~1% of good condition fish returned from that sample. Clearly more research is needed to better understand the influence of abiotic factors on kelt survival and returns.

We did find that early-migrating kelts returned at relatively higher rates than later migrants, 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), kelt survival might be expected to be highest during peak passage, particularly as this period is closer in time to the spring flood when fish would benefit from rapid transport to the ocean. However, in this impounded system the benefits of migrating during historically optimal times may be offset by greatly reduced kelt migration speeds. If there are strong selection pressures for rapid outmigration and ocean re-entry 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 rates for early migrants. Alternately, early migrants may have had greater energetic reserves or encountered more favorable river or ocean conditions. A combination of environmental and other factors likely influenced the reported return rates, and we emphasize that these hypotheses remain untested.

Return timing and breeding interval of successfully iteroparous steelhead was strongly associated with kelt outmigration timing. Compared to kelts that spent a winter at sea 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. In part, these patterns reflect the time kelts require to restore lost somatic and gonadal energy reserves (Niemalä et al. 2006). Early Columbia River outmigrants may have adequate time at sea to complete this process in a single season, whereas late migrants that miss productive ocean conditions in late spring may require additional ocean residency. Recovery times may also differ among populations as a function of freshwater migration distance or difficulty (Schaffer and Elson 1975; Willson 1997). This may explain why Snake River kelts overwinter in the ocean at substantially higher rates than kelts collected at lower Columbia River sites. On average, consecutive repeat spawners spent about four months in the ocean compared to approximately 15 months for skip repeat spawners. The latter breeding interval is somewhat more typical among anadromous iteroparous species (Dutil 1986; Behnke 1992; Jonsson et al. 1991; Willson 1997).

The general Columbia River steelhead iteroparity and migration timing patterns described above were inter-related in complex ways. For example, kelt coloration and condition varied seasonally and differed between sexes and between wild and hatchery fish. River conditions and dam operations also varied within season, 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., population effects or ocean conditions). The statistical results were therefore useful for identifying broad patterns (i.e., the importance of collection site, kelt condition and sex, and migration timing), but these models are an oversimplification of the processes affecting iteroparity and should not be used to infer causality.

Conservation and management implications

Iteroparity estimates for the aggregate Columbia River samples (5-6%, across years) were comparable to 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 the Columbia River study. The aggregate 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 relatively low rate may be attributable to long, energetically demanding migrations that favor high single-episode reproductive investment (Crespi and Teo 2002; Fleming and Reynolds 2004). Low repeat spawning may have been the norm historically, particularly for those interior Columbia and Snake River populations that have among the longest freshwater migrations recorded for the species (Busby et al. 1996).

The lack of historic data makes it difficult to assess how iteroparity patterns may have changed in Columbia basin steelhead, but the proliferation of hatchery fish has almost certainly affected the number and proportion of returning fish. Over the last decade, annual counts of summer-run steelhead at Bonneville Dam averaged ~339,000 fish, with more than 80% typically of hatchery origin (U.S. Army Corps of Engineers 2006). Pre-dam steelhead runs have been estimated at about 500,000 fish (Chapman 1986), suggesting a nearly 10-fold decrease in wild spawners. In our samples, wild kelts were disproportionately abundant (66-69% of the lower Columbia River samples and 52% of the Lower Granite Dam sample). In part, this reflects greater harvest mortality for hatchery fish and hatchery culling of broodstock. However, lower postspawn survival for hatchery fish may also be a contributing factor. Our results consistently indicated that wild fish returned at higher rates than hatchery-origin steelhead that presumably spawned in the wild, consistent with other studies showing reduced reproductive performance in hatchery steelhead, including those spawning in the wild (e.g., Chilcote et al. 1986; Kostow et al. 2003; Araki et al. 2007a).

An essential management challenge for both wild and hatchery kelts in the Columbia River basin is to reduce the direct and indirect mortality risks associated with dams and reservoirs. In many respects, the risks for kelts parallel those for smolts. Direct mortality hazards include contact with turbine blades, rapid pressure changes in powerhouses, and trauma from passage over high spillways (e.g., Čada 2001; Ferguson et al. 2005). A partial list of indirect effects include energetically costly migration delays, accumulated physiological stress, delayed effects of injuries sustained during dam passage, and possible asynchrony between migration timing and physiological readiness for the ocean environment (Venditti et al. 2000; Budy et al. 2002; Schaller and Petrosky 2007). Despite similar outmigration risks for steelhead kelts and many juvenile salmonids, the expansive programs designed to reduce juvenile migration mortality (e.g., Bickford et al. 2001; Muir et al. 2001; Buchanan et al. 2006; Ferguson et al. 2006) have largely circumvented kelt passage issues. In part, this omission was due to a common assumption that iteroparity was uniformly low or non-existent among interior steelhead populations.

While it is probable that bypass systems and operational changes designed for smolts (e.g., increased spill during outmigration, surface flow bypass systems) may also benefit kelts, these assumptions have not been directly tested. The large numbers of kelts collected in juvenile bypass systems and kelt use of a surface bypass structure at Bonneville Dam (Wertheimer 2007) indicate that these facilities can effectively pass kelts. Similarly, kelts and prespawn adults appear to readily pass downstream via spillways when adequate flow is available (Boggs et al. 2004; Wertheimer and Evans 2005). However, relative use patterns and mortality risks associated with passage routes at each dam are largely unknown. Route-specific survival likely differs as a function of body size, with large-bodied kelts at potentially greater risk than smolts while passing via turbines, debris sluiceways, and relatively constricted bypass systems designed for juveniles. The kelt telemetry data provided some support for differential return rates by kelt passage routes at dams, but sample sizes were limiting and only three dams were evaluated. Returns were generally highest for kelts that passed via juvenile bypass systems. The relatively high return rates for kelts tagged in 2001, when there was little or no spill during much of the kelt outmigration, also suggests that kelt passage via bypass systems may be preferable to passage over spillways. These are largely qualitative conclusions, however, and further assessment of route-specific survival differences may help mitigate dam-related kelt mortality.

The broader changes in river environment, such as reduced peak flows during outmigration, may be a more intractable problem. Better guidance and surface flow structures at dams can reduce kelt passage delays (Wertheimer and Evans 2005; Wertheimer 2007), but probably not enough to compensate for reduced water velocities in hundreds of kilometres of reservoir. Downstream kelt migration rates in the impounded Columbia River system have averaged 13-16 km•d^{-1} in Snake and upper Columbia River reaches and 38 km•d^{-1} in lower Columbia River reaches where spill tends to be more constant and total flow volume is higher (Wertheimer and Evans 2005; English et al. 2006). In comparison, these authors reported mean steelhead kelt outmigration rates of 42-54 km•d^{-1} in the Skeena River, 100 km•d^{-1} in the Fraser River, and 99-111 km•d^{-1} in unimpounded Columbia River reaches. These differences were not an artifact of river gradient (i.e., all estimates were for relatively low gradient main stem reaches), but rather were attributed to passage barriers and reduced water velocity in reservoirs versus free-flowing rivers. Operations that mimic normative river conditions during the kelt outmigration, such as increased spill volume, may ameliorate some kelt migration delay. However, such changes are unlikely given demands for power generation, irrigation withdrawals, and flood control (National Research Council 1996).

Two additional strategies to increase iteroparity in Columbia River summer-run steelhead are currently being evaluated: transportation and reconditioning. Kelt transportation seeks to circumvent the mortality risks associated with dam and reservoir passage by collecting kelts at main stem dams or other diversion sites and then transporting them downstream in fish barges or trucks. This effort is modeled after the smolt transportation program, which has been a central salmon and steelhead recovery strategy in the basin for several decades (Ruckelshaus et al. 2002; Buchanan et al. 2006). Transportation has successfully increased the number of juveniles that reach the ocean (e.g., Sandford and Smith 2000), though overall population benefits have been mixed due to delayed mortality (Budy et al. 2002; Muir et al. 2006). A kelt transportation evaluation was conducted in conjunction with the current study using kelts collected and then transported downstream from Lower Granite and John Day dams (see Chapter 2). Preliminary results indicate that transported kelts returned at slightly higher rates than in-river migrants. The greatest apparent transport benefits were for kelts with the longest migrations (i.e., those collected at Lower Granite Dam). The second mitigation strategy, kelt reconditioning, involves culturing postspawned fish in a captive environment until they are able to reinitiate feeding, grow, and develop mature gonads for another spawning event. Successful reconditioning of iteroparous species has been achieved with Arctic charr (Boyer and Toever 1993), Atlantic salmon (Johnston et al. 1992, Crim et al. 1992, Moffett et al. 1997) and steelhead (Wingfield 1976). Reconditioning trials in the Columbia system indicate higher kelt survival and rematuration rates in reconditioned fish relative to controls (Hatch et al. 2004). The relative costs and benefits of in-river passage improvements versus more direct actions like reconditioning and transportation are currently being debated. We expect success will likely differ among populations and as a function of environmental conditions; hence a comprehensive kelt management program will likely include a combination of strategies.

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 implies that the genetic potential for repeat spawning is continuously present within these populations, perhaps unsurprisingly given the broad phenotypic and reproductive plasticity of *O. mykiss* (e.g., Behnke 1992). It is not yet possible, however, to quantify the current population-level or stock-specific contribution of repeat spawners in the Columbia River system. In the Snake River, several thousand mixed-stock steelhead kelts pass through juvenile bypass systems each year (Evans et al. 2003; 2004a; Narum et al. 2008) and an unknown number of additional kelts pass via other routes (e.g., spillways). Assuming a 1% return rate for these fish, 10s to perhaps 100s of repeat spawners likely return to the Snake River each year. Higher return rates for kelts passing lower Columbia River dams (~5%) and larger populations passing these sites suggest 100s to 1000s of repeat spawner returns each year, with dispersal throughout the interior basin. While these estimates are relatively modest, both their distribution among populations and the relative reproductive contribution of these fish may be important. We expect repeat spawners may be more successful on average than maiden spawners given previous spawning experience and larger size. As the current results show, repeat spawners are also disproportionately female and of wild origin. These traits are desirable for populations below carrying capacity given greater reproductive success in wild steelhead (e.g., Chilcote 2003; Araki et al. 2007a,b) and the tendency for females to be limiting in male-skewed mating systems (Fleming and Reynolds 2004). These demographic benefits, as well as the genetic and stabilizing effects of iteroparity, are currently not fully realized in Columbia River steelhead. Efforts to recover protected populations in the basin should therefore include provisions to promote iteroparity and—more generally—encourage the full expression of genetic and life history diversity of steelhead.

References

Altukhov, Y.P., Salmenkova, E.A., and Omelchenko, V.T. 2000. Salmonid fishes: population biology, genetics and management. Blackwell Science, Oxford, U.K.

Araki, H., Cooper, B., and Blouin, M.S. 2007*a*. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science 318:100-103.

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. Molecular Ecology 16:953-966.

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.

Augerot, X. 2005. Atlas of Pacific salmon: the first map-based assessment of salmon in the north Pacific. University of California Press, Berkeley, CA.

Behnke, R.J. 1992. Native trout of western North America. American Fisheries Society Monograph 6.

Bickford, S.A., and Skalski, J.R. 2000. Reanalysis and interpretation of 25 years of Snake-Columbia River juvenile salmonid survival studies. North American Journal of Fisheries Management 20:53-68.

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. Transactions of the American Fisheries Society 133:932-949.

Booth, R.K., Bombadier, E.B., Mckinley, R.S., Scruton, D.A., and Gossney, R.F. 1997. Swimming performance of post spawning (kelts) and juvenile (smolts) Atlantic salmon, *Salmo salar*. Canadian Manuscript Report of Fisheries and Aquatic Sciences No. 2406.

Boyer, J.N., and Van Toever, W. 1993. Reconditioning of Arctic char (*Salvenius alpinus*) after spawning. Aquaculture 110:279-284.

Brannon, E.L., Powell, M.S., Quinn, T.P., and Talbot, A. 2004. Population structure of Columbia River basin chinook salmon and steelhead trout. Reviews in Fisheries Science 12:99-232.

Buchanan, R.A., Skalski, J.R., and Smith, S.G. 2006. Estimating the effects of smolt transportation from different vantage points and management perspectives. North American Journal of Fisheries Management 26:460-472.

Buckland, S.T., Burnham, K.P., and Augustin, N.H. 1997. Model selection: an intergral part of inference. Biometrics 53:603-618.

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. North American Journal of Fisheries Management 22:35-51.

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. International North Pacific Fisheries Commission Bulletin 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(9):147-123.

Chapman, D. 1986. Salmon and steelhead abundance in the Columbia River in the nineteenth century. Transactions of the American Fisheries Society 115:662-670.

Chilcote, M.W., Leider, S.A., and Loch, J.J. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. Transactions of the American Fisheries Society 115:726-735.

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). Canadian Journal of Fisheries and Aquatic Sciences 60:1057-1067.

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. Transactions of the American Fisheries Society 129:946-961.

Cooke, S.J., Crossin, G.T., Patterson, D.A., English, K.K., Hinch, S.G., Young, J.L., Alexander, R.F., Healey, M.C., Kraak, G.V.D., 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. Journal of Fish Biology 67:1342-1358.

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.

Crim, L.W., Wilson, C.E., So, Y.P., D. R. Idler, 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.

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. Fisheries Management and Ecology 11:387-402.

Dodson, J.J. 1997. Fish migration: an evolutionary perspective. *In* Behavioural Ecology of Teleost Fishes. Oxford University Press.

Downing, S., and Prentice, E. 2003. Overview of the performance of PIT-tag interrogation systems for adult salmonids at Bonneville and McNary Dams. BPA Report DOE/BP-00013411-1, Bonneville Power Administration, Portland, Oreg.

Dutil, J.-D. 1986. Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). Copeia 4:945-955.

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. Transactions of the American Fisheries Society 135:739-754.

Evans, A.F. 2003. Development and application of steelhead (*Oncorhynchus mykiss*) kelt identification techniques. M.S. thesis. Oregon State University, Corvallis.

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. Transactions of the American Fisheries Society 133:1089-1099.

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. North American Journal of Fisheries Management 24:967-978.

Evans, A.F., Wertheimer, R.H., Keefer, M.L., Boggs, C.T., Peery, C.A., and Collis, K. *In prep*. Transportation of steelhead kelts to increase return rates of repeat spawners in the Snake and Columbia rivers.

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, Report NMFS-NWFSC-64, Northwest Fisheries Science Center, NOAA-Fisheries.

Ferguson, J.W., Absolon, R.F., Carlson, T.J., and Sandford, B.P. 2006. Evidence of delayed mortality on juvenile Pacific salmon passing through turbines at Columbia River dams. Transactions of the American Fisheries Society 135:139-150.

Fleming, I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Reviews in Fish Biology and Fisheries 6:379-416.

Fleming, I.A. 1998. Pattern and variability in the breeding system of Atlantic salmon (Salmo salar), with comparisons to other salmonids. Canadian Journal of Fisheries and Aquatic Sciences 55(Suppl. 1):59-76.

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.

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, USA.

Gibbons, J.W., and Andrews, K.M. 2004. PIT tagging: simple technology at its best. Bioscience 54(5):447-454.

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, British Columbia.

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, Oreg. Rep. DOE/BP-00004185-5.

Hosmer, D.W., and Lemeshow, S. 2000. Applied Logistic Regression, 2nd Edition. Wiley-InterScience, Hoboken, New Jersey.

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.

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. Journal of Animal Ecology 60:937-947.

Jonsson, B., and L'Abee-Lund, J.H. 1993. Latitudinal clines in life-history variables of anadromous brown trout in Europe. Journal of Fish Biology 43:1-16.

Keefer, M.L., Boggs, C.T., Peery, C.A., and Caudill, C.C. 2008. Overwintering distribution, behavior, and survival of adult summer steelhead: variability among Columbia River populations. North American Journal of Fisheries Management 28:81-96.

Keefer, M.L., Peery, C.A., and Caudill, C.C. 2008. Migration timing of Columbia River spring Chinook salmon: effects of temperature, river discharge, and ocean environment. Transactions of the American Fisheries Society 137:1120-1133.

Kinnison, M.T., Unwin, M.J., and Quinn, T.P. 2003. Migratory costs and contemporary evolution of reproductive allocation in male chinook salmon. Journal of Evolutionary Biology 16:1257-1269.

Kostow, K.E., Marshall, A.R., and Phelps, S.R. 2003. Naturally spawning hatchery steelhead contribute to smolt production but experience low reproductive success. Transactions of the American Fisheries Society 132:780-790.

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. Canadian Journal of Fisheries and Aquatic Sciences 43:1398-1409.

Lohr, S.C., and Bryant, M.D. 1999. Biological characteristics and population status of steelhead (*Oncorhynchus mykiss*) in Southeast Alaska. Gen. Tech. Rep. PNW-GTR-407. US Forest Service, Pacific Northwest Research Station, Portland, Oreg.

Long, J.B., and Griffin, L.E. 1937. Spawning and migratory habits of the Columbia River steelhead trout as determined by scale studies. Copeia 1937:62.

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(S1):77-92.

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, Maryland. pp.47-82.

Mills, D. 1989. Ecology and Management of Atlantic Salmon. Chapman and Hall, New York, NY.

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.

Muir, W.D., Smith, S.G., Williams, J.G., and Hockersmith, E.E. 2001. Survival estimates for migrant yearling Chinook salmon and steelhead tagged with passive integrated transponders in the Lower Snake and Lower Columbia Rivers, 1993-1998. North American Journal of Fisheries Management 21:269-282.

Muir, W.D., Marsh, D.M., Sandford, B.J., Smith, S.G., and Williams, J.G. 2006. Post-hydropower system delayed mortality of transported Snake River stream-type Chinook salmon: unraveling the mystery. Transactions of the American Fisheries Society 135:1523-1534.

Narum, S.R., Hatch, D., Talbot, A.J., Moran, P., and Powell, M.S. 2008. Iteroparity in complex mating systems of steelhead trout. Journal of Fish Biology 72:45-60.

National Marine Fisheries Service. 1997. Endangered and threatened species: listing of several evolutionarily significant units (ESUs) of West Coast steelhead. Federal Register 62:159(18 August 1997):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.

National Research Council. 1996. Upstream: Salmon and Society in the Pacific Northwest. National Academy Press, Washington, D.C.

Niemelä, E., Erkinaro, J., Julkunen, M., Hassinen, E., Länsman, M., and Brørs, S. 2006. Temporal variation in abundance, return rate and life histories of previously spawned Atlantic salmon in a large subarctic river. Journal of Fish Biology 68:1222-1240.

Pirhonen, J., and Schreck, C.B. 2003. Effects of anaesthesia with MS-222, clove oil, and CO_2 on feed intake and plasma cortisol in steelhead trout (*Oncorhynchus mykiss*). Aquaculture 220:507-514.

Prince, A., and Powell, C. 2000. Clove oil as an anesthetic for invasive field procedures on adult rainbow trout. North American Journal of Fisheries Management 20:1029-1032.

Quinn, T.P., and Adams, D.J. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology 77:1151-1162.

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.

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. Transactions of the American Fisheries Society 131:523-536.

Rounsefell, G.A. 1958. Anadromy in North American *Salmonidae*. Fisheries Bulletin 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. Annual Review of Ecology and Systematics 33:665-706.

Sandford, B.P., and Smith, S.G. 2002. Estimation of smolt-to-adult return percentages for Snake River basin anadromous salmonids, 1990-1997. Journal of Agricultural, Biological and Environmental Statistics 7:243-263.

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.

Schaller, H.A., and Petrosky, C.E. 2007. Assessing hydosystem influence on delayed mortality of Snake River stream-type Chinook salmon. North American Journal of Fisheries Management 27:810-824.

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.

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 managment. California Department of Fish and Game, Fish Bulletin 98:1-375.

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.

US Army Corps of Engineers. 2006. Annual fish passage report. US Army Corps of Engineers, Portland, Oreg., and Walla Walla, Wash.

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. North American Journal of Fisheries Management 20:41-52.

Wagner, T., and Congleton, J.L. 2004. Blood chemistry correlates of nutritional condition, tissue damage, and stress in migrating juvenile chinook salmon (*Oncorhynchys tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 61:1066-1074.

Wedemeyer, G.A., Saunders, R.L., and Clarke, W.C. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Marine Fisheries Review 42:1-14.

Wertheimer, R.H. 2007. Evaluation of a surface flow bypass system for steelhead kelt passage at Bonneville Dam, Washington. North American Journal of Fisheries Management 27:21-29.

Wertheimer, R.H., and Evans, A.F. 2005. Downstream passage of steelhead kelts through hydroelectric dams on the lower Snake and Columbia rivers. Transactions of the American Fisheries Society 134:853-865.

Whitt, C.R. 1954. The age, growth, and migration of steelhead trout in the Clearwater River, Idaho. M.S. thesis, University of Idaho, Moscow.

Wilbur, H.M., and Rudolf, H.W. 2006. Life-history evolution in uncertain environments: bet hedging in time. American Naturalist 168:398-411.

Willson, M.F. 1997. Variation in salmonid life histories: patterns and perspectives. Res. Pap. PNW-RP-498. US Forest Service, Pacific Northwest Research Station, Portland, Oreg.

Wingfield, B. 1976. Holding summer steelhead adults over to spawn a second time. Northwest Fish Culture Conference 27:63-64

Withler, I.L. 1966. Variability in life history characteristics of steelhead trout (*Salmon gairdneri*) along the Pacific coast of North America. Journal of the Fisheries Research Board of Canada 23:365-393.

Appendix 1

Appendix Figures 1-4 show additional summary details (origin, sex, condition, coloration, and migration timing) for the full kelt samples collected at John Day, McNary, and Lower Granite dams during the study years.

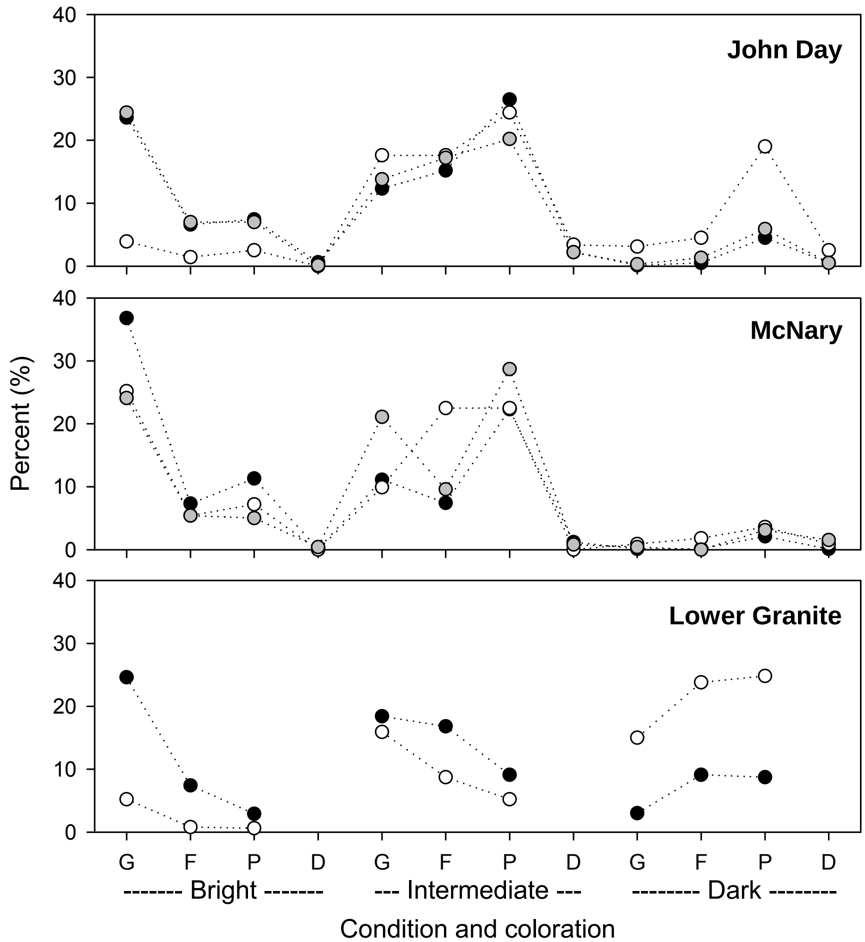

Figure A1. Condition and coloration of female (●), male (○) and unknown-sex (●) kelts sampled at John Day, McNary and Lower Granite dams. All years combined.

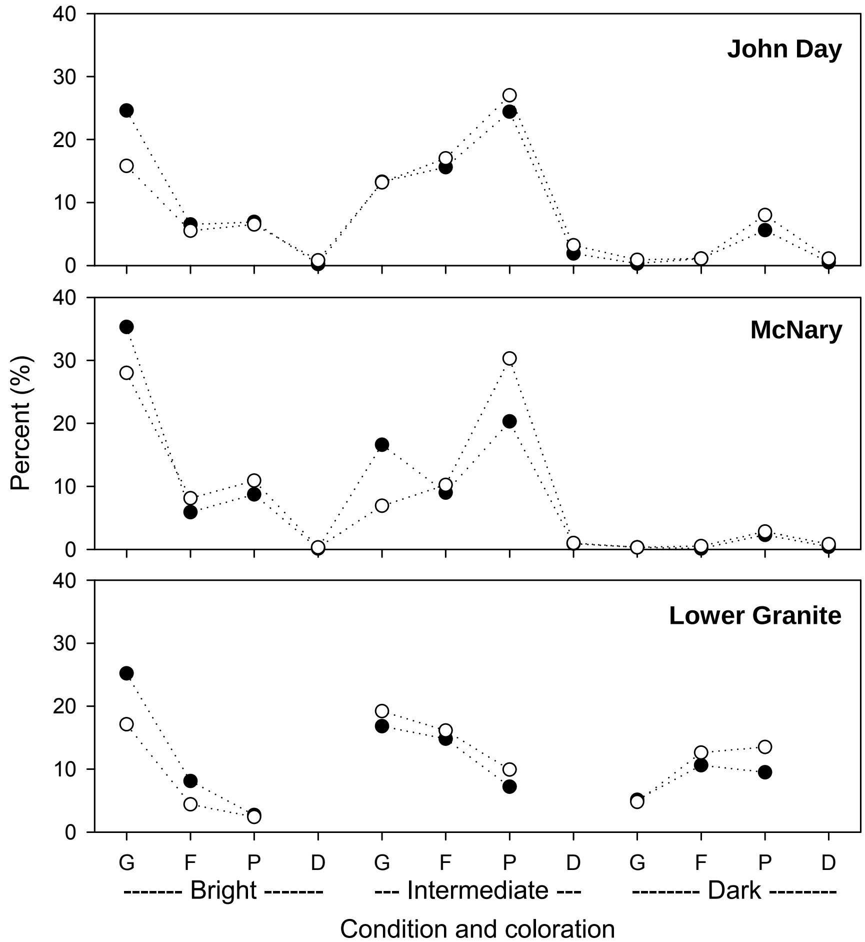

Figure A2. Condition (good, fair, poor, dead) and coloration (bright, intermediate, dark) of wild (●) and hatchery (○) kelts sampled at John Day, McNary and Lower Granite dams. All years combined.

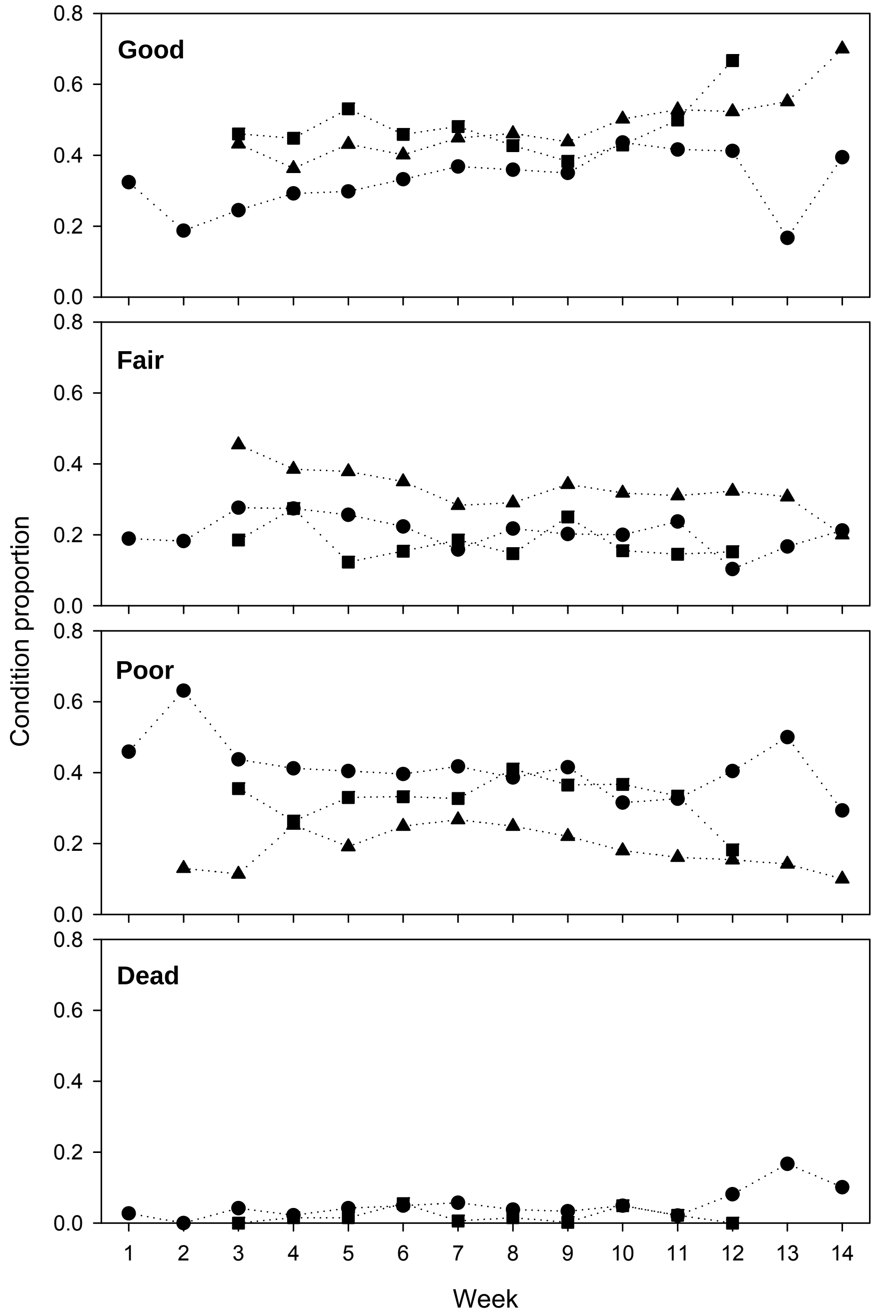

Figure A3. Mean weekly proportions of all sampled kelts that were in good, fair or poor condition or were dead at John Day (●), McNary (■) and Lower Granite (▲) dams by sampling week.

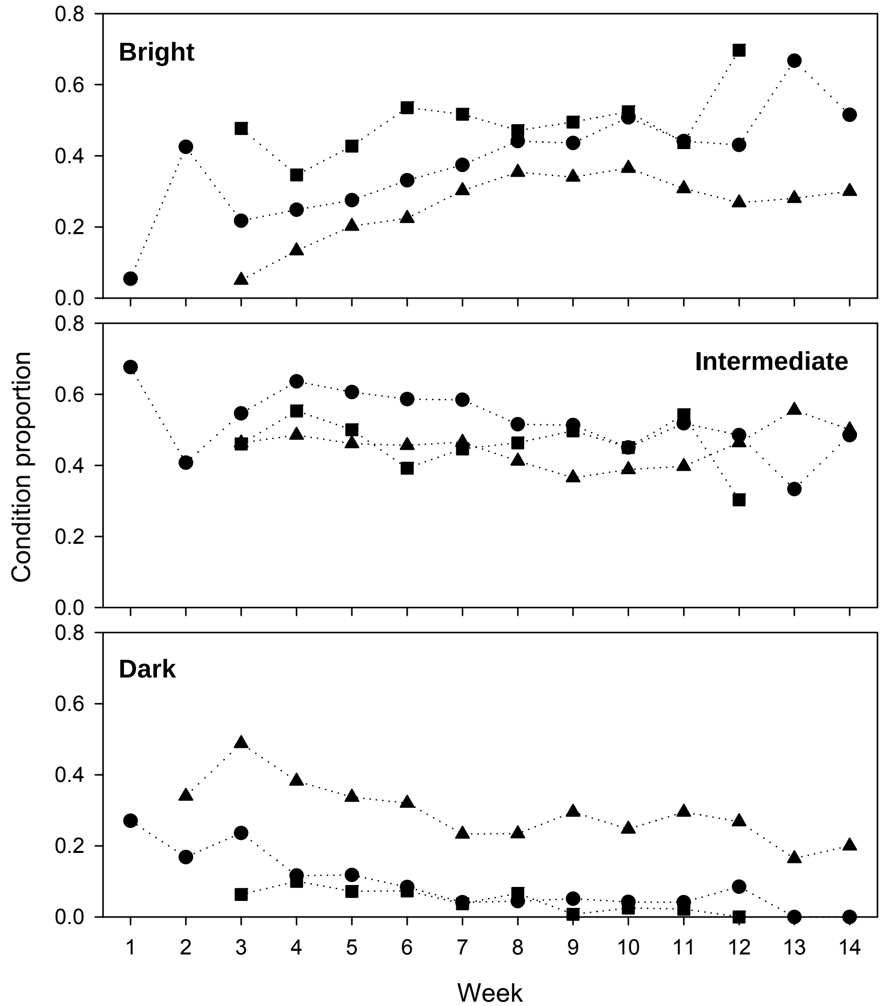

Figure A4. Mean weekly proportions of all sampled kelts that were dark, intermediate, or bright colored (●), McNary (■) and Lower Granite (▲) dams by sampling week.

CHAPTER 2

TRANSPORTATION OF STEELHEAD KELTS TO INCREASE ITEROPARITY IN THE COLUMBIA AND SNAKE RIVERS

Abstract

We tested the feasibility of transporting steelhead (*Oncorhynchus mykiss*) kelts (post-spawned adults) around hydroelectric dams on the Snake and Columbia rivers to increase returns of repeat spawners. In total, 5,878 kelts were collected, tagged with Passive Integrated Transponder tags, and assigned to transport or in-river treatment groups at Lower Granite Dam (n = 5,320, 2002-2004) on the Snake River and at John Day Dam (n = 558, 2002) on the Columbia River. Returns of repeat spawners differed by site and year with 11.1% (62/558) for the 2002 John Day Dam sample, and 1.4% (27/1,959), 0.5% (6/1,241), and 0.8% (17/2,120) for the Lower Granite Dam samples in 2002, 2003, and 2004, respectively. Transportation tests indicated kelts transported from the Snake River were 2.3 times more likely to return than fish allowed to migrate in-river. Transport benefits were greatest for wild-origin female kelts, a demographic with high conservation value. There was no significant benefit for kelts transported from John Day Dam, although transported fish returned at a slighter higher rate (1.1 times greater). Comparisons between treatment groups (in-river versus transport) and locations (Snake versus Columbia) indicated the greatest potential transport benefit may be for Snake River kelts due to the population's low overall iteroparity rate and numerous potential kelt collection sites. Small sample sizes of returning fish limited our ability to examine more complex trends and environmental effects on return rates. Additional research is needed to fully evaluate the efficacy of kelt transportation in the context of regional steelhead recovery efforts.

Introduction

Unlike most Pacific salmonids (*Oncorhychus* spp.), steelhead (*O. mykiss*) may spawn more than once during their lifetime (Quinn 2005). Repeat spawning (iteroparity) is both a hedge against catastrophic reproductive failure and a life history strategy that provides population-level genetic and demographic benefits (Crespi and Teo 2002; Fleming and Reynolds 2004). In the Columbia River basin, repeat spawning steelhead have been documented returning to natal streams for decades (Long and Griffin 1937; Whitt 1954; Leider et al. 1986; Busby et al. 1996). However, very little is known about postspawned steelhead (referred to as "kelts") or to what extent repeat spawners might help rebuild depleted populations in the region, including those listed under the U.S. Endangered Species Act (ESA, Good et al. 2005).

To address these questions, a series of research projects were initiated in 2000 to broaden the understanding of steelhead kelts and iteroparity in the Columbia River basin. Methods were developed to accurately differentiate kelts from adult steelhead on pre-spawn migrations using rapid, non-invasive ultrasound imaging techniques (Evans et al. 2004a). Subsequent kelt abundance data revealed that thousands of Columbia River basin kelts attempt outmigration to the Pacific Ocean each spring (approximately April through June), and many of these fish are from ESA-listed populations (Evans et al. 2004b; Narum et al. 2008). Although abundant, many kelts die before reaching the free-flowing section of the Columbia River below Bonneville Dam (235 river kilometers [rkm] from the Pacific Ocean). Mortality estimates for radio-tagged kelts ranged from 20-40% for fish tagged at lower Columbia River dams and from 84-96% for kelts tagged at the uppermost passable dam on the Snake River (Lower Granite Dam, eight dams upstream from the ocean at rkm 695; Wertheimer and Evans 2005). High downstream kelt mortality directly contributes to the relatively low iteroparity estimates for these populations. In the portion of this study unrelated to kelt transportation, annual repeat spawning estimates for summer-run (freshwater maturing) steelhead that migrated in-river ranged from 2.9-7.8% for kelts collected at John Day Dam (third main-stem dam, Columbia River rkm 347) to 0.4-1.2% for kelts collected at Lower Granite Dam (see Part 1).

Researchers have hypothesized that more kelts from interior Columbia basin populations may survive to spawn again if they were: (1) protected from turbines at dams by increasing flow over spillways (Wertheimer and Evans 2005); (2) provided seasonally operated surface flow outlets to specifically accommodate downstream passage of adults (Wertheimer 2007); (3) collected and transported downstream past dams and reservoirs (Evans et al. 2004b); and/or (4) reconditioned in temporary holding facilities before release for natural spawning (Wingfield 1976; Hatch et al. 2004). Research presented here evaluates the use of kelt transportation (option 3) to increase returns of repeat spawners in the Columbia and Snake rivers. Fish transportation in barges or trucks has been used as a means to circumvent mortality risks from dams and reservoirs for juvenile salmonids in the Snake and Columbia rivers since the early 1970's (e.g., Bickford and Skalski 2000; Buchanan et al. 2006). Transporting kelts around main-stem dams may similarly mitigate downstream migration losses by allowing a larger proportion of outmigrants to reach the ocean, resume feeding sooner, undergo gonad recrudescence, and return to spawn again.

Study Site

Research was conducted at the Lower Granite Dam (LGR) and John Day Dam (JDA) juvenile bypass facilities, located on the Snake (695 rkm from the Pacific Ocean) and Columbia (347 rkm from the ocean) rivers, respectively (Figure 1). Bypass facilities divert downstream traveling fishes around the dam via large screens placed in front of turbine intakes. Like other bypass facilities on the Snake and Columbia rivers, only a portion of the fish in a dam's forebay pass surface flow outlets or bypass systems and many fish use other passage routes (e.g., via spillways or turbines). Research was conducted at LGR because more adult steelhead kelts are counted at LGR's bypass than at any other

Snake or Columbia River bypass facility (Evans et al. 2004b). Furthermore, the LGR bypass is the first main-stem dam collection point at which emigrating kelts can be sampled on the Snake River. Research was conducted at JDA because steelhead kelts from multiple upstream Evolutionary Significant Units (e.g., Snake, Upper Columbia and Middle Columbia River ESU's; NMFS 2004) could be sampled at this location. The closer proximity of JDA to the Pacific Ocean, relative to LGR, also provided a spatial comparison for different kelt collection and transportation points.

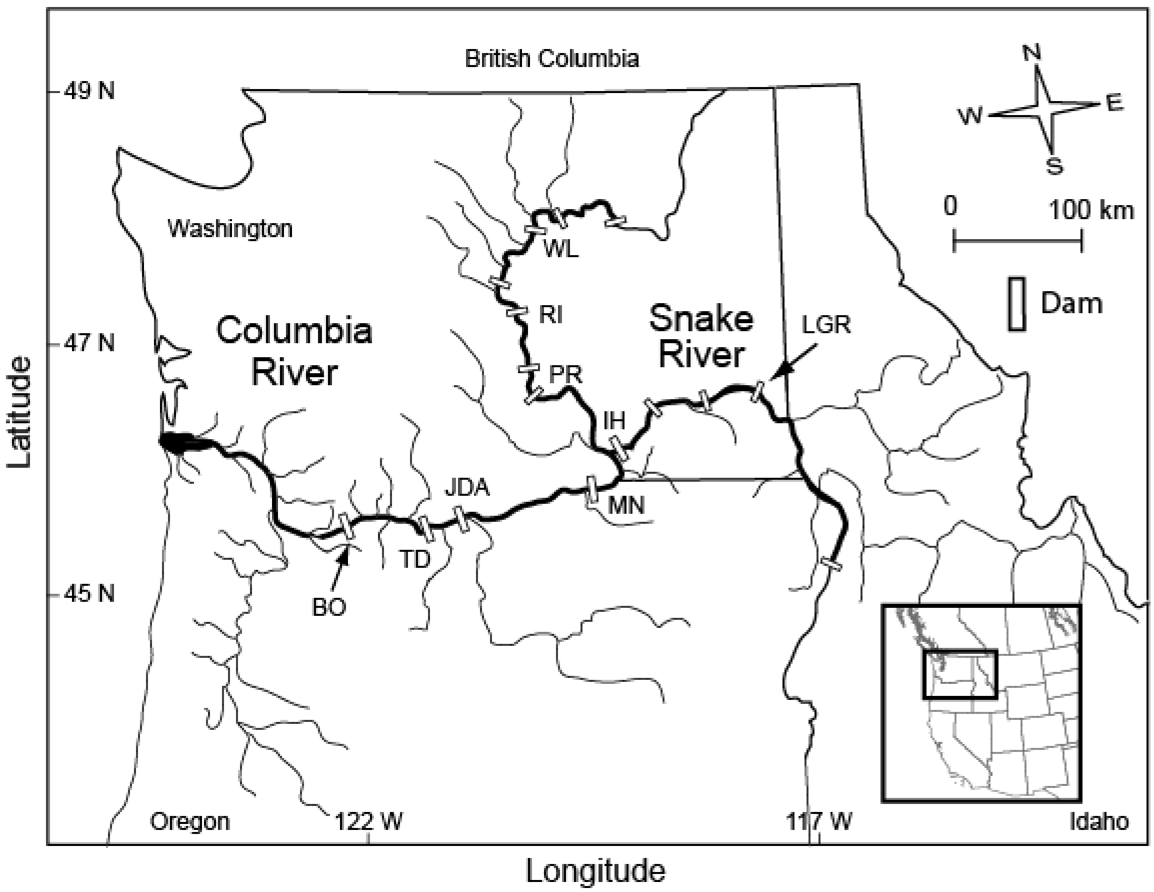

Figure 1. Map of the Columbia and Snake rivers showing main-stem dams and major tributaries. Steelhead (*Oncorhynchus mykiss*) kelts were collected at John Day (JDA, 2002) and Lower Granite (LGR, 2002-2004) dams for transportation evaluations. Repeat spawners could be detected at PIT-tag interrogators at Bonneville (BO), McNary (MN), and Wells (WL) dams in all years and Ice Harbor (IH), Priest Rapids (PR), and Rock Island (RI) dams in 2003 and 2004. TD = The Dalles Dam.

Methods

Kelt Collection

We sampled adult steelhead from the LGR juvenile bypass facility in the spring of 2002, 2003, and 2004 and from the JDA bypass in the spring of 2002. Adult steelhead arriving at each bypass facility were diverted into a temporary holding tank (3.0 x 1.2 x 1.8 m) prior to each daily sampling period. Kelts were collected during day and night, with sample numbers proportional to the number of fish entering the facility during any sample period. At LGR, sampling was conducted an average of six days per week over a 9 or 10 week sampling period (31 March to 5 June). At JDA, sampling was conducted 5 days per week on average over 11 weeks (17 March to 1 June). Sampling at both sites spanned the peak arrival of adult steelhead in the juvenile bypass facilities.

Following collection, adult steelhead were transferred via dipnet to a nearby 190-L sampling tank containing fresh river water, where they were anesthetized (60 ppm tricaine methanesulfonate [MS-222] or 30-mg/L of clove oil) and scanned with an ultrasound machine to assess maturation status. Kelt identification was based on the size, number, location, and density of gonads using the techniques in Evans et al. (2004a). Following ultrasound examination of each adult steelhead, we recorded maturation status (prespawn or kelt), sex, fish length (cm), condition ("good", "fair", or "poor"; see Evans 2003), and origin (hatchery or wild, based on presence/absence of an adipose fin). Those fish determined to be prespawn (i.e., mature) were immediately released to resume upstream migration. Kelts in good or fair morphological condition were tagged with passive integrated transponder (PIT) tags and assigned to one of two treatment groups: in-river or transport. Kelts were randomly assigned to treatments at LGR in 2002 and 2003 using a computer-based number generator. Kelts were opportunistically assigned to a treatment group at LGR in 2004 and at JDA in 2002, with all (100%) of the kelts sampled being transported when a barge (LGR) or truck (JDA) was available at the dam. Conversely, when a transportation barge or truck was not available, all fish were released in-river. The sampling system resulted in more fish being assigned to the in-river treatment group at LGR because a transportation barge was absent more than present, especially early in the season.

Kelt Transportation

Kelts transported from LGR were placed in a barge hold originally designed to transport juvenile salmonids. Within the hold, kelts were confined to a specially designed aluminum mesh net pen (2.1 x 1.2 x 2.4 m) to minimize interaction between kelts and juvenile salmonids that were also being transported. Kelt densities within the net pen enclosure were less than 0.1-kg/L. Kelts from LGR were transported around seven main-stem dams on the Lower Snake and Columbia rivers and released below the Bonneville Dam tailrace (rkm ~225; the most downstream dam on the main-stem Columbia River), a total transportation distance of 471 rkm (Figure 1). Kelts collected at JDA were transported by truck around two main-stem dams in an insulated 1,135 L aerated tank and released below Bonneville Dam near Dalton Point, OR (rkm 214), a total transportation distance of 133 rkm (Figure 1). Kelt densities within the transport truck were less than 0.2-kg/L. In-river migrants from both sites were released via a flume into the dam's tailrace to resume downstream migration following sampling.

Analysis

The numbers of returning kelts (i.e., repeat spawners) from each treatment group were based on the number of fish subsequently detected at PIT tag interrogators in adult fishways at Bonneville Dam (the first main-stem dam returning fish would encounter). A fish was not considered a repeat spawner unless the release-to-return time to Bonneville Dam was a minimum of 100 days, thereby excluding any kelts that might have used the Bonneville Dam fishway as a downstream migration route in the days following release. Repeat spawners were characterized by their return timing as "consecutive" or "skip" spawners based on whether they returned the same year they were tagged and released (between 100 and 365 days post-release) or the year following release (> 365 days post-release). All comparisons were limited to weeks in which samples from both treatment groups were collected (i.e., we excluded surplus in-river fish that were sampled during weeks when transportation did not take place). Independence tests (Chi-square or Fisher Exact; depending on sample sizes) were used to determine if sample composition (as defined by the kelts' condition, sex, and origin) differed among in-river or transported treatment groups.

The likelihood of steelhead returning on repeat spawning migrations was examined using a combination of univariate analyses and stepwise logistic regression models (Hosmer and Lemeshow 2000). Predictor variables included the study treatment (in-river, transport), kelt characteristics (condition, fork length, sex, origin), and outmigration metrics (year, release timing). The release timing term was defined as early (weeks 1-7) or late (weeks 8-14), and was created because weekly sample sizes were limiting in some analyses. More complete analyses of the explanatory variables associated with kelt return rates and patterns for the larger sample of in-river kelts are described in Part 1.

Results

Kelt Sampling

In total, 5,878 kelts were sampled, tagged, and assigned to transport or in-river treatment groups at LGR (n = 5,320, 2002-2004) and JDA (n = 558, 2002) (Figure 2). Of these, 3,483 (59.3%) were released in-river and 2,395 (40.7%) were transported. Although kelts were transported and released in-river throughout the kelt migration period of March/April to June, the late arrival of fish transportation barges at LGR resulted in the early portion of the kelt run being missed (Figure 2), especially in 2003 and 2004. The majority of tagged kelts were in good overall external condition (n = 3,348, 56.9%), female (n = 4,893, 83.2%), and of wild origin (n = 3,199, 54.4%). In 2002, when kelts were sampled at both JDA and LGR, good condition kelts were proportionately more abundant at LGR (62.7%) than at JDA (53.6%).

There were kelt composition differences between in-river and transport treatment groups in some years at both locations (Table 1). More good than fair condition kelts were transported from JDA in 2002 (χ^2 = 11.79, P < 0.001) and from LGR in 2003 (χ^2 = 7.03, P = 0.008). In addition, proportionately more females and unsexed fish were transported from JDA (χ^2 = 10.46, P = 0.005). Transport versus in-river composition differed significantly (P < 0.001) among weeks for all site×year samples, with early-migrating kelts being disproportionately assigned to the in-river treatment group as a result of limited barge availability early in the season (Figure 2). All other kelt composition comparisons between treatment fish were non-significant (Table 1). Kelt size (cm fork-length) did not differ ($P \geq$ 0.145, Kruskal-Wallis tests) among treatments in any samples.

Kelt returns

Of the 5,878 kelts PIT-tagged during the study, 112 (1.9%) were detected passing Bonneville Dam as repeat spawners, and two fish from the JDA releases were detected passing Bonneville Dam in successive years (i.e., on second and third repeat spawning migrations). Returns by site and year were 11.1% (62/558) for the 2002 JDA sample, and 1.4% (27/1,959), 0.5% (6/1,241), and 0.8% (17/2,120) for the LGR samples in 2002, 2003, and 2004, respectively. Of 112 returning fish, 56 fish (50.0%) returned in the same year they were tagged and released (i.e., consecutive repeat spawners) and 56 (50.0%) returned the following year (i.e., skip repeat spawners). Among repeat spawners, skip spawners were more prevalent in the LGR sample (60.0%, 30/50) than the JDA sample (41.9%, 26/62).

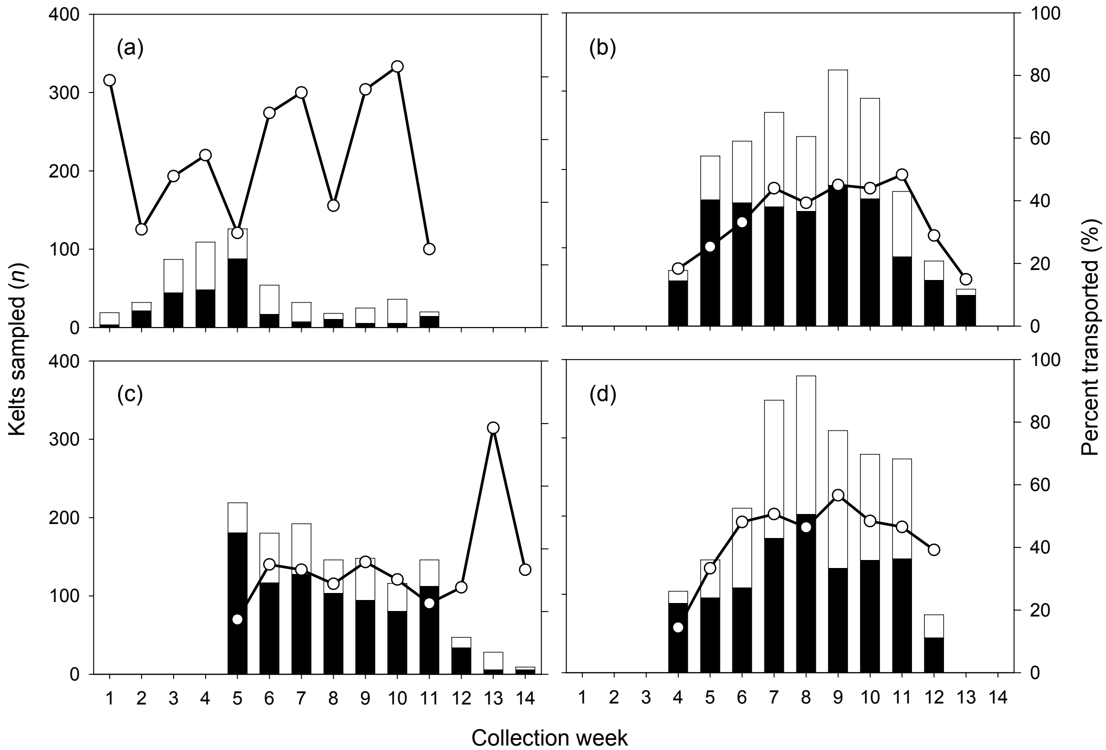

Figure 2. Weekly numbers of steelhead kelts assigned to in-river (black bar) and transportation (white bar) treatment groups at John Day Dam in 2002 (a) and at Lower Granite Dam in 2002 (b), 2003 (c), and 2004 (d). Line depicts the percentages of fish transported.

Table 1. Condition, sex, and origin of kelts tagged and allocated to in-river and transportation treatment groups at Lower Granite (LGR) and John Day (JDA) dams from 2002 to 2004. The percentage (number) of fish within each category is given for each treatment group. P-values are based on Pearson chi-square tests.

		Sample percent (*n*)					
		Condition		Origin		Sex[a]	
Site, Year	Treatment	Good	Fair	Wild	Hatchery	Female	Male
LGR 2002	In-river	63.3 (765)	36.7 (444)	51.2 (619)	48.8 (590)	85.7 (1036)	14.3 (173)
	Transport	61.9 (464)	38.1 (286)	54.0 (405)	46.0 (345)	84.7 (635)	15.3 (115)
	P		*0.531*		*0.228*		*0.534*
LGR 2003	In-river	61.3 (530)	38.7 (335)	55.4 (479)	44.6 (386)	85.3 (738)	14.7 (127)
	Transport	69.2 (260)	30.8 (116)	51.3 (193)	48.7 (183)	85.9 (323)	14.1 (53)
	P		*0.008*		*0.189*		*0.788*
LGR 2004	In-river	50.1 (570)	49.9 (568)	56.4 (642)	43.6 (496)	84.7 (964)	15.3 (174)
	Transport	46.8 (460)	53.2 (522)	54.3 (533)	45.7 (449)	84.5 (830)	15.5 (152)
	P		*0.136*		*0.323*		*0.904*
JDA 2002	In-river	46.1 (125)	53.9 (146)	55.7 (151)	44.3 (120)	59.4 (161)	12.2 (33)
	Transport	60.6 (174)	39.4 (113)	61.8 (177)	38.3 (110)	71.8 (206)	6.6 (19)
	P		*< 0.001*		*0.153*		*0.005*

[a]Sex was not determined in 139 kelts sampled at JDA; 77 were in-river and 62 were transported

In the stepwise logistic regression model, repeat spawner return rates for kelts tagged at LGR were statistically associated with several variables, including transportation (Table 2). Kelt condition was the best predictor in the model that included all LGR kelts, with good condition kelts 10.75 times more likely to return than fair condition kelts. In addition, returns were 4.34 times more likely for females than males, 2.52 times more likely for wild than hatchery fish, 2.26 times more likely for early than late migrants, and more likely for smaller fish (Table 2). In the JDA stepwise model, kelt condition was the only variable associated with repeat spawner returns. Good condition JDA kelts were 2.50 times more likely to return than fair condition kelts (95% CI = 1.37-4.35; $\chi^2 = 9.00$; P = 0.003).

Table 2. Stepwise logistic regression results of return rates for kelts PIT-tagged at Lower Granite, 2002-2004. Effects not selected include: year and all 1-way interactions.

Effect	*df*	χ^2	*P*	Effect	Odds ratio	95% CI
Condition	1	15.73	< 0.001	Good vs. Fair	10.75	3.32-34.48
Origin	1	8.44	0.004	Wild vs. Hatchery	2.52	1.35-4.69
Transport	1	8.22	0.004	Barge vs. In-river	2.30	1.30-4.08
Length	1	7.65	0.006		0.94	0.90-0.98
Timing	1	7.65	0.006	Early vs. Late	2.26	1.27-4.02
Sex	1	4.07	0.044	Female vs. Male	4.34	1.04-18.07

In univariate analyses, return rates of in-river and transportation groups differed by location, year, and kelt characteristics (Figure 3, Table 3). With all fish included, return rates for JDA samples were 10.3% for in-river releases versus 11.9% for transported kelts, a non-significant difference ($\chi^2 = 0.32$, $P = 0.569$). Differences were also non-significant ($P > 0.05$) when JDA samples were separated by origin, sex, and sex×origin categories except that wild, unsexed kelts that were transported returned at a higher rate (18.2%) than in-river fish (4.7%) ($\chi^2 = 3.91$, $P = 0.048$) (Figure 4).

Transport treatment effects were significant for the LGR sample in 2002 (*return rate* = 0.66% for in-river fish and 2.53% for transported kelts; $\chi^2 = 11.93$, $P < 0.001$) and for all years combined (0.65% for in-river and 1.38% for transport; $\chi^2 = 7.12$, $P = 0.008$). At LGR, good condition females were consistently the most likely to return (Figure 4) and the highest return rate was for wild, good condition females that were transported in 2002 (5.7%, Table 3). Across years, good condition females that were transported returned at higher rates than their in-river counterparts in almost every week, with the greatest benefits early and late in the migrations (Figure 5). Return rates were lowest for fair condition kelts (0.13%, 3/2,271) and males (0.25%, 2/794), with no fish in these categories returning in some years. At JDA, where a much larger proportion of tagged kelts returned, there was no evidence that fish condition, origin, or sex was associated with return rate differences between treatment groups ($P > 0.15$ for all comparisons, Table 3).

Finally, a higher proportion of transported fish returned as consecutive repeat spawners (48.3%, 14/29) relative to fish that migrated in-river (28.6%, 6/21) from LGR. Return cycles among JDA-sampled kelts were similar between in-river and transported kelts, with 57.1% (transported) and 58.8% (in-river) being consecutive repeat spawners. The small number of returning fish from each treatment group by year (see Table 3), however, limited the usefulness of further statistical comparisons.

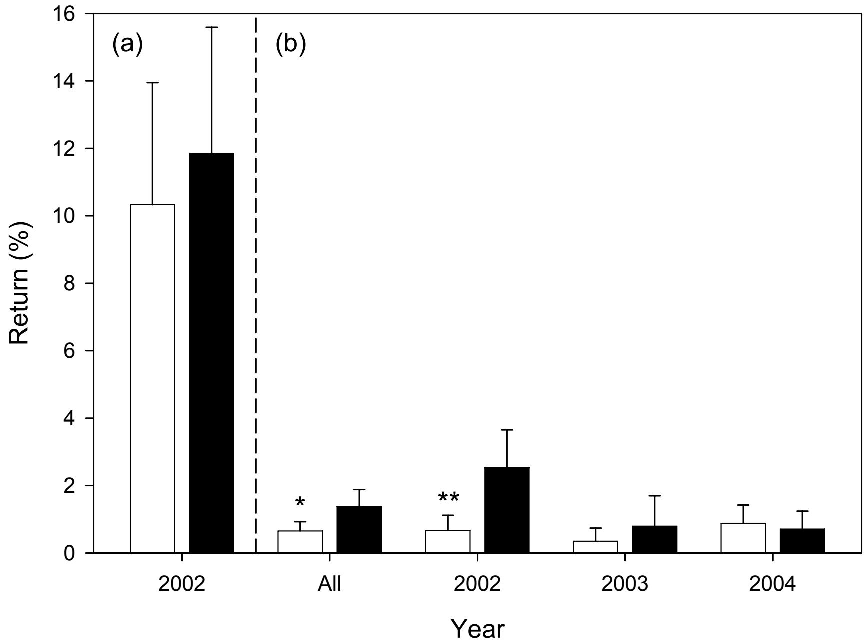

Figure 3. Repeat spawner return rates (+ 1 SD) for in-river (white bar) and transported (black bar) steelhead kelts tagged at John Day (a) and Lower Granite (b) dams. * $P < 0.05$; ** $P < 0.005$, Fischer's exact tests.

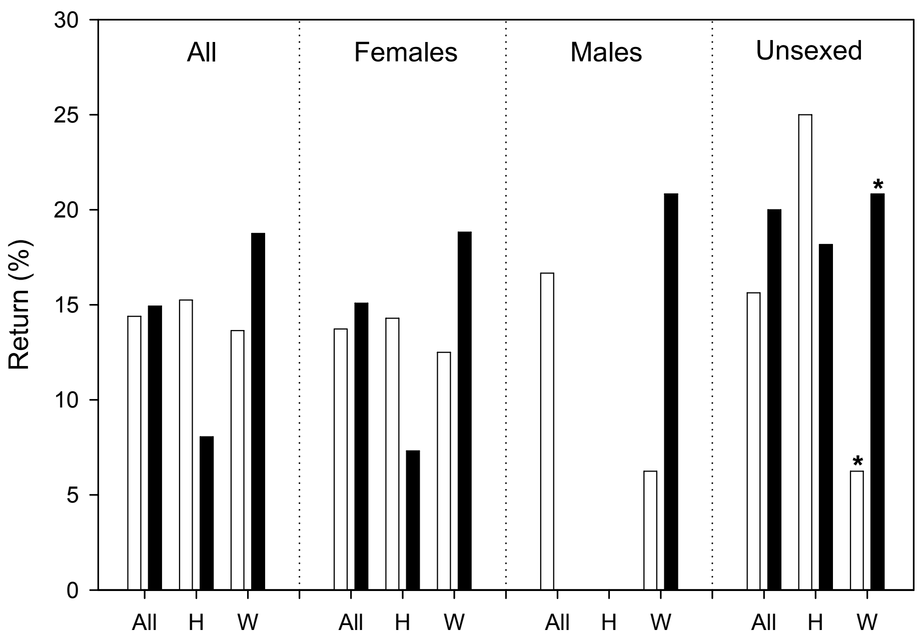

Figure 4. Repeat spawner return rates for in river (white bar) and transported (black bar) steelhead kelts tagged at John Day Dam in 2002, by origin (H = hatchery, W = wild) and sex. * $P < 0.05$, Fisher's exact test.

Table 3. Return rates of repeat spawners based on their condition (good or fair), sex (male or female), and origin (hatchery or wild) from kelts tagged at Lower Granite (LGR) and John Day (JDA) dams, 2002-2004. Percentage (number) of repeat spawners within each category is given for each treatment group. † $P < 0.10$; ** $P < 0.005$, Fisher's exact tests.

					Return percent (*n*)			
					Hatchery		Wild	
Site	Year	Treatment	Condition	*n*	F	M	F	M
LGR	2002	In-river	Good	765	†1.2 (327)	0.0 (36)	**1.2 (344)	0.0 (58)
		Transport	Good	464	†3.5 (171)	0.0 (26)	**5.7 (227)	0.0 (40)
		In-river	Fair	444	0.0 (196)	0.0 (31)	0.0 (169)	0.0 (48)
		Transport	Fair	286	0.0 (129)	0.0 (19)	0.0 (108)	0.0 (30)
LGR	2003	In-river	Good	530	0.0 (197)	0.0 (35)	1.2 (259)	0.0 (39)
		Transport	Good	260	2.0 (100)	0.0 (20)	0.8 (121)	0.0 (19)
		In-river	Fair	335	0.0 (124)	0.0 (30)	0.0 (158)	0.0 (23)
		Transport	Fair	116	0.0 (57)	0.0 (6)	0.0 (45)	0.0 (8)
LGR	2004	In-river	Good	570	0.0 (213)	0.0 (30)	2.5 (282)	2.2 (45)
		Transport	Good	460	1.1 (182)	3.6 (28)	1.4 (218)	0.0 (32)
		In-river	Fair	568	0.5 (209)	0.0 (44)	0.4 (260)	0.0 (55)
		Transport	Fair	522	0.5 (193)	0.0 (46)	0.0 (237)	0.0 (46)
JDA[a]	2002	In-river	Good	93	14.3 (35)	0.0 (8)	12.5 (40)	30.0 (10)
		Transport	Good	139	7.3 (41)	0.0 (10)	18.8 (85)	0.0 (3)
		In-river	Fair	101	5.1 (39)	0.0 (4)	12.8 (47)	0.0 (11)
		Transport	Fair	86	2.7 (37)	0.0 (4)	7.0 (43)	0.0 (2)

[a] Unsexed fish at JDA: in-river, hatchery, good (return percent = 25.0%, *n* = 16); transport, hatchery, good (18.2%, *n* = 11); in-river, wild, good (6.3%, *n* = 16); transport, wild, good (20.8%, *n* = 24); in-river, hatchery, fair (5.6%, *n* = 18); transport, hatchery, fair (14.3%, *n* = 7); in-river, wild, fair (3.7%, *n* = 27); transport, wild, fair (15.0%, *n* = 20)

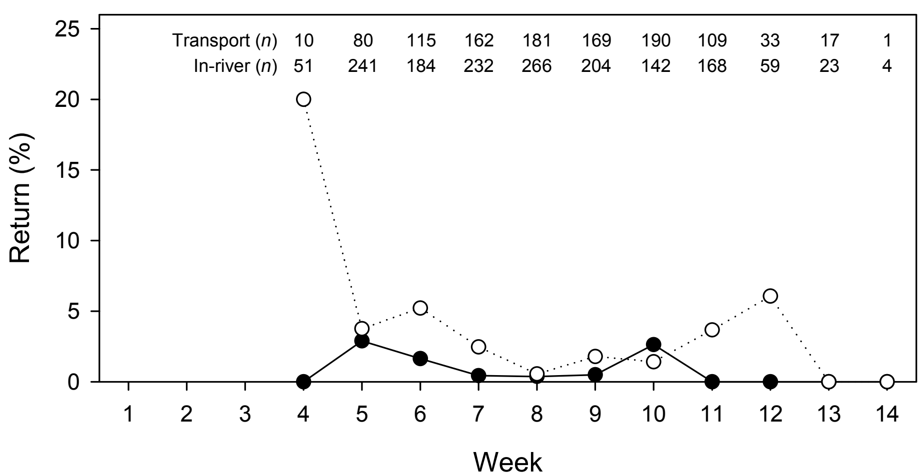

Figure 4. Repeat spawner return rates by outmigration week, for good condition females collected at Lower Granite Dam that were transported (○) or migrated in-river (●). All years pooled.

Discussion

Mitigation for dam passage mortalities of salmonids in the Columbia River basin has focused primarily on assisting outmigrating juveniles and upstream-migrating adults. Conversely, management practices to assist downstream-migrating kelts have not been fully explored or implemented. Although overlooked, kelts and the repeat spawners they become may be an important life history and genetic resource for rebuilding depleted steelhead populations in the region (Evans et al. 2004b; NMFS 2004). Kelt transportation has been hypothesized as a means to rebuild natural populations expeditiously by decreasing dam and reservoir passage mortality and preserving the finite energy reserves of kelts (Wertheimer and Evans 2005). Data presented here indicate that it is feasible to increase returns of repeat spawners by transporting kelts around main-stem dams on the Columbia and Snake rivers.

Return Rates

The incidence of repeat spawning was significantly higher in kelts tagged at JDA relative to LGR, with ~12 times as many good and fair condition kelts returning from JDA. Higher proportions of repeat spawners in the population are generally believed to increase relative to distance from the ocean in the Columbia River basin (Meehan and Bjornn 1991) and elsewhere (Wilson 1997). Wertheimer and Evans (2005) found that kelts radio-tagged and released at dams in the lower Columbia River had significantly higher downstream migration survival rates than kelts radio-tagged on the Snake River. Part 1 of this evaluation similarly shows a negative correlation between kelt migration distance and repeat spawner rates, with kelts tagged closer to the ocean returning at rates 2 to 10 times higher than kelts tagged further inland. Data presented here also indicated that good condition, wild female kelts returned at the highest overall rate, although fair condition, male, and hatchery kelts also returned. Substantially higher return rates for females are typical for steelhead and other iteroparous salmonids, presumably because breeding competition is more costly for males (Withler 1966; Fleming 1998; Lohr and Bryant 1999).

Repeat spawners exhibited one of two different spawning cycles: consecutive and skip spawning. Skip spawners were significantly more prevalent in kelts sampled from LGR relative to JDA. This suggests that migration distance and/or postspawn energy reserves are factors associated with not only iteroparity rates but spawning cycles as well (Niemelä et al. 2006). Interestingly, two of the repeat spawners from JDA-sampled kelts were observed on a third spawning migration, indicating iteroparity in interior summer-run steelhead populations is not limited to two spawning events. It is also possible that some proportion of the sampled kelts had spawned more than once previously.

Overall, transported kelts returned at a higher rate than kelts that migrated in-river. The relative difference in return rates was greatest for LGR-sampled kelts compared to JDA-sampled kelts. Across all years, return rates were 2.3 times higher for kelts transported from LGR compared to their in-river counterparts and benefits were more dramatic for wild females. Despite this cumulative difference, the finding was only statistically significant in one of three study years (2002). Furthermore, the net benefits (transport returns minus in-river returns) of transporting kelts from the Snake River were slight for the full samples, with a net iteroparity increase of just 0.73% (ranging from -0.17% in 2004 to +1.87% in 2002). There was also some evidence that a higher proportion of transported kelts from LGR returned as consecutive repeat spawners relative to their in-river counterparts, although sample sizes for this comparison were small. If true, this finding suggests that transportation may have preserved kelt energy reserves — reserves that would have otherwise been invested in downstream migration — and ultimately allowed a larger proportion of kelts to return on a consecutive rather than skip spawning cycle. At JDA, return rate differences between treatment groups were not statistically significant, suggesting that kelts received little to no benefit from being transported around two lower river main-stem dams (The Dalles and Bonneville; a distance of 133 rkm). However, samples were small and data were limited to one relatively average water flow year. Taken as a whole, results suggest that the benefits of kelt transportation may be greater the further kelts have to travel and the more dams they have to pass.

The small numbers of returning fish from both in-river and transport groups limit the study's ability to reveal more complex trends and interactions, including the effects of environmental conditions and dam operations. For example, how returns were associated with river conditions, outmigration timing, and ocean conditions remain unknown and may influence when, if, and under what conditions, transportation is most beneficial. The delayed start of transportation evaluations, particularly in the Snake River, is another factor that may have influenced return rates and comparisons. Part 1 shows that return rates were significantly higher early in the kelt run, a segment largely missed by the Snake River transport evaluations. Finally, it is difficult to ascertain the impact of additional handling on transported kelts. Prior research has demonstrated elevated stress indices in adult salmonids subjected to transportation (Mazeaud et al. 1977; Dabrowski and Ciereszko 1993) and it is possible the procedures used to transport kelts in this study were less than ideal. Reduced handling times, longer acclimation periods, and larger transport tanks could prove beneficial, and such improvements may warrant future investigation.

Management Implications

Results from this study suggest that there are some potential benefits to transporting kelts. These benefits are variable (i.e., depend on year, location and possibly season), and might be considered marginal from the standpoint of the increase in return rates alone, particularly at JDA. Nevertheless, the return rates of kelts transported from LGR was increased by as much as 2% or twice that of their in-river counterparts. The finding that wild, female kelts were the most likely to benefit from transportation should also be taken in consideration as this group of fish is the most likely to augment threatened populations. Wild steelhead tend to have greater reproductive success in the wild than hatchery-origin fish (Chilcote 2003; Araki et al. 2007), while females can strongly affect overall productivity through their influence on nest site selection and spawn timing (Fleming 1996). Finally, evidence that kelts transported from LGR returned as consecutive repeat spawners at higher rates than in-river fish supports our hypothesis that transportation conserves kelt energy reserves and that iteroparity is particularly energy-dependent. An energy-dependent response is supported by results in Part 1, where individual steelhead were observed alternating between consecutive and skip-spawning cycles.

Evaluations of the potential efficacy of transportation in increasing the repeat spawning rates of kelts must also take into consideration the total number of available kelts at upriver dams and bypass facilities. Kelt abundance estimates generated by Evans et al. (2004a) and Boggs and Peery (2004) suggest that thousands of good and fair condition kelts are intercepted passing dams on the lower Snake River each year. In these evaluations, it was estimated that up to 23% of the entire ESA-listed Snake River steelhead population was bypassed at LGR as kelts. If all suitable steelhead kelts encountered at Snake River dam bypass facilities were annually transported and returns were similar to those measured in 2002, the net benefits of transportation would likely be about 100 repeat spawners per year (assuming a net benefit of 1.9% from 5,000 transported Snake River kelts). Determining the "value" of these additional ~100 repeat spawners requires further consideration of several factors, including the fish's ESA-status, the cost of transportation relative to the other restoration options, and the general importance of maintaining and managing for iteroparity as a steelhead life history trait. Identifying the among-stock contributions of both kelts (e.g., Narum et al. 2008) and repeat spawners may also inform management decisions.

Finally, kelt transportation is not the only option available to increase steelhead iteroparity rates in the region. Kelt reconditioning and improvements to in-river passage options/strategies for kelts also hold promise. Kelt reconditioning, the culturing of post-spawned fish via feeding and other fish husbandry techniques, has been successfully achieved with Arctic charr (Boyer and Toever 1993), Atlantic salmon (Johnston et al. 1990; Crim et al. 1992) and steelhead (Wingfield 1976). Reconditioning trials in the Columbia system indicate significantly higher kelt survival and rematuration rates in reconditioned fish relative to in-river controls, with kelt-to-repeat spawner success rates observed in excess of 25% (Hatch et al. 2004). Passage evaluations by Wertheimer (2007) and Wertheimer and Evans (2005) indicate that surface oriented passage routes at dams provide the best passage efficiencies for kelts. Conversely, turbine intakes, which are typically deeper in the water column, appear to be associated with the highest kelt mortality rates; effects of passage over spillways are unknown, but are likely mixed. Ultimately, a Columbia River basin kelt management program will likely include a combination of approaches (e.g., reconditioning, improved transportation practices, and improved in-river passage), based upon location, collection capability, and kelt availability. We expect strategies that maximize repeat spawner return rates will vary among years, populations, and mitigation sites.

References

Araki, H., B. Cooper, and M. S. Blouin. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science 318:100-103.

Bickford, S. A., and J. R. Skalski. 2000. Reanalysis and interpretation of 25 years of Snake-Columbia River juvenile salmonid survival studies. North American Journal of Fisheries Management 20:53-68.

Boggs, C. T., and C. A. Peery. 2004. Steelhead (*Oncorhynchus mykiss*) kelt abundance, condition, passage, and survival in the lower Snake and Columbia Rivers, 2003. Idaho Cooperative Fish and Wildlife Research Unit, Technical Report 2004-1, Moscow, Idaho. Available: www.cnr.uidaho.edu/uiferl.

Boyer, J. N., and W. Van Toever. 1993. Reconditioning of Arctic char (*Salvenius alpinus*) after spawning. Aquaculture 110:279-284.

Buchanan, R. A., J. R. Skalski, and S. G. Smith. 2006. Estimating the effects of smolt transportation from different vantage points and management perspectives. North American Journal of Fisheries Management 26:460-472.

Busby, P. J., T. C. Wainwright, E. J. Bryant, L. J. Lierheimer, R. S. Waples, F. W. Waknitz, and I. V. Lagomarsino. 1996. Status review of west coast steelhead from Washington, Idaho, Oregon, and California. NOAA Tech. Memo. NMFS-NWFSC-27.

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*). Canadian Journal of Fisheries and Aquatic Sciences 60:1057-1067.

Crespi, B. J., and R. Teo. 2002. Comparative phylogenetic analysis of the evolution of semelparity and life history in salmonid fishes. Evolution 56:1008-1020.

Crim, L. W., C. E. Wilson, Y. P. So, D. R. Idler, and C. E. Johnston. 1992. Feeding, reconditioning, and rematuration responses of captive Atlantic salmon (*Salmo salar*) kelt. Canadian Journal of Fisheries and Aquatic Sciences 49:1835-1842.

Dabrowski, K. and A. Cieresxko. 1993. Influence of fish size, origin, and stress on ascorbate concentration in vital tissue of hatchery rainbow trout. The Progressive Fish Culturist. 55:109-113.

Evans, A. F. 2003. Development and application of steelhead (*Oncorhynchus mykiss*) kelt identification techniques. Master's thesis. Oregon State University, Corvallis.

Evans, A. F., M. S. Fitzpatrick, and L. K. Siddens. 2004a. Use of ultrasound imaging and steroid concentrations to identify maturational status in adult steelhead. North American Journal of Fisheries Management 24:967–978.

Evans, A. F., R. E. Beaty, M. S. Fitzpatrick, and K. Collis. 2004b. Identification and enumeration of steelhead kelts at Lower Granite Dam. Transactions of the American Fisheries Society 133:1089-1099.

Fleming, I. A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Reviews in Fish Biology and Fisheries 6:379-416.

Fleming, I. A. 1998. Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. Canadian Journal of Fisheries and Aquatic Sciences 55 (Supplement 1):59-76.

Fleming, I. A., and J. D. Reynolds. 2004. Salmon breeding systems. Pages 264-294 *in* A. P. Hendry, and S. C. Stearns, editors. Evolution illuminated: salmon and their relatives. Oxford University Press, New York, USA.

Good, T. P., R. S. Waples, and P. Adams. 2005. Updated status of federally listed ESUs of West coast salmon and steelhead. NOAA Tech. Memo. NMFS-NWFSC-66.

Hatch, D., R. Branstetter, J. Whiteaker,, J. Blodgett, B. Bosch, D. Fast, and T. Newsome. 2004. Kelt reconditioning: a research project to enhance iteroparity in Columbia basin steelhead (*Oncorhynchus mykiss*). Bonneville Power Administration Report DOE/BP-00004185-5. Portland, Oregon.

Hosmer, D. W., and S. Lemeshow. 2000. Applied Logistic Regression, 2nd Edition. Wiley-Interscience, Hoboken, New Jersey.

Johnston, C. E., S. R. Farmer, R. W. Gray, and M. Hambrook. 1990. Reconditioning and reproductive responses of Atlantic salmon kelts (*Salmo salar*) to photoperiod and temperature manipulation. Canadian Journal of Fisheries and Aquatic Sciences 47:701-710.

Leider, S. A., M. W. Chilcote, and J. J. Loch. 1986. Comparative life history characteristics of hatchery and wild steelhead trout (*Salmo gairdneri*) of summer and winter races in the Kalama River, Washington. Canadian Journal of Fisheries and Aquatic Sciences. 43:1398-1409.

Lohr, S. C., and M. D. Bryant. 1999. Biological characteristics and population status of steelhead (*Oncorhynchus mykiss*) in Southeast Alaska. Gen. Tech. Rep. PNW-GTR-407. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Long, J. B. and L. E. Griffin. 1937. Spawning and migratory habits of the Columbia River steelhead trout as determined by scale studies. Copeia 1937:62

Mazeaud, M., F. Mazeaud, and E. M. Donaldson. 1977. Primary and secondary effects of stress in fish: some new data with a general overview. Transactions of the American Fisheries Society 106:201-212.

Meehan, W. R., and T. C. Bjornn. 1991. Salmonid distributions and life histories. Pages 47-82 *in* W. R. Meehan, editor. Influences of forest and rangeland on salmonid fishes and their habitats. *Edited by* W.R. Meehan. American Fisheries Society, Bethesda, Maryland.

Narum, S. R., D. Hatch, A. J. Talbot, P. Moran, and M. S. Powell. 2008. Iteroparity in complex mating systems of steelhead trout. Journal of Fish Biology 72:45-60.

NMFS (National Marine Fisheries Service). 2004. 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, Washington.

Niemelä, E., J. Erkinaro, M. Julkunen, E. Hassinen, M. Länsman, and S. Brørs. 2006. Temporal variation in abundance, return rate and life histories of previously spawned Atlantic salmon in a large subarctic river. Journal of Fish Biology 68:1222-1240.

Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. American Fisheries Society, Bethesda, Maryland.

Wertheimer, R. H. and A. F. Evans. 2005. Downtream passage of steelhead kelts through hydroelectric dams on the lower Snake and Columbia Rivers. Transactions of the American Fisheries Society 25:275-286.

Wertheimer, R. H. 2007. Evaluation of a surface flow bypass system for steelhead kelt passage at Bonneville Dam, Washington. North American Journal of Fisheries Management 27:21-29.

Whitt, C. R. 1954. The age, growth, and migration of steelhead trout in the Clearwater River, Idaho. Master's thesis, University of Idaho, Moscow.

Willson, M. F. 1997. Variation in salmonid life histories: patterns and perspectives. Research Paper PNW-RP-498. US Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Wingfield, B. 1976. Holding summer steelhead adults over to spawn a second year. Northwest Fish Culture Conference 27:63-64.

Withler, I. L. 1966. Variability in life history characteristics of steelhead trout (*Salmon gairdneri*) along the Pacific coast of North America. Journal of the Fisheries Research Board of Canada 23:365-393.