ARTICLE

Relationship of baseline and maximum glucocorticoid concentrations to migration propensity: a field test with wild subadult brown trout (*Salmo trutta*)

S.M.R. Jain-Schlaepfer, J.D. Midwood, M.H. Larsen, K. Aarestrup, G.D. King, C.D. Suski, and S.J. Cooke

Abstract: There is considerable variation in glucocorticoid (GC) baseline status and stress responses of individuals, yet the cause and consequence of this variation remains ambiguous. Attempts to relate GC levels to fitness and life-history trade-offs have yielded variable results. In this study, we evaluated whether baseline and poststressor GC hormone concentrations predicted migration strategy (i.e., resident or migrant) and successful seaward migration in a partially migrating population of juvenile brown trout (*Salmo trutta* Linnaeus, 1758). Baseline ($N = 99$) or poststressor ($N = 102$) plasma cortisol concentrations were obtained from brown trout and they were tagged with passive integrated transponder (PIT) and released in a natural Danish stream. Subsequently, fish were tracked with PIT reader systems and the stream was resampled for resident individuals. GC levels were not found to be associated with recapture of resident individuals or migration propensity to our first tracking station (S1), but increased baseline (and not poststressor) GC levels were associated with increased passage from S1 to our second tracking station, which anecdotally was an area of high predation or challenge. Our study found no evidence to suggest that cortisol regulates the migration life history in juvenile brown trout, but intermediate increases in baseline GC (and not poststressor GC) levels may favor migration performance.

Key words: cortisol, fish, glucocorticoid, migration, stress response, brown trout, *Salmo trutta*.

Résumé : Si les concentrations de glucocorticoïdes (GC) de référence et en réponse au stress d'individus présentent des variations considérables, les causes et conséquences de ces variations demeurent ambiguës. Des tentatives visant à relier les concentrations de GC à l'aptitude et à des compromis évolutifs ont donné des résultats variables. Nous avons évalué si les concentrations de référence et post-stress d'hormones GC prédisaient la stratégie de migration (c.-à-d. résident ou migrateur) et le succès de la migration vers la mer dans une population partiellement migratrice de truites brunes (*Salmo trutta* Linnaeus, 1758) juvéniles. Des concentrations de référence ($N = 99$) et post-stress ($N = 102$) de cortisol plasmatique ont été obtenues de truites qui ont été dotées de radioétiquettes passives intégrées (PIT) et relâchées dans un cours d'eau naturel danois. Les poissons ont ensuite été suivis à l'aide de systèmes de lecture des PIT et le cours d'eau a été rééchantillonné pour en prélever les spécimens résidents. Aucune association n'a été relevée entre les concentrations de GC et la recapture de spécimens résidents ou la propension à migrer jusqu'à la première station de surveillance (S1), mais des concentrations de GC de référence (mais non post-stress) accrues étaient associées au déplacement accru de S1 vers la deuxième station de surveillance qui, par ailleurs, était un secteur de forte prédation ou difficulté. L'étude n'a fait ressortir aucun indice de régulation par le cortisol du cycle de migration chez les truites brunes juvéniles, mais des augmentations modérées des concentrations de GC de référence (mais non post-stress) pourraient favoriser la performance de migration. [Traduit par la Rédaction]

Mots-clés : cortisol, poisson, glucocorticoïde, réaction au stress, truite brune, *Salmo trutta*.

Introduction

The study of the physiological basis of stress is useful for understanding physical, chemical, social, and perceived challenges faced by organisms, and the functional responses employed by organisms to deal with those stressors (Denver 2009). In vertebrates, real or perceived stressors stimulate the hypothalamic–pituitary–adrenal axis (HPA; or the hypothalamic–pituitary–interrenal (HPI) axis in fish) resulting in the release of glucocorticoid (GC) hormones into the blood stream (Sapolsky et al. 2000; Barton 2002). Thus, circulating concentrations of GC hormones are often measured to understand an organism's stress response (Dantzer et al. 2014). Within a species, individuals often show repeatable baseline (prior to a stressor) GC levels and a repeatable GC response following a stressor (Pottinger and Carrick 2001; Ouedraogo et al. 2004; Wada et al. 2008; Rensel and Schoech 2011; Cook et al. 2012; Narayan et al. 2013; Love et al. 2015) resulting in different reactive scope profiles (difference between GC response and baseline) be-

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tween individuals (Romero et al. 2009). The biological functionality, as well as the individual and evolutionary consequences of such variability among individual, are still debated (Breuner et al. 2008; Bonier et al. 2009).

To define the biological consequences of individual variation in GC levels during the stress response, researchers have attempted to relate interindividual differences in baseline and poststressor GC concentrations to performance (e.g., migration, parental care, territorial behavior) and fitness (e.g., Comendant et al. 2003; Cabezas et al. 2007; Breuner et al. 2008). From a theoretical point of view, it is often hypothesized that individuals with greater poststressor GC levels should have increased long-term fitness (Breuner et al. 2008), because an individual's stress response increases chances of surviving the stressor (e.g., predation attempt) and mediates trade-offs between reproduction and survival. Indeed, experimental studies show variability in the relationship between magnitude of the stress response and performance or fitness measures (reviewed by Breuner et al. 2008). This relationship is increasingly understood as context dependent, because an elevated stress response in an emergency situation shifts resources from reproduction to survival (Wingfield et al. 1998); however, an elevated stress response when the perception of stressors is exaggerated can lead to the misallocation of resources, thereby limiting investment in growth and reproduction (Hawlena and Schmitz 2010). There is a paucity of studies directly examining interindividual differences in stress response while concurrently measuring performance or fitness (Romero and Wikelski 2001; Blas et al. 2007; Cook et al. 2011).

In contrast to the theorized positive association between elevated poststressor GC levels and performance or fitness, higher baseline GC levels are often inferred to indicate reduced condition, because it suggests an organism is experiencing greater environmental stressors (Cort-Fitness hypothesis; reviewed by Bonier et al. 2009). Higher GC levels are in circulation when exposed to a stressor and are associated with the reallocation of resources from fitness-related factors, such as growth and reproduction, towards the restoration of physiological homeostasis. Despite the potential negative consequences associated with higher baseline GC levels, some studies have found that moderate long-term increases in GCs can actually increase individual performance (Comendant et al. 2003; Pravosudov 2003; Cabezas et al. 2007). Further investigation is therefore warranted to understand the relationship between baseline GC hormones and performance.

Both baseline and poststressor GC concentrations have a heritable component in some species (Evans et al. 2006; Jenkins et al. 2014) and are associated with a suite of other traits that can lead to different life-history and coping strategies (Koolhaas et al. 1999; Pottinger and Carrick 1999; Blas et al. 2007; Øverli et al. 2007; Wada et al. 2008). Selection on heritable variation in GC levels and response is thought to drive the evolution of life-history traits (Bolnick et al. 2003; Williams 2008), such as migration behavior. Migration, in particular, requires large amounts of energy and often exposes individuals to many stressors including predation and changes in environmental condition (Dingle 2014). Thus, GC levels have the potential to be an important factor determining successful migration (Holberton 1999; Piersma et al. 2000; Angelier et al. 2009), which could affect fitness and potentially drive the evolution of migration strategies. Migration success, meaning successfully reaching the migration destination, has been linked to GC levels in a single species of fish, adult sockeye salmon (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)), where upriver migration success was found to increase with stress responsiveness but not baseline stress levels (Cook et al. 2014). GC levels have also been related to the smoltification process in anadromous salmonids. Smolting fish generally have higher baseline and peak GC, which appears to induce the physiological changes required to cope with the transition from freshwater to saltwater (e.g., increased osmoregularity capacity; Barton et al. 1985; Redding et al. 1991; Björnsson et al. 2011). Stressors that cause a GC re-

sponse may cause a reallocation of energy towards immediate survival resulting in a change in life-history and coping strategies (Landys et al. 2006; Shepard et al. 2008). Thus, GC variation resulting from past or current conditions may influence the "decision" to migrate. Alternative migration strategies have the potential to be heritable through heritable GC regulation (Zera and Harshman 2001; Williams 2008).

For our study species, the brown trout (*Salmo trutta* Linnaeus, 1758), migration success provides a measure of performance and also acts as an indicator of alternate life-history strategies. More specifically, European populations of brown trout show a continuum of migration strategies, where subpopulations are capable of anadromous activity, smaller scale migrations within freshwater systems (potamodromous), and residency in natal streams (Cucherousset et al. 2005). This phenomenon is termed partial migration and reflects the fact that only a component of the population engages in migration, a common trait among some salmonid species (Jonsson and Jonsson 1993). Previous studies on the propensity of migration in brown trout have found that individuals with high metabolisms and high growth rates tend to migrate, likely due to higher resource requirements (Jonsson and Jonsson 1993; Forseth et al. 1999).
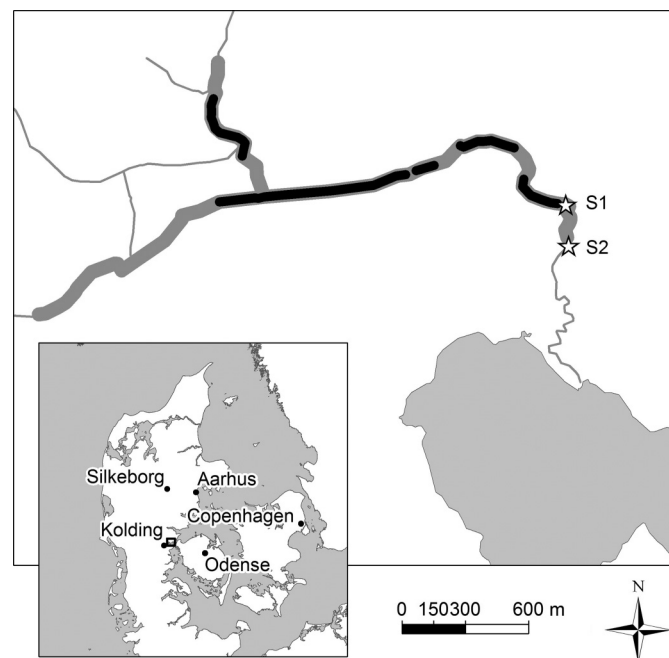
The goal of this study is to define relationships between GC levels (baseline and poststressor) and migration propensity in juvenile brown trout. Given the role of GCs in smoltification, we would expect to see higher poststressor and baseline GC levels in migrating individuals. The effects of individual body condition and size (length, mass) in relation to migration propensity will also be quantified.

Materials and methods

Experimental design

Brown trout were captured using a backpack electrofisher (Scubla ELT 60 II GI; run at 300 V) in four regions of the Gudsø Stream, Jutland, Denmark (Fig. 1) between 11 March and 18 March 2013. This time period was selected because it fell prior to the spring migration, which typically occurs in mid-April (Midwood et al. 2014). Individuals between 120 and 182 mm in total length were used to minimize the effects of allometry on results. To evaluate an individual's resting plasma cortisol levels (baseline), blood was collected (~0.2 to 0.3 mL) from a subset of fish within 3 min of capture via caudal puncture of the haemal arch using a 1 mL syringe and a 25-gauge needle. A separate subset of fish (Table 1) were exposed to a standardized 3 min air exposure and then held in a 20 L container with 5 L of fresh water for 30 min prior to the collection of a poststressor blood sample. Blood was sampled in the same manner as above at 30 ± 3 min after air exposure corresponding with the approximate peak in GCs in brown trout (Pickering and Pottinger 1989). Blood samples were held in a water–ice slurry for no more than 2 h until centrifuged for 5 min (10 000 r/min) to isolate plasma. Plasma isolate was decanted, flash frozen, and stored (–80 °C) for later analysis of plasma cortisol concentrations. Total length and wet mass of each individual were then measured. Next, a uniquely coded 23 mm passive integrated transponder (PIT) tag (RI-TRP-RRHP, half duplex, 134 kHz, diameter 3.85 mm, and a mass of 0.6 g in air; Texas Instruments, Plano, Texas, USA) was inserted into the body cavity through a small incision made with a scalpel. Previous tag retention studies on salmonids have found negligible effects on survival and growth (Larsen et al. 2013) and generally low PIT tag rejection rates (<4% after 7 months; Ombredane et al. 1998). Following tagging, fish were placed in a 60 L container of fresh river water and monitored for a minimum of 30 min to ensure recovery before they were ultimately released back into the stream near their point of capture. All fish recovered. Length (cm) and mass (g) were used to calculate Fulton's condition factor (K) for each sampled fish, where $K = (mass/length^3) \times 100$ (Ricker 1975).

Fig. 1. Location of Gudsø Stream in Denmark is shown as a black box in the bottom left panel (northeast of Kolding). The portions of the stream where brown trout (*Salmo trutta*) were captured are shown as thick black lines and the areas re-sampled in June 2013 are shown as thick grey lines. The positions of the two passive integrated transponder (PIT) antennas, tracking station 1 (S1) and tracking station 2 (S2), are also shown in the larger map. Light grey areas represent water and the outflow location of Gudsø Stream into Kolding Fjord. Map data from the European Environment Agency.

Table 1. Sample size, plasma cortisol concentration, individual fish length, mass, and Fulton's condition factor (*K*) for juvenile brown trout (*Salmo trutta*) collected from the Gudsø Stream, Denmark.

Treatment	Baseline	Poststressor
Sample size	99	99
Cortisol (ng/mL)	5.6±6.7 (0.1–25.5)	69.2±40.1 (7.2–197.6)
Length (mm)	146±126 (120–182)	147±13 (122–171)
Mass (g)	28.2±7.6 (15.8–48.5)	29.2±8.1 (17.1–45.8)
K	0.90±0.07 (0.66–1.06)	0.90±0.06 (0.72–1.09)

Note: Collected fish were blood sampled either within 3 min of capture (baseline) or 30 min following a standardized 3 min air exposure (poststressor). Values are mean ± SD, with the range in parentheses.

Table 2. Number of individuals recaptured, number of sampled individuals that were detected at tracking station 1 (S1) and tracking station 2 (S2), and mean (±SD) cortisol concentration of these individuals for baseline (sampled within 3 min of capture) and poststressor (sampled 30 min following a standardized 3 min air exposure) treatment groups of juvenile brown trout (*Salmo trutta*) collected from the Gudsø Stream, Denmark.

Treatment	Baseline	Poststressor
Number of recaptured brown trout	13	6
Cortisol of recaptured brown trout (ng/mL)	5.6±5.0	69.9±40.1
Number of brown trout at S1 passage	37	46
Cortisol on passing S1 (ng/mL)	5.8±7.7	76.2±42.3
Number of brown trout at S2 passage	19	26
Cortisol on passing S2 (ng/mL)	8.4±9.0	79.2±42.4

16 km in length; however, given the shallow and narrow nature of the stream and the relatively high efficiency of capture for salmonid species using electrofishing (Kennedy and Strange 1981; Hayes and Baird 1994), efforts were likely sufficient to provide a relative estimate of residency.

Cortisol analysis

Plasma cortisol (ng/mL) was quantified using a commercially available enzyme-linked immunosorbant assay (ELISA) (Enzo Life Sciences, Cortisol EIA Kit (901-071), BioAssay Systems) previously validated for use in fishes (Sink et al. 2008). This assay has a detection limit of 0.0567 ng/mL; therefore, the five samples with undetectable cortisol concentrations were assigned values equal to this detection limit (Haddy and Pankhurst 1999; Liss et al. 2013).

Tracking

To track movements of individuals from their point of release to the sea, two tracking stations were placed approximately 1 km upstream of Kolding Fjord on Gudsø Stream, which was the closest feasible place to the ocean. The first station (S1) was placed upstream of a millpond and the second station (S2) was placed downstream of the millpond, approximately 150 m from S1. Each station consisted of a paired set of PIT gates spaced approximately 10 m apart. This allowed for an assessment of the direction of movement for individuals at each station. The same array was used by Midwood et al. (2015) and was found to have a detection efficiency at S1 of 96.3%; detection efficiency could not be evaluated at S2, but missed detections were assumed to affect all brown trout equally and therefore should not bias conclusions related to baseline GC or poststressor GC correlations with relative migration success to S1 and S2.

To estimate the proportion of individuals that stayed resident and did not migrate to the ocean, the stream was re-sampled using a backpack electrofisher on 18 and 19 June 2013, at which point migratory individuals should have left the stream. Surveys started near the antenna and proceeded upstream through all areas where brown trout were initially captured (Fig. 1). It was not possible to resample the entire system because it is greater than

Statistical analyses

Multiple linear regression was used to quantify relationships between plasma cortisol concentrations (for both poststressor and baseline groups) and timing of migration (time from sampling to S1 passage) while controlling for *K*, length, or mass. Assumption of homogeneity of variance and normal distribution for the models were ensured by visual inspection of residual plots. If violated, then the response variable was log-transformed or square root transformed. Multiple binomial logistic regression was used to test for the effect of plasma cortisol concentration (baseline and poststressor) on the probability of successful migration to S1 (used as a proxy of migration strategy) and on the probability of successful migration to S2 given successful passage of S1 (used as a measure of migration success through the millpond for migrating individuals). Again, separate tests were conducted using mass, length, or *K* as a covariate in the model. Length, mass, and *K* were also tested separately for effects on all migration response variables with the baseline and poststressor fish subsets pooled. Two outliers were removed before analyses because they were outside the standard deviation of the mean: a baseline cortisol value of 44.5 ng/mL and a peak cortisol value of 3.43 ng/mL. All significant results found without the outliers were also found when the outliers were included in the analyses.

Variation in association with recorded mean values is given as standard deviation (±SD) throughout. Statistical significance for all analyses was set at $\alpha = 0.05$ and all statistical analyses were conducted in R version 3.2.2 (R Core Team 2016).

Results

Of the 198 fish tagged, 19 were recaptured in mid-June, 83 were detected passing S1, and 45 were detected passing S2 (Table 2). All fish detected at S2 were also detected at S1, suggesting a detection

Fig. 2. The probability of recapture (*a*), successful tracking station 1 (S1) passage (*b*), and successful passage between S1 and tracking station 2 (S2) (*c*) as a function of individual baseline cortisol plasma concentration collected within 3 min of capture for individual juvenile brown trout (*Salmo trutta*) on the Gudsø Stream, Denmark. The probability of recapture (*d*), successful S1 passage (*e*), and successful passage between S1 and S2 (*f*) as a function of individual cortisol plasma concentration 30 min after 3 min air exposure. Open circles represent actual values found for individuals and the line represents the values predicted using a binary logistic regression with no covariates. Binary logistic regression found no significant relationships except for panel *c*: increased baseline cortisol was associated with greater probability of successful S2 passage for fish that had completed S1 passage, with marginal significance when mass (*p* = 0.05) or length (*p* = 0.04) was included in the model as a covariate, but not when Fulton's condition factor was included as a covariate.
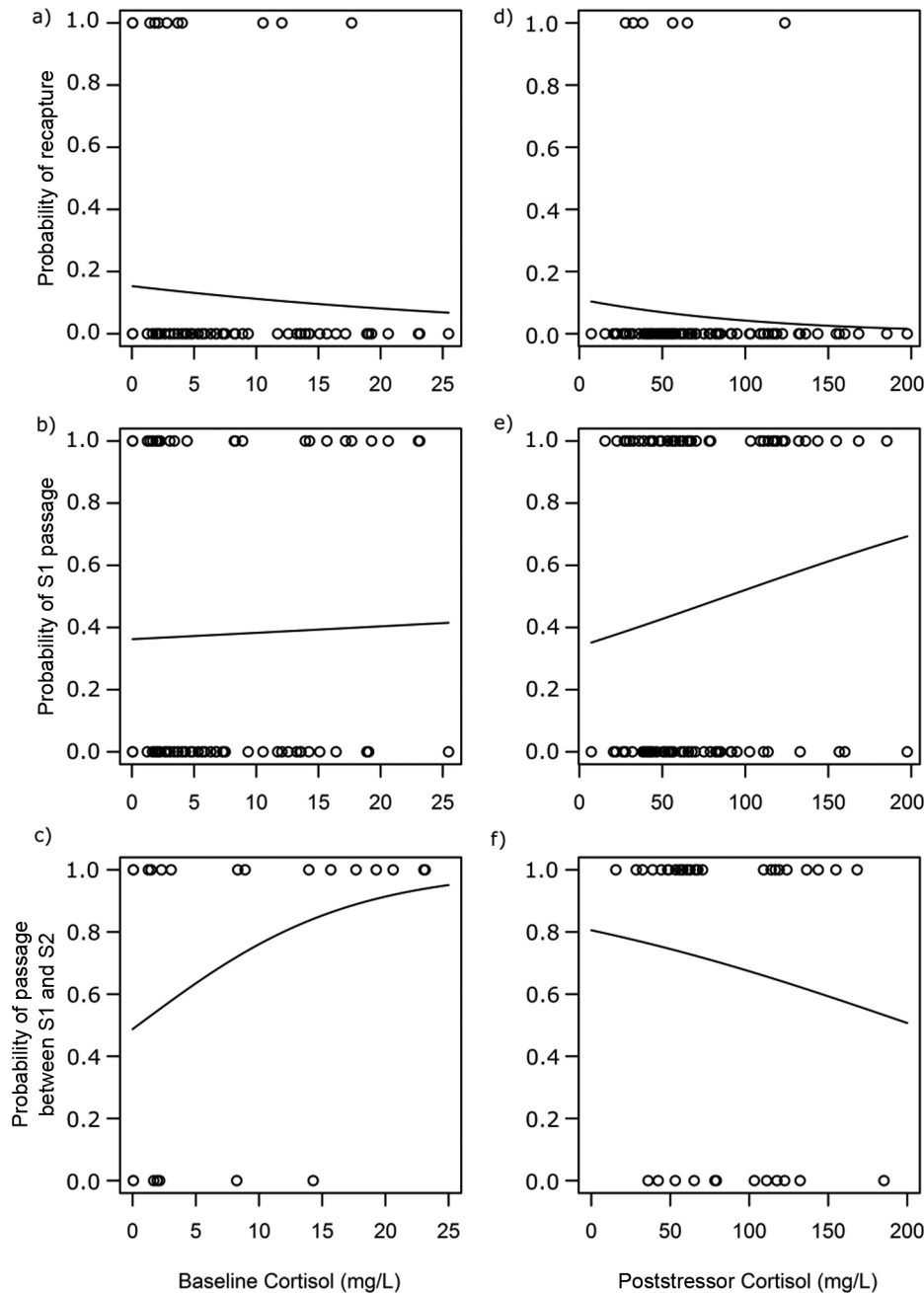
efficiency of 100% at S1. Mean (±SD) baseline cortisol was 5.6 ± 6.7 ng/mL and poststressor cortisol was 69.2 ± 40.1 ng/mL (Table 1). Poststressor (multiple logistic regression: $Z_{[2,96]} = 1.44$, $p = 0.15$) and baseline (multiple logistic regression: $Z_{[2,96]} = 0.15$, $p = 0.89$) plasma cortisol concentrations did not have a significant effect on the probability of successful passage at S1 when controlling for K, mass, or length ($p > 0.1$; Figs. 2*b*, 2*e*). For fish that passed S1, the probability of successful passage to S2 increased with increasing individual baseline cortisol when controlling for mass (multiple

logistic regression: $Z_{[2,27]} = 1.96$, $p = 0.05$) and length (multiple logistic regression: $Z_{[2,27]} = 2.01$, $p = 0.045$), but not for K ($p > 0.05$). For fish that passed S1, the probability of successful passage to S2 showed no relationship with poststressor cortisol (all: $p > 0.1$).

Mean (±SD) migration time from blood sampling to S1 passage was 33.4 ± 19.1 days and mean (±SD) time from S1 to S2 was 3.2 ± 7.6 days. Multiple regression showed no significant relationship between migration duration or date of passage and poststressor or baseline cortisol when controlling for mass, length, or K (all:

$p > 0.1$). Migration time decreased with increasing fish length (linear regression: $F_{[1,79]} = 6.82$, $p = 0.01$, $R^2 = 0.8$) and fish mass (linear regression: $F_{[1,79]} = 4.4$, $p = 0.04$, $R^2 = 0.05$), but no relationship was found with K (linear regression: $F_{[1,79]} = 3.14$, $p = 0.08$, $R^2 = 0.04$).

Multiple logistic regression revealed no effect of poststressor and baseline cortisol on the probability of recapture in resident streams when controlling for K, length, or mass (all: $p > 0.1$; Figs. 2a, 2d). Length, mass, and K also were found to have no effect on the probability of recapture in resident streams (all — logistic regression: $p > 0.1$). No relationship was found between K, mass, or length and baseline or poststressor cortisol (all — linear regression: $p > 0.1$). The probability of S1 passage and the probability of passage between S1 and S2 had no relationship with K, fish length, and fish mass (all: $p > 0.08$; Figs. 2c, 2f).

Discussion

As previous studies have found cortisol to be elevated during smoltification (Barton et al. 1985), we expected individual brown trout with higher baseline and poststressor cortisol to have a higher probability of migrating downstream to S1 and S2, coupled with a lower probability of recapture as resident. However, no such relationships were found.

We found no evidence suggesting that migration is correlated with endocrine regulation in juvenile brown trout, despite several studies having documented that cortisol levels rise during smoltification in andromous fish (Barton et al. 1985; Redding et al. 1991; Björnsson et al. 2011), and also that GC regulation has the potential to play a role in determining alternative coping strategies (Zera and Harshman 2001; Landys et al. 2006; Williams 2008). Mass, length, and body condition were also not found to have a relationship with plasma cortisol (baseline or poststressor). Fish of greater mass and length (but not condition) were found to have shorter migration times similar to previous findings (Bohlin et al. 1996). Body condition, length, and mass were not found to affect migration propensity to S1. The lack of a correlation between our condition metrics and migration propensity is counter to previous findings of reduced condition leading to increased migration propensity (Peiman et al. 2017); however, it is possible that the comparatively limited recapture rate in the present study ($N = 19$) prevented the detection of a size-based effect.

Baseline, but not poststressor, cortisol concentration was found to be positively associated with passage through the millpond (i.e., from S1 to S2). Previous studies have found brown trout baseline cortisol without chronic stressors to be 0–5 ng/mL, whereas those exposed to chronic stressors such as confinement or crowding have shown baseline cortisol elevated to 10 ng/mL (Pickering and Pottinger 1989). The mean baseline cortisol found in individuals recaptured in resident streams, individuals that passed S1, and individuals that passed S2 was 5.6, 5.8, and 8.4 ng/mL, respectively (Table 2). Thus, individuals that passed through the millpond had baseline cortisol levels of individuals approaching chronically stressed levels, on average, whereas other fish had cortisol levels closer to what would be expected for fish not showing chronic stress.

The distance between S1 and S2 is only 150 m, thus it is unlikely that S1 passage versus S2 passage would be indicative of migration strategy. The millpond may therefore be an area of increased mortality, suggesting S1 passage is more indicative of migration strategy (resident and potamodromous versus anadromous), whereas passage between S1 and S2 is more indicative of migration success of migrant individuals. Forty-five percent of all brown trout that passed S1 were not detected passing S2, which is only 150 m downstream, and those that did migrate through the millpond took much longer than when migrating through the stream, taking, on average, 3.2 days to move 150 m. Similar patterns are found in other studies of migrating fish at Gudso (Midwood et al.

2014, 2015). This indicates the millpond was challenging for migrating brown trout. We suggest that many of these individuals likely suffered mortality, as it is unlikely for such a large proportion of migrants to take up residency in such a small area. Furthermore, there is anecdotal evidence of high concentration of foraging Grey Herons (*Ardea cinerea* Linnaeus, 1758) and other birds at the outflow of millpond. Previous studies on salmonid smolts have documented large losses resulting from predation in lakes (Jepsen et al. 1998; Koed et al. 2006) and at weirs and related millponds (Aarestrup and Koed 2003). For example, Jepsen et al. (1998) found 90% of smolts died while passing through Lake Tange, Denmark, with 56% of the mortality cause by northern pike (*Esox lucius* Linnaeus, 1758) and 31% by birds. Another possibility for the reduced passage and long migration time through the millpond is that there is only one small exit and brown trout may have had a hard time getting out. Although it is possible that overall lower passage at S2 is driven by reduced detection efficiency at this station, these missed detections would affect all brown trout equally and thus would not affect the relationship found between baseline cortisol and passage between S1 and S2 other than by reducing statistical power. Our results, therefore, do not support the link between GC levels and migration strategy in brown trout, but they do suggest that baseline GC (and not poststressor GC) is positively associated with migration success.

Generally, it is hypothesized that increased baseline GC are associated with decreased survivorship because increased baseline GC are associated with increased chronic stressors (Cort-Fitness hypothesis: Bonier et al. 2009). Our findings appear to support the opposite trend because migratory fish with lower baseline cortisol appear to have lower successful passage through the millpond (Figs. 2a–2f). Several other studies have also found higher baseline cortisol to be correlated with increased survivorship: Cabezas et al. (2007) found moderately elevated corticosterone was associated with decreased body condition but increased probability of survival in European wild rabbits (*Oryctolagus cuniculus* (Linnaeus, 1758)); Comendant et al. (2003) found higher corticosterone in female Side-blotched Lizards (*Uta stansburiana* Baird and Girard, 1852) to be associated with increased survival to second ovulation; and Cote et al. (2006) found increased corticosterone to modify behaviour (locomotor and social activity), increasing survival in male adult Viviparous Lizards (*Lacerta vivipara* Jacquin, 1787).

Another possible explanation for why our results are not consistent with the Cort-Fitness hypothesis is that it is difficult to discern whether higher baseline cortisol indicates exposure of the individual to greater chronic stress (which is assumed to be the case by the Cort-Fitness hypothesis; Bonier et al. 2009), or indicates a more competent ability to cope with chronic stressors. The first would likely lead to decreased survivorship with increasing baseline GC level, whereas the later would likely result in the opposite trend. In our study, all individuals may be subjected to similar chronic stressors because they were all reared in the same stream reach. Thus, baseline stress may be a better indicator of better ability to cope with chronic stressors than exposure to greater environmental stressors.

Poststressor cortisol, a proxy for stress responsiveness, was not found to be a significant predictor of migration timing, survival, or success. Potentially, the effect of stress responsiveness was masked, because we were not able to control for individual variability in baseline since fish were too small to obtain both a baseline and a poststressor cortisol sample. However, poststressor cortisol was more variable (SD = 40.7 ng/mL) than baseline cortisol (SD = 7.7 ng/mL). Cockrem (2013) reviewed studies on baseline and stress-induced GCs and determined that there tended to be more variation in baseline GCs among individuals than in stress-induced levels. Although our findings are not consistent with that generalization, Cockrem (2013) did note that it was not ubiquitous with a number of exceptions. It is unclear why that pattern was

observed here, but reasons, among others, could include inter-individual differences in how the stressor was perceived or different stress histories. Despite the widely accepted belief that acute stress responses are adaptive, similar to our study, several other studies have failed to find a relationship between stress responsiveness and performance (Romero and Wikelski 2001; Blas et al. 2007), or may even reduce performance. These results may be an indication that different reactive scope profiles may allow individuals to adequately cope with stressors. Additionally, the benefits of stress responsiveness are increasingly viewed as context dependent, because traits induced by a stress response can have variable consequences on the performance of organisms depending on the nature of the stressor (Breuner et al. 2008).

Similar to our findings in brown trout, the only other study that we are aware of which examines individual variation in endocrine regulation in relation to migration in fish (anadromous semelparous sockeye salmon) found no correlation between GC levels and migration timing or rate. They also found individuals with higher stress responsiveness to have greater migration success, but that baseline cortisol was not a significant predictor of migration success (Cook et al. 2014). Differences in the relationship between GC secretion and migration success found by our study may be attributed to differences in the stressors experienced. For example, salmon may have more chronic stressors such that their baseline levels are at the turning point of the baseline cortisol survivorship curve hypothesized by Cabezas et al. (2007), where differences in baseline levels have negligible effects on survivorship. The inconsistency between findings may also be reflective of differences in physiology between species.

Conclusions

In summary, we found no evidence suggesting that cortisol regulates the migration life-history trade-off in juvenile brown trout. But, slightly higher levels of baseline GC (and not post-stressor GC) may favor migration performance. Further study is warranted to help determine the relationship between migration success and GC, with special focus on stress responsiveness within an individual.

Acknowledgements

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