North American Journal of Fisheries Management

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1002/nafm.10042

ARTICLE

Population-Specific Migration Patterns of Wild Adult Summer-Run Chinook Salmon Passing Wells Dam, Washington

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Abstract
Summer-run Chinook Salmon *Oncorhynchus tshawytscha* migrating over Wells Dam, Washington, enter a habitat characterized by blocked upstream access, high tributary water temperature regimes, and robust tribal and recreational fisheries. In 2011, we initiated a 2-year radiotelemetry study to identify population-specific run timing, movement, and mortality of naturally produced fish passing the dam. Five hundred seventeen salmon were radio-tagged at Wells Dam over 2 years of study. The highest proportion (44%) of tagged fish escaped to the Okanogan River, but spawning populations from the Methow River (16%), Wenatchee River (6%), Entiat River (5%), and the Columbia River upstream (14%) and downstream of Wells Dam (14%) were also represented. In general, tributary-spawning fish had significantly earlier run timing than did main-stem–spawning fish. We observed very little movement among spawning tributaries, but a significant proportion of fish (~30%) were detected holding in the tailrace of Chief Joseph Dam on the Columbia River prior to spawning, including fish from populations many kilometers downstream of Wells Dam. Fallback was common in each year of the study, and we calculated that passage at Wells Dam was overestimated by 27.5% in 2011 and 32.0% in 2012 due to fallback and re-ascension. Of the fish that remained upstream, 16% in 2011 and 22% in 2012 were estimated to have died prior to spawning, excluding fish that were known or suspected to have been harvested. In 2012, warm water temperatures (>20°C) in the Okanogan River resulted in a thermal barrier that delayed migration but did not affect spawning distribution within the river compared with 2011, when no significant thermal barrier was detected. Our results highlight some of the complex migration and distribution patterns of natural-origin Chinook Salmon passing Wells Dam and should assist managers in upstream population and fishery modeling efforts.

The Columbia River has changed from a free-flowing river to a series of connected hydroelectric impoundments, with more than 10 significant main-stem projects being completed between 1933 and 1971. Significant declines in the abundance of anadromous salmonids *Oncorhynchus* spp. in the Columbia River over the last century have been attributed to commercial fisheries (Van Hyning 1973; Chapman 1986), hatchery production (Chilcote et al. 2011; Christie et al. 2011), habitat degradation (Nehlsen et al. 1991), and anthropogenic changes related to the hydroelectric system (Raymond 1988; Sanford et al. 2012). Hydroelectric dams alter the flow regime, water temperature, and other variables (e.g., dissolved gasses, predator populations) that affect the migration and survival of adult and juvenile salmonids (Weitkamp and Katz 1980; Giorgi et al. 1997; Connor et al. 2003). More directly, large areas of the upper Columbia River historically available as salmon spawning and rearing habitat were made inaccessible by the completion of Grand Coulee Dam (river kilometer [rkm] 965, measured from the mouth of the Columbia River) and Chief Joseph Dam (rkm 877; Fish and Hanavan 1948; Fulton 1968; Dauble et al. 2003). Habitat for adult salmonids migrating above Wells Dam (rkm 830), the last dam on the Columbia River with fish passage facilities, is now limited to a short (47-km) section of the Columbia River and two

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Received August 22, 2017; accepted December 27, 2017

tributaries, the Methow and Okanogan rivers. Thermal and hydrological regimes vary among these three areas and likely elicit differing prespawn movement and distribution patterns of adult Chinook Salmon *O. tshawytscha*, depending on their population of origin (Goniea et al. 2006; Salinger and Anderson 2006).

The migration timing of adult salmonids is a heritable trait (Ramstad et al. 2003; Keefer et al. 2004b) that promotes survival related to specific environmental conditions (Unwin et al. 2003; Strange 2012). In the Columbia River, water temperature and discharge are determinant variables in the upstream movement of adult fish (Quinn et al. 1997; Keefer et al. 2004a; Goniea et al. 2006). Significant changes to these environmental variables (and others) likely elicit a genetic response from affected populations over time. Thus, monitoring the migration timing and movement of salmon stocks can characterize differences between stocks in an altered environment like the contemporary Columbia River and identify the correlated effects of important environmental variables. Keefer et al. (2004b) described the migration timing of Chinook Salmon stocks in the Columbia River passing Bonneville Dam and detected stream–specific migration timing patterns influenced by environmental variables (e.g., river discharge) within each year. However, Chinook Salmon stocks (e.g., spring versus summer) upstream of Wells Dam were not differentiated by Keefer et al. (2004b) because monitoring at the subbasin level (i.e., the Methow and Okanogan rivers) was limited. Monitoring at this finer spatial scale is necessary to describe migration characteristics and influential variables for specific populations with different conservation concerns.

Fish passage facilities at Wells Dam enumerate Chinook Salmon (and other species) and make fish passage statistics (daily, weekly, and annual totals) available through various online sources. These data are extremely valuable to resource managers monitoring trends in salmonid abundance, distribution, survival, and migration timing. In particular, managers use fish passage data to model annual abundance and make decisions regarding fishery duration and harvest rates and to estimate the subsequent number of postharvest fish available for spawning ground escapement. However, the precision of these modeling efforts is decreased by the common occurrence of fallback and re-ascension at hydroelectric facilities (see Boggs et al. 2004), as well as prespawn mortality that occurs between dams and spawning grounds. To improve the strength of abundance and distribution models, managers need to incorporate estimates of fallback and re-ascension to refine hydroelectric facility fish passage estimates. Our objectives were to identify population-specific migration patterns and prespawn movement and to estimate postpassage mortality rates for summer-run Chinook Salmon populations upstream of Wells Dam.

METHODS

Adult collection and tagging.— Chinook Salmon are counted annually between May 1 and November 15 as they migrate over Wells Dam (Figure 1). Counted fish are grouped into distinct runs based on passage date (Fish Passage Center data available at http://www.fpc.org), namely, spring run (prior to June 29), summer run (June 29–August 28), and fall run (after August 28). Although some fish are counted during the first half of November, the proportion is small relative to the overall run at large (2011–2012 mean = 0.9%) and no genetic distinction between summer-run and fall-run Chinook Salmon passing Wells Dam has been identified (Utter et al. 1995; Kassler et al. 2011). Because of this, we trapped fish between late June and late October in 2011 and 2012 (Figure 2) and considered all trapped fish to be summer run Chinook Salmon based on timing and a morphological inspection of the fish. Fish with an intact adipose fin and without a coded wire tag were considered wild.

Within each year, collection of wild adult Chinook Salmon for tagging occurred up to 4 d per week, with overall weekly tagging objectives derived from the mean (10-year) weekly proportion of the run passing the dam. Salmon were trapped at the east shore and west shore fish ladders at Wells Dam by lowering a barrier screen into the ladder. To circumnavigate the barrier, fish ascended a Denil fish ladder adjacent to the barrier that led to a 21-m^3 concrete holding area at each ladder. Each holding area had a sloped flume entering at one end with a continual upwelling of surface water to provide attraction flow. Fish attracted by the flow were entrained in the flume. At the west shore ladder, salmon were diverted from the flume into a 9-m^3 holding pond using a pneumatically controlled gate and were sorted and tagged the following day. At the east shore ladder, fish were diverted from the flume with a pneumatic gate and deposited directly into a 3-m^3 anesthetic tank for sorting and tagging. Trapped fish were anesthetized using tricaine methanesulfonate (MS-222) at a targeted concentration of 60 mg/L. Anesthetized fish were scanned for passive integrated transponder (PIT) tags, coded wire tags, and adipose fin clips. Wild fish were also collected for local hatchery broodstocks concurrently with the trapping for radio-tagging purposes. On these days, every other fish meeting the minimum size requirement was tagged.

Mideye-to-hypural length (cm), fork length (cm), and sex were recorded for all tagged fish. Scale samples were collected to confirm fish origin (hatchery or wild), and PIT tags were applied if no PIT tag was already present. The physical condition of each tagged fish was ranked from 1 to 3 based on the presence of externally visible injuries; 3 indicated good condition with no or minimal injuries, 2 indicated moderate condition with healed or scarred injuries, and 1 indicated poor condition with open

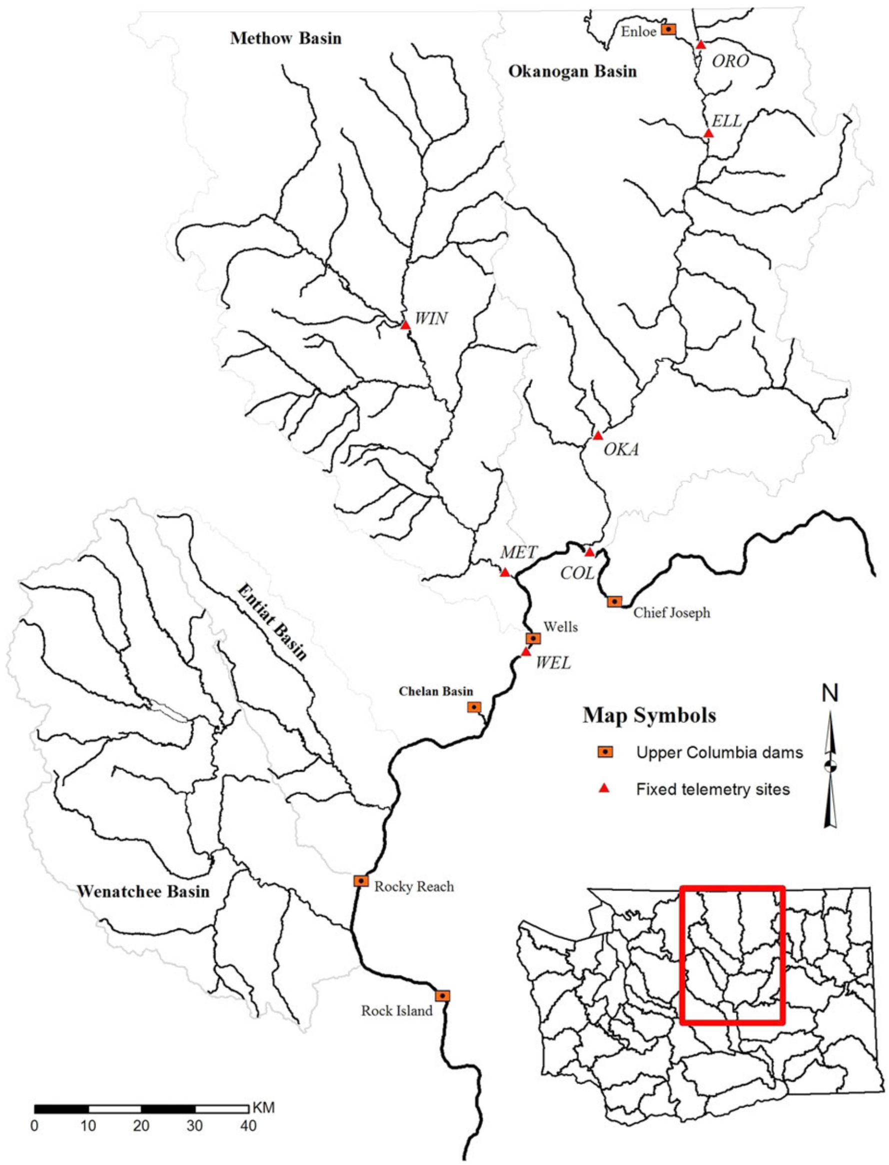

FIGURE 1. Map of the main study area (rectangle), including infrequently monitored tributaries downstream of Wells Dam. The main study area was defined as the sections of the Columbia River from Wells Dam to Chief Joseph Dam, the Methow River upstream to the town of Winthrop, Washington, and the Okanogan River upstream to Zosel Dam, including the Similkameen River upstream to Enloe Dam.

wounds or a collection of scarred wounds possibly impacting postrelease survival. This condition index was used to evaluate the postrelease movement of tagged fish. A radio transmitter (Lotek Wireless MCFT2-3EM, 12 × 53 mm, 10 g in air, 4.5 g in water; or MCFT2-3A, 16 × 46 mm, 16 g in air, 6.7 g in water) was coated in food grade glycerin for lubrication and inserted gastrically using a dowel rod trocar. The tagging procedures were conducted or supervised by a biologist with multiple years of radio tag insertion experience. Some wild fish under 70 cm were rejected because they could not physically accommodate the transmitters. Radio transmitters (i.e., tags) were equipped with a mortality sensor that activated when a tag was motionless for 24 h. Two 4-mm bands of surgical tubing were placed around each tag prior to implantation to discourage regurgitation. Each tagged fish also received a numbered spaghetti-type anchor tag adjacent to the dorsal fin which served as a secondary identification of radio tag presence and as an identifier to allow exclusion from an ongoing sport fishery in the Columbia River. In 2012, a subsample of 106 radio-tagged fish were also fitted with an internal temperature recorder (iBCod model 22L, 12 g in air, 5.5 g in water) attached to each radio tag. The recorders collected temperature readings at

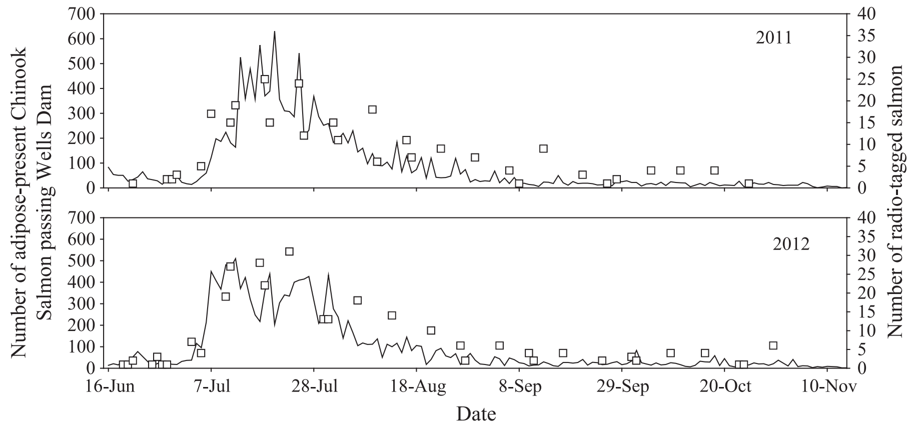

FIGURE 2. Number of wild Chinook Salmon counted at Wells Dam (solid line) and the number collected, radio-tagged, and released (squares) into the fish ladders at the dam in 2011 and 2012.

30-min intervals at a resolution of 0.0625°C. After tagging, fish were allowed to recover in freshwater, then released into the ladder from which they were collected upstream of the barrier.

Radio-tracking.— We installed six fixed-site radiotelemetry receivers in 2011 and a seventh site in 2012 in order to monitor movement patterns (Figure 1). Each fixed site consisted of a Yagi 6-element antenna and a SRX 400 receiver with W7AS firmware (Lotek Wireless), which detected transmitters and stored telemetry records. Two fixed sites were located in the Methow River basin, one in the town of Winthrop downstream of the Chewuch River confluence (WIN; rkm 83.6, measuring from the Methow River's confluence with the Columbia River), and one just upstream of the Wells Dam reservoir inundation zone (MET; rkm 3.6). Three sites were located in the Okanogan River basin, one at the town of Malott above the inundation zone (OKA; rkm 27.5, measuring from the Okanogan River's confluence with the Columbia River), one at the bridge in the town of Ellisforde (ELL; rkm 104.5 [installed in 2012 only]), and a third upstream of Zosel Dam (ORO; rkm 126.4) in the town of Oroville. The ORO site was above all spawning areas in Washington State and was primarily installed to monitor escapement into Canada. Two additional fixed sites were located on the Columbia River, one near Cassimer Bar (COL), a natural constriction point 2 km upstream of the mouth of the Okanogan River, and one approximately 1.25 km downstream of Wells Dam (WEL) to monitor any posttagging downstream movement. Each site was powered by 12-V direct current batteries charged on-site from available grid power (WIN and OKA) or by 135-W solar panels installed annually (all other sites).

To eliminate false-positive detections, we required that a tag be recorded at least twice to be considered a true detection. In general, multiple records are logged for individual fish as they approach or pass fixed sites. A detection was thus defined as the block of time that a fish was within range of the site. A separate detection required a fish be absent from the site for a minimum of 2 h. Using these protocols, a single fish could have multiple detections at the same fixed site within the same day, but the data better represented movement patterns within the system for analysis.

We conducted mobile tracking surveys via boat or vehicle between late June and late November each year throughout the study area. Surveys were conducted using SRX 400 receivers with W5XG firmware to obtain the locations of tagged fish between fixed-site receivers. Tributaries were monitored by automobile using two 4-element Yagi antennas mounted in opposite directions, attached to the automobile trailer hitch. The Methow River upstream to the town of Winthrop and the Okanogan River from Monse Bridge (rkm 6.6) upstream to Zosel Dam, including the Similkameen River upstream to Enloe Dam (Figure 1), were surveyed by automobile weekly. The latitude and longitude of the approximate detection point were recorded using hand-held GPS devices and adjusted to the nearest river location using geospatial computer software (ArcMap by ESRI). The Columbia River between the Wells and Chief Joseph dams and the Okanogan River downstream of Monse Bridge were tracked weekly using a 5.2-m aluminum boat powered by a gas-operated, jet-driven outboard engine. The boat was equipped with a 6-element Yagi antenna attached to a pole allowing 360-degree antenna rotation. Each shore was monitored separately, and fish location (generally to within 30 m) was obtained using triangulation techniques. Once a fish was detected, the latitude and longitude and shoreline being utilized were recorded using hand-held GPS devices.

We also monitored additional areas on a biweekly or monthly schedule, as availability allowed, where spawning of summer Chinook Salmon is uncommon (the Methow River upstream of the town of Winthrop and the Chewuch River) or to determine whether fish moved downstream after tagging (the main-stem Columbia River downstream of Wells Dam to Rock Island Dam, the Entiat and Wenatchee rivers). Areas downstream of Wells Dam were monitored twice before spawning (August and September) and once after spawning was predicted to have concluded (early November) in order to mark the final locations of tagged fish that may have moved below Wells Dam. The Entiat River was monitored up to Lake Creek Campground (rkm 28.9), upstream of identified summer Chinook Salmon spawning. The Wenatchee River, including approximately 1 rkm of Icicle Creek at its confluence, was monitored up to Tumwater Dam (rkm 43.7), which has a passage facility operated by Washington Department of Fish and Wildlife (WDFW) and at which study fish would be detected.

Population assignment.— Fish were assigned to a spawning population based on their detection histories at fixed sites and during mobile surveys. We also utilized detections at existing PIT tag antennas and interrogation systems on dams and in streams installed and maintained by WDFW and many other cooperating agencies in the Columbia River watershed. Information from PIT tag records was supplementary and most beneficial for assignment of downstream populations where radiotelemetry coverage was less frequent and no fixed radiotelemetry sites existed. Data from these interrogation sites are housed within the Columbia Basin PIT Tag Information System database maintained by Pacific States Marine Fisheries Commission and are available for public use (Pacific States Marine Fisheries 2017). Fish that were not detected after tagging and those that were known to have been harvested based on reported captures were excluded from further analyses. Harvest could also be confirmed if tags were tracked to residences and had records indicative of vehicle travel, such as brief detection at fixed sites (<20 s) on a reoccurring schedule. Fish were assigned to one of six populations: the Okanogan River, Methow River, Columbia River above Wells Dam, Columbia River below Wells Dam, Entiat River, and Wenatchee River. We also included two subpopulations within these categories, the Similkameen River (a tributary to the Okanogan River) and the Chelan River (a tributary to the Columbia River below Wells Dam). Fish in the Chelan River were not considered a separate spawning population because less than 1 rkm is accessible to anadromous fish, so the spawning population was presumed to be the same stock as that of the Columbia River below Wells Dam (Kassler et al. 2011). Kruskal–Wallis ANOVA tests compared the distributions of migration timing, as indicated by the day of the year on which a fish was tagged, by population (STATISTICA). Pairwise comparisons of mean ranks were used post hoc to compare individual populations. Values for all statistical tests were considered significant at $\alpha \leq 0.05$.

Temperature monitoring.— Water temperature (°C) was collected from stream gauging stations operated by the U.S. Geological Survey (USGS) in the Okanogan River (station 12447200 at Malott) or from a Web-based query to the Columbia River Data Access in Real Time online database (Columbia Basin Research 2017). We compared Okanogan River water temperatures during the radiotracking season using ANOVA and Tukey post hoc tests to examine differences between monthly temperature data between years (STATISTICA). Fish movement in relation to water temperature was assessed from 25 temperature recorders recovered from pre- and postspawn salmon carcasses in 2012.

Downstream movement.— Fish that were known to have passed upstream of Wells Dam after tagging but were later detected downstream of the dam were considered fallbacks. Fish that were detected downstream of Wells Dam after tagging without having first been detected upstream of Wells Dam were considered to have moved out of the ladder immediately after tagging and were labeled dropouts. Upstream passage at Wells Dam was assumed for tagged fish detected at PIT tag antennas at the upstream end of each fish ladder, in tributary PIT tag interrogation sites, or by any mobile- or fixed-site radio tag detection upstream of the dam. Fallback was monitored by radio tag detections at the WEL fixed site, through mobile-tracking surveys downstream of the dam, or through detection at PIT tag arrays in tributaries downstream of the dam. Logistic regression models were used to assess whether the occurrence of fallback or dropout (yes or no) was influenced by condition index, fish length, tag date, and tagging site (predictor variables). Fish removed by angling (confirmed) and fish that regurgitated their tags were excluded from these analyses.

Escapement.— As a supplement to dam counts, we estimated more precise spawning escapement numbers using data collected from the radio-tagged salmon in this study. Because Chinook Salmon race (e.g., spring or summer run) is determined at Wells Dam by passage date, annual variations in run timing may result in summer Chinook Salmon being counted as spring Chinook Salmon and vice versa. Fish passage videos at Wells Dam are reviewed annually to adjust ladder counts when spring and summer Chinook Salmon passage overlaps (WDFW, unpublished data). These adjustments were applied to the dam passage counts. An adjustment factor (AF) described by Boggs et al. (2004) was then calculated on the corrected summer Chinook Salmon passage counts for each ladder to better represent the number of fish upstream. The Wells Dam adjustment factor was calculated by the formula:

$$AF = (LP_U - FB_U + R_U)/TLP,$$

where

LP_U = the number of unique radio-tagged fish known to have passed the dam
FB_U = the number of unique radio-tagged fish that fell back at the dam one or more times
R_U = the number of unique radio-tagged fish that fell back one or more times, re-ascended the dam, and were assigned to a population upstream of the dam
TLP = the total number of times unique radio-tagged fish were known to have passed the dam.

Boggs et al. (2004) also incorporated values for the number of fish known to have migrated upstream via navigation locks, but no navigation locks exist at Wells Dam and that component of the formula was omitted. Dropout fish were excluded from AF estimates to reduce the influence of a tagging effect on passage estimates. The total wild harvest was estimated from radio-tagged fish based on the ratio of tagged fish confirmed harvested above Wells Dam to the total number of radio-tagged fish above Wells Dams multiplied by the adjusted ladder counts. The total estimated spawners was then estimated by multiplying our overall prespawn mortality rate by the adjusted ladder counts, minus our wild harvest estimate and the hatchery fish harvested from the recreational and tribal fisheries. The number of hatchery fish harvested was obtained from creel surveys conducted by WDFW and the Confederated Colville Tribes (CCT). The total spawners were estimated for each of the populations above Wells Dam based on the percent of radio-tagged spawners with final locations in each. These values were compared with traditional redd-based escapement estimates (Hillman et al. 2012, 2013).

Survival to spawning.— Final upstream locations, mortality sensor data, migration history, and relation to known spawning areas were collectively used to assign fate for individuals upstream of Wells Dam. Fish were considered to have spawned if they were detected at a location and time when spawning was occurring (after September 25 for tributaries and October 25 for the main-stem Columbia River). When possible, spawning success was verified by egg retention estimates of radio-tagged Chinook Salmon carcasses identified by survey crews. Fish that were tracked to known prespawn holding areas and that were tracked throughout the spawning period without moving to spawning areas were considered to be prespawn mortalities, as were fish whose carcasses or radio tags were recovered prior to spawning (September 25 for tributaries and October 25 for the main-stem Columbia River). Fish that disappeared prior to the commencement of spawning were considered to have been harvested if a fishery was ongoing (Okanogan basin and main-stem Columbia) or prespawn mortalities if no fishery was occurring (Methow basin). Although some harvest was confirmed by the voluntary return of radio tags or through fishery monitoring efforts, many fish were suspected (but not confirmed) to have been removed in recreational or tribal fisheries based on their tracking history. These groups (confirmed harvested and suspected harvested) were excluded from survival to spawning analysis. Confidence intervals for survival estimates were calculated as normal approximation intervals at $\alpha \leq 0.05$.

RESULTS

Fish Collection and Tagging

Over the 2 years of this study, we placed radio transmitters in 517 wild summer-run Chinook Salmon passing Wells Dam (Table 1), representing 1.8% of the wild adult return in 2011 and 1.6% of the wild return in 2012 (Figure 2). All radio-tagged fish were also PIT-tagged prior to release, with the exception of five fish with existing PIT tags, which had all been tagged in the lower Columbia River as adults.

Distribution and Final Fate

We assigned 482 of the 517 radio-tagged Chinook Salmon released to a spawning population. Fish distribution by spawning area was similar over the 2 years of the study. The greatest proportion of radio-tagged fish were assigned to the Okanogan River population (44.0%; Table 2). The Methow River population accounted for 16.4% of the released fish, the main-stem Columbia River above Wells Dam for 14.3%, and the main-stem Columbia River below Wells Dam for 13.9%. Tributaries downstream of Wells Dam (the Entiat and Wenatchee rivers) accounted for 11.4% of the radio-tagged fish released.

TABLE 1. Number and disposition of wild adult summer-run Chinook Salmon radio-tagged and released at Wells Dam in 2011 and 2012. Harvest was confirmed through voluntary tag returns or analysis of telemetry records; n/a = not applicable.

Variable	2011	2012	Total
Summer-run Chinook Salmon radio-tagged	255	262	517
Tagged fish harvested	16	12	28
Radio-tags regurgitated	5	2	7
Net tagged fish tracked to final location	234	248	482
Temperature recorders deployed	0	106	106
Temperature recorders recovered	n/a	25	25

In 2011, run timing at Wells Dam was not significantly different between the four tributary groups (the Okanogan, Methow, Entiat, and Wenatchee populations); however, the two main-stem Columbia River groups (above and below Wells Dam) had significantly later run timing than the four tributary groups (Figure 3; all comparisons $P < 0.02$, except that between the Okanogan River and the Columbia River below Wells Dam groups [$P = 0.19$]), but did not differ significantly from each other. Similarly, in 2012 run timing did not differ significantly among the tributary groups or between the two main-steam groups; however, all tributary groups were significantly different from the later-arriving main-stem Columbia River above Wells group (all comparisons $P < 0.05$), but only the Wenatchee River group was significantly different from the Columbia River below Wells Dam group (Figure 3; $P < 0.001$).

Movement Patterns

Many tagged fish were tracked to the main-stem Columbia River near Chief Joseph Dam (CJD), although the nearest spawning tributary (the Okanogan River) was about 19 rkm downstream of the dam. During the 2011 season, 80 tagged fish (34% of all those tagged) were detected at least once within a 6-rkm section downstream of the dam. In 2012, 71 tagged fish (27%) were detected at least once in this area. Sport and tribal fisheries occurred in this (and other) areas during both years of this study, and we estimate that 21 tagged fish were removed in fisheries in this area over the 2 years of the study; these fish were excluded from further analysis.

Fish movement to the area below CJD was highly variable, depending on population origin (Table 3). Excluding main-stem Columbia River fish above Wells Dam, Methow River fish had the highest utilization of the area directly downstream of CJD, despite their (presumably) natal tributary being about twice the distance downstream (35 rkm) as the closest tributary population (the Okanogan River [19 rkm below]). Similarly, fish assigned to the Entiat River (99 rkm below) were detected downstream of CJD at a higher rate than Okanogan fish in both years of this study, and Wenatchee River basin fish (124 rkm below) had a higher detection rate in the area than did Okanogan River basin fish in 2011. Although many fish were observed in the Columbia River upstream of their final destination tributary, we observed very little prespawn movement between tributaries. Across both years, only 23 fish (4.8%) had confirmed detections in two tributaries, and no fish were observed in more than two tributaries. Most of these detections were in the lowest portion of the receiving tributaries. Interestingly, although the Okanogan River had the highest total proportion of tagged fish in each year, no fish strayed to other tributaries prior to their final detection in the Okanogan River. In 2011, Entiat River fish had the highest rate of temporary straying into other tributaries (33.3%), most of which occurred into the Methow River (75% of straying Entiat fish).

Downstream Movement

Thirty of the tagged fish released were never detected at PIT tag arrays in the fish ladders and were presumed to have moved downstream through the fish ladders immediately after tagging (dropouts). Logistic regression analysis within each year indicated dropout differed significantly by ladder ($P < 0.001$) but not by tag date, length, or condition index. Dropout rates were similar between years, with 8% of tagged fish in 2011 and 5% in 2012 dropping out and not re-ascending the dam. Because the fish enumeration facilities at Wells Dam are located upstream of our release location in each ladder, we assumed that dropout fish were never counted and thus no estimate of the impact of dropouts on upstream escapement estimates was necessary.

TABLE 2. Population assignment based on the detection history of wild adult summer-run Chinook Salmon radio-tagged at Wells Dam in 2011 and 2012. The Similkameen and Chelan River groups were considered subpopulations of the Okanogan and Columbia River below Wells Dam populations, respectively, and are included within the primary population totals.

Population (subpopulation)	2011		2012		Overall	
	n	%	*n*	%	*n*	%
Okanogan (Similkameen)	110 (38)	47.0 (16.2)	102 (24)	41.1 (9.7)	212 (62)	44.0 (12.9)
Methow	36	15.4	43	17.3	79	16.4
Columbia above Wells	33	14.1	36	14.5	69	14.3
Columbia below Wells (Chelan)	31 (3)	13.2 (1.3)	36 (5)	14.5 (2.0)	67 (8)	13.9 (1.7)
Entiat	15	6.4	9	3.6	24	5.0
Wenatchee	9	3.8	22	8.9	31	6.4
Total	234	100	248	100	482	100

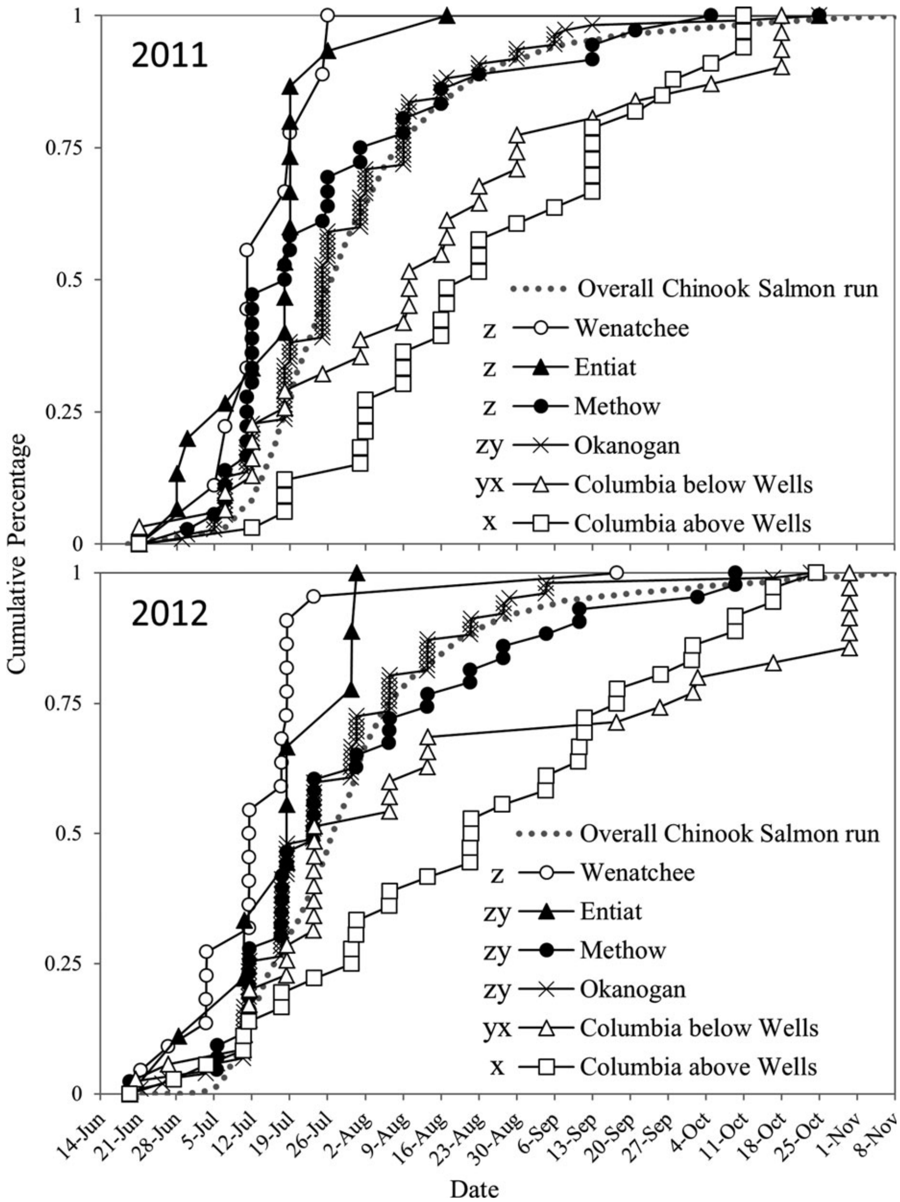

FIGURE 3. Cumulative frequency plots of population-specific arrival timing at Wells Dam based on the detection history of tagged fish. Run times for basins with the same lowercase letters were not significantly different (Multiple comparisons of mean ranks; $P < 0.05$).

For fish confirmed to have passed upstream of Wells Dam after release, 51 individuals in 2011 fell back below the dam at least once (24%) and 68 individuals fell back below the dam at least once in 2012 (30%). In both years, some of these individuals eventually re-ascended the dam, some of which fell back and re-ascended the dam multiple times (up to three fallbacks and four re-ascensions). Logistical regression analysis within years found a significant effect of tag date on fallback ($P < 0.01$), suggesting that the occurrence of fallback increased later in the migration season, but no significant effects for fish length, ladder, or condition index.

Survival to Spawning

Nine Columbia River above Wells Dam fish and six Okanogan fish were suspected of being harvested in 2011 and were not included in the totals for survival to spawning. Additionally, 10 Columbia River above Wells Dam fish and three Okanogan fish were suspected of being harvested in 2012. These fish are in addition to the 16 fish in 2011 and 12 fish in 2012 that were confirmed harvested by anglers, which had previously been removed from analysis (Table 3). Overall survival to spawning above Wells Dam was estimated to be 84.1% and 78.0% for 2011 and 2012, respectively (Table 4).

TABLE 3. Number and percentage of fish detected in the 6-km section downstream of Chief Joseph Dam based on their ultimate destination. The total percentage for each year is the percentage of all radio tags assigned to a population; n/a = not applicable.

	2011		2012		All	
Population	*n*	%	*n*	%	*n*	%
Columbia above Wells Dam	27	81.8	20	55.5	47	68.1
Columbia below Wells Dam	7	22.6	7	19.4	14	20.9
Okanogan	12	10.9	12	11.8	24	11.3
Methow	16	44.4	20	46.5	36	45.6
Entiat	4	26.7	2	22.2	6	25.0
Wenatchee	1	11.1	2	9.1	3	9.7
Fishery removal	13	n/a	8	n/a	21	n/a
Total	80	32.0	71	27.3	151	29.6

TABLE 5. Calculation of the adjustment factor (AF) as AF = (LP_U – FB_U + R_U)/TLP. LP_U is the number of unique, radio-tagged fish known to have passed the dam, FB_U is the number of unique fish that fell back at the dam one or more times, and R_U is the number of unique fish that fell back one or more times, re-ascended the dam, and were assigned to a population upstream of the dam. TLP is the total number of times unique radio-tagged fish were known to have passed the dam (Boggs et al. 2004).

Year	Ladder	LP_U	FB_U	R_U	TLP	AF
2011	East	173	46	13	201	0.697
	West	38	5	1	39	0.872
	Combined	211	51	14	240	0.725
2012	East	203	58	16	229	0.703
	West	23	10	0	27	0.481
	Combined	226	68	16	256	0.680

Escapement

The calculated adjustment factor at Wells Dam was 0.725 in 2011 and 0.680 in 2012 when ladders were combined, representing an overcount of 11,717 fish in 2011 and 18,824 in 2012 (Table 5). Radiotelemetry-based escapement estimates were higher than tradition redd-based estimates for both tributaries in both years of the study (Table 6).

Temperature Monitoring

Mean daily water temperature in the Columbia River (measured at the CJD tailrace) peaked at about 18°C in September of each year of the study. Conversely, mean daily water temperatures in the Okanogan River were at or above levels expected to inhibit salmonid migration (21°C) for 30 d between August 6 and September 13, 2011, and for 47 d between July 10 and August 27, 2012 (Figure 4). The overall mean water temperature in the Okanogan River during the tracking period was significantly warmer in 2012 than in 2011 ($P < 0.05$). Post hoc analysis of monthly temperature data between years indicated that mean monthly July and November temperatures were significantly warmer in 2012 than in 2011 ($P < 0.0001$ in each case), but significant differences were not detected between the other months tested.

Individual fish experienced large differences in temperature exposures across the populations upstream of Wells Dam in 2012, as indicated by the internal temperature recorders (Figure 5). The Methow River was generally cooler than the main-stem Columbia River but exhibited large diurnal fluctuations of more than 5°C. The Okanogan River temperatures exceeded those in the main stem by as much as 8°C until September; however, the diurnal fluctuations in that river were approximately half those of the Methow River. The smallest diurnal fluctuations were observed in the inundated main-stem Columbia River.

The posttagging travel time of adult salmon into the Okanogan River was significantly different between 2011 and 2012 ($P < 0.0001$). Adult salmon took longer on average between release and first detection at the OKA site in 2012 (25 d) than in 2011 (8 d; Figure 4), presumably due to the extended thermal barrier in 2012. Post hoc tests showed significant between-year differences for the months of August ($P < 0.001$) and September ($P < 0.0001$) but no difference in July ($P = 0.999$) and October

TABLE 4. Number of radio-tagged fish that survived to spawning (Spawn) or were assumed to be prespawn mortalities (PSM), together with the percent survival to spawning (%) for the populations upstream of Wells Dam. Confidence intervals were calculated using the normal approximation interval method; $\alpha = 0.05$.

	2011			2012			Overall		
Population	Spawn	PSM	%	Spawn	PSM	%	Spawn	PSM	%
Okanogan	98	6	94.2 ± 4.5	89	10	89.9 ± 5.9	187	16	92.1 ± 3.7
Methow	34	2	94.4 ± 7.5	35	8	81.4 ± 11.6	69	10	87.3 ± 7.3
Columbia above Wells Dam	6	18	25.0 ± 17.3	7	19	26.9 ± 17.0	13	37	26.0 ± 12.2
Total	138	26	84.1 ± 5.6	131	37	78.0 ± 6.3	269	63	81.0 ± 4.2

TABLE 6. Wells Dam fish count adjustment used to estimate escapement. Adjustment factors are show in italics; prespawn mortality estimates are shown in bold italics. Negative numbers represent net losses to the total spawners. Redd-based (redd) and radiotelemetry-based (RT) escapement estimates are for both ladders combined; n/a = not applicable.

	2011				2012			
	East ladder		West ladder		East ladder		West ladder	
Value/basin	Tags	Fish	Tags	Fish	Tags	Fish	Tags	Fish
Summer Chinook Salmon count	173	28,171	38	14,437	203	41,242	23	17,527
Count adjustment								
Adjustment factor		*0.697*		*0.872*		*0.703*		*0.481*
Adjusted ladder count		19,635		12,589		28,993		8,430
Escapement adjustment								
Hatchery fish harvested (WDFW)	n/a	−352	n/a	−180	n/a	−1,331	n/a	−566
Tribal harvest hatchery (CCT)	n/a	−562	n/a	−288	n/a	−2,028	n/a	−862
Wild harvest confirmed	13	−1,372	2	−629	12	−1,618	0	0
Prespawn mortality	***15.9%***	−2,758	***15.9%***	−1,827	***22.0%***	−5,284	***22.0%***	−1,541
Total estimated spawners	114	15,963	24	10,294	122	20,351	9	5,462
Columbia River	3	420	3	1,287	5	834	2	1,214
Methow	28	3,921	6	2,573	32	5,338	3	1,821
Okanogan	82	11,482	15	6,434	84	14,012	4	2,428
Canada	1	140	0	0	1	167	0	0
Escapement method comparison								
	Redd	RT			Redd	RT		
Methow	2,917	6,494			2,947	7,159		
Okanogan (U.S. total only)	9,681	17,916			8,225	16,440		

(P = 0.872); June was not analyzed due to low sample sizes. Analysis of temperature recorders recovered from fish affected by the thermal barrier indicates staging at the Okanogan–Columbia confluence, a definitive Okanogan River entrance, and for many fish, refuge from elevated water temperatures by entrance into the Similkameen River, which has mean daily water temperatures about 2°C cooler than those in the Okanogan River (data not shown; Figure 6). We did observe three fish move upstream through the lower Okanogan River while the thermal barrier was established from July 28 to August 23. No temperature recorders were recovered from these fish.

DISCUSSION

We found that the migration of wild summer-run Chinook Salmon passing Wells Dam was composed of salmon from five primary spawning populations. Four of these were Columbia River tributary populations (the Entiat, Methow, Okanogan, and Wenatchee rivers), and the fifth was composed of fish spawning in the main-stem Columbia River downstream of the Chief Joseph and Wells dams. We relied heavily on mobile tracking to determine the final destinations of fish; however, fixed sites were also utilized in population assignment. Detection range and depth were tested at the Methow and Okanagon fixed sites, and detection efficiency was assumed to be 100% based on these tests (barring any power outage of the receivers). No outages occurred for the sites verifying escapement (the MET and OKA sites). Main-stem sites were not assumed to have 100% detection efficiency due to the constraints of deep water and, in limited cases, high interference. We were satisfied with these assumptions, because (1) the mobile tracking efforts were intensive and (2) the main-stem sites were not imperative to population assignment and were designed only to provide opportunistic marks to inform mobile tracking.

Adult fish from tributary populations in general had an earlier run timing over Wells Dam than did Columbia River fish; however, tributary populations could not be differentiated from each other based on run timing. The Columbia River above Wells Dam was the final destination for about 15% of our tagged fish over the 2 years of the study. This value was much lower than the 36% (excluding harvested fish) that was documented by Ashbrook et al. (2008), most of which (87%) were documented to have final locations within the 6 km downstream of CJD. Given the later migration timing of Columbia River fish observed in both studies, the slightly skewed tagging effort toward later-returning fish (Ashbrook et al. 2008) may explain the considerably higher proportion of tagged fish

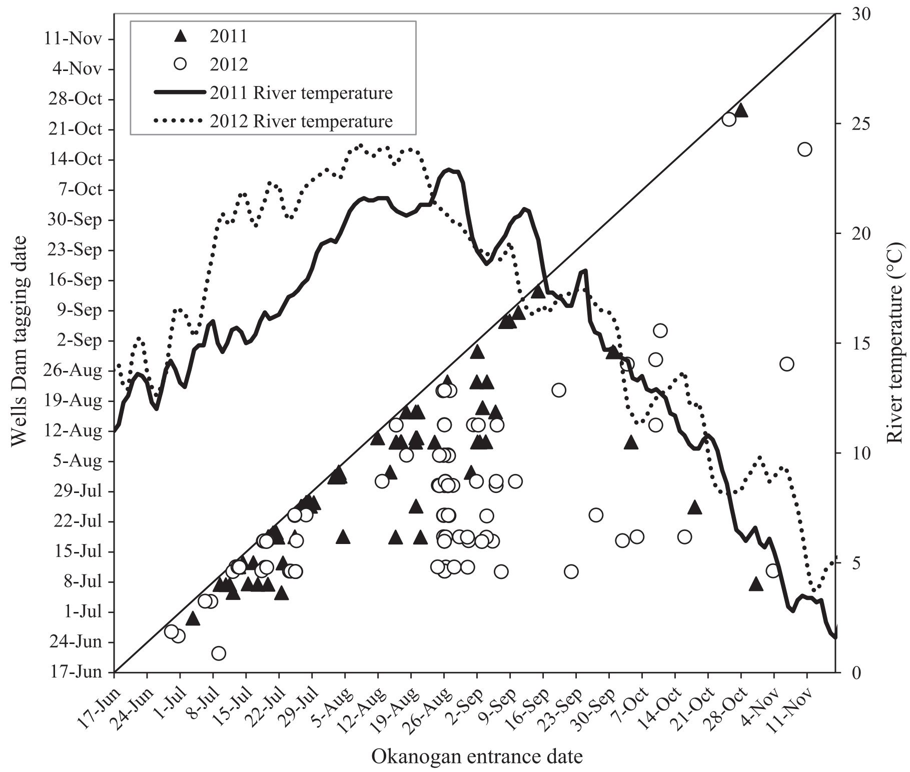

FIGURE 4. Migration delay between posttagging release at Wells Dam and first observation at the OKA fixed site in the Okanogan River. Each triangle or circle represents one radio-tagged fish. The farther from the diagonal line a point is, the greater the delay between release and Okanogan River detection. River temperature data are daily average temperatures queried from the USGS gauge site 12447200 at Malott, which is also the location of the OKA fixed site.

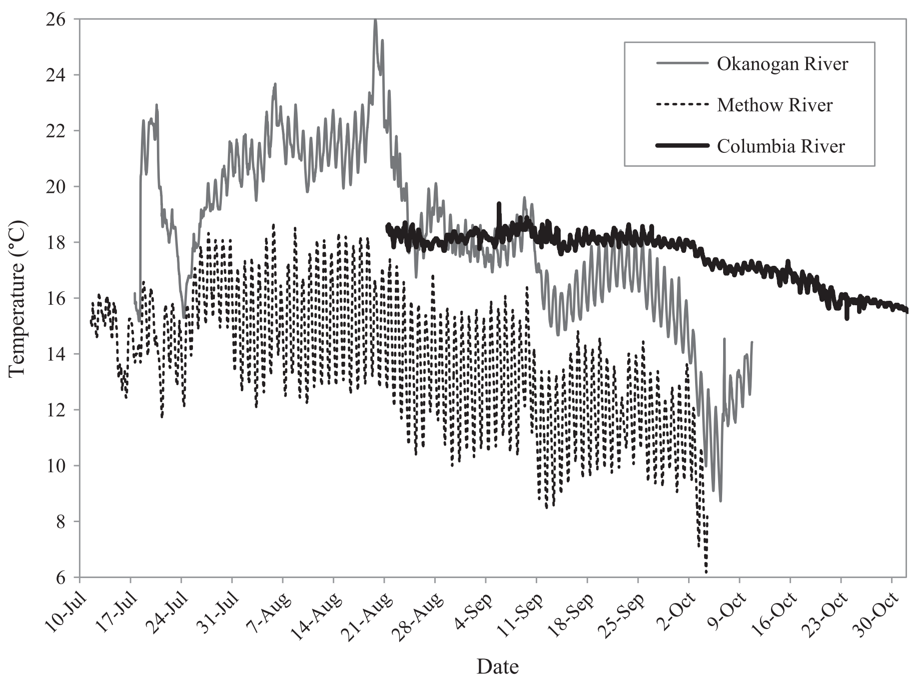

FIGURE 5. Example temperature profiles recorded every 30 min from the three main populations upstream of Wells Dam. The profiles begin at the time of tagging at Wells Dam and end when the recorder was recaptured from a carcass.

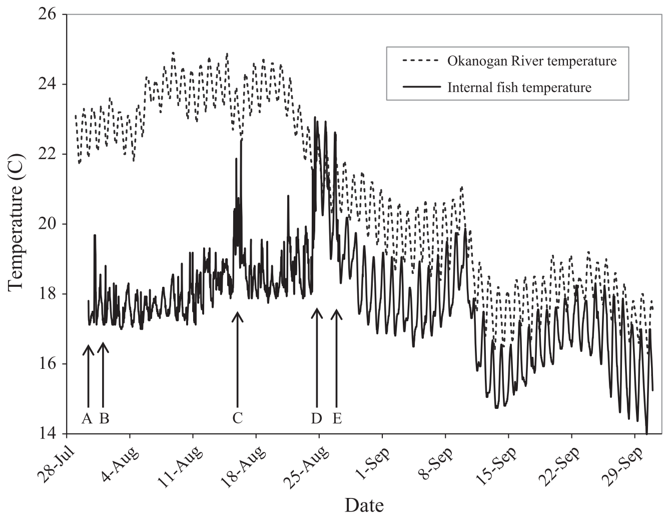

FIGURE 6. Temperature profile recorded every 30 min for a typical radio-tagged fish delayed by a thermal barrier at the mouth of the Okanogan River. River temperature data were queried from the USGS gauge 12447200 at Malott. This fish was tagged on July 30 (**A**), detected outside the mouth of the Okanogan between August 1 and August 23 (**B** to **D**), briefly entered and exited the Okanogan River (**C**), re-ascended the Okanogan River and crossed the OKA site late on August 24 (**D**), reached the Similkameen River on August 26 (**E**), and remained there until spawning.

with a final destination in the Columbia River below CJD. Nevertheless, the area below CJD is demonstrably an important holding area for local populations. Because CJD is a complete fish passage barrier (i.e., no navigation locks or fish ladders), it is not unexpected that adult salmonids would stage there.

The action of falling back after passing a hydroelectric dam is common in the upstream migration of Pacific salmon in Columbia River basin (Matter and Sandford 2003; Boggs et al. 2004; Naughton et al. 2006). Fallback rates are influenced by the hydroelectric project structure and location in relation to natal tributaries as well as river conditions during migration (Boggs et al. 2004; Keefer et al. 2004a, 2004b). However, the downstream movement of fish during a spawning migration is also known to occur after encountering other obstacles or interruptions such as hook-and-line angling (Thorstad et al. 2007; Richard et al. 2013). Fish may continue migration after a period of delay or remain in downstream areas or tributaries throughout the spawning period. We observed between 32–37% of radio-tagged fish in each year downstream of Wells Dam at some point after tagging, counting both fallback and dropout fish. This downstream group includes fish from all tributary destinations. About 27% and 24% of fallback fish eventually re-ascended Wells Dam in 2011 and 2012, respectively, and had final destinations upstream of the dam. It is possible that the release of study fish back into the fish ladders at Wells Dam facilitated downstream movement after release. However, most fish detected at some point downstream after tagging had their first detection at the top of the fish ladders (based on PIT tag records) before falling back in 2011 (68%) and 2012 (76%). PIT tag detection at the top of the fish ladders very accurately represented passage over Wells Dam. We found that 99.8% of the study fish detected upstream of Wells Dam through radiotelemetry were detected by the PIT tag array at the top of the fish ladders.

The percentage of fish that fell back at Wells Dam in 2011 (24.2%) and 2012 (30.1%) was higher than the values reported for lower Columbia River dams (1.4–14.6%; Boggs et al. 2004). At lower Columbia and Snake River dams, Boggs et al. (2004) found that the percent of fish that re-ascend fishways after falling back decreases as upstream distance increases. Thus, net fallback rates at Wells Dam would be expected to exceed those of other main-stem dams because it is the farthest upstream dam on the Columbia River with salmon passage facilities, and correspondingly has the highest number of populations downstream that could contribute overshooting fish. However, since hatchery fish were excluded from our study, the total fallback of fish passing Wells Dam (hatchery and wild) is unclear.

Based on our adjustment factors, which rely heavily on fallback rates and on the assumption that our radio-tagged fish represented the run at large, we estimated that dam counts overestimated the populations of summer-run Chinook Salmon above Wells Dam by over 10,000 fish in each year. Although high, the proportion of overcount is consistent with estimations for Chinook Salmon at some Snake River impoundments within the Columbia River hydrosystem, especially for upstream impoundments, though release methods differed from those in the present study (Boggs et al. 2004). We did observe a difference in fallback by ladder, which translated into a difference in adjustment factor by ladder. This difference could be attributed to increased sampling late season at the west ladder, particularly in 2012. This was done in order to reach minimum sampling goals as overall passage slowed and to have large enough sample sizes to accurately represent this portion of the run. Our analyses of run timing suggested late-returning fish were more likely to have final destinations below Wells Dam and thus theoretically more likely to fall back. Although minor, the disproportionally higher late-season tagging would cause the adjustment factor to be biased downward. Despite this, it appears that fallback and re-ascension can significantly reduce the accuracy of Wells Dam ladder counts and any management metrics that rely on them, such as escapement estimates and harvest quotas (Dauble and Mueller 2000). Managers should explore methods to account for fallback at other structures, such as the adjustment factor presented here, when precise metrics are needed. Radiotelemetry may be an impractical approach considering its high annual costs; however, caution should be taken when utilizing PIT tag records alone to estimate fallback. A fallback event will go undocumented if that fish does not re-ascend or is not detected by PIT arrays downstream. To emphasize this point, we observed a number of fish that fell back over Wells Dam but were never subsequently detected by another PIT tag array to indicate this fallback event outside of our radiotelemetry monitoring. This is particularly important for summer and fall Chinook Salmon because these fish can spawn in main-stem systems where instream PIT tag coverage is limited or infeasible.

Movement patterns of adult salmonids in the main-stem Columbia River are influenced by environmental variables such as water temperature and flow regime (Quinn and Adams 1996; Quinn et al. 1997; Keefer et al. 2008). Previous radiotelemetry studies in the Columbia River have not distinguished stock-specific migration timing and distribution differences in relation to thermal barrier effects for populations above Wells Dam because they employed broad-scale approaches focusing primarily on the main-stem Columbia River (e.g., Keefer et al. 2004a, 2004b, 2004c; Goniea et al. 2006). The majority of the fish that we tagged in both years were from the Okanogan River, a population that encounters elevated water temperatures during migration that can result in migration delay of returning fish (Major and Mighell 1966; Hatch et al. 1992; Ashbrook et al. 2008). The Okanogan River has a warmer average daily temperature than other spawning tributaries in the upper Columbia during the summer months, often exceeding 21°C—the level at which migration is generally impacted (Major and Mighell 1966; Hyatt et al. 2003; Goniea et al. 2006), although Chinook Salmon have been reported to migrate at higher temperatures (Strange 2010, 2012). We observed a significant barrier effect in 2012 (but not in 2011), evidenced by a significant decrease or complete cessation of upstream migration.

However, negative effects to delayed fish were not clear. The proportion of radio-tagged fish that spawned in the main-stem Columbia River below CJD did not increase in 2012 relative to 2011, suggesting that delayed fish were not displaced to a different spawning area. In both years, Methow River fish made up the majority of radio-tagged fish from other spawning populations holding downstream of CJD prior to spawning. This finding was surprising given that Methow River fish do not experience a thermal migration barrier and their natal tributary is 16 rkm farther downstream from CJD than the Okanogan River. Further, the Okanogan River supports a larger population of summer-run Chinook Salmon than does the Methow River (Hillman et al. 2012), which we expected would make Okanogan River fish more prevalent in nearby prespawn holding areas, especially during periods of thermally blocked migration into the tributary.

It was evident from the internal temperature tag data that migrating fish made attempts to move upstream in the Okanogan River in both years when temperatures were at or above 21°C, despite these temperatures severely deterring most passage. We documented upstream and downstream movement past our fixed telemetry site near the mouth when we considered a thermal barrier to be in place. Although we were unable to recover any temperature-recording tags from these fish, they were likely exposed to prolonged temperatures in excess of 24°C based on their distance traveled and the lack of known thermal refugia in the main-stem Okanogan River near the monitoring site. These values border the upper limits of thermal tolerance for adult Chinook Salmon reported by Richter and Kolmes (2005) but are similar to the upper limits reported by Strange (2010). Despite this exposure, we believe the fish that migrated through the thermal barrier survived to spawn. The low sample sizes of recovered temperature recorders limited our investigation of the effects of temperature exposures on fish movement and survival to spawning; we recognize the need for further examination of these relationships in the upper Columbia River and other systems where high river temperatures or high temperature gradients exist.

Delayed fish were likely exposed to Columbia River fisheries longer than they would have been if no thermal barrier had been in place. Salmon fisheries in the reservoir upstream of Wells Dam are diverse and robust. In 2012, for example, sport anglers were estimated to have harvested 2,364 summer-run Chinook Salmon, and additional tribal snag and purse seine fisheries occurred at CJD and at the Okanogan–Columbia confluence, respectively (R. Jateff, WDFW, personal communication). Fisheries in 2011 and 2012 removed 13 and 8 tags, respectively, despite regulations prohibiting retention of tagged fish. These should be considered minimum values because some fish were suspected to have been harvested and not reported. Most (reported) tagged fish were harvested in the CJD snag fishery. Although the decrease in harvest between 2011 and 2012 may corroborate the tracking data suggesting that delayed fish did not appear to be displaced to the area below CJD, the decrease could also be attributed to increased compliance with the release regulation over the course of the study.

We estimate that 77–85% of our radio-tagged fish above Wells Dam successfully survived to spawning. We often could not verify that fish surviving to spawning successfully spawned without more intensive monitoring of fish on spawning grounds. This was not feasible with the resources available and the large scope of this project. Despite this, we feel confident that between monitoring fish locations and having precise locations and timing of all spawning sites through concurrent spawning grounds surveys, we accurately represented a fish's likelihood of successfully spawning.

Traditional spawning ground surveys in the upper Columbia region generally report lower prespawn mortality rates than those estimated by our survival-to-spawning rates (Hillman et al. 2012, 2013). However, these surveys typically begin immediately prior to spawning and do not account for mortality that occurs during most of the prespawn holding period. Further, in the upper Columbia tributaries and in many other regions, these estimates are typically based on female fish because of the relative ease of determining whether the fish spawned (i.e., egg voidance sampling). As male gametes are typically always present in carcasses regardless of spawning success, determining whether the fish contributed to the spawning population is difficult. We observed a large proportion of mortality before spawning ground surveys would typically begin and within the lower migration corridor, an area not typically covered by traditional surveys. Although this mortality may fall outside the temporal and spatial bounds of the traditional definition of prespawn mortality, it is nonetheless important for managers to consider (Bowerman et al. 2016). Managers should be aware that mortality rates could be significantly underestimated if they rely solely on carcass inspections during redd surveys.

Prespawn mortality was proportionally much higher within the main-stem Columbia River than in tributaries, despite the former's having more tolerant temperatures through much of the summer. Spawning habitat is severely limited within the main-stem Columbia River between Wells Dam and CJD, and main-stem prespawn mortality could be inherently higher than in tributaries. We observed a number of fish that survived until spawning commenced but that did not spawn, presumably because they never located areas with suitable spawning substrate and flow. This was substantiated by underwater video surveys conducted concurrently as part of a related study. The higher main-stem prespawn mortality, however, is primarily a result of our methods of assigning fish to populations. Because no distinction between the populations of the wild fish that we tagged was possible during sampling, we had to observe movement into or spawning in a tributary to assign the fish to that population. Our data show that fish from multiple populations hold in the main-stem Columbia River prior to tributary entry. Thus, prespawn mortality estimates for that area undoubtedly include fish from tributary populations that could not locate their natal tributary or had depleted energy reserves within the main stem. Redd survey data suggest that most prespawn mortality in the main-stem Columbia was experienced by fish from tributary populations, given that main-stem Chinook Salmon redd counts upstream of Wells Dam averaged only 1.9% of all redds counted upstream of the dam between 2011 and 2013 (WDFW, unpublished data). Our assignment method overestimates the true prespawn mortality rates within the main-stem spawning population and underestimates mortality for the tributary spawning populations.

Understanding the stock-specific migration patterns of summer-run Chinook Salmon populations and the factors that influence them is integral to developing effective management policy and risk assessment for these populations. Our results suggest that local hatchery programs aiming to preserve the genetic integrity of local spawning populations should not rely on broodstock collections at main-stem dams because they include fish from multiple spawning populations. We observed very little movement between tributary locations prior to spawning, further suggesting that tributary broodstock collection would be the most effective way to ensure that genetic contributions from nontarget populations are reduced. Although upper Columbia River summer-run Chinook Salmon are not currently listed under the U.S. Endangered Species Act (NMFS 2005), substantial risks to the continuing abundance of these populations exist. In addition to the commonly cited effects of hatcheries, harvest, habitat, and hydroelectric causes, it is estimated that mean air temperatures will rise 2.4°C and that snowpack levels in Washington State will decrease by about 40% by midcentury as the result of global climate change (Snover et al. 2013). This is likely to exacerbate already-poor migration conditions for some local summer-run Chinook Salmon populations and decrease the availability of coolwater refugia where it currently exists. Radiotelemetry remains one the best methods for obtaining detailed information about the environmental variables experienced by migrating adult anadromous salmonids. Further, anthropogenic effects related to the Columbia River hydropower system and genetic effects from existing and expanding hatchery supplementation programs should be monitored routinely to ensure that these populations of fish are viable and likely to persist into the future.

Management Implications

Our research project intended to examine stock-specific migration patterns of summer-run Chinook Salmon above Wells Dam and to evaluate the influences of environmental variables (e.g., water temperature) on migration. Further, telemetry monitoring allowed us to estimate prespawn mortality and the contribution of wild summer-run Chinook Salmon to spawning populations (among other metrics). Understanding these metrics is important to implementing an effective, information-driven management plan for the species. We have shown that the summer-run Chinook Salmon passing Wells Dam constitutes a mixed stock of fish, including spawning populations above and below the dam, some with unique migration characteristics.

Managers rely on dam passage counts when estimating adult returns and evaluating whether returns are healthy enough to support recreational and tribal fisheries, broodstock collection, and spawning escapement. Utilizing existing techniques, we have shown that Wells Dam counts overestimate the populations of fish upstream unless corrections for fallback and re-ascension are applied. Additionally, other factors (including mortality occurring en route to spawning grounds) may bias estimates of the number of fish available for harvest or spawning. Our calculated adjustment factor and prespawn mortality estimates should provide managers the best current data available to model the postpassage availability of fish for broodstock, spawning escapement, and harvest. Further, radiotelemetry tracking indicated that migration into some tributaries (e.g., the Okanogan River) can be delayed for a prolonged period by increased water temperatures in tributary habitats (i.e., thermal barriers). Presumably, the occurrence of a thermal barrier would result in a greater exploitation rate of affected fish when tribal or recreational fisheries are occurring in the area where affected fish must linger. Interestingly, we found that a greater proportion of Methow River fish were detected in one such holding area, the Chief Joseph Dam tailrace, than Okanogan River fish, even though the Methow River was not subject to a thermal barrier (as was present in the Okanogan River) and is a greater distance from Chief Joseph Dam. This finding should give managers caution that stock exploitation in fisheries may not mirror geographically based expectations.

ACKNOWLEDGMENTS

Many people provided their time and assistance during the course of this study. Specifically, we thank T. R. Divis and the crew from the WDFW Methow Field Office for help with field work and data collection; Jayson Wahls and Scott Moore and the crew from Wells Hatchery for assistance in trapping; Andrew Murdoch and Alf Haukenes for early reviews; Casey Baldwin for initial project development and funding acquisition; the Douglas County Public Utility District for access to Wells Dam; Patrick Miller and the U.S. Geological Survey for use of stream gauge stations for fixed telemetry sites; and the U.S. Bureau of Reclamation for allowing fixed telemetry sites on their property. We also thank the many collaborating agency personnel and staff for providing spawning surveys and tag collections. We greatly appreciate NOAA Fisheries and the Pacific States Marine Fisheries Commission for their funding and support of this research. There is no conflict of interest declared in this article.

REFERENCES

Ashbrook, C. E., E. A. Schwartz, C. M. Waldbillig, and K. W. Hassel. 2008. Migration and movement patterns of adult Chinook Salmon (*Oncorhynchus tshawytscha*) above Wells Dam. Washington Department of Fish and Wildlife Technical Report FPT 06-11.

Boggs, C. T., M. L. Keefer, C. A. Peery, T. C. Bjornn, and L. C. Stuehrenberg. 2004. Fallback, re-ascension, 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.

Bowerman, T., M. L. Keefer, and C. C. Caudill. 2016. Pacific Salmon prespawn mortality: patterns, methods, and study design considerations. Fisheries 41:738–749.

Chapman, D. W. 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., K. W. Goodson, and M. R. Falcy. 2011. Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish. Canadian Journal of Fisheries and Aquatic Sciences 68:511–522.

Christie, M. R., M. L. Marine, R. A. French, and M. S. Blouin. 2011. Genetic adaptation to captivity can occur in a single generation. Proceedings of the National Academy of Sciences of the United States of America 109:238–242.

Columbia Basin Research. 2017. Columbia River data access in real time [online database]. Columbia Basin Research, School of Aquatic and Fishery Sciences, University of Washington, Seattle. Available: www.cbr.washington.edu/dart/. (February 2018).

Connor, W. P., H. L. Burge, J. R. Yearsley, and T. C. Bjornn. 2003. Influence of flow and temperature on survival of wild subyearling fall Chinook Salmon in the Snake River. North American Journal of Fisheries Management 23:362–375.

Dauble, D. D., T. P. Hanrahan, D. R. Geist, and M. J. Parsley. 2003. Impacts of the Columbia River hydroelectric system on main-stem habitats of fall Chinook Salmon. North American Journal of Fisheries Management 23:641–659.

Dauble, D. D., and R. P. Mueller. 2000. Difficulties in estimating survival for adult Chinook Salmon in the Columbia and Snake rivers. Fisheries 25(8):24–34.

Fish, F. F., and M. G. Hanavan. 1948. A report on the Grand Coulee Fish Maintenance Project, 1939–1947. U.S. Fish and Wildlife Service Special Scientific Report 55.

Fulton, L. A. 1968. Spawning areas and abundance of Chinook (*Oncorhynchus tshawytscha*) in the Columbia River basin: past and present. U.S. Fish and Wildlife Service Special Scientific Report Fisheries 571.

Giorgi, A. E., T. W. Hillman, J. R. Stevenson, S. G. Hays, and C. M. Peven. 1997. Factors that influence the downstream migration rates of juvenile salmon and steelhead through the hydroelectric system in the mid–Columbia River basin. North American Journal of Fisheries Management 17:268–282.

Goniea, T. M., M. L. Keefer, T. C. Bjornn, C. A. Peery, D. H. Bennett, and L. C. Stuehrenberg. 2006. Behavioral thermoregulation and slowed migration by adult fall Chinook Salmon in response to high Columbia River water temperatures. Transactions of the American Fisheries Society 135:408–419.

Hatch, D. R., A. Wand, A. Porter, and M. Schwartzberg. 1992. The feasibility of estimating Sockeye Salmon escapement at Zosel Dam using underwater video technology. Columbia River Inter-Tribal Fish Commission, Annual progress report for Public Utility District No. 1 of Douglas County, Portland, Oregon. Available: www.fishlib.org/library/Documents/CRITFC/zosel1992.pdf (July 2014).

Hillman, T., M. Miller, L. Keller, J. Murauskas, T. Miller, M. Tonseth, M. Hughes, and A. Murdoch. 2013. Monitoring and evaluation of the Chelan County PUD hatchery programs: 2012 annual report. Report to the HCP Hatchery Committee, Wenatchee, Washington.

Hillman, T., M. Miller, J. Murauskas, L. Keller, T. Miller, M. Tonseth, M. Hughes, and A. Murdoch. 2012. Monitoring and evaluation of the Chelan County PUD hatchery programs: 2011 annual report. Report to the HCP Hatchery Committee, Wenatchee, Washington.

Hyatt, K. D., M. M. Stockwell, and D. P. Rankin. 2003. Impact and adaptation responses of Okanogan River Sockeye Salmon (*Oncorhynchus nerka*) to climate variation and change effects during freshwater migration: stock restoration and fisheries management implications. Canadian Water Resources Journal 28:689–713.

Kassler, T. W., S. Blankenship, and A. R. Murdoch. 2011. Genetic structure of upper Columbia River summer Chinook and evaluation of the effects of supplementation programs. Washington Department of Fish and Wildlife, Olympia.

Keefer, M. L., C. A. Peery, T. C. Bjornn, M. A. Jepson, and L. C. Stuehrenberg. 2004a. Hydrosystem, dam, and reservoir passage rates of adult Chinook Salmon and steelhead in the Columbia and Snake rivers. Transactions of the American Fisheries Society 133:1413–1439.

Keefer, M. L., C. A. Peery, and C. C. Caudill. 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.

Keefer, M. L., C. A. Peery, M. A. Jepson, K. B. Tolotti, T. C. Bjornn, and L. C. Stuehrenberg. 2004b. Stock-specific migration timing of adult spring–summer Chinook Salmon in the Columbia River basin. North American Journal of Fisheries Management 24:1145–1162.

Keefer, M. L., C. A. Perry, R. R. Ringe, and T. C. Bjornn. 2004c. Regurgitation rates of intragastric radio transmitters by adult Chinook Salmon and steelhead during upstream migration in the Columbia and Snake rivers. North American Journal of Fisheries Management 24:47–54.

Major, R. L., and J. L. Mighell. 1966. Influence of Rocky Reach Dam and the temperature of the Okanogan River on the upstream migration of Sockeye Salmon. U.S. National Marine Fisheries Service Fishery Bulletin 66:131–147.

Matter, A. L., and B. P. Sandford. 2003. A comparison of migration rates of radio- and PIT-tagged adult Snake River Chinook Salmon through the Columbia River hydropower system. North American Journal of Fisheries Management 23:967–973.

Naughton, G. P., C. C. Caudill, M. L. Keefer, T. C. Bjornn, C. A. Peery, and L. C. Stuehrenberg. 2006. Fallback by adult Sockeye Salmon at Columbia River dams. North American Journal of Fisheries Management 26:380–390.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.

NMFS (National Marine Fisheries Service). 2005. Endangered and threatened species: final listing determinations for 16 ESUs of West Coast salmon and final 4(d) protective regulations for threatened salmonid ESUs. Federal Register 70:123(28 June 2005):37160–37204.

Pacific States Marine Fisheries Commission. 2017. PTAGIS (Columbia Basin PIT Tag Information System) [online database]. Pacific States Marine Fisheries Commission, Portland, Oregon. Available: www.ptagis.org.

Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American Shad and Sockeye Salmon. Ecology 77:1151–1162.

Quinn, T. P., S. Hodgson, and C. Peven. 1997. Temperature, flow, and the migration of adult Sockeye Salmon (*Oncorhynchus nerka*) in the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 54:1349–1360.

Ramstad, K. M., C. J. Foote, J. B. Olsen, and D. Rogers. 2003. Genetic and phenotypic evidence of reproductive isolation between seasonal runs of Sockeye Salmon in Bear Lake, Alaska. Transactions of the American Fisheries Society 132:997–1013.

Raymond, H. L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer Chinook Salmon and steelhead in the Columbia River basin. North American Journal of Fisheries Management 8:1–12.

Richard, A., M. Dionne, J. Wang, and L. Bernatchez. 2013. Does catch-and-release affect the mating system and individual reproductive success of wild Atlantic Salmon (*Salmo salar* L.)? Molecular Ecology 22:187–200.

Richter, A., and S. A. Kolmes. 2005. Maximum temperature limits for Chinook, Coho, and Chum salmon and steelhead trout in the Pacific Northwest. Reviews in Fisheries Science 13:23–49.

Salinger, D. H., and J. J. Anderson. 2006. Effects of water temperature and flow on adult salmon migration swim speed and delay. Transactions of the American Fisheries Society 135:188–199.

Sanford, B. P., R. W. Zabel, L. G. Gilbreath, and S. G. Smith. 2012. Exploring latent mortality of juvenile salmonids related to migration through the Columbia River hydropower system. Transactions of the American Fisheries Society 141:343–352.

Snover, A. K., G. S. Mauger, L. C. Whitely Binder, M. Krosby, and I. Tohver. 2013. Climate change impacts and adaptation in Washington State: technical summaries for decision makers. State of Knowledge Report prepared for the Washington State Department of Ecology, Climate Impacts Group, University of Washington, Seattle.

Strange, J. S. 2010. Upper thermal limits to migration in adult Chinook Salmon: evidence from the Klamath River basin. Transactions of the American Fisheries Society 139:1091–1108.

Strange, J. S. 2012. Migration strategies of adult Chinook Salmon runs in response to diverse environmental conditions in the Klamath River basin. Transactions of the American Fisheries Society 141: 1622–1636.

Thorstad, E. B., T. F. Naesje, and I. Leinan. 2007. Long-term effects of catch-and-release angling on ascending Atlantic Salmon during different stages of spawning migration. Fisheries Research 85:330–334.

Unwin, M. J., M. T. Kinnison, N. C. Boustead, and T. P. Quinn. 2003. Genetic control over survival in Pacific salmon (*Oncorhynchus* spp.): experimental evidence between and within populations of New Zealand Chinook Salmon (*O. tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 60:1–11.

Utter, F. M., D. W. Chapman, and A. R. Marshall. 1995. Genetic population structure and history of Chinook Salmon of the upper Columbia River. Pages 149–165 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Van Hyning, J. M. 1973. Factors affecting the abundance of fall Chinook Salmon in the Columbia River. Research Reports of the Fish Commission of Oregon 4:1–87.

Weitkamp, D. E., and M. Katz. 1980. A review of dissolved gas supersaturation literature. Transactions of the American Fisheries Society 109:659–702.