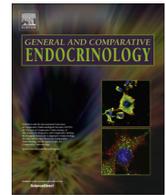




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The stress response predicts migration failure but not migration rate in a semelparous fish



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ABSTRACT

Recent findings from iteroparous species suggest that glucocorticoid secretion following acute stress can mediate behavior and survival strategies, ultimately influencing fitness. However, these correlates of the stress response may not exist in semelparous animals given the inability to maximize fitness by delaying reproduction. We measured baseline and stress-induced cortisol concentrations in semelparous sockeye salmon (*Oncorhynchus nerka*) following exposure to an acute stressor at the mouth of the Fraser River in British Columbia. The homing fish were then radio-tagged and tracked throughout their in-river migration. Findings reveal that the stress response (i.e. change from baseline to stress-induced cortisol) was predictive of mortality; fish failing to leave the release site had a significantly greater stress response (mean \pm SE = 1004.0 \pm 75.3 ng/mL) compared to fish capable of successfully migrating beyond one of the most difficult areas of passage over 100 river kilometers upstream (mean \pm SE = 780.7 \pm 66.7 ng/mL). However, there were no associations between swimming behaviors, both immediately following release and to last point of detection, and the stress response. This study also introduced a unique method of tagging migrating salmon that allows for rapid capture and sampling and thus provides the first assessment of true baseline cortisol concentrations at river-entry for migrating Pacific salmon in the wild. Results show the stress response to be linked to survival in a semelparous species and therefore set the stage for further exploration into how the evolutionary theories underlying relationships between stress responsiveness and fitness may differ between semelparous and iteroparous species.

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1. Introduction

Recent studies presenting evidence that glucocorticoid (GC) hormone secretion mediates life-history trade-offs and behavioral traits has led to attempts of linking the stress response with individual quality. Exposure to acute stress activates a series of responses that culminate in the synthesis and release of GCs (Barton, 2002), which in turn increase activity, enhance cognition and mobilize fat reserves and energy stores (Wingfield et al., 1998). These processes enable an animal to overcome an immediate challenge or cope with the perceived stress and as such, the stress response is assumed to be an adaptive mechanism. Indeed,

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during physiologically demanding periods, the stress response is typically elevated (e.g. in juvenile salmonids undergoing smoltification (Barton et al., 1985).

The assumption of the stress response being adaptive emerges from the presence of trade-offs; in challenging or stressful environments, animals maximize lifetime fitness by adjusting behavior and diverting resources to immediate survival (Ricklefs and Wikelski, 2002; Wingfield et al., 1998). There has consequently been continued interest in linking variation in stress-induced GC titres with measures of individual fitness but the direction of the relationship is increasingly context-dependent and remains ambiguous (Breuner et al., 2008). Although the theory stands that greater GC reactivity favours self maintenance (Ricklefs and Wikelski, 2002), several studies have found elevated acute levels of GCs to decrease survival (Blas et al., 2007; MacDougall-Shackleton et al., 2009; Romero and Wikelski, 2001).

In iteroparous species, individual variability in stress responsiveness has also been shown to have consistent behavioral correlates. Considerable work on lines of rainbow trout bred for high or low responsiveness has demonstrated a tight coupling between stress physiology and behavior whereby distinct “coping styles” emerge (Øverli et al., 2005). However, given that correlates of the stress response are driven by age, experience and reproductive investment, the relationships observed in iteroparous species may not transfer to semelparous systems. Additionally, concentrations of cortisol, the primary GC in fish (Barton, 2002), are very high during semelparity in fish (Hruska et al., 2010; McBride et al., 1986), and much higher when compared to iteroparous life histories, even within a single species (Barry et al., 2001). The presence of trade-offs between survival and reproduction are likely to be strongest in long-lived species with multiple reproductive opportunities (Angelier et al., 2007), but in short-lived or semelparous species with minimal chances at reproduction, evolutionary theory predicts the stress response to be decoupled from behavior as reproduction must occur despite stressful conditions (Wingfield and Sapolsky, 2003). Supporting this is a study on spawning pink salmon where although baseline cortisol was elevated in behaviorally subordinate fish compared to dominant fish, no relationships between the observed behavioral hierarchies and stress-induced cortisol were observed (Cook et al., 2011a).

Few studies assessing consequences of the stress response have incorporated measures of direct fitness and most have used captive subjects (reviewed in Breuner et al., 2008). There is evidence suggesting that Pacific salmon do maintain an acute stress response during migration that varies considerably among individuals [e.g. when encountering hydraulic changes (Hinch et al., 2006) or elevated water temperatures (Mathes et al., 2010)] but little remains known regarding the significance of this variation. Additionally, measuring a full response from baseline concentrations in wild migrating salmon is difficult given the inability to obtain true baseline cortisol concentrations with standard capture techniques.

The spawning migrations of Pacific salmon (spp.) from ocean to their natal streams are among the longest and most challenging of all animal migrations and are completed entirely with fixed somatic energy reserves (Hendry and Berg, 1999). This upriver migration therefore acts as a strong selective force for Pacific Salmon populations and cortisol plays an adaptive and integral role throughout (Carruth et al., 2002). Therefore, the main objective was to examine whether the stress response influences probability of survival throughout migration by radio-tracking wild homing sockeye salmon (*O. nerka*) that were bio-sampled prior to and following exposure to an acute stressor. We also aimed to describe individual variation in cortisol secretion as well as assess links between cortisol concentrations and swim speeds. Cortisol concentrations have been linked to fitness and behavior in Pacific salmon on the spawning grounds (Cook et al., 2011a), but we wish to explore if these relationships are present from the beginning of migration. Additionally, given the literature on coping styles in fish (Koolhass et al., 1999; Øverli et al., 2005), we would expect more “proactive” individuals, those with a reduced GC response, to respond actively to an acute stressor and have faster swim speeds upon release.

An experimental design based in biotelemetry of a semelparous model makes for a novel addition to the growing literature attempting to understand the context-dependent relationships between fitness and acute glucocorticoid secretion. Further, we introduce a unique method of capturing migrating salmon that allows for rapid sampling and thus we present the first assessment of true baseline cortisol concentrations at river-entry for wild migrating Pacific salmon.

2. Materials and methods

2.1. Study site and sampling

This study was conducted in strict accordance with Canadian Council on Animal Care guidelines under an animal care permit obtained from Carleton University (B10-06) and Fisheries and Oceans Canada (DFO-2010 UBC SGH Permit). Sockeye salmon were sampled and tagged from dusk to dawn on 17-Aug-2010 from a fishwheel located on the Fraser River near Mission, British Columbia, Canada (49°10'3.4291"N and 122°26'22.9513"W; Fig. 1). A fishwheel operates as a water-powered mill wheel. As the wheel rotates with the current, baskets scoop up fish travelling upstream. Near the apex of rotation, fish descend from the baskets into holding tanks. Fish ($n = 54$) were intercepted for sampling prior to landing in holding tanks and blood samples (~2 mL) were immediately drawn by caudal venipuncture with a 3.8 cm, 21-gauge needle and a 3 mL vacutainer (BD, Franklin Lakes, NJ). During sampling (and after, as applicable), fish were exposed to a 2-min air exposure treatment that acted as an acute standardized stressor ensuring all fish experienced the same magnitude of stress. From first encounter with the fishwheel to time of sampling took approximately 45 s and therefore cortisol concentrations measured in these samples were representative of baseline physiological condition given current in-river conditions. Most individuals were sampled in under 1 min from capture; samples collected after 2 min were not used. Following initial sampling and air exposure, fish were held for 25 min. in black nylon flow-through fish bags (25 cm diameter, 100 cm length) placed in the river alongside the fishwheel prior to obtaining a second blood sample. This replicate sampling procedure has been used previously in semelparous Pacific salmon and known to evoke a stress response (Cook et al., 2011a). Holding in black opaque bags ensured that all fish experienced the same conditions of sensory deprivation (i.e. reduced light and no interaction with other fish) throughout the holding period. At termination of the 25 min. holding period, fish were sampled for stress-induced cortisol levels (~1 mL). Coded radio transmitters (16 × 50 mm; Lotek Wireless Inc. or Sigma Eight Inc., Newmarket, ON) were implanted gastrically (see Cooke et al., 2005 for methodology). Blood samples were centrifuged for 5 min at 10,000g (Compact II Centrifuge, Clay Adams, Parsippany, NJ) on site and immediately stored in liquid nitrogen until transferred to a -80 °C freezer. Reproductive hormones (testosterone and 17β – estradiol), used to determine sex, were assayed in duplicate (enzyme linked immunosorbent assay, Neogen Co., Lexington, KY). Plasma cortisol concentrations were quantified using a commercial ImmunoChem Cortisol ¹²⁵I RIA kit (MP Biomedicals, Orangeburg, NY) and a Cobra Auto-Gamma counter (Hewlett-Packard, Palo Alto, CA) validated for use in fish (Gamperl et al., 1994). Intra-assay variability was 8.76 (% CV). Because we were interested in the ability to elicit a stress response while accounting for the high baseline concentrations naturally occurring during migration, analyses were performed on the response (change from baseline to maximum stress-induced concentrations).

True baseline cortisol concentrations have never before been established in wild migrating Pacific salmon due to an inability to sample captured fish immediately using traditional gear (e.g. netting or angling). In pink salmon on the spawning grounds, baselines have averaged (±SE) between 297 ± 21 ng mL⁻¹ (Cook et al., 2011a) and 436 ± 78 ng mL⁻¹ (McConnachie et al., 2012) but a progressive increase in baseline plasma cortisol concentrations is known to occur as fish approach the spawning grounds (McBride et al., 1986; Robertson and Wexler, 1959). As such, we expected to observe high and/or variable baselines in fish captured at

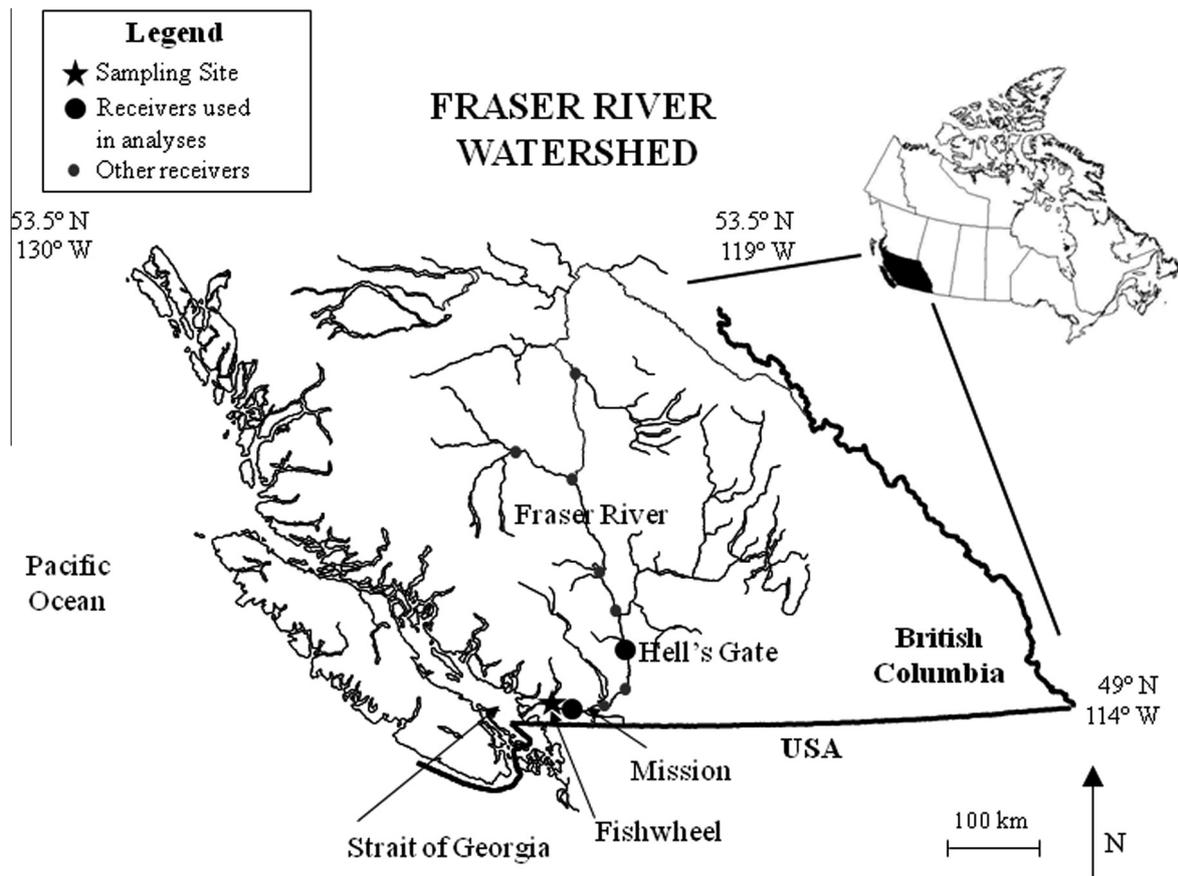


Fig. 1. Map of the Fraser Watershed in British Columbia, Canada where 54 sockeye salmon (*Onchorynchus nerka*) were sampled and tagged from a fishwheel (star on map). Receivers (black and grey circles) located throughout the river recorded their success. The first receiver past release was at Mission, 10 rkm from release; fish classified as “successful” were those that past the receiver at Hell’s Gate.

river-entry. However, despite rapid sampling, baseline samples from wild fish are inevitably influenced by previous stress history and environmental conditions at time of sampling that cannot be controlled for.

2.2. Migration success

The coded radio transmitters allowed for detection of individual fish when passing within range of fixed receiver stations (SRX400 or SRX400A, Lotek Wireless Inc., Newmarket, ON) that were strategically deployed on the mainstem Fraser River (see [Cooke et al., 2006](#) for a full description of the system and [Fig. 1](#)). Fish were classified as “en-route mortality” at the location of last detection. For analyses we classified fish as “successful” or “unsuccessful”, on a relative scale. All sockeye sampled in this study were destined for spawning locations upstream of Hell’s Gate (~144 river kilometers from release; [Fig. 2](#)) which is also the most difficult portion of their migration ([Hinch and Bratty, 2000](#)). Therefore, those fish detected passing the receiver following Hell’s Gate, a receiver line also known to have high probabilities of detection, were considered “successful”. Although some tagged fish did reach the spawning grounds beyond Hell’s Gate, sample sizes were much too small (4 individuals) for these fish to be grouped separately for analyses. Therefore, the classification of “successful” is a relative comparison to the unsuccessful group and does not indicate successful spawning. Fish classified as “unsuccessful” include those never detected or fish only detected on the first receiver [approximately 10 river kilometers (rkm) from release] but on no other subsequent receiver. These fish likely fell downstream and were unable to recover

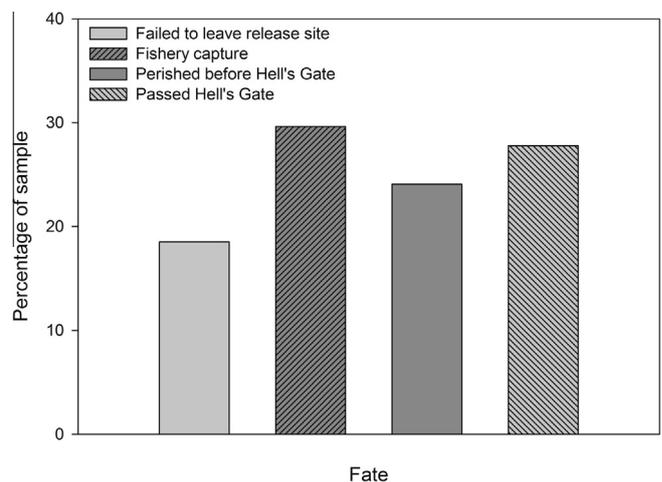


Fig. 2. Fate of sockeye salmon (*Onchorynchus nerka*) sampled and tagged at river-entry from the Fraser River, British Columbia and their classification for analysis. Fish failing to leave the release site (i.e. those that were never detected or those only detected on the first receiver and no other) were considered “unsuccessful” in analyses. Those individuals detected passing Hell’s Gate, an area of extremely difficult passage, were considered as “successful” for the purpose of analyses. All of fish (i.e. those detected past the first receiver but that perished before Hell’s Gate as well as fishery captures) were excluded from analyses.

to continue migration. All analyses were documented as a relative comparison between these two groups. All reported captures from commercial, recreational or tribal fisheries were excluded.

Similarly, fish that travelled beyond the first receiver but that disappeared prior to Hell's Gate were excluded as this area experiences intense fishing pressure and uncertain capture reporting rates. Sockeye densities were exceptionally high in 2010 and the fishery harvest was one of the largest recorded. Despite having low survival overall and small sample sizes, this methodology of comparing two groups allows for the best comparison of the physiological attributes of definitely unsuccessful fish (i.e. failing to migrate beyond 10 rkm from release) relative to stronger individuals that were capable of migrating at least 150 rkm from release and through very difficult stretches of river.

Assessments of activity included immediate post-release swim speeds (i.e. behavioral response to the experimental stressor) and swim speed overall. Migratory rates were calculated in all fish as the time elapsed between release and detection at the first receiver (immediate post-release behavior) and Hell's Gate (swim speed overall) divided by the corresponding distances. All statistical analyses were conducted with SPSS Statistics (Version 19.0.0, IBM Company, Somers NY) using $\alpha = 0.05$. Fish were immature at time of sampling and lacked external sexual characteristics. Therefore, sex was determined by regressing estradiol with testosterone concentrations (Cooke et al., 2006). The resulting graph reveals two clusters: males with high testosterone and low estradiol and females with the opposite characteristics.

3. Results

Of the 54 fish tagged, 15 were classified as successful (passed Hell's Gate; Fig. 1) and 10 were unsuccessful [only detected at the first receiver and not on subsequent receivers ($n = 6$) or never detected ($n = 4$; Fig. 2)]. Fishery captures were high; 16 fish were reported as commercial or recreational harvests (Fig. 2). Fish detected past the first receiver but that disappeared en-route to Hell's Gate ($n = 13$; Fig. 2) were also excluded given uncertainty surrounding their fate. A multivariate analysis of variance (MANOVA) testing for sex differences in cortisol concentrations revealed no significance ($F_{(4,54)} = 1.26$, $p = 0.29$). Therefore, sexes were pooled for all analyses. Baseline cortisol concentrations had greater variation (172 % CV; Table 1) than response values and did not influence absolute stress-induced concentrations ($R^2 = 0.057$, $F_{(1,50)} = 3.02$, $p = 0.09$).

Binary logistic regression modeling revealed the probability of leaving the release site and passing Hell's gate was predicted by the cortisol stress response (Model: $X^2_{(1)} = 6.10$, $R^2 = 0.33$, $p = 0.014$) but not baseline cortisol (Model: $X^2_{(1)} = 0.946$, $R^2 = 0.57$, $p = 0.62$). Unsuccessful fish had a greater stress response (Wald = 3.99, $P = 0.046$; Fig. 3). The stress response (mean \pm SE) was 1004.0 ± 75.3 ng/mL for unsuccessful fish and 780.7 ± 66.7 ng/mL for successful fish.

It took fish an average of 0.67 d to reach the first receiving station and an average of 4.53 d to pass Hell's Gate. Multiple regression showed neither baseline cortisol concentrations nor the stress response to predict swim speed immediately following release, reflective of a response to the experimental stressor

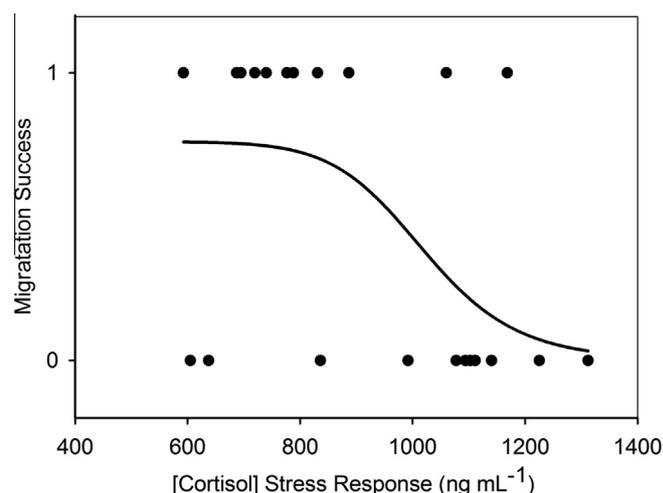


Fig. 3. The stress response (stress-induced [cortisol] – baseline [cortisol]) predicts migratory success of sockeye salmon (*Oncorhynchus nerka*) sampled and tagged at river-entry from the Fraser River, British Columbia ($n = 25$). Each point represents an individual fish. Fish categorized as “successful” (coded as 1) are those that passed Hell's Gate, an area of extremely difficult passage and those categorized as “unsuccessful” (coded as 0) are those that failed to leave the release site. Logistic regression revealed the stress response to predict success whereby unsuccessful fish had an elevated glucocorticoid stress response relative to fish passing Hell's Gate.

($F_{(2,27)} = 0.51$, $p = 0.61$), or overall migration rates ($F_{(2,20)} = 0.38$, $p = 0.69$).

There are many differing stocks of sockeye salmon, each with distinct physiological characteristics. Therefore, given the chance of mixed stocks, the data was explored for correlations between swim speed and reproductive hormones. A mixed stock composition would result in maturity levels (i.e. reproductive hormones) and swim speeds variable among the sample as a whole but consistent within an individual stock. Therefore, a significant relationship between reproductive hormones and swim speed suggests variable stock composition. However, multiple regression modeling revealed neither testosterone nor estradiol to be significant predictors of swim speed upon release ($R^2 = 0.049$, $F_{(2,29)} = 0.74$, $p = 0.48$) or overall ($R^2 = 0.039$, $F_{(2,22)} = 0.45$, $p = 0.65$). Although it cannot be confirmed, this provides evidence for low stock variability in the sample in the absence of conclusive genetic information.

4. Discussion

The likelihood of survival to the spawning grounds was diminished in fish with a high stress response, suggesting that the magnitude of the cortisol stress response is associated with individual fitness in migrating sockeye salmon at river-entry. En-route mortality for Pacific salmon can be very high in some years (Cooke et al., 2004), and despite receiving considerable research attention, the mechanisms underlying this variability remain unknown. A finding of reduced survival in individuals with a higher stress response aligns with previous research from iteroparous species (e.g. Blas et al., 2007; MacDougall-Shackleton et al., 2009; Romero and Wikelski, 2001). Although evolutionary theory would state that the stress response may not mediate trade-offs or behavioral traits in a semelparous species (Wingfield and Sapolsky, 2003), launching a high stress response could have the same detrimental effect on survival as it has shown to in some iteroparous species.

The rapid sampling from a fishwheel conducted in this study provided the first descriptive characteristics of cortisol concentrations at river-entry for migrating sockeye salmon. Standard capture methods for wild fish (i.e. seining, angling, etc.) do not allow

Table 1
Range of baseline cortisol concentrations and the stress response for migrating sockeye salmon (*Oncorhynchus nerka*) sampled at river entry from the Fraser River in British Columbia, Canada ($n = 54$).

	[Cortisol] (ng mL ⁻¹)					
	Min	Max	Mean	SEM	SD	CV (%)
Baseline	3.52	470.83	66.08	15.46	113.62	171.94
Response	280.48	1322.49	857.52	36.82	268.09	31.26

Values represent entire sample, inclusive of those excluded in regression analyses.

for immediate sampling and thus baselines, in addition to the ability to quantify the entire magnitude of a stress response following acute stress, were previously unknown. Cortisol concentrations exhibited considerable individual variability that exceeds published values. For example, Guimont and Wynne-Edwards (2006) reported 50–60% CV in corticosterone concentrations as exceptionally high. It is possible that the measured baselines are indeed an individual trait (i.e. repeatable over time within an individual) and that such variability exists naturally in wild Pacific salmon in an unstressed state. However, previous repeated sampling of wild fish in their natural environment failed to find consistency in baseline cortisol concentrations (Cook et al., 2011b). Given that these values are from wild and actively migrating fish, they are likely higher and much more variable than those that would be collected from fish at rest or those held in captivity. However, baseline samples taken from wild animals at will are inevitably and uncontrollably influenced by short-term condition and an immediate stress history and therefore we may not expect to see correlations with other repeatable traits. Additionally, these potential previous stress encounters could influence the subsequent response as acute disturbances are known to evoke cumulative stress responses (Barton et al., 1986). It is also of note that in addition to intrinsic variability there are also differences attributed to maturity level and stock that we were unable to control for. However, all individuals were sampled over a very short time period (~12 h) and stocks tend to travel together in groups. Further, there was little observed variation in external sexual characteristics and no relation between sex hormones and swim speeds which drastically reduces the likelihood of variable stock composition.

No association was detected between measured cortisol concentrations and swim speeds overall or upon release. The literature from captive fish populations suggests that cortisol stimulates locomotor activity (Øverli et al., 2002) and that “low responders” are generally more aggressive when faced with stress (e.g. territorial intruder test; Øverli et al., 2005). Therefore, we may have expected the “high responders” from the study group to have faster swim speeds upon release as an active escape response from the stressor. Failure to see this relationship could support the theory from Wingfield and Sapolsky (2003) that behavior becomes decoupled from the stress response with limited breeding opportunities (e.g. semelparity). However, we caution that the swim speed variables measured may not represent a true individual behavior given the myriad of external factors that may affect swim speeds such as in-river experience (e.g. predator exposure, river flow), and spawning destination. Furthermore, the telemetry tags used in this study measure only directionality (i.e. whether a fish passed certain check points or not) but not locomotory activity. Tags such as accelerometers can be used to measure activity levels which may be more appropriate for a detailed assessment of individual locomotory behavior.

Despite an extensive theoretical framework explaining the relationship between GCs and fitness, factors mediating negative consequences of the stress response remain ambiguous. Cortisol is known to play an important role for homing Pacific salmon (Carruth et al., 2002); findings of a negative relationship between the stress response and fitness therefore do not disregard all previous research suggesting that the cortisol stress response is an adaptive response (see Ricklefs and Wikelski, 2002; Wingfield et al., 1998). Nor do results explicitly suggest the stress response is maladaptive as survival differences could be reflective of those high responders showing evidence of an elevated and cumulative stress response due to previous (i.e. prior to sampling) exposure to stress, as has been shown to occur in captive juvenile Chinook salmon (Barton et al., 1986).

Romero et al. (2009) introduced the reactive-scope model where factors such as neural, epigenetic and immune mechanisms

also act as mediators of the stress response. A mechanistic approach to studying stress and survival that combines multiple aspects would therefore be beneficial to unravel factors mediating the relationship, in addition to a comparative exploration into how the evolutionary theories underlying relationships between stress responsiveness and fitness may differ between semelparous and iteroparous models.

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