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Field assessments of heart rate dynamics during spawning migration of wild and hatchery-reared Chinook salmon

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During spawning, adult Pacific salmonids (*Oncorhynchus* spp.) complete challenging upriver migrations during which energy and oxygen delivery must be partitioned into activities such as locomotion, maturation and spawning behaviours under the constraints of an individual's cardiac capacity. To advance our understanding of cardiac function in free-swimming fishes, we implanted migrating adult Chinook salmon (*Oncorhynchus tshawytscha*) collected near the mouth of the Sydenham River, Ontario, with heart rate (f_H) biologgers that recorded f_H every 3 min until these semelparous fish expired on spawning grounds several days later. Fundamental aspects of cardiac function were quantified, including resting, routine and maximum f_H, as well as scope for f_H (maximum−resting f_H). Predictors of f_H were explored using generalized least-squares regression, including water temperature, discharge, fish size and fish origin (wild versus hatchery). Heart rate was positively correlated with water temperature, which aligned closely with daily and seasonal shifts. Wild fish had slower resting heart rates than hatchery fish, which led to significantly higher scope for f_H. Our findings suggest that wild salmon may have better cardiac capacity during migration than hatchery fish, potentially promoting migration success in wild fish.

This article is part of the theme issue 'Measuring physiology in free-living animals (Part I)'.

1. Introduction

Pacific salmon species (*Oncorhynchus* spp.) undertake some of the most challenging migrations in the animal kingdom, often travelling hundreds of kilometres up rivers to reproduce [1]. Like most fish, the capacity of salmonids to perform physical activities (e.g. swimming) depends on their aerobic metabolic capacity to produce energy, which in turn is determined by the cardiovascular system's ability to supply tissues with oxygen and nutrients [2–6]. Fish can adjust cardiovascular function by altering stroke volume, but for most fish, this is primarily achieved through increases in heart rate (f_H; [7]). During migrations, cardiovascular function is critical to whole animal performance, as these movements are often the most challenging periods of an animal's life cycle [8,9]. This is particularly so for semelparous salmonid species, which have a single opportunity to reproduce following a migration, which often requires prolonged periods of aerobic swimming and repeated burst (anaerobic) swimming events to traverse high-velocity river reaches [10–12]. Indeed, the collapse of cardiac function during migration has been hypothesized as the physiological mechanism behind pre-spawn mortality in Pacific salmon [5,13]. A thorough understanding

of cardiac performance during migration and the factors affecting cardiac physiology is, therefore, prudent to effectively conserve and manage Pacific salmon populations [14].

Various biotic and abiotic factors may influence cardiac performance during salmonid spawning migrations. Warm water temperatures place a higher demand on the cardiovascular system to maintain tissue oxygen supply ([15]; see [16]). At high temperatures the heart may not have sufficient capacity to deliver necessary oxygen throughout the body, potentially leading to migration failure, and even death [5,13]. Similarly, biotic factors such as the body size or sex of a fish are known to influence metabolic rate [17,18]. Oxygen consumption rate and heart rate should scale universally with body mass in animals with closed circulatory systems (in theory: [19]), though this is often not the case [20]. This notion of cardiovascular scaling has yet to be thoroughly investigated in fish, although a study in Chinook salmon did not find evidence that heart rate scales with body mass [21].

Individual life-history, including rearing conditions, can influence animal phenotypes and has been shown to alter both cardiac morphology and physiology [22–24]. This suggests that cardiac performance could differ for fish reared in wild versus hatchery environments (a common practice for salmonid species; [25]). Farmed salmonids often display abnormalities associated with the orientation, shape and alignment of the heart in comparison with their wild counterparts [23]. According to Brijs *et al*. [24], a major contributing factor to cardiac abnormalities may be accelerated growth rates associated with early rearing stages—an outcome common in hatcheries where fish may be overfed and where metabolic expenditures are lower than in the wild [26]. Moreover, the speed of growth during early rearing stages (up to smoltification) has been linked to cardiac abnormalities (e.g. rounded ventricles) 1 year after hatchery exposure [27]. Morphological abnormalities associated with farmed and hatchery salmonids (i.e. ventricle shape and alignment) can result in impaired cardiac function, lowered swimming performance and elevated risk of mortality [23,27,28]. Indeed, it has been observed that reproductive fitness is lower in hatchery versus wild salmonids, indicating early rearing conditions do have long-term consequences on fitness-related traits [29,30]. Nevertheless, little is known about whether differences in rearing conditions can have lifelong impacts on heart function in salmonids. It has been documented that hatchery rearing environments explain a significant proportion of epigenetic variation in Pacific salmonids [31,32] and that conceivably these changes could lead to lifelong phenotypic alterations [33,34].

Whereas a substantial amount of information exists on cardiac function in salmonids, much of what we know has been derived from experiments conducted in captivity, which may oversimplify conditions in natural environments (discussed in [35]). Moreover, most information from previous assessments of cardiac performance during swimming stems from experiments conducted in a laboratory setting where fish have been tethered to recording equipment, while swimming in enclosed spaces, e.g. swim tunnels [5,8,36,37]. However, recent developments in biologging technology have increased our ability to assess the physiological performance of free-swimming fish in their natural environments [38]. To advance our understanding of cardiac function in fish within the natural environment, we implanted adult Chinook salmon (*Oncorhynchus tshawytscha*) from the Sydenham River (located in Owen Sound, Ontario) with heart rate (f_H) biologgers that monitored f_H during their upstream migration until fish expired on spawning grounds. Fundamental aspects of cardiac function were quantified, including resting, routine and maximum f_H, as well as scope for f_H (maximum−resting f_H; as per [39]). The influence of various biotic and environmental predictors was explored including the origin (wild versus hatchery), water temperature and body size of fish, as well as discharge. It was predicted that wild fish would have greater cardiac performance than hatchery fish (i.e. lower f_H and greater scope for f_H), that water temperature and discharge would both be positively correlated with f_H, and that larger fish would have lower f_H. Findings from this research will expand our knowledge on the cardiac physiology of wild fish in natural environments.

2. Methods

(a) Experimental animals and study site

Chinook salmon from the Great Lakes Basin have a similar life-history to that of anadromous Chinook salmon in their native range (i.e. the Pacific Ocean), but migrate into a large freshwater lake (Lake Huron) instead of migrating to the marine environment. Notably, the river migration of Chinook salmon in the Sydenham River is relatively short (less than 7 km) and not nearly as long or challenging as those completed in other watersheds such as the Columbia, Fraser, or Yukon River, where they may migrate over 1000 km upriver to reach natal spawning grounds. A wild population has become established in the Sydenham River in Owen Sound, Ontario, but is supported by hatchery supplementation that is completed by the local Sportsmen Association [40]. Broodstock are collected from the Mill Dam Fishway in Owen Sound (figure 1) in September and October and juveniles are raised at a hatchery on Weaver Creek, a tributary located approximately 3 km upstream from the mouth of the Sydenham River. Water is diverted to the hatchery from Weaver Creek, and fish are fed using timed feeding systems. Age-0 Chinook salmon are released back to the river each spring (discussed in [41]) and return as adult salmon to spawn after 2–4 years of feeding in Lake Huron [42,43]. These fish likely travel widely throughout the lake over the course of their life cycle before returning to natal streams [44].

Twenty male Chinook salmon were sampled from 8 to 11 October 2019 at the Mill Dam, located approximately 2 km upstream of the mouth of the Sydenham River, Ontario (figure 1). Fish were dip netted either from a collection basket at the exit of the Mill Dam fishway, or from a side channel that was temporarily filled with water to facilitate fish capture. Upon capture, the origin of each fish (wild versus hatchery) was determined based on the presence or absence of an adipose fin. Spawning sites are dispersed upstream of the dam throughout an approximately 5 km stretch of river below Inglis Falls (an impassable waterfall). The section of the river consisting of spawning grounds is generally quite shallow and fish likely must undertake burst-swimming to traverse high-velocity sections (see habitat footage: https://www.youtube.com/watch?v=faWQz_ANI_c). A hydrometric station (Environment Canada) records discharge every 5 min just upstream of Inglis Falls.

(b) Surgical procedures

A fish was transferred from its collection site to a surgical trough and was immobilized using a pair of electric fish handling gloves (Smith-Root, Vancouver, USA) operated at an output current of 10 mA (similar to [39]). Electric fish handling gloves are known to allow rapid physiological and behavioural recovery in

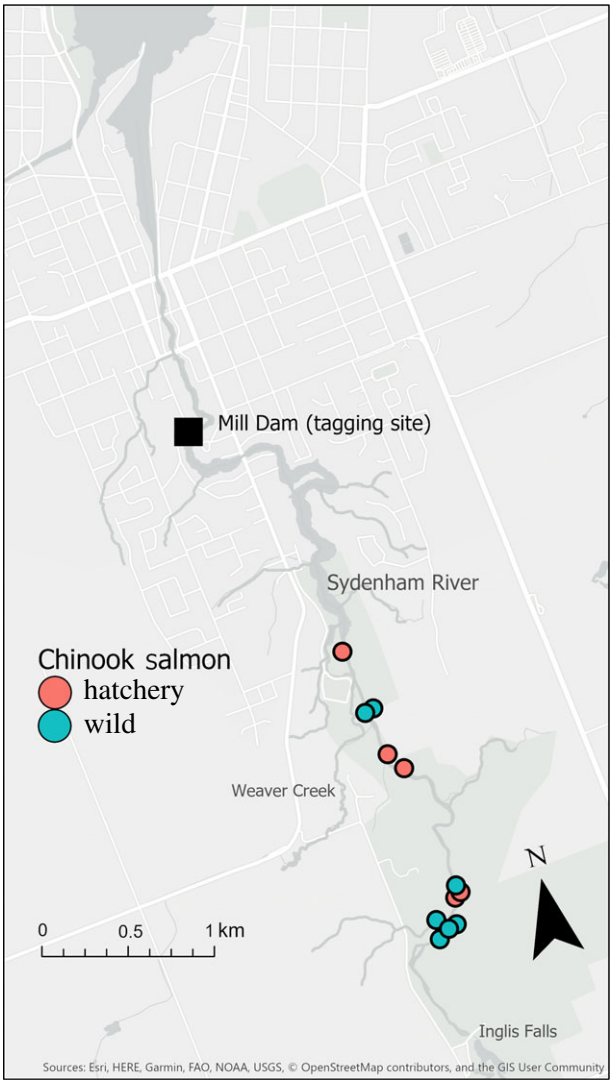

Figure 1. The study site, located on the Sydenham River, Ontario. Chinook salmon (*Oncorhynchus tshawytscha*) migrate from Georgian Bay (Lake Huron), south to the Sydenham River. Salmon were tagged at the Mill Dam, located 2 km upstream of the river mouth. Terminal locations are shown for hatchery (red symbols) and wild origin (blue symbols) Chinook salmon implanted with f_H loggers and radio telemetry transmitters. (Online version in colour.)

immobilized fish compared with chemical sedatives [45–47]. River water was pumped continuously over the gills during the entire surgical procedure. An incision of approximately 5 cm was made along the midline of the ventral surface of the fish, approximately 3 cm posterior to the pectoral girdle. An f_H logger (DST milli HRT (13 × 39.5 mm, 11.8 g), Star-Oddi, Iceland; http://www.star-oddi.com/) was placed adjacent to the pericardial membrane in the dorsal–ventral direction and was secured directly to the body wall using a 2–0 monofilament suture (PDS II polydioxanone suture). The f_H logger was attached to a radio telemetry transmitter (I80 (27 × 10 mm, 4.2 g), Sigma Eight, Aurora, Canada) with an approximately 8 cm piece of monofilament. The radio tag was placed in the body cavity posterior to the logger to reduce the likelihood of electrical interference on the f_H logger. The antenna of the radio telemetry transmitter was coiled and secured around the transmitter for ease of implantation, and to minimize internal tissue irritation from the antenna. Tag burden for the combined f_H logger and radio transmitter (16 g) was approximately 0.3% based on length–weight relationships for Chinook salmon in Ontario [48]. A study evaluating the influence of a 0.7% tag burden (15.1 g) and intracoelomic surgery in Atlantic salmon (*Salmo salar*) adults found no difference in endurance or blood physiology at various swim speeds compared with untagged controls ([49]; see [50]), suggesting our tag burden was suitable for our study animals. The incision was sealed using three single interrupted sutures (PDS II polydioxanone suture) and a spaghetti tag was tied behind the dorsal fin for visual identification. Following these procedures, the fish was immediately released upstream of the dam. Surgery equipment was immersed in povidone–iodine (Betadine) for sterilization prior to reuse in successive fish. Fish capture and surgery were conducted in accordance with the Canadian Council on Animal Care guidelines set by Carleton University (AUP no. 103 128).

(c) Data collection, processing and calculations

The f_H loggers were programmed to record temperature and f_H every 3 min at 125 Hz with a 4.8 s measurement period as recommended by the manufacturer for work on fish. Raw electrocardiogram (ECG) traces were measured every 9 min to validate the quality of calculated f_H measurements. Radio telemetry transmitters were programmed to emit a 10 ms pulse every 2.6 s. A radio telemetry receiver (SRX800, Lotek, Newmarket, Canada) and a three-prong Yagi antenna were used for active tracking to recover loggers from tagged fish. Active radio tracking surveys of the entirety of the spawning grounds were completed by foot on days four, nine and fifteen after the final fish had been tagged. Fish were located using zero-point tracking (i.e. successive gain reductions), which allowed tags to be identified to within 2 m^2. In most cases, tags were found along the shore or in shallow water outside of the carcass, with evidence of predation and/or scavenging nearby (e.g. scat, scales, vertebrae). f_H data were initially processed in the data logging software Mercury (Star-Oddi, Iceland) by determining the average R–R interval, i.e. the time between two consecutive R waves of the ECG (reflecting ventricular depolarization). Manual inspections of ECGs was completed in Pattern Finder (Star-Oddi, Iceland) for a subset of measurements (approx. 50 per logger) to validate f_H calculations. Based on this validation, only f_H data with a quality index of 0 were retained (a software-assigned measure of quality on a scale of 0–3) and all other observations were removed (as per [24]). For one logger, data with a quality index of 1 was retained because it had high alignment with validated ECG data. All measurements with a corresponding ECG were manually calculated to replace measurements that had a quality index of 1 or 2. A small proportion of ECGs (less than 1%) did not have discernable R waves and could not be calculated manually. The first 7.5 h of measurements were removed when quantifying f_H parameters for each fish to account for the f_H elevation associated with capture and surgical procedures (similar to recovery times in [3,39] for migrating salmonids). A fish was considered to have recovered from surgery once f_H had plateaued after an initial peak and had returned to or below routine f_H. All f_H measurements during the few hours (1–13 h per fish) prior to death when f_H quickly plummeted were also removed from calculations of resting/routine f_H, and were instead used in a separate analysis of the ECGs prior to death, including quantifications of R-wave amplitude (i.e. the largest upward deflection in a typical ECG) and the presence of arrhythmias (electronic supplementary material, figure S4). R-wave amplitude was measured as the difference (in mV) from the peak of the R-wave to the mean baseline during a measurement period (with the median value taken for that measurement period). Arrhythmias were identified as measurement sequences with irregular heart beats, and/or missing QRS complexes (i.e. the three graphical deflections on an ECG corresponding to ventricular depolarization). Longevity (days) was taken as the elapsed time between tagging and the last valid f_H observation before the fish expired. Migration distance was calculated as the distance along the river between

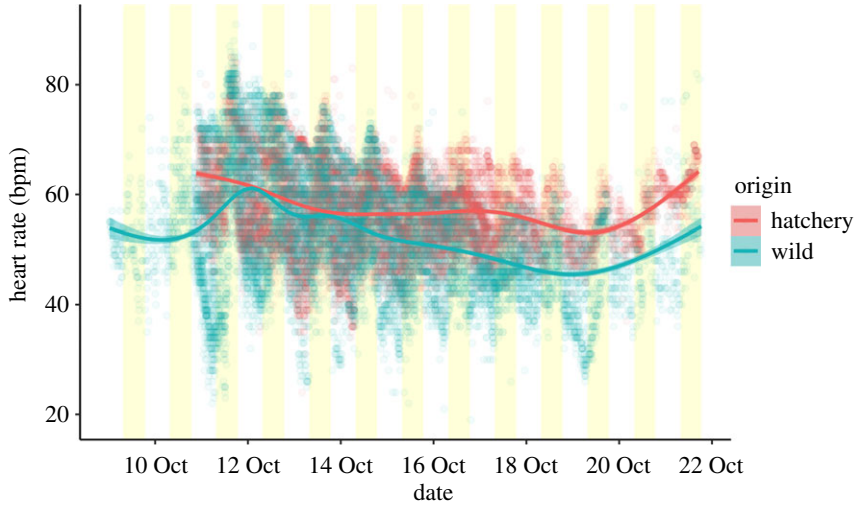

Figure 2. Diel cycles in the heart rate response in the hatchery ($n = 5$) and wild ($n = 7$) Chinook salmon (*Oncorhynchus tshawytscha*) from the Sydenham River, Ontario during the spawning migration. Data are presented over daylight (yellow) and night-time hours (white) though individual salmon would have been distributed throughout various locations in the river at any given point in time. A generalized additive model smoother is fitted for both hatchery and wild fish. (Online version in colour.)

Table 1. Water temperature and discharge (calculated as means over the study period), longevity, fork length and migration distance for wild and hatchery groups (i.e. origin). Values are presented as the means within groups with minimum and maximum values in parentheses, in addition to *t*- and *p*-values produced through one-way ANOVA models.

parameter	wild	hatchery	*t*-value	*p*-value
water temperature (°C)	10.7 (10.1–11.4)	10.4 (9.9–10.9)	1.0	0.4
discharge ($m^3\ s^{-1}$)	0.68 (0.65–0.75)	0.69 (0.65–0.77)	−0.3	0.8
longevity (days)	7.3 (4.9–11.3)	7.7 (5.5–10.7)	−0.3	0.8
fork length (mm)	708 (648–775)	668 (578–749)	1.3	0.2
migration distance (m)	3552 (2401–4141)	3042 (2024–3864)	1.1	0.3

Mill Dam and the recovery location of the carcass or tag on spawning grounds. Distances along the river were calculated using the *riverdist* package in R (see https://CRAN.R-project.org/package=riverdist). Resting f_H was calculated as the mean of the lowest 10% of f_H values over the course of the migration, routine f_H was taken as the mean of all f_H, whereas maximum f_H was taken as the highest 10% of f_H values (which likely underestimated maximum f_H, but we did not keep fish captive so could not force peak f_H through exercise; similar to [39]). Scope for f_H reflected the difference between maximum and resting f_H in an individual fish.

(d) Statistical analysis

Differences in water temperature, system-wide discharge (5 min resolution), longevity (days), migration distance (km) and fork length (mm) between wild and hatchery fish were assessed using separate one-way analysis of variance (ANOVA) tests. A linear regression model was used to evaluate the relationship between fork length and migration distance. Differences in resting f_H, maximum f_H, and scope for f_H between hatchery and wild salmon were assessed by separate one-way ANOVAs. The relationship between resting f_H and scope for f_H was modelled using linear regression. Predictors of f_H over the course of the migration were modelled using generalized least-squares regression with the 'gls' function in the *nlme* package in R [51]. The model included origin, water temperature, discharge and fork length as predictors. Nested effects by individual and temporal autocorrelation (time | ID) were specified using the correlation structure 'corAR1' [52] to account for repeated (temporally correlated) measurements taken from each individual (as per [53]). Visual inspection of residual plots did not reveal significant deviations from model assumptions [52]. No model reduction was attempted from the initial candidate model. Statistical significance was accepted at $p \leq 0.05$. Data and code for all analyses are available as electronic supplementary material.

3. Results

(a) Overview

Surgery was completed on 20 male salmon, with the entire procedure from tagging to release lasting 10.7 (8.5–16.7) min. f_H recovered to routine levels within a few hours of tagging (4.4 (1.75–6.4) h; electronic supplementary material, figure S1). Most fish ($n = 18$) completed their 2 km upstream migration to spawning grounds, and tags were recovered from 12 of these fish, including 7 of wild and 5 of hatchery origin. Environmental conditions over the course of the migration, including water temperature (10.5 (7.5–14.1)°C) and discharge (0.7 (0.6–1.3) $m^3\ s^{-1}$), did not vary significantly between wild and hatchery fish (i.e. origin, table 1). Similarly, no biotic

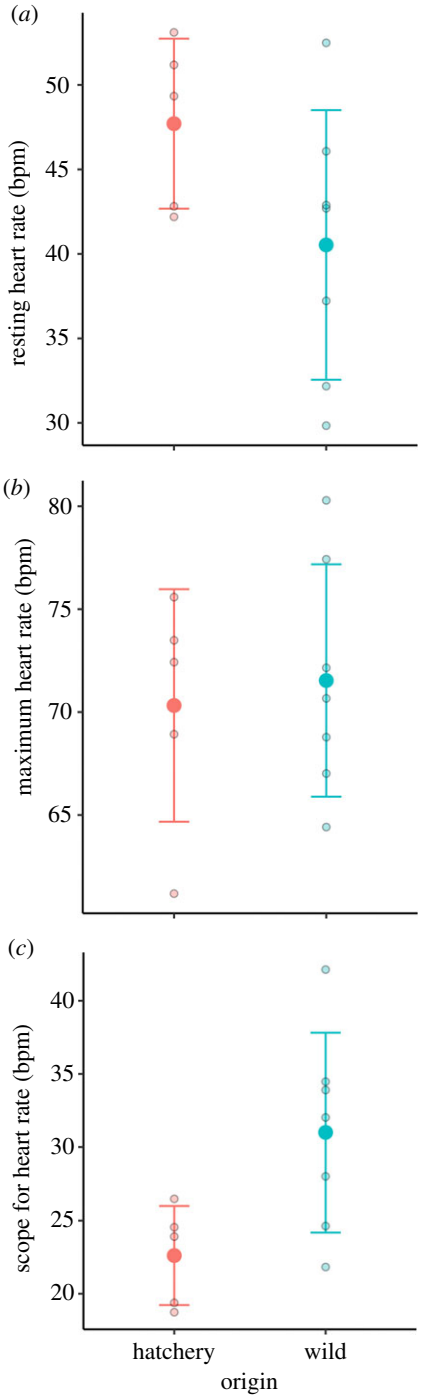

Figure 3. The figure illustrates (*a*) resting heart rate ($p = 0.09$), (*b*) maximum heart rate ($p = 0.75$) and (*c*) scope for heart rate ($p = 0.03$) in the hatchery ($n = 5$) and wild ($n = 7$) Chinook salmon (*Oncorhynchus tshawytscha*) from the Sydenham River, Ontario during the spawning migration. The data are presented as mean ± s.d. (Online version in colour.)

factors, including fork length (691 (578–774) mm), longevity after tagging (7.4 (4.9–11.3) days) or migration distance (3339 (2024–4141) m), differed significantly between fish origins (all $p > 0.05$; table 1). Larger fish migrated significantly further upstream to reach spawning sites relative to smaller fish ($R^2 = 0.47$, $T_{11} = 3.0$; $p = 0.01$). f_H tended to decline within a few hours before death (electronic supplementary material, figure S3). Although a controlled study was not completed to evaluate their influence, it did not appear as though the radio transmitters significantly influenced f_H logger traces over the course of the measurement period.

Table 2. Generalized least-squares regression ('gls' function in *nlme* R package) modelling heart rate in Chinook salmon (*Oncorhynchus tshawytscha*) from the Sydenham River, Ontario during the spawning migration. The model incorporated time nested within the individual in a linear correlation structure to account for temporal autocorrelation in the model residuals.

fixed effect	coefficient ± s.e.	*t*-value	*p*-value
intercept	41.18 ± 1.00	41.25	<0.01
origin	−3.18 ± 0.11	−28.80	<0.01
water temperature	3.43 ± 0.05	73.92	<0.01
discharge	3.74 ± 0.52	7.20	<0.01
fork length	−0.83 ± 0.03	−31.77	<0.01

(b) Predictors of heart rate and scope

f_H varied between 13 beats per minute (bpm; near death) and 91 bpm in migrating Chinook salmon (figure 2 and electronic supplementary material, figure S2), with an average routine f_H of 56.9 ± 6.1 bpm. Salmon had an average resting f_H of 43.5 ± 7.6 bpm and average maximum f_H of 71.0 ± 5.4 bpm, resulting in an average scope of 27.5 ± 6.9 bpm. While resting f_H tended to be lower in wild versus hatchery salmon (40.5 ± 8.0 versus 47.7 ± 5.0 bpm, respectively, *t*-value = −1.77, $p = 0.11$), $f_{H\ max}$ was similar (71.5 ± 5.6 bpm versus 70.3 ± 5.7 bpm, respectively) which meant that scope for f_H was significantly higher in wild compared with hatchery fish (31.0 ± 6.8 versus 22.6 ± 3.4 bpm; *t*-value = 2.51, $p = 0.03$; figure 3). Moreover, the scope for f_H was negatively correlated with resting f_H in Chinook salmon (*t*-value = −3.28, $p < 0.01$).

Generalized least-squares regression indicated f_H was significantly different in wild fish compared with hatchery fish over the course of the migration (table 2 and figure 2). Visual inspection of violin plots suggested that f_H tended to be lower and more variable in wild fish compared with hatchery fish (55.6 ± 6.9 versus 58.7 ± 4.9 bpm, respectively; figure 4). The water temperature had a significant and positive effect on f_H ($R^2 = 0.16$; figure 5), resulting in temperature-related diel and seasonal patterns in f_H during the course of migration as temperatures cooled from 14.1 to 7.5°C (table 2 and figure 2). The discharge had a significant effect on f_H but the relationship with f_H was not consistent across individual fish (i.e. in some fish the relationship was positive while in others it was neutral or negative). Body size was also significantly and negatively correlated with f_H, though the effect size was small and likely biologically insignificant (table 2).

4. Discussion

Free-swimming male Chinook salmon were monitored in their natural environment during the spawning migration using f_H biologgers. Notable and significant differences in f_H were observed between hatchery and wild origin salmon, including lower resting f_H, overall f_H and higher scope for f_H in wild salmon. Our findings suggest that wild fish have better cardiac performance than hatchery fish during spawning migrations, implying that hatchery rearing conditions may have lifelong impacts on cardiac function (see [25]). f_H was also found to vary on both a diel and seasonal timescale consistent with

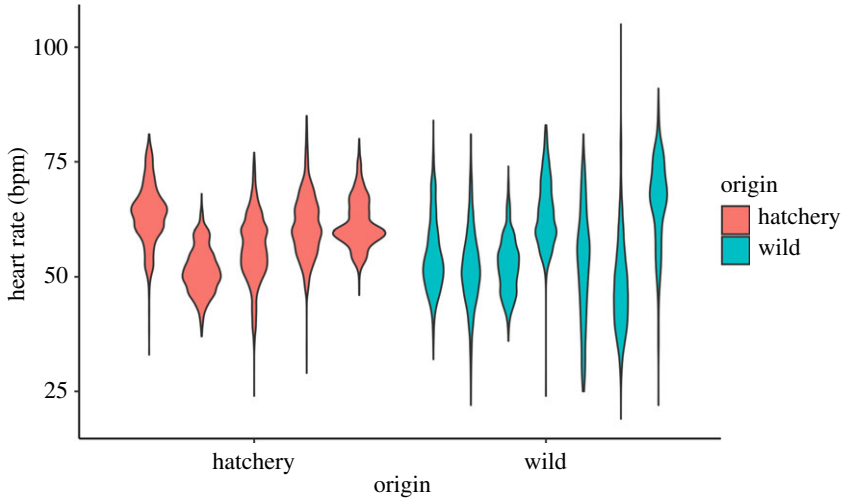

Figure 4. Violin plots depicting heart rates in the hatchery ($n = 5$) and wild ($n = 7$) Chinook salmon (*Oncorhynchus tshawytscha*) from the Sydenham River, Ontario during the spawning migration ($p < 0.01$). (Online version in colour.)

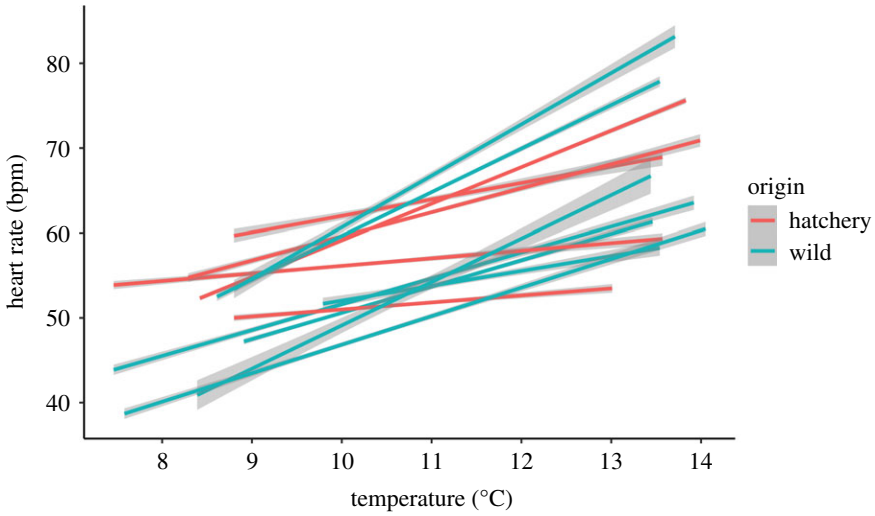

Figure 5. Linear relationships (grey shading, 95% CI) between water temperature and heart rate ($p < 0.01$) for individual hatchery and wild Chinook salmon (*Oncorhynchus tshawytscha*) from the Sydenham River, Ontario during the spawning migration. (Online version in colour.)

changes in water temperature. Aside from identifying the influence of various factors on f_H, including origin, temperature, discharge, and fork length, this study also increased knowledge on basic Chinook salmon cardiac physiology.

(a) Heart rate responses in Chinook salmon during their spawning migration

This is the first study to our knowledge, to investigate f_H responses *in situ* during the upriver spawning migration in adult Chinook salmon. Chinook salmon in this study survived and were monitored for an average of 7.4 days after tagging, and seemingly impacts of logger implantation on longevity were not severe. Fraser River sockeye salmon had 7.2 days of longevity on the spawning grounds after f_H logger implantation [39]. Similarly, a longevity–migration timing model for this population of Chinook salmon estimates males should have approximately 9 days of longevity after passing Mill Dam over the tagging dates used in the current study [54]. A few studies have attempted to investigate heart rate in Pacific salmon in their natural environment [39,55], though most have used heart rate loggers in captivity (e.g. [4,6,21,46,47]). Compared with other studies, the resting, peak and scope for f_H in Sydenham River Chinook salmon appear to be within a normal range for Pacific salmon despite differences in species, sex, water temperatures and laboratory conditions across studies (table 3). However, absolute resting f_H may have been lower than that observed here had we measured resting f_H in a holding tank with no external stimuli and low water velocity (as per previous laboratory studies). Further, our study likely did not allow tagged salmon to return to true 'resting' levels after surgery, as previous work has indicated that f_H recovery to resting levels can take more than 24 h (e.g. [6]) and up to several days [60]. By contrast to previous studies completed in captivity that consider 'recovery' as a return to resting levels, actively migrating fish (as in this study) are not likely to ever return to true resting levels of f_H. As such, we considered recovery in this study as a return to routine f_H, which occurred within a maximum of 6.4 h of tagging and for many fish occurred within just a couple hours of tagging. While it is unclear how long it may theoretically take a fish to recover to resting levels in the wild, we believe it is likely that recovery is faster in natural versus captive environments because holding can be stressful for fish (e.g. adverse water quality conditions, confinement; [61]). It should also be noted that

Table 3. A literature synthesis recording the resting, peak and scope for f_H in various Pacific salmon species and populations across a range of temperatures.

species (salmon)	study location (source)	temp. (°C)	rest. (bpm)	peak (bpm)	scope (bpm)	references
Chinook	*ex situ* (Harrison River)	*ca* 8	34.5	—	—	[21]
Chinook	*ex situ* (aquaculture)	14	49	—	—	[56]
Chinook	*ex situ* (aquaculture)	12.5	44	—	—	[57]
Chinook	*ex situ* (Chilliwack River)	13	58	—	—	[3]
Chinook	*ex situ* (aquaculture)	9–10	53–57	65–70	12–23	[58]
sockeye	*ex situ* (Fraser River)	16	48.0	91.3	43.3	[46,47]
sockeye	*ex situ* (Fraser River)	19	43.3	104.9	61.6	[46,47]
sockeye	*ex situ* (Fraser River)	21	47.9	117.2	69.3	[46,47]
coho	*ex situ* (Chehalis River)	8	31.5	58.7	27.2	[4]
sockeye	*ex situ* (Fraser River)	8–9	70.1	93.1	23.0	[8]
sockeye	*ex situ* (Fraser River)	9–13	67.3	94.4	27.1	[8]
sockeye	*ex situ* (Fraser River)	5–6	60.9	94.0	33.1	[8]
sockeye	*ex situ* (Harrison River)	*ca* 12	48	—	—	[59]
sockeye	*ex situ* (Fraser River)	15	65.2	—	—	[36]

we cannot be certain that the absolute maximum f_H was measured in our study because no standardized test (e.g. by a chase or swim protocol) was conducted on fish to swim maximally, and much higher peak f_H have been recorded in Pacific salmon (table 3). Nonetheless, it seems likely that the shallow, high-velocity migration undertaken here elicited close to maximal aerobic swimming effort at times. We argue, however, for further effort to measure cardiac parameters in the natural environment to increase the ecological relevance of these measurements. Moreover, our study provides further evidence that differences in scope for f_H across individual fish appear to be driven by changes in resting f_H (rather than maximum f_H). Previous work with rainbow trout (*Oncorhynchus mykiss*) has shown that higher resting f_H leads to a lower scope for f_H [62].

(b) Differences in f_H between hatchery and wild salmon

Although only a small number of hatchery and wild origin salmon were monitored for f_H, and individual fish had unique migratory experiences (e.g. severity of the surgery, the timing of movements, fine-scale positioning, longevity, etc.), interesting differences were observed across these groups. Hatchery salmon had lower scope for f_H, and less variable f_H, and tended to have higher resting f_H relative to wild fish. There are a number of potential mechanisms that could lead to these disparities relating to differences in the life-history of hatchery and wild salmon. First and foremost, broodstock fish selected for use in a hatchery to produce offspring are often collected part way through a migration and may not have successfully completed their migration and spawned otherwise (discussed in [63]). If cardiac performance is an important determinant of migration and spawning success [39] and hatcheries artificially increase the spawning success of fish with poorer cardiac performance, this could explain the lowered cardiac performance in returning hatchery fish. Dunmall & Schreer [64] explored maximum cardiac function in adult wild and hatchery Atlantic salmon (*Salmo salar*) reared in identical conditions from the eyed egg stage to adulthood and found no difference in f_H between groups. This common garden experiment suggested that the artificial selection of broodstock fish is not responsible for differences in f_H between groups, though this is sure to vary based on the broodstock selection practices of a given hatchery. Alternatively, differences between hatchery and wild rearing conditions could lead to altered selection regimes or phenotypic plasticity with respect to heart morphology and cardiac performance. Fish raised in captivity are often subject to much more homogeneous conditions (e.g. constant temperature, flow and food availability, lack of predators) than would be experienced in the wild. The Sydenham River Hatchery salmon are reared under the natural thermal regime (creek water is diverted to the hatchery), but have no predator exposure and are fed using a timed feeding system. These conditions may yield physiological, morphological and behavioural differences in hatchery fish [65–67]. Hatchery salmonids have exhibited misshaped hearts characterized by a more rounded ventricle relative to wild counterparts, which is typical of more sedentary fish species [23,25]. Salmonids raised in captivity also tend to have greater fat deposition around the heart and cardiac deformities [25]. Cardiac deformities may lead to lowered cardiac and swimming performance [28]. Although we did not quantify heart morphology in the present study, hatchery salmon differed with respect to cardiac performance and swam shorter distances upstream than wild salmon to reach spawning sites. A study on Atlantic salmon (*Salmo salar*) from the River Namsen, Norway, found evidence that wild salmon have higher routine f_H at age 1+ and lower f_H at age 2+ compared with farmed salmon [68]. Similarly, age 1+ hatchery brown trout (*Salmo trutta*) displayed greater elevations in f_H than wild fish when exposed to predators [69]. Few studies have compared f_H in wild and hatchery adult salmonids to examine to what extent differences in f_H remain throughout the life cycle. However, some parallels can be drawn from Gallaugher *et al*. [58], who examined plasticity in cardiac function of saltwater acclimatized Chinook salmon following either constant low flow conditions (akin

to a hatchery) or variable flow conditions (as in the wild). Chinook salmon held at constant low flow conditions had higher resting f_H, and lower scope for f_H, and tended to reach a plateau in f_H much faster than those previously held in variable flow conditions.

It is well documented that hatchery salmonids typically have lower reproductive success than their wild counterparts [29,70]. This indicates that just 1 year of rearing in captivity can lead to lasting changes in lifetime fitness. There is considerable evidence for morphological, physiological and behavioural differences between adult hatchery and wild salmonids that may contribute to this decrease in fitness [71–73]. Our study is, however, the first to our knowledge to find that the hearts of hatchery salmon did not perform as well as the hearts of wild fish during spawning migrations. This may provide a mechanistic physiological explanation for reduced migratory and reproductive performance in hatchery salmonids, though research on other cardiac performance metrics (e.g. cardiac output, stroke volume) will contribute to solidifying evidence for differences in cardiac phenotype between wild and hatchery salmon. Notably, the river migration of Chinook salmon in the Sydenham River is relatively short and not nearly as difficult as those in systems such as the Columbia, Fraser or the Yukon River where the salmon may migrate over 1000 km upriver to reach natal spawning grounds. As such, we might predict that such differences would be even more apparent during more arduous migrations. Regardless, our study builds on the substantial amount of evidence suggesting that hatchery fish are not a like-for-like replacement for wild fish.

(c) Temperature effects on f_H

The f_H in migrating adult Chinook salmon tended to increase with water temperature, which is consistent with the fact that the elevation in metabolic rate and tissue oxygen demand with warming necessitates an elevation in cardiac output, which in teleosts is achieved primarily through elevations in f_H and secondarily by adjustments to stroke volume [16,55]. For instance, peak f_H in sockeye salmon increased progressively with warming (being lowest at 16°C and highest at 21°C) [46,47]. Beyond thermal optima, cardiovascular collapse is common, which is primarily driven by the insufficient scope for f_H [5,13,74]. While temperatures in the Sydenham River were not beyond thermal optima for the species, there is substantial evidence that populations differ in their thermal tolerance based on local conditions [75]. As temperatures warm, performance may be compromised in species like Chinook salmon that are reliant on sufficient cardiac scope to overcome O_2 limitations during migration [76].

5. Conclusion

The current study investigating the f_H responses of Chinook salmon during their spawning migration has advanced our understanding of cardiac function in free-swimming wild and hatchery-reared fish in the natural environment. The tendency for higher resting f_H and consequently lower f_H scope of hatchery salmon suggests that hatchery Chinook salmon exhibit a lower cardiac capacity during migration, which may decrease their capacity to migrate and thus lifetime fitness [55]. Water temperature was found to have a positive correlation with f_H in salmon [39,74], which will likely have implications for salmonids as fresh waters warm with predicted climate change [77]. We encourage researchers to further explore the relationships identified here, particularly the observation that hatchery salmon cardiac performance differed from that of wild salmon during spawning migrations. Our study provides a mechanistic understanding of the migration performance of Pacific salmonids and creates opportunities for conducting similar studies in systems that represent more arduous migrations.

Ethics. Sampling was conducted under the Ontario Ministry of Natural Resources and Forestry Licence to Collect Fish for Scientific Purposes no. 1094299.

Data accessibility. Data and code for all analyses are available as electronic supplementary material.

Authors' contributions. W.M.T.: designed study, led data collection, analysed data, wrote the manuscript. A.E.: informed study design, advised analysis, revised manuscript. E.J.E.: advised analysis, revised manuscript. R.J.L.: advised analysis, revised manuscript. E.T.: informed study design, data collection, revised manuscript. A.E.I.A.: data collection, revised manuscript. A.L.J.: data collection. S.J.C.: provided equipment and funding, informed study design, revised manuscript.

Competing interests. We declare we have no competing interests

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