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CHUM SALMON SPAWNING ACTIVITY IN TRIBUTARIES BELOW BONNEVILLE DAM: THE RELATIONSHIP WITH TAILWATER ELEVATION AND SEASONAL PRECIPITATION†

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ABSTRACT

Chum salmon (*Oncorhynchus keta)* below Bonneville Dam migrate through as well as hold and spawn in both tributaries and mainstem areas of the Columbia River, USA. Whether fluctuations in tailwater elevation influence spawning in tributaries is unclear. We examined the relationship between Bonneville Dam tailwater elevation, seasonal precipitation and chum salmon spawning activities in three tributary spawning areas. In these tributaries, we assessed initial date of entry, time required to enter and length of spawning season, as well as the proportion of the total population that spawned in tributaries and the distribution of spawners among tributaries. Using linear regression, these variables were compared to cumulative hours of tailwater elevation ≥ 3.5 m and cumulative precipitation. Increased Bonneville Dam tailwater elevation was associated with later and longer lasting chum salmon spawning activities, but was not associated with the distribution of chum salmon spawners in tributaries. Increased seasonal precipitation was associated with a more prolonged spawning season and relatively even distribution of adult chum salmon, but was unrelated to the timing of chum salmon spawning in tributaries. The regulation of tailwater elevation downstream from Bonneville Dam can influence the spawning process for chum salmon in tributaries that enter the regulated area. How important this influence is to the decline of chum salmon in the Columbia River is unclear. Published in 2011 by John Wiley & Sons, Ltd.

KEY WORDS: chum salmon; tailwater regulation; tributaries; spawning activity; precipitation; Columbia River

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INTRODUCTION

The regulation of water level below dams has been shown to influence a variety of aquatic organisms, including fish and invertebrates (see Helesic and Sedlak, 1995; Scheidegger and Bain, 1995; Collier *et al*., 2000; Freeman *et al*., 2001; Vinson, 2001; Cortes *et al*., 2002; Anderson *et al*., 2006; Lundqvist *et al*., 2008; Robinson and Uehlinger, 2008). Although research associated with water regulation at dams is abundant, the majority of this work has been focused in mainstem areas of the regulated river (Raymond, 1988; Williams, 1989; Murchie *et al.*, 2008). Many of these studies have examined the impact of streamflow or tailwater manipulations on the spawning behaviour of adult salmon in mainstem areas downstream from hydroelectric projects (see Chapman *et al.*, 1986; Hunter, 1992; Tiffan *et al.*, 2002, 2004, 2005, 2010; Garland *et al.*, 2003; Connor and Pflug, 2004; McMichael *et al.*, 2005). Although the importance of tributaries that enter regulated areas of rivers below dams has also been recognized (Rice *et al*., 2001), relatively little research has been focused on the response of fish in these tributaries to the regulated conditions (see Murchie *et al*., 2008). Studies that have been conducted on fish in these tributaries have generally focused on larval or juvenile fish (Robinson *et al*., 1998; Mérigoux and Ponton, 1999).

In the Pacific Northwest, USA, chum salmon abundance is severely depressed over much of its historical range. Although there are no official estimates of chum salmon abundance in the Columbia River basin prior to the 1930's (Myers *et al*., 2006), maximum historical commercial fishery landings were reported to be as high as 425 000 fish in 1942 (WDFW, 2000). By the mid-1950s, chum salmon returns to the Columbia River had declined to a fraction of historic levels and today, returns are $<1\%$ of historic levels (Johnson *et al*., 1997). It is estimated that up to 88% of historic populations are extirpated from the basin (McElhany, 2005). In 1999, chum salmon in the lower Columbia River were legally protected to aid in their conservation (NOAA, 1999).

Historical records suggest chum salmon were distributed throughout the lower Columbia River, spawning in virtually all tributaries downstream from Celilo Falls (river kilometer (Rkm) 320) (LCFRB, 2004; Myers *et al*., 2006). Present day confirmed spawning distribution is limited to tributaries and mainstem areas below Bonneville Dam (Rkm 235) (Johnson *et al*., 1997). Currently, the majority of spawning occurs in three focal areas. The Grays River (Rkm 34), a lower Columbia River tributary, the Woods Landing (Rkm 183) area of the mainstem Columbia River, and the area immediately downstream of Bonneville Dam. The spawning area near Bonneville Dam (Figure 1) includes two tributaries

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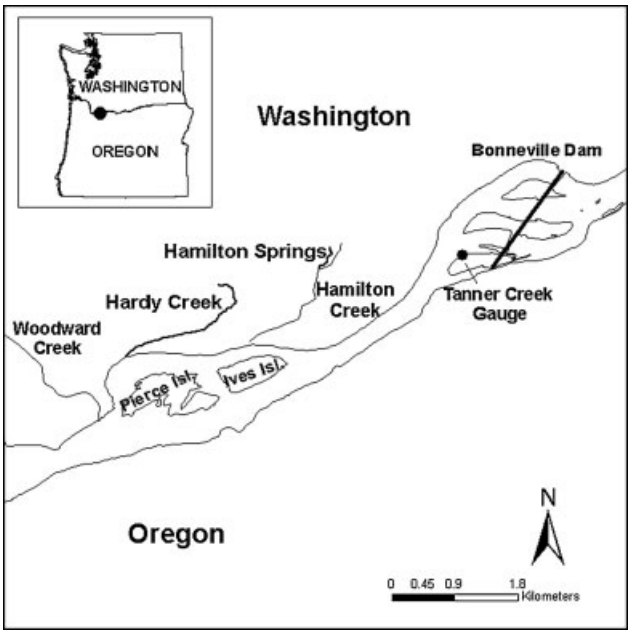

Figure 1. Map of study area.

(Hardy Creek and Hamilton Creek), an artificial spawning channel (Hamilton Springs) that enters Hamilton Creek (Rkm 1.6), and the Ives Island area which is a Columbia River side channel adjacent to Pierce and Ives Islands (McElhany, 2005; Myers *et al*., 2006; McElhany *et al*., 2007). Each of these areas is influenced to varying degrees by the regulation of Bonneville Dam.

The mainstem Columbia River immediately downstream from Bonneville Dam is susceptible to frequent fluctuations in tailwater elevation and discharge resulting primarily from the operation of Bonneville Dam for hydropower production, backwater effects from the Willamette River near Portland, Oregon (Rkm 162), and from Pacific Ocean tides. Chum salmon in the Columbia River begin their spawning migration in October (Johnson *et al*., 1997), when river discharge is typically at its lowest level of the year (Tiffan *et al*., 2002; Garland *et al*., 2003). As adults begin to arrive in the Ives Island area (early to mid-November), tributaries and a majority of the mainstem spawning habitat are often inaccessible because river flow and water surface elevations are too low for fish to enter these areas (Garland *et al*., 2003). Low Bonneville Dam tailwater levels at the onset of spawning (i.e. <3.5 m) may exclude fish from potential spawning habitat (such as the Ives channel, Hamilton Creek and Hardy Creek), forcing fish to spawn in the resulting reduced area, and possibly creating competition with other adults for access to limited habitat (Schroder, 1973; Fish Passage Center (FPC), 2006; Thorstad *et al*., 2008). Following a review of historical spawning ground survey data and hydrodynamic modeling studies (Tiffan *et al*., 2002; Garland *et al*., 2003), the US Army Corps of Engineers and Bonneville Power Administration have recommended a sustained minimum Columbia River tailwater elevation of 3.5 m to provide spawning habitat over at a portion of the area historically used for spawning below Bonneville Dam (see FPC, 2004; NOAA, 2008). Fisheries managers have speculated that this recommended minimum tailwater elevation would increase the availability of spawning habitat in the Ives spawning area (including mainstem spawning areas downstream of Ives), and would improve access to the Ives spawning area as well as the tributaries which enter the Ives Island area (i.e. Hamilton and Hardy Creek) (see FPC, 2004; NOAA, 2008).

The tributaries immediately downstream from Bonneville Dam (e.g. Hamilton Creek and Hardy Creek), experience highly intermittent stream flows during the summer and early fall. In early November, the lower reaches of these tributaries often remain dry until the first significant rain of the season (FPC, 2001; Tiffan *et al*., 2002, 2005, 2010; Garland *et al*., 2003). General opinion based on knowledge of the area suggests that access into tributaries is influenced by tailwater elevation, and must be coupled with sufficient precipitation and tributary discharge levels for salmon to successfully ascend to the spawning grounds (Garland *et al*., 2003; Tiffan *et al*., 2005; NOAA, 2008). However, it is unknown whether a 3.5 m tailwater elevation is either necessary or adequate for adult chum salmon to enter into the tributaries, particularly when tributary discharge is low. It is also unknown whether tailwater elevation or precipitation influences the spawning activity of chum salmon in these tributaries.

The objective of this study was to examine relationships between Bonneville Dam tailwater elevation and seasonal precipitation to chum salmon spawning activities in Hamilton Creek, Hamilton Springs and Hardy Creek. We evaluated five hypotheses: (1) Bonneville Dam tailwater elevation of 3.5 m is not required for chum salmon to successfully enter tributaries; (2) the amount of time Bonneville Dam tailwater elevation is at least 3.5 m is unrelated to the timing of chum salmon entry into and duration of spawning activity in tributaries; (3) seasonal precipitation is unrelated to the timing of chum salmon entry into and duration of spawning activity in tributaries; (4) the amount of time Bonneville Dam tailwater elevation is at least 3.5 m is unrelated to the distribution of chum salmon spawning in and among tributaries; and (5) seasonal precipitation is unrelated to the distribution of chum salmon spawning in and among tributaries.

STUDY AREA

Ives Island area

The Ives Island area is located in the mainstem Columbia River between Rkm 226.9 and 231.5 (Figure 1), approxi-

mately 3.5 km downstream from Bonneville Dam (the most downstream dam on the Columbia River). The area is composed of two side channels located along the Washington shoreline near Pierce and Ives islands. Three tributaries (Hardy Creek, Hamilton Creek, and Woodward Creek) flow into the side channels. Adult chum salmon that ultimately enter into Hamilton or Hardy creeks must swim through, and often hold in, the Ives Island area.

Hamilton Creek and Hamilton Springs

Hamilton Creek is a 13 km long stream, which enters the Columbia River at Rkm 230 (Figure 1). The mouth of Hamilton Creek is located approximately 4.3 km downstream from Bonneville Dam. The lower 1.6 km of the creek flows through the town of North Bonneville to its confluence with the Columbia River near the center and north end of Ives Island. Hamilton Springs is a 530 m long artificial spawning channel that enters Hamilton Creek at approximately Rkm 1.6 (Figure 1). The Hamilton Springs channel was originally constructed in the early 1960s. Natural groundwater springs provide water to Hamilton Springs which typically flows during late fall through late spring and is dry during the summer and early fall. Chum salmon spawn in both Hamilton Creek and Hamilton Springs.

Hardy Creek

Hardy Creek is a 6 km long stream, which enters the Columbia River at Rkm 227 (Figure 1). The mouth of Hardy Creek is located approximately 6 km downstream from Bonneville Dam. The lower 2 km of the creek is located on Pierce National Wildlife Refuge. Chum salmon spawning is restricted to the lower 2.1 km of the creek because a railroad culvert creates an impassable barrier.

METHODS

Data

Spawning ground surveys. Adult fish sampling in Hamilton Springs and Hardy Creek was conducted by the US Fish and Wildlife Service, Columbia River Fisheries Program Office. From 2000–2006, the US Fish and Wildlife Service conducted adult spawning ground surveys for chum salmon by foot, one to three times per week from November through early January. Detailed field survey and data collection methods are described in Johnson *et al.* (2006). Adult fish sampling in Hamilton Creek and the Ives Island area was conducted jointly between state and federal fisheries agencies (Oregon Department of Fish and Wildlife, Washington Department of Fish and Wildlife, Pacific States Marine Fisheries Commission, US Fish and Wildlife Service). From 2000–2006, these agencies conducted spawning ground surveys for chum salmon by jet boat in the Ives Island area and by foot in Hamilton Creek, one to three times per week from October through January (see Keller, 2006; Tomaro *et al.*, 2007).

Adult abundance estimates. We compiled estimates of abundance of adult chum salmon for the 2000–2006 spawning seasons (see Johnson *et al.*, 2006; Keller, 2006; Tomaro *et al.*, 2007). Total adult abundance in Hamilton Springs and Hardy Creek was estimated with a trapezoidal approximation of the area-under-the-curve method (Hilborn *et al.*, 1999) applied to daily totals of live chum salmon enumerated during spawning ground surveys. In Hamilton Creek, total abundance was estimated in 2000, and from 2002–2006 using the area-under-the-curve method, and in 2001 by subtracting the area-under-the-curve estimates for Hamilton Springs and Hardy Creek from the lower gorge tributary abundance estimate (K. Keller, WDFW personal communication). In the Ives Island area, total abundance was estimated in 2000 and 2001 using the area-under-the-curve method, and from 2002–2006 using a modified Jolly-Seber POPAN carcass mark recovery method [as described in Schwarz and Arnason (1996) and Rawding and Hillson (2003)].

Bonneville Dam tailwater elevation. Historical Bonneville Dam tailwater elevations were obtained from the US Army Corps of Engineers, Columbia Basin Water Management Division database (www.nwd-wc.usace.army.mil/perl/dataquery.pl). Hourly and daily average tailwater elevations for the years 2000–2006, from 28 October through 10 January were retrieved from the Tanner Creek gage (United States Geological Survey, gage # 14128870), which is located 0.85 km downstream from Bonneville Dam at Rkm 232.5, and approximately 2 km upstream from the Ives Island area (Figure 1). Minimum sustained tailwater elevation (MSTE) was defined as the lowest tailwater elevation value recorded during a given period.

Precipitation. Precipitation records for Bonneville Dam (Oregon climate station 350897), were compiled from the Oregon Climatic Services climate data archives (www.ocs.OregonState.edu). The Bonneville Dam climate station is located approximately 4 km from Hamilton Creek and 6 km from Hardy Creek. Daily precipitation was obtained for the same time periods as tailwater elevation (28 October through 10 January, 2000–2006). Precipitation (which is positively related to water elevation in Hamilton Springs and Hardy Creek) was used as a surrogate for stream discharge. There are no permanent stream gages in the Bonneville tributaries, and little information exists on historic streamflow conditions in these areas.

Fish variables

When attempting to relate adult chum counts to environmental conditions, the inability to predict the availability of

chum salmon downstream from a spawning site can dramatically influence results (Trépanier *et al*., 1996). Therefore, we used the observation of adult chum salmon in the Ives Island area to indicate when fish were present downstream from and available to move into the spawning tributaries. Although the specific efficiency of these observations is unknown, to minimize potential bias spawning ground surveys were performed using a standardized effort (i.e. similar frequency, time of year and method). We calculated values for each year and tributary based on the times when live chum salmon were observed in the Ives Island area or in tributaries. Calendar dates were converted to Julian day values for the analysis.

Spawn timing. We used three spawn timing metrics as dependent variables in the assessment. Date of entry ($Entry_{date}$) was defined as the first date an adult chum salmon was observed in a tributary spawning area. Time required for entry ($Entry_{time}$) was defined as the total number of days between the first time an adult chum salmon was observed in the Ives Island area and the first time a fish was observed in a given tributary spawning area. Length of spawning season ($Season_{length}$) was defined as the total number of days live chum salmon were observed in a given tributary spawning area.

Spawning distribution. We used two spawning distribution metrics as dependent variables in the assessment. Proportion in tributaries ($Trib_{\%}$) was defined as the total number of chum salmon spawning in the tributaries divided by the sum of the total number spawning in the tributaries and the Ives Island area. To evaluate how evenly spawners were distributed among tributaries, tributary variation ($Trib_{variance}$) was defined as the variance in the proportion of total tributary spawners among the three tributary spawning areas.

Tailwater variables

We used three tailwater elevation metrics as independent variables in the assessment. Ives to first-MSTE ($MSTE_{first}$) was defined as the cumulative hours of MSTE $\geq$ 3.5 m between the period when the first chum salmon was observed in the Ives Island area and the first chum salmon was observed in a respective tributary spawning area. Ives to first-MSTE ($MSTE_{first}$) was defined separately for each tributary spawning area. Ives to last-MSTE ($MSTE_{last}$) was defined as the hours of MSTE $\geq$ 3.5 m between the period when the first chum salmon was observed in the Ives Island area and the last chum salmon was observed in a respective tributary. Ives to last-MSTE ($MSTE_{last}$) was defined separately for each tributary spawning area. Ives to final-MSTE ($MSTE_{final}$) was defined as the hours of MSTE $\geq$ 3.5 m between the period when the first chum salmon was observed in the Ives Island area and the last chum salmon was observed in any of the tributary spawning areas.

Precipitation variables

We used three precipitation (P) metrics as independent variables in the assessment. Ives to first-P (P_{first}) was defined as the cumulative amount of precipitation between the period when the first chum salmon was observed in the Ives Island area and the first chum salmon was observed in a respective tributary spawning area. Ives to first-P (P_{first}) was defined separately for each tributary spawning area. Ives to last-P (P_{last}) was defined as the amount of precipitation between the period when the first chum salmon was observed in the Ives Island area and the last chum salmon was observed in a respective tributary. Ives to last-P (P_{last}) was defined separately for each tributary spawning area. Ives to final-P (P_{final}) was defined as the amount of precipitation between the period when the first chum salmon was observed in the Ives Island area and the last chum salmon was observed in any of the tributary spawning areas.

Data analysis

To test if a MSTE of 3.5 m was required for adult chum salmon to enter into spawning tributaries we evaluated whether, once they were observed at Ives Island, chum salmon were subsequently observed in a tributary prior to any hour or full day of MSTE $\geq$ 3.5 m. This was done for each spawning area (Hamilton Creek, Hamilton Springs and Hardy Creek) in each year.

Linear regression analysis was used to test for relationships between specific spawning, tailwater and precipitation variables. To test whether a MSTE of $\geq$3.5 m was associated with the timing of chum salmon entry and duration of spawning activity we evaluated three relationships. We regressed date of entry ($Entry_{date}$) and time required for entry ($Entry_{time}$) on Ives to first-MSTE ($MSTE_{first}$) as well as length of spawning season ($Season_{length}$) on Ives to last-MSTE ($MSTE_{last}$). To test whether precipitation was associated with the timing of chum salmon entry and duration of spawning activity we evaluated three relationships. We regressed date of entry ($Entry_{date}$) and time required for entry ($Entry_{time}$) on Ives to first-P (P_{first}) as well as length of spawning season ($Season_{length}$) on Ives to last-P (P_{last}). To test whether a MSTE of $\geq$3.5 m was associated with the distribution of spawning chum salmon we evaluated two relationships. We regressed the proportion in tributaries ($Trib_{\%}$) and among-tributary variation ($Trib_{variance}$) on Ives to final-MSTE ($MSTE_{final}$). To test whether precipitation was associated with the distribution of spawning chum salmon we evaluated two relationships. We regressed the proportion in tributaries ($Trib_{\%}$) and among-tributary variation ($Trib_{variance}$) on Ives to final-P (P_{final}). Independent

Table I. Summary of total chum salmon abundance (includes Hamilton Creek, Hamilton Springs, Hardy Creek and the Ives Island area), cumulative seasonal precipitation and range in Bonneville Dam tailwater elevation during 28 October through 10 January, 2000–2006

Year	Total abundance of adult chum salmon	Cumulative precipitation (cm)	Range in tailwater elevation (m)
2000	869	43.6	3.2–5.9
2001	2292	99.4	2.2–5.8
2002	6054	57.9	2.7–5.0
2003	2121	77.7	2.5–6.4
2004	1166	38.2	3.2–6.1
2005	675	89.6	2.5–6.5
2006	1040	129.0	2.1–6.9

variables were tested for collinearity using linear regression analysis. All statistical comparisons were assessed for significance at $\alpha = 0.10$.

RESULTS

Tributary access

In all seven spawning seasons (2000–2006), chum salmon were not observed in any tributary spawning area prior to the MSTE being $\geq$3.5 m for at least 1 h. Among the seven spawning seasons, chum salmon were observed in tributaries prior to any full day (i.e. consecutive 24 h) of MSTE $\geq$ 3.5 m three times in Hamilton Creek (2001, 2003, 2004), twice in Hamilton Springs (2001, 2003) and three times in Hardy Creek (2001, 2003, 2005).

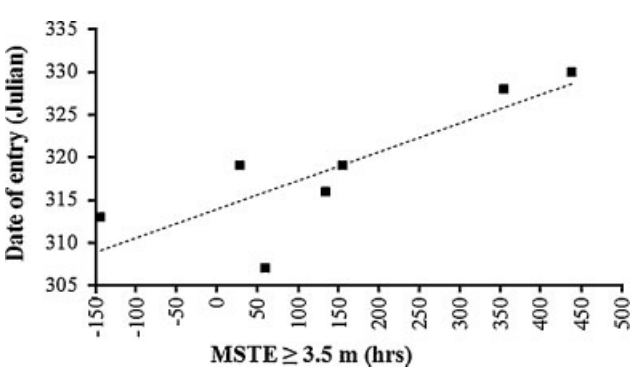

Figure 2. Relationship between tailwater elevation and date of entry. Date of entry represents the first date adult chum salmon were observed in a tributary spawning area. MSTE $\geq$ 3.5 m represents the cumulative number of hours MSTE was at or above 3.5 m between when the first chum salmon was observed in Ives and the first chum salmon was observed in a respective tributary spawning area, 2000–2006. Tailwater elevation was positively related to the first day chum salmon were observed in Hardy Creek ($p = 0.022$, $R^2 = 0.68$).

Spawn timing

Overall, Bonneville Dam tailwater elevation ranged from 2.1–6.9 m and cumulative seasonal precipitation ranged from 38.2–129.0 cm (Table I). The first day (Julian) adult chum salmon were observed in a tributary ($\text{Entry}_{\text{date}}$) ranged from day 313–323 in Hamilton Creek, day 311–323 in Hamilton Springs and day 307–330 in Hardy Creek. Cumulative hours of MSTE $\geq$ 3.5 m ($\text{MSTE}_{\text{first}}$) was positively related to the first day adult chum salmon were observed in Hardy Creek ($p = 0.022$, $R^2 = 0.68$) (Figure 2), but not in Hamilton Creek ($p = 0.536$, $R^2 = 0.08$) or Hamilton Springs ($p = 0.495$, $R^2 = 0.10$). No relationship was found between cumulative precipitation (P_{first}) and the first day chum were observed in Hamilton Creek ($p = 0.428$, $R^2 = 0.13$), Hamilton Springs ($p = 0.305$, $R^2 = 0.21$) or Hardy Creek ($p = 0.865$, $R^2 = 0.01$). Although there was no linear relationship between precipitation and time of entry, the data suggest that a unimodal relationship may exist where entry date was latest when precipitation is approximately 15 cm. However, since 2005 was the only year precipitation exceeded 15 cm, additional data would be required to confirm this unimodal relationship.

The length of time (days) between when adult chum salmon were observed in the Ives Island area and a tributary ($\text{Entry}_{\text{time}}$) ranged from 1–14 days in Hamilton Creek, from −1–14 days in Hamilton Springs and from −5–20 days in Hardy Creek. In 2006, adult chum salmon were observed in Hamilton Springs and Hardy Creek prior to when they were observed in the Ives Island area (reflected by the negative numbers on the range). Cumulative hours of MSTE $\geq$ 3.5 m ($\text{MSTE}_{\text{first}}$) was positively related to the length of time between when adult chum salmon were observed in the Ives Island area and Hamilton Creek ($p = 0.085$, $R^2 = 0.48$) and Hardy Creek ($p = 0.002$, $R^2 = 0.88$) (Figure 3), but not in Hamilton Springs ($p = 0.128$, $R^2 = 0.40$). No relationship was found between cumulative precipitation (P_{first}) and the length of time between when adult chum salmon were observed in the Ives Island area and Hamilton Creek ($p = 0.165$, $R^2 = 0.35$), Hamilton Springs ($p = 0.233$, $R^2 = 0.27$) or Hardy Creek ($p = 0.108$, $R^2 = 0.43$).

The length of the spawning season ($\text{Season}_{\text{length}}$) ranged from 34–58 days in Hamilton Creek, 32–53 days in Hamilton Springs and 23–62 days in Hardy Creek. Cumulative hours of MSTE $\geq$ 3.5 m ($\text{MSTE}_{\text{last}}$) was positively related to the length of spawning season in Hamilton ($p = 0.011$, $R^2 = 0.76$) and Hardy Creeks ($p = 0.047$, $R^2 = 0.58$) (Figure 4), but not in Hamilton Springs ($p = 0.202$, $R^2 = 0.30$). Cumulative precipitation (P_{last}) was positively related to the length of the spawning season in Hamilton Springs ($p < 0.001$, $R^2 = 0.91$) and also Hardy Creek ($p = 0.002$, $R^2 = 0.87$) (Figure 5), but not in Hamilton Creek ($p = 0.916$, $R^2 < 0.01$).

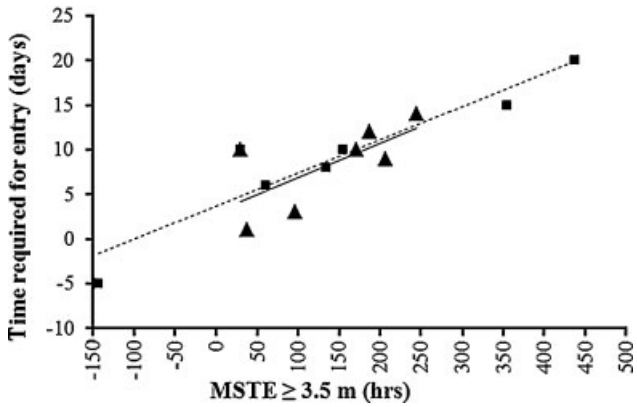

Figure 3. Relationship between tailwater elevation and time required for entry. Time required for entry represents the total number of days between when the first chum salmon was observed in Ives, and the first chum salmon was observed in a tributary spawning area. MSTE $\geq$ 3.5 m represents the cumulative number of hours MSTE was at or above 3.5 m between when the first chum salmon was observed in Ives and the first chum salmon was observed in a respective tributary spawning area, 2000–2006. Tailwater elevation was positively related to the length of time between when adult chum salmon were observed in the Ives Island area and Hamilton Creek (triangles) ($p = 0.085$, $R^2 = 0.48$) and Hardy Creek (squares) ($p = 0.002$, $R^2 = 0.88$).

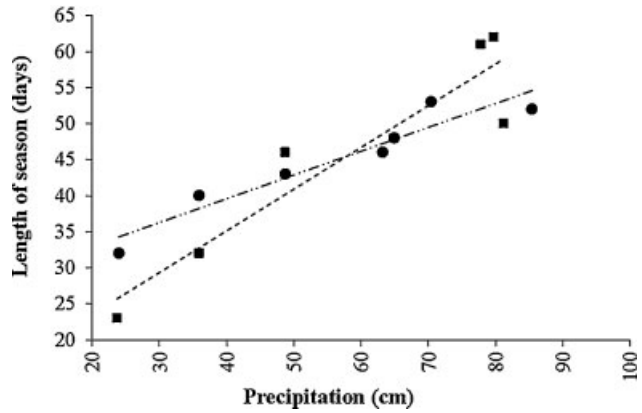

Figure 5. Relationship between precipitation and length of season. Length of season represents the total number of days live chum salmon were observed in a tributary. Precipitation represents cumulative centimeters of precipitation between when the first chum salmon was observed in Ives and the last chum salmon was observed in a respective tributary spawning area, 2000–2006. Precipitation was positively related to the length of the spawning season in Hamilton Springs (circles) ($p < 0.001$, $R^2 = 0.91$) and Hardy Creek (squares) ($p = 0.002$, $R^2 = 0.87$).

Spawning distribution

Overall, estimates of adult chum salmon abundance ranged from 675–054 fish (Table I). The proportion of the total chum salmon population spawning in tributaries ($\text{Trib}_{\%}$) ranged from 0.30–0.77. No significant relationship was found between cumulative hours of MSTE $\geq$ 3.5 m ($\text{MSTE}_{\text{final}}$) and the proportion of chum salmon in tributaries ($p = 0.822$, $R^2 = 0.01$). No significant relationship was found between cumulative precipitation (P_{final}) and the proportion of chum salmon in tributaries ($p = 0.250$, $R^2 = 0.25$).

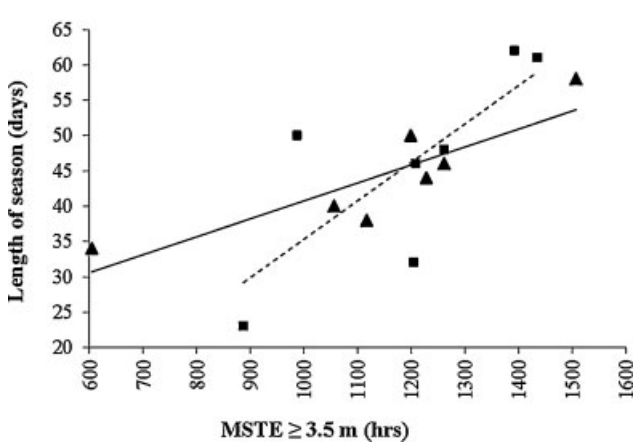

Figure 4. Relationship between tailwater elevation and length of season. Length of season represents the total number of days live chum salmon were observed in a tributary spawning area. MSTE $\geq$ 3.5 m represents the cumulative number of hours MSTE was at or above 3.5 m between when the first chum salmon was observed in Ives and the last chum salmon was observed in a respective tributary spawning area, 2000–2006. Tailwater elevation was positively related to the length of spawning season in Hamilton Creek (triangles) ($p = 0.011$, $R^2 = 0.76$) and Hardy Creek (squares) ($p = 0.047$ $R^2 = 0.58$).

Of the total chum salmon population spawning in tributaries, the proportion within a given tributary ranged from 0.16–0.69 in Hamilton Creek, from 0.30–0.47 in Hamilton Springs and from 0.05–0.47 in Hardy Creek. The yearly variance of the proportion of total spawners among tributaries ($\text{Trib}_{\text{variance}}$) ranged from 0.0074–0.0706. No significant relationship was found between cumulative hours of MSTE $\geq$ 3.5 m ($\text{MSTE}_{\text{final}}$) and the variance of the proportion of chum salmon among tributaries ($p = 0.358$, $R^2 = 0.17$). Cumulative precipitation (P_{final}) was negatively related to the variance of the proportion of chum salmon among tributaries ($p = 0.028$, $R^2 = 0.65$) (Figure 6). One particularly dry year (2004) had a relatively great influence on the relationship between P_{final} and $\text{Trib}_{\text{variance}}$. Omitting 2004 from the regression resulted in a stronger relationship between P_{final} and $\text{Trib}_{\text{variance}}$ ($R^2 = 0.79$), which remained significant ($p = 0.018$). We found no relationship between any of our tailwater elevation variables and the corresponding precipitation variables (i.e. no collinearity).

DISCUSSION

The timing of chum salmon spawning in tributaries that enter the regulated area of the Columbia River below Bonneville Dam is related to regulation of tailwater elevation. In this study, the greater the number of hours that MSTE was at or above 3.5 m; the later chum salmon

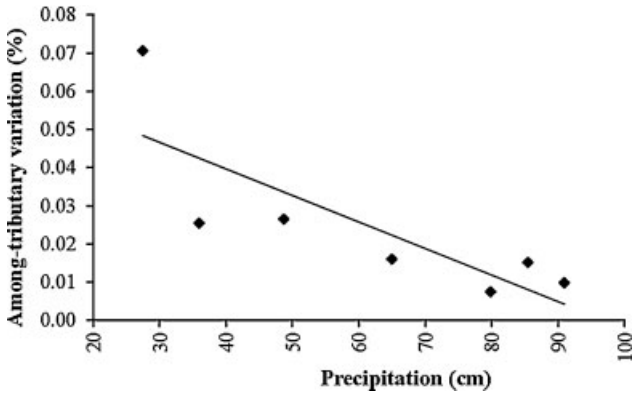

Figure 6. Relationship between precipitation and among-tributary variation. Among-tributary variation represents the variance in the proportion of total tributary spawners among the three tributary spawning areas. Precipitation represents cumulative centimeters of precipitation between when the first chum salmon was observed in Ives and the last chum salmon was observed in any tributary, 2000–2006. Precipitation was negatively related to the variance of the proportion of chum salmon among tributaries ($p = 0.028$, $R^2 = 0.65$).

entered into Hardy Creek, the longer it took chum salmon to move from the Ives Island area into Hardy Creek and Hamilton Creek, and the longer the duration of spawning activity in both creeks. In general, this finding is consistent with other studies from mainstem areas showing that flow regulation at dams can influence the timing of migratory and spawning behaviour of adult salmon (Gerlier and Roche, 1998; Linnik *et al*., 1998; Bunt *et al*., 1999; Murchie and Smokorowski, 2004; Geist *et al*., 2008; Thorstad *et al*., 2008; Tiffan *et al*., 2010). To ensure adequate water levels for chum salmon access to primary spawning grounds in mainstem and tributary spawning areas, managers have prescribed a MSTE of 3.5 m at Bonneville Dam (see FPC, 2004; NOAA, 2008). Thus, we anticipated that tailwater elevations 3.5 m or higher would result in chum salmon moving into tributaries more quickly and being observed in tributaries earlier than when tailwater elevations were below 3.5 m. Unexpectedly, we found that tailwater levels of 3.5 m or higher, or more water in the mainstem, was related to delays in chum salmon entering spawning tributaries. Tiffan *et al*. (2010) reported that tailwater levels which exceed 3.5 m may cause chum salmon to move away from established redd sites because of the energetic cost associated with holding behaviour, suggesting that elevated tailwater levels may delay spawning activity. Reports of increased streamflow resulting in fish modifying their behaviour and seeking cover are not uncommon (Salo, 1991; Linnik *et al*., 1998; Bunt *et al*., 1999; Murchie and Smokorowski, 2004). It is conceivable that the relationship we observed between tailwater elevation and the timing of entry in tributaries reflected a general delay in the spawning decisions made by the chum salmon. Alternatively, chum salmon may have been attracted to the increased flows associated with increased tailwater elevations in the mainstem (Arnekleiv and Kraabøl, 1996; Rivinoja *et al*., 2001; Karppinen *et al*., 2002; Scruton *et al*., 2007). Such an attraction could also have delayed their upstream migration into tributaries (Gerlier and Roche, 1998).

Whether maintaining a 3.5 m tailwater elevation below Bonneville Dam is necessary for chum salmon to enter spawning tributaries remains unclear. We did not observe any adult chum salmon in tributaries prior to the MSTE being $\geq$3.5 m for at least 1 h during the spawning season. However, we did observe adult chum salmon in tributaries prior to the first full day (24 consecutive hours) of a 3.5 m MSTE. Although there may be a diel component to their migratory behaviour, chum salmon are active during the day and night (Tiffan *et al*., 2005). Furthermore, Stober *et al*. (1982) found that female fall Chinook salmon on the Skagit River would initiate and eventually complete redds in areas that were covered by water for only a few hours each day, suggesting that relatively brief changes in water elevation may influence spawning behaviour. Thus, short periods of the MSTE being $\geq$3.5 m may be adequate for chum salmon to migrate into tributaries. In contrast, Chapman *et al*. (1986) found no evidence that hourly streamflow fluctuations affected the distribution of fall Chinook salmon redds downstream from the Priest Rapids Dam on the Columbia River. Furthermore, Tiffan *et al*. (2004, 2010) indicated that Columbia River tailwater elevation is more likely to influence chum salmon spawning behaviour if the level is sustained for a prolonged period. This suggests that hourly fluctuations in water elevation may be too short a period to influence significant changes in fish behaviour. The duration of tailwater elevation necessary for adult chum passage into tributaries may ultimately depend on seasonal climate conditions (i.e. precipitation). In general, during years with relatively low seasonal precipitation (2000, 2002, 2004), chum salmon tended to enter Bonneville tributaries after the first 24 consecutive hours of 3.5 m MSTE. In contrast, during years with relatively high seasonal precipitation (2001, 2003, 2005), chum salmon tended to enter tributaries before the first 24 consecutive hours of 3.5 m MSTE. To enter tributaries of the regulated area, adult chum salmon likely benefit from some period of 3.5 m MSTE, perhaps occurring at certain times of the day and dependent on precipitation and streamflow.

The regulation of tailwater elevation does not appear to be associated with the spawning distribution of chum salmon in tributaries below Bonneville Dam. Cumulative hours of MSTE $\geq$ 3.5 m was not related to the proportion of chum salmon that spawned in the tributaries (compared to the mainstem Columbia River) or the variance of the proportion of total chum salmon spawners among tributaries. Although chum salmon generally spawn in tributaries (Johnson *et al*.,

1997), in the Columbia River, most spawning occurs in the mainstem below Bonneville Dam (Tomaro *et al*., 2007). The majority of research on streamflow regulation and fish distribution below a dam, specifically the distribution of spawning salmon, has focused on fish within the regulated river. Several studies have reported streamflow management leading to a significant shift in the spawning distribution of fish below dams. For example, in response to minimized daily flow fluctuations and increased minimum daily flows on the upper Skagit River (Washington), Connor and Pflug (2004) observed a significant shift in the spawner density of pink and chum salmon below the Skagit Hydroelectric Project. Furthermore, on the Feather River in California, Sommer *et al*. (2001) observed a shift in the distribution of Chinook salmon, which they attributed in part to an increase in minimum base flows and larger flow allocation, to a channel downstream from Oroville Dam. Tailwater fluctuations can shift the availability and reduce the amount of suitable spawning habitat within the mainstem channel (Garland *et al*., 2003; Hatten *et al*., 2009) or alter the upwelling cues used by salmon to select spawning sites (Geist *et al*., 2008). For chum salmon in the Ives Island area of the mainstem Columbia River, spawning distribution (Geist *et al*., 2008) can be influenced by tailwater fluctuations. However, once fish begin to construct redds, spawning distribution does not appear to be influenced by tailwater fluctuations (Tiffan *et al*., 2010). While tailwater fluctuations can alter spawning distribution within regulated rivers, similar changes are not well documented in tributaries to regulated areas below dams. We anticipated that regulated streamflows below Bonneville Dam would alter the overall spawning distribution of the population (Johnson *et al*., 1997; Thorstad *et al*., 2008), including in tributaries, but found no evidence to support this hypothesis. This suggests that the influence of Bonneville Dam tailwater elevation may be limited to mainstem and confluence areas. While a 3.5 m MSTE might improve passage conditions at the confluence of tributaries (NOAA, 2008), tailwater elevation may have no significant affect on overall spawning site selection within tributaries. Instead, as long as some habitat suitable for spawning exists, adult chum salmon may exhibit a strong homing fidelity to their natal areas (see Dittman and Quinn, 1996; Shoji *et al*., 2003) in both mainstem and tributary areas.

The variability observed in the spawning distribution of chum salmon could be explained, at least in part, by seasonal precipitation. The proportion of total spawners in the tributaries was unrelated to seasonal precipitation. However, among tributaries, the evenness of spawning distribution was negatively related to the amount of rain during the spawning season. In years when precipitation was relatively high, chum salmon spawning tended to be evenly distributed among the tributary spawning areas. Conversely, in years when precipitation was relatively low, chum salmon spawning tended to be concentrated in Hamilton Creek and limited in Hardy Creek. In general, this finding is largely consistent with other reports that there is yearly variation in where chum salmon spawn in tributaries (Connor and Pflug, 2004), and that stream discharge has a significant influence on the upstream migration of adult salmonids (Banks, 1969; Jonsson, 1991; Thorstad *et al*., 2008). In particular, chum salmon frequently stage at the confluence of smaller natal tributaries for several days before moving upstream in response to environmental cues such as precipitation or an increase in stream discharge (Hunter, 1959; Hale *et al*., 1985; Salo, 1991). Columbia River discharge has been shown to influence the mainstem distribution of chum salmon in the Ives Island area by changing the physical location or quantity of suitable habitat (Garland *et al*., 2003). As such, it is reasonable to speculate that the amount and accessibility of suitable spawning habitat in tributaries may also change as stream discharge levels rise with increased precipitation. Specifically, our data suggests that the quantity of and accessibility to spawning habitat in Hardy Creek increases with precipitation. Although the mechanism for this response is not clear, it is possible that when seasonal precipitation is relatively low, chum salmon may have difficulty gaining access to, moving through or finding suitable spawning habitat in Hardy Creek. Alternatively, when seasonal precipitation is high, adult chum salmon may be particularly attracted to an increase in discharge (see Hawkins, 1989; Tetzlaff *et al*., 2005) from Hardy Creek.

Seasonal precipitation had little influence on the timing of chum salmon entry in tributaries of the regulated area. Although there was a positive relationship with the length of the spawning season in Hamilton Springs and Hardy Creek, no relationship was observed between precipitation and the date when fish were first observed in any of the tributary spawning areas, or the time it took them to get from the Ives Island area to any of the tributary spawning areas. This finding is contrary to the notion that low flows often result in later and less regular entry of adult salmon into spawning tributaries (see Webb and Hawkins, 1989; Tetzlaff *et al*., 2005), and that increased discharge typically stimulates or allows spawners to enter tributaries (Hawkins, 1989). In addition, extremely low flow levels in tributaries can act as a barrier to the upstream migration of salmon (Hale *et al*., 1985; Tetzlaff *et al*., 2005; Thorstad *et al*., 2008). When adult chum salmon begin to arrive below Bonneville Dam in early November, flow conditions within Hamilton and Hardy creeks can be low, or the channels can be dry (FPC, 2001; Tiffan *et al*., 2002, 2004, 2010; Garland *et al*., 2003). It is likely that we did not observe a substantial relationship between precipitation and spawn timing because the influence of tailwater elevation superseded that of precipitation. Alternatively, precipitation and associated

streamflows during our investigation may not have been high or low enough at the time when chum salmon desired to enter tributaries to have a substantial influence on their spawn timing.

Various anthropogenic factors (e.g. hydroelectric dams, irrigation withdrawals, climate change) have fundamentally altered the hydrograph of numerous river systems, including the Columbia River (NRC, 2004; Bottom *et al*., 2005; Hatten and Batt, 2010). To the best of our knowledge, the work presented here is one of the first illustrations that streamflow regulation in a mainstem river, and corresponding tailwater elevations, are related to chum salmon spawning activities in tributaries that enter the regulated area of a mainstem river below a hydroelectric dam. To interpret how this relationship impacts the population, it would be valuable to know the conditions chum salmon encountered prior to when Bonneville Dam was constructed. Unfortunately, we are unaware of any documentation comparing current tailwater elevations below Bonneville Dam to pre-dam river levels or evaluating whether the channel structure has changed since the dam was constructed. While the findings of this study suggest that dam regulation influences chum salmon spawning activity in tributaries, how important this is to the decline of chum salmon in the Columbia River is unclear.

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