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Using an integrative research approach to improve fish migrations in regulated rivers: a case study on Pacific Salmon in the Seton River, Canada

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Abstract Many of the world's rivers are dammed, altering the physiology, behaviour, ecology and survival of fish. Integrative research has the potential to improve our understanding of these impacts and could enable environmental managers to develop effective solutions for population conservation. Such approaches, however, are not yet prevalent. We use a case study on Pacific salmon (*Oncorhynchus* spp.) in British Columbia, Canada, to demonstrate how regulated rivers may be used as experimental systems, allowing for applied research that can advance our understanding of the biology of migratory fish as well as our ability to manage them. Through the integration of multiple research approaches (i.e. biotelemetry, behavioural tests, physiological and molecular analyses, and hydraulic monitoring), we characterized the effects of natal water dilution and dam flow releases on upstream navigation, passage success and post-passage survival of returning adult salmon. Our findings confirmed previously established operational guidelines for natal water dilution and informed the adoption of new operational conditions for dam flow releases, providing an example of the successful application of

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integrative research to the management of a fisheries resource in a regulated river. We encourage researchers to consider using an experimental approach that integrates multiple research disciplines to inform science-based management action.

Keywords Fish passage · Fishway · Regulated rivers · Migratory fish · Freshwater conservation · Integrated approach

Introduction

The number of dams on the world's largest rivers is continuing to rise (Zarfl et al., 2015), and the majority of large rivers are no longer free-flowing (Grill et al., 2019). This phenomenon is truly global—dams can be found on every continent aside from Antarctica and are proliferating in many of the world's most biodiverse basins, such as the Amazon, Congo and Mekong (Winemiller et al., 2016). Flow modification can have a significant impact on geomorphology (Petts and Gurnell 2005), species abundance and diversity (Bain et al., 1988; Bunn & Arthington 2002; Poff & Zimmerman 2010) and the behaviour and physiology of aquatic organisms (Dewson et al., 2007; Murchie et al., 2008; Pavlov et al., 2008). As a consequence, flow modification has been identified as a major threat to freshwater biodiversity (Dudgeon et al., 2006; Arthington et al., 2010; Reid et al., 2019) and is likely a significant contributor to the accelerated global extinction rates of freshwater fauna over the past century (Ricciardi & Rasmussen, 1999; Strayer & Dudgeon, 2010).

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The variety and complexity of ecological responses to dams make management-relevant research in regulated rivers especially challenging (Power et al., 1996). The effects of dam infrastructure and operation on river ecosystems can be wide-ranging and are influenced by the geomorphology, environmental conditions and biotic assemblages that are unique to each system. Researchers and natural resource managers have repeatedly called upon a more integrated approach to address the complex issues facing sustainable freshwater management (Brett, 1957; Naiman et al., 1995; Alcamo et al., 2008), but this approach is often not put into practice. Traditional approaches that attempt to compartmentalize problems are outmoded as they fail to yield the level of nuanced and integrated understanding that is needed to truly solve complex problems (Dick et al., 2016). Murchie et al. (2008) conducted a comprehensive review of articles studying the effects of river regulation on fish, and while the authors found consensus that flow modification does indeed influence fish and fish habitat, they also identified persistent limitations to methodological approaches that restricted the conclusions being drawn. In particular, the authors highlighted a lack of integrative approaches in fisheries management research (but see Patterson et al., 2016). Connecting research from different natural science disciplines (for example, linking behavioural responses that are mediated by complex flow dynamics to physiology or molecular biology) would allow researchers to not only observe trends but also identify the mechanisms driving the trends. Such an approach was encouraged over 60 years ago, when Brett (1957) asserted that the challenges dams pose to fish migrations could only be addressed through integrated research.

Here, we review a large-scale, multi-year study that aimed to assess the effects of dam operations on Pacific salmon (*Oncorhynchus* spp.) in the Seton River—a tributary of Canada's Fraser River—and to identify and evaluate operational strategies that would mitigate these effects. Previous research in this river indicated potential negative effects of the dam on the return migration of adult salmon (Andrew & Geen, 1958; Fretwell, 1989). Through the involvement of ecologists, physiologists, hydraulic engineers, natural resource managers and fisheries practitioners from academia, industry, government and First Nations, we examined the molecular, behavioural, physiological, and population-level responses of migrating adult sockeye salmon (*Oncorhynchus nerka*, Walbaum, 1792) to dam operations. Our methods included laboratory analyses, controlled behavioural tests and large-scale management experiments involving the manipulation of dam flow releases. We applied innovative technologies to these procedures and in some instances our applications were novel to the field of fisheries science. Our research builds on Brett's (1957) assertion and demonstrates that integrating research approaches from several disciplinary perspectives can lead to management actions that are informed by rigorous science. In addition, our work underscores a potential benefit of research in regulated rivers: that the ease in which wild fish may be captured from (and studied in) fishways, in conjunction with the ability to directly manipulate flow, enables researchers to address fundamental scientific questions. We review our approach and findings and lay out the key lessons learned about integrative research in regulated rivers.

Pacific Salmon in the Fraser River's Seton-Anderson Watershed, British Columbia, Canada

The Fraser River is Canada's most productive salmon-bearing river system, and the fourth largest river in the country, with a drainage area of 240,000 km^2. Covering much of the southern half of British Columbia, the Fraser River receives annual returns reaching tens of millions of adult Pacific salmon migrating to natal spawning grounds (PSC, 2018). Populations that migrate through the Seton River, a tributary of the Fraser River, are some of the few in the watershed that must pass through a dam (BC Hydro's Seton Dam). These include two populations of sockeye salmon, as well as pink salmon (*Oncorhynchus gorbuscha*, Walbaum, 1792), Chinook salmon (*Oncorhynchus tshawytscha*, Walbaum, 1792), coho salmon (*Oncorhynchus keta*, Walbaum, 1972), and steelhead (*Oncorhynchus mykiss*, Walbaum, 1792).

Water in this region flows from the Gates Creek headwaters and through Anderson and Seton Lake before flowing into the Seton River through Seton Dam (Fig. 1). Hydroelectric development in the mid-20th century resulted in several significant changes to the system. BC Hydro constructed a tunnel to allow water to flow into Seton Lake from Carpenter Reservoir (of the adjacent Bridge River watershed) and the 18-m tall Seton Dam was built to divert water exiting Seton Lake to a power canal, which leads to a generating station on the bank of the Fraser River. After travelling through the Seton River, returning salmon must pass a vertical slot fishway at Seton Dam to enter Seton Lake and continue migrating to spawning grounds at Gates Creek.

In addition to the challenge of dam passage, adult salmon migrating through this system encounter confusing directional cues as a consequence of hydroelectric development (Andrew & Geen, 1958). Water released through the generating station, which is impassable to fish, enters the mainstem Fraser River 1 km downstream of the Seton-Fraser confluence (Fig. 2). Pacific salmon are guided to spawning grounds primarily by the odour of their natal streams and lakes (Hasler & Scholz, 1983; Bett & Hinch, 2016), and these attractive odours are present in the water passing through the generating station. Salmon migrating up the Fraser River that are bound for the Seton system therefore encounter their natal water in two places: first, at the tailrace of the generating station, and second, at the mouth of the Seton River. This issue is compounded by the fact that the concentration of natal water is higher in the generating station tailrace than at the Seton River mouth. This is due to the fact that Cayoosh Creek, which originates in a different watershed and does not contain natal odours, flows into the Seton River downstream of Seton Dam, reducing the concentration of natal water in the Seton River. Salmon were first observed delaying at the generating station tailrace immediately after construction of the dam and generating station was completed (Andrew & Geen, 1958). Nearly three decades later, Fretwell (1989) used radio telemetry to demonstrate that some salmon returned to the generating station tailrace after having migrated upstream to the Seton-Fraser confluence. Fretwell (1989) suggested these individuals might return to the tailrace due to its higher concentration of natal cues (relative to the concentration of natal cues at the confluence), and supported this theory with controlled behavioural tests. In response to this issue, temporary rock and gravel dams were constructed on Cayoosh Creek in the 1980s so that water could be diverted away from Seton River and through a tunnel connecting to Seton Lake (the tunnel was originally used following the construction of Seton Dam in 1956 to augment discharge

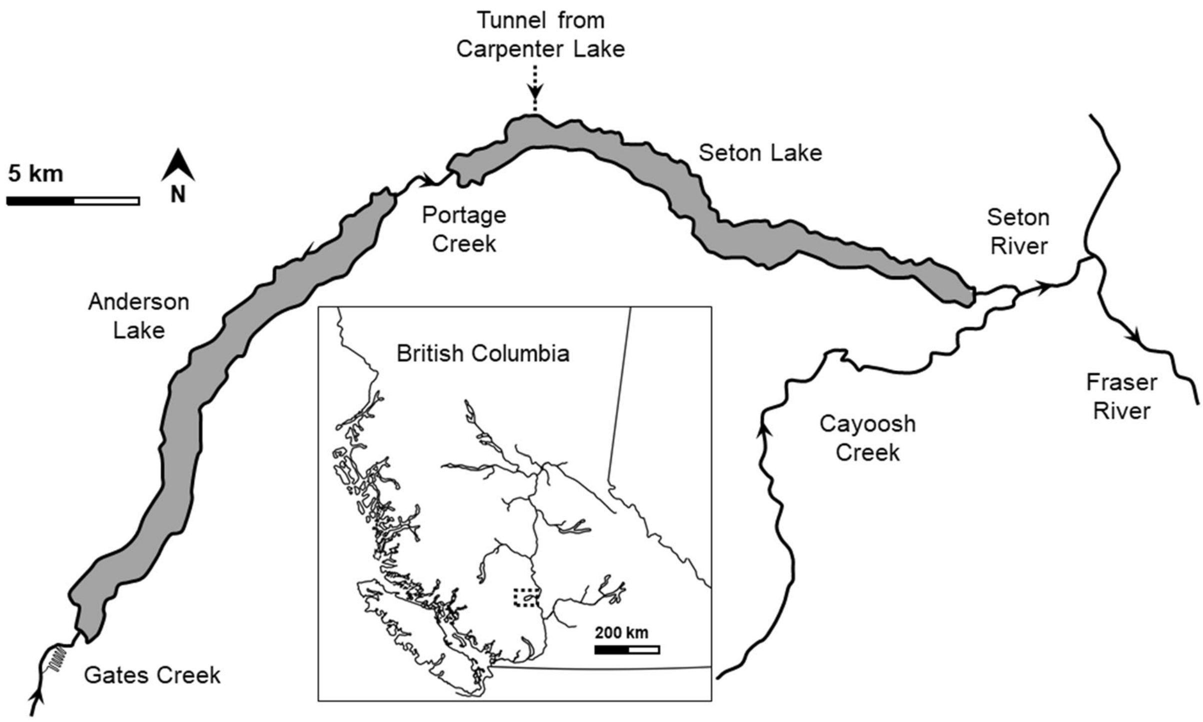

Fig. 1 Study area and its location within the Fraser River in British Columbia, Canada (inset)

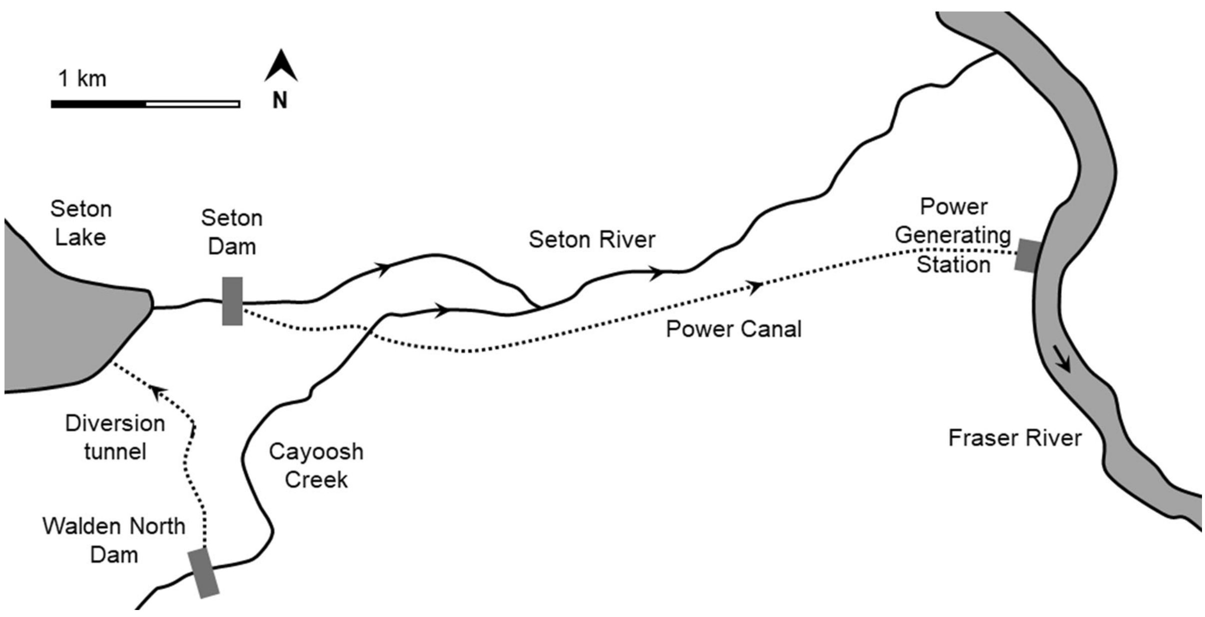

Fig. 2 Movement of water through the Seton River. Some of the water exiting Seton Lake is diverted at Seton Dam to a power canal that leads to a generating station on the bank of the Fraser River. A diversion tunnel can be used to divert water from Cayoosh Creek to Seton Lake

at the generating station, but was blocked off a few years later when the diversion of water from the Bridge River system was increased [Fretwell, 1989]). This alteration reduced the amount of water from Cayoosh Creek directly entering the Seton River, thereby reducing the level of natal water dilution at the Seton-Fraser confluence. In 1992, the temporary rock and gravel dams were replaced with a more permanent dam facility known as Walden North (Fig. 2). A threshold for maximum allowable dilution of natal water in the Seton River during the return migration was set at 20% to minimize the effects of dilution.

Following the construction of Walden North and the water diversion tunnel, Pon et al. (2009a, b) and Roscoe et al. (2010, 2011) studied the biological effectiveness of the fishway at Seton Dam. At the time our study began, however, there had been little directed research examining the causes of passage success or failure at Seton Dam (e.g. fish physiology, flow dynamics, water temperature), or the carry-over effects of dam passage (i.e. the influence of dam passage on post-passage survival and reproductive success). And while Andrew & Geen (1958) had observed that upstream migration did not seem "seriously impaired" so long as water was not released through a radial gate (used to spill excess water), the effects of different water release strategies through different dam syphons had never been experimentally tested. Further, all of the past research on dam passage was conducted using fish that had successfully passed the fishway rather than using fishway-naïve fish, which could introduce potential bias to the previous results. There had also been no examination of the effects of natal water dilution that were first observed by Fretwell (1989), despite the construction of Walden North on Cayoosh Creek.

In 2012, we began a 6-year study to understand the effects of dam infrastructure and operations on migrating adult Pacific salmon, and to learn from large-scale management experiments. Our work was completed under BC Hydro's Bridge River Power Development Water Use Plan, which aimed to assess the effects of operational practices of hydroelectric infrastructure in the Seton-Anderson watershed. Specifically, the study was part of the BRGMON-14 monitoring programme (BC Hydro, 2012), under which we sought to (1) examine the effect of dilution on return migrations and confirm whether the dilution threshold applied by management was appropriate, (2) examine the physiological factors that affect dam passage and determine whether migrating salmon might benefit from alternative dam operational scenarios, (3) measure the carry-over effects of dam passage and (4) observe salmon movement behaviours in response to flow dynamics through the application of computational fluid dynamics analyses. More generally, we also aimed to further our understanding of salmon migration biology, which, as noted by Brett (1957), is of critical importance to addressing any management problems, either current or future. While we studied pink salmon and two populations of sockeye salmon, here we report our analysis of the Gates Creek sockeye salmon population, which were the primary focus of our research. This population spawns at Gates Creek, located 55 km upstream of Seton Dam.

Instruments and methods used to examine fish in the Seton River

Due to the complexities associated with regulated rivers and the use of wild fish, many of the research questions and management objectives addressed in this project could not be answered through the use of a single instrument, technique or disciplinary expertise. Instead, we needed to adopt an integrative approach, which combined several types of instruments (e.g. passive tags, active transmitters, experimental chambers, flow profilers, fish counters) measuring different biological levels (cellular, organismal, population) and environmental variables. Below, we outline the techniques we employed, including the methods we used to collect data and the analytical procedures that were necessitated by our integrative approach. In bringing together different techniques it follows that we also had to bring together a diverse team spanning disciplinary expertise in ecology, fish physiology and hydraulic engineering, among others.

Telemetry

We used telemetry to characterize migration behaviour (e.g. migration speed, migration success, and energetics) as fish moved through the area. We employed three types of transmitters: passive integrated transponders (PIT), radio and acoustic. Transmitters were inserted into fish following their capture

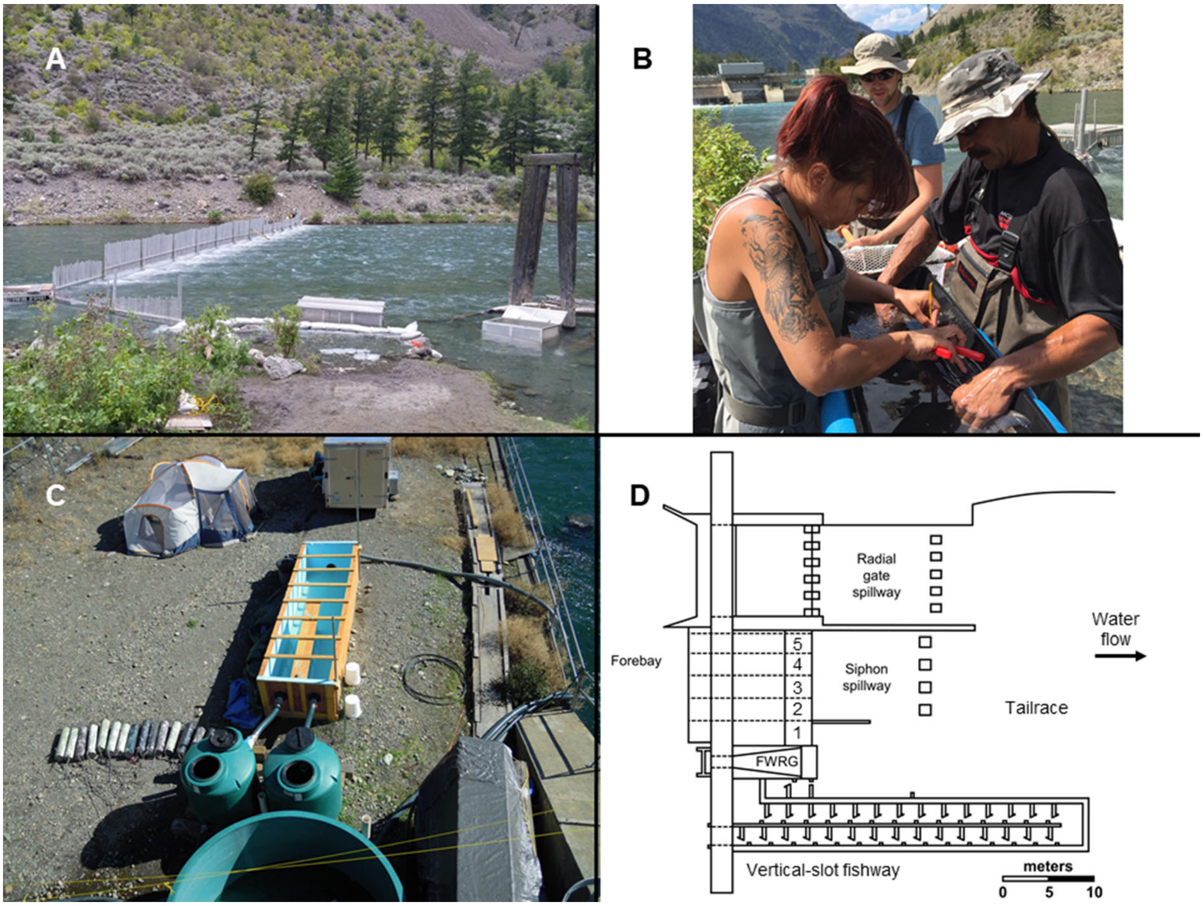

Fig. 3 **A** Full-spanning fence used to collect salmon in the Seton River downstream of Seton Dam (photograph taken by: AG Lotto). **B** Gastric implantation of a radio transmitter and identification tagging of a Gates Creek sockeye salmon (photograph taken by: SM Drenner). **C** Behavioural choice chamber (Y-maze) used for controlled behavioural tests (photograph taken by: NN Bett). **D** Schematic of Seton Dam, including locations of the five syphons used to release water

from a full-spanning fence located 200 m downstream of Seton Dam (Fig. 3a). PIT tags are the smallest, least invasive and most inexpensive of the three, allowing researchers to tag a large number of individuals (Brännäs et al., 1994). To be detected, however, a fish with a PIT tag must pass directly through or over an antenna, making this method of telemetry difficult to incorporate in large rivers. We used PIT tags to measure passage success or failure through the fishway and survival to spawning grounds. Radio transmitters, which can be gastrically implanted (Fig. 3b) in returning salmon (Pacific salmon are not feeding during their final few weeks of life), emit signals that can be detected by a land-based fixed station, allowing for individuals to be tracked through large river systems. We used an array of 11 fixed stations to track the movement of fish from in the Fraser River, downstream of the generating station tailrace, to spawning grounds in Gates Creek. Acoustic transmitters are designed specifically for aquatic habitats, emitting transmissions to submerged receivers that contain integrated hydrophones. This technology works better than radio for detecting fish in lakes and deep rivers. Acoustic transmitters equipped with an accelerometer sensor that has been calibrated in the laboratory (Wilson et al., 2013) can provide estimates of swim speed, allowing researchers to monitor energetic use (i.e. aerobic versus anaerobic swimming, oxygen consumption) through hydraulically challenging reaches. We used an array of 24 acoustic receivers to track salmon from the dam tailrace to spawning grounds, and accelerometers to estimate the recruitment of anaerobic muscle fibres during dam passage and the level of excess post-exercise oxygen consumption (EPOC; Lee et al., 2003) following passage.

Behavioural tests

There had been no studies since the construction of the Walden North dam to confirm the effects of natal water dilution in the Seton River first identified by Fretwell (1989). To explore the effects of natal water dilution on migratory behaviour, we assessed the preference of salmon for different odours in controlled experiments using a Y-maze (or two-choice chamber; Fig. 3C). This method is commonly used in the study of behaviour—particularly in aquatic organisms—as it allows for relatively easy analysis of preference or avoidance behaviours and can address a broad range of research questions (Jutfelt et al., 2017). We recorded several indicators of avoidance or preference, including time spent in the presence of an odour, number of entrances into either arm of the Y-maze and number of surfacing events. We used behavioural tests to examine the behavioural response of salmon to diluted natal water, conspecific cues and chemical disturbance cues. Fish used in the behavioural tests were captured from the most upstream pool of the fishway using dipnets and transported via an aerated tank on the back of a transport truck to experimental tanks on the bank of the river, adjacent to Seton Dam. The Y-maze was 4.88-m long, 1.22-m wide, 1.22-m high and received a constant flow of water (40 L min^{-1}) into each of the two arms.

Physiological and molecular analyses

Blood parameters such as hormones or plasma ion levels are known to affect salmon migrations (Schmidt & Idler, 1962; Cooke et al., 2006). We measured the concentration of reproductive hormone levels and metabolic stress indices in fish, prior to telemetry tracking and following Y-maze tests, to determine how physiological factors may influence migration behaviour and survival. We also conducted gene expression analyses of olfactory receptors to provide a mechanistic explanation of the olfactory-mediated behaviours observed in the Y-maze tests.

Environmental monitoring

We used an acoustic Doppler current profiler (ADCP; Channel Master 1200 kHz, Teledyne RD Instruments, Poway CA) to determine the magnitude and direction of flows in the dam tailrace that salmon must navigate to enter the fishway. We linked this information with fine-scale acoustic telemetry data to relate movement behaviours in the dam tailrace to flow patterns. We measured water velocity across 43 transects in the dam tailrace and immediately downstream: 38 transects were taken directly downstream of the dam at a depth of 0.5 m, and 5 transects were taken at different depths (every 0.5 m, from the river bed to the water surface) at the entrance to the fishway. The ADCP cannot effectively characterize flows in highly turbulent aerated waters due to the fast deterioration of acoustic signals caused by bubbles, so in some regions we used particle tracking to determine surface water velocities.

We also monitored water temperature (which influences many aspects of fish physiology and behaviour) and conductivity (which provides insight into the degree to which water odours differ between rivers) at multiple sites throughout the river system. Such information was combined with telemetry data and incorporated into statistical models to understand the influence of water temperature and conductivity on observed behaviours. Using archival temperature loggers implanted in a subset of fish in the study, we identified the temperatures individuals experienced as they travelled through the region, which highlighted thermoregulatory behaviours and potential underlying mechanisms driving observed movement patterns or survival.

Population enumeration

To place our findings within the larger context of the Gates Creek sockeye salmon population, we estimated the number of fish passing the fishway using resistivity counters and arriving at the Gates Creek spawning grounds using mechanical counters. Resistivity counters detect fish by changes in the resistance of water as they pass through sensor tubes (McCubbing et al., 2000), and we validated counts and species identification by using video footage of the sensor tubes. These continuous estimates of fish passage through the entire migration period allowed us to scale up the projected impact of operational changes to the population as a whole. They also provide an indication of post-passage success by comparing the difference in estimates between the top of the fishway and the spawning grounds, which would have otherwise been difficult to estimate. A spawning channel at Gates Creek enabled us to locate tagged migrants and estimate reproductive success.

River manipulation

Critical to our objective of improving the management of dam infrastructure was the experimental manipulation of dam operations. Aside from Andrew & Geen's (1958) observation that releasing excess water through a radial gate might impair migration, there had been no previous analysis of the effects of experimental manipulation of dam operations on returning salmon in the Seton River. By using telemetry to track salmon in experimentally manipulated river conditions, we were able to identify potential operational changes that could improve migratory or reproductive success. We separately tested two major manipulations: (1) a decrease in the amount of water diverted at Walden North from Cayoosh Creek to Seton Lake, thereby increasing dilution levels in the Seton River, and (2) a change in the flow patterns of the Seton Dam tailrace by switching the location of water discharge from a syphon directly adjacent to the fishway (Syphon 1; Fig. 3d) to a syphon located further from the fishway (Syphon 4).

Research questions and findings

Our overall study was guided by four main research questions. These questions cover different physiological, behavioural and ecological aspects of salmon migrations through the region. As such, the findings we describe below demonstrate the potential for an integrative approach to provide managers with knowledge needed to make informed, science-based management decisions.

Does natal water dilution negatively affect migration success or migration speed?

We combined telemetry with behavioural tests, physiological analyses and environmental monitoring to assess whether the dilution of natal water in the Seton River slows down the migration or discourages returning salmon from entering the Seton River. Confusion caused by natal water dilution has the potential to reduce the likelihood of migration success, and we aimed to identify whether this issue might be mitigated by restricting the amount of dilution in the Seton River.

First, we examined the relative importance of natal water as a directional cue for returning adults. Pacific salmon are known to imprint on the odour of their natal waters and use this odour as a directional cue while navigating upstream (Hasler & Scholz, 1983). Dilution of natal water could therefore disrupt the upstream migration by negatively affecting the salmons' ability to detect the imprinted cues. An alternate hypothesis suggests that salmonids do not follow their natal water, but instead are guided by conspecific odours, or pheromones (Nordeng, 1971). This hypothesis has been debated, however, and has failed to gain support among salmon researchers (Ueda, 2011). We integrated behavioural choice experiments with molecular analyses to examine the relative importance of imprinted and conspecific cues in the Seton-Anderson watershed. For the behavioural experiments, we tested the response of Gates Creek sockeye salmon to the addition of conspecific odours in one of the two arms of a Y-maze (Bett & Hinch, 2015). When the tests were conducted using natal water from Seton Lake, the salmon did not respond to conspecific odours. However, when tested in water from Cayoosh Creek, which does not contain the imprinted natal odour, the salmon exhibited a preference for the conspecific odours. The results from the first test using natal water support the prevailing theory that salmon are not guided by conspecific cues, but the results from the second test suggest that salmon might be guided by conspecific cues when the imprinted cues are absent. These findings contributed to the development of a novel hypothesis for salmon homing, which posits that salmon use imprinted cues as their primary directional cue and have the ability to use conspecific cues secondarily (Bett & Hinch, 2016). Molecular analyses determined that a suite of olfactory genes are differentially expressed in sockeye salmon depending on whether natal imprinted cues are present or absent (Bett et al., 2018b). This result suggests that the behaviours observed in the Y-maze might be driven by differential expression of olfactory receptor genes.

After identifying the relative importance of imprinted and conspecific cues to the spawning migration, we examined the effects of altered dilution levels on the behaviour of returning Gates Creek sockeye salmon. First, we tested their sensitivity to the dilution of natal water cues in a controlled, stream-side experiment. The Y-maze was used to replicate the olfactory conditions experienced by the migrating salmon, with undiluted natal water (the same as discharged by the generation station) in one arm of the maze, and diluted natal water (the same as in the Seton River) in the other arm. By manipulating the dilution level, we could determine the threshold at which the salmon exhibit a preference for the undiluted water. Concurrently, we used radio and PIT telemetry to observe the behaviour of salmon migrating through the system under routinely occurring conditions (i.e. dilution levels were not manipulated, but rather fluctuated in accordance with the routine dam operational scenarios). We captured individuals using the full-spanning fence downstream of Seton Dam, then tagged and transported them by truck for release in the Fraser River downstream of the generating station. Blood physiology was linked to movement behaviour through analysis of blood samples obtained during tagging. Following the Y-maze experiment and observational study, we conducted a field experiment to determine the effects of high dilution on migration behaviour. Dilution was manipulated such that it exceeded the estimated threshold level as determined by the water preference tests and observational tracking. This was accomplished by inhibiting the diversion of water from Cayoosh Creek directly into Seton Lake above the Dam, allowing all the water in Cayoosh Creek to flow into the Seton River. The manipulated conditions were maintained for 1 week out of the roughly 6-week migration so as to limit adverse effects to the migrants and were done with the support of regulators (Department of Fisheries and Oceans Canada and British Columbia Ministry of Forests, Lands, Natural Resources Operations and Rural Development). As with the observational tracking study, fish were captured using the full-spanning fence in the Seton River, tagged with a radio transmitter, then transported and released in the Fraser River downstream of the generating station.

In the water preference tests, Gates Creek sockeye salmon exhibited a preference for undiluted natal water when paired with water diluted by 30% or more (Bett et al., 2018a). The fish did not exhibit any preference between undiluted natal water and water diluted by 20% or less. Observational tracking found that the salmon slowed their migration at the outlet of the generating station, where undiluted natal water flows into the Fraser River (Middleton et al., 2018). Seventeen percent of tagged fish made back-and-forth movements between receivers located at the generating station and the mouth of the Seton River, indicating some level of confusion over the presence of directional cues at both locations. Circulating glucose levels were negatively associated with migration speed and circulating lactose levels were negatively associated with back-and-forth movements, which might suggest individuals with higher levels of stress are less likely to spend time at the outlet of the generating station or return to it after arriving at the mouth of the Seton River.

In our flow manipulation experiment, movement behaviours were tracked while dilution was elevated to 30%. These movement behaviours were compared to those when the Seton River was relatively undiluted (8%). The elevated dilution was associated with 80% reduced odds of salmon entering the Seton River (Drenner et al., 2018; Fig. 4), and for salmon that did enter the river, migration times were longer. The experiment also identified potential sex-linked differences in the response to natal water dilution, with males spending more time in the outlet of the generating station during the elevated dilution conditions while females took a longer amount of time to enter the Seton River. Responses to dilution did not differ between sexes, though, in the Y-maze experiment.

Migration time increased and likelihood of entry into the Seton River decreased when dilution was high, in accordance with the early observations of Fretwell (1989). The results are consistent with a preference for undiluted natal water, as demonstrated with the behavioural choice tests. Environmental monitoring, which was conducted in conjunction with the studies, allowed us to identify variables that might contribute to these behaviours. We found stark differences in the conductivity of the Seton River and Cayoosh Creek (Bett et al., 2018a), indicating different chemical constituents in the two waters and suggesting there are detectable odours that are different between the two sources (Vrieze et al., 2011). We also monitored water temperature, which can influence migration speed and

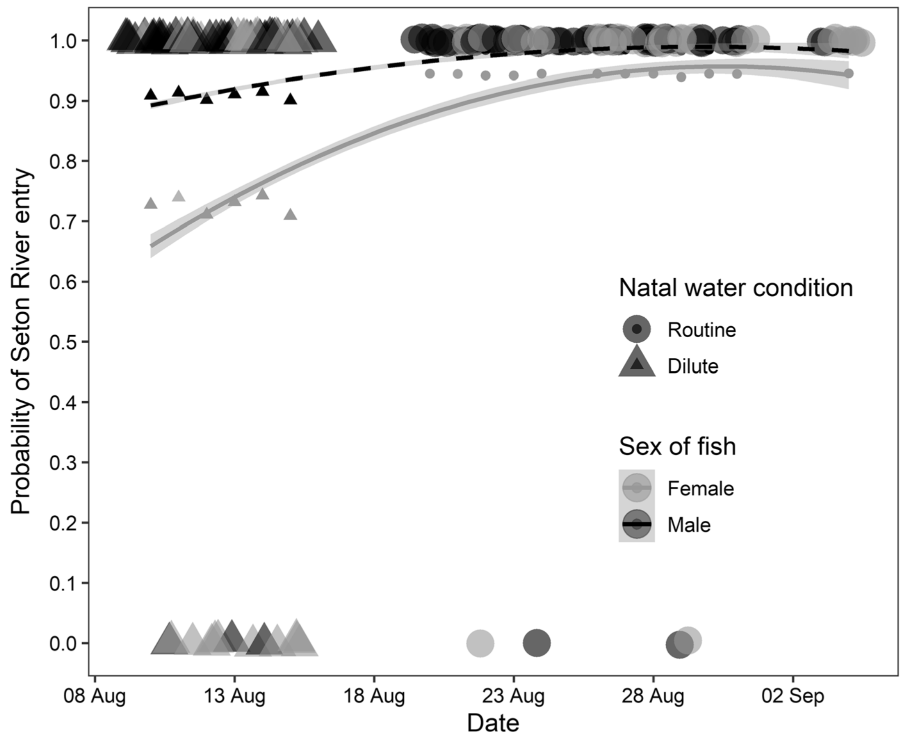

Fig. 4 Probability of entry into Seton River by Gates Creek sockeye salmon during routine natal water dilution levels (< 8% dilution; circles) and elevated natal water dilution levels (30% dilution; triangles). Data are binomial (entry or no entry) and are shown as large points. Small points and regression lines give predicted results of generalized linear mixed models and provide 95% confidence intervals on the line of best fit. Figure modified from Drenner et al. (2018)

other movement behaviours of migrating salmon (Goniea et al., 2006). Temperature in the Fraser River and Seton River did not appear to affect speed or entry into the Seton River in either the flow manipulation experiment or observational tracking study.

The integrative approach used to address this research question allowed for a comprehensive understanding of the influence of dilution on migration speed and navigation. The behavioural tests with conspecific cues identified migrating adult salmons' reliance on natal water as their primary directional cue. The behavioural tests with different levels of natal water dilution identified the dilution threshold at which preference behaviours emerged. The observational tracking study provided evidence that such preferences are exhibited in the natural environment and can result in slower migrations. The flow manipulation experiment confirmed that migration speed and migration success (i.e. entry into the Seton River) decrease when dilution is elevated above the 20% threshold level. Although the energetic cost of migratory delay when dilution levels were elevated was modest (Harrower et al., 2018), olfactory-related confusion in more heavily modified river systems could have a more significant effect on migration speed and energy use. Environmental monitoring confirmed that these behaviours are not driven by temperature and are likely due to differential olfactory properties of the Seton River and Cayoosh Creek, as indicated by differences in their conductivities.

Do dam operations influence fish passage?

A second major concern regarding the management of salmon populations in the Seton-Anderson watershed is the effect of dam operations on fish passage. Pon et al. (2009a, b) found a potential effect of flow conditions on passage time and also observed tagged salmon actively seeking a means of upstream passage, but the authors were unable to identify the cause of passage failure. We integrated acoustic accelerometer transmitters with environmental monitoring to assess the effects of dam operations on dam passage. Combining these measurements allowed us to map swim speed and estimated oxygen consumption on to the environmental conditions experienced during passage, providing a mechanistic understanding of dam passage success and failure. By using these transmitters, we were able to estimate the amount of anaerobic recruitment (i.e. the degree to which anaerobic metabolism contributed to swimming, which occurs during burst swimming) required to navigate through fishway attraction flows, providing insight into the energetic costs associated with dam passage. Salmon were tracked throughout the dam tailrace during two consecutive years, and specific behavioural, physiological and environmental factors influencing passage were discovered. Fish appeared to have less difficulty passing the fishway than they did locating and entering it (Burnett et al. 2014b), with passage efficiency reaching 98% in the second year of study (Burnett et al., 2014a). These results supported the findings of Pon et al. (2009b). Difficulty locating the fishway entrance was associated with the spilling of excess water through the dam's radial gate (Burnett et al. 2014b). The research also found that anaerobiosis was required to reach the fishway entrance, and fish that experienced higher velocities near the fishway entrance showed increased anaerobic recruitment (Burnett et al., 2014a; Fig. 5). Comparing sexes, female salmon exhibited higher anaerobic recruitment in these high velocities than did males and were less likely to pass Seton Dam (Burnett et al., 2014a, b). An effect of water temperature was also discovered during the second year, when shut downs of the generating station resulted in surface waters heating behind the Seton Dam, exposing fish to supraoptimal temperatures. Fish that were exposed to these warmer temperatures were less likely to locate, enter and pass the fishway (Burnett et al., 2014a).

What are the carry-over effects of dam passage on post-dam passage survival and reproductive success?

The immediate effects of passage on the behaviour, physiology and survival of migratory fish have been studied in many different regulated systems (Caudill et al., 2007; Bunt et al., 2012; Noonan et al., 2012). Most studies do not address, however, whether the effects of fish passage or early migratory experience might carry over (see O'Connor et al., 2014) to

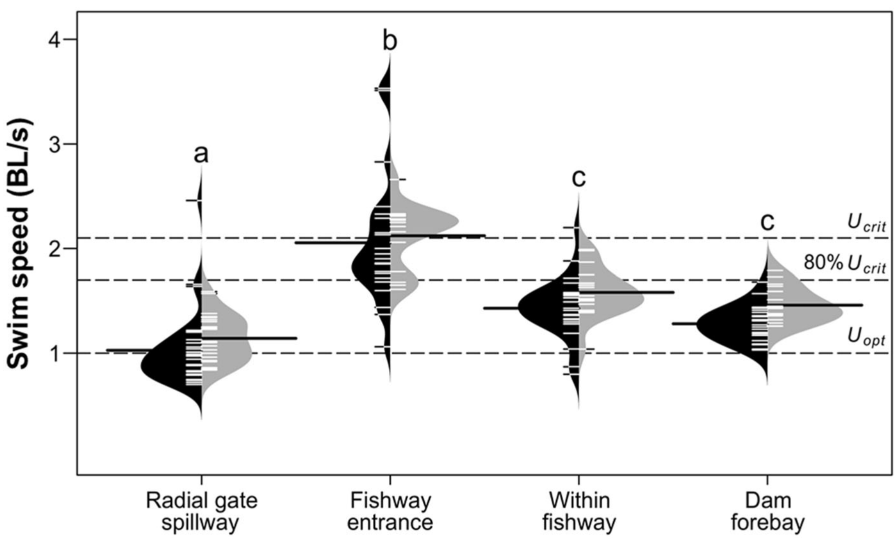

Fig. 5 Swim speed in body lengths per second of male (black) and female (grey) Gates Creek sockeye salmon. Shaded curved polygons show estimated density of the distribution of individual swimming speed values (white lines). Black lines indicate mean swim speeds. Optimal swimming speeds (U_{opt}), critical swimming speeds (U_{crit}) and 80% of critical swimming speeds (80% U_{crit}; when anaerobic muscle fibres start to be recruited) are shown as dashed horizontal lines. Lowercase letters represent significant differences ($P < 0.05$) from one-way ANOVA and Tukey 's post hoc tests. Figure modified from Burnett et al. (2014a)

influence survival to spawning grounds and/or reproductive success. We integrated dam passage analyses with upstream tracking and spawning ground assessments in the second year of our research on dam operations to estimate carry-over effects of dam passage. We found that increased anaerobic recruitment during dam passage was associated with increased mortality upstream of the dam, demonstrating the occurrence of carry-over effects resulting from dam passage (Burnett et al., 2014a). Following this discovery, we conducted an in situ experiment to test whether altering Seton Dam operations would mitigate carry-over effects and improve survival to spawning grounds. Passage success and survival to spawning grounds were compared under two flow conditions: the routine operational scenario (in place since construction of Seton Dam in the 1950s) that released fishway attraction flows directly adjacent to the fishway entrance, and an alternative operational scenario that reduced flows near the fishway and instead released water 10 m away from the fishway entrance (Fig. 6). The experiment was first conducted in 2014, and then replicated in 2016. Over the 2 years, a total of 1070 acoustic- and PIT-tagged salmon were tracked, and the results indicated modest increases in dam passage under the alternative operational scenario compared to the routine operational scenario (ranging from a 1% increase in 2016 [Harrower et al., 2018] to a 9% increase in 2014 [Burnett et al., 2017]). Post-dam passage survival to spawning grounds was 10% higher during the alternative scenario in 2014 (Burnett et al., 2017) and 14% higher in 2016 (Harrower et al., 2018). This effect of operational scenario on post-dampassage survival is likely associated with differences in anaerobic recruitment: salmon in the routine operational scenario spent twice as long recovering in the dam forebay following passage than did fish exposed to the alternative operational scenario (Burnett et al., 2017).

The carry-over effects of dam passage may be compounded by previous migratory experience, and the effects of these experiences may influence not just survival but also reproductive success. Building from our experiment on the effects of dam operations on post-dam passage survival, we integrated spawning assessments with telemetry, environmental monitoring, injury assessments and physiological analyses to determine the influence of physiological state and migratory experience (including dam passage) on the

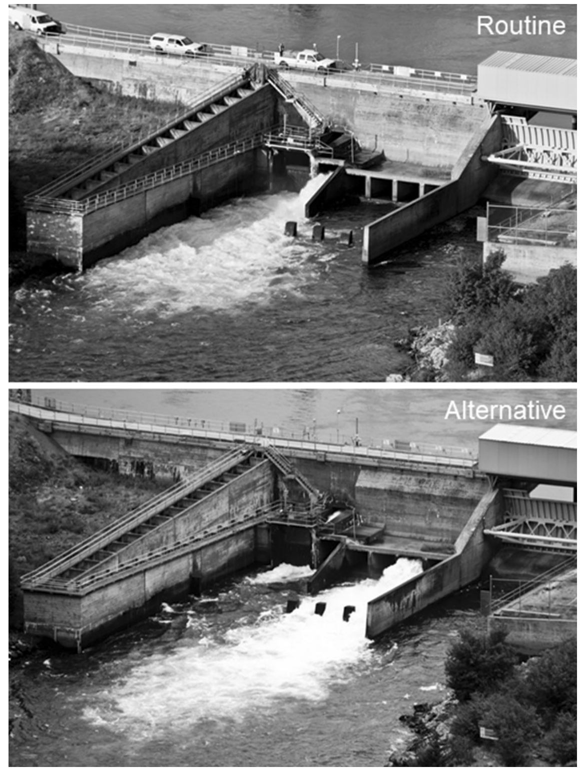

Fig. 6 Flow patterns in the dam tailrace during the routine operational scenario and alternative operational scenario (photographs taken by: NJ Burnett)

reproductive success of returning migrants. By conducting visual injury assessments of salmon arriving at Seton Dam before tracking their survival to spawning grounds (using PIT telemetry) and monitoring the reproductive success of females, we discovered a significant effect of gillnet-induced injury on survival to spawning grounds and reproductive success. Fish exhibiting gillnet wounds, which made up 21–29% of females and 13–22% of males during the 3 years of monitoring, had a 16% lower probability of surviving to spawning grounds (Bass et al., 2018). Furthermore, females with gillnet injuries had an 18% lower probability of releasing their eggs. We also blood-sampled fish and tagged them with archival temperature loggers and radio transmitters, then tracked them from the dam forebay to spawning grounds. Females that spent more time in their optimal temperature window while migrating through the two lakes lived longer on spawning grounds and had greater probability of releasing their eggs (Minke-Martin et al., 2018). Also, individuals that arrived earlier in the migration spent longer in the lakes, and plasma glucose levels were lower in fish that successfully reached spawning grounds, which align with previous research on this population (Roscoe et al., 2011). In addition, fish exposed to a higher dam discharge exhibited reduced reproductive longevity and reduced probability of egg-release on spawning grounds (although survival to spawning grounds was not lower in these fish; Minke-Martin et al., 2018). The results from this research provide further examples of the complex interplay between physiological state and migration success and also highlight the influence of migratory experience on reproductive success.

How do salmon use different flow fields and navigate complex flow patterns in the dam tailrace?

Because sockeye salmon rely solely on endogenous energy reserves when migrating to spawning grounds, energy-saving behaviours can be important to migration success, particularly in areas of difficult passage. For example, salmon might swim at hydrologic or metabolic optimum speeds (Webb, 1995), take advantage of low-velocity or reverse-current pathways (Webb, 1995; Hinch & Rand, 1998, 2000), or adopt a different form of locomotion to reduce muscle activity (Liao et al., 2003). The study of flow-mediated behaviours during the upstream migration, however, requires a detailed assessment of flow patterns. Flow patterns can be exceedingly complex, varying with bathymetry, depth in the water column, the level of discharge and river channel geometry. Laboratory studies that monitor swimming behaviours of migratory fish in constant flow velocities have yielded insight into the optimization of swim speeds while traversing velocity barriers (Castro-Santos, 2005). Fine-scale profiling of river currents, though, can be difficult to accomplish, and descriptions of flow-mediated migratory behaviours in the field often rely on speculation (e.g. Hinch & Rand, 2000; Hinch et al., 2002; Milner et al., 2012).

To evaluate flow-mediated behaviours in the dam tailrace, we linked salmon movements measured using acoustic telemetry with computational fluid dynamics and fine-scale flow profiling using an ADCP. The application of such a method to understand the flows that fish encounter when migrating upstream is limited (McElroy et al., 2012). Measurements were taken for both the routine operational scenario (water released directly adjacent to the fishway entrance) and the alternative operational scenario (water released 10 m away from the fishway entrance) to compare differences in the magnitude and direction of flows in the dam tailrace (Fig. 7) and to strengthen our understanding of fish movement under the two flow scenarios. In the routine operational scenario, discharge from the syphon closest to the fishway (Syphon 1, or "SSV1" in Fig. 7A) was 19.8 m^3 s^{-1}, and discharge from the fish water release gate (located between the fishway and nearest syphon) was 7.6 m^3 s^{-1}. In the alternative operational scenario, discharge from the syphon 10 m away from the fishway (Syphon 4, or "SSV4" in Fig. 7B) was 25.5 m^3 s^{-1}, and discharge from the fish water release gate was 1.9 m^3 s^{-1}. The total discharge was 28.5 m^3 s^{-1}in both scenarios, with 1.1 m^3 s^{-1} of discharge in the fishway.

In the routine operational scenario, water near the fishway entrance was highly turbulent, preventing accurate ADCP measurements through much of this area. Particle tracking, however, estimated that surface flow velocities exceeded 4.0 m s^{-1}. Downstream of the fishway entrance, where ADCP measurements were possible, peak flow velocities at a depth of 0.5 m were between 4.5 and 4.8 m s^{-1} (Fig. 7). Fish are required to navigate through these high-velocity areas to approach the fishway entrance. Some upstream flows occurred adjacent to the area of high turbulence (on the opposite side of the river), providing opportunities for salmon to take advantage of reverse flow fields and reduce energy expenditure (Liao et al., 2003). Three large vortices were created under the routine operational scenario: two were located along the north bank of the Seton River, opposite from the fishway, and a smaller third vortex was located on the south bank downstream of the fishway. Flow velocities up to 1 m s^{-1} were measured in each vortex.

In the alternative operational scenario, highly turbulent flows were shifted further from the fishway entrance, thereby reducing the amount of turbulent flows that fish must experience while approaching the fishway (Fig. 7). Peak velocities in the area of primary discharge reached 6.6 m s^{-1}, and velocities up to 4.3 m s^{-1} extended 75 m downstream. Below this discharge plume, however, velocities decreased to < 1 m s^{-1} as the tailrace widened into the Seton River. Two vortices were created along the north bank

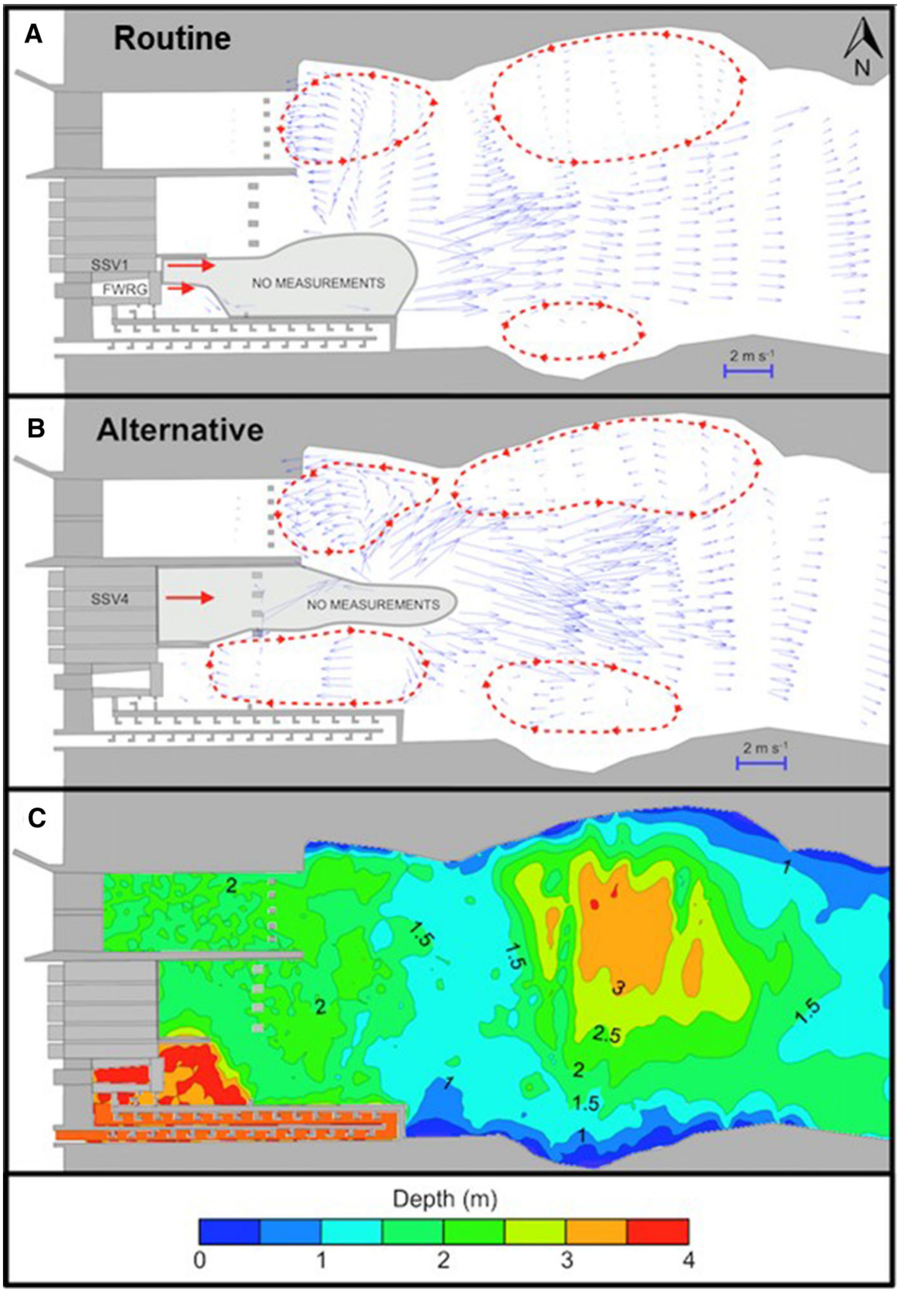

Fig. 7 Water velocity field 0.5 m below the surface downstream of Seton Dam during the **A** routine operational scenario and **B** alternative operational scenario. Water was released through the fish water release gate (FWRG) and the syphon closest to the fishway (SSV1) or a syphon 10 m from the fishway (SSV4). Also shown is water depth **C** downstream of Seton Dam

of the river, similar to those present under the routine operational scenario. On the south bank, the vortex that occurred downstream of the fishway in the routine scenario increased in size in the alternative scenario. Another vortex developed in the entrance area adjacent to the fishway outer wall. Upstream flows from this vortex created a flow interface with discharge from the fishway attraction flows. This interface occurred 8–10 m downstream of the entrance. Downstream flows were < 0.5 m s^{-1} and upstream flows were 0.5–1.0 m s^{-1}. As a result, the fishway attraction flows under the alternative scenario may have been reduced, although direct comparison to the routine scenario was not possible due to the high turbulence in this area under the routine scenario. Regardless, flow velocities around the entrance area were reduced under the alternative scenario, and upstream flows were present.

In the routine operational scenario, the salmon regularly made dozens of movements to and from the fishway entrance from the north bank (P. Li, University of Alberta, unpublished data). In the alternative operational scenario, however, this behaviour was restricted, typically occurring only twice per fish (P. Li, University of Alberta, unpublished data). The total volume of water in the tailrace with a velocity that necessitates burst swimming and anaerobic recruitment was much larger in the routine operational scenario compared to the alternative operational scenario (285 m^3 vs 243 m^3), which might explain the repeated attempts required to navigate through high velocities to reach the fishway entrance. This is particularly true for the region just downstream of the fishway entrance in the routine scenario, where the high velocity and turbulent flow field may disorient fish. Linkage of hydrodynamic results and fish migration routes also suggest that fish avoided the high-velocity region (> 2.4 m s^{-1}) in both scenarios, and fish appeared to be able to locate and take advantage of low-velocity areas near the outer wall of the fishway before entering the fishway (P. Li, University of Alberta, unpublished data).

Lessons learned from using an integrative approach

Over the course of 6 years, we gained significant insight into the biology and physiology of salmon spawning migrations, and our findings had a direct impact on local management decisions (Fig. 8). We characterized the effect of natal water dilution on the movement behaviour of returning salmon and confirmed that existing management targets for dilution levels are appropriate. We found differential energy use patterns and levels of anaerobiosis under routine and alternative dam operational scenarios, which were associated with differences in post-dam passage survival. In doing so, we identified a more beneficial operational scenario that could improve survival to spawning grounds by 10–15%. These results have been rapidly incorporated by BC Hydro in the management of dam operations in the Seton-Anderson watershed: the alternative operational scenario is operated at the Seton Dam, and dilution levels continue to be regulated in accordance with the target confirmed through our research (i.e. dilution levels are not permitted to exceed beyond 20% during the Gates Creek sockeye migration). Forebay temperature monitoring has also been linked with generating station operations to manage Seton River temperatures.

Integrative research is regularly motivated by a desire to tackle complex problems such as those found in regulated rivers, and may in fact be necessary (Rhoten & Parker, 2004). Even when the level of integration is relatively small in scale, the benefits gained by linking different perspectives can be significant. Past salmon research has demonstrated these benefits, such as Fretwell's (1989) pairing of field observations with experimental tests to reveal the back-and-forth movements of salmon between the generating station and the Seton River and to identify a potential mechanism driving the behaviour. Other studies have combined tagging with measurements of biological parameters (Williams et al., 1986) or field observations with laboratory behavioural experiments (Brannon, 1972) to explore environmental and physiological factors affecting salmon migrations. Our research drew from these approaches and extended the level of integration through the use of new technologies. We discovered carry-over effects of dam passage by integrating telemetry with physiological measurements (levels of anaerobic recruitment) and assessments of spawning success. Had we only measured passage rates of tagged salmon, we would not have discovered these carry-over effects and therefore would not have identified the benefits of the alternative dam operational scenario. We also would not have been able to identify how salmon use flow fields below the dam without the integration of telemetry data with computational fluid dynamics and fine-scale flow profiling. Similarly, we would not have provided conclusive evidence of the negative effect of high dilution on the return migration had we not applied the results of controlled behavioural tests to the manipulation of field conditions. These examples, among many others, provide further evidence that integrative research can lead to discoveries that may be critical to management and conservation efforts (Dick et al., 2016).

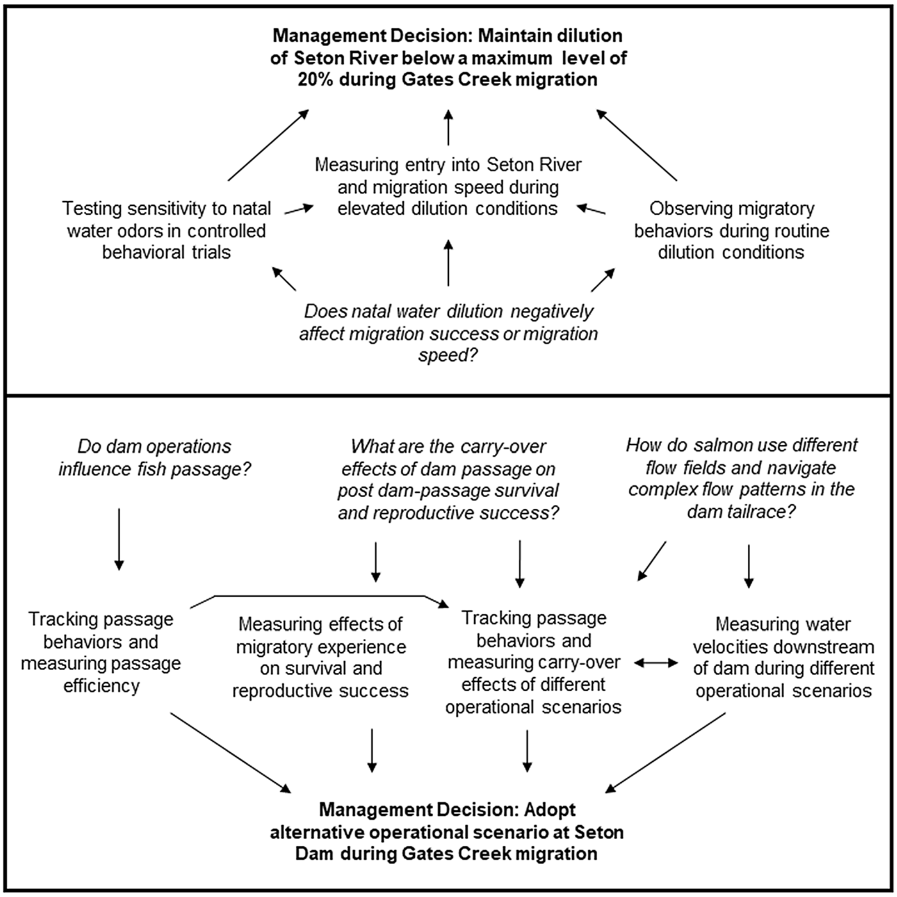

Fig. 8 Contributions of research activities to addressing research questions (in italics) and informing management decisions (in bold). Research activities took place within a multi-year programme assessing the effects of hydroelectric operations on adult salmon migrations in the Seton-Anderson watershed

In their synthesis of research in regulated rivers, Murchie et al. (2008) found that many studies do not incorporate controls, and few tested the effects of operational changes. While observational studies can document the effects of flow modification on aquatic communities, their ability to inform effective management practices is limited. An adaptive management framework—defined as "an integrated, multidisciplinary and systematic approach to improving management and accommodating change by learning from the outcomes of management policies and practices" (Holling, 1978)—on the other hand, can be used to mitigate the negative effects of flow modification. Indeed, adaptive management is frequently recommended for regulated systems (Poff et al., 1997; Schreiber et al., 2004; Stoffels et al., 2018), yet it is rarely applied (Richter et al., 2006). Our research incorporated elements of an adaptive management framework (specifically, analysing the outcomes of management practices with respect to salmon migrations, then identifying improved management practices that were subsequently adopted in management policies), and has set the stage for continued future monitoring within this system that can carry on with this approach. Where possible, researchers should use regulated rivers as experimental systems, allowing for a more rigorous assessment of local policy or management actions. In fact, regulated rivers provide some of the best opportunities to conduct true adaptive management research (Walters & Hilborn, 1978; Bradford et al., 2011), as they are often amenable to large-scale experimental manipulation.

In addition to the benefits of integrative approaches, we identified a few key lessons from our research. One of the lessons is the necessity of studying organisms at multiple levels of biological organization (molecular, organismal, population) in order to make any reasonable claims or suggestions with respect to population conservation or management. We were able to place behavioural and physiological results (such as the sensitivity of salmon to natal waters, or the energetic costs of dam passage) within the broader context of population persistence by linking these factors to survival and reproductive success. Fine-scale analyses, such as the expression of olfactory receptor genes or estimates of anaerobic recruitment, provided mechanistic understanding of the responses we observed, which helped to interpret our findings. Another lesson is the importance of multi-year studies, which can allow us to detect issues that may not be apparent every year. For example, there was an increase in dam passage under the alternative operational scenario in 2014, but the increase was barely noticeable in 2016. Multi-year studies can be especially important given that the operational benefit may only occur under certain conditions, such as during years when water temperatures are elevated.

Our experience with large-scale manipulation also highlights the important and underappreciated opportunity that regulated rivers provide for studying fundamental scientific questions. While our research was conducted within a management framework, we were able to make broadly applicable discoveries that could only be accomplished in a system that is open to manipulation. In addition, fish passage structures can be used to easily capture migratory fish in a relatively benign fashion, which is particularly favourable for physiological or behavioural studies, as more intrusive methods can have immediate and significant effects on a fish's physiological condition (Cooke et al., 2008b). Regulated rivers therefore provide an opportunity to conduct experimental research in a relatively natural setting, allowing for detailed exploration of basic issues such as the effects of flooding or drought on fish survival or spawning (Bradford et al., 2011; King et al., 2008) and unravelling the effects of flow variability on fish (Rytwinski et al., 2017). Studies that capitalize on these benefits of working in regulated systems could yield novel findings in the behaviour, physiology and ecology of aquatic organisms. We also acknowledge, however, that dams pose a risk to salmon populations (Ferguson et al., 2011), and the research benefits we have highlighted should not invalidate conservation efforts to restore salmon populations by decommissioning structures in some rivers.

Large-scale flow experiments and integrative approaches are not without their challenges and risks. There are several considerations that can influence the degree to which a system might be manipulated. Our experience has taught us that cooperation and continual dialogue between researchers, First Nations and regulators of the hydroelectric facility are absolutely necessary for manipulation experiments to occur. Water release changes often cannot deviate from existing water-use policies without regulatory approval or review of safety protocols. In addition, experiments must be coordinated with scheduled operational procedures that may be planned years in advance (such as equipment service or replacement), and—in regions such as ours—must obtain endorsement by local First Nations. Effective coordination is also important when taking an integrative approach. Our research relied on input from experts of various disciplinary backgrounds, all working together to ensure that data collected on different aspects of salmon biology or hydrology would complement one another. More broadly, our research involved various stakeholders (including members of government, industry, academia, First Nations and environmental organizations), all of whom needed to agree on the management questions to be addressed and the approach most likely to succeed. A diverse set of stakeholders may have fundamental conflicts over ecological values that can lead to disagreement over management questions or appropriate management actions (Walters, 1997), although disagreements can be effectively managed with transparent decision-making processes, such as structured decision-making (Failing et al., 2012) guided by larger planning frameworks. Other potential issues include competing uses for water (a public resource in Canada), physical limitations to the dam infrastructure, concerns about impacts on at-risk species or the possibility of collateral effects on non-targeted organisms (Konrad et al., 2011). If possible, methods should be adapted to limit potential negative effects on local species (in our case, for example, we restricted the manipulation of dilution levels to 1 week out of the 6-week migration period) and data should be monitored in real time so that issues can be rapidly detected should they arise (for example, we actively monitored fish passage when testing the alternative operational scenario at the dam). Some stakeholders may also view large-scale experimentation as too time consuming, too costly or too complex (Medema et al., 2008). Many of these issues could be exacerbated in large regulated rivers, where the risk of unintended consequences of experimental manipulation is greater, and where economic costs or project complexity could be prohibitively high. Experiments directly involving power-generating facilities, as opposed to diversion dams such as the Seton Dam, may also not be possible if power production is adversely impacted. Nevertheless, most regulated rivers have the potential for some level of manipulation, and barriers to experimental manipulation are not always insurmountable. Fisheries managers should consider using these systems where possible.

Our research emphasizes the usefulness of integrated research when studying migratory fish species and adds to a growing trend in fisheries research of pairing telemetry with physiological and molecular analyses, environmental data, and lab- or field-based experiments to better understand fish movements and behaviour (Cooke et al., 2008a; Patterson et al., 2016). Freshwater biodiversity faces significant threats in the coming decades, which includes flow modification but also overexploitation, water pollution, habitat loss and invasive species (Reid et al., 2019). Freshwater fish are encountering sharp declines in many areas of the world (Harrison et al., 2018), and the declines are projected to accelerate with future changes in climate and water consumption (Xenopoulos et al., 2005). The implementation of well-planned, integrative research could play a key role in helping us track losses to biodiversity and identify potential actions for mitigation related to environmental flows and connectivity (Tickner et al., 2020). We hope that our experience provides an example for future research programmes to adopt similar approaches when tackling emerging issues in aquatic ecology and management.

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