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ORIGINAL ARTICLE

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Physiological consequences of an altered flow regime on Alabama bass (*Micropterus henshalli*)

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Abstract

There are numerous studies on the effects of dams on aquatic biota, yet relatively little is known about whether hydropeaking activities cause physiological change in fish. Using Alabama bass (*Micropterus henshalli*) as a model, we evaluated whether hydropeaking in a regulated river altered glucocorticoid stress responsiveness relative to fish from an unregulated tributary. Blood samples were collected at the time of capture (baseline) and then collected again after a 1-hr period of confinement (response). Leukocyte profiles (blood smears) were created and plasma was extracted to assess plasma cortisol levels and neutrophils and lymphocyte (N:L) ratios, between sites and times to evaluate differences between sites and the two sampling periods. Baseline cortisol levels were higher in fish collected from the regulated river compared to those from unregulated site, but response levels of cortisol were similar between sites. Baseline and response level N:L ratios did not differ between sites. High baseline levels of cortisol suggested that fish exposed to regulated flows expressed an altered stress response and were likely in an allostatic state, i.e., attempting to acclimate. Further research is needed to understand how altered stress responses due to hydropeaking flows may be affecting fish.

KEYWORDS

centrarchids, cortisol, hydropeaking, Leukocyte profiles, stress response

1 | INTRODUCTION

The field of physiological ecology has expanded over the last several decades to incorporate concerns regarding the effects of anthropogenic disturbances on animals, including the endocrine response (Romero, 2004). When animals become stressed, their physiology and behaviour are often altered. Typically, this response is adaptive, but with more intense or prolonged stressors, the response can become maladaptive and possibly even physiologically dysfunctional (Barton, 2002; Wendelaar Bonga, 1997). The acute type of stress is experienced for brief periods, causing a temporary disturbance in homeostasis (Van Weerd & Komen, 1998). Chronic stress is associated with prolonged challenges where there is a continued loss of homeostasis and adaptation is either not possible or is only achieved after a long time (Schreck, 1981, cited in Van Weerd & Komen, 1998). Chronic stress has been observed to affect growth, physiological condition, immune function, feeding behavior, competitive ability, and swimming performance of fishes (Barton, Schreck, & Barton, 1987; Gregory & Wood, 1999; Van Weerd & Komen, 1998). The stress response in teleosts is similar to other vertebrates that are exposed to environmental challenges (Baker, Gobush, & Vynne, 2013) with glucocorticoids often used as indicators of stress (Dantzer, Fletcher, Boonstra, & Sheriff, 2014).

Altered flows resulting from hydropeaking operation from power-generating dams have been found to have profound effects on aquatic ecosystems (Ligon, Dietrich, & Trush, 1995). Peaking operation usually results in rapid changes in the quantity, quality, and location of different habitats (Garcia, Jorde, Habit, Caamano, & Parra, 2011). Bain, Finn, and Booke (1988) documented that highly variable and unpredictable flow modifications can cause a disturbance to fish due to the inaccessibility of certain habitats. This rapid change in habitat quality and quantity creates an unstable environment (Pert & Erman, 1994). Although some habitats become available because of higher flows, the rapidly falling water levels characterized by ending peaking operations disconnects these same habitats from the main channel, leading to fish stranding (Bradford, 1997). Aarts, Brink, and Niemhuis (2004) found that there was a decrease in fish species richness and diversity with decreasing hydrological connectivity between river and floodplain. Thus, alteration of habitats in these riverine ecosystems resulting from hydropeaking operations may have major impact on aquatic organisms, especially fishes.

Numerous studies have focused on how altered flow regimes from dams may disrupt biological and ecological processes in fish populations and individuals that inhabit these aquatic systems (Poff & Zimmerman, 2010). Dam operations influence survival of fish larvae, reduce biomass of prey, and alter feeding behaviors (Humphries & Lake, 2000; Lagarrigue et al., 2002; Moog, 1993). Additionally, energetic costs occur for fishes found in stream reaches exposed to altered flow regimes (Puffer et al., 2014; Scruton et al., 2008). However, very few studies have focused on the individual and sub-organismal responses to hydropower peaking operations, including energetic and endocrine responses (Flodmark et al., 2009; Hasler et al., 2009; Taylor, Cook, Hasler, Schmidt, & Cooke, 2012).

In an attempt to explore the physiological consequences of an altered flow regime on fish in the Tallapoosa River, Alabama, USA, we evaluated the acute stress response of a native black bass species (*Micropterus* spp.). If these fish were chronically stressed, we expected to observe little to no response in the cortisol levels for fish exposed to a stressor, which for this study was confinement (Hontela, Rassmussen, Audet, & Chevalier, 1992; Norris et al., 1999). We also anticipated higher baseline levels of stress biomarkers in fish that were constantly exposed to altered flows (Bonier, Martin, Moore, & Wingfield, 2009). Using two bio-markers, we evaluated the baseline levels, the stress response (response) and the efficiency of these two biomarkers and allowed for the evaluation of the stress response of Alabama bass (*Micropterus henshalli*) to hydropeaking flows in a river. Alabama bass are a generalist species endemic to the Mobile River Basin in Alabama, Georgia, and Tennessee, where they inhabit a variety of habitats (Baker, Johnston, & Folkerts, 2008). Alabama bass adult sizes range from 300 to 600 mm, which is typical for black bass species, and is an economically important sport fish in Alabama (Rider & Maceina, 2015).

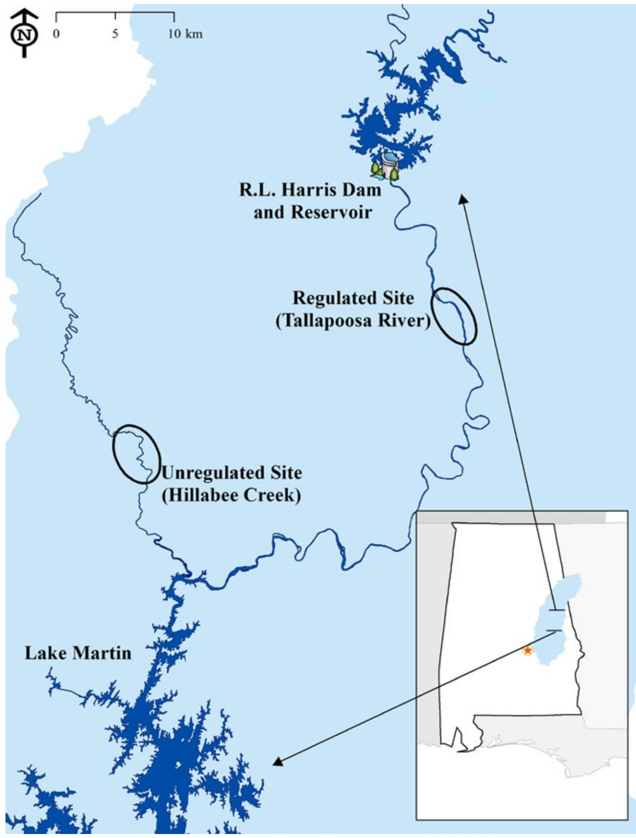

FIGURE 1 An overview map of the Tallapoosa watershed, the sampling locations on the Tallapoosa River and Hillabee Creek circled

2 | MATERIALS AND METHODS

2.1 | Study site

Originating in northwestern Georgia, the Tallapoosa River flows 421 km southwesterly across east-central Alabama to its confluence with the Coosa River, forming the Alabama River (Figure 1). This study was conducted on the section of river 21 km downstream of R.L. Harris Dam. This portion of the river is located in the Piedmont Upland physiographic region and is characterized by a physically stable channel, with low-gradient habitats with silt substrate as well as high-gradient shoal habitats dominated by bedrock and boulders. Discharge is highly regulated by Harris Dam, which normally is operated in hydropeaking mode, where water is released in pulses for 4–6 hr through one or two turbines (capacity of 226 m^3/s) and power generation can occur once or twice a day from Monday thru Friday (Irwin & Freeman, 2002). The mean annual discharge in the river reach below R.L. Harris Dam is 68.36 m^3/s, but dam operation results in extreme fluctuation in discharge and stage, especially in the first 20 km downstream of the dam, creating highly variable habitats (Figure 2). Although continued adaptive management procedures are currently underway, at the time of our study there were minimal regulations on the magnitude or the duration of water releases.

Although the Tallapoosa River above Harris Dam is unregulated, we did not elect to use it as a reference site due to much lower fish abundances, different geomorphology, and land-use impacts. In order to stay within the lower Tallapoosa watershed, we selected Hillabee Creek (mean annual discharge = 8.29 m^3/s) as the reference site, which is the largest unregulated tributary stream entering the Tallapoosa River in the regulated stretch downstream of Harris Dam (Figure 1). Similar to the impacted site, Hillabee Creek is located in the Piedmont Upland physiographic region and shares similar geomorphology of the impacted site.

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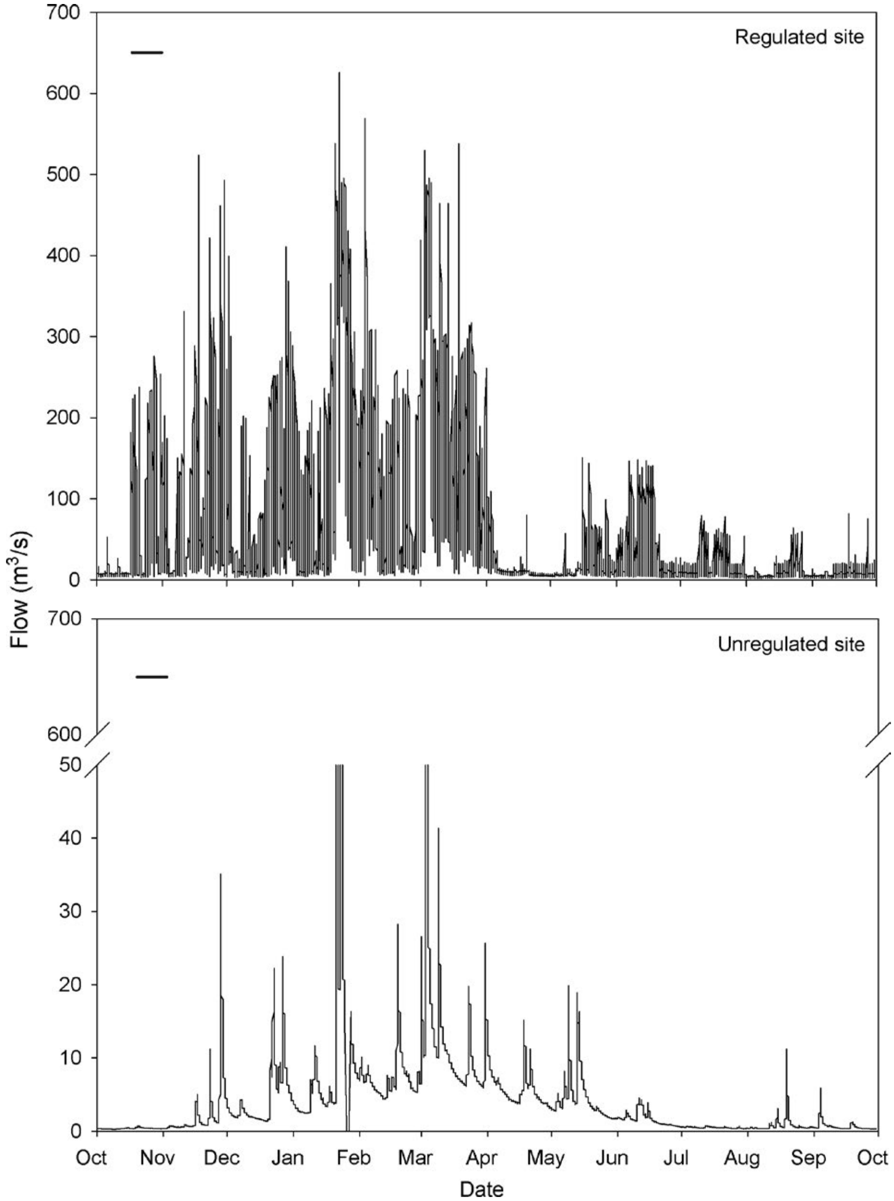

FIGURE 2 Hydrographs of the Tallapoosa River and Hillabee Creek for Water Year (WY) 2012. The line indicates the time period that sampling was completed

2.2 | Collection and sampling

Following Martínez-Porchas, Martínez-Córdova, and Ramos-Enriquez (2009), we examined the stress responses by measuring plasma cortisol, along with leukocyte profiles (Davis, Maney, & Maerz, 2008; Dhabhar, Miller, McEwen, & Spencer, 1996; Müller, Jenni-Eiermann, & Jenni, 2011) because of the variability in plasma cortisol. Changes in leukocyte distribution (increasing neutrophils and decreasing lymphocytes, herein referred to as N:L ratios) are considered to be induced by the release of glucocorticoids into the bloodstream (Dhabhar et al., 1996). We sampled fish by angling in the fall 2011 to reduce any confound effects associated with sampling fish close to spawning (Faught & Vijayan, 2018). We also sampled at a time where temperatures were similar amongst the two sites and was not considered as a covariate (Suski, Killen, Kieffer, & Tufts, 2006). Fish were collected from the Tallapoosa River (regulated site) on October 24, 25, and 29, 2011 and mean discharge on these days ranged from 5.72 to 30.24 m^3/s during the sampling periods. Based on daily dam operations, fish were exposed to higher discharge (>113 m^3/s) anywhere from 7 to 60 hr prior to capture, which represented typical hydropeaking operations. We sampled fish from Hillabee Creek (unregulated site) on November 7, 2011 when the mean discharge was 0.56 m^3/s. Rainfall 7 days prior to sampling at all sites was <1.0 cm (NCDC NOAA, www.ncdc.noaa.gov/cdo-web, Alexander City, AL, US; 000010160) and streamflow ranged from 0.59 to 0.70 m^3/s within 7–60 hr prior to capture. We collected 12 Alabama bass from the regulated site ($\bar{x}$ = 318 mm; range: 252–424 mm; TL) and 11 fish from the unregulated site ($\bar{x}$ = 357 mm; range: 307–424 mm; TL).

On each sample date, fish were collected over a 6.5-hr sampling period in the middle of the day, to avoid any confounding effects due to diel differences in baseline blood parameters (Biron & Benfey, 1994). Once a fish was caught, we collected blood samples within 180 s (Clements, Schreck, Larson, & Dickhoff, 2002; Romero & Reed, 2005; Sumpter, Dye, & Benfey, 1986), and each fish was sampled at two different time intervals (baseline and response). Immediately after capture, about 1.00 ml of blood was extracted (baseline sample) from the caudal vein of the fish using a 26-gauge needle. Samples were placed on ice until these were centrifuged. Fish were floy-tagged for identification purposes and placed in a 114-L cooler outfitted with an aerator; no more than 4 fish were held in a cooler at one time (target biomass density ~21g/L) and water exchanges did not occur. Fish were resampled 1 hr after confinement (response sample) and were then sacrificed. The response sample in our study was based upon a 1-hr confinement period, following Norris et al. (1999). Suski et al. (2004) and Suski et al. (2006) used confinement in black boxes for >24 hr to generate baseline values in black bass, therefore response we observed may have been from the capture and sampling rather than from confinement. Regardless, the purpose of the 1-hr response was to expose these fish to an acute stressor and the source of the stressor was is irrelevant to our findings. After collecting the second sample, the fish were sacrificed using 300 mg/L solution of Tricaine Methanesulfonate (MS-222) until expired and then placed on ice. Fish were measured (total length, mm), weighed (g), and sexed.

Blood samples were centrifuged at 6,000 rfc for 7 min.; plasma was extracted and placed on ice until it was returned to the lab, where samples were frozen until they were assayed. Levels of cortisol were measured after returning to the lab using ELISA kits (Cayman Chemical, Ann Arbor, MI). The samples were assayed in duplicate using the appropriate dilution based on the sample period (baseline samples = 1:10; response samples = 1:150) and the collected blood samples variability between inter-assay and intra-assay was <10%.

About 0.50 ml of blood was used to create a blood smear. Blood smears were fixed with methanol and were stained with a Hema-3 kit (Wright-Giemsa staining method; Fisher Scientific Company L.L.C., Middletown, VA). Slides were then dried, cover-slipped, and stored until analysis. Each slide was examined using a compound microscope under transmitted light (1,000× magnification), and relative counts of the blood cells were conducted. Each type of white blood cell was tallied until 100 different leukocytes were identified following similar methods of Müller et al. (2011). The proportion of neutrophils to lymphocytes was calculated by dividing the number of neutrophils by the number of lymphocytes (N:L ratios).

2.3 | Statistical analysis

Differences in cortisol concentrations and N:L ratios were assessed between regulated and unregulated sites for both the baseline and response sample periods. We used a linear mixed-effects model to test biomarker differences with each individual fish set as the random variable to account for repeated sampling. Collection time, sample period, sex, and site were included in the model as covariates. Post-hoc analysis was completed using an unbalanced two-way analysis of variance (ANOVA) for each sample time to determine if there was a difference between site. All data analysis was completed using R with the CAR and NLME packages (version 3.11.1; www.r-project.org).

3 | RESULTS

The initial analysis found that cortisol was higher for the response sample period than the baseline period ($t = 6.67$; $df = 35$; $p = 0.000$; Table 1), otherwise collection time ($t = 1.65$; $df = 35$; $p = 0.108$), sex ($t = -0.248$; $df = 46$; $p = 0.805$), and site ($t = 0.91$; $df = 46$; $p = 0.364$) did not have an effect. However, the post-hoc analysis found that baseline cortisol was higher in fish collected from the regulated site compared to those from the unregulated site ($F = 7.71$; $df = 1,15$; $p = 0.014$). Response cortisol levels were similar between sites ($F = 0.00$; $df = 1,19$; $p = 0.976$), suggesting no difference between the regulated and unregulated sites.

The initial analysis found that collection time ($t = 0.81$; $df = 8$; $p = 0.439$), sample period ($t = 0.89$; $df = 8$; $p = 0.401$), sex ($t = 0.70$; $df = 25$; $p = 0.491$), or site ($t = 0.18$; $df = 25$; $p = 0.860$) did not have an effect on the N:L ratios (Table 1). *Post-hoc* analysis found that the N:L ratios were similar between sites for baseline ($F = 0.27$; $df = 1,11$; $p = 0.611$), and response ($F = 2.42$; $df = 1,15$; $p = 0.140$).

4 | DISCUSSION

Baseline cortisol levels were higher in fish collected from the regulated site than those collected from the unregulated site, indicating that Alabama bass experienced higher stress levels in the regulated site than in the unregulated site. The significance of higher baseline levels to the overall health of organisms has been debated among scientists for years. Although studies have shown that fish exposed to stressors show a decrease in growth (O'Connor et al., 2011) there was no evidence that growth of Alabama bass was impacted by hydropeaking operations in the Tallapoosa River (Earley & Sammons, 2018). Response levels were high and typical of fish exposed to a stressor, and these response levels were similar among sites. Fish N:L ratios were similar between the regulated and unregulated site, possibly indicating that fish acclimated to the stressor, or those in

TABLE 1 Mean ± SE CORT levels and N:L ratios for Alabama bass collected from the Tallapoosa River and Hillabee Creek. The sample sizes are presented in parenthesis

	CORT		N:L Ratios	
Sample	Tallapoosa	Hillabee	Tallapoosa	Hillabee
Baseline	27.99 ± 21.60 (8)	1.87 ± 0.96 (8)	0.06 ± 0.02 (6)	0.05 ± 0.01 (5)
Response	205.44 ± 69.69 (10)	215.87 ± 95.85 (9)	0.24 ± 0.08 (7)	0.11 ± 0.03 (9)

the impacted site were trying to re-establish homeostasis (McEwen & Wingfield, 2003; Romero, Dickens, & Cyr, 2009).

Alternatively, Alabama bass in the regulated portion of the Tallapoosa River may be in a state of allostasis. Animals in an allostatic state for a long period of time, can suffer from allostatic overload, which can lead to an allostatic state independent of the environment and have major impacts on life history stages, such as sexual maturity and seasonal migrations (McEwen & Wingfield, 2003). Wingfield and Kitaysky (2002) stated that higher baseline levels of cortisol, as observed in the fish from the Tallapoosa River in our study, could represent a form of an altered life-history strategy. Thus, this species may be experiencing allostatic overload in the Tallapoosa River, or are functioning under an emergency life history strategy. Based on the evidence from our study, the results would suggest these fish are likely functioning in an allostatic state but additional research should be conducted.

Flodmark et al. (2009) concluded that brown trout (*Salmo trutta*) in an artificial channel showed rapid habituation (within 4 days) to daily fluctuations to discharge because cortisol responses were no longer observed. However, laboratory studies may not adequately explain what is actually happening to fish in their aquatic habitats (Norris, 2000). Taylor et al. (2012) found that changes in discharge did not affect the physiological response of mountain whitefish (*Prosopium williamsoni)* in a regulated river. Other researchers predicted fish found in cold water, such as mountain whitefish and brown trout, would have lower immune responses than fish found in warm water, such as Alabama bass (Avtalion & Clem, 1981; Bly & Clem, 1992; Rijkers, Teunissen, Oosterom, & Muiswinkel, 1980), which may also be true for the physiological response and may explain the difference in our results compared to Flodmark et al. (2009) and Taylor et al. (2012).

The leukocyte profiles were similar between the sites for both sample times. We expected to see higher baseline N:L ratios from fish collected in the Tallapoosa River, but our sample size may have been too small to detect a difference. Futhermore, the 1-hr sample may have been too short of a duration to observe any effects on the N:L ratios. Changes in the leukocyte profile may not respond as quickly as other secondary stress responses, and although there was a minor increase though not significant, between the baseline and response samples, we would suggest to increase the duration of time in between sampling. Davis (2005) reviewed several studies that examined the variation in temporal sampling and concluded that it may take up to 4 hr after exposure to a stressor for an increase in N:L (or H:L) ratios to be observed. However, results from this study generally agreed with the recommendations of Müller et al. (2011) that N:L ratio and plasma cortisol concentrations should be done concurrently to fully assess the stress response of fishes and do not duplicate each other as a biomarker.

5 | CONCLUSION

Despite the limitations, this study demonstrated higher baseline cortisol for fish living under hydropeaking conditions compared to those living in a natural flow regime. While this study is only correlative and does not show causation that an altered flow regime is the reason for the altered stress response, we feel that this study provides background information for further research to be conducted on the stress response of fish in hydrologically altered environments. Further field investigations may help to determine if these fish are in an altered state, i.e. allostasis, are chronically stressed, or if there is a downregulation in the hypothalamic-pituitary-interrenal axis. Additionally, studies such as a 24-hr stress test, an adrenocorticotropic hormone challenge (Norris, 2000), or simply completing more field studies with a larger sample size and more sites, will likely increase understanding of the stress response of this species and the response to an altered flow regime.

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