

REGULAR PAPER

Metabolic constraints and individual variation shape the trade-off between physiological recovery and anti-predator responses in adult sockeye salmon

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Abstract

Metabolic scope represents the aerobic energy budget available to an organism to perform non-maintenance activities (e.g., escape a predator, recover from a fisheries interaction, compete for a mate). Conflicting energetic requirements can give rise to ecologically relevant metabolic trade-offs when energy budgeting is constrained. The objective of this study was to investigate how aerobic energy is utilized when individual sockeye salmon (*Oncorhynchus nerka*) are exposed to multiple acute stressors. To indirectly assess metabolic changes in free-swimming individuals, salmon were implanted with heart rate biologgers. The animals were then exercised to exhaustion or briefly handled as a control, and allowed to recover from this stressor for 48 h. During the first 2 h of the recovery period, individual salmon were exposed to 90 ml of conspecific alarm cues or water as a control. Heart rate was recorded throughout the recovery period. Recovery effort and time was higher in exercised fish, relative to control fish, whereas exposure to an alarm cue had no effect on either of these metrics. Individual routine heart rate was negatively correlated with recovery time and effort. Together, these findings suggest that metabolic energy allocation towards exercise recovery (i.e., an acute stressor; handling, chase, etc.) trumps anti-predator responses in salmon, although individual variation may mediate this effect at the population level.

KEYWORDS

cardiac, heart rate, metabolism, migration, Pacific salmon, predator-prey interactions

1 | INTRODUCTION

In vertebrates, the amount of aerobic energy available to an individual is primarily dictated by their metabolic scope. Metabolic scope,

determined by the difference between maximal (MMR) and standard metabolic rates (SMR; Fry, 1947), represents the amount of aerobic energy that can be allocated towards fitness-related processes (Fry, 1947; Guderley & Pörtner, 2010; Portner & Farrell, 2008).

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Nonetheless, this energy is finite and requires that individual's partition energetic resources among their various life-history traits to maximize performance and fitness resulting in fitness-related trade-offs (Sokolova, 2013). For example, sub-populations of Atlantic silversides (*Menidia menidia*) that specialize in accelerated growth demonstrate greater susceptibility to predation as well as reduced swimming capacity relative to slow-growing conspecifics (Arnott et al., 2006; Lankford et al., 2001; Munch & Conover, 2003). These phenotypes are likely direct consequences of differential metabolic scope budgeting and highlight the importance of energy-limited trade-offs linking physiological processes with ecological characteristics.

Metabolic scope is also an important determinant of the ability of an organism to cope with environmental challenges. Stressor mitigation can be an energy-intensive process and adds considerable metabolic load to the energy budget of an individual (Barton & Schreck, 1987; Chan & Woo, 1978; Lawrence, Eliason et al., 2019; Morgan & Iwama, 1996). In some instances, stressor exposure can constrain aerobic scope and limit energy available for performing other tasks or responding to subsequent environmental challenges (Lankford et al., 2005; Sandblom et al., 2014). Thus, stress-induced metabolic loading can have the potential to alter individual energy budgets, driving life-history trade-offs that could constrain performance attributes.

Metabolic scope also plays an important role in dictating migratory activities in Pacific salmonids. Salmon frequently encounter stressful events along their migratory route forcing the animals to engage in exhaustive exercise (Cooke et al., 2006). In such cases, tissue oxygen demand can often exceed uptake/supply resulting in an acute reliance on anaerobic metabolism resulting in an oxygen debt (Wood, 1991), using a large proportion of the metabolic scope [i.e., excess post-exercise oxygen consumption (EPOC); Clark et al., 2012; Donaldson et al., 2011; Lee et al., 2003; Prystay et al., 2017]. Conceivably, this may have consequences for the animal responding to subsequent stressors and challenges, especially those that are metabolically demanding such as predator avoidance (Lawrence et al., 2022; Lawrence, Godin, et al., 2019; Raby et al., 2018). Our understanding of metabolic power allocation under competing metabolic demands is poor.

Metabolic budgeting is particularly important in the context of anti-predator behaviour. Predation detection and avoidance requires significant allocation of metabolic energy (Godin, 1997). In juvenile Atlantic salmon (*Salmo salar*), anti-predator behaviours (i.e., increased vigilance) can cause metabolic rate to increase by as much as 30% in conditions where there is no available shelter cover (Millidine et al., 2006). Largemouth bass (*Micropterus salmoides*) demonstrated a significant increase in cardiovascular activity after a simulated avian predation event with the magnitude of response tightly coupled to the size of the bird (Cooke et al., 2003). Furthermore, fish with greater aerobic scopes were able to support greater degrees of anti-predator vigilance than those with comparatively smaller scopes (Killen et al., 2015). Both chronic and acute stressors appear to increase rates of predator-induced mortality in teleosts (Danylchuk et al., 2007; Marine & Cech, 2004; Mesa et al., 1994; Ryer et al., 2004). Together,

these works suggest a metabolic basis for vulnerability of prey to predators, but this area of research remains poorly characterized.

Aquatic organisms rely, in part, on chemical cues to acquire information about their environment (Ferrari et al., 2010; Wisenden, 2000). In teleost fish, predation risk can be assessed through the detection of chemical alarm cues that are passively released from the epidermis following mechanical damage, as would likely occur during a predation event (Chivers & Smith, 1998; Smith, 1992). Detection of these chemical cues by conspecific receivers elicits a species-specific suite of anti-predator behavioural responses (Brown, 2003), with the magnitudes of response influenced by similarity in life-history stage and size (Harvey & Brown, 2004). In addition, unrelated sympatric species exposed to similar predation pressures can learn to respond to heterospecific cues (Elvidge & Brown, 2015), supporting the idea that chemical alarm cues serve as reliable indicators of elevated predation risk. In addition to behavioural responses, detection of alarm cues elicits primary stress responses in focal fish (Rehnberg & Schreck, 1987; Sanches et al., 2015), implying that anti-predator responses impose metabolic costs beyond those associated with altered activity levels and sacrificed foraging opportunities.

The goal of this study was to evaluate the role that heart rate (f_H) scope plays in mediating exercise recovery and anti-predator responses in a wild teleost fish. The authors evaluated how heart rate scope is partitioned in fish balancing two activities: recovery from exhaustive exercise and exposure to a chemical alarm cue. They hypothesized that if metabolic scope energy is prioritized towards recovery from exhaustive exercise, maintaining anti-predator activities should be constrained, thereby increasing vulnerability to predation. Conversely, if metabolic scope is partitioned to both exercise recovery and anti-predator activity, then the trade-off should result in prolonged recovery duration. In testing this, they fitted adult sockeye salmon (*Oncorhynchus nerka*) with heart rate biologgers to track heart rate responses after exhaustive exercise chase events (i.e., an acute stressor) in the presence of conspecific chemical alarm cues. In sockeye salmon, f_H serves as a proxy for metabolic rate (Clark et al., 2010), and using f_H biologgers allows measurements to be made in free-swimming individuals that can respond to alarm cues in a more natural experimental context.

2 | MATERIALS AND METHODS

2.1 | Animal care and surgical procedures

Migrating adult sockeye salmon (*O. nerka*; Walbaum 1792) were captured using beach seine nets in the lower Fraser River (49.300689 N, -121.667184 W) during late August 2015. During this time of year, a number sockeye stocks make their migration runs through this part of the river system (Gable & Cox-Rogers, 1993). Given the timing of capture, our fish likely consisted of a summer stock composition. As indicated in Prystay et al.

(2017), which used the same pool of salmon, stock composition for the summer of 2015 consisted of mostly of Chilko and Quesnel stocks ($60.75 \pm 1\%$) with a mix of other stocks including Raft North Thompson ($2.75 \pm 1\%$), Late Stuart Stellako ($13.75 \pm 1\%$) and Harrison Widgeon ($4.75 \pm 2\%$). Thus, our cohort of fish was likely a mixed population consisting predominately of Chilko/Quesnel stock individuals ($>50\%$). Salmon ($N = 59$; average mass = 2.10 ± 0.05 kg, average fork length = 58.89 ± 0.4 cm) were immediately transported back to the Cultus Lake Salmon Research Laboratory (Cultus Lake, BC, Canada) via a pick-up truck with a well-oxygenated holding tank (1250 l; $>90\%$ O₂ saturation) with the transport time taking roughly 1 h (Transplant permit: ITC#13730). The fish were then transferred from the vehicle and held in large, flow-through tanks (c. 15 fish/tank; 6000 l) at $12 \pm 1^\circ\text{C}$ with sufficient oxygen (DO $>83\%$). Animals were held under a natural photoperiod (c. 12 h L:12 h D) and were not fed during the duration of their captivity because they had naturally ceased feeding. All experimental procedures were conducted in compliance with the Canadian Council for Animal Care under permit from the Carleton University Animal Care Committee (AUP #103128). Sockeye salmon were collected under a Department of Fisheries and Oceans Canada permit #XR2362015.

Salmon were initially anaesthetised using a buffered tricaine methanesulfonate (MS-222; 100 mg l^{-1} ; $200 \text{ mg l}^{-1} \text{ NaHCO}_3$) and were sustained on a lighter MS-222 dosage being pumped over the branchial epithelium throughout the surgical procedures (50 mg l^{-1} MS-222; $100 \text{ mg l}^{-1} \text{ NaHCO}_3$). f_{H} biologgers (Star Oddi, Gardabaer, Iceland) were then implanted into each fish by means of a ventral incision, midline to the pectoral girdle and stitched to the body wall as described in Prystay *et al.* (2017). The incision was sutured shut (2-0 PDS II monofilament; Ethicon, NJ, USA), and the animal was recovered under a flow of fresh water over the gills until equilibrium was regained in the fish. At this time, each fish was fitted with a colour-coded visual ID tag (35.56 cm FT-4 spaghetti tag; Floy Tag & Mfg Inc. WA, USA) through the dorsal musculature to aid in the identification of the fish during the experimental series. After surgical procedures, salmon were subsequently transferred to a separate holding tank (c. 2200 l; $T = 15 \pm 0.5^\circ\text{C}$; dissolved O₂ $> 90\%$) and allowed to recover over the following 24 h. The surgical holding tank only ever held a single cohort of four salmon at any one time. Here, each f_{H} logger was programmed to turn on at 5 min intervals, recording for a duration of 3 s at 200 Hz as reported in previous studies (Clark *et al.*, 2010; Prystay *et al.*, 2017). To ensure high-quality and representative data, an ECG recording was saved alongside a heart rate value once per hour.

2.2 | Experimental series

On the day of the experimental trials, salmon were haphazardly allocated to one of four treatment groups pairing stressor and chemical cue in a 2×2 crossed design: stressor and alarm cue

($N = 15$), control and alarm cue ($N = 15$), stressor and sham cue ($N = 14$), control and sham cue ($N = 15$). On any given day, four salmon were assigned to one of the experimental treatments with all four of the treatments being conducted simultaneously (i.e., $N = 1/\text{day}$ for each treatment combination). All fish used in these exposures were fitted with a f_{H} logger. Experimental conditions were comparable to the holding tank conditions ($T = 15 \pm 0.5^\circ\text{C}$; dissolved O₂ $> 90\%$).

The stressor consisted of a 3-min chase followed by a 1-min air exposure as described in Prystay *et al.* (2017). For the chase, fish were removed directly from the recovery tank and placed into a designated chase tank (500 l, circular shape; c. 15°C). After the chase, fish were placed in separate holding tanks (c. 1250 l; $T = 15 \pm 0.5^\circ\text{C}$; dissolved O₂ $> 90\%$), where they were allowed to recover from the chase event over the next 48 h. Control fish (i.e., no exercise) were simply netted and moved from the surgical recovery tank to the holding tanks with care being taken to minimize air exposure and struggling.

After introduction to the holding tanks, the fish were exposed to one of two olfactory cues: conspecific chemical alarm cues or a sham cue consisting of distilled water. The conspecific alarm cues were generated by mechanically homogenizing lateral skin filets from freshly euthanized donors (four adult, male sockeye salmon; c. 61 cm; c. 2.5 kg) filtered, and diluted with distilled water to a final concentration of $0.1 \text{ cm}^2 \text{ skin ml}^{-1}$ following established protocols (750 cm^2 in 750 ml distilled water, diluted $10\times$ thereafter); (Brown *et al.*, 2006; Ferrari *et al.*, 2008). The alarm cue was frozen and stored at -20°C as 50 ml aliquots in falcon tubes. This concentration of alarm cue ($0.1 \text{ cm}^2 \text{ skin l}^{-1} \text{ ml water}$) has been previously shown to elicit strong and reliable anti-predator responses in salmonid fishes after exposure to 10 ml volumes of alarm cues, equivalent to 1 cm^2 of damaged skin tissue (Brown & Smith, 1997; Leduc *et al.* 2006). Each tank (four tanks total; c. 1200 l, c. 182 cm diameter; $T = 15 \pm 0.5^\circ\text{C}$; dissolved O₂ $> 90\%$) was injected with 90 ml of chemical cue, equivalent to 9 cm^2 of damaged skin tissue (alarm or sham), delivered through a c. 38 cm long piece of aquarium tubing from a 50 ml syringe. During cue injection, water flow into the tank was turned off for c. 120 min to avoid dilution and removal of the chemical cues. At 48 h post-chase, salmon were euthanized via cerebral percussion and the logger removed. Following this, animals were weighed and measured for fork length.

2.3 | Heart rate and statistical analyses

Logger downloads and initial data manipulations were carried out in Mercury (Star Oddi, Gardabaer, Iceland). Erroneous data, which consisted of f_{H} data that were outside of 21–130 BPM (i.e., the typical physiological range of f_{H} in pacific salmonids); see (Clark *et al.*, 2011; Donaldson *et al.*, 2010; Eliason *et al.*, 2013a; Prystay *et al.*, 2017), or had a quality index of 3, were removed from the data set. A number of f_{H} parameters were computed during this assessment and included resting, routine and maximal f_{H} , f_{H} scope (absolute and factorial), recovery time and recovery effort (excess post-exercise heart beats;

EPHB). Resting f_H was determined by taking the average of the lowest 10th percentile of f_H values during the overnight period just prior to the onset of experimental series. Routine f_H represented the average of all heart rate values during this time. Peak f_H (i.e., maximal) was the single highest f_H value following the chase period within 2 h of this event (or after relocation of the control fish). Absolute heart rate scope was calculated as the difference between peak and resting heart rate ($HS_a = \text{peak } f_H - \text{resting } f_H$), whereas factorial scope was derived from peak f_H divided by resting f_H ($HS_f = \text{peak } f_H / \text{resting } f_H$). Recovery time constituted that amount of time that the fish took to return to routine f_H levels for an individual fish. Specifically, this was when the heart rate reached four consecutive values that were at or below routine f_H . The last time value of these four points was then used at the point at which the fish reached recovery. EPHB was derived from the total area under the curve representing time vs. f_H and subtracting off routine f_H . More specifically, this involved splitting the heart rate values into hourly blocks following the treatment (e.g.,

0–1, 1–2, 2–3 h) up until the recovery timepoint. The block containing the recovery timepoint proceeded the last full hour block of time meaning that this value was usually less than a full hour (e.g., 20, 15 min). f_H was then averaged in each of the binned time blocks and was then multiplied by the interval timeframe to express f_H in heart beats (e.g., $f_H * 60 \text{ min}$). The routine f_H , expressed in heart beats (i.e., routine f_H multiplied by recovery time), was then subtracted off the recovery beats value to derive net EPHB. This same procedure was also used to determine EPHB at discrete time intervals of 1, 6, 12, and 24 h post-exercise rather than the precise recovery time interval.

All statistical analyses were conducted in SigmaPlot version 11.0 (Systat Software Inc., San Jose, CA, USA) where significance was accepted at $\alpha = 0.05$. Unless otherwise noted, values are presented as mean ± 1 S.E.M. A two-way ANOVA was used to determine differences between the various treatment groups for all f_H metrics. All *post hoc* analyses for ANOVA models were handled using a Tukey's test.

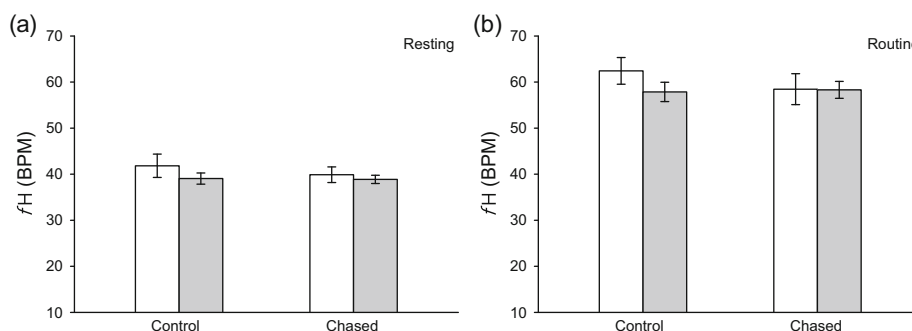


FIGURE 1 (a) Resting and (b) routine heart rates (f_H) of sockeye salmon being either chased to exhaustion (right bars; $N = 29$) or left as handling controls (left bars; $N = 27$) which were subsequently exposed to either a sham cue (90 ml of distilled water; white bars) or a conspecific alarm cue (90 ml of $0.1 \text{ cm}^2 \text{ skin ml}^{-1}$ alarm cue; grey bars). No significant effects of either main effect on these parameters were observed ($P > 0.05$). Values are reported as means ± 1 S.E.M. □, Sham cue; ■, Alarm cue.

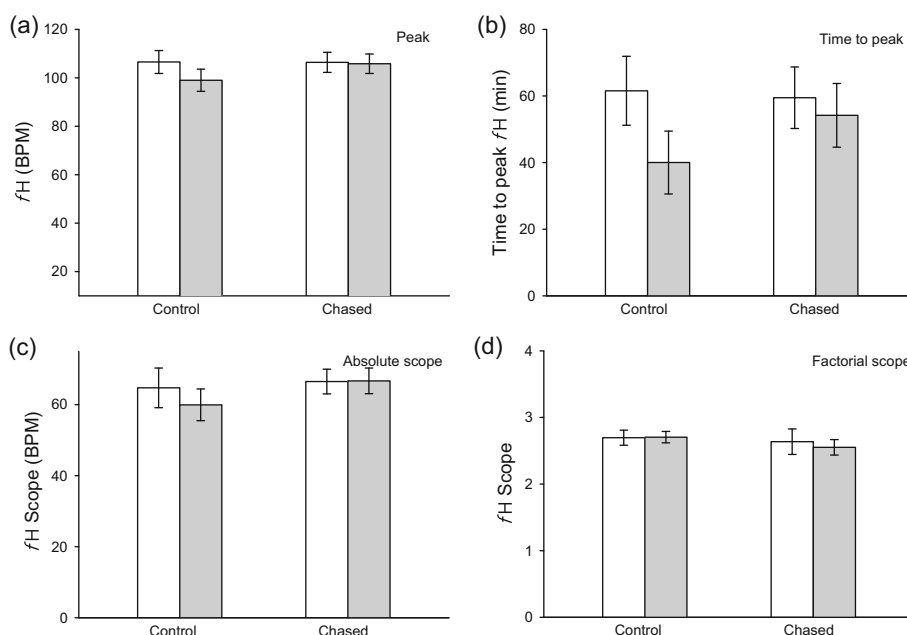


FIGURE 2 (a) Peak heart rates (f_H), (b) time to peak f_H , (c) absolute f_H scope and (d) factorial f_H scope of sockeye salmon being either chased to exhaustion (right bars; $N = 25$) or left as handling controls (left bars; $N = 24$) which were subsequently exposed to either a sham cue (90 ml of distilled water; white bars) or a conspecific alarm cue (90 ml of $0.1 \text{ cm}^2 \text{ skin ml}^{-1}$ alarm cue; grey bars). No significant effects of either main effect on these parameters were observed ($P > 0.05$). Values are reported as means ± 1 S.E.M. □, Sham cue; ■, Alarm cue.

For ANOVA models, conformity of data to normality and variance were assayed using a Kolmogorov–Smirnov test (Massey Jr, 1951) and Levene's test (Schultz, 1985), respectively. A simple linear regression was used to determine the relationship between f_H scope and recovery time. Nonetheless, regression normality and variance were verified using Shapiro–Wilk test (Shapiro & Wilk, 1965) and a Spearman rank correlation (Zar, 2005), respectively. In instances where the data did not meet model assumptions, a $\log_{10}$ transformation was used. The overall f_H and time plot was analysed using a two-way repeated measures ANOVA model. Statistical analyses of discrete EPHB values (i.e., at 1, 6, 12, 24 h post-exercise) were analysed in R Studio using a linear mixed effect model (package “nlme”; Pinheiro *et al.* 2013) with EPHB as the response variable and chase state and alarm cue as independent variables. Fish ID was treated as a random effect to account for repeated measures. EPHB values were square root transformed to satisfy the assumption of normality.

3 | RESULTS

3.1 | Baseline f_H metrics

Both resting and routine f_H were comparable among all treatment groups, mean values were c. 39 and 58 BPM, respectively (Figure 1a,b). Peak f_H was unaffected by chase status ($df = 1$; $F = 0.581$; $P = 0.450$) or by the presence of alarm cue in water ($df = 1$; $F = 0.856$; $P = 0.360$) (Figure 2a). There were no detectable interactive effects between our treatment groups ($df = 1$; $F = 0.639$; $P = 0.428$). Similarly, the time to peak f_H was comparable among all treatment groups with fish generally taking close to an hour to reach maximal values.

Absolute heart rate scope and factorial heart rate scope were found to be comparable across all treatment groups in this study. Here, sockeye salmon were capable of raising their f_H to c. 66 BPM above resting levels (Figure 2c) or by a factor of nearly $2.6\times$ (Figure 2d).

3.2 | Recovery dynamics

Figure 3 shows the overall recovery profile of each group of fish. Chase state was found to have a significant influence on the recovery timing of sockeye salmon whereby animals subject to the chase and air exposure treatment had significantly longer recovery durations when compared to control fish ($df = 1$; $F = 9.192$; $P = 0.004$; Figure 4a). Nonetheless, there was no influence of alarm cue exposure ($df = 1$; $F = 0.223$; $P = 0.639$). Similarly, total recovery effort (EPHB) was higher in fish subject to a chase event, relative to control treated fish ($df = 1$; $F = 15.965$; $P < 0.001$; Figure 4b) with alarm cue having no impact on EPHB either ($df = 1$; $F = 0.522$; $P = 0.474$). In both of these instances, there was no significant interaction between the main effects ($df = 1$; $F = 0.537$; $P = 0.467$). Similar effects were observed when looking at EPHB over discrete time intervals (i.e., 1, 6, 12, 24 h post-chase) where chased fish had a greater EPHB against controls

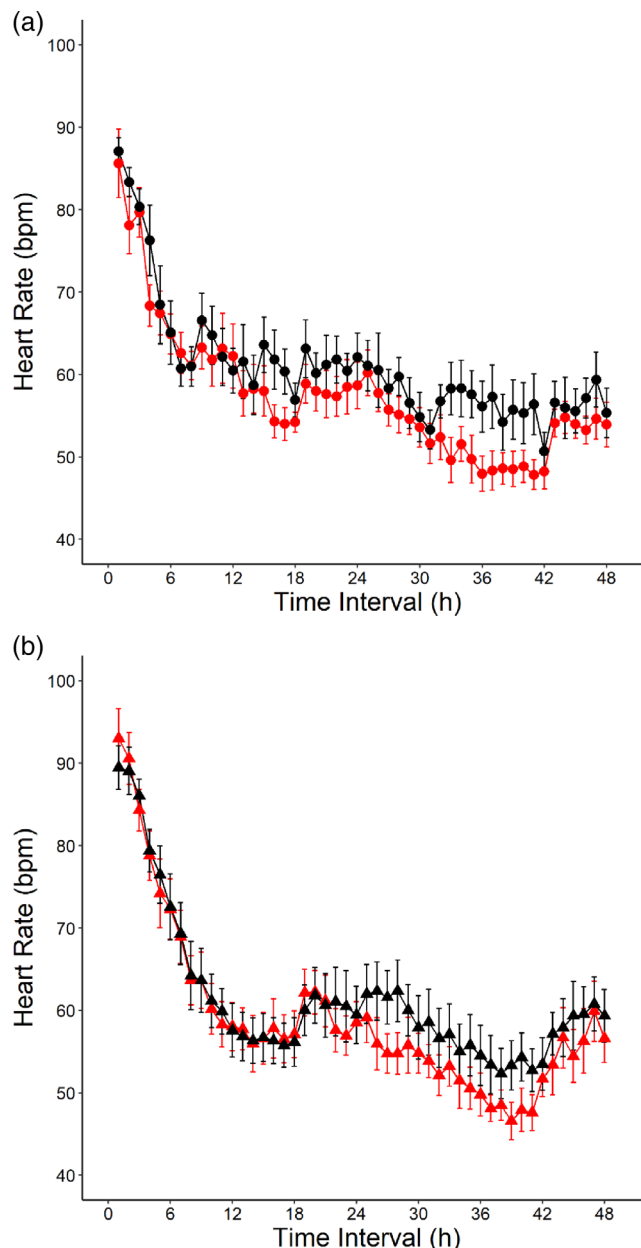


FIGURE 3 Overall recovery profile detailing the relationship between heart rate (f_H) and time of handling controls (circles; a) or proceeding an exhaustive chase (triangles; b) with animals allowed to recover under a sham cue (90 ml of distilled water; black points) or a conspecific alarm cue (90 ml of 0.1 cm² skin ml⁻¹ alarm cue; red points). Values are reported as means ± 1 S.E.M. for each time point. ♦, Alarm & Control; ♦, Sham & Control; ▲, Alarm & Chased; ▲, Sham & Chased.

($df = 45$; $F = 8.62$; $P = 0.005$; Figure 5) with no effect of alarm cue observed ($df = 45$; $F = 0.26$; $P = 0.615$). This effect was time dependent where EPHB decreased as the animal was allowed to recover ($df = 141$; $F = 74.8$; $P < 0.001$; Figure 5). A significant interaction between chase state and time was detected ($df = 141$; $F = 4.54$; $P = 0.035$) but was not observed for the alarm cue-time interaction term ($df = 141$; $F = 0.15$; $P = 0.701$).

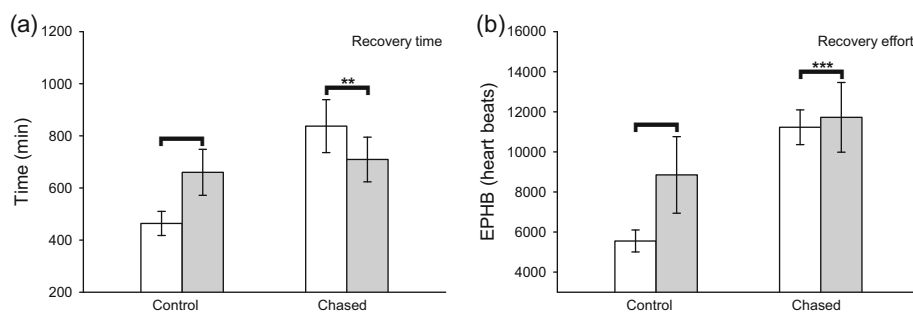


FIGURE 4 Time to heart rate (f_H) (a) recovery and (b) recovery effort [excess post-exercise heart beats (EPHB)] of sockeye salmon being either chased to exhaustion (right bars; $N \geq 24$) or left as handling controls (left bars; $N = 24$) which were subsequently exposed to either a sham cue (90 ml of distilled water; white bars) or a conspecific alarm cue (90 ml of $0.1 \text{ cm}^2 \text{ skin ml}^{-1}$ alarm cue; grey bars). Asterisks denote statistically significant differences (** $P < 0.01$, *** $P < 0.001$) between chased and control fish. No effect of the alarm cue was detected. Values are reported as means ± 1 S.E.M. □, Sham cue; ■, Alarm cue.

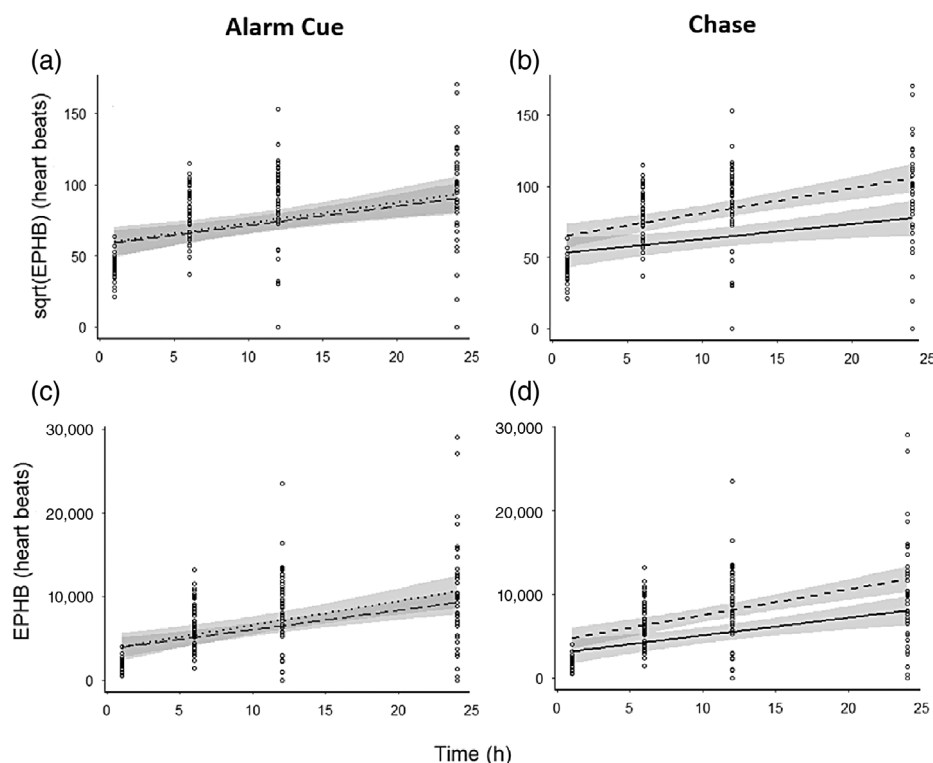


FIGURE 5 Regression plot showing the variability of square root transformed cumulative excess post-exercise heart beats (EPHB) and raw EPHB in sockeye salmon when exposed to an alarm cue and/or exhaustive chase, where (a) shows the change in square root transformed EPHB (heart beats) over time (hours) in fish exposed to a predator alarm cue (dotted regression line; $N = 96$) compared to fish that were not exposed to a predator alarm cue (long dashed regression line; $N = 96$); (b) shows the change in square root transformed EPHB over time in fish exposed to an exhaustive chase (short dashed regression line; $N = 96$) compared to fish that were not exposed to an exhaustive chase (solid regression line; $N = 96$); (c) shows the change in raw EPHB over time in fish exposed to a predator alarm cue (dotted regression line; $N = 96$) compared to fish that were not exposed to a predator alarm cue (long dashed regression line; $N = 96$); and (d) shows the change in raw EPHB over time in fish exposed to an exhaustive chase (short regression dashed line; $N = 96$) compared to fish that were not exposed to an exhaustive chase (solid regression line; $N = 96$). Square root transformed EPHB is presented given that the linear mixed effect model required the data be transformed to satisfy normality. Hollow circles denote the raw EPHB of each individual at each hour. The shaded area around each regression line represents the 95% confidence region. Time 0 represents the start of the recovery after both treatments. □, No predator cue; ■, Predator cue; □, Chase; ■, No chase.

Individual-level effects seemed to be involved in determining recovery dynamics. Individual salmon with high routine f_H demonstrated a comparatively lower recovery time [$t = -3.118$;

$P = 0.003$; $\log \text{ recovery} = 3.332 - (0.00923 * \text{routine } f_H)$; Figure 6a] alongside a lower recovery effort, relative to salmon with low routine f_H [$t = -2.881$; $P = 0.006$; $\log \text{ EPHB} = 4.571 -$

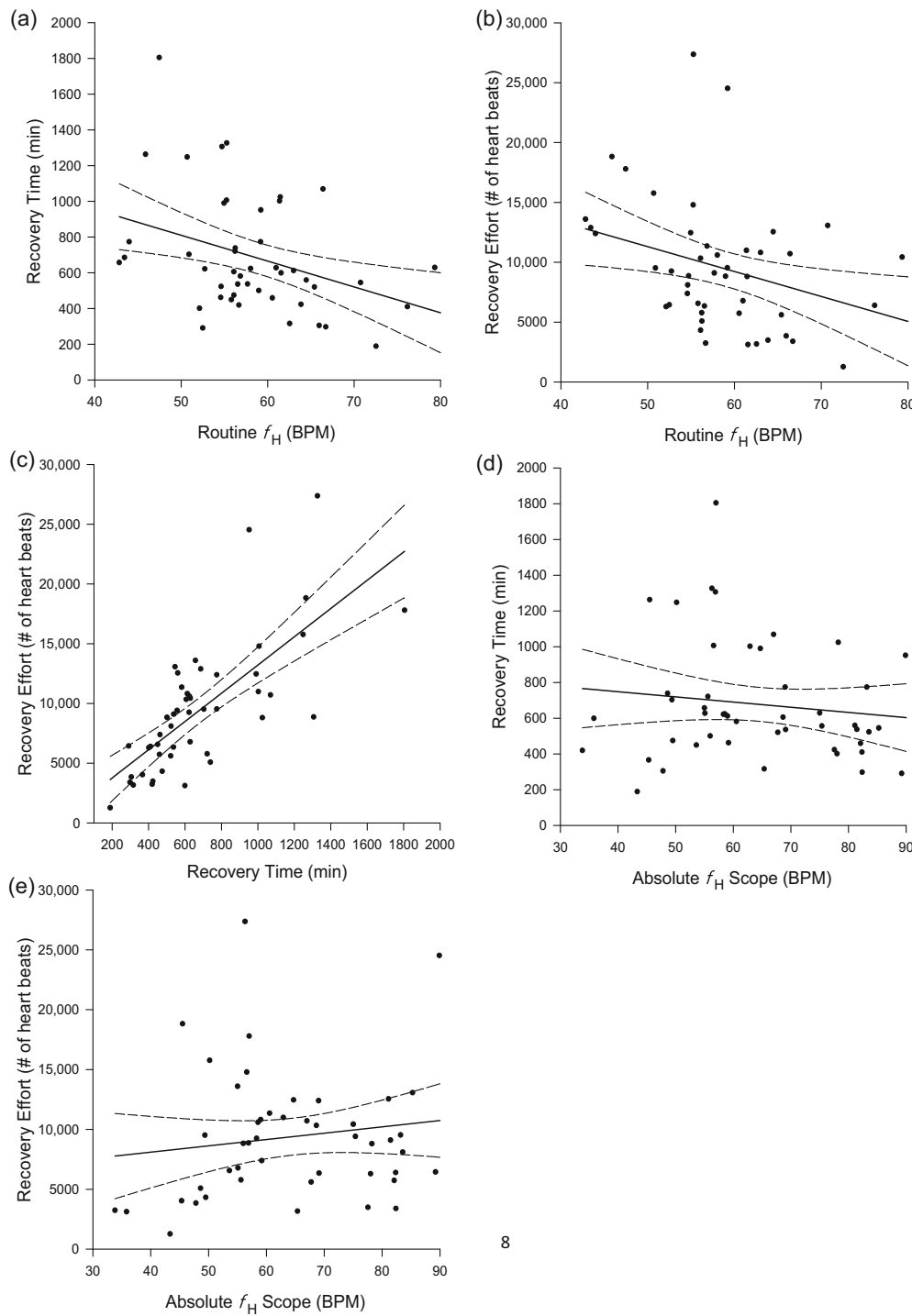


FIGURE 6 Simple linear regression plots detailing the relationships between (a) recovery time and routine heart rate (f_H ; $N = 48$), (b) recovery effort [excess post-exercise heart beats (EPHB)] and routine f_H ($N = 48$), (c) recovery effort and recovery time ($N = 48$), (d) recovery time and absolute f_H scope ($N = 48$) and (e) recovery effort and absolute f_H scope ($N = 48$) in sockeye salmon. Each point on the plot represents a single individual fish used in the experimental series across all treatment groups. Dashed lines represent the 95% C.I. for the model

(0.0113 * routine f_H); Figure 6b]. Furthermore, recovery time was found to be quite strongly related to recovery effort ($t = 8.585$; $P < 0.001$) with timing being able to explain 60.7% of the variation in effort (Figure 6c). Yet, f_H scope was not able to explain any of the variation in recovery timing ($t = -0.526$; $P = 0.601$; $r^2 = 0.00$) or effort ($t = 1.795$; $P = 0.079$; $r^2 = 0.05$) in the sockeye salmon measured here.

4 | DISCUSSION

4.1 | Overview

The authors looked to characterize how f_H scope would be partitioned among competing processes: recovery from exhaustive exercise and anti-predator activities. Yet, they remain cautious in this interpretation

as sockeye salmon regulate both stroke volume and heart rate (Eliason *et al.*, 2013a). Recovery dynamics were unaffected by the alarm cue treatment. Allocation of f_H scope energy appeared to be directed towards recovery from the exhaustive exercise event. Presumably, this was used to re-establish homeostasis (e.g., ion and acid–base regulation, energy substrate reformation) after the chasing event (Wood, 1991). The lack of alarm cue effects on f_H recovery dynamics suggests that there is a diminished capacity to avoid a predator as both anti-predator responses and avoidance require large sums of metabolic energy (Cooke *et al.*, 2003; Killen *et al.*, 2013). Yet, masking effects associated with handling (Dick *et al.*, 2018), an inability to respond to alarm cues in adult fish, or anti-predator responses requiring minimal metabolic inputs may confound this interpretation. Baseline f_H metrics were comparable between the treatment groups suggesting a similar capacity to deal with environmental challenges. Individual scale effects appeared to be an important mediator of f_H responses in sockeye salmon.

4.2 | f_H scope and the prioritization of metabolic power

The authors speculate that migratory activities, which would involve a great deal of burst/aerobic swimming coupled with recovery events, may take priority over responding to an indirect predation threat due to the fitness costs associated with not reaching the spawning ground (Farrell *et al.*, 2008). They tested the hypothesis that stressor mitigation should compromise anti-predator responses because of trade-offs associated with a finite metabolic scope. Indeed, teleosts experiencing a pre-existing stressor (*i.e.*, exhaustive exercise, chemicals, hypoxia, handling) demonstrated enhanced susceptibility to a predator-induced mortality (Danylchuk *et al.*, 2007; Mesa *et al.*, 1994; Raby *et al.*, 2014; Ryer *et al.*, 2004) and can show impaired swimming performance and disrupted shoaling behaviour (Danylchuk *et al.*, 2007; Handeland *et al.*, 1996; Piato *et al.*, 2011; Ryer *et al.*, 2004), suggesting a metabolic basis for this effect (Guderley & Pörtner, 2010; Lawrence, Godin, *et al.*, 2019). As metabolic scope is finite, we would expect that conflicts in metabolic energy allocation, such as in Killen *et al.* (2015), to be a driving force in dictating prey vulnerability to a predator.

The chasing treatment appeared to be the primary draw of f_H scope energy. As expected, exhaustive exercise recovery corresponded with a higher recovery duration and effort, compared to control, unchased fish with no effects of alarm cue. Together, this suggests that physiological recovery after the chase event was prioritized over metabolic expenditure into anti-predator activities. Recovery from a chase event is a metabolically demanding process requiring a significant portion of the animal's aerobic scope (Lawrence *et al.*, 2022; Priede, 1985; Redpath *et al.*, 2010), with scope energy being used for restoring hydromineral and energy imbalances associated with prolonged anaerobic metabolism (Wood, 1991). Consequently, metabolic rate is often elevated for a

sustained period during recovery (Clark *et al.*, 2012; Lawrence, Eliason, *et al.*, 2019; Lee *et al.*, 2003; Scarabello *et al.*, 1991) with comparable responses being observed with respect to post-recovery f_H in sockeye salmon (Clark *et al.*, 2012; Donaldson *et al.*, 2010; Eliason *et al.*, 2013a; Prystay *et al.*, 2017). Presumably, chased sockeye here had a larger deviation in acid–base/ionoregulatory status than unchased controls leading to higher recovery indices (Gale *et al.*, 2014; Robinson *et al.*, 2013). During the migratory period, salmon are not feeding, and metabolic resources are scarce (Eliason & Farrell, 2016) making the proper allocation of metabolic resources a key feature in determining spawning success (Cooke *et al.*, 2006; Farrell *et al.*, 2008; Hinch & Bratty, 2000). Thus, from a fitness perspective, it may be optimal for a salmon to devote the majority of its metabolic scope towards exercise recovery given the high costs of failing to reach spawning grounds and the comparatively low cost of failing to meet other auxiliary demands (e.g., predator avoidance).

The high usage of f_H scope energy here may limit the available metabolic responses in dealing with a predation threat in the moments immediately after exhaustive exercise. Successful avoidance of a predator requires the integration of a number of physiological and behavioural processes that can be of considerable metabolic cost (Killen *et al.*, 2015; Millidine *et al.*, 2006; Moran *et al.*, 2015; van Ginneken *et al.*, 1996). Consequently, anti-predator responses may be muted after exhaustive exercise as metabolic scope energy is prioritized towards physiological recovery potentially enhancing predator vulnerability (Cooke *et al.*, 2014; Killen *et al.*, 2007, 2015; Raby *et al.*, 2014; Raby *et al.*, 2018). In addition, allocation of f_H scope energy towards anti-predator responses should result in delayed recovery durations as metabolic power is diverted from exercise recovery processes (Killen *et al.*, 2015), but this was not the case here. The lack of alarm cue effect may be explained by a potentially low degree of predation risk in the freshwater portion of the sockeye's migration. Here, only a few predators that are able to predate upon adult salmon exist (e.g., bears, seals, eagles; Quinn & Buck, 2001), particularly in the deeper, main stem reaches of the river (Quinn *et al.*, 2001). Perhaps anti-predator activities are unnecessary if the predation risk is quite low with those resources being better allocated towards migration and spawning activities. Nonetheless, predation risk has not been quantified in the Fraser River system to any great extent (Patterson *et al.*, 2017). Alternatively, it may be that adult salmon do not use chemosensory cues to perceive predation risk. To date, literature on this topic has been restricted to juvenile salmonids (e.g., Elvidge & Brown, 2014; Hawkins *et al.*, 2004; Martel & Dill, 1993) and has not been characterized in adults. Yet, migrating adult sockeye salmon appear to behaviourally avoid stressed conspecifics *via* olfactory cues, which could suggest that they may be able to use olfactory cues to perceive risk in their environment (Bett *et al.*, 2016). This notion remains speculative, but an assessment of the role of olfaction in an adult salmon's perception of the environment could prove useful in furthering our knowledge of migratory behaviours.

A few aspects of this study's experimental design may help to shed light on the findings. The experimental series only evaluated cardiovascular responses to an alarm cue of fish that were held in a tank (c. 1200 l). In response to a predation threat, salmonids exhibit a diversity of anti-predator behaviours that include sheltering, changes in spatial use patterns and shoaling (Brown & Smith, 1997; Davidsen *et al.*, 2008; Leduc *et al.*, 2004; Mirza & Chivers, 2001; Valdimarsson & Metcalfe, 1998). In addition, salmonid predation studies typically use juveniles and not adults engaged in spawning migrations. Thus, the circumstances of the experimental design may have precluded natural anti-predator behaviours. In addition, some anti-predator responses may not include a significant metabolic component (*i.e.*, change in spatial use patterns; Davidsen *et al.*, 2008; Vilhunen & Hirvonen, 2003) that would be unlikely to impart a meaningful change in our sockeye's f_H . Together, these attributes signify a need to address cardiovascular responses, in the context of multiple stressors, under a more natural setting that would permit for a larger range of behavioural responses.

4.3 | Baseline cardiovascular parameters

Sockeye salmon in this study demonstrated typical baseline f_H metrics. Here, resting and routine f_H were 39 and 58 BPM, respectively, and were comparable to wild sockeye salmon, acclimated to 15°C water temperatures, in previous works (Brett, 1971; Eliason *et al.*, 2013b; Prystay *et al.*, 2017; Smith *et al.*, 1967; Steinhausen *et al.*, 2008). Interestingly, the magnitude of peak f_H was consistent across all groups. This was unexpected as the handling control fish were not subject to the same strenuous chase event and had minor air exposure (<10 s) when transferring between tanks. Nonetheless, simple tank transfers can cause increases in f_H above basal levels (Laitinen & Valtonen, 1994). Furthermore, stress effects associated with handling, at the level of circulatory metrics, have been shown to mask treatment-level outcomes in migrating sockeye salmon (Dick *et al.*, 2018). Together, these factors may have contributed to a relatively “high” peak f_H in control fish.

4.4 | The role of the individual in mediating f_H responses

Cardiovascular responses in this study appeared to be dictated, in part, by intraspecific variation. Here, the authors found that individuals that demonstrated a high routine f_H had a lower recovery time and effort. Characterization of this phenomenon in teleosts is rather limited, but some work has shown that individuals with higher routine/resting metabolic rates can recover faster from a metabolic challenge (Marras *et al.*, 2010; Millidine *et al.*, 2009). Intraspecific variation in routine metabolism is often linked to the energetic costs associated with maintaining aerobically demanding organs in teleosts that permit high-performance activities (Burton *et al.*, 2011; Farrell, 1996; Killen *et al.*, 2010; Priede, 1985). Consequently, resting and maximal

metabolic rates have been found to be highly correlated in fishes (Killen *et al.*, 2016; Norin *et al.*, 2016; Norin & Malte, 2012; Svendsen *et al.*, 2014; this study). In this study, the relationship between recovery time/effort and routine f_H may stem from differences in inherent cardiovascular performance among individuals, thus generating additional variation in physiological recovery after the chase (Marras *et al.*, 2010).

Individual metabolic scope was not related to recovery dynamics in sockeye salmon. In previous works, a larger magnitude of available metabolic scope energy in teleost fishes often corresponds with a shorter recovery duration after exhaustive exercise (Killen *et al.*, 2014; Marras *et al.*, 2010). Contrastingly, recovery timing and effort was not related to f_H scope in sockeye salmon used in this study. The relationship between metabolic scope and recovery timing is not ubiquitous and, like this work, has been observed to have no role in dictating recovery dynamics in teleost fishes (Killen *et al.*, 2015; Marras *et al.*, 2013). Although individual responses in resting f_H may help dictate recovery responses in sockeye salmon (above), f_H scope may be less of a crucial factor here.

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