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# Thermal selection and delayed migration by adult sockeye salmon (*Oncorhynchus nerka*) following escape from simulated in-river fisheries capture

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# ABSTRACT

Two hypotheses were tested concerning the consequences to adult sockeye salmon (Oncorhynchus nerka) of escape from commonly used fishing gear (gillnet, seine net and tangle net). First, by experimentally exposing 214 fish to three commonly used fishing gear types (gillnets, tangle nets, or seine nets) and releasing to complete migration after PIT-tagging, we tested the hypothesis that migration success and behaviour are differentially impacted according to the type of fishing gear interaction and escape. Also, by fitting salmon with thermal loggers, we tested whether salmon behaviourally selected cooler lake water following an escape encounter. Migration success was unaffected after escape from the simulated gear types compared to control fish. Surviving sockeye salmon that had gillnet or seine net encounter, but not a tangle net encounter, on average took approximately 2 days longer to migrate to the spawning area (averaging 14.7 days and 14.9 days, respectively) compared to control fish (12.6 days). Furthermore, escaped fish migrated at cooler temperatures through a lake system (average of 14.0 °C) compared to control fish (15.3 °C), which would reduce their absolute cost of transport during this migration by reducing the standard metabolic rate by about 10%. Consequently, in addition to demonstrating that fish escapement from a fishing gear will alter their subsequent migration behaviour, we introduce the possibility that the associated increase in energy expenditure and migration delay can be partially compensated for by behavioural selection of cooler water, if it is available, to lower basic energy turnover in a fish that is entirely reliant on energy stores to fuel its spawning migration.

# 1. Introduction

Pacific salmon (*Oncorhynchus* spp.) are important culturally (Lichatowich, 2013), ecologically (Cederholm et al., 1999), and economically (Gislason et al., 2017a, 2017b) and are targeted by numerous marine and freshwater fisheries. In riverine areas, the most common harvesting of salmon targets adult fish during their spawning migration using either gillnets, tangle nets, beach seine nets, or rod-and-reel angling (Patterson et al., 2017a). As a result, incidental encounters and by-catch are

common, with many fish being released after capture, while others escape from fishing gear (Raby et al., 2015; Bass et al., 2018a, 2018b; Kanigan et al., 2019), which we collectively defined here as 'nonretention' fish. The frequency and fate of non-retention fish post-net encounter is of importance for fisheries managers who need to quantify total fishing-related mortality for specific fisheries and estimate predictions of spawner abundance to manage salmon populations (Ricker, 1976; Patterson et al., 2017a, 2017b).

Most research to date has focused on the consequences of release

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from common fishing gears (reviewed in: Raby et al., 2015; Patterson et al., 2017a) and estimates of short-term post-release mortality are included in some fishing impact models used to predict spawner abundance (DFO, 2019). In contrast, the incidence and consequences of escape are poorly understood (Patterson et al., 2017a), and most fisheries models quantifying fishing-related incidental mortality for salmon do not explicitly account for escapees (Baker et al., 2014; Patterson et al., 2017b). The importance of escapees is perhaps best understood for the gillnet fishery because survivors of encounters carry characteristic entrapment wounds. In Bristol Bay, Alaska, for example, 6-44% of sockeye salmon (Oncorhynchus nerka) were observed on spawning areas with scars consistent of a gillnet entanglement, and of fish with these injuries, approximately half failed to reproduce (Baker and Schindler, 2009). Similar scarring was seen on 10 to > 40% of certain populations of Fraser River sockeye salmon in British Columbia (BC), Canada (Clarke et al., 1994), on their spawning grounds between 1987 and 1994. Between 2014 and 2016, 19-27% of sockeye salmon captured on the Seton River (a tributary of the Fraser River) had gillnet scars and compared with uninjured fish, their en-route and pre-spawn mortality increased by 16–18% (Bass et al., 2018a). Moreover, a higher gillnet fishing effort in the lower Fraser River was positively correlated with a higher proportion of gillnet injuries to sockeve salmon captured in Seton River (Kanigan et al., 2019). This high prevalence of gillnet wounds could, in fact, suggest a current underestimation of the percentage of salmon escaping gillnets if fish die post-entanglement and pre-observation. Clearly, further experimental study is needed on salmon escapements from common fishing gears to more accurately estimate the frequency and consequences of gear escape at different locations.

Different fishing gear types can cause different types of injuries, levels of exhaustion, and levels of stress for fish that escape or are released, which then may trigger different consequences for survival and spawning (Davis, 2002; Cooke et al., 2013; Broadhurst et al., 2006). Fraser River sockeye salmon, for example, can encounter gillnets, tangle nets, or beach seines during their spawning migrations. Gillnet entanglement can cause exhaustion, suffocation, lacerations (sometimes extensive and severe), and mucus removal that provides an entry point for infectious agents (Kojima et al., 2004; Baker and Schindler, 2009). Post-release survival for Fraser River sockeye salmon following manual release after an experimental gillnet entanglement can differ among populations (17.8% for Harrison and 34.2% for Weaver populations; Donaldson et al., 2012), between sexes (30% survival for females and 66% survival for males experiencing 20 min gillnet entanglement; Teffer et al., 2017), and with maturation state (35% for less mature and 75% for more mature; Bass et al., 2018b). The smaller mesh size and larger hang-ratio of tangle nets compared with gillnets is intended to entangle a fish's fins, mouth, or teeth rather than ensnaring and constricting their body. Nevertheless, while an entanglement with a tangle net can still exhaust, lacerate, and cause mucus loss, survival has been shown to be higher than with gillnet encirclement (Vander Haegen et al., 2004; Donaldson et al., 2012) with an estimated 68.6% survival of adult Columbia River Chinook salmon (Oncorhynchus tshawytscha) released from a tangle net (Ashbrook et al., 2008). Beach seines potentially harm fish by removing mucus and possibly through suffocation if oxygen is depleted by a high fish density in the net sets (Raby et al., 2014). However, injures following beach seine escape are typically mild, and post-release survival for Pacific salmon has been shown to be higher for than gillnets (Bass et al., 2018b). Survival to spawning areas after a beach seine encounter is reported from 33% to 82% for adult sockeye salmon (Donaldson et al., 2011; Robinson et al., 2015; Bass et al., 2018b).

Despite this knowledge, no study has directly compared the effects of the three fishing gear types commonly used to intercept adult sockeye salmon during their river migration (gillnet, tangle net, and seine net) within a single fishery. Therefore, we aimed to investigate the consequences of simulated escapes from these three gear types. This study focused on a subset of a population of Fraser River sockeye salmon that had likely not encountered previous net entanglement. A volitional escape from entrapment in fishing gear prior to landing differs from bycatch release because escapees do not experience air exposure or direct human handling (Patterson et al., 2017a). Also, because the escape is most often unobserved, the exact process of escape is largely unknown. Increased energy expenditure and stress for the fish are expected as they struggle to free themselves, typically using burst swimming to push their way through, or out of, mesh entanglement. Beach seine escaped fish would likely swim under the lead line or jump over the float line. We tested the hypothesis that migration success and behaviour are differentially impacted according to the type of fishing gear interaction by PIT-tagging fish before they were released back to the river for short (200 m to negotiate a dam raceway) and a longer (50 km to their spawning area) migrations. Consistent with previous studies (Mäkinen et al., 2000; Frank et al., 2009, 2019), we predicted that escapees would have reduced migration success and an increase in migration duration for fish that escape gear compared with control fish, and that interaction with gillnets would have a greater impact compared with tangle net and seine net interactions.

Also, by fitting the fish with a thermal logger, we could test the hypothesis that escapees would behaviourally select cooler water while migrating through deep lakes enroute to their spawning area compared with fish that did not experience a gear escape simulation. Behavioural thermoregulation of Pacific salmon is well documented (Newell and Quinn, 2005; Mathes et al., 2009; Keefer and Caudill, 2015), with fish potentially seeking out cooler water in response to supra-optimal water temperature (Goniea et al., 2006), and for energetic and reproductive benefits (Roscoe et al., 2010). Of course, these behaviours, which can increase survival to spawning grounds (Mathes et al., 2009), may become increasingly important in an era of warming water temperatures. Moreover, recent evidence suggests that gillnet-injured adult sockeye salmon seek cool water during their up-river migration (Bass, 2018). Escaping fishing gears requires increased energy expenditure and migration delay (Mäkinen et al., 2000, 2019) and often leaves fish with lacerations (which may serve as an entry point for opportunistic infectious agents). Behavioural thermoregulation following fishing gear interactions may therefore offer benefits for a migrating salmon using a fixed energy store as basic energy needs (the standard metabolic rate) would be reduced, and it would slow the proliferation of opportunistic pathogen infections.

# 2. Methods

# 2.1. Study site

Fish interception, tagging, fishing gear treatment, and release took place on the Seton River, a tributary of the Fraser River, British Columbia, approximately 5 km upstream from the Seton River-Fraser River confluence (Fig. 1). Gates Creek sockeye salmon are an early summer-run population that had already migrated approximately 364 km from the Fraser River mouth to reach our experimental field site in the year of this study (2017). Their destination, the spawning area at Gates Creek, involves a further 50 km migration through the Seton and Anderson Lakes, as well as negotiating the Seton Dam and fishway situated 100 m upstream of the field site. Successful passage of the Seton Dam fishway by adult sockeye salmon has been estimated at  $\sim$  90% over the past decade (Harrower et al., 2020). A manually operated gate at a fish weir located 800 m upstream from the mouth of Gates Creek diverts fish either to the entrance of an artificially enhanced spawning channel or allows them to pass further upstream into Gates Creek.

# 2.2. Fish interception

In 2017, sockeye salmon were intercepted using a river-spanning picket fence and trap constructed at the tagging site on the Seton River (Fig. 1). When all pickets were in place, salmon could not migrate



Fig. 1. Map of the Seton system. The location of the Seton system in Canada is shown by a diamond in the lower part of the figure. The locations of both PIT receivers are indicated by a star. The locations of Seton Dam and fish fences are also indicated on the map.

past the fence, except through a gap entrance to an enclosed holding area. Sockeye salmon were intercepted during their peak hours of migration by closing the fence for 10 h throughout the night and leaving it open during daylight hours for free fish passage upstream. Salmon were captured daily in the holding area between Aug 8th and Aug 20th, 2017.

A total of 214 fish (96 females and 118 males) were intercepted at the fish fence for this study. Of these fish, 96 were treated as controls (i.e., experienced no additional gear escape simulations), 39 experienced gillnet escape simulations, 37 experienced tangle net escape simulations, and 42 experienced seine net escape simulations. A subset of 120 fish had temperature-logging iButtons (iButton Thermochron model DS1921Z or DS1922L; Maxim Integrated, San Jose, CA, USA) installed on their PIT tags: 55 controls, 23 gillnet, 22 tangle net, and 20 seine net treated individuals.

# 2.3. Control fish and tagging

We used gastric tagging and biopsy procedures that have previously been validated for use with adult sockeye salmon with minimal impact on survival (Cooke et al., 2005). Individual control fish were removed from the holding area with a dipnet and transferred to a trough continuously supplied with river water for a condition assessment (wounds or scars, especially previous gillnet markings, and scale loss). Fish were excluded if they had pre-existing severe wounds, > 25%overall body scale loss, or old gillnet markings. This allowed us to eliminate fish that had been suspected to have previously encountered fishing gear prior in their migration, as we aimed to limit our study to single fishing gear encounters. Gross somatic energy (GSE; measured using a fish FatMeter Model FM 692, Distell, West Lothian, Scotland, UK) was used was to distinguish Gates Creek sockeye salmon from strays from other populations (Casselman et al., 2016), which were also excluded. Only sockeye salmon with FatMeter readings less than 2.7 (equivalent of a GSE less than 7.2 MJ/kg) were tagged as part of this study. Next, a 32 mm half duplex (HDX) passive integrated transponder (PIT) tag (Oregon RFID, Portland, OR, USA) was implanted into smoothed acetal Delrin tube sections (1.59 cm in diameter, 3.81 cm in length) to allow the tag to be inserted into the stomach (with a smoothed plunger) of Gates Creek sockeye salmon. The temperature logger (iButton Thermochron model DS1921Z or DS1922L; Maxim Integrated, San Jose, CA, USA) was installed on the PIT tag and programmed to record temperature every 30 min throughout the remaining migration.

These internal tags were waterproofed using Plasti Dip (Plasti Dip International, St. Louis Park, MN, USA). Visual identification of a tagged fish was possible by implanting an external 7.62 cm T-bar anchor tag (Floy Tag & Mfg. Inc., Seattle, TA, USA) into the dorsal musculature (Drenner et al., 2012). Small gill biopsies were also taken from each fish (approximately 3 mm from the tips of 2–3 gill filaments). These gill biopsies were taken for functional genomics analyses as part of a separate study. This biopsy procedure has been previously validated for use with adult sockeye salmon, and no impact on survival was found (Cooke et al., 2005).

# 2.4. Escape from fishing gear

A total of 118 sockeye salmon were subjected to a simulated escape from one of three fishing gear types: gillnet (N = 39), tangle net (N = 37), or beach seine net (N = 42). A 5.25-inch (13.3 cm) mesh gill net (the size most commonly used to target Fraser River sockeye) was either loosely strung as a tangle net with a high hang ratio or tightly strung as a gillnet with low hang-ratio. The beach seine net consisted of a sinking lead line, floating line, and 2-inch mesh netting strung in between (the mesh size was small enough to preclude net entanglement). A simulated escape from the fishing gear was performed immediately prior to tagging using an enclosed experimental arena that allowed recapture of the fish should they escape by themselves ahead of a timed encounter.

For a simulated gillnet entanglement, a fish was released directly in front of a small (60 cm  $\times$  60 cm) section of the gillnet into which they swam and remained entangled for up to 1 min (or less if they escaped by themselves). A dipnet strategically held behind the gillnet enabled immediate capture of volitional escapees. Escape was simulated by quickly cutting the netting after 1 min so that the fish could escape directly into the awaiting dipnet without air exposure. For a simulated tangle net exposure, fish were wrapped in a loosely strung section of netting suspended underwater by two floats. Tangle net contact was from head to tail, unlike the tight opercular contact with the gillnet treatment. Again, after a maximum of 1 min of tangle net entanglement, escape was simulated by quickly unwrapping and/or cutting the netting. For a simulated seine net exposure, a fish was corralled towards a sandy-rocky bank within the experimental arena using a small section of seine net, which forced the fish to escape under the lead line into the waiting dipnet within 1 min. All treatment fish were transferred by dipnet to the trough for tagging and biopsy.

#### 2.5. PIT telemetry

Fish were released on the upstream side of the fish fence to continue their migration. Migration was monitored by three PIT receiver antennas installed between the Seton fish fence and the Gates Creek spawning channel (see Fig. 1). The first two antennas (see Casselman et al., 2016 for a full description) were located at the Seton Dam fishway entrance and exit. Fish detected at the final antenna (a 16 m long and 1 m diameter pass-through antenna constructed from PVC piping installed approximately 100 m upstream from the mouth of Gates Creek and spanning the entire creek) were considered to have successfully completed their spawning migration.

#### 2.6. Recovery of carcasses

Daily surveys at the artificial spawning channel and weekly walking surveys of the lower 6 km of Gates Creek allowed the research team to identify carcasses of tagged fish. Temperature loggers were recovered from these fish that had completed their spawning migration. A total of 47 temperature loggers were retrieved from carcasses. For females, spawning success was assessed from egg retention in carcasses. Female carcasses were dissected and visually assessed for egg retention. Those females with fewer than 500 eggs remaining (as estimated through the visual assessment) were determined to be successful spawners. Females with greater than 500 eggs remining were determined to be unsuccessful spawners as egg retention was too high (see Shaw, 1994; Bass et al., 2018a).

# 2.7. Time for gillnet escape

A separate study used a different set of Gates Creek sockeye salmon (N = 155) to investigate a much longer simulated gillnet entanglement (up to 35 min). Exactly the same procedures as described above were used except that the maximum gillnet entanglement time was 35 min (unless they successfully escaped earlier) at which time fish were released by cutting the gill net. The number of fish that were capable of volitional escape and their duration of gillnet entanglement was recorded.

#### 2.8. Statistical analyses

Migration into the dam fishway, through the fishway (200 m) and to the spawning area (50 km) was determined from PIT detections at the receivers. The data were treated as binary: a presence or absence at a receiver. Migration success to each of these sites was compared among the treatment groups (control, gillnet, tangle net, and seine net) through mixed effects factorial logistic regression models using the glmer() function of the "lme4" package (Bates et al., 2015). In these models, treatment, sex, fork length, and GSE were included as fixed effects and tagging date was included as a random effect to account for any differences in migration success due to date of tagging. Beyond migration success through the Seton Dam raceway and to Gates Creek, migration time (in days, hours, and mins) was determined as the difference in time between fish release and first detection at each PIT receiver (separate models were constructed for migration time to Seton Dam fishway exit receiver and Gates Creek). Data were tested for normality using the Shapiro-Wilk test and log transformed where data were determined not to be normally distributed. Normality of log transformed data was confirmed again using the Shapiro-Wilk test. Differences in migration time between treatment groups were tested using linear mixed effects models using the *lmer(*) function from the "lme4" package (Bates et al., 2015). These models included treatment, sex, fork length, and GSE as fixed effects and tagging date as a random effect. Where no significant effect was found, gear treatment groups (gillnet, tangle net, and seine net escape) were pooled into a single treatment group to increase statistical power to repeat the above comparison of migration success or migration rate for escaped fish against control fish.

Egg retention in female carcasses was used to assess spawning success as a binary factor: either successful or failed spawners. The impact of gear escape on spawning success was tested using mixed effects factorial logistic regression models using the *glmer()* function from the "Ime4" package (Bates et al., 2015). In this model, treatment, fork length, and GSE were included as fixed effects. Date of arrival to Gates Creek (first detection at Gates Creek PIT receiver) was included as a random effect to account for any differences due to date of arrival to spawning grounds. Again, where no significant effect was found, gear treatment groups were pooled into a single treatment group to increase statistical power to compare spawning success for escaped fish against control fish.

Thermal experience of individual fish was downloaded from the temperature logger and compared with PIT receiver records. The average temperature during migration was calculated through Seton Lake, Anderson Lake, and both lakes combined. The temperature on entry into Seton Lake was determined as the first temperature recording following the last PIT detection at the fishway exit. The temperature on leaving Anderson Lake was determined as the final temperature recording before the first detection at the Gates Creek PIT receiver. Portage Creek separates Seton and Anderson Lakes and the time spent in Portage Creek was determined by looking at individual thermographs, which were much higher (typically 19 - 20 °C) compared with lake

migration (typically below 16 °C) and from which the timespan between exit from Seton Lake and entry into Anderson Lake could be estimated. We also calculated the proportion of time fish spent migrating at temperatures within their optimal temperature window. The optimum temperature for maximum aerobic scope ( $T_{OPT}AS$ ) of Gates Creek sockeye salmon is 16.4 °C and Fraser River sockeye salmon are thought to require 90% of this maximum to their complete migration (Eliason et al., 2011), which is possible between 13.4 and 19.5 °C. We therefore calculated the proportion of lake migration at a temperature that permitted 90% of maximum aerobic scope as per Minke-Martin et al. (2018).

Associations between average migration temperature and the proportion of time spent at or above 90% of  $T_{OPT}AS$  were tested using Pearson's correlation analysis. We performed Shapiro-Wilk's normality tests and log transformed where data were determined not to be normally distributed. Additionally, differences in average migration temperature and proportion of time spent at or above 90% of  $T_{OPT}AS$  were tested among treatment groups using linear regression models. These models included treatment (control fish or 'escapee' fish that experienced gear escape) and sex as covariates. Due to the low treatment sizes for fish fitted with temperature loggers, gear treatment groups previously determined to cause significant behavioural changes compared with the control (the gillnet and seine net escapes) were pooled into a single treatment group for comparison with control fish.

#### 3. Results

#### 3.1. Migration and spawning success

Overall, 95.2% of the 214 tagged Gates Creek sockeye salmon successfully exited the Seton Dam fishway and 78.2% successfully reached Gates Creek. Neither treatment group (gillnet, tangle net or seine net) nor any other explanatory variables (sex, fork length, or GSE) significantly affected migration success though the Seton Dam fishway or to Gates Creek (Table 1). When pooled into a single group, the gear escape treatment group also had similar migration success though the Seton Dam fishway (97.5% success) compared with control fish (95.8%; logistic mixed effects model; p = 0.50), and similar migration success to Gates Creek (83.1% success) when compared with control fish (77.1% success; logistic mixed effects model; p = 0.34).

Of the 44 recovered female carcasses, 47.7% had successfully spawned. No explanatory variables were found to significantly affect spawning success (Table 1). Similarly, when all gear escape treatment groups were pooled, we found the gear escape treatment group had similar spawning success (41.7%) compared to control fish (55.0%; logistic mixed effects model;p = 0.52).

# 3.2. Migration duration

Fish in both the gillnet escape and beach seine escape treatment groups took significantly longer to migrate through the Seton Dam fishway and to Gates Creek (Fig. 2) compared to control fish (Table 1). To negotiate the Seton Dam fishway, fish in the gillnet treatment took 53% longer (20.0  $\pm$  16.5 h; p=0.008) and fish in the seine treatment 64% longer (21.5  $\pm$  16.5 h; p=0.0009) compared with control fish  $(13.1 \pm 13.3 \text{ h})$ . The tangle net treatment took 19% longer (15.6  $\pm$  12.4 h; p = 0.26) to pass the Seton Dam fishway compared to the control fish, however this difference was not statistically significant. To migrate to Gates Creek, the gillnet treatment took 17% longer (14.7  $\pm$  4.2 days; p=0.02) and the seine treatment 18% longer (14.9  $\pm$  4.2 days; p=0.014) compared with control fish (12.6  $\pm$  3.6 days). The tangle net treatment took 13% longer (14.2  $\pm$  4.5 days; p=0.11) to migrate to Gates Creek compared with control fish, however this difference was not statistically significant. The full statistical comparison of migration success rates and migration times across all treatment groups is presented in Table 3. We also found that GSE was positively associated

#### Table 1

Model results for logistic and linear regression models testing the effects of treatment, and sex on various response variables related to migration success, time, and temperature. Significant findings (p < 0.05) are boldened. Treatments refer to either gillnet (G), seine net (S), or tangle net (T) escape simulations.

				Model Parameters		
Response variable	Model Type	Ν	Explanatory variable	β	SE	р
Success past Seton Dam	Logistic mixed effects	214	Treatment (G)	-0.06	0.95	0.95
			Treatment (S)	0.61	1.15	0.60
			Sex (M)	0.43	0.88	0.63
			Fork Length	-0.17	0.14	0.21
			GSE	-0.10	0.78	0.90
Migration time past Seton Dam	Linear mixed effects	206	Treatment (G)	0.49	0.18	0.008
			Treatment (S)	0.59	0.18	0.0009
			Treatment (T)	0.21	0.18	0.26
			Sex (M)	-0.08	0.14	0.60
			Fork Length	-0.02	0.02	0.36
			GSE	-0.08	0.15	0.57
Success to	Logistic	214	Treatment	-0.18	0.46	0.69
Gates Creek	mixed effects		(G)			
			Treatment (S)	0.39	0.49	0.43
			Treatment (T)	1.25	0.66	0.06
			Sex (M)	0.21	0.39	0.59
			Fork Length	0.02	0.06	0.81
			GSE	-0.26	0.37	0.48
Migration time to Gates Creek	Linear mixed effects	172	Treatment (G)	1.58	0.87	0.02
Gutes Greek	cifeetb		Treatment (S)	2.02	0.81	0.014
			Treatment (T)	0.99	0.82	0.23
			Sex (M)	0.20	0.65	0.76
			Fork Length	-0.16	0.11	0.13
			GSE	2.52	0.68	0.00031
Spawning	Logistic	44	Treatment	-1.52	1.23	0.22
success	mixed effects		(G)			
			Treatment (S)	0.28	0.82	0.73
			Treatment (T)	-0.7	0.88	0.43
			Fork Length	0.03	0.14	0.85
			GSE	-0.87	0.69	0.21

with increased migration duration to Gates Creek (p = 0.00031; Table 1). We found no effect of sex or fork length on migration duration in this study (Table 1).

# 3.3. Thermal selection

Temperature loggers were recovered from 47 carcasses. The average migration temperature through Seton Lake was 14.9  $\pm$  1.6 °C. The average migration temperature through Anderson Lake was significantly lower compared with Seton Lake (12.7  $\pm$  1.12 °C; Welch's two sample t-test; t = 7.64, p = <0.0001). The combined gillnet and seine treatment group experienced a significantly cooler average temperature (14.0  $\pm$  1.7 °C) migrating through Seton Lake compared with control fish (15.3  $\pm$  1.7 °C; p = 0.035, Fig. 3), but not while migrating through Anderson Lake (p = 0.78, Table 2). Average Seton Lake migration temperature of tangle net treatment fish was cooler than that of control fish, however this difference was not significantly significant (14.7  $\pm$  1.4 °C; p = 0.36). The treatment groups also spent the same proportion of time at or above 90% of their T<sub>OPT</sub>AS (p = 0.54; Table 2).

During tagging in the Seton River, fish experienced temperatures from 16.5 °C to 20 °C. Those fish that experienced warmer temperatures during tagging migrated through both Seton and Anderson Lake at a cooler temperature (Pearson correlation; p = 0.041, r = -0.32; Fig. 4A). Warmer tagging temperature was also associated with spending more



**Fig. 2.** (A) Migration time to pass Seton Dam (as defined by time of release following tagging to final detection at dam fishway exit PIT receiver) across all treatment groups for both sexes combined. Fish that experience gill net and seine net escape simulation take significantly longer to pass Seton Dam compared to control fish. (B) Migration time to Gates Creek spawning grounds (defined as time of release following tagging to first detection at PIT receiver located at the mouth of Gates Creek). Fish that experience gill net and seine net escape simulation take significantly longer to Gates Creek compared to control fish. For each boxplot, the centre black line of the box indicates the median, the upper and lower box limits represent the first and third quartiles, the whiskers represent 1.5 times the inter-quartile range, and the points represent outliers. For each group, the mean migration time in days to Gates Creek is shown by a large black circle.

time below 13.4 °C in both lakes, a temperature below 90% of their  $T_{OPT}AS$  (Pearson correlation; p = 0.066, r = -0.29; Fig. 4B).

#### 3.4. Time for volitional gillnet escape

Of 155 fish tested with a longer simulated gillnet entanglement, 72 (46.5%) escaped volitionally in less than 35 min, ranging from 1 s to 22 min entanglements. Of the escaped group, 56.9% of salmon escaped in less than 10 s and 72.2% escaped in less than 1 min

#### 4. Discussion

We compared the consequences of escape from three gear types on migration success and behaviour of a single population of sockeye salmon (Gates Creek) that had been intercepted during the late stages of riverine spawning migration. Contrary to our initial hypothesis, we found escape from a simulated gear entanglement had no effect on either migration success or spawning success in this study. Instead, migration duration increased significantly after escape from gillnet and seine net entanglement, but not for tangle net escapees or immediate dipnet

#### Table 2

Linear regression model results for thermal experience during migration through Seton Lake, Anderson Lake, and proportion of time spent in  $T_{OPT}AS$  (13.4 – 19.5 °C) during lake migration. Explanatory variables included in these models include treatment (control fish vs fish that experienced gillnet and seine net escape combined 'GS' or fish that experienced tangle net escape 'T'), sex, tagging temperature (the water temperature the fish experienced during tagging procedures), and wound (scored as either 0, 1, or 2 depending on severity of the wound). Significant explanatory variables (at p < 0.05) are boldened.

				Model Parameters		
Response variable	Model Type	Ν	Explanatory variable	β	SE	р
Mean temp Seton Lake	Linear regression	47	Treatment (GS)	-1.01	0.50	0.036
	-		Treatment (T)	-0.60	0.64	0.36
			Sex (M)	0.34	0.53	0.52
			Wound (1)	-0.10	0.63	0.88
			Wound (2)	-0.26	0.78	0.74
Mean temp	Linear	47	Treatment	0.10	0.34	0.78
Anderson Lake	regression		(GS)			
			Treatment (T)	0.23	0.42	0.60
			Sex (M)	0.15	0.36	0.68
			Wound (1)	-0.02	0.43	0.96
			Wound (2)	-0.37	0.54	0.50
Proportion of	Linear	47	Treatment	0.02	0.04	0.56
time in T <sub>OPT</sub> AS	regression		(GS)			
			Treatment (T)	0.08	0.05	0.14
			Sex (M)	0.03	0.04	0.44
			Wound (1)	-0.01	0.05	0.79
			Wound (2)	0.03	0.07	0.69

#### Table 3

Summary of migration success and migration time ( $\pm$  standard error) of fish to both Seton Dam fishway exit and Gates Creek spawning grounds for each gear escape treatment group (C = control, G = gillnet escape, S = seine net escape, T = tangle net escape) and for both males (M) and females (F). The average migration temperatures ( $\pm$  standard error) of fish through both Seton and Anderson Lakes is also shown.

	Treatment			Sex		
	С	G	S	Т	М	F
Success past Seton Dam (% surviving)	95.8	94.9	97.6	100	96.6	96.9
Migration time past Seton Dam (hrs)	$\begin{array}{c} 13.1 \\ \pm \ 13.3 \end{array}$	20 ± 17.1	$\begin{array}{c} 21.5 \\ \pm \ 16.5 \end{array}$	15.6 ± 12.4	$\begin{array}{c} 15 \\ \pm \ 13.4 \end{array}$	$\begin{array}{c} 18.3 \\ \pm \ 16.4 \end{array}$
Success to Gates Creek (% surviving)	77.1	74.4	83.3	91.8	82	78
Migration time to Gates Creek (days)	$\begin{array}{c} 12.6 \\ \pm \ 3.6 \end{array}$	$\begin{array}{c} 14.7 \\ \pm \ 4.2 \end{array}$	$\begin{array}{c} 14.9 \\ \pm \ 4.2 \end{array}$	$\begin{array}{c} 14.2 \\ \pm \ 4.5 \end{array}$	$\begin{array}{c} 13.5 \\ \pm \ 3.4 \end{array}$	14.1 ± 4.9
Number of fish per group	96	39	42	37	118	96
Spawning success	55	20	60	33.3	-	-
Number of fish per group	20	5	10	9	-	44
Average Temperature Seton Lake (°C)	15.3 ± 1.7	$\begin{array}{c} 13.8 \\ \pm \ 2.2 \end{array}$	14.1 ± 1.5	14.7 ± 1.4	15.2 ± 1.6	14.4 ± 2.1
Average Temperature Anderson Lake (°C)	12.6 ± 1.0	13.0 ± 1.5	$\begin{array}{c} 12.3 \\ \pm \ 1.0 \end{array}$	$\begin{array}{c} 12.9 \\ \pm \ 0.3 \end{array}$	$\begin{array}{c} 12.7 \\ \pm \ 0.9 \end{array}$	$\begin{array}{c} 12.6 \\ \pm \ 1.2 \end{array}$
Number of fish per group	21	5	7	9	27	15



Fig. 3. Temperature of migration through both Seton and Anderson lakes. Fish from gillnet and seine net escape treatment groups were pooled into a single treatment group and compared with control fish. Because differences in behaviour following tangle net simulations had previously been identified, fish from this treatment group were kept separate for these analyses. Fish that experienced gillnet or seine net escape migrated at significantly cooler temperatures through Seton Lake compared with control fish that did not encounter any fishing gear. For each boxplot, the centre black line of the box indicates the median, the upper and lower box limits represent the first and third quartiles, the whiskers represent 1.5 times the interquartile range, and the points represent outliers. Group means are shown by a large black

в

0

8 o

19.5

0

19.0

Fig. 4. Plots showing the relationship between water temperature at the time of tagging and average temperature during Anderson Lake migrations (A), and proportion of time fish spent in T<sub>OPT</sub>AS window (13.4 – 19.5 °C) during their lake migration (B).

release. Thus, we provide experimental support for our hypothesis that migration behaviour is differentially impacted according to the type of fishing gear interaction, with a simulated tangle net escapement being the least impactful of the gears compared. In addition, we found support for our second hypothesis that fish will behaviourally select cooler water following fishing gear interactions because fish experiencing gillnet and seine net entanglements typically migrated through Seton Lake at cooler temperatures compared with control fish. Consequently, despite simulated gear escape having no direct impacts on mortality or spawning success for this population of sockeye salmon, escape from a gillnet or a seine net did modify their behaviour to facilitate recovery and enhance survival following their escape (in a manner proposed below).

Our discovery of no impact on migration survival or spawning success of simulated gear escape for Gates Creek sockeye salmon captured on the Seton River contrasts with earlier studies (Donaldson et al., 2012; Bass et al., 2018b). Indeed, such a difference adds to the recognized importance of context, in that any negative consequences of fishing gear interactions can depend on both the population and the fishery location. For example, survival of late-run Shuswap sockeye salmon following gillnet and seine net capture increased substantially as they got closer to their spawning areas (Bass et al., 2018b). Faced with 500 km river and lake migration, salmon survival after capture with either gillnets or seine nets improved considerably at locations closer to spawning grounds (35% survival after 10% of the migration, 46% after 26% of the migration and 75% after 72% of the migration). Our study followed Gates Creek sockeye salmon after they had already completed about 88% of their freshwater migration, and so subsequent survival was expected to be high. Clearly, resilience to fisheries interactions that impose stress and injury increases as a salmon matures and has left seawater. The physiological changes that promote this resilience likely include a

thickening of skin (Robertson and Wexler, 1960), scale reabsorption (Kacem et al., 1998), an increase in baseline plasma cortisol levels (Baker and Vynne, 2014), and completion of the physiological changes needed to transition from sea water to fresh water (Shrimpton et al., 2005). Also, a post-escape river migration (e.g., the Shuswap salmon study; Bass et al., 2018b) is more challenging than a post-escape lake migration, as in our study, which has an added benefit of offering thermal refugia and no hydraulic challenges after Seton Dam fishway passage. Thus, from a fisheries management perspective, survival to spawning grounds can be more favorable when the salmon fishery is closer to the spawning area. Moreover, tangle net simulations were less likely to impact migration rate for Gates Creek sockeye salmon than either gillnet or seine net simulations. The mechanistic basis for this gear-type difference warrants investigation. Further considerations for fishery managers include the roles of handling, forceful removal, and air exposure. While previous research on fisheries interactions has involved air exposure, we deliberately simulated a volitional escape by avoiding air exposure, reducing handling, and using no forceful removal from gear.

Our observation that salmon experiencing a simulated gillnet or seine net escape took longer to reach spawning grounds is consistent with other telemetry research assessing migration rate following fisheries interactions (Mäkinen et al., 2000; Frank et al., 2009, 2019). Such migration delays likely relate in part to 'repaying' an oxygen debt (Lee et al., 2003) from anaerobic swimming while escaping before continuing their migration. Complete recovery from full exhaustion may take up to 24 h (Zhang et al., 2018), but fatigued salmon can resume swimming much sooner (after 40-60 min; Jain et al., 1998; Lee et al., 2003; Jain and Farrell, 2003; Wagner et al., 2006). The  $\sim$  6 h delay to negotiate the Seton Dam fishway is consistent with these sorts of known recovery

periods. In fact, Gates Creek sockeye salmon seemed adept at escaping the gillnet since we observed nearly three quarters of the fish escape within 1 min. We also found that higher GSE in sockeye salmon was associated with increased migration time to spawning grounds for these fish. GSE values represent endogenous energy reserves which Pacific salmon rely on to fuel the entirety of their upstream migrations and sexual maturation (Gilhousen, 1980; Crossin et al., 2004). Our finding complements that of Bass et al. (2018a) who found that higher GSE was associated with reduced migration survival and spawning success for Gates Creek sockeye salmon tagged at the Seton River fish fence. The authors suggest that higher GSE late in the migration could be indicative of previous stress (Baker et al., 2013) and failure to mature and develop secondary sexual characteristics, and thus contributed to reduced migration and/or spawning success.

A migration delay has been previously shown to be associated with reduced Pacific salmon survival (Caudill et al., 2007) and potentially maladaptive spawning ground activity (Dickerson et al., 2005; Richard et al., 2014). An obvious reason for such impacts of a migration delay for salmon is that they do not feed during the migration and must fuel both the migration and the sexual maturation with an endogenous lipid store. Indeed, Rand et al. (2006), who modelled the energetics of sockeve salmon migrations in the Fraser River, found that transit time is one of the largest determinants of energy use. All the same, the  $\sim$ 2-day delay after a gillnet and seine net encounter that we observed here did not negatively impact survival or egg retention in Gates Creek sockeye salmon. We believe that the temperature-logging iButtons provided a valuable insight into why this was the case. Fish migrated at an average temperature through Seton Lake that was > 1 °C cooler compared with control fish (14.0 °C vs 15.3 °C). While previous research has shown Gates Creek sockeye salmon with more severe gillnet injuries selected cooler temperatures in Seton and Anderson Lakes (Bass, 2018), and that this form of behavioural thermoregulation could reduce stress (Goniea et al., 2006), aid in healing wounds (Jensen et al., 2015), and defend against infection (Mathes et al., 2009; Bradford et al., 2010), our data allows us to quantify the potential benefit of conserving energy (Roscoe et al., 2010). Because the basic energy need of a fish (SMR, standard metabolic rate) decreases by about 10% per degree Celsius (Brett, 1971; Lee et al., 2003; Steinhausen et al., 2008; Eliason et al., 2011), a Gates Creek sockeye salmon would accrue an approximately 10% saving of their energy store by behaviourally choosing to migrate at a 1 °C cooler temperature, all things being equal. Remarkably, the increased SMR energy cost of the  $\sim$ 2 day delay to a normally  $\sim$ 12 day lake migration was quantitatively similar (17-18%). Indeed, female Gates Creek sockeye salmon with lower gross somatic energy (GSE) levels have previously been shown to migrate at cooler temperatures through Seton and Anderson Lakes, perhaps as an energy saving behaviour (Roscoe et al., 2010).

To further examine energetic considerations, cost of transport (COT) was estimated from the standard metabolic rate (SMR), average migration speed and water temperature of the current study for Gates Creek sockeye salmon based on empirical data found in Lee et al. (2003). The SMR of Gates Creek sockeye salmon migrating would be 13.1 mg O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup> at 15.3 °C (the average migration temperature of control fish in this study) versus 12.6 mg O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup> at 14.0 °C (the average Seton Lake migration temperature of escaped fish in this study). Migration at the cooler temperature, therefore, would reduce SMR of escaped Gates Creek sockeye by 4.1% compared with control fish. Consequently, the average COT (COT = SMR / migration speed) for control fish migrating through Seton Lake at an average speed of 2.66 m/min (49 km in 12.7 days) and at an average temperature of 15.3 °C, COT would be 4.93 mg  $O_2$  kg<sup>-1</sup> m<sup>-1</sup>. For the gillnet and seine net escapees migrating at an average speed of 2.29 m/min (49 km/14.8 days) and at an average temperature of 14.0 °C, COT increased by 11.8% to 5.51 mg O<sub>2</sub> kg<sup>-1</sup>m<sup>-1</sup> and would be 16.6% higher had they not selected a cooler lake migration. These calculations support the idea that thermal selection for cooler water following gear escape is a behavioural response to slow the

progressive depletion of GSE. Consequently, the potential for behavioural thermoregulation following a fisheries interaction is an important consideration for fishery managers.

Finally, previous observational studies on salmon spawning grounds found a high percentage of fish with external markings consistent with earlier gillnet entanglement and escape (Baker and Schindler, 2009; Bass et al., 2018a; Kanigan et al., 2019). While such observation can infer volitional escape, the previous experience of that fish is unknown and also a lack knowledge of the number of fish that died before reaching the research sampling sites. The implication is that the number of escapees is higher than estimated, some having died en-route. Indeed, we observed that, of the sockeye experimentally entangled in gillnets, 46.5% escaped within 35 min, which is considerably higher than escapee estimates for observational studies at the same location (19-27% from 2014 to 2016; Bass et al., 2018a; Kanigan et al., 2019). Thus, a significant proportion of escapees may not reach the spawning area. Indeed, Bass et al. (2018a) found that for fish with gillnet markings, en-route mortality was increased by 16% and female pre-spawn mortality was increased by 18%. Furthermore, 51% of fish with gillnet markings (assumed to have escaped) failed to reproduce (Baker and Schindler, 2009). Thus, clear evidence exists for gear escape having numerous lethal and sub-lethal impacts on sockeye salmon. Yet, gear escape is not explicitly incorporated into fishery impact models for sockeye salmon in Canada.

# 5. Conclusions

We found no impact on survival for migrating Gates Creek sockeye that escaped from a simulated experimental gillnet and seine net encounter, but their migration was significantly delayed, and they behaviourally selected a cooler temperature for their lake migration in possible response to gear escape. Gear escape is currently not considered in escapement estimate models used by fisheries managers to sustainably regulate salmon fisheries. Here we demonstrate that gillnet escape is a common occurrence with the potential to reduce survival and spawning success, and thus current escapement estimates may be an over-inflation (previously recognized by Baker and Schindler, 2009 and Baker et al., 2014). We present calculations that indicate the behavioural thermoregulation represented a possible energy-saving strategy that would have helped offset the added depletion of energy stores incurred by the delay in migration. The observation of differential thermal experience by fish that escaped is fascinating and more work is needed to understand if the fish are actively seeking out cooler temperatures or if the consequences of the fisheries interaction is such that impaired behaviour simply results in cooler thermal experiences. To our knowledge this is one of the first studies of fish that suggests the potential for behavioural thermoregulation to be a mechanism for mediating fisheries stressors.

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#### CRediT authorship contribution statement

Laura K. Elmer: Methodology, Formal analysis, Investigation, Writing – original draft, Visualization. David L. Moulton: Methodology, Writing – review & editing. Andrea J. Reid: Methodology, Writing – review & editing. Anthony P. Farrell: Conceptualization, Writing – review & editing, Funding acquisition. David A. Patterson: Conceptualization, Writing – review & editing. Brian Hendriks: Investigation, Writing – review & editing. Steven J. Cooke: Conceptualization, Writing – review & editing, Supervision, Funding acquisition. Scott G. **Hinch**: Conceptualization, Writing – review & editing, Supervision, Funding acquisition.

#### **Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### L.K. Elmer et al.

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