Technical Report 2014-1

ESTIMATING ITEROPARITY IN COLUMBIA RIVER STEELHEAD USING RECORDS ARCHIVED IN THE COLUMBIA RIVER PIT TAG INFORMATION SYSTEM (PTAGIS) DATABASE

A Report for Study Code ADS-P-12-2

by

M. L. Keefer & C. C. Caudill
Department of Fish and Wildlife Sciences
University of Idaho, Moscow, ID 83844-1136

For

U.S. Army Corps of Engineers
Portland District, Portland OR

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Executive Summary

We used steelhead PIT-tag detection data archived in the Columbia River PTAGIS database to estimate the incidence of repeat spawning migration (i.e., iteroparity) in the multi-stock metapopulation upstream from Bonneville Dam. We evaluated migration histories from 53,282 adult steelhead detected at Bonneville Dam over 11 adult migration years (2000-2010). The dataset included winter- and summer-run life history types, wild- and hatchery-origin fish, and were from a wide variety of populations and management groups.

In total, 7 winter steelhead and 132 summer steelhead were considered to have initiated a second spawning migration based on appropriately-timed detections at Bonneville Dam in two migration years. Six of the seven winter steelhead were consecutive year spawners and the seventh was a skip year spawner. The summer group was half consecutive spawners and half skip spawners. With all years combined, Bonneville-to-Bonneville iteroparity estimates for the primary life history×origin groups were: 2.78% (winter, wild), 0.44% (winter, hatchery), 0.56% (summer, wild), and 0.16% (summer, hatchery).

At several geographic scales, wild steelhead had iteroparity estimates that were several times higher than those for hatchery steelhead. This was likely the result of more liberal harvest regulations for hatchery fish and the collection of hatchery adults for broodstock (i.e., limited survival to kelting). Younger steelhead (i.e., 1-sea, or ‘A-group’) tended to have higher iteroparity estimates than older steelhead (i.e., 2-sea, or ‘B-group’), though this pattern was not universal across populations. Winter steelhead had higher iteroparity than summer steelhead, but there were no direct comparisons of life history groups within individual tributaries. Iteroparity rates for wild steelhead decreased as freshwater migration distance increased, presumably reflecting higher kelt mortality for interior Columbia and Snake River populations.

Annual iteroparity estimates for wild steelhead were positively correlated with river discharge during the kelt outmigration. After accounting for this effect, we found limited but indirect evidence that installation and increased operation of surface flow outlets (SFOs) at Columbia and Snake River dams may have contributed to increasing steelhead iteroparity rates during the study period. However, we also concluded that the PTAGIS dataset was not particularly well suited to address this management question because sample sizes in the response variable (repeat-spawners) were small in several years and there was high year-to-year variability in which steelhead populations were PIT-tagged. No management groups (e.g., wild steelhead from individual populations or Snake River ‘B-group’ steelhead) had sufficient numbers of PIT-tagged fish in all study years. We provide several recommendations for evaluating the efficacy of SFOs for increasing iteroparity.

The PTAGIS-based iteroparity estimates do provide important baseline data, both as a time series of estimates for aggregated steelhead populations and as estimates for a range of individual management groups. These data can be used for future conservation and management initiatives for Columbia basin steelhead.

Introduction

Steelhead (*Oncorhynchus mykiss*) are unusual among the anadromous Pacific salmonids in their expression of iteroparity (i.e., repeat spawning). Iteroparity rates vary by orders of magnitude among steelhead populations and tend to be higher in winter-run populations in coastal watersheds and lower for summer-run fish and those with long distance migrations (Withler 1966; Busby et al. 1996; Quinn and Myers 2004; Keefer et al. 2008). Repeat spawners contribute a variety of genetic and demographic benefits to populations (Crespi and Teo 2002) and are therefore desirable for addressing management and conservation objectives. By spawning in multiple years, iteroparous individuals increase their number of mates and genetic crosses. Repeat spawners also have greater average lifetime production than single-year spawners, have greater fecundity given their larger size, and are thought to have competitive advantages over first-time spawners (Fleming and Reynolds 2004). Females and wild fish – two desirable demographic groups – typically have higher iteroparity rates than males and hatchery fish, respectively.

The Columbia River basin is located near the center of the steelhead distribution in North America and historically supported a great diversity of steelhead and other *O. mykiss* life history types (Brannon et al. 2004; Augerot 2005). However, historical iteroparity estimates are rare in the Columbia River basin literature, particularly for interior summer-run populations. In the current multi-dam environment, iteroparity estimates have ranged from <1-2% for mixed-stock Snake River summer steelhead (e.g., Whitt 1954; Keefer et al. 2008) to > 15% for some winter-run populations downstream from Bonneville Dam (e.g., Leider et al. 1986; Jepson et al. 2013). There are currently few benchmark iteroparity data for individual steelhead populations or specific management groups in the Columbia basin (e.g., ESA-listed populations, Snake River 'B-group' steelhead, etc).

The expression of iteroparity is often substantially reduced in impounded rivers (Kraabøl et al. 2009). Dams and reservoirs can select against post-spawn survival by slowing kelt migration to the ocean and by increasing direct and indirect mortality risks via increased energy consumption through delay (Castro-Santos and Letcher 2010) and passage through turbines or over spillways (Wertheimer and Evans 2005; Wertheimer 2007; Scruton et al. 2008; Colotelo et al. 2013). Kelts are particularly vulnerable to outmigration delays because they are often energetically exhausted. In fact, large numbers of steelhead kelts have been detected initiating downstream migration in the mid- and upper Columbia River basins (English et al. 2006; Hatch et al. 2013) and many are observed in bypass systems at lower Snake and lower Columbia River dams (e.g., Evans et al. 2004; Narum et al. 2008). However, PIT-tag studies have shown that few kelts survive to spawn again (Keefer et al. 2008).

A variety of management approaches have been undertaken to increase kelt survival and the expression of iteroparity in Columbia River steelhead over the last decade. These include increased operation of surface flow outlets (SFOs) for kelts at many FCRPS dams (e.g., Wertheimer 2007; Weiland et al. 2009; Khan et al. 2013), downstream transportation of kelts in juvenile fish barges (Evans et al. 2008), and kelt reconditioning in hatchery facilities (Hatch et al. 2013). The SFOs were designed to pass juvenile salmonids (Johnson and Dauble 2006) but their installation and expanded seasonal operations potentially benefit run-of-river kelts from all upriver populations. Radio and acoustic telemetry studies have shown that kelts use SFOs (Khan et al. 2010; Colotelo et al. 2013) and that fish that pass via these routes have a survival advantage over those that pass via turbines (Wertheimer 2007).

The primary objective in this study was to use the steelhead migration histories stored in the Columbia River PIT Tag Information System (PTAGIS) to generate 'baseline' iteroparity rate estimates for a variety of Columbia and Snake River steelhead populations and management groups.

Within this broad objective, we assessed five hypotheses: (1) winter steelhead have higher iteroparity rates than summer steelhead; (2) wild steelhead have higher iteroparity rates than hatchery steelhead; (3) 1-sea (i.e., 'A-group') steelhead have higher iteroparity rates than 2-sea (i.e., 'B-group') steelhead; (4) iteroparity rates decrease as freshwater migration distance increases; and (5) iteroparity rates in the Columbia River basin have increased as SFO installation and operation has increased.

Methods

Data Source and Data Screening

We used existing migration histories from steelhead that were PIT-tagged as juveniles at sites throughout the Columbia River basin upstream from Bonneville Dam. These data were archived by the Pacific States Marine Fisheries Commission (PSMFC) and accessed using the PTAGIS web portal (www.ptagis.org). Steelhead in the PTAGIS database were tagged by many different Federal, state, and Tribal organizations. Study objectives for these tagged fish rarely included estimation of iteroparity rates. Instead, they were typically used to evaluate juvenile survival rates, smolt-to-adult return rates, and other routine monitoring objectives. Most importantly, the data were not a random sample of the steelhead life history types, age classes, origins (wild, hatchery), or unique populations that were present in the Columbia basin in any year. The presented iteroparity estimates should be interpreted with these caveats in mind.

We used the following series of PTAGIS queries, joins, and data screens to generate the data set that we used for iteroparity analyses:

1.) We queried PTAGIS for all steelhead interrogations (i.e., detections) at adult fishways at Bonneville Dam. Sites included B2A (Washington-shore adult), BO1 (Bradford Island ladder), BO2 (Cascades Island ladder), BO3 (Washington-shore ladder/Adult Fish Facility), and BO4 (Washington-shore ladder slots). Separate queries were run for each year from 2000 through 2010 (n = 11 years). The start year (2000) was selected because it was the first we considered to have sufficient numbers of returning adult PIT-tagged steelhead. The end year (2010) was selected because it was the last year for which skip-year repeat spawners (i.e., those that returned in 2012) could be accounted for. Output from these queries included PIT code, juvenile release site and date, life history type (winter, summer), origin (wild, hatchery), and first and last detection dates and times at the Bonneville Dam fishway sites.

2.) From the above queries, we compiled a master list of unique steelhead PIT tag codes detected in the 11 study years. The master code list was then joined to each annual list using PIT code as the shared field. Codes with detections in adult fishways at Bonneville Dam in more than one calendar year were flagged as potential repeat spawners.

3.) We additionally queried PTAGIS for steelhead detected at adult fishways at Bonneville Dam in more than one calendar year (i.e., calendar year 1 plus calendar year 2 or 3). As with the joined fields in step 2 above, these queries helped identify steelhead that potentially made more than one spawning migration. Both methods also identified steelhead that were at Bonneville Dam in calendar year 1, overwintered, and were again at Bonneville Dam in calendar year 2 prior to spawning.

4.) Full detection histories for all potential repeat spawners in the master list and the multi-year PTAGIS queries were examined individually. Steelhead were designated as overwintering (calendar year 1 detection plus pre-spawning detection date in year 2), consecutive repeat spawners (calendar year 1 detection plus post-spawning detection date in calendar year 2), or skip repeat spawners (detections in calendar years 1 and 3).

5.) We used several data screens to exclude steelhead from the iteroparity analyses. These included: fish that were PIT-tagged as adults (primarily at Bonneville Dam, but also in some tributaries), fish that were PIT-tagged as juveniles but were collected and radio-tagged as adults (primarily at Bonneville Dam), fish that were PIT-tagged as kelts (primarily at John Day, McNary, or Lower Granite dams), and fish that were detected at the Bonneville adult fishways but were likely smolts or kelts (based on release dates and/or reviews of migration histories). We also excluded some PIT tag release groups due to ambiguous origin (e.g., small samples collected at some main stem sites, unknown life history type, etc.).

6.) For the screened dataset, we ran additional PTAGIS queries for detections as juveniles and as post-spawn kelts in juvenile bypass systems (JBS) during their outmigrations at Lower Granite, Little Goose, Lower Monumental, Rocky Reach, McNary, John Day, and Bonneville dams (including the Bonneville corner collector [BCC]). The juvenile detection data were used to establish whether steelhead spent one or two years in the Pacific Ocean before their maiden spawning migration. The kelt detection data were used to estimate minimum kelting rates and kelt-to-adult iteroparity estimates. (Note: juvenile and kelt detections at Ice Harbor Dam were not included because PTAGIS did not differentiate between juvenile and adult detections).

7.) Last, we queried PTAGIS for adult steelhead detections at dams upstream from Bonneville Dam. These data were used to identify fish that passed Bonneville Dam but were presumably harvested, died of natural causes, or strayed during their first migration year before reaching upstream dams. PIT interrogation sites were at McNary (installed 2002), Priest Rapids (2003), Rock Island (2003), Rocky Reach (2006), Wells (2002), Ice Harbor (2005), and Lower Granite (1989) dams.

Population Assignments

The initial queries generated a master database with 63,614 steelhead. The subsequent screens reduced the sample by ~10,000 fish to 53,282. The steelhead in this dataset were from 198 juvenile release sites distributed throughout the Columbia and Snake River basins upstream from Bonneville Dam (Appendix B). To simplify data presentation and analyses, these groups were consolidated into 26 loosely-defined ‘populations’ within three geographic regions (Figure 1). The regions included (1) sites downstream from the Columbia River-Snake River confluence; (2) sites within the Snake River basin; and (3) sites upstream from the Columbia River-Snake River confluence. The populations included major tributaries, groups PIT-tagged at main stem dams (Lower Granite, Rock Island, Rocky Reach, Wells), and at two hatcheries located adjacent to the main stem (Lyons Ferry, Ringold) (Figure 1). Within the 26 populations, the data were further separated by life history type (winter, summer), origin (wild, hatchery), and sea age (1-sea, 2-sea, unknown-sea). A majority of the summer steelhead in the Columbia basin has a 1-sea life history, but several sub-basins also produce 2-sea fish (Busby et al. 1996). The latter primarily include Clearwater and Salmon rivers in the Snake River as well as the Methow River and other sites in the upper Columbia River basin (Chapman et al. 1994; Wells HGMP 2011).

Data Analyses

The primary metric used to evaluate iteroparity was the percentage of PIT-tagged steelhead that was detected at Bonneville Dam on two spawning migrations (i.e., pre-spawn adult-to-adult iteroparity). The metric included repeat spawners that returned within several months of their kelt outmigration (‘consecutive spawners’ with a few months between events) or in the calendar year after

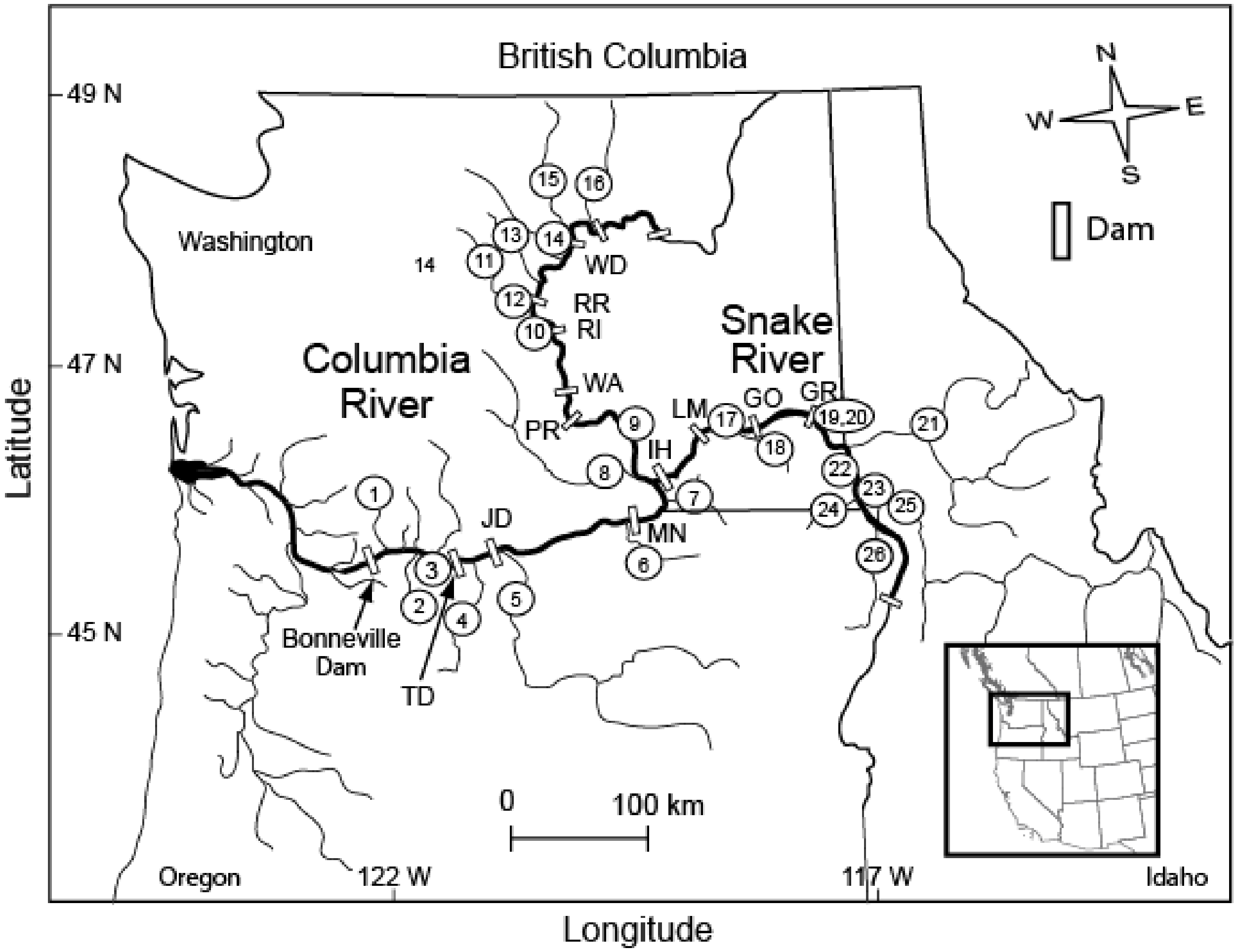

Figure 1. Map of the Columbia and Snake rivers indicating where PIT-tagged steelhead were tagged as juveniles (numbered circles) and monitored as adults (dams). Tagged fish were assigned to one of 26 populations upstream from Bonneville Dam based on their juvenile release site: Wind River (1), Hood River (2), Fifteenmile Creek (3), Deschutes River (4), John Day River (5), Umatilla River (6), Walla Walla River (7), Yakima River (8), Ringold Hatchery (9), Rock Island Dam (10), Wenatchee River (11), Rocky Reach Dam (12), Entiat River (13), Wells Dam (14), Methow River (15), Okanogan river (16), Lyons Ferry Hatchery (17), Tucannon River (18), Lower Granite Dam (19,20), Clearwater River (21), Asotin Creek (22), upper Snake River (23), Grande Ronde River (24), Salmon River (25), and Imnaha River (26). PIT tag interrogation systems used in the analyses included juvenile bypass systems (Lower Granite [GR], Little Goose [GO], Lower Monumental [LM], Rocky Reach [RR], McNary [MN], John Day [JD], and Bonneville dams) and adult fishways (Bonneville, McNary, Ice Harbor [IH], Lower Granite, Priest Rapids [PR], Rock Island [RI], Rocky Reach, and Wells [WL] dams).

their kelt outmigration ('skip spawners' with a year or more at sea). Bonneville was selected because all study populations had to pass this site and detection efficiency for PIT-tagged fish was near 100%. The criteria used to establish a second migration were detection at Bonneville Dam during two calendar years and detection during the typical upstream migration period. This was approximately May-November for summer steelhead. Winter steelhead timing was somewhat more ambiguous, with some fish migrating upstream from November-April and others passing Bonneville Dam during the summer months. Fish were not considered repeat spawners if their detections in the second year were prior to typical spawning dates. These fish were likely overwintering and did not have time to spawn, return to the ocean, and initiate a second migration. Importantly, we generally could not determine whether steelhead returned to their natal site or whether repeat spawners spawned successfully in either year. Some fish may have strayed and spawned at non-natal sites and others may not have survived to the spawning period after passing Bonneville Dam.

The adult PIT tag detections at dams upstream from Bonneville Dam were used to estimate 'adjusted' iteroparity rates that accounted for upstream migration mortality during the first steelhead migration year. This essentially reduced the denominators in calculations by excluding fish that likely had no opportunity for repeat spawning (with the exception of strays). Unlike the Bonneville-to-Bonneville estimates, the adjusted estimates were not directly comparable across populations because different groups had to pass different dams and had different opportunities for straying. We calculated the percentages of steelhead that were detected at McNary, Priest Rapids, or Lower Granite dams on their first migrations that were subsequently detected at Bonneville Dam on their second migrations (i.e., McNary-to-Bonneville, Priest Rapids-to-Bonneville, and Lower Granite-to-Bonneville). Only the years 2004-2010 were included (Priest Rapids PIT antennas were fully operational in 2004 and relatively small samples in 2000-2003 reduce the value of these data).

Lastly, we calculated kelt-to-adult iteroparity estimates for the much smaller sample of PIT-tagged steelhead detected during outmigration. This metric was defined as the percentage of kelts that were detected at main stem dams during outmigration that were subsequently detected on second spawning migrations at Bonneville Dam. These estimates were more directly comparable to the PIT-tagged kelt-to-adult iteroparity estimates reported by Keefer et al. (2008). It is important to note that many of the repeat spawners we identified in the PTAGIS dataset were not detected at any site as kelts (i.e., they passed dams via turbines, spillways, or other unmonitored routes) and were thus excluded from kelt-to-adult iteroparity estimates.

Comparisons of Bonneville-to-Bonneville iteroparity among life history types, origin groups, age classes, populations, and years were qualitative for this summary because the data were collected opportunistically. There was no controlled experimental design and PIT tag groups varied considerably through the study years. SFO operations and river environment also varied from year to year and site to site, making it difficult to directly evaluate the effects of these installations. Installation years for SFOs were: 2002 (Lower Granite), 2004 (Bonneville corner collector), 2005 (Ice Harbor), 2007 (McNary), 2008 (Lower Monumental), and 2009 (Little Goose) (R. Wertheimer, *personal communication*). We used logistic regression to evaluate the relationship between freshwater migration distances and repeat spawning. Migration distance for each steelhead was assigned as the distance to the Pacific Ocean in river kilometers from the dam or mouth of the tributary where they were tagged, or from Lyons Ferry or Ringold Hatchery. These distances were conservative (i.e., minimum) for the dam and tributary groups. Separate logistic models were run for each origin×age combination.

Results

Sample Summary

A total of 53,282 maiden steelhead detected inside adult fishways at Bonneville Dam were included in repeat spawner analyses (Table 1). Annual sample sizes ranged from 298 in 2000 to 11,775 in 2009 (*annual mean* = 4,843, SD = 3,558). The life history×origin components were: 144 (winter, wild), 676 (winter, hatchery), 12,114 (summer, wild), and 40,348 (summer, hatchery) steelhead. Winter fish were released at 6 sites in two tributaries to the Bonneville reservoir (Hood River and Fifteenmile Creek). Summer fish were released at 193 locations upstream from Bonneville

Dam. Within year, the PIT-tagged steelhead used in the analyses were 0.1-2.2% (*mean* = 1.2%) of the total steelhead counts at Bonneville Dam, which ranged from 275,806-636,460 (*mean* = 403,202). Mean percentages of PIT-tagged fish in annual samples were 0.9% (*range* 0.1-1.7%) for wild steelhead and 1.4% (*range* = 0.1-2.8%) for hatchery steelhead.

Repeat Spawner Identification and Timing

A total of 49 winter and 320 summer steelhead were detected at Bonneville Dam adult fishways in two calendar years. Detection histories and migration dates for 86% (*n* = 42/49) of the winter and 59% (*n* = 188/320) of the summer fish suggested that they overwintered somewhere in the lower Columbia River prior to their first spawning attempt. Detections of overwintering fish at Bonneville in the second year were mostly in January-March, suggesting that overwintering occurred both upstream and downstream from Bonneville Dam. The remaining 7 (14%) winter and 132 (41%) summer fish were likely repeat spawners.

The seven repeat spawners in the winter group were detected inside Bonneville Dam fishways from 5 April through 19 August (*median* = 22 June) on their first migration year. Six of the seven were consecutive spawners that were detected on their second migration from 25 February through 3 September (*median* = 20 July). The seventh was a skip spawner. The detection dates suggest that some may have been summer or hybrid fish.

The 132 repeat spawners in the summer group were first detected at Bonneville Dam from 4 June through 17 October (*median* = 4 August; Figure 2). This distribution was earlier than the steelhead run at large (2000-2010 *median* = 14 August). The repeat group was half consecutive spawners (*n* = 66) and half skip spawners (*n* = 66). Most consecutive spawners were detected later in the run during their second migration (*median* = 29 August, *range* = 18 June to 29 October) than skip spawners (*median* = 2 August, *range* = 20 June to 19 October).

The ratios of consecutive:skip repeat spawners differed slightly by region and more substantially by ocean age. Consecutive spawners were proportionately more common among older fish and in populations originating closer to the Pacific Ocean. Consecutive:skip repeat spawner ratios for 1-sea steelhead were 12:10 (lower Columbia), 11:16 (upper Columbia), and 15:24 (Snake). Ratios for 2-sea steelhead were 3:1 (lower Columbia), 7:2 (upper Columbia), and 8:4 (Snake). Ratios for unknown-sea fish were 2:2, 7:7, and 1:0, respectively.

Bonneville-to-Bonneville Iteroparity by Life History Type and Origin

Winter Run.– The 144 wild winter steelhead were from Fifteenmile Creek. In total, 2.78% (*annual mean* = 1.88%) of this group was detected on a second spawning migration (Table 1, Figure 3). The 676 hatchery winter steelhead from the Hood River had a total repeat spawning estimate of 0.44% (*annual mean* = 0.37%).

Summer Run.– Across all years and all summer steelhead populations, total iteroparity estimates were 0.56% (*annual mean* = 0.55%) for wild fish and 0.16% (*annual mean* = 0.11%) for hatchery fish (Table 1). Total estimates for the group of populations downstream from the Columbia River–Snake River confluence were 1.27% (wild) and 0.35% (hatchery). Estimates were 1.12% (wild) and 0.20% (hatchery) for Columbia River populations above the Snake River confluence and 0.38% (wild) and 0.09% (hatchery) for Snake River populations.

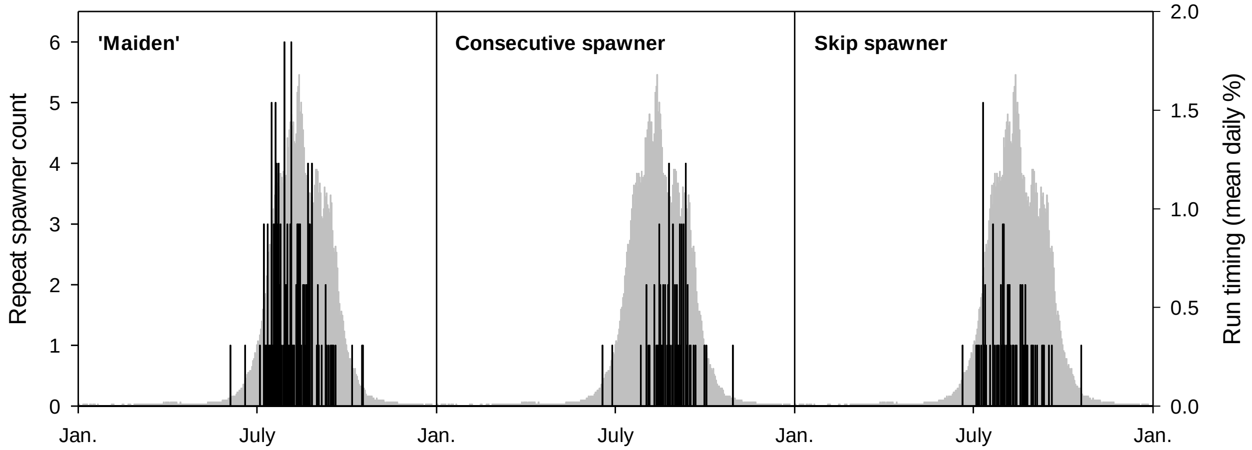

Figure 2. Migration timing of 132 PIT-tagged summer steelhead at Bonneville Dam on the year they were first detected as adults ('Maiden') and on their second spawning migration year at Bonneville Dam (either Consecutive spawner or Skip spawner). Gray shaded areas show steelhead run timing at Bonneville Dam, expressed as mean daily percent passage during the study years (2000-2010).

Table 1. Annual and total numbers of steelhead that were detected as maiden spawners at Bonneville Dam and the percentages that were estimated to have made two spawning migrations, by life history type (winter, summer) and origin (wild, hatchery). All age classes and populations combined.

		Wild			Hatchery		
Run	Year	Maiden	Repeat	Repeat (%)	Maiden	Repeat	Repeat (%)
Winter	2006	-	-	-	1	0	0.00
	2007	-	-	-	32	0	0.00
	2008	11	0	0.00	76	1	1.32
	2009	45	1	2.22	200	0	0.00
	2010	88	3	3.41	367	2	0.54
	Total	**144**	**4**	**2.78**	**676**	**3**	**0.44**
Summer	2000	43	0	0.00	255	0	0.00
	2001	1,018	4	0.39	916	0	0.00
	2002	1,204	3	0.25	393	0	0.00
	2003	799	5	0.63	324	0	0.00
	2004	701	1	0.14	3,745	7	0.19
	2005	526	5	0.95	6,419	10	0.16
	2006	360	3	0.83	7,158	9	0.27
	2007	840	10	1.19	3,219	9	0.28
	2008	1,442	6	0.42	3,626	6	0.17
	2009	2,685	16	0.60	8,845	8	0.09
	2010	2,495	15	0.60	5,448	5	0.09
	Total	**12,045**	**68**	**0.56**	**40,348**	**64**	**0.16**

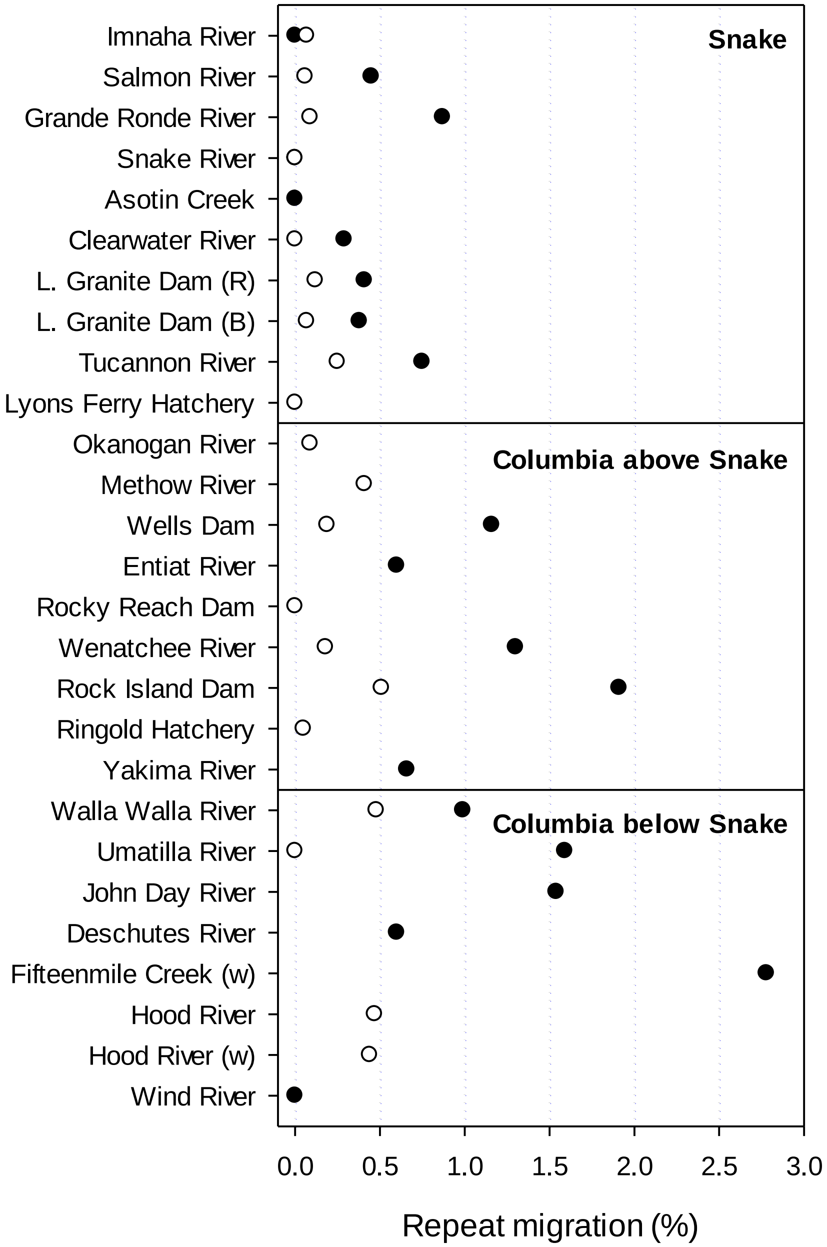

Figure 3. Percentages of wild (●) and hatchery (○) steelhead that were estimated to have made two spawning migrations based on PIT-tag detections at Bonneville Dam. All years, age classes, and release groups were combined within individual sub-basins, main stem release sites, and hatcheries. ‘w’ indicates winter steelhead. ‘R’ and ‘B’ indicate in-river and barged juveniles at Lower Granite Dam. (See Appendix Table 1 for sample sizes).

Iteroparity was also consistently higher for wild steelhead than hatchery steelhead from individual sub-basin populations and for groups PIT-tagged at main stem dams (Figure 3). In tributary sub-basins where both wild and hatchery fish had non-zero estimates, rates for wild fish were 2.1-9.7 times higher than rates for hatchery fish. Similarly, rates were 3.4-5.4 times higher for wild versus hatchery fish PIT-tagged at Snake and upper Columbia River dams. The only exception to this pattern was for Imnaha River steelhead, which had estimates of 0.00% (wild) and 0.09% (hatchery).

Unknown Life History.– One group of presumed wild-origin steelhead with unknown life history type was excluded from all analyses but warrants mention. This was the 346 steelhead from the Wind River for which the total iteroparity estimate was 4.05%, among the highest for any category. Maiden migration timing for the repeat Wind River spawners ranged from late April through October (*median* = 1 July), suggesting a mix of winter and summer life history types.

Bonneville-to-Bonneville Iteroparity by Ocean Age

Winter run.– Total estimates for the Fifteenmile Creek wild winter steelhead were 4.04% for 1-sea fish and 0.00% for unknown-sea age fish (Table 2). Estimates for the Hood River hatchery group were 0.00% (1-sea) and 0.57% (unknown-sea).

Summer run.– Across all years and all summer steelhead populations, total estimates were 0.67% (1-sea), 0.35% (2-sea), and 0.96% (unknown-sea) for wild fish and 0.18% (1-sea), 0.09 (2-sea), and 0.19% (unknown-sea) for hatchery fish (Table 2). Total iteroparity estimates for lower Columbia River wild populations were 1.34% (1-sea), 1.81% (2-sea), and 0.83% (unknown-sea). Estimates were 0.29%, 1.92%, and 1.88%, respectively, for upper Columbia wild populations and were 0.53%, 0.22%, and 0.41%, respectively, for wild Snake River fish. At this geographic scale, estimates for hatchery steelhead ranged from 0.11-0.51 (1-sea), 0.00-0.14% (2-sea), and 0.00-0.22% (unknown-sea). Note the small sample sizes in some comparisons (Table 2).

At the population scale there were fewer consistent differences in iteroparity rates among sea-age classes (Table 2). For wild-origin steelhead, 1-sea fish had higher rates in some populations (e.g., John Day, Umatilla, Grande Ronde, and Salmon River groups and both Lower Granite Dam groups) while 2-sea fish had higher rates in others (e.g., Deschutes River, Yakima River, Tucannon River, and Rock Island Dam). Unknown-sea age fish had higher rates in the wild Wenatchee, Entiat, Methow, and Clearwater River populations. Note the small sample sizes in some comparisons (Table 2).

Bonneville-to-Bonneville Iteroparity by Migration Distance

The relationship between freshwater migration distance and repeat migration was not the same across origin and sea-age classes (Figure 4). The predicted probability of repeat migration decreased as migration distance increased for wild 1-sea (logistic regression, $\chi^2 = 14.9$, $P < 0.001$) and wild 2-sea steelhead ($\chi^2 = 10.0$, $P < 0.001$), with summer and winter run fish combined. In contrast, the predicted probability increased with migration distance for 2-sea hatchery fish ($\chi^2 = 5.3$, $P = 0.022$). The relationships were equivocal ($P > 0.05$) for 1-sea hatchery, unknown-sea hatchery, and unknown-sea wild fish ($\chi^2 \leq 0.5$, $P \geq 0.47$).

Table 2. Percentages of wild and hatchery steelhead that were estimated to have made two spawning migrations based on PIT-tag detections at Bonneville Dam, by estimated time at sea (1-sea, 2-sea or Unknown [U]). All years and release groups combined within individual sub-basins, main stem release sites, and hatcheries. 'w' indicates winter steelhead. 'R' and 'B' indicate in-river and barged juveniles at Lower Granite Dam.

	Wild						Hatchery					
	1-sea		2-sea		U-sea		1-sea		2-sea		U-sea	
Juvenile release site	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Columbia below Snake							-	-	-	-	-	-
Wind River	3	0.00	-	-	61	0.00	-	-	-	-	-	-
Hood River (w)	-	-	-	-	-	-	148	0.00	-	-	528	0.57
Hood River	-	-	-	-	-	-	64	1.56	-	-	157	0.00
Fifteenmile Creek (w)	99	4.04	-	-	45	0.00	-	-	-	-	-	-
Deschutes River	229	0.44	17	5.88	89	0.00	-	-	-	-	-	-
John Day River	758	1.72	143	0.70	267	1.50	-	-	-	-	-	-
Umatilla River	81	2.47	22	0.00	23	0.00	283	0.00	70	0.00	105	0.00
Walla Walla River	122	0.00	39	5.13	41	0.00	836	0.60	92	0.00	108	0.00
Total (w)	**99**	**4.04**	**-**	**-**	**45**	**0.00**	**148**	**0.00**	**-**	**-**	**528**	**0.57**
Total (s)	**1,193**	**1.34**	**221**	**1.81**	**481**	**0.83**	**1,183**	**0.51**	**162**	**0.00**	**363**	**0.00**
Columbia above Snake												
Yakima River	94	0.00	16	5.88	41	0.00	-	-	-	-	-	-
Ringold Hatchery	-	-	-	-	-	-	4,711	0.08	1,235	0.00	1,654	0.00
Rock Island Dam	83	1.20	74	2.70	-	-	221	0.90	173	0.00	-	-
Wenatchee River	48	0.00	31	0.00	75	2.67	1,873	0.21	604	0.00	853	0.23
Rocky Reach Dam	-	-	-	-	-	-	125	0.00	101	0.00	-	-
Entiat River	87	0.00	25	0.00	54	1.85	-	-	-	-	-	-
Wells Dam	-	-	-	-	-	-	681	0.15	915	0.22	-	-
Methow River	34	0.00	9	0.00	43	2.33	3,624	0.41	1,088	0.37	1,650	0.42
Okanogan River	-	-	-	-	-	-	525	0.00	234	0.00	305	0.33
Total	**346**	**0.29**	**156**	**1.92**	**213**	**1.88**	**11,760**	**0.22**	**4,350**	**0.14**	**4,462**	**0.22**
Snake River												
Lyons Ferry Hatchery	-	-	-	-	-	-	119	0.00	20	0.00	2	0.00
Tucannon River	146	0.68	87	1.15	34	0.00	1,628	0.31	251	0.00	157	0.00
Lower Granite Dam (b)	1,915	0.57	1,814	0.17	-	-	3,423	0.09	2,241	0.04	1	0.00
Lower Granite Dam (r)	1,637	0.55	1,560	0.26	-	-	1,118	0.18	523	0.00	1	0.00
Clearwater River	158	0.00	459	0.22	70	1.43	157	0.00	868	0.00	127	0.00
Asotin Creek	49	0.00	40	0.00	4	0.00	-	-	-	-	-	-
Snake River[1]	69	0.00	42	0.00	6	0.00	412	0.00	62	0.00	9	0.00
Grande Ronde River	174	1.72	143	0.00	26	0.00	1,862	0.05	356	0.28	77	0.00
Salmon River	177	0.56	194	0.52	77	0.00	2,707	0.07	410	0.00	101	0.00
Imnaha River	421	0.00	177	0.00	24	0.00	1,252	0.08	159	0.00	25	0.00
Total	**4,746**	**0.53**	**4,516**	**0.22**	**241**	**0.41**	**12,678**	**0.11**	**4,890**	**0.04**	**500**	**0.00**
Total	**6,286**	**0.67**	**4,893**	**0.35**	**935**	**0.96**	**25,621**	**0.18**	**9,402**	**0.09**	**5,325**	**0.19**

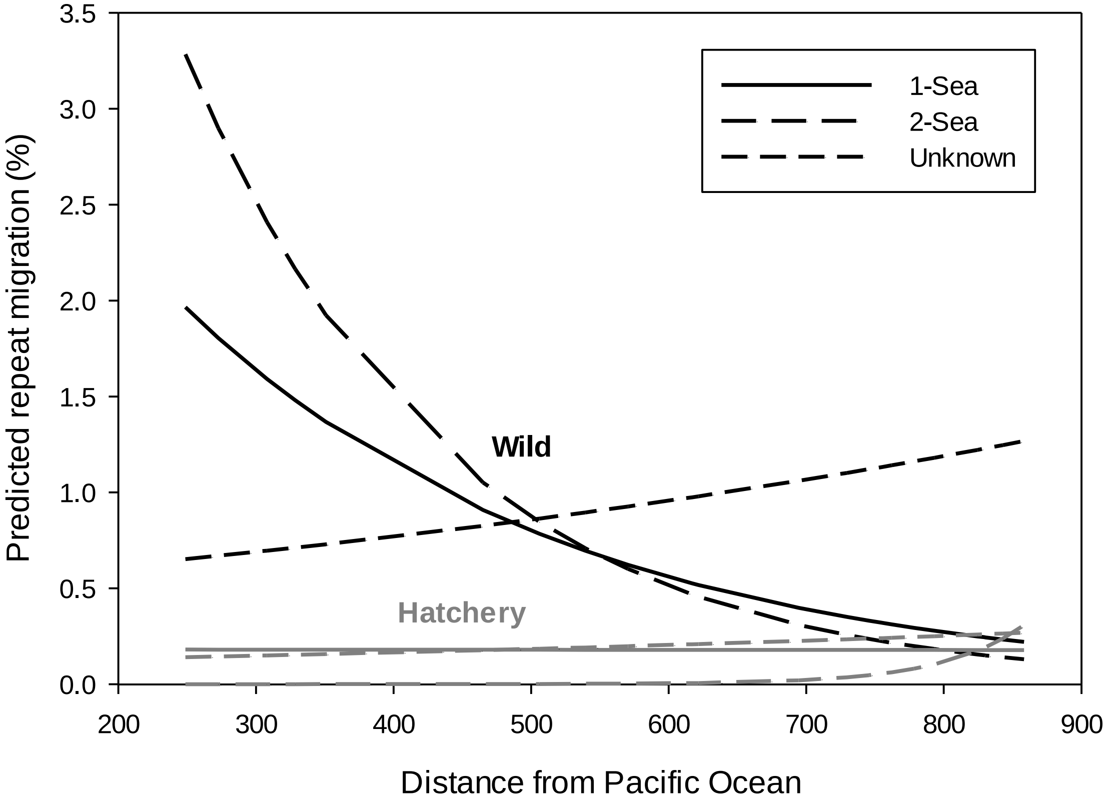

Figure 4. Probabilities that PIT-tagged steelhead would make two spawning migrations as predicted by distance to the Pacific Ocean from natal sub-basin or juvenile release site, by origin (wild, hatchery) and sea age (1-sea, 2-sea, unknown). Probabilities were generated using logistic regression models that included all steelhead in the respective study samples.

Bonneville-to-Bonneville Iteroparity through Time

Small sample sizes, especially for the response variable ‘repeat spawners’, precluded many meaningful comparisons of how iteroparity rates changed (or did not change) through time. At the broadest scale of all populations combined, annual iteroparity estimates for wild steelhead generally increased from 2000 to 2007 and then declined in 2008-2010 (quadratic regression, $r^2 = 0.48$, $P = 0.073$; Figure 5). A similar quadratic relationship was observed for all hatchery steelhead ($r^2 = 0.63$, $P = 0.020$). When the models were weighted by the number of maiden steelhead in each year, model fit was reduced for wild steelhead ($r^2 = 0.26$, $P = 0.293$) but increased for hatchery steelhead ($r^2 = 0.72$, $P = 0.006$).

Columbia River discharge during the kelt outmigration period of April-June was positively associated with wild steelhead iteroparity rates (Figure 6). The relationship was statistically significant ($r^2 = 0.51$, $P = 0.014$) in an unweighted linear regression but was not significant ($r^2 = 0.21$, $P = 0.153$) when the regression was weighted by annual maiden steelhead abundance. Neither weighted nor unweighted linear models were significant ($P > 0.05$) for hatchery steelhead (Figure 6). Residuals from the flow×iteroparity regressions were not associated with migration year for either wild or hatchery fish (Figure 6). The lack of a linear year effect was also

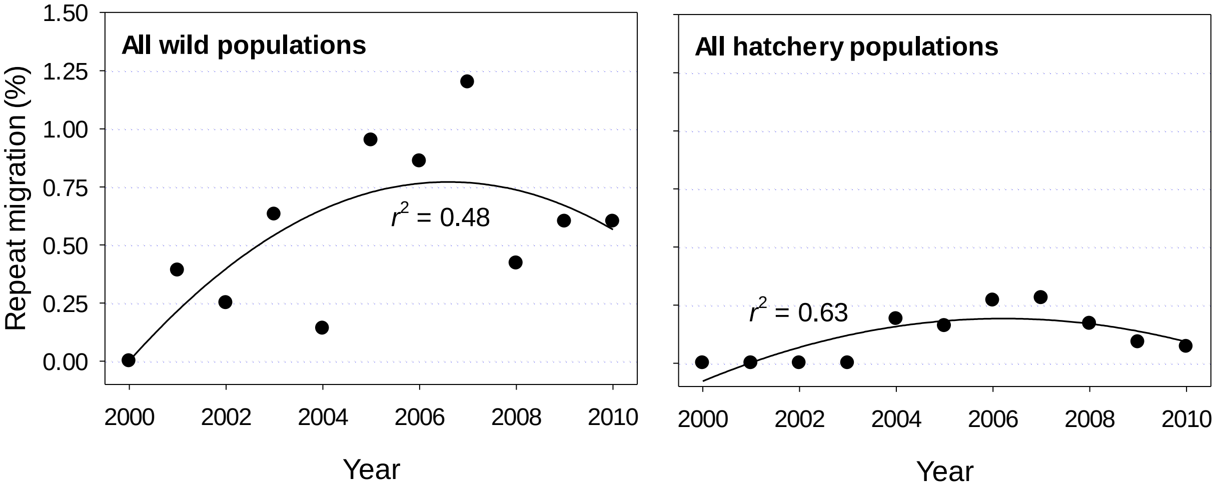

Figure 5. Quadratic relationships between maiden migration year and the percentage of repeat spawning steelhead. Solid lines show unweighted quadratic regression results.

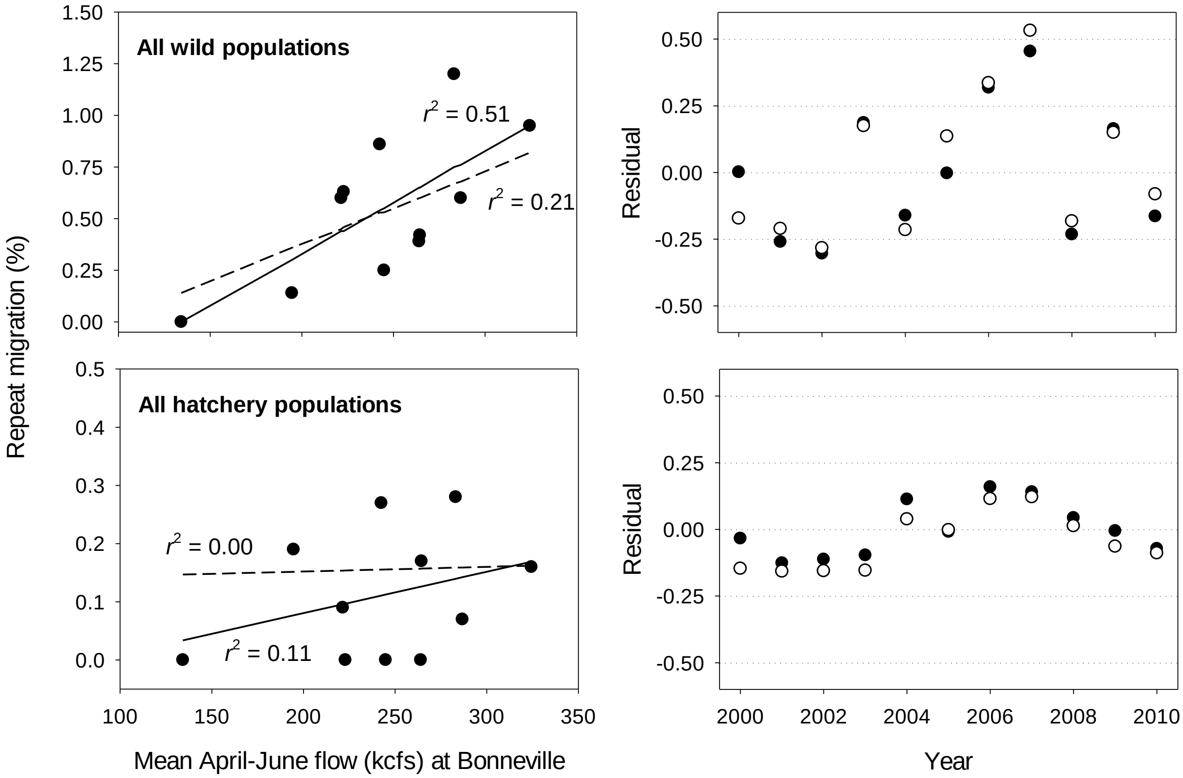

Figure 6. Relationships between mean April-June Columbia River flow and the percentage of repeat spawning steelhead (left panels). Solid lines show unweighted linear regression results and dashed lines show linear regressions weighted by the number of maiden steelhead in each year. Right panels show the relationship between migration year and the residuals from the unweighted (●) and weighted (○) flow models. Flow data were from Bonneville Dam in the kelt outmigration year (e.g., maiden spawners from the 2000 migration were matched to flow data from April-June 2001).

evident in regression models that included both flow and year as predictor variables (all $P >$ 0.05 for year effects). Notably, the residual analyses suggest that iteroparity was lower than expected once accounting for flow in 2000-2002, higher than expected from 2004-2008, and lower again in 2009-2010. This pattern may indicate multi-year effects that were unaccounted for in the model (e.g., ocean conditions, composition of the PIT-tagged sample, etc), a quadratic effect like the one evident in the year-only models, or merely statistical noise.

A similar set of evaluations for the Snake River steelhead groups produced qualitatively similar results. Iteroparity rates for both hatchery and wild Snake River steelhead were positively correlated ($P < 0.05$) with flow in the kelt emigration season and year effects were non-significant ($P > 0.05$) in models that included flow and year.

'Adjusted' Iteroparity Estimates

McNary-to-Bonneville iteroparity estimates for wild steelhead were ~25% higher than Bonneville-to-Bonneville estimates for the upper Columbia and Snake River wild groups (Table 3). Similarly, McNary-to-Bonneville estimates were higher than Bonneville-to-Bonneville estimates by 43% for the upper Columbia group and 22% for the Snake group.

The Priest Rapids-to-Bonneville estimate for upper Columbia wild steelhead (1.24%) was higher than the Bonneville-to-Bonneville (0.91%) estimate by 36%. The Priest Rapids-to-Bonneville estimate for upper Columbia hatchery fish (0.43%) was more than double the Bonneville-to-Bonneville estimate (0.21%). In contrast, Lower Granite-to-Bonneville estimates were only slightly higher (11-15%) than Bonneville-to-Bonneville estimates for wild and hatchery groups that originated above Lower Granite Dam (Table 3).

Kelt-to-Bonneville Iteroparity

Winter run.– In total, 4.2% (6/144) of maiden wild and 0.9% (6/676) of maiden hatchery steelhead were subsequently detected as kelts at Bonneville Dam. None of these detected kelts was among the seven repeat spawners in the winter group and hence kelt-to-adult iteroparity estimates were 0.00% (Table 4).

Summer run.– Across all years, 4.8% (580/12,045) of maiden wild and 1.0% (418/40,348) of maiden hatchery steelhead were subsequently detected as kelts at one or more main stem sites. The 580 detected wild kelts included 15 of the 68 wild repeat spawners (i.e., 22% of the wild repeat spawners were detected as outmigrating kelts). Similarly, the 418 detected hatchery kelts included 14 of 64 (22%) hatchery repeat spawners. The remaining repeat spawners (53 wild, 50 hatchery) were not detected as kelts.

Estimates of kelt-to-adult iteroparity for wild steelhead ranged from 0.00% for kelts detected at John Day, McNary, Lower Monumental, Little Goose, and Lower Granite dams (n = 33-78 kelts) to > 7% for kelts detected at Bonneville (n = 142) and Rocky Reach (n = 27) dams (Table 4). Estimates for hatchery steelhead ranged from 0.00% at Lower Granite Dam (n = 46) to 6.12% at John Day Dam (n = 49).

Table 3. ‘Adjusted’ percentages of wild and hatchery steelhead that were estimated to have made two spawning migrations based on adult PIT-tag detections at Bonneville (BO), McNary (MN), Priest Rapids (PR), and Lower Granite (GR) dams. All release groups combined within individual sub-basins, main stem release sites, and hatcheries ‘r’ and ‘b’ indicate in-river and barged juveniles at Lower Granite Dam. Years were restricted to 2004-2010.

	Wild				Hatchery			
	BO-BO	MN-BO	PR-BO	GR-BO	BO-BO	MN-BO	PR-BO	GR-BO
Columbia below Snake								
Walla Walla River	0.99	1.17	-	-	0.49	0.62	-	-
Columbia above Snake								
Yakima River	0.76	0.91	-	-	-	-	-	-
Ringold Hatchery					0.05	0.08	-	-
Rock Island Dam	0.81	0.99	1.03	-	0.89	1.23	1.22	-
Wenatchee River	1.30	1.72	1.72	-	0.18	0.24	0.24	-
Rocky Reach Dam	-	-	-	-	0.00	0.00	0.00	-
Entiat River	0.60	0.82	0.83	-	-	-	-	-
Wells Dam	-	-	-	-	0.28	0.37	0.38	-
Methow River	1.16	1.41	1.41	-	0.41	0.55	0.56	-
Okanogan River	-	-	-	-	0.10	0.13	0.13	-
Total	**0.91**	**1.15**	**1.24**	**-**	**0.21**	**0.30**	**0.43**	**-**
Snake River								
Lyons Ferry Hatchery	-	-	-	-	0.00	0.00	-	0.00
Tucannon River	0.85	1.09	-	-	0.25	0.25	-	-
Lower Granite Dam (b)	0.41	0.51	-	0.45	0.07	0.08	-	0.10
Lower Granite Dam (r)	0.43	0.56	-	0.58	0.16	0.20	-	0.20
Clearwater River	0.36	0.43	-	0.46	0.00	0.00	-	0.00
Asotin Creek	0.00	0.00	-	0.00	-	-	-	-
Snake River[1]	0.00	0.00	-	0.00	0.00	0.00	-	0.00
Grande Ronde River	0.68	0.88	-	0.94	0.09	0.12	-	0.13
Salmon River	0.51	0.64	-	0.65	0.06	0.08	-	0.08
Imnaha River	0.00	0.00	-	0.00	0.07	0.10	-	0.11
Total	**0.40**	**0.50**	**-**	**0.46**	**0.09**	**0.11**	**-**	**0.10**

Table 4. Percentages of wild and hatchery steelhead kelts that were estimated to have made two spawning migrations based on PIT-tag detections at juvenile bypass systems or at the Bonneville Dam corner collector during kelt outmigration. All years and release groups combined. BO = Bonneville, JD = John Day, MN = McNary, LM = Lower Monumental, GO = Little Goose, GR = Lower Granite, RR = Rocky Reach.

		Wild			Hatchery		
Run	Dam	Kelt	Repeat	Repeat (%)	Kelt	Repeat	Repeat (%)
Winter	BO	6	0	0.00	6	0	0.00
Summer	BO	142	11	7.80	183	10	5.43
	JD	51	0	0.00	49	3	6.12
	MN	33	0	0.00	85	1	1.18
	LM	39	0	0.00	35	1	2.86
	GO	78	0	0.00	75	1	1.33
	GR	86	2	2.33	46	0	0.00
	RR	27	2	7.41	143	1	0.70
	Any	**580**	**15**	**2.59**	**418**	**14**	**3.35**

Discussion

Surface Flow Operations at Dams

Although wild steelhead iteroparity estimates generally increased over the study period, the correlative nature of our analysis made it impossible to attribute the increase to increased SFO installation and operation. Many environmental and biological factors may influence repeat spawning rates and our analysis of covariates was limited. We accounted for inter-annual variability in Columbia River discharge in the spring because previous research has shown that flow is positively correlated with steelhead kelt survival (Wertheimer and Evans 2005). This makes intuitive sense because kelt residence times in reservoirs are reduced and more water may be passed via surface flow routes during high flow. However, residuals from our flow×iteroparity rate relationship did not indicate a clear increase in iteroparity rates for wild aggregate populations over the 2000-2010 study period. Instead, the residual analysis suggested a possible multi-year periodicity in iteroparity rate, which may be related to unmeasured covariates. We did not conduct a more comprehensive analysis (i.e., one that included other potential covariates like spill volume, SFO operations, or measures of ocean productivity upon kelt re-entry into salt water because steelhead in the PTAGIS samples were not consistent from year to year. Even the largest sample groups (e.g., steelhead PIT-tagged at Lower Granite Dam, Ringold Hatchery, and the Methow River) had small samples or no samples in some years.

It was also difficult to assess the timing and consistency of SFO operations across years and at individual dams (R. Wertheimer, *personal communication*). We considered the covarying environmental conditions and SFO operations, along with small kelt sample sizes and inconsistent PTAGIS samples across years to be sufficiently confounding to preclude a full data mining exercise, particularly given the low observed sample sizes for repeat spawners. To better understand and potentially model the effects of SFO operations on steelhead iteroparity in the Columbia River basin we recommend:

- consistent use of clearly defined study populations, such as PIT-tagged wild steelhead from populations of management concern; year-to-year consistency is important for detecting trends and for evaluating effects of environmental and operational covariates;

- increased PIT monitoring at downstream migration routes to detect a higher proportion of outmigrating kelts; sites like the Bonneville corner collector provide valuable kelt detection data and similar systems should be considered at other SFOs to compliment kelt detections in juvenile bypass systems;

- increased PIT-tagging of kelts at collection facilities (e.g., Keefer et al. 2008; Evans et al. 2008; Hatch et al. 2013); kelt-to-adult iteroparity estimates are more useful for operations-related questions than adult-to-adult estimates based on fish tagged as juveniles;

- better estimation of kelt abundance along the outmigration route; the scope of any iteroparity-related conservation efforts depends upon the available kelt population;

- experimental designs that directly address SFO operations in relation to route-specific kelt passage and survival at dams; studies that use kelts tagged with active transmitters (e.g., Wertheimer 2007; Colotelo et al. 2013) can provide the route-specific estimates needed to model potential population-level benefits of SFO operations.

Iteroparity Estimation Methods

The iteroparity estimates we report here were derived from a diverse but clearly non-random sampling of Columbia and Snake River steelhead populations. Juveniles were PIT-tagged for a variety of reasons by many organizations, and we could not confirm the suitability of some samples for our analyses. Nonetheless, we think that the screened PTAGIS dataset was broadly representative of the steelhead metapopulation upstream from Bonneville Dam as adults passed Bonneville Dam throughout the migration season in approximate proportion to the runs at large. We included as many of the returning PIT-tagged adults as possible and consequently evaluated more than 13,000 migration histories for wild fish and more than 43,000 histories for hatchery fish. This ratio of hatchery to wild steelhead (~3.3:1) was within the typical annual range at Bonneville Dam.

We think the multi-year iteroparity estimates of 2.78% (winter, wild), 0.44% (winter, hatchery), 0.56% (summer, wild), and 0.16% (summer, hatchery) should be representative of Bonneville-to-Bonneville repeat spawner rates. The closest comparison estimates have been generated by aging scales from adult steelhead collected during routine monitoring at Bonneville Dam from April through October. Scale-age repeat spawner estimates from the 2008-2012 steelhead migrations were 0.9% (Torbeck et al. 2009), 0.2% (Fryer et al. 2011), 0.3% (Fryer et al. 2012), 0.5% (Fryer et al. 2013), and 1.9% (Nowinski et al. 2013). These were calculated across life history types, age classes, and origin groups, but were also broadly consistent with the PTAGIS-based estimates. We note that PTAGIS-based iteroparity estimates are likely to be biased slightly low because we were more likely to fail to identify a repeat spawner then to mis-classify a single year spawner as a repeat spawner. It was also possible to miss PIT detections at Bonneville Dam during the first, second or both spawning migrations. However, the latter bias should be trivially low given estimated detection efficiencies of >97% at most adult fishways (PSMFC, unpublished data).

A primary objective was to provide benchmark iteroparity estimates that can be used in more controlled future evaluations of individual populations, management groups, or FCRPS operations. The several iteroparity metrics we reported (i.e., Bonneville-to-Bonneville, McNary-to-Bonneville, kelt-to-Bonneville, etc.) each had a different ‘maiden’ steelhead population as the denominator and hence can be interpreted differently. The Bonneville-to-Bonneville estimates were the most conservative because steelhead that were harvested, died naturally, or were collected in hatcheries prior to spawning were all included. Repeat spawning migrations for these fish was clearly not possible, and including them in calculations results in underestimation of the rate of iteroparity expression in the study populations. In contrast, the kelt-to-Bonneville estimates relied solely on steelhead that survived the spawning period, initiated downstream migration, and were detected at dams. Unfortunately, detection probabilities for outmigrating kelts were much lower than for upstream migrating adults and the number of outmigrating kelts is low. Thus, few kelts were detected and the resulting iteroparity estimates were imprecise, with limited information for individual years, kelt detection sites, populations, or management groups. Managers and researchers interested in monitoring or increasing iteroparity rates in Columbia River steelhead – particularly for specific populations – will need to weigh the tradeoffs associated with these different estimation methods.

We also note that the PTAGIS data could not be used to estimate what may be the most biologically relevant metric: spawer-to-spawner iteroparity. It may be possible to collect the data needed for spawner-to-spawner iteroparity for populations where in-stream PIT antenna arrays are installed. However, generating reliable estimates at these sites will require significant investment in juvenile and/or adult PIT-tagging projects and monitoring infrastructure. The costs of such estimation approaches should be weighed against other approaches such as scale analyses which may be more cost effective for populations where adults can be readily sampled at weirs or other locations (e.g., Seamons et al. 2009).

Winter Versus Summer Steelhead

We hypothesized that winter steelhead would have higher iteroparity rates than summer steelhead based on previous studies (e.g., Busby et al. 1996), and this was generally supported by the PTAGIS data. However, several factors reduced our ability to make clear distinctions. First, the sample sizes for winter steelhead were small and geographically limited to Fifteenmile Creek for wild fish and the Hood River for hatchery fish. There were no direct comparison groups of summer run steelhead for these sub-basins. Second, the life history assignments were somewhat ambiguous for presumptive winter run fish from Fifteenmile Creek. Although Fifteenmile Creek is considered a winter population with little introgression from summer strays (ODFW 2010), many of the PIT-tagged fish had adult migration timing at Bonneville Dam that was more typical of summer steelhead. Third, we excluded the ‘unknown’ life history steelhead from the Wind River which had high Bonneville-to-Bonneville iteroparity estimates (>4%). If the Wind River fish were mostly winter run steelhead, then our hypothesis would have been further supported. If they were summer steelhead, then the results would have been inconclusive.

Wild Versus Hatchery Steelhead

As expected, wild steelhead consistently had higher iteroparity rates than hatchery steelhead. Wild fish estimates were higher – often several times higher – within almost every population and sea-age class that included both wild and hatchery fish. This was unsurprising given the many adult mortality risks that are higher for hatchery than wild steelhead. These include higher recreational harvest of hatchery fish along the migration corridor and especially on and near spawning grounds as well as hatchery collection.

Our results suggest that the percentage of maiden spawners that were subsequently detected as kelts is about 5 times higher for wild than hatchery steelhead. This is consistent with previous Columbia and Snake River studies. For example, the proportions of maiden fish collected at kelts at main stem dams (Evans et al. 2004; Keefer et al. 2008; Narum et al. 2008) and other facilities (Hatch et al. 2013) indicate a several-fold higher kelting rate for wild versus hatchery steelhead. Notably, the kelt-to-adult iteroparity estimates we generated from the PTAGIS data suggested slightly higher survival for hatchery (3.35%) than wild kelts (2.59%), though these estimates did not account for differences in sea-age or origin population. These estimates were generally within the range of kelt-to-adult iteroparity estimates of 5.45%, 5.37%, and 0.69% for mixed-origin kelts that were PIT-tagged at John Day, McNary, and Lower Granite dams, respectively (Keefer et al. 2008).

Ocean Age

In general, 1-sea steelhead had higher iteroparity estimates than 2-sea steelhead, supporting our hypothesis that younger fish would be more likely to repeat spawn. However, this pattern was not universal within sub-basin populations, as some 2-sea groups had higher estimates than their 1-sea conspecifics. The tendency for older fish to be semelparous (i.e., one-time spawners) has been reported for several iteroparous species (e.g., Atlantic salmon *Salmo salar*, Jonsson et al. 1991; Arctic char *Salvelinus alpinus*, Dutil 1986), including steelhead in the Columbia and Snake rivers (Keefer et al. 2008; Narum et al. 2008). Older age at maturity, larger body size, and long migrations have all been associated with increased likelihood of semelparity (Crespi and Teo 2002). Therefore, we expect that the overall age-related iteroparity pattern in the PTAGIS data was reinforced by the tendency for older steelhead to have originated at sites more distant from the Pacific Ocean (i.e., the 'B-group' steelhead from the Clearwater and Salmon rivers and from upper Columbia tributaries).

Unfortunately, sea age could not be confidently assigned to many of the steelhead in the screened PTAGIS dataset. We were conservative in our age assignments, requiring juvenile outmigration detection in addition to return year to determine sea-age class. Although juvenile PIT-tagging and release dates were almost universally available, some juveniles clearly did not migrate seaward in their release year but instead spent additional time rearing in freshwater. Iteroparity estimates for the unknown-sea groups were mixed in relation to the 1-sea and 2-sea estimates. Some unknown-sea estimates were more similar to those for 1-sea fish and others were more similar to those for 2-sea fish, but we do not think that age assignment for the unknown group would have changed the overall conclusion about age effects on iteroparity.

Migration Distance

Wild steelhead iteroparity rates (both Bonneville-to-Bonneville and kelt-to-Bonneville) decreased as freshwater migration distance increased, consistent with our expectations. Results for hatchery fish were equivocal, with little variation by distance. The wild steelhead results corroborate the inverse distance relationship reported for radio-tagged Snake and Columbia River kelts by Wertheimer and Evans (2005) and for PIT-tagged kelts by Keefer et al. (2008). These authors hypothesized that kelt survival was relatively lower for populations that had to pass multiple dams. Slow outmigration through reservoirs, combined with and the hazards associated with downstream dam passage, presumably reduce kelt survival. For example, steelhead kelts outmigrate much more rapidly through the unimpounded Fraser River than through the Columbia system (English et al. 2006). As noted above, the concentration of 2-sea fish in more interior tributaries may also have contributed to the inverse distance-by-iteroparity relationship.

We also found that repeat spawner timing was associated with freshwater migration distance. Consecutive-year spawners were proportionately more common in populations closer to the Pacific Ocean. This may indicate that kelts with short seaward migrations entered saltwater in better overall condition or at a more favorable time than their long-distance counterparts. Kelt research on other species has indicated that condition upon ocean entry is a good predictor of repeat spawning interval (Schaffer and Elson 1975; Willson 1997).

Conclusions

The life history and behaviors of steelhead in the Columbia River basin can be complex, making it challenging to interpret some of the data stored in PTAGIS. In addition to exhibiting iteroparous behaviors, the detection histories indicated that steelhead overwinter throughout the main stem Columbia and Snake rivers, fall back downstream over dams, and stray into non-natal tributaries. Steelhead in other large west coast rivers have additionally been recorded residualizing in freshwater after spawning (Null et al. 2013; Teo et al. 2013), a behavior that may also occur in the Columbia system. These behaviors all highlight the importance of providing safe and efficient passage opportunities for upstream and downstream movement past dams throughout the year. We recommend that conservation efforts to increase the abundance and productivity of iteroparous steelhead need to consider the survival effects of Hydrosystem operations at broad spatial and temporal scales. This wider perspective is increasingly incorporated into the management of iteroparous species in regulated rivers worldwide (e.g., Arnekleiv et al. 2007; Calles and Greenberg 2009; Kraabøl et al. 2009).

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Appendix A. Sample Sizes for Sub-Basin Populations

Table A1. Percentages of wild and hatchery steelhead that were estimated to have made two spawning migrations based on PIT-tag detections at Bonneville Dam. All years, age classes, and release groups combined within individual sub-basins, main stem release sites, and hatcheries. ‘w’ indicates winter steelhead and ‘s’ indicates summer. ‘R’ and ‘B’ indicate in-river and barged juveniles at Lower Granite Dam.

	Wild			Hatchery		
Juvenile release site	Maiden	Repeat	Repeat (%)	Maiden	Repeat	Repeat (%)
Columbia below Snake						
Wind River	64	0	0.00			
Hood River (w)	-	-	-	676	3	0.44
Hood River	-	-	-	214	1	0.47
Fifteenmile Creek (w)	144	4	2.78	-	-	-
Deschutes River	335	2	0.60	-	-	-
John Day River	1,168	18	1.54	-	-	-
Umatilla River	126	2	1.59	458	0	0.00
Walla Walla River	202	2	0.99	1,036	5	0.48
Total (w)	**144**	**4**	**2.78**	**676**	**3**	**0.44**
Total (s)	**1,895**	**24**	**1.27**	**1,708**	**6**	**0.35**
Columbia above Snake						
Yakima River	152	1	0.66	-	-	-
Ringold Hatchery	-	-	-	7,600	4	0.05
Rock Island Dam	157	3	1.91	394	2	0.51
Wenatchee River	154	2	1.30	3,330	6	0.18
Rocky Reach Dam	-	-	-	226	0	0.00
Entiat River	166	1	0.60	-	-	-
Wells Dam	-	-	-	1,596	3	0.19
Methow River	86	1	1.16	6,362	26	0.41
Okanogan River	-	-	-	1,064	1	0.09
Total	**715**	**8**	**1.12**	**20,572**	**42**	**0.20**
Snake River						
Lyons Ferry Hatchery	-	-	-	141	0	0.00
Tucannon River	267	2	0.75	2,036	5	0.25
Lower Granite Dam (b)	3,729	14	0.38	5,665	4	0.07
Lower Granite Dam (r)	3,197	13	0.41	1,642	2	0.12
Clearwater River	687	2	0.29	1,152	0	0.00
Asotin Creek	93	0	0.00	-	-	-
Snake River[1]	117	0	0.00	483	0	0.00
Grande Ronde River	343	3	0.87	2,295	2	0.09
Salmon River	448	2	0.45	3,218	2	0.06
Imnaha River	622	0	0.00	1,436	1	0.07
Total	**9,503**	**36**	**0.38**	**18,068**	**16**	**0.09**

[1] main stem upstream from Lower Granite Dam

Appendix B. Sample Sizes by Release Site

Table B1. Numbers of adult steelhead included in the iteroparity evaluation, by PTAGIS release site code.

Site	*n*	Site	*n*	Site	*n*	Site	*n*
15MILC	144	GEDNEC	15	MEACHC	45	SATUSC	14
AHTANC	6	GOLD2C	3	MEAD2C	54	SAWT	71
AMERR	6	GRAND2	34	METHR	2605	SAWTRP	678
ASOTIC	93	GRANDR	58	METTRP	14	SECESR	17
BARGAC	3	GRBLDC	1	MILL2C	20	SECTRP	10
BCANF	452	GRNTRP	453	MILLC	9	SELWYR	1
BEAR2C	8	HAYDNC	22	MINAMR	49	SFSTRP	19
BEARVC	33	HAZARC	1	MINP	128	SGOLDC	2
BIG2C	64	HOODEF	218	MOOS2C	2	SIMILR	710
BIGBEC	61	HOODMF	49	MOS2N	10	SLAT2C	62
BIRCHE	1	HOODR	333	MXWLCN	27	SLATEC	7
BIRCHW	2	HOODWF	162	NASONC	1042	SNAKE4	201
BLKBAS	30	HORSEC	8	NATCHR	1	SNDTAP	3
BONP	10	IMNAHR	4	NEWSOC	5	SNKTRP	399
BOULDC	2	IMNTRP	848	NFTEAN	9	SQAW2C	131
BRIDGC	58	IMQP	13	OHARAC	1	SQUAWC	1
BRUSHC	3	JDAR	1	OKANR	223	SQUAWP	22
BSHEEC	502	JDAR1	18	OMAKC	118	STAPAC	13
CAMASC	19	JDAR2	311	PAHSIW	15	STORMC	2
CAMP2C	4	JDARMF	165	PAHTRP	330	SULFUC	2
CATHEC	40	JDARNF	7	PANT2C	8	TANEUC	4
CFCTRP	68	JDARSF	465	PARK	95	TEANAR	7
CHAMBC	57	JOHNC	1	PENP	93	THOP	6
CHAMWF	2	JOHNSC	1	PESHAR	1	TMFFBY	5
CHANDL	1	JOHTRP	31	PINE2C	3	TMFTAL	14
CHEWUR	1690	JSFBC	49	POTR	4	TOPPEC	106
CHIP	31	JSFDC	3	POTREF	5	TOUCHR	508
CHIWAC	2	JSFMC	75	RAPIDR	7	TROU2C	335
CHIWAR	689	KNOXB	18	RAPR	2	TROUTC	27
CHIWAT	30	LAKEC	7	REDP	143	TUCR	2303
CLEARC	75	LBEARC	2	REDR	69	TWIS2P	234
CLWR	5	LCATHC	1	REDRSF	1	TWISPR	1520
CLWRSF	235	LEMHIR	54	RI2BYP	317	UMAR	222
CLWTRP	61	LEMHIW	23	RINH	7600	VALEYC	94
COLTKC	19	LGRRBR	9394	RIS	234	WALH	1061
COTP	363	LGRRRR	4839	RPDTRP	18	WALLAR	446
CROOKP	16	LIBBYC	5	RRE	134	WALLSF	1
CROOKR	65	LICKC	3	RRETAL	92	WBIRDC	2
CROTRP	4	LOCHSA	1	SALEFT	43	WELH	993
DAYP	269	LOLOC	41	SALMF2	2	WELTAL	603
DRYFBY	1	LOOKGC	64	SALR	31	WENATR	1657
DWOR	1	LOONC	3	SALR1	7	WENATT	31
DWORMS	437	LOSTIR	64	SALR3	512	WHITSC	2
ENTIAR	154	LSALR	740	SALR4	61	WIND2R	29
FEEDCN	15	LSFTRP	5	SALREF	94	WINT	342
FISHC	16	LSHEEF	141	SALRMF	1	YAKIMR	4
FISTRP	377	MADRVR	12	SALRNF	4	YANKFK	199
GABLEC	3	MARTRP	2	SALRSF	1	YELHKC	5
GEDCWF	2	MCKAYC	3	SALTRP	158	YELLJC	5