

Stress in Fishes: A Diversity of Responses with Particular Reference to Changes in Circulating Corticosteroids¹

BRUCE A. BARTON²

Department of Biology and Missouri River Institute, University of South Dakota, Vermillion, South Dakota 57069

SYNOPSIS. Physical, chemical and perceived stressors can all evoke non-specific responses in fish, which are considered adaptive to enable the fish to cope with the disturbance and maintain its homeostatic state. If the stressor is overly severe or long-lasting to the point that the fish is not capable of regaining homeostasis, then the responses themselves may become maladaptive and threaten the fish's health and well-being. Physiological responses to stress are grouped as primary, which include endocrine changes such as in measurable levels of circulating catecholamines and corticosteroids, and secondary, which include changes in features related to metabolism, hydromineral balance, and cardiovascular, respiratory and immune functions. In some instances, the endocrine responses are directly responsible for these secondary responses resulting in changes in concentration of blood constituents, including metabolites and major ions, and, at the cellular level, the expression of heat-shock or stress proteins. Tertiary or whole-animal changes in performance, such as in growth, disease resistance and behavior, can result from the primary and secondary responses and possibly affect survivorship.

Fishes display a wide variation in their physiological responses to stress, which is clearly evident in the plasma corticosteroid changes, chiefly cortisol in actinopterygian fishes, that occur following a stressful event. The characteristic elevation in circulating cortisol during the first hour after an acute disturbance can vary by more than two orders of magnitude among species and genetic history appears to account for much of this interspecific variation. An appreciation of the factors that affect the magnitude, duration and recovery of cortisol and other physiological changes caused by stress in fishes is important for proper interpretation of experimental data and design of effective biological monitoring programs.

INTRODUCTION

Hans Selye once defined stress as “the nonspecific response of the body to any demand made upon it” (Selye, 1973). A common misconception among fishery biologists is that stress, in itself, is detrimental to the fish. This is, however, not necessarily the case. The response to stress is considered an adaptive mechanism that allows the fish to cope with real or perceived stressors in order to maintain its normal or homeostatic state. Quite simply, stress can be considered as a state of threatened homeostasis that is re-established by a complex suite of adaptive responses (Chrousos, 1998). If the intensity of the stressor is overly severe or long-lasting, however, physiological response mechanisms may be compromised and can become detrimental to the fish's health and well-being, or maladaptive, a state associated with the term “distress” (Selye, 1974; Barton and Iwama, 1991) and the important concern of managers and aquaculturists.

Physiological responses of fish to environmental stressors have been grouped broadly as primary and secondary (Fig. 1). Primary responses, which involve the initial neuroendocrine responses, include the release of catecholamines from chromaffin tissue (Randall and Perry, 1992; Reid *et al.*, 1998), and the stimulation of the hypothalamic-pituitary-interrenal (HPI) axis culminating in the release of corticosteroid hor-

mones into circulation (Donaldson, 1981; Wendelaar Bonga, 1997; Mommsen *et al.*, 1999). Secondary responses include changes in plasma and tissue ion and metabolite levels, hematological features, and heat-shock or stress proteins (HSPs), all of which relate to physiological adjustments such as in metabolism, respiration, acid-base status, hydromineral balance, immune function and cellular responses (Pickering, 1981; Iwama *et al.*, 1997, 1998; Mommsen *et al.*, 1999). Additionally, tertiary responses occur (Fig. 1), which refer to aspects of whole-animal performance such as changes in growth, condition, overall resistance to disease, metabolic scope for activity, behavior, and ultimately survival (Wedemeyer and McLeay, 1981; Wedemeyer *et al.*, 1990). This grouping is simplistic, however, as stress, depending on its magnitude and duration, may affect fish at all levels of organization, from molecular and biochemical to population and community (Adams, 1990).

Much of our present knowledge about physiological responses of fish to stress has been gained from studying the primary responses of the brain-chromaffin and HPI axes to stressors and the subsequent or secondary effects associated with neuroendocrine stimulation on metabolism, reproduction, and the immune system (Randall and Perry, 1992; Pickering, 1993; Iwama *et al.*, 1997; Reid *et al.*, 1998; Mommsen *et al.*, 1999). The majority of past research on stress physiology in fish during the last few decades has focused on aquaculture because of the interest in managing for stress while maximizing production in artificial environments. Many reviews have been published in that con-

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² E-mail: bbarton@usd.edu

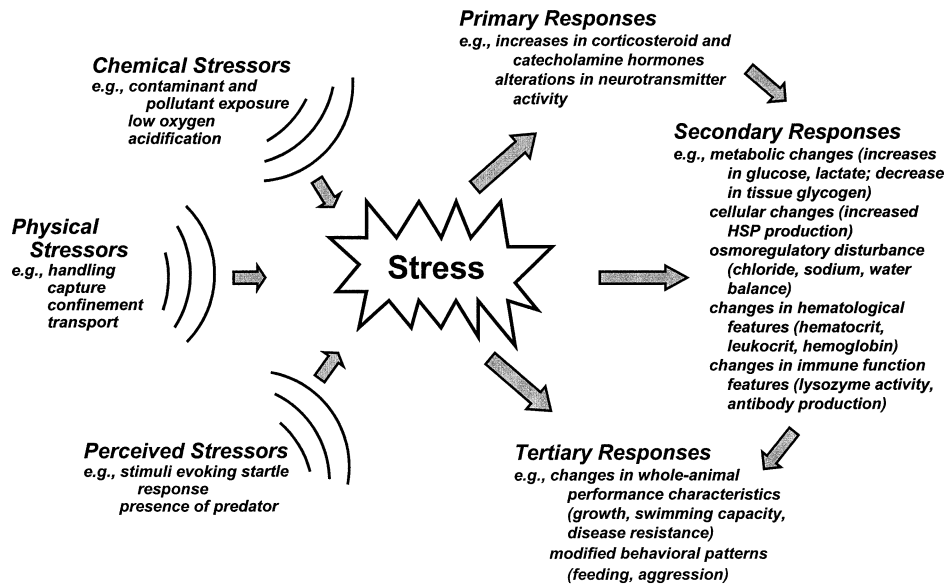


Fig. 1. Physical, chemical and other perceived stressors act on fish to evoke physiological and related effects, which are grouped as primary, secondary and tertiary or whole-animal responses. In some instances, the primary and secondary responses in turn may directly affect secondary and tertiary responses, respectively, as indicated by the arrows.

text (Barton and Iwama, 1991; Iwama *et al.*, 1997; Pickering, 1998) and a few have dealt with the nature of stress responses and manipulations of stress-hormone levels in fish (Mazeaud *et al.*, 1977; Pickering, 1981; Gamperl *et al.*, 1994; Wendelaar Bonga, 1997; Mommsen *et al.*, 1999). Comparatively less information is available on physiological responses of fish to environmental perturbations associated with natural or anthropogenic stressors, particularly water-borne contaminants (Cairns *et al.*, 1984; Adams, 1990; Niimi, 1990; Brown, 1993; Hontela, 1997). The purpose of this paper is to illustrate the diversity of corticosteroid stress responses that occurs among fishes in the context of their genetic, developmental and environmental history.

ENDOCRINE RESPONSES TO STRESS IN FISH

When fish are exposed to a stressor, the physiological stress response is initiated by the recognition of a real or perceived threat by the central nervous system (CNS). The sympathetic nerve fibers, which innervate the chromaffin cells, stimulate the release of catecholamines via cholinergic receptors (Reid *et al.*, 1996, 1998). The chromaffin tissue (adrenal medulla homologue) is located mainly in the anterior region of the kidney in teleostean fishes (Reid *et al.*, 1998). Because catecholamines, predominantly epinephrine in teleostean fishes, are stored in the chromaffin cells, their release is rapid and the circulating levels of these hormones increase immediately with stress (Mazeaud *et al.*, 1977; Randall and Perry, 1992; Reid *et al.*, 1998).

The release of cortisol in teleostean and other bony fishes is delayed relative to catecholamine release. The pathway for cortisol release begins in the HPI axis with the release of corticotropin-releasing hormone (CRH), or factor (CRF), chiefly from the hypothala-

mus in the brain, which stimulates the corticotrophic cells of the anterior pituitary to secrete adrenocorticotropin (ACTH). Circulating ACTH, in turn, stimulates the interrenal cells (adrenal cortex homologue) embedded in the kidney to synthesize and release corticosteroids into circulation for distribution to target tissues. The interrenal tissue is located in the anterior kidney in teleosts and exhibits considerable morphological variation among taxonomic groups (Nandi, 1962), but is found throughout the kidney in chondrosteans (Idler and O'Halloran, 1970). Cortisol is the principle corticosteroid in actinopterygian (*i.e.*, teleostean, other neopterygian and chondrosteans) fishes (Sangalang *et al.*, 1971; Idler and Truscott, 1972; Hanson and Fleming, 1979; Barton *et al.*, 1998) whereas 1α -hydroxycorticosterone is the major corticosteroid in elasmobranchs (Idler and Truscott, 1966, 1967). Cortisol synthesis and release from interrenal cells has a lag time of several minutes, unlike chromaffin cells, and, therefore, proper sampling protocol can allow measurement of resting levels of this hormone in fish (Wedemeyer *et al.*, 1990; Gamperl *et al.*, 1994). As a result, the circulating level of cortisol is commonly used as an indicator of the degree of stress experienced by fish (Barton and Iwama, 1991; Wendelaar Bonga, 1997). Control of cortisol release is through negative feedback of the hormone at all levels of the HPI axis (Fryer and Peter, 1977; Donaldson, 1981; Bradford *et al.*, 1992; Wendelaar Bonga, 1997). Regulation of the HPI axis is far more complicated than this description implies, however. For additional details, Sumpter (1997), Hontela (1997) and Wendelaar Bonga (1997) provide more complete descriptions of the endocrine stress axis in fish.

Other peripheral hormones can become elevated during stress, including notably thyroxine (Brown *et*

TABLE 1. Examples of mean (\pm SE) plasma cortisol concentrations in selected juvenile freshwater fishes before and 1 hr after being subjected to an identical 30-sec aerial emersion (handling stressor).*

Species	Cortisol (ng/ml)	
	Pre-stress	Post-stress
Pallid sturgeon <i>Scaphirhynchus albus</i>	2.3 \pm 0.3	3.0 \pm 0.3
Hybrid sturgeon <i>S. albus</i> \times <i>platyrhynchus</i>	2.2 \pm 0.4	3.2 \pm 0.3
Paddlefish <i>Polyodon spathula</i>	2.2 \pm 0.6	11 \pm 1.8
Arctic grayling <i>Thymallus arcticus</i>	1.1 \pm 0.3	26 \pm 4.4
Rainbow trout (domestic) <i>Oncorhynchus mykiss</i>	1.7 \pm 0.5	43 \pm 3.5
Common carp <i>Cyprinus carpio</i>	7.4 \pm 2.9	79 \pm 14
Brook trout <i>Salvelinus fontinalis</i>	4.0 \pm 0.6	85 \pm 11
Yellow perch <i>Perca flavescens</i>	3.4 \pm 1.1	85 \pm 12
Bull trout <i>Salvelinus confluentus</i>	8.1 \pm 1.2	90 \pm 11
Brown trout <i>Salmo trutta</i>	1.0 \pm 0.3	94 \pm 11
Lake trout <i>Salvelinus namaycush</i>	2.8 \pm 0.4	129 \pm 11
Walleye <i>Stizostedion vitreum</i>	11 \pm 4.4	229 \pm 16

* All species were acclimated to their respective environmental preferences and are listed in order of increasing magnitude of their plasma cortisol concentration 1 hr after the disturbance (from Barton and Zitzow, 1995; Barton and Dwyer, 1997; Barton *et al.*, 1998, 2000; Barton, 2000; and unpublished data for common carp [N. Ruane, Wageningen University], yellow perch [A. H. Haukenes, University of South Dakota] and Arctic grayling [B. A. B. and W. P. Dwyer, U.S. Fish and Wildlife Service, Bozeman Fish Technology Center]).

al., 1978), prolactin (Avella *et al.*, 1991; Pottinger *et al.*, 1992a) and somatolactin (Rand-Weaver *et al.*, 1993; Kakizawa *et al.*, 1995). Also, stress may suppress reproductive hormones in circulation (Pickering *et al.*, 1987; Pankhurst and Dedual, 1994; Haddy and Pankhurst, 1999), as does an elevated level of cortisol (Carragher *et al.*, 1989; Carragher and Sumpter, 1990). However, these other hormones have not yet been demonstrated to be useful stress indicators *per se* and, therefore, are not discussed herein. Interest has focused recently on the responses of central brain monoamines, specifically the catecholamines and indoleamines in response to stress (Winberg and Nilsson, 1993). Serotonin, in particular, has been implicated in both epinephrine and cortisol regulation in fish during stress (Fritsche *et al.*, 1993; Winberg and Nilsson, 1993; Winberg *et al.*, 1997).

FACTORS INFLUENCING CORTICOSTEROID STRESS RESPONSES

Genetic factors

Fishes exhibit a wide variation in their responses to stressors, particularly endocrine responses (Barton and Iwama, 1991; Gamperl *et al.*, 1994). Earlier studies on corticosteroid stress responses tended to center on freshwater fishes, particularly salmonids, because of their importance in government and commercial aquaculture (Barton and Iwama, 1991; Barton, 1997), but interest has focused recently on commercially important marine species (Thomas and Robertson, 1991; Pankhurst and Sharples, 1992; Morgan *et al.*, 1996; Waring *et al.*, 1996; Barnett and Pankhurst, 1997; Rottlant *et al.*, 2000). Elevations in plasma cortisol range at least as much as two orders of magnitude among fishes following an identical stressor (Table 1) and can be much higher, depending on species.

Characteristic cortisol elevations of fishes in response to acute stressors tend to range within about 30 and 300 ng/ml (Wedemeyer *et al.*, 1990; Barton and

Iwama, 1991) but there are notable exceptions. Barton *et al.* (1998, 2000) observed that peak levels in cortisol following an acute handling stressor were low (Table 1) in scaphirhynchid sturgeons (*Scaphirhynchus* spp.) and paddlefish (*Polyodon spathula*). Their results suggest a trend toward lower stress responses in those chondrosteans compared with teleosts. Belanger *et al.* (2001), however, found that peak plasma cortisol in white sturgeon (*Acipenser transmontanus*) following an acute disturbance was about 40 ng/ml, indicating that a low corticosteroid stress response may not be a universal phenomenon in this fish group.

Among teleosts, some species also exhibit low corticosteroid responses to acute stressors. Atlantic cod (*Gadus morhua*), for example, had a peak increase in plasma cortisol to <15 ng/ml after handling (Hemre *et al.*, 1991). At the high end of the response range, Maule *et al.* (1988) during their physiological monitoring studies of migrating juvenile chinook salmon (*Oncorhynchus tshawytscha*) found that peak post-disturbance cortisol concentrations often reached 400 ng/ml during and after transport. However, Congleton *et al.* (2000) later measured cortisol titers in outmigrating chinook salmon from the same system that were considerably lower. Mazik *et al.* (1991) documented plasma cortisol increases in striped bass (*Morone saxatilis*) to nearly 2,000 ng/ml during recovery following 5 hr of hauling, which represent some of the highest levels reported.

Response differences to stressors are clearly evident among closely related fish species and such differences appear to be consistent. Barton (2000) and Ruane *et al.* (1999) both showed that brown trout (*Salmo trutta*) exhibited greater cortisol increases after brief handling and short-term confinement, respectively, than did rainbow trout (*Oncorhynchus mykiss*). This difference was also consistent with glucose responses between these two species. Similarly, both McDonald *et al.* (1993) and Barton (2000) found that lake trout (*Sal-*

velinus namaycush) were more sensitive to a transport stressor than brook trout (*Salvelinus fontinalis*), a closely related char species.

A few studies have subjected fish to continuous severe stressors in an attempt to characterize maximum corticosteroid responses to stress. Plasma cortisol in sturgeons and paddlefish reached maximum levels of about 13 and 60 ng/ml, respectively, when subjected to severe continuous confinement accompanied by handling (Barton *et al.*, 1998, 2000), but in juvenile rainbow trout, this plateau was about 160 ng/ml using the same experimental protocol (Barton *et al.*, 1980). In similar studies, peak plasma cortisol concentrations exceeded 500 ng/ml in juvenile chinook salmon (Strange *et al.*, 1978) and approached 1,400 ng/ml in striped bass (Noga *et al.*, 1994), further emphasizing the wide variations in stress responses apparent among fish species.

Most fish species tested show their highest plasma increase in cortisol within about 0.5–1 hr after a stressful disturbance (Barton and Iwama, 1991), but there are exceptions to this general pattern. Vijayan and Moon (1994) found that circulating cortisol in the sea raven (*Hemitripterus americanus*), a sedentary, benthic marine fish, took about 4 hr to reach its peak level of about 260 ng/ml following an acute stressor. Those authors suggested that the slow rate of response to the stressor may help conserve energy in a normally inactive species having a slow metabolic rate.

Differences in corticosteroid stress responses also exist among strains or stocks within the same species (Iwama *et al.*, 1992; Pottinger and Moran, 1993), their hybrids (Noga *et al.*, 1994), and between wild and hatchery fish (Woodward and Strange, 1987). Within a single strain or population, variation in stress responses also has a genetic component (Heath *et al.*, 1993) and some fish may be predisposed to consistently exhibit high or low cortisol responses to stressors (Pottinger *et al.*, 1992b; Tort *et al.*, 2001), a pattern that appears to have a behavioral correlate (Øverli *et al.*, 2002). The tendency for major differences in stress responses between and among taxa is a trait that appears to be at least partly heritable (Fevolden *et al.*, 1991; Fevolden and Røed, 1993; Pottinger *et al.*, 1994). Fevolden *et al.* (1999) estimated a heritability value of 0.56 for the plasma cortisol increases measured in adult rainbow trout after being exposed to three stressful events, each spaced more than 1 mo apart. Similarly, Tanck *et al.* (2001) recently attempted to calculate heritability estimates for stressor-induced plasma cortisol elevations in common carp (*Cyprinus carpio*) and determined, with reservation, a relatively high mean heritability value of 0.60 for an androgenetic stock. It is unclear, however, whether fishes that display relatively high or low corticosteroid stress responses are actually “more or less stressed” than others or simply have different capacities to respond to stressors. Differences in physiological mechanisms that would account for wide variations remain largely unexplored, but Pottinger *et al.* (2000) found recently

that high cortisol levels exceeding 1,500 ng/ml in chub (*Leuciscus cephalus*) following a disturbance were associated with low corticosteroid receptor affinity.

Developmental factors

The developmental stage of the fish can also affect its responsiveness to a stressor. A fish's ability to respond to a disturbance develops very early in life. Larval turbot (*Scophthalmus maximus*) at 23 days post-hatch and before metamorphosis showed elevations of whole-body cortisol after they were exposed to high levels of crude oil in a laboratory setting (Stephens *et al.*, 1997). Pottinger and Mosuwe (1994) determined that the HPI axis in both rainbow and brown trout was responsive to an acute stressor as early as 5 wk post-hatch. Barry *et al.* (1995a) subsequently determined that rainbow trout could elicit a significant plasma cortisol response to an acute stressor within 2 wk after hatching, 1 wk before they started to feed. Barry *et al.* (1995b) also noted that, although the fish did not respond to the stressor immediately after hatching, the interrenal tissue at this stage was capable of secreting cortisol upon stimulation by ACTH *in vitro*, suggesting there may be a brief post-hatch period at which time the HPI axis is not yet functional. Fish with a more rapid rate of development may be capable of eliciting a stress response much earlier. Stouthart *et al.* (1998) observed that the HPI axis in embryonic carp, as measured by whole-body cortisol, was activated and produced a cortisol response 50 hr after fertilization, 6 hr before hatching, when eggs were subjected to mechanical pressure. High cortisol content in embryos or larvae may actually affect larval quality. McCormick (1998, 1999) found that elevated cortisol in female damselfishes (*Pomacentrus amboinensis*) transferred to the egg yolk can result in smaller larvae at hatching. Whether endogenously produced cortisol resulting from stress at this life stage would have a similar negative effect on early growth of larvae is unknown although Weil *et al.* (2001) demonstrated a positive correlation between speed of recovery of circulating cortisol and growth rate in juvenile rainbow trout.

Limited evidence exists to suggest that fish show a consistent increase in stress responses as they develop, but they do appear to have heightened responses during periods of metamorphosis. Anadromous salmonid fishes, for example, appear to be especially sensitive to certain stressors, particularly physical disturbances, during the period of parr-smolt transformation, a time of physiological metamorphosis during which juvenile salmon prepare for seawater entry. Barton *et al.* (1985a) reported a two-fold increase in the response of plasma cortisol at 1 hr following a brief handling stressor in juvenile coho salmon (*Oncorhynchus kisutch*) during the 3–4-mo period of parr-smolt transformation as the juvenile fish switch from a freshwater to saltwater existence. Maule *et al.* (1987) noted that coho salmon smolts also appear to be particularly sensitive to stressors during this transformation and Shrimpton and Randall (1994) concluded that addi-

tional stress on smolting fish may also impair certain necessary physiological changes that occur at this time. As fish mature, primary stress responses may actually decrease in magnitude, possibly as a result of a reduced threshold for regulatory feedback with the onset of maturity (Pottinger *et al.*, 1995).

Environmental factors

Almost all environmental factors tested can influence the degree to which fish respond to stressors. External factors include acclimation temperature (Strange, 1980; Davis *et al.*, 1984; Barton and Schreck, 1987; Davis and Parker, 1990), salinity (Strange and Schreck, 1980; Mazik *et al.*, 1991; Barton and Zitzow, 1995), time of day (Davis *et al.*, 1984; Barton *et al.*, 1986), wave length of light (Volpato and Barreto, 2001) and even background color of the tanks (Gilham and Baker, 1985). Internal environmental factors, including the fish's nutritional state (Barton *et al.*, 1988) and presence of disease (Barton *et al.*, 1986), may also affect the magnitude of the stress response.

In certain instances, stress-modifying factors that are themselves chronically stressful, such as poor water quality or toxicants, can actually exacerbate (Barton *et al.*, 1985b) or attenuate (Pickering and Pottinger, 1987; Hontela, 1997; Wilson *et al.*, 1998) the cortisol response to a second stressor. Continual interrenal activity will down-regulate the HPI axis as a result of negative feedback by cortisol, which causes the attenuation of the response to additional stressors. Thus, when a second acute stressor subsequently challenges fish exposed to a chronic stressor, the corticosteroid response to the additional stressor may be reduced considerably relative to controls (Hontela, 1997). Impaired interrenal function from chronic stress has been demonstrated *in vivo* by subjecting fish to an acute physical disturbance after being exposed to various contaminants (Hontela *et al.*, 1992; Wilson *et al.*, 1998; Norris *et al.*, 1999; Laflamme *et al.*, 2000).

This apparent interrenal dysfunction has also been assessed by measuring the functional integrity of the interrenal tissue *in vitro* as a bioassay approach for environmental monitoring. Brodeur *et al.* (1997) developed a relatively simple perfusion protocol and, more recently, Leblond *et al.* (2001) described a method of preparing and using interrenal cell suspensions for quantifying the extent of *in vitro* steroidogenic inhibition of ACTH-stimulated interrenal tissue at the cellular level. These and similar approaches have been used by this group of investigators and others to evaluate the mechanisms involved in the depression of interrenal capacity following exposure to contaminants including heavy metals and organochlorine compounds (Brodeur *et al.*, 1998; Girard *et al.*, 1998; Wilson *et al.*, 1998; Leblond and Hontela, 1998; Benguira and Hontela, 2000; Laflamme *et al.*, 2000).

Repeated stressors

Fish can exhibit a cumulative response to repeated stressors (Carmichael *et al.*, 1983; Flos *et al.*, 1988;

Maule *et al.*, 1988). Barton *et al.* (1986) found that when juvenile chinook salmon were given multiple handling stressors, the peak cortisol responses after the final disturbance were cumulative. This phenomenon was demonstrated in this species at the secondary physiological level with plasma glucose (Barton *et al.*, 1986; Mesa, 1994) and also at the whole-animal level using response time to avoid a noxious stimulus or a predator as an indicator (Sigismondi and Weber, 1988; Mesa, 1994).

However, repeated exposures to mild stressors can desensitize fish and attenuate the neuroendocrine and metabolic responses to subsequent exposure to stressors (Reid *et al.*, 1998; see also last section). For example, Barton *et al.* (1987) subjected juvenile rainbow trout to one of three different brief handling stressors once a day for 10 wk and at the end of that time, measured their response to acute handling. The response of plasma cortisol was about half of that observed in naive, previously unstressed fish indicating possible desensitization of the HPI axis to the repeated disturbances. A matching and significant decline in the response of plasma glucose in the treatment group, which implies the involvement of the catecholamine response, suggests a general habituation to the repeated stressor.

The length of time between discrete stressors, the effect of multiple stressors, and the severity of continuous stressors are important factors that will likely influence how fish respond. Unless stressors, singularly or in combination, are severe enough to challenge the fish's homeostatic mechanisms beyond their compensatory limits or permanently alter them, which ultimately may cause death, physiological processes generally adapt to compensate for the stress (Schreck, 1981, 2000). In these cases, blood chemistry features, such as cortisol, used to evaluate stress may appear "normal" and alternative approaches, such as determining the magnitude of response to an additional acute stressor, may be needed to assess the fish's physiological state.

SUMMARY

Knowledge and understanding of what constitutes stress in fish has increased immensely in the past few decades, notably in the area of physiological mechanisms and responses that lead to changes in metabolism and growth, immune functions, reproductive capacity, and normal behavior. Primary stress responses in actinopterygian fishes include a number of hormonal changes, but particularly those in circulating levels of cortisol and catecholamines. Secondary responses, which may or may not be caused directly by the endocrine response, include measurable changes in blood glucose, lactate or lactic acid, and major ions (*e.g.*, chloride, sodium, and potassium), and tissue levels of glycogen and HSPs. Tertiary responses, including changes in growth, disease resistance and behavior, may result directly or indirectly from these primary and secondary responses. Many other apparent factors,

however, influence characteristic stress responses in fish and include genetic (*e.g.*, species, strain), developmental (*e.g.*, life history stage), and environmental (*e.g.*, temperature, nutrition, water quality) factors.

Interpreting the changes that occur in physiological variables can be more problematic than actually measuring the responses for two reasons. First, various genetic, developmental and environmental factors can have a modifying effect on the magnitude and duration of the stress response. Without knowing the extent to which these other factors may have affected the response, it is difficult to interpret the biological significance of that response in a specific context. A second factor complicating data interpretation is the variation and apparent inconsistency among fishes in the responses of different blood chemistry characteristics. For example, a species that shows the greatest plasma cortisol response increase compared with other taxa may not be the same species that elicits the greatest increase in a secondary response, such as glucose or lactate, when subjected to the identical stressor. Thus, a species or group that appears “most stressed” as indicated by one particular indicator or level of response may not necessarily reflect that same degree of stress if measured by another aspect of the response.

The response to a stressor is a dynamic process and physiological measurements taken during a time course are only representative instantaneous “snapshots” of that process. A significant delay, depending on the level and type of response, can occur from initial perception of the stressor by the CNS to the time when plasma cortisol or other feature of interest reaches a peak level of response. Thus, the measurement of plasma cortisol alone may not necessarily reflect the degree of stress experienced by the fish at that instant but more likely be representative of the extent of the earlier or initial response.

An appreciation of the factors that affect the magnitude, duration and recovery of cortisol and other physiological changes in fishes during the stress response is important for proper interpretation of experimental data and design of effective biological monitoring programs. Moreover, understanding trends in changes that occur in fish in response to stressors can often provide clues that help relate the physiological responses of individuals with changes in performance manifested at the population level that could affect their health and survivorship.

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