General and Comparative Endocrinology 202 (2014) 44–49

Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen

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

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ARTICLE INFO

Article history:
Received 30 November 2012
Revised 21 February 2014
Accepted 7 April 2014
Available online 24 April 2014

Keywords:
Cortisol
Glucocorticoid secretion
Migration
Oncorhynchus nerka
Sockeye salmon
Stress response

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 ± SE = 1004.0 ± 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 ± SE = 780.7 ± 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 an 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.

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, 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).

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http://dx.doi.org/10.1016/j.ygcen.2014.04.008
0016-6480/

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 an 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-guage 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 10,000*g* (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 ^{125}I RIA kit (MP Biomedicals, Orangeburg, NY) and a Cobra Auto-Gammer counter (Hewlett–Packard, Palo Alta, 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