SPECIAL ISSUE

CSIRO PUBLISHING

Marine and Freshwater Research, 2018, **69**, 1995–2007
https://doi.org/10.1071/MF18124

Reservoir provides cool-water refuge for adult Chinook salmon in a trap-and-haul reintroduction program

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Abstract. Trap-and-haul is a mitigation strategy at many hydropower dams lacking upstream fish-passage facilities, and protocols are needed to maximise its effectiveness. We used biotelemetry to assess the potential benefits of releasing transported adult Chinook salmon (*Oncorhynchus tshawytscha*) into a cold-water reservoir *v.* a relatively warm-water tributary before spawning. Over 5 years, we released 160 salmon into Foster Reservoir (Oregon, USA) and another 102 into the South Santiam River near historical salmon spawning areas further upstream. In total, 70% of reservoir-released salmon entered an upriver tributary after spending a median of 3–95 days annually in the reservoir. Data recovered from 61 archival temperature loggers indicated that salmon were ~3–6°C cooler per day in the reservoir than in the river. We estimated that cumulative exposure of reservoir-released fish was reduced by 64 degree days, on average (range = −129 to 392), relative to river-released fish. Release into the reservoir was not risk free; 14% of all reservoir-released fish fell back downstream *v.* 1% of river-released fish. We conclude that reduced transport distance, reduced thermal exposure and potential survival benefits of releasing salmon into reservoirs should be weighed against risks of factors such as fallback and homing errors.

Additional keywords: behavioral thermoregulation, biologger, homing, mitigation, native species, philopatry.

Received 24 March 2018, accepted 21 June 2018, published online 25 September 2018

Introduction

Dams have blocked fish from accessing their historical habitats worldwide (Gehrke *et al.* 2002; Agostinho *et al.* 2008; Liermann *et al.* 2012) and are particularly deleterious to migratory species (Gustafson *et al.* 2007; DeHaan and Bernall 2013; Ziv *et al.* 2012). Fish reintroduction above barriers without passage facilities is an increasingly common strategy for restoring or augmenting imperiled populations (George *et al.* 2009; Anderson *et al.* 2014; Lusardi and Moyle 2017). Fish reintroduction requires suitable upstream habitat and, for many diadromous or otherwise migratory species, collection and transport of reproductive-aged adults and, in some cases, emigrating juveniles (Shute *et al.* 2005; Anderson *et al.* 2014). Unfortunately, trap-and-haul strategies also present a variety of risks because collection, transport and release are each potentially stressful events where fish mortality risks are elevated (Lusardi and Moyle 2017). Collection facilities and transport operations often temporarily place fish in artificial, high-density environments where disease transmission increases (Ögut *et al.* 2005; Harmon 2009), and release into post-transport habitats can be physiologically taxing or put fish at increased risk of predation or harvest (Schreck *et al.* 1989; DeWeber *et al.* 2017). Furthermore, natal origin of transported fish may be important to post-release behaviour and metapopulation dynamics if prespawn adults originating below dams are transported above dams, particularly in philopatric species.

In the Willamette River basin (Oregon, USA), high-head hydroelectric dams without fish-passage facilities block access to spawning and rearing habitat of spring-run Chinook salmon (*Oncorhynchus tshawytscha*) in several large tributaries. Willamette River spring Chinook salmon were listed as threatened under the *USA Endangered Species Act* (National Marine Fisheries Service 1999) following large populations declines. Several other endemic fishes, including threatened winter-run steelhead (anadromous rainbow trout, *O. mykiss*), bull trout (*Salvelinus confluentus*) and Pacific lamprey (*Entosphenus tridentatus*), also experienced large declines as a result of habitats being fragmented or blocked by dams (Sheer and Steel 2006; Mesa *et al.* 2010; US Fish & Wildlife Service 2011; National Marine Fisheries Service 2016). Hatchery programs have been a primary mitigation method for maintaining spring Chinook salmon in the upper Willamette River, along with habitat restoration and a significant reduction in salmon harvest. Despite considerable investment in these programs, populations of wild Chinook salmon have continued to decline.

In the mid-1990s, managers of Willamette River fisheries initiated an experimental trap-and-haul program to release Chinook salmon into historical spawning and rearing habitat above dams in the upper basin, so as to increase natural production and expedite recovery efforts (Keefer *et al.* 2010; Sard *et al.* 2015; Evans *et al.* 2016). The program has expanded to several tributaries and now includes winter-run steelhead. Since the start of the Chinook salmon trap-and-haul program, episodically high prespawn mortality of outplanted adults has been observed in some years and locations. Prespawn mortality rates vary widely among years and among sub-basin populations, but have exceeded 90% (Keefer *et al.* 2010; Bowerman *et al.* 2016; DeWeber *et al.* 2017), rates that may significantly reduce the efficacy of the adult trap-and-haul program. The mechanisms that precipitate premature mortality on the spawning grounds are not fully understood, but are likely to include handling and transport effects (Mosser *et al.* 2013; DeWeber *et al.* 2017), infectious disease processes (Benda *et al.* 2015) and energetic exhaustion (e.g. Rand *et al.* 2006). Salmon exposure to warm water temperatures exacerbates many of these processes and has also been linked to increased stress (Jeffries *et al.* 2014), reduced reproductive potential and fitness (McCullough *et al.* 2009) and elevated prespawn mortality (Hinch *et al.* 2012; Bowerman *et al.* 2016). In the Willamette River basin, premature mortality by Chinook salmon has been associated with warm-water exposure along the migration corridor downstream from hydroelectric dams (Keefer *et al.* 2010; Bowerman *et al.* 2018), and near release sites used in the trap-and-haul program (DeWeber *et al.* 2017).

Release of transported adult Chinook salmon into reservoirs rather than directly into spawning tributaries upstream from reservoirs is being considered as a management alternative in the Willamette River basin. Deep, thermally stratified reservoirs offer a potential temperature refuge for adult Chinook salmon during summer and early fall when some spawning tributaries warm to stressful levels (i.e. >18°C; Richter and Kolmes 2005; McCullough *et al.* 2009). The underlying hypothesis is that maturing adult salmon will select and hold in cool water below reservoir thermoclines before movement into spawning tributaries, thereby reducing exposure to stressful river temperatures. Similar thermoregulatory behaviours, where Pacific salmonids select preferred temperatures during prespawn holding or staging, have been widely reported as a strategy to conserve energy, regulate sexual maturation and reduce the effects of thermal stress, parasites and pathogens (e.g. Berman and Quinn 1991; Newell and Quinn 2005; Keefer *et al.* 2009; Mathes *et al.* 2010; Armstrong *et al.* 2016). Release into reservoirs could also reduce trap-and-haul transport distances and times and may increase homing to natal tributaries in locations where multiple spawning tributaries enter a reservoir. Potential risks of release into reservoirs include failure to return to natal sites and possible fallback downstream past a dam (Evans *et al.* 2016; Kock *et al.* 2016).

In the present study, we paired radio-telemetry with salmon-borne archival temperature loggers to test three hypotheses about releasing adult Chinook salmon into a stratified Willamette River basin reservoir. Our hypotheses included the following: (1) all salmon released into the reservoir would eventually enter upstream spawning tributaries; (2) reservoir-released salmon would fall back downstream past the dam at rates similar to salmon released into their presumed natal river; and (3) reservoir-released salmon would have substantially lower cumulative thermal exposure than do river-released fish.

Materials and methods

Study area

The main stem Willamette River is the largest river in Oregon by volume and flows for ~299 km before entering the Columbia River at river kilometre (rkm) 206 from the Pacific Ocean. The Willamette River basin is ~29 730 km^2 and is home to approximately two-thirds of the human population of Oregon (Nilsen *et al.* 2014) with most of development in the valley lowlands. The Willamette Valley Project is a group of 13 dams and reservoirs authorised by the US Congress as part of the *Flood Control Act* of 1936. Project dams currently block access to most major salmon-bearing tributaries in the upper Willamette Valley. The South Santiam River is a tributary to the Santiam River, which is a major Willamette River tributary basin with several dams (Fig. 1). The South Santiam River has a 2694-km^2 watershed, with elevations ranging from 67 m in the Willamette Valley to 1744 m on the western slope of the Cascade Mountains. Foster Dam is a high-head, rock-fill dam (1391 m long and 38 m high) located on the South Santiam River at rkm 418.2. It was constructed in 1968 and is an impassable barrier that blocks adult spring-run Chinook salmon and other species from accessing historical spawning habitat. Foster Dam created Foster Reservoir, which is ~5.6 km long and covers ~500 ha. Foster Reservoir is held at or near full-pool elevation in summer to support recreation and is drawn down for flood control in the winter and spring. The Middle Santiam River enters Foster Reservoir at approximately rkm 426.8 and extends upstream to Green Peter Dam located at rkm 429.2; there is remnant suitable Chinook salmon spawning habitat between the reservoir and Green Peter Dam but the reach is difficult to survey and there is little evidence of recent spawning. The South Santiam River above the reservoir has ~30 km of spawning and rearing habitat and is the basin targeted in the trap-and-haul program.

Adult spring-run Chinook salmon enter the Columbia River estuary in late winter and early spring, ascend the Columbia River and most major tributaries from March to July (Keefer *et al.* 2004*a*), and spawn during August and September (Hoffnagle *et al.* 2008; Bowerman *et al.* 2016). Chinook salmon from the Willamette River basin have a similar phenology and migrate through a corridor that includes dense urban areas and irrigated agricultural lands, before reaching their natal tributaries. Spring Chinook salmon arrive at the Foster Dam fish trap between May and September and adult trap-and-haul operations generally occur once or twice weekly, but vary according to the number of fish trapped. In recent years, only Chinook salmon with intact adipose fins (presumed wild origin) were transported to release sites above the dam, as part of the effort to increase natural production and reduce hatchery influence in the population (Evans *et al.* 2016).

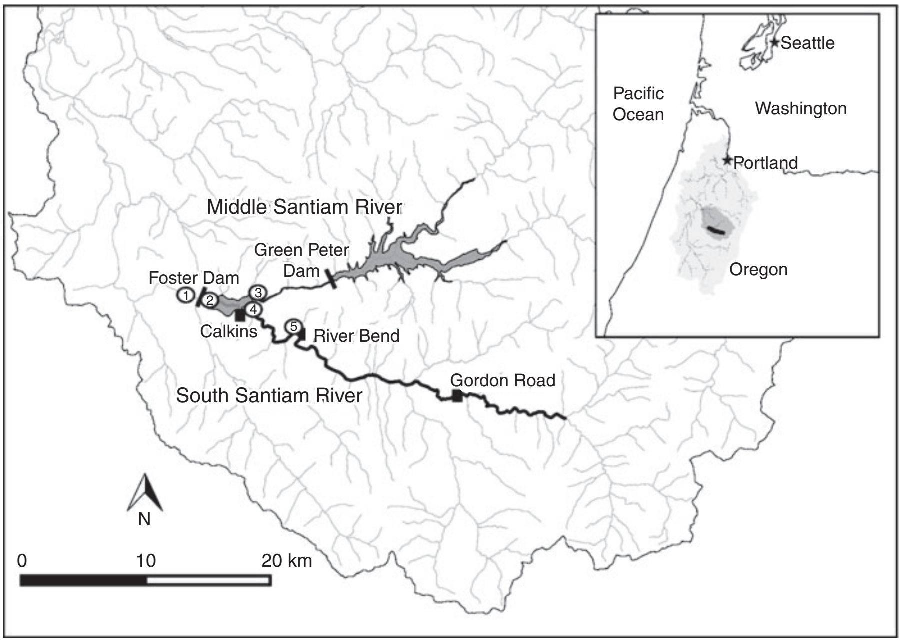

Fig. 1. Map showing Foster Dam on the South Santiam River and Green Peter Dam on the Middle Santiam River. Rectangles indicate sites where tagged Chinook salmon were released in Foster Reservoir (Calkins) and the South Santiam River upstream from the reservoir (River Bend, Gordon Road). Numbered circles indicate telemetry sites: 1, Foster Dam tailrace; 2, dam forebay; 3, Middle Santiam River; 4, South Santiam River; and 5, River Bend. Inset shows the locations of the Willamette River basin (light grey) and Santiam River basin (dark grey) in western Oregon.

Chinook salmon collection and tagging

Adult Chinook salmon were collected and tagged in 2012–2015 and 2017 at the Foster Dam trap (Fig. 1). The trap is operated by the Oregon Department of Fish and Wildlife (ODFW) to collect fish for hatchery broodstock and for an adult trap-and-haul operation. Sampled fish were provided for this study as part of routine trap operations and all trap- and handling-related protocols other than release location were the same for river- and reservoir-release groups. In 2012–2013, the Foster trap consisted of a ladder that led to a large collection area where a mechanical sweep was used to crowd trapped fish. ODFW personnel crowded fish into an anaesthetic tank with CO_2 and then sorted and transferred fish to be radio-tagged to a secondary tank containing tricaine methanesulfonate (MS-222; Argent Chemical Laboratories, Ferndale, WA, USA). A new fish facility was constructed in 2014, which consists of a lower ladder, transport channel, upper ladder and pre-sort pool, where fish were anesthetised using a 15–20 mg L^{-1} solution of AQUI-S 20E (AquaTactics Fish Health, Kirkland, WA, USA) and sorted by ODFW personnel. In 2014–2015 and 2017, fish were transferred to a secondary tank containing a 5 mg L^{-1} concentration of AQUI-S 20E for evaluation and tagging. Only fish with intact adipose fins, indicating likely natural origin, were included in the study.

While anesthetised, fish were measured for fork length (to the nearest 0.5 cm), assigned a sex on the basis of external characteristics, inspected for fin clips or markings, and assessed for condition (see Keefer *et al.* 2017 for details). In 2012–2015, fish were tagged with a passive integrated transponder (PIT, Model HPT12, Biomark, Boise, ID, USA) in the dorsal sinus and gastrically implanted with a 3-V radio-transmitter (Model MCFT2-3A, 46 × 16 mm in diameter, 16 g in air, Lotek Wireless Inc., Newmarket, Ontario, Canada). In 2012–2015, we used iButton submersible temperature loggers (Models DS1922L and DS1921G, 17.35 × 5.89 mm, 3.3 g in air, Embedded Data Systems, LLC, Lawrenceburg, KY, USA) to record internal body temperatures (every 30 min in 2012–2014; every 15 min in 2015) on a subsample of radio-tagged fish in each year. The loggers were waterproofed (Plasti Dip multipurpose rubber coating; Plasti Dip International, Blaine, MN, USA; see Donaldson *et al.* 2009) and attached to the bottom of the radio-tags with electrical tape and then inserted gastrically. In 2017, we used 3-V radio-transmitters that recorded temperature (±0.8°C resolution) and pressure (±1-PSI resolution) every 8 min (Model MCFT3-3A-TP-L, 61 × 16 mm in diameter, 23 g in air, Lotek Wireless Inc.). In all years, a silicone band was placed on each transmitter to reduce regurgitation (Keefer *et al.* 2004*b*).

After tagging, fish were loaded into a transport truck and then released into either Foster Reservoir near the transition area between the reservoir and the South Santiam River (Calkins Park boat launch, rkm 421.7) or directly into the South Santiam River, upstream from the reservoir at River Bend (rkm 428.3) or Gordon Road (rkm 444.7; Fig. 1). Transport times were shorter by ~10–30 min for reservoir-released groups than for river-released groups, but total time from tagging to release was slightly higher for the reservoir-released fish (3 h 0 min, on median) than for river-released fish (2 h 30 min). No mortalities

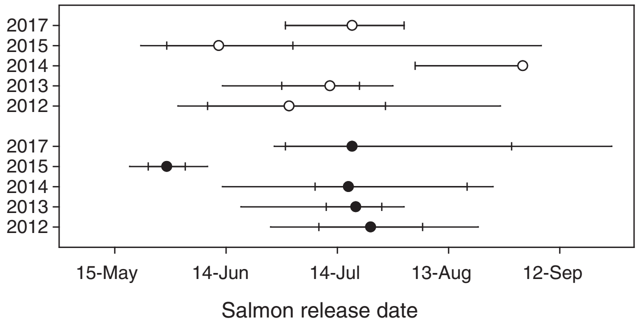

Fig. 2. Tag-date distributions, including median, 10th, 25th, 75th and 90th percentiles for Chinook salmon tagged with temperature loggers and radio-transmitters at Foster Dam and released in the South Santiam River (open circles) and Foster Reservoir (black circles) in 2012–2015 and 2017.

occurred during transport and no moribund fish were observed in any release group. Median tag dates for fish released in the South Santiam River were generally from mid-June to mid-July in all years, except in 2015 when eight river-released salmon were temporarily held at the Foster hatchery facility when managers decided that water temperatures were too high for immediate transport and release (Fig. 2). Tag dates for reservoir-released fish were more protracted owing to logistical constraints within the broader trap-and-haul program; median dates were in mid- to late-July in all years except 2015 (Fig. 2).

After transport to reservoir or river release sites upstream from Foster Dam, salmon were allowed to spawn naturally and spawning areas were monitored to collect carcasses and assess spawning success. Carcass surveys were conducted by personnel from the University of Idaho and ODFW approximately one or two times per week from the first release dates through the spawning period (June through early October). The South Santiam River survey area extended from Menear's Bend (rkm 425.1) to an impassable falls located at rkm 460.5; no surveys were conducted on the Middle Santiam River because of deep water, difficult access and limited suitable spawning sites. The iButton loggers and archival transmitters were recovered during spawning-ground surveys and returned by anglers and others. Recovered female carcasses in good physical condition were assessed for egg retention and prespawn mortality by using established methods (DeWeber *et al.* 2017; Bowerman *et al.* 2018). As is common in carcass-based prespawn mortality studies (e.g. Naughton *et al.* 2018), just a small percentage (<4%) of the total sample released was females recovered in assessable condition, so no formal prespawn mortality analysis was conducted.

Temperature and telemetry monitoring

Water temperature recorders (HOBO V2 Pro Onset, Inc., Bourne, MA, USA) were installed in Foster Reservoir (rkm 422), the Middle Santiam River (rkm 424), and at the following three locations in the South Santiam River: the River Bend release site (rkm 428.3), Cascadia (rkm 437.3) and the Gordon Road release site (rkm 444.7). Depth of temperature loggers ranged from ~0.5 to 1.5 m. Temperatures were logged at 15-min intervals from mid-May to mid-October. The US Army Corps of Engineers (USACE) collected Foster Reservoir water-temperature data at 11 depths (range = 0.2–24.4 m) in the dam forebay.

Fixed-site radio-telemetry antennas and receivers were used to monitor radio-tagged adult salmon in Foster Reservoir, in upstream tributaries, and in the Foster Dam tailrace, and mobile antennas were used during carcass surveys and to help locate transmitters in the South Santiam River. Fixed-site monitoring effort varied slightly among years. In 2012 (the pilot-study year), two telemetry stations were located on the South Santiam and Middle Santiam river banks near where the rivers enter the reservoir (rkm 422.0 and 424.1 respectively). In 2013–2014, additional receivers were used in the South Santiam River at River Bend (rkm 427.6) and downstream from Foster Dam (rkm 416.6). In 2015 and 2017, a fifth telemetry site was added to monitor salmon in the Foster Dam forebay (see Fig. 1 for telemetry locations). A combination of records from fixed-site receivers and mobile-tracking surveys was used to identify movement events, movement direction and final fish fate. We note that the single receivers in the Middle Santiam River (all years) and in the South Santiam River (2012) made it more difficult to confidently infer salmon movement direction, which contributed some uncertainty to fate assignment.

Data analyses

We used the radio-telemetry data to assess when Chinook salmon moved out of Foster Reservoir into tributaries (or *vice versa*), moved between tributaries, and when they passed downstream over Foster Dam (i.e. fallback). We note that it was often impossible to determine whether fish that fell back were alive, moribund or dead and that it is likely that some fish entered tributaries without detection because of receiver outages or transmitter malfunction. Final salmon locations were sometimes ambiguous as a result of the incomplete monitoring effort and uncertainty regarding fish-movement direction. Temperature and depth data from recovered loggers were reviewed for each salmon and were integrated with radio-telemetry detections to help assess movements among habitats. Logger data that appeared to have been collected after fish death were discarded; examples include temperature signals that tracked air temperatures (i.e. when a carcass or transmitter was on a river bank) and unvarying depth data (i.e. fish carcass or transmitter at the bottom of a pool). Reservoir-released fish were considered to have entered the South or Middle Santiam rivers when their final detections were at tributary receiver sites, when they were detected further upstream using mobile receivers, and when transmitters were recovered in the rivers.

We used the temperature-logger data to assess the potential thermal benefit of fish release into the reservoir in two ways. First, we calculated mean daily temperatures for each salmon on the basis of their presumed location in the reservoir, the South Santiam River, or the Middle Santiam River. We then calculated the mean daily difference in body temperatures for salmon in the South Santiam River *v.* those in the reservoir or the Middle Santiam River, which many fish used before entering the South Santiam River. We restricted the comparison to only those fish that were last recorded in the South Santiam River (the majority of the salmon; see Results). In a second evaluation, we calculated cumulative temperature exposure for each fish in degree-days (DD), defined as the cumulative average daily temperature exposure above 0°C. The DD metric has been correlated with a

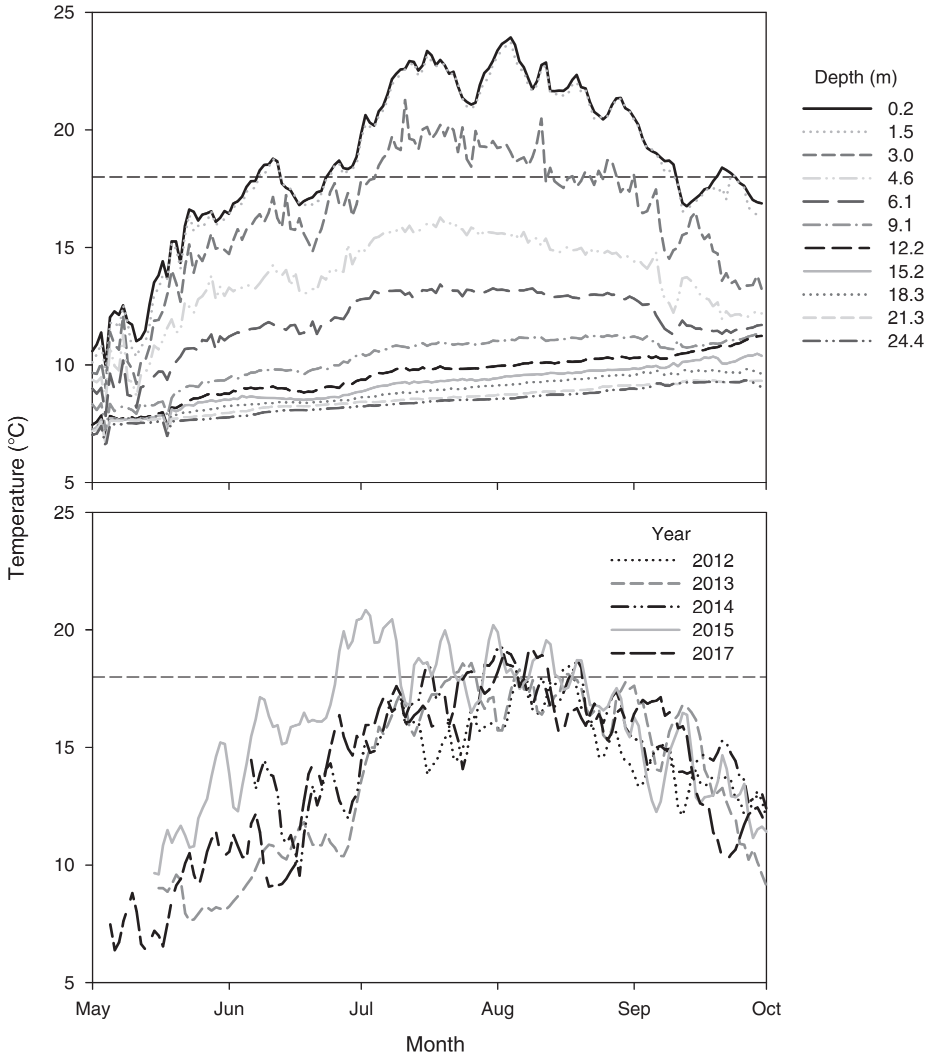

Fig. 3. Foster Reservoir mean daily water temperatures collected at 11 depths between 1 May and 30 September 2014 (top panel; US Army Corps of Engineers). Daily mean water temperatures in 2012–2015 and 2017 collected in South Santiam River at the Gordon Road release site (bottom panel). Dashed line at 18°C represents temperature considered to be physiologically stressful for adult Chinook salmon.

variety of physiological processes, and has been used in many adult-salmonid studies (e.g. Wagner *et al.* 2005; Mathes *et al.* 2010; Keefer *et al.* 2015). For the reservoir-released individuals, we estimated what their cumulative DD would have been had they instead been released into the South Santiam River, by using the daily mean of all fish in the river on each date of the thermal history of the reservoir-released fish. The thermal 'benefit' was calculated as the difference between the observed DD and estimated DD for each fish.

We used Pearson's Chi-Square tests to compare the proportions of salmon that fell back at Foster Dam after release into the South Santiam *v.* into Foster reservoir. Linear regression was used to assess how DD accumulations were related to salmon release date and to the total number of days at large for each salmon. All statistical analyses were conducted using SAS (ver. 9.2, SAS Institute, Cary, NC, USA).

Results

Environmental temperatures

Mean daily water temperatures collected by the USACE at 11 depths in Foster Reservoir typically ranged from ~19 to 21°C at 0.2 m below the surface and from ~8 to 10°C at 24 m. Annual near-surface maxima ranged from 23.5 to 24.8°C and typically occurred from early July to mid-August (Fig. 3). The reservoir thermocline was at ~6–9 m and temperatures below 9 m generally remained ≤15°C in all years. Water temperatures in the South Santiam River upstream from the reservoir at the Gordon Road release site warmed seasonally from ~7–12°C in early June to ~18–20°C in mid-summer and then cooled through September and October. Patterns were similar at the River Bend monitoring site. Annual daily maxima ranged from 18.5°C in 2012 (17 August) to 20.8°C in 2015 (2 July; Fig. 3). Diel

Table 1. Chinook salmon tagging, final distribution, and logger recovery summary

Annual numbers of Chinook salmon tagged with radio-transmitters and temperature loggers, the numbers and percentages last detected in the reservoir, in upstream tributaries, or in the Foster Dam tailrace, and the numbers of loggers recovered with usable temperature data (and depth data in 2017). The river-release group was released near Gordon Road ($n = 61$) or River Bend ($n = 41$)

Year	Release site	n	Final detection, n (%)				Number of loggers recovered
			Reservoir	South Santiam	Middle Santiam	Tailrace	
2012	River	41	2 (5)	37 (90)	1 (2)	1 (2)	6
	Reservoir	33	14 (42)	11 (33)	6 (18)	2 (6)	2
2013	River	25		25 (100)			6
	Reservoir	50	7 (14)	30 (60)	7 (14)	6 (12)	3
2014	River	8		8 (100)			5
	Reservoir	44	3 (7)	19 (43)	12 (27)	10 (23)	15
2015	River	23		23 (100)			14
	Reservoir	14	1 (7)	6 (43)	5 (36)	2 (14)	4
2017	River	5		5 (100)			4
	Reservoir	19	1 (5)	15 (79)	1 (5)	2 (11)	9
Total	River	102	2 (2)	98 (96)	1 (1)	1 (1)	35
	Reservoir	160	26 (16)	81 (51)	31 (19)	22 (14)	33

variation in temperature was greater in the South Santiam River than in the reservoir hypolimnion.

Chinook salmon sample summary

In total, 262 adult Chinook salmon were tagged with radio-transmitters and temperature loggers over the 5 study years; 160 were released in Foster Reservoir and 102 were released in the South Santiam River above the reservoir (Table 1). We recovered 33 (21%) radio-archival tag pairs from reservoir-released fish and 35 (34%) from fish released into the South Santiam River. Logger data from seven reservoir-released salmon were excluded from temperature analyses because salmon were last recorded in the Middle Santiam River ($n = 1$) or downstream from Foster Dam ($n = 6$). Across years, we recovered four river-released and five reservoir-released females whose carcasses were in good enough condition to assess egg retention. Pre-spawn mortality estimates for the two groups were 75 and 80% respectively.

Hypothesis 1: reservoir-released salmon will enter tributaries

Reservoir-released salmon entered tributaries, although proportionately fewer reservoir-released salmon than river-released salmon were last detected in tributaries. Of the 160 radio-tagged salmon released in Foster reservoir over 5 years, 70% were last detected in an upstream tributary *v.* 97% of the 102 salmon released directly into the South Santiam River (Table 1). Across years, 51% of reservoir-released fish were last detected in the South Santiam River (33–79% per year) and 19% were last detected in the Middle Santiam River (5–36% per year). Salmon that did not enter tributaries were last detected in the reservoir (5–42% per year) or downstream from Foster Dam (6–23% per year). Many salmon were recorded moving between the South and Middle arms of the reservoir, before eventually entering and apparently remaining in a tributary.

The time that reservoir-released salmon spent in the reservoir was highly variable within and among years (Fig. 4). With all years combined, salmon spent median times of 13.2 days (range = 0–131 days, $n = 78$) before entering the South Santiam River and 14.8 days (range = 4–114 days, $n = 30$) before entering the Middle Santiam River. With fish from the two tributaries combined within year, median reservoir residence times were 6.5 days (2012), 35.4 days (2013), 10.9 days (2014), 92.5 days (2015) and 7.7 days (2017). The very long residence times in 2015 were due, at least in part, to earlier arrival and release timing in that year (see Fig. 2). More generally, salmon released early in the season in all years were more likely to have longer reservoir-residence times than those released in August and September (Fig. 4).

Hypothesis 2: fallback rate between release groups

Reservoir-released salmon fell back past Foster Dam at a higher rate than did river-released salmon. Across years, 13.8% of 160 reservoir-released salmon fell back at Foster Dam *v.* 1.0% of 102 river-released fish (Pearson's $\chi^2 = 12.7$, $P = 0.0004$). Annual fallback estimates for the reservoir group ranged from 6.1% in 2012 to 22.7% in 2014. Sample size limited statistical power in individual years (annual: $0.6 \leq \chi^2 \leq 3.5$, $0.062 \leq P \leq 0.449$).

Hypothesis 3: thermal exposure between release groups

In total, 61 salmon with archival data were last detected in the South Santiam River and had thermal histories that averaged 53.9 days (range = 7–116 days). Body temperatures of salmon released into the South Santiam River generally tracked ambient river temperatures, with clear diel fluctuations and additional variation related to the river segment that the fish occupied (i.e. upstream reaches and reaches with tributaries tended to be slightly cooler than reaches closer to the reservoir). Thermal histories of reservoir-released salmon showed considerable among-individual variation in behaviour. Some fish quickly entered tributaries, some moved among several thermal layers in the reservoir, and others moved between the South and Middle Santiam branches of the reservoir (Fig. 5). The pressure-sensor loggers used in 2017 helped confirm that salmon had frequent

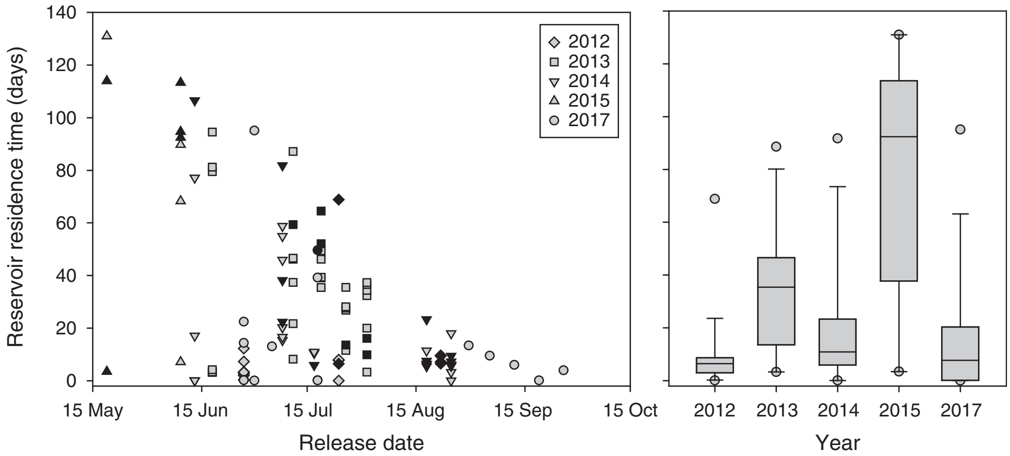

Fig. 4. Relationship between Chinook salmon release date and the time (days) that fish spent in the reservoir before entering either the South Santiam River (grey symbols) or Middle Santiam River (black symbols) in 2012–2017 (left panel). Box plots (5th, 10th, 25th, 50th, 75th, 90th, 95th percentiles) show annual reservoir residence times for salmon from both tributaries (right panel).

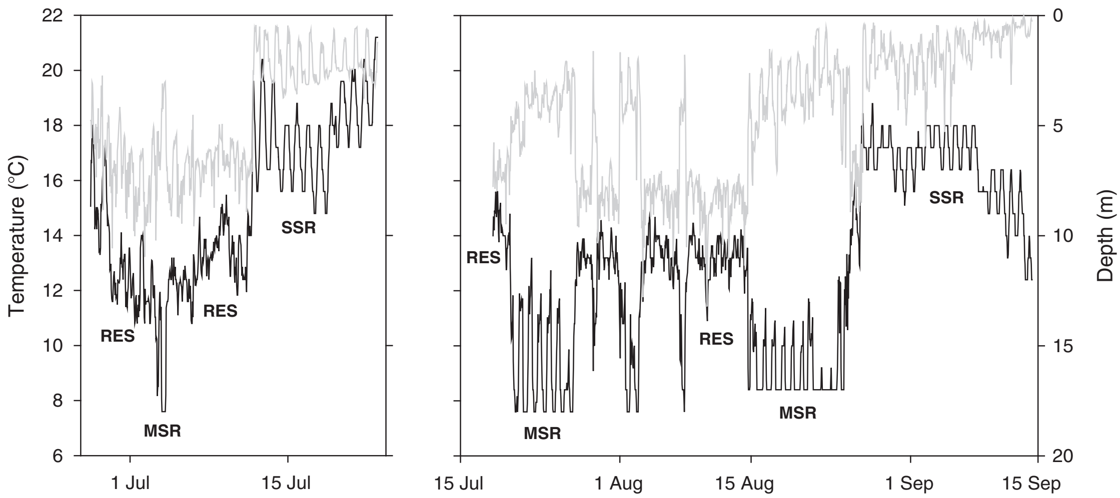

Fig. 5. Mean hourly temperature (°C, black lines) and depth (m, grey lines) profiles of two logger-tagged Chinook salmon that were released in the Foster Reservoir and eventually entered the South Santiam River upstream from the reservoir in 2017. Labels indicate blocks of time when salmon were likely to be in the reservoir (RES), Middle Santiam River (MSR) or South Santiam River (SSR), on the basis of thermal profiles and telemetry detections.

vertical movements in the reservoir and also appeared to routinely move from shallow runs and riffles in the South Santiam River into deeper pools (Fig. 5).

Chinook salmon were generally ~3–6°C cooler in the reservoir than in the South Santiam River on most days from late May through early September (Fig. 6). Exceptions occurred when individuals were in near-surface reservoir water (see 2012 panel in Fig. 6) and when fish were temporarily within the influence of the much colder Middle Santiam River (Fig. 5, 6).

Cumulative thermal exposure was strongly, positively correlated with days at large and negatively correlated with fish release date for both release groups, as expected (Fig. 7). In linear regressions, release date explained 53–54% of the DD variation for the two release groups and days at large explained 97–98% of the variation. Slopes of the regression lines for days at large indicated that reservoir-released fish accumulated lower DD totals than did river-released fish across the range of observed values. Across years, the 26 reservoir-released salmon with recovered loggers that eventually entered the South Santiam River were at large for 63 days, on average, and accumulated from 167 to 1913 DD (mean = 931 DD, s.d. = 544 DD). The 35 river-released fish were at large for 47 days, on average, and accumulated from 115–1585 DD (mean = 765 DD, s.d. = 488 DD).

In the thermal-benefit analysis for the 26 reservoir-released salmon that entered the South Santiam River, 19 fish (73%) accumulated fewer DD than we estimated they would have accumulated had they been released directly into the South Santiam River (Fig. 7). Individual benefits tended to be highest

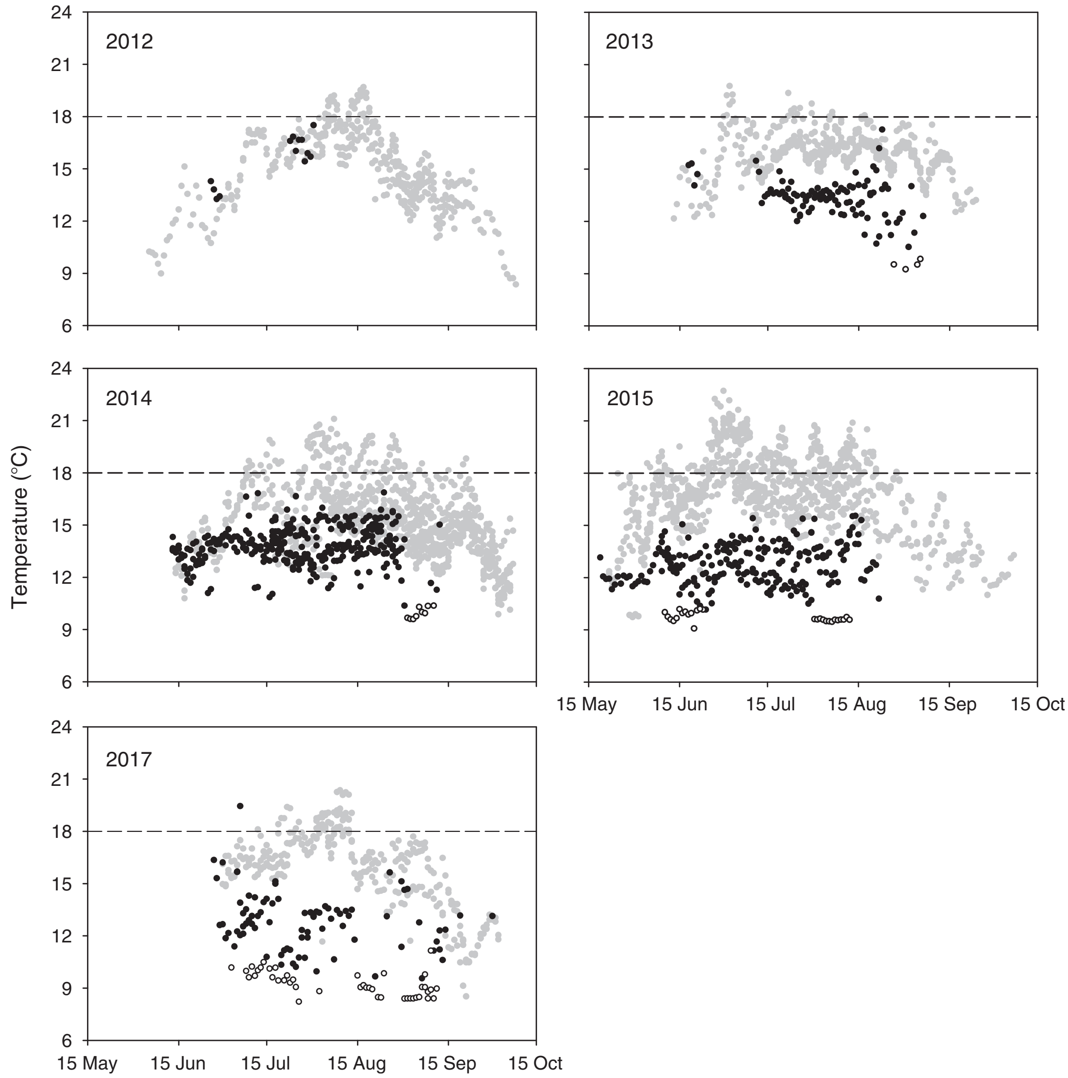

Fig. 6. Mean daily body temperatures of logger-tagged Chinook salmon recorded while they were in Foster Reservoir (black circles), the South Santiam River upstream from the reservoir (grey circles) or the Middle Santiam River (white circles). All reservoir-released salmon depicted here eventually entered the South Santiam River. Annual sample sizes in Table 1.

for fish released early in the season, with a general decline as the release date increased. No clear pattern was evident in the relationship between time at large and individual benefits. The difference between observed and estimated DD accumulations for the 19 fish with a thermal benefit ranged from 11 to 392 DD (mean = 107 DD, s.d. = 98 DD). Differences for the seven fish with a thermal deficit ranged from −109 DD to −3 DD (mean = −54 DD, s.d. = 47 DD); differences for all 26 salmon averaged 64 DD (s.d. = 113).

Discussion

The present study provided important data regarding a strategy to improve the success of a Chinook salmon trap-and-haul reintroduction program. The combination of radio-telemetry and salmon-borne biologgers led us to affirm two of our three hypotheses. First, adult salmon released into a deep reservoir downstream from historical spawning sites entered upstream tributaries before or during the typical spawning period for the population; second, reservoir-released salmon exhibited extended thermoregulatory behaviours by selecting water considerably cooler than the water available near the reservoir surface or in upstream spawning reaches. Release into the reservoir also may have increased the rate of fallback because only one river-released salmon fell back past the barrier dam during the five study years, but some reservoir-released salmon fell back each year. That Chinook salmon extensively used the thermal refuge provided by the reservoir suggests that direct release into the reservoir may be a viable strategy to directly reduce thermal exposure and indirectly reduce the incidence of prespawn mortality, a serious potential constraint on re-establishment of the study population. We anticipate that releasing adult salmon into reservoirs may be effective in many similar dammed river systems where warm water temperatures are a challenge for salmon conservation.

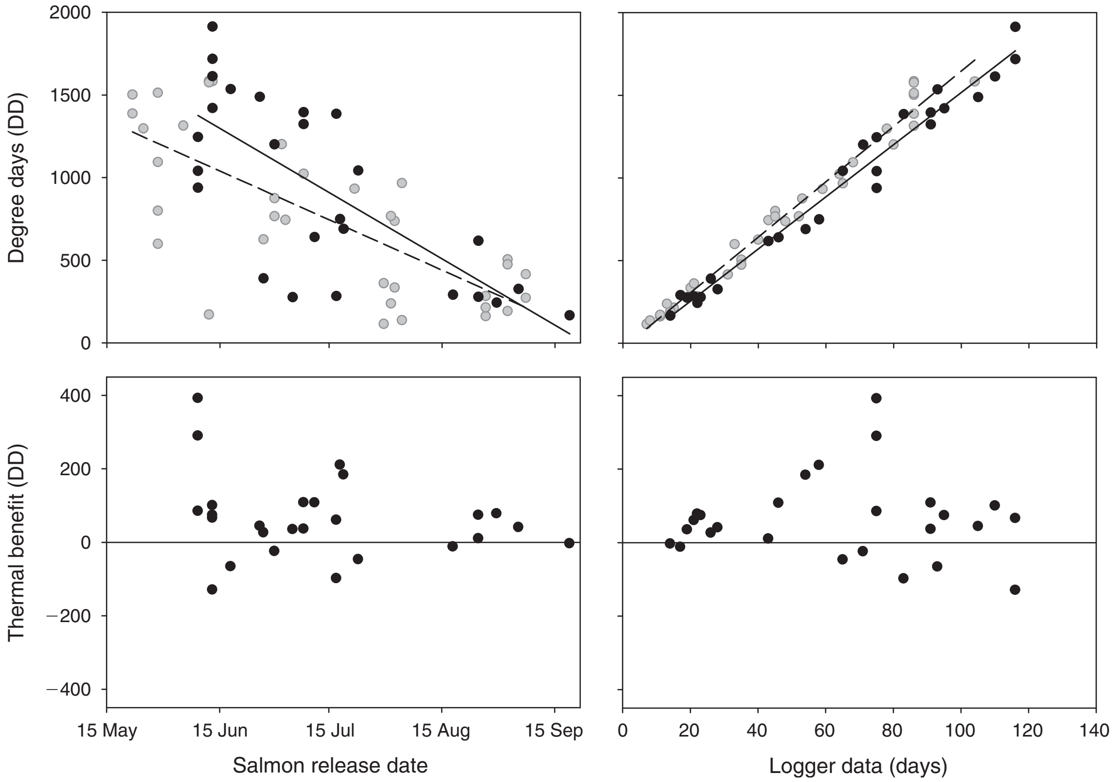

Fig. 7. Degree-day (DD) accumulations by logger-tagged Chinook salmon released in the South Santiam River (grey circles) or Foster Reservoir (black circles) in relation to release date (top left) and the number of days loggers collected salmon body-temperature data (top right), 2012–2017. Regression lines in the top panels are dashed for river-released fish and solid for reservoir-released fish. Bottom panels show the total estimated thermal benefit (positive values) or cost (negative values) for salmon released into the reservoir relative to mean thermal load of salmon in the tributary, expressed in DD. Only salmon that eventually entered the South Santiam River were included.

Tributary entry

A substantial majority (70%) of reservoir-released Chinook salmon eventually entered either the South or Middle Santiam River upstream from the reservoir. The 70% estimate is a minimum measure of escapement to tributaries given the limited monitoring effort (i.e. a single antenna per tributary in some years). We were particularly likely to underestimate tributary entry in 2012, a pilot study year when only ~51% of the 33 reservoir-released salmon were detected upstream. Across years, ~16% of reservoir-released fish were last detected in the reservoir; the fate of these salmon was unknown, but may have included premature mortality, unreported fisheries harvest, undetected tributary entry, or undetected downstream fallback. This level of uncertainty regarding final fates is fairly typical for radio-telemetry studies of adult salmon because carcasses are infrequently recovered and monitoring gaps occur for a variety of reasons (Keefer *et al.* 2005; Patterson *et al.* 2007; Naughton *et al.* 2018). Unaccounted-for fish are particularly likely when tagged samples are at large for weeks to months and when the study area is large, as was the case in the present study.

Importantly, last detection in a tributary should not be considered equivalent to successful spawning. Although 70% of reservoir-released fish were last detected in tributaries *v.* 97% of river-released fish, the overall spawning success of both groups was unknown. Recent estimates of prespawn mortality for Chinook salmon released directly into the South Santiam River above the reservoir averaged 28% over 5 years, and was especially high (74%) in 2013 (DeWeber *et al.* 2017). An effective assessment of whether release into the reservoir affected spawning success would require recovery of far more female carcasses from both river- and reservoir-release groups than was possible here, preferably in a paired-release study design. If more tagged carcasses could be collected, one could also directly test whether thermal-exposure histories differed among successful *v.* unsuccessful spawners.

More Chinook salmon were last detected in the Middle Santiam River than we expected, and this is an area of uncertainty. The short reach between the reservoir and Green Peter Dam is difficult to access and so we did not attempt carcass or mobile telemetry surveys there and do not know whether any salmon last detected at the Middle Santiam receiver spawned in the river. Potential fates for this group include: (1) successful spawning; (2) natural mortality in the river or reservoir; (3) illegal harvest in the large recreational fishery that occurs in the lower Middle Santiam River and reservoir; (4) undetected fallback at Foster Dam; or (5) undetected entry into the South Santiam River. Non-detection is a possibility, given potential transmitter loss during the weeks to months between reservoir release and the onset of spawning. Regardless, if the group last detected in the Middle Santiam River was mostly unsuccessful, then the overall efficacy of releasing adults into the reservoir would be substantially reduced. Future studies should attempt to resolve this uncertainty.

Downstream fallback

A concern regarding in-reservoir releases is that some fish may fall back past the dam after release. Fallback by reservoir-released salmon was recorded in all years and ranged from 6 to 23%. Our results are similar to those of Kock *et al.* (2016) who found that 19% of adult Chinook salmon released in the reservoir upstream from Cowlitz Falls Dam (Washington, USA) fell back, *v.* 15% of those released in the Cowlitz River above the reservoir. Fallback percentages in our study were also comparable to those reported for Chinook salmon at dams with adult fishways. For example, Boggs *et al.* (2004) found that fallback percentages for spring-run Chinook salmon at four Columbia River (Oregon–Washington, USA) dams ranged from 1 to 15% annually. However, the negative consequences of falling back at dams such as Foster Dam or Cowlitz Falls Dam is potentially higher because fish cannot re-ascend via fishways and fallback routes are often limited to high-head spillways or powerhouses.

It is unclear why Chinook salmon in our study fell back at Foster Dam, but one hypothesis is that their natal site was downstream from the dam and fallback was related to homing or orientation. In a genetic parentage study, Evans *et al.* (2016) found that up to 35% of Chinook salmon adults in the South Santiam River trap-and-haul program were not produced upstream from Foster Dam. Reservoir-released fish that originated downstream may actively search for natal sites, which is common near spawning areas (Dittman *et al.* 2010). Lacking familiar olfactory cues, some may eventually find downstream routes at dams and fall back, a behaviour that is sometimes referred to as 'overshoot' fallback in regulated rivers (Keefer *et al.* 2008). Distinguishing between volitional fallback by adults attempting to return to downstream natal sites *v.* incidental fallback by entrainment is an important information gap in the South Santiam River trap-and-haul program. Insomuch as possible, a cost–benefit analysis of salmon release into the reservoir should consider volitional fallback by downstream-origin fish differently from entrained fallback by upstream-origin fish. For example, management agencies in the Willamette River Basin are moving towards treating some areas above dams as 'wild-fish sanctuaries' in an effort to minimise hatchery–wild fish interactions and maximise the potential for local adaptation to habitats upstream from dams (US Army Corps of Engineers 2007). Thus, fallback fish could be an undesirable loss of transported fish from the translocated population or may be net beneficial if those salmon had originated from downstream populations and strayed into the transport trap. Volitional fallback may effectively reduce introduction of non-natal spawners, including unrecognised hatchery-origin or hatchery-wild hybrids.

Thermal benefits of fish release into the reservoir

The Chinook salmon thermal histories we collected clearly indicated that Foster Reservoir provided a thermal refuge from exposure to potentially acutely stressful temperatures in the South Santiam River during the critical period preceding spawning. Salmon released in the reservoir rarely experienced temperatures >18°C while in the reservoir, and those that surpassed this threshold appeared to only briefly enter near-surface reservoir waters. In contrast, some river-released individuals had maxima of >19–20°C in the river in all years and several had body temperatures of >22°C in 2015 when South Santiam River temperatures approached record high levels. Temperatures greater than ~18°C are generally considered stressful for adult Chinook salmon (Coutant 1977; McCullough *et al.* 2001; Richter and Kolmes 2005), so release into the reservoir provided individual salmon refuge from stressfully high temperatures for days to weeks within each year.

The cumulative thermal benefit of time spent in the reservoir was substantial for some salmon. Median reservoir residence time was ~2 weeks over the full study, but many individuals remained in the reservoir for many weeks and even months before moving upstream for presumed spawning in late summer and fall. The recovered temperature loggers indicated that reservoir-released salmon were exposed to ~3–6 fewer DD per day than fish released in the river, which translated to a DD benefit averaging 64 DD and ranging as high as 392 DD; this translated to a ~12% reduction in total thermal accumulation, on average. On the basis of the median reservoir residence times of all radio-tagged salmon that entered tributaries (~14 days), we further estimated that fish were likely to accrue benefits ranging from 42 to 84 DD on the basis of daily benefits of 3–6°C. Salmon with longer reservoir residencies (i.e. 30–60 days) may have accrued benefits of 90–360 DD. We expect that the thermal benefits of release into the reservoir were highest in 2015, when South Santiam River temperatures were exceptionally warm, migration timing was early, and prespawn holding durations were longer than average.

There is considerable empirical support for the relationship between the cumulative temperature exposure of salmonids and increased risk of lethal and sublethal effects from bacterial and fungal infections and pathogens (e.g. Kocan *et al.* 2004; Bradford *et al.* 2010; Kent *et al.* 2013). Although DD thresholds are somewhat arbitrary, exposures as low as 500 DD have been predictive of disease expression and prespawn mortality in some populations (Wagner *et al.* 2005; Mathes *et al.* 2010). Previous research showed that South Santiam River Chinook salmon accumulate several hundred to >1000 DD during their migration through the Willamette and South Santiam rivers and many encounter temperatures >18°C before reaching Foster Dam (Keefer *et al.* 2015). Similarly high acute and cumulative exposure occurs for Chinook salmon returning to other Willamette River tributaries (Keefer *et al.* 2015); pathogen loads in these populations can be very high (Benda *et al.* 2015), and prespawn mortality rates have been among the highest recorded for the species (Keefer *et al.* 2010; Bowerman *et al.* 2016, 2018; DeWeber *et al.* 2017). The very high cumulative temperature exposure before trap-and-haul suggests to us that better management strategies to minimise exposure after release are needed.

Release into reservoirs allows transported fish the opportunity to find and use cool- and cold-water sources, thereby taking advantage of a highly adaptive thermoregulatory behaviour.

In our study, Foster Reservoir and the Middle Santiam River provided large and stable thermal refuges for South Santiam River Chinook salmon. These cool and cold sites provide a clear opportunity for managers of the South Santiam River trap-and-haul program to reduce temperature exposure during the final stages of migration. Notably, the wider scope for behavioural thermoregulation in the reservoir, (i.e. greater opportunity for salmon to select preferred temperatures) may have provided benefits beyond the absolute reduction in thermal accumulation. Parallel opportunities exist in other deep-water reservoirs in the Willamette River basin and in many salmonid-bearing river systems of the western United States and Canada. Nonetheless, we recommend monitoring for trade-offs between benefits and potential costs to releasing fish in reservoirs, including hypolimnetic dissolved-oxygen concentration in mesotrophic and eutrophic systems, relative fishing pressure between tributary and reservoir habitats, and potential for fallback before implementation of a release program. The tactic may also be viable for other temperature-sensitive migratory species in fragmented river systems worldwide.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Acknowledgements

Many people assisted with work on this study and its successful completion was made possible through their efforts. This project was funded by the US Army Corps of Engineers (USACE). We thank: Michael Jepson, Mark Morasch, Charles Erdman, Jeff Garnett, Eric Johnson, Grant Brink, Eric Powell, Dan Joosten, Karen Johnson, Mike Turner, Ryan Mann and Chuck Boggs (University of Idaho) for assisting with field work and data collection; David Griffith, Rich Piaskowski, Fenton Khan and Robert Wertheimer (USACE Portland District); special thanks go to Brett Boyd (ODFW) for logistical support at Foster Hatchery and transporting fish to release sites; Mike Sinnott, Justin Huff, Dan Coffman, Naomi Halpern, Reed Fischer and Bob Mapes (ODFW), for assistance with spawning ground surveys, tagging and data collection. Permitting and animal care procedures were facilitated by Joy Vaughn, Michele Weaver, Shivonne Nesbit, Holly Huchko (ODFW), Stephanie Burchfield, Kim Hatfield, Diana Dishman (NOAA-Fisheries), Bonnie Johnson (US Fish & Wildlife Service), and the UI Animal Care and Use Committee. This study was conducted under Cooperative Ecosystems Study Unit (CESU) agreement CESU W912HZ-12-2-0004 funded by the USACE, Portland District.

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