

Stress Responses in Teleosts

Physiological Stress Responses in Teleost: Cortisol, Catch and Release Fishing, and Fish Fitness

Alexis Anderson

Honors Senior Capstone

Bergman

April 2016

I. Introduction

Stress responses in vertebrates are chemical messaging systems associated with potentially negative physiological consequences. The particular glucocorticoid, cortisol, is a predominant hormone released in response to stressful stimuli in animal species. Ray-finned fishes (teleosts) demonstrate cortisol-driven stress responses when exposed to certain stimuli. But, analysis of recovery after stressful stimuli is difficult to quantify and, therefore, not well understood. With recreational catch and release fishing increasing globally, scientists and anglers are beginning to question whether the stress associated with catch and release fishing is negatively affecting teleost populations. Understanding the mechanisms and repercussions of stressful stimuli in these species is integral to understanding if catch and release fishing is leading to adverse consequences for highly used fish populations.

The infraclass teleostei includes the ray-finned fishes, which are characterized by their tail-fin symmetry and jaw mobility. This infraclass includes a wide variety of fish including eels, salmon, trout, pike, herring, anchovies, and many more (Klappenbach 2015). Salmon and trout are target fish for many recreational fly-fishing enthusiasts worldwide so the following deductions will focus on these species. As one of the most recreationally fished classes, teleosts generally encounter repetitive human induced stressors, but the negative effects of catch and release fishing practices on fish have only recently been considered and studied.

Fish, like most other animals, use stress response systems when confronted with negative stimuli. Stress responses are important in the case of natural negative stimuli as they enhance a fish's ability to escape by initiating a fight or flight response. Catch and

release fishing heightens physiological stress responses as it prolongs stimulation and steroid secretion. Similar to mammals, exposure to large and sustained amounts of stress—and therefore cortisol release—elicits many negative physiological effects on fish. The process of catching, removing from, and returning fish to their aqueous environment by anglers presents teleosts with an unnatural, negative stimulus. The scientific community has focused on distinguishing the difference between stress responses in teleosts, determining if the stress of recreational fishing is significantly increasing cortisol production, and examining whether such stressors affect the fitness of fish populations. By reviewing literary sources from previous research on teleost stress responses, this paper examines the mechanistic response to cortisol and other stress hormones in fish. The paper also compares corticosteroid messaging mechanisms between mammals and fish with the intent of comparing physiological effects of prolonged cortisol release. Concurrently, the paper examines the effect of high levels of cortisol on reproduction and fitness of fish. Overall, we will analyze the physiological effects of elevated cortisol due to recreational fishing along with a summary of potential stress alleviation techniques for highly stressed fish populations.

II. Hormone Action in Mammals and Fish

Corticosteroids are important in organisms due to their role in ion and water regulation and movement (ion and osmoregulation) as well as their regulation of metabolism and growth. In mammals, two distinctive hormone groups mediate these functions: mineralocorticoids and glucocorticoids. The most important mineralocorticoid in mammals is aldosterone and the most important glucocorticoid is cortisol. These

hormones work in the body through specific receptors. The ability of an organism to produce a hormone is important, but the existence of receptors for the hormone is possibly even more important. An analogy for how these systems work could be that of a lock and a key. Each synthesized hormone acts as a key, but the key is useless unless it has a lock to open. And in the same way that locks will only accept certain keys, receptors will only accept certain ligands. The most important aspect of these messaging systems, in terms of gene expression, is the activity of steroid receptors and ability of cells to receive certain messages. Three characteristics of hormone receptors are specificity, affinity, and signaling. Each receptor is specific for a hormone and a cell type, each will have affinities for specific hormones and bind selectively because of it; they will then elicit a biological response, called a signal, once bound. Fish may secrete mineralocorticoid, however, their cells may not have the correct receptors to bind such a steroid. If this class of hormone were working in fish cells, the signals they create may look very different than in mammals. Overall, aldosterone receptors in mammals elicit specific responses for osmoregulation while different cortisol receptors regulate metabolic and growth changes. In fish, however, metabolism, growth, ion balances, and water balances are all regulated by different families of receptors that respond to glucocorticoids. Let's examine a brief chart detailing the differences between stress hormone actions in mammals and freshwater fish:

Overview of Cortisol Secretion and Effects in Mammals and Teleosts

	Mammals	Teleosts
Adrenal Hormones Released	Aldosterone and Cortisol	Only Cortisol
Cortisol Release Pathway	Hypothalamic-Pituitary-Adrenal Axis Corticotropin Releasing Hormone	Hypothalamic-Adenohypophysis-Interrenal Axis CRH→ACTH→Cortisol

	(CRH)→adrenocorticotrophic hormone (ACTH)→Cortisol	
Ion and Water Balance	Regulated by aldosterone Increased and decreased through ingestion and kidneys.	Regulated by Na/K ATPase in gills and ions/water taken directly from external freshwater environment.
Effects of Cortisol	Increased gluconeogenesis (increased ATP) for more energy Activation of anti-inflammatory pathways	Increased gluconeogenesis and more (to be discussed in this paper)

As seen in the chart above, corticotropin releasing hormone (CRH) and adrenocorticotrophic hormone (ACTH) act as signaling molecules in fish and mammals, however they intersect at different tissues. From a physiological standpoint, the mechanisms by which mammals and fish gain or lose electrolytes and water are immensely different. Mammals rely on ingestion for their water and ions and that could explain why a different class of hormone messaging is necessary. Mammals eat food and drink water, then various parts of the digestive tract and hormone systems work to retain these ingested materials. The kidney, specifically, is the target of the mineralocorticoid aldosterone. Here, aldosterone works to promote retention of sodium and water follows through osmosis. Mammalian osmoregulation is, overall, much different from that of fish because, unlike fish, mammals lack constant exposure to water and ions. Mammalian systems have evolved to draw in water/ions once they have been internalized, whereas fish can draw ions and water in from their environment. This substantially differentiates the physiological hormone action mechanisms of fish and mammals.

Hormones are difficult to study because they generally circulate in very low concentrations. To determine the presence of a secreted hormone, biological products are generally measured as opposed to specific hormone levels. An example is ion and water

concentration regulation via mineralocorticoids, which connects aldosterone secretion to sodium-potassium pump (Na^+/K^+ ATPase) activity in mammals. When blood volume or sodium concentrations in interstitial fluids are low, aldosterone is secreted. Subsequently, the activity of Na^+/K^+ ATPase in the nephrons of the kidneys increases. As sodium and water are closely linked in mammalian tissues, Na^+/K^+ ATPase firing moves three molecules of sodium into the interstitial fluid causing water to follow. This system allows for osmoregulation and, therefore, increased reception of mineralocorticoids will up-regulate Na^+/K^+ ATPase activity. Based on this knowledge, the firing of this pump can be monitored after introduction of a hormone to determine if receptor binding and activation is happening. If the activity increases, scientists may deduce that receptors for the given hormone are present. This method is a common way to study the presence of hormone receptors in organisms.

Although osmoregulation is much different in fish, bi-products are still analyzed as a means of determining the presence of specific receptors. As previously stated, mammals do not draw from aqueous environments as do fish, so the water and ions that we introduce into our body have to come from what we ingest and then our kidneys filter what is retained from what is excreted. Freshwater fish also excrete some extra substances through dilute urine, but more importantly, they move ions into and out of their bodies through their gills. In freshwater fish, water passively enters the body while ions diffuse out. To combat this, they produce a dilute urine and actively pump ions into their bodies through their gills. For saltwater fish, this process works in reverse; the fish drink saltwater, retain the water and excrete excess ions through concentrated urine while pumping ions out of their bodies, back into the water, through their gills. Both of these

processes utilize the Na^+/K^+ ATPase in the gill, so to determine if a hormone is able to effect osmoregulation, the activity of these pumps and body or surrounding water osmolarity can be measured to see if ligand binding is occurring. This knowledge is important for understanding what is happening at a mechanistic level in response to stress.

A study conducted in 2008 by Stephen McCormick et al., tested the presence of mineralocorticoid receptors (MRs) in freshwater fish by monitoring their Na^+/K^+ ATPase activity to see if aldosterone would affect osmoregulation. McCormick examined whether Atlantic salmon—a type of teleost—responded to artificial aldosterone to determine if teleosts have MRs. Theoretically, if MRs were present in tissues, hormone binding would up-regulate ATPase activity in the gills. To test this, scientists injected fish with varying levels of cortisol or deoxycorticosterone, DOC, (a mineralocorticoid similar to aldosterone found in fish). The results demonstrated a lack of receptors for mineralocorticoids in salmon (McCormick 2008;Figure 1).

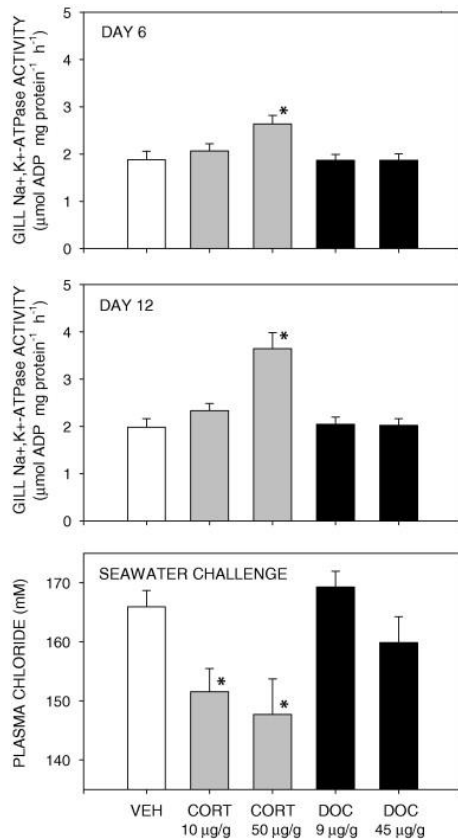


Figure 1:
Gill Na⁺/K⁺ ATPase activity over six and 12 days in juvenile Atlantic salmon treated with various amounts of cortisol or deoxycorticosterone, DOC. The white boxes indicate a control group and the final graph indicates a different, seawater group. The graphs illustrate the lack of MRs and presence of glucocorticoid receptors (GRs) in teleosts. (McCormick 2008)

As shown, in a 12-day trial, salmon treated with cortisol had increased gill Na⁺/K⁺ ATPase activity while fish treated with DOC—aldosterone—experienced no change. The results are consistent with the fact that GRs (bound by cortisol) affect osmoregulation, and MRs are absent in Atlantic Salmon. These findings can be generalized to indicate a lack, or minimal activity, of MRs in other teleosts. Overall, these data indicate that glucocorticoids are the primary hormones released naturally in fish associated with osmoregulation in teleosts (McCormick 2008).

A. Mammalian Cortisol Mechanism

Mammalian and fish cortisol pathways are relatively similar in terms of secretions and targets for these secretions. In mammals, cortisol release is promoted by activation of the hypothalamic-pituitary-adrenal axis. The brain registers a stressor—or a variety of other

stimuli that elicit hypothalamic responses—and a CRH, ACTH, Cortisol cascade ensues. In the human body, release and binding of cortisol has two main effects: 1. Increase of gluconeogenesis, and 2. Activation of anti-inflammatory systems. These function to increase the energy/viability of an organism in response to a stressor as they increase the amount of ATP in the body. Cortisol also serves as an immune-suppressor by inhibiting release of antibodies and cytokines in mammalian tissues (Cortisol 2015).

B. Fish Cortisol Mechanism

The pathway leading to secretion of cortisol in fish is very similar to that of mammals; the only thing that differs is the tissues targeted by each intermediate factor in the cascade. In the mammal system, the cascade goes from the hypothalamus to pituitary to adrenal cortex. In fish the stimulus starts at the hypothalamus which sends a messenger (CRH) to the adenohypophysis which sends ACTH to interrenal tissue which releases cortisol. The main physiological impacts of cortisol in fish is examined later in this paper (Neson 2013).

C. Comparison

Glucocorticoids, in fish and mammals, increase metabolic rate by influencing numerous biochemical pathways. A study by G. Tripathi on changes in metabolic pathways related to cortisol secretion was conducted to target the reactions exhibited in various biochemical-messaging systems after exposure to cortisol. Many enzymes are influenced, but the major change discussed in this study focused on increased activity of gluconeogenic enzymes. Stress responses increase metabolic rates in animals to provide more ATP to muscles allowing for increased strength or speed to get away from dangerous situations. To do this, mRNA transcription and protein synthesis must increase at the cellular level. The newly created proteins can then signal to other tissues and initiate gluconeogenesis.

Gluconeogenesis refers to the process of synthesizing glucose from non-carbohydrates when carbohydrates are not available to feed glycolytic pathways. This process is important, as glycolysis catabolizes glucose to produce ATP, which is the functional energy unit used in tissues. Therefore, Tripathi's study proved that "cortisol increases all key gluconeogenic enzymes" which allows fish to create more ATP without ingesting carbohydrates (Tripathi 2003). In stressful situations, cortisol acts as a metabolic "fight or flight" response in an effort to help fish escape from potential predators, yet many other consequences stem from unusually high levels of the steroid.

III. Experimental vs. Natural levels of Cortisol

Cortisol increases in catch and release studies are difficult to measure, yet secretion of the steroid can be quantified in fish subjected to a variety of stressful sounds. These measurements can then be compared to experimentally injected quantities to determine how realistic the results of injection studies are. In this European study from 2006, scientists exposed three species of fish to pre-recorded ship noises and measured the cortisol emissions found in their aqueous environments after exposure. These graphs compare cortisol secretion between stressful and non-stressful noise stimuli (Wysocki 2006).

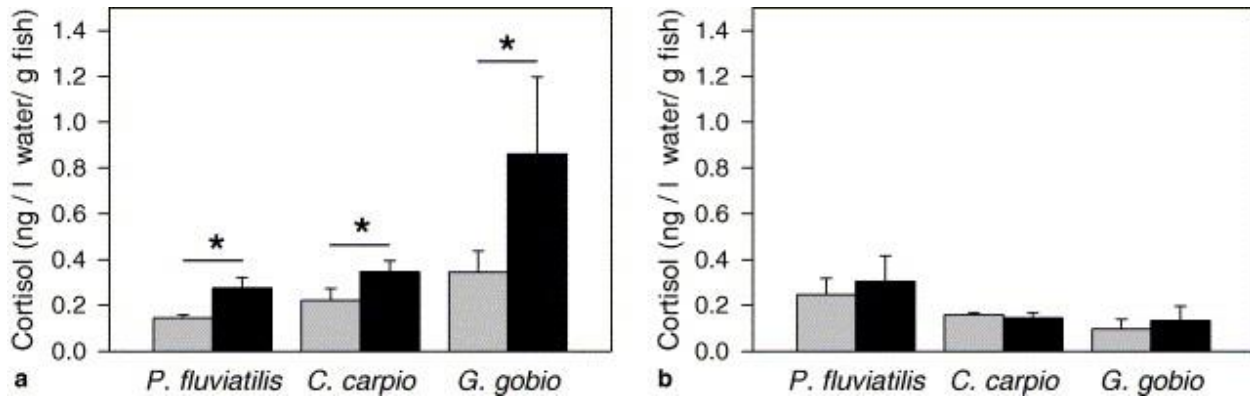


Figure 2: Cortisol content in ng/liter of water/ g of fish for three fish species. In graph A, the black bars represent secretions for fish exposed to ship noises while grey is a control. In graph B, the black bars represent fish exposed to Gaussian noises and grey bars are control fish again. Cortisol levels in water increases up to 1.2 ng/l/g in some fish when stimulated by ship noises. (Wysocki 2006)

Although these data were collected in response to noise stimuli, they generalize to cortisol secretions during catch and release fishing. Noise stimuli are shorter lived and require less physical reaction than the act of being reeled in by a fisher; hence, it is easy to assume that cortisol secretions would be higher in response to a catch and release scenario.

Furthermore, fish have to actively, and for a prolonged amount of time, fight against a line while being reeled in leading to exhaustion. In summation, the amount of cortisol released and effort exerted in caught fish likely exceeds cortisol levels found in the study shown above (Wysocki 2006).

Many studies on fish stress responses are conducted to evaluate cortisol levels in response to rising water temperature. Thermal shock, as a large stressor in natural populations, can be used to determine quantitative levels of stress hormones in fish. In a study published by the Canadian Journal of Fisheries and Aquatic Sciences, the effects of thermal cycling in warm water and cold water fish were analyzed to determine if cortisol levels were rising, how much they were rising, and the effects these rises had on fish. To do

this, researchers documented biogenetic changes (changes in mass), longevity, and cortisol levels in a variety of test groups. Seven different species of fish were tested in two different variable environments—cool season and warm season. The fish were kept initially in water containers that simulated “cool season” temperatures or “warm season” temperatures and were then exposed to water temperature cycling. Although stress from temperature changes has recently been attributed to rising levels of stress and mortality in fish, this study found that there were no differences in longevity between cold and warm test groups. More importantly, however, in all species, cortisol levels were tracked and the results show that fish are able to adapt quickly to stressors and therefore did not experience increased cortisol after continual thermal cycling. The analysis of cortisol levels revealed that:

After 44 days of rapid temperature change, cortisol levels in all species were not higher than the control for any rate of temperature change (Tukey’s HSD, $p > 0.05$). In fact, cortisol concentrations in bluntnose minnow and spotfin shiner were lower than the control for some rates of change (Tukey’s HSD, $p < 0.05$). During the warm season, cortisol concentrations after 1 day of temperature change were higher in walleye for the $0.8\text{ }^{\circ}\text{C}\cdot\text{h}^{-1}$ treatment (Tukey’s HSD, $p < 0.05$; Fig. 3). After 29 days, the cortisol concentrations were similar to the control in all species and rates of temperature change (Tukey’s HSD, $p > 0.05$) (Sweeney 2015).

These data are important in showing the compensatory responses in an animal’s physiology as, under stressed conditions, stress hormone levels did not change, and even decreased in some cases. Generalizing these results may be difficult, however, due to the difference in stress patterns between chronic thermal cycling and acute catch and release fishing. In this experiment, researchers were determining the effects of a chronic stress, therefore fish were constantly exposed to temperature changes. In contrast, most catch and release fishing would be classified as a repeated acute stressor. Distinction between

stressor type is important as often, for chronic stress, compensatory responses work to normalize physiological reactions allowing organisms to function normally even in the presence of a long-lasting stressor. Acute stressors are more impactful as they each illicit a stress response which is difficult to compensate for. Although this study is important in ruling out cortisol-related changes in fish after chronic exposure to stressors, it is also important to examine physiological changes in response to acute stressors.

Acute stressors, such as introduction of a predatory species or capture of a fish, initiate acute physiological responses. These types of stressors generally do not elicit compensatory defenses from animals as they are too infrequent to do so. Such stressors are important in determining the stress on fish in hatcheries, therefore, a telling study on acute stress responses examines the effects of stressors experienced in a hatchery situation. These triggers are much more similar to catch and release fishing than a chronic thermo-cycling experiment. As shown in figure 3, cortisol was measured at various intervals after catching, transporting, and returning fish to their environments. These data show the spike and fall in cortisol levels after an acute stressor.

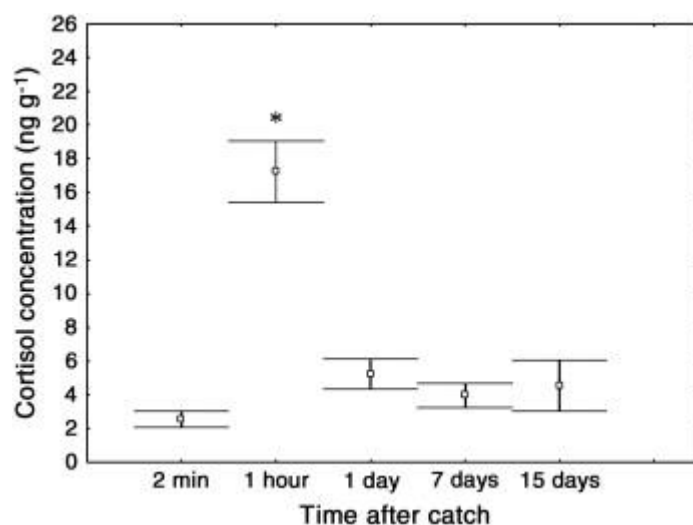


Figure 3: Whole body cortisol levels in ng/g in flounder after catch and transport for 1 hour. The times refer to time after initial catch. Cortisol levels increased from an average of 2.56 ng/g to an average of 17.23 ng/g after transport (Bolasina 2011).

As is demonstrated from the figure, cortisol levels spike dramatically after exposure to an acute stressor and remain slightly elevated, though not significantly, from normal for up to 15 days after the stressor. Although hormone levels seem to remain slightly elevated on the graph, the journal does state that “twenty-four hours after fish capture and transportation, cortisol concentration...returned to the basal level and no immediate mortality was registered” demonstrating the rapid homeostatic recovery of the fish (Bolsina 2011). Because this study was conducted in a closed system and measured the actual body content of cortisol, we can say that the data generalizes to catch and release fishing. The stressors are very similar and, therefore, the physiological responses should be similar.

Another study measured the whole body cortisol of zebrafish after exposure to acute restraint stress in which individual fish were isolated to very small tubes for varying amounts of time. Bodily levels of cortisol were then measured and documented in figure 4:

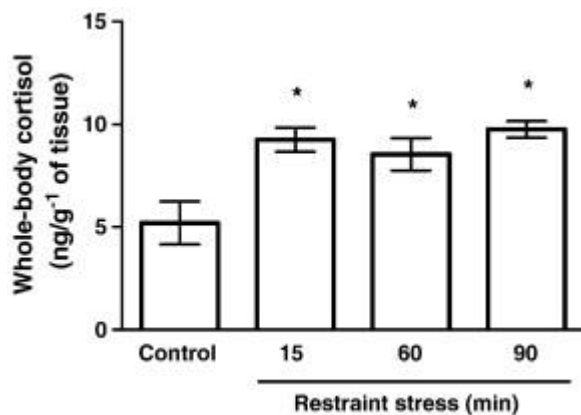


Figure 4: Whole-body cortisol in ng/g of zebrafish after exposure to restraint stress for 15, 60, or 90 minutes. The cortisol levels of animals exposed to stress averaged between 8.5 and 9.7 ng/g while the control group exhibited a maintained level of cortisol at 5.2ng/g (Ghisleni 2012).

These results differ from the cortisol levels in flounder as basal cortisol levels were lower in flounder than the zebrafish (Ghisleni 2012). Cortisol levels were still much higher in flounder after their exposure to handling stress than in zebrafish after exposure to restraint stress. Once again, handling stress in the previous experiment proves to correlate

more closely to fishing based on the stressor used, but both studies are important in establishing the difference between basal and elevated cortisol levels.

IV. Glucocorticoid Effects on Female Reproduction

Increased sodium-potassium ATPase function and changes in female reproductive cycles are both consequences of cortisol exposure. In some species of female fish, gestation periods last anywhere from 60-75 days in viviparous species. Depending on the fish species, a brood can contain between 1200 and 7800 viable eggs (Mendoza 1962). The most costly part of this process for female fish occurs during vitellogenesis. Vitellogenin is secreted from the liver half way through the reproductive cycle as a function of estrogen control. This molecule is a “high molecular weight glycolipoprotein” which is transported through the blood to the ovaries (Tingaud-Sequeira, Angèle 2012). At its final binding site—the female gonad—the growing oocytes take up the protein through endocytosis where it is utilized as a yolk pre-cursor and increases energy/fat storage in the oocytes.

The Oregon Cooperative Fishery Research Unit, led by Contreras-Sanchez, examined the physiological effects of increased cortisol on various periods of reproduction. They used vitellogenesis as a marker in a study conducted to evaluate reproductive quality in female fish after exposure to high levels of cortisol. In this study, they tested the effects of cortisol in various stages of the reproductive cycle to measure the effect it would have on female fish and their offspring. There were three test groups: vitellogenic or early-stress, final maturation or late-stress, whole period, and control. For each test group, the fish were given cortisol or a substance lacking cortisol during a specific interim in their reproductive cycle. Then, differences in egg size and quality, ovulation, fecundity, mortality, and growth in the fish and their offspring were examined. The study concluded that egg production did

not change in control, early vitellogenesis, late vitellogenesis, or whole period test groups, but egg and offspring quality did.

The same study proved that excess cortisol imposes negative consequences on fish broods when mothers are injected during specific times in their reproductive cycles. The study revealed that mothers in whole and late-period test groups were less likely to produce viable offspring. Analysis of the data presented an indirect correlation between stress level and egg size in female teleosts. In these fish, stressful conditions create a physiological ultimatum: maintain a constant body weight and decrease egg quality or keep egg production constant and decrease somatic tissue supplies (Contreras-Sanchez 1998). As stated by Contreras-Sanchez, “the fact that females stressed for 6 [weeks] during early vitellogenesis produced smaller eggs suggests that these fish selected for body maintenance and survival, thus compromising the size but not the number of eggs” (Contreras-Sanchez 1998). Clearly, high amounts of glucocorticoids during vitellogenesis decreased the fitness of eggs and fry. Furthermore, Contreras-Sanchez concluded that, “results of this study with respect to egg and fry quality agree with other studies that demonstrated that size of the fry is highly correlated with egg size” (Contreras-Sanchez 1998). So if egg sizes are much smaller due to reallocation of resources during reproductive cycling, the fry, and adult fish, will be smaller. Correlation between exposure to high levels of stress in reproducing female fish and brood quality alludes to the physiological consequences of increased cortisol in fish.

V. Behavioral Responses to Increased Cortisol

A recent study examined the behavioral changes exhibited in fish post stress. In an experiment, fish caught using a rod-and-reel—in the typical catch and release style— were given injections from one of three categories: control, sham, or cortisol. All fish were captured, anesthetized, and injected in the same way to maintain consistency; then behavioral and statistical data were collected. From these data, scientists documented that “fish receiving cortisol or ACTH became less excitable and were more easily netted than the sham-injected controls after 5-7 days” (Langdon 1984). Cortisol has negative consequences on fish because it leaves them less energetic and increases chances of capture after a given amount of time. Cortisol-treated fish apparently experienced a decrease in fitness in this experiment.

Similarly, the survival rates of cortisol-injected fish were measured during an overwintering episode in another study. An overview of the procedure and results regarding fish mortality follows:

Cortisol- treated fish were injected intraperitoneally with 10mg/ml of cortisol...this dose raises plasma cortisol from approximately 5 ng/ml to 2,000 ng/ml, a supraphysiological level that is higher than that elicited by exposure to a typical stressor such as exhaustive exercise....Interestingly, the timing of mortality differed significantly among the treatment groups. The cortisol-treated individuals succumbed significantly earlier in the winter than individuals in the other groups....fish treated with cortisol traveled greater daily distances than did fish in the control group....bass that experienced cortisol treatment during the fall suffered accelerated mortality and displayed altered behavior when compared with sham-treated or control fish during a subsequent winterkill event. (O'Connor 2010)

This study illuminates the decreased fitness experienced in fish with high accumulations of cortisol. The amount of cortisol injected was significantly more than would be expected naturally, but smaller amounts of cortisol secretion could have the same effect to a smaller extent.

While examining the hypothalamic-pituitary-interrenal axis in fish, a different group of scientists determined behavioral differences associated with elevated levels of serum CRH (a precursor to cortisol). This study exposed 6-8 month old zebrafish to an acute stressors (being confined to a very small tube for various amounts of time) and then observed their behavior and locomotion. Analysis of turn angles is important here because normative turn angles—therefore demonstrating an organized swim pattern—do not exceed 180 degrees. Scientists found that higher amounts of time in restraint control tubes correlated directly with higher amounts of angular velocities above 180 degrees. The zebrafish subjected to restraint control therefore demonstrated much higher levels of angular variation and an overall disorganized swim pattern after an acute stressor (Ghisleni 2012). Clearly, the locomotive and behavioral patterns of zebrafish experienced drastic changes with the introduction of a negative stimulus, thereby demonstrating some detrimental effects of cortisol secretion in fish.

VI. Conclusion

Glucocorticoid responses vary across fish species and populations, but there are some commonalities that can be applied to most teleostean fish. In terms of recreational fishing—as shown above—consistent, elevated levels of cortisol can reduce fish's abilities to function normally and maintain energetic responses to stimuli. In areas with high amounts of recreational fishing, repetitive stress to fish is common. In terms of their response to such stressors, if prolonged, the fish will likely experience lower energy, and therefore higher levels of predation. Cortisol secretion in fish increases gluconeogenesis, but also leads to negative side effects on brood fitness, overwintering success rates, and escapeability. In many cases, commonly fished bodies of water may result in individuals

being captured frequently in a short amount of time thereby compounding cortisol responses. Likewise, capture of reproducing female fish introduces cortisol to growing eggs which can decrease fitness of future generations of fish. These problems are prominent, but can easily be fixed with the creation and enforcement of catch and release regulations.

Already implemented in many areas, prohibiting fishing during spawning seasons would allow female fish to experience fewer stressors. Such a decrease would result in higher maternal and offspring fitness as the fish would be able to produce larger eggs while maintaining their body weight. Similarly, limiting accessibility to popular fishing areas would decrease exposure of fish to the stress of capture and lower cortisol related consequences in populations. Although catch and release fishing imposes a negative consequence for fish, the implications would not be as drastic as demonstrated above. Hormone secretions occur in small dosages naturally and many cortisol injection studies introduce supraphysiological amounts of hormone to organisms. Such high levels of hormones are rarely, if ever, found naturally in animals. Thus, injection studies are useful in understanding responses to drastic levels of hormone secretion but cannot be directly applied to natural secretion patterns.

In conclusion, it is difficult to address the issue of whether catch and release fishing is detrimental to populations with a yes or no: it really depends. The number of studies conducted specifically on cortisol secretion as a response to recreational fishing are limited. Also, physiological responses to many hormones are variable, leaving fully catalogued hormonal responses to stressors unknown. Although stress is portrayed negatively, some corticosteroidal responses are important, if not necessary to organismal homeostasis. Therefore, the imposition and enforcement of various regulations in regions

with dwindling fish populations would be beneficial in helping maintain or reestablish populations, but many recreational fishing areas maintain healthy populations already. Although fish can have exaggerated, negative responses to supraphysiological levels of glucocorticoids, truly deleterious levels are generally not secreted naturally in teleosts and preventative measures protect many populations from experiencing abnormal amounts of stressful stimuli.

Bibliography

- Ayson, Felix G. "The Effect of Stress on Spawning of Brood Fish and Survival of Larvae of the Rabbitfish, *Siganus Guttatus* (Bloch)." *Aquaculture* 80.3 (1989): 241-6.
- Barry, Terence P., et al. "Ontogeny of the Cortisol Stress Response in Larval Rainbow Trout." *General and comparative endocrinology* 97.1 (1995): 57-65.
- Barton, Bruce A., and George K. Iwama. "Physiological Changes in Fish from Stress in Aquaculture with Emphasis on the Response and Effects of Corticosteroids." *Annual Review of Fish Diseases* 1 (1991): 3-26.
- Barton, Bruce A. "Stress in Fishes: A Diversity of Responses with Particular Reference to Changes in Circulating Corticosteroids." *Integrative and Comparative Biology* 42.3 (2002): 517-25.
- "Cortisol." *Encyclopaedia Britannica*. Encyclopaedia Britannica. 6/14/2015. Web. 24 February 2015.
- Contreras-Sánchez, W. M., et al. "Effects of Stress on the Reproductive Performance of Rainbow Trout (*Oncorhynchus Mykiss*)." *Biology of reproduction* 58.2 (1998): 439-47.
- DONKIN, RICHARD. "Do Fish Feel Pain? Animal Rights Groups Looking for a Ban on Fishing Say Yes; Anglers, Unsurprisingly, Insist Not. but, Says Weekend Fishing Ist Richard Donkin, both Sides may Find there is a More Pressing Debate to be had: LONDON 1ST EDITION." *Financial Times*: 1. 2006.
- Gesto, Manuel, et al. "Is Plasma Cortisol Response to Stress in Rainbow Trout Regulated by Catecholamine-Induced Hyperglycemia?" *General and comparative endocrinology* 205 (2014): 207.
- Ghisleni, Gabriele, et al. "The Role of CRH in Behavioral Responses to Acute Restraint Stress in Zebrafish." *Progress in Neuro-Psychopharmacology and Biological Psychiatry* 36.1 (2012): 176-82. Web.
- Godwin, John. "Neuroendocrinology of Sexual Plasticity in Teleost Fishes." *Frontiers in neuroendocrinology* 31.2 (2010): 203-16.
- Klappenbach, Laura. "Teleosts". *AboutEducation*. About.com. 2015. Web. 9 April 2015.

- Langdon, J. S., J. E. Thorpe, and R. J. Roberts. "Effects of Cortisol and Acth on Gill Na⁺/K⁺-ATPase, SDH and Chloride Cells in Juvenile Atlantic Salmon *Salmo Salar* L." *Comparative Biochemistry and Physiology -- Part A: Physiology* 77.1 (1984): 9-12.
- Leatherland, JF, M. Li, and S. Barkataki. "Stressors, Glucocorticoids and Ovarian Function in Teleosts." *Journal of fish biology* 76.1 (2010): 86-111.
- McCormick, Stephen D., et al. "Are we Missing a Mineralocorticoid in Teleost Fish? Effects of Cortisol, Deoxycorticosterone and Aldosterone on Osmoregulation, Gill Na⁺,K⁺-ATPase Activity and Isoform mRNA Levels in Atlantic Salmon." *General and comparative endocrinology* 157.1 (2008): 35-40.
- Mendoza, Guillermo. "The Reproductive Cycles of Three Viviparous Teleosts, *Allophorus Robustus*, *Goodea Luitpoldii* and *Neophorus Diazii*." *Biology Department of Grinnell College*, Grinnell Iowa: 1962. Web.
- Milla, S., et al. "Corticosteroids: Friends Or Foes of Teleost Fish Reproduction?" *Comparative Biochemistry and Physiology, Part A* 153.3 (2009): 242-51.
- Mommsen, Thomas P., Mathilakath M. Vijayan, and Thomas W. Moon. "Cortisol in Teleosts: Dynamics, Mechanisms of Action, and Metabolic Regulation." *Reviews in Fish Biology and Fisheries* 9.3 (1999): 211-68.
- Nesan, Dinushan, and Mathilakath M. Vijayan. "The Transcriptomics of Glucocorticoid Receptor Signaling in Developing Zebrafish: E80726." *PLoS One* 8.11 (2013) Web.
- O'Connor, Constance M., et al. "Seasonal Carryover Effects Following the Administration of Cortisol to a Wild Teleost Fish." *Physiological and Biochemical Zoology* 83.6 (2010): 950-7.
- Silva, Patricia I. M., et al. "Stress and Fear Responses in the Teleost Pallium." *Physiology & Behavior* 141 (2015): 17-22.
- Soerensen, Christina, Ida B. Johansen, and Oeyvind Oeverli. "Neural Plasticity and Stress Coping in Teleost Fishes." *General and comparative endocrinology* 181 (2013): 25-34.
- Sweeney, Bernard W., William H. Eldridge, and J. Mac Law. "Fish Growth, Physiological Stress, and Tissue Condition in Response to Rate of Temperature Change during Cool Or Warm Diel Thermal Cycles." *Canadian Journal of Fisheries and Aquatic Sciences* 72.10 (2015): 1527-37. Web.

Tingaud-Sequeira, Angèle, et al. "Vitellogenin Expression in White Adipose Tissue in Female Teleost Fish." *Biology of reproduction* 86.2 (2012; 2011): 38.

Tripathi, G., and Priyanka Verma. "Pathway-Specific Response to Cortisol in the Metabolism of Catfish." *Comparative Biochemistry and Physiology, Part B* 136.3 (2003): 463-71.

Van Weerd, J. H., and J. Komen. "The Effects of Chronic Stress on Growth in Fish: A Critical Appraisal." 120 Vol. Elsevier Inc, 1998.

Wunderink, Yvette S., et al. "Chronic and Acute Stress Responses in Senegalese Sole (*Solea Senegalensis*): The Involvement of Cortisol, CRH and CRH-BP." *General and Comparative Endocrinology* 171.2 (2011): 203-10. Web.

Wysocki, Lidia Eva, John P. Dittami, and Friedrich Ladich. "Ship Noise and Cortisol Secretion in European Freshwater Fishes." *Biological Conservation* 128.4 (2006): 501-8.