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Effect of dietary cortisol administration on growth and reproductive success of channel catfish

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The effect of cortisol administration on reproductive performance was investigated in channel catfish *Ictalurus punctatus* broodfish. Cortisol was added to a commercial catfish feed by dissolving in ethanol and spraying the feed to yield a dietary concentration of 150 mg kg^{-1} feed. The cortisol diet and the control (no cortisol) diet were offered at a rate of 1% of biomass to three replicate ponds each containing 28 female and 14 male broodfish, respectively, three times per week for 11 weeks. Spawning began 10 days after the start of the experiment, and continued for 10 weeks. In fish fed cortisol, body mass and the hepato-somatic index were reduced ($P \leq 0{\cdot}02$) and concentrations of plasma cortisol and glucose were significantly higher ($P \leq 0{\cdot}0003$) compared to those of controls. The relative frequency of spawning was similar between the two treatments; however, cortisol-fed channel catfish had an average of 47·1% more spawns than the control-fed fish. On average, there were 25·5 spawns per pond in the treated groups compared to 12·3 spawns per control pond ($P = 0{\cdot}10$). No effect was observed on egg production, with individual egg mass, fecundity, and hatching success being similar ($P \geq 0{\cdot}27$) for both treatments. Despite the observed negative effects of cortisol on somatic and hepatic growth, the increased reproductive output coupled with no observable effects on the eggs or hatching success demonstrates that cortisol does not suppress channel catfish reproduction.

Key words: channel catfish; cortisol; *Ictalurus punctatus*; reproduction.

INTRODUCTION

Channel catfish *Ictalurus punctatus* (Rafinesque) are widely distributed throughout the southern U.S.A. and are an important aquacultural species. Reproduction of channel catfish is characterized by an annual spawning cycle that is highly dependant on water temperature, with spawning typically occurring during the spring and early summer (Clemens & Sneed, 1957; Silverstein & Small, 2004). Reproductive success of this economically important species is highly variable. Typical spawning rates in broodfish ponds can range from 8 to 80% and may average as low as 30% (Silverstein & Small, 2004). Research to improve reproductive success suggests that, like other captive silurids, *e.g. Clarias gariepinus* (Burchell) (de Leeuw *et al.*, 1985), *Clarias batrachus* (L.) (Manickam & Joy, 1989) and *Heteropneustes fossilis* (Bloch) (Tharakan & Joy, 1996), final oocyte maturation is often inhibited (Silverstein *et al.*, 1999).

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Many researchers have demonstrated that stress has the capacity to inhibit reproductive performance (Schreck *et al.*, 2001), as exhibited by stress in pike *Esox lucius* L. (de Montalembert *et al.*, 1978), white sucker *Catostomus commersonii* (Lacepède) (Stacey *et al.*, 1984) and rainbow trout *Oncorhynchus mykiss* (Walbaum) (Campbell *et al.*, 1994). The association between stress, elevations in plasma cortisol (F) and concomitant depressions in plasma testosterone (T) and 17β-oestradiol (E_2) levels in brown trout *Salmo trutta* L. (Pickering *et al.*, 1987) and snapper *Pagrus auratus* (Forster) (Carragher & Pankhurst, 1991) together with evidence that exogenous F produces inhibitory effects on reproduction in salmonids (Carragher *et al.*, 1989; Pottinger *et al.*, 1991), tilapia *Oreochromis mossambicus* (Peters) (Foo & Lam, 1993), red gurnard *Chelidonichthys kumu* (Cuvier) (Clearwater & Pankhurst, 1997), snapper (Cleary *et al.*, 2000) and spiny damselfish *Acanthochromis polyacanthus* (Bleeker) (Pankhurst, 2001), has lead to the general assumption that the effect of stress on fish reproduction is mediated through the action of F on the gonad. In an attempt to clarify the action of F on ovarian steroidogenesis in rainbow trout, Pankhurst & Van Der Kraak (2000) demonstrated no effect of elevated plasma cortisol levels on E_2 or maturational gonadotropin (GtH), but found plasma T levels to decline in a stepwise manner over time. From their results, it was concluded that the potential inhibitory effects of cortisol on reproduction do not involve inhibition of GtH secretion, and may possibly be at the level of GtH signal transduction.

In vitro studies with goldfish *Carassius auratus* (L.), common carp *Cyprinus carpio* L., and snapper suggest no inhibitory effect on steroidogenesis following treatment of follicles with F, and in several cases demonstrated augmented GtH-induced E_2 production (Pankhurst *et al.*, 1995). Much of the positive information on the effects of F on oocyte maturation in teleosts is based on data obtained from research on *H. fossilis* (Sundararaj & Goswami, 1977; Lamba *et al.*, 1983). This research established perhaps the only clear physiological role for F in teleost reproduction, providing evidence that gonadotropic action on oocyte maturation in *H. fossilis* is mediated through its heterocorticotrophic action on oocytes to induce maturation. Goswami *et al.* (1985) demonstrated that gonadotropin-induced oocyte maturation in this catfish requires steroidogenesis in both interrenal and ovary.

Even with the substantial amount of literature regarding the effects of stress and cortisol on steroidogenesis in fishes, a careful review reveals only a very limited amount of information pertaining to the direct effects of stress and cortisol on reproductive success. Consideration of these effects is given in reviews by Leatherland (1999) and Schreck *et al.* (2001). In the present study, the effect of dietary F administration on channel catfish reproductive success was examined. It was hypothesized that a moderate increase in plasma F concentration, as a result of administering F in the feed, would negatively affect reproductive output (number of spawning events) and fitness (overall fecundity and hatching success).

MATERIALS AND METHODS

In April, adult channel catfish (mean ± S.E. mass = 2·68 ± 0·03 kg) of the NWAC103 strain were stocked into six 0·0405 ha ponds in Stoneville, MS, U.S.A. at a stocking density of 28 females and 14 males. Fish were acclimated for 3 weeks prior to starting the

experiment and fed at 1% body mass on Monday, Wednesday and Friday. For the experiment, ponds were randomly assigned to treatments and control (36% protein, floating, catfish feed; Farmland Industries, Inc., Kansas City, MO, U.S.A.) or cortisol-treated feed was fed to broodfish in triplicate ponds between 1100 and 1200 hours on Monday, Wednesday and Friday for 11 weeks. The cortisol-treated feed was prepared by dissolving crystalline cortisol (Sigma Chemical Co., St Louis, MO, U.S.A.) in 100% ethanol, and spraying the commercial catfish feed using an atomizer while turning in a small concrete mixer to produce a concentration of 150 mg cortisol kg^{-1} feed, a concentration sufficient to cause a moderate, sustained increase in plasma cortisol after 2 h of feeding (Davis *et al.*, 2003). The feed was air-dried and stored at 4° C until fed. At the start of the experiment, six spawning containers were placed into each pond.

At the conclusion of the experiment, blood was rapidly collected from 10 fish per pond anaesthetized in a solution of 6 mg l^{-1} metomidate hydrochloride to determine circulating levels of F and glucose. The cortisol-blocking properties of metomidate hydrochloride prevented handling-associated cortisol increases often observed with other anaesthetics (Small, 2003). The fish were fed according to schedule that day, then caught by seining 6 h after feeding. Plasma was stored at −80° C for later analysis. Cortisol was measured using a modified time-resolved fluoroimmunoassay (Perkin–Elmer Life Sciences, Boston, MA, U.S.A.) validated for channel catfish plasma (Small & Davis, 2002). Plasma glucose concentrations were determined using an Accucheck Advantage glucometer (Boehringer Mannheim Diagnostics, Indianapolis, IN, U.S.A.). Following blood collection, the fish were euthanized in a solution of tricaine methanesulphonate (200 mg l^{-1}), weighed (M), livers removed and weighed (M_L), and the hepato-somatic index (I_L) calculated ($I_L = 100\, M_L\, M^{-1}$).

During the experiment, spawning containers were checked for egg masses three times a week between 0800 and 0900 hours. Egg masses were collected and transported to the hatchery. Once in the hatchery, the entire egg mass was weighed then sub-sampled to determine individual egg mass and fecundity (eggs per spawn). Hatching success (%) was calculated from the total number of hatched larvae (determined volumetrically) divided by the total number of eggs spawned (fecundity).

Number of spawns, egg mass, fecundity, hatching success, final body mass, I_L, plasma F and glucose were subjected to statistical comparisons conducted using the SAS software system version 8.00 (SAS Institute Inc., Cary, NC, U.S.A.). Pond was the experimental unit, and pond within treatment was used as the error term in tests of significance. Assumptions for homogeneity of variance and normality of the data were tested by examination of correlation between absolute residuals and predicted values, and the Shapiro-Wilkes test for normality. Data not meeting these assumptions were arcsine-transformed prior to applying ANOVA using mixed-model procedures.

RESULTS

Plasma F levels were higher ($P = 0{\cdot}0003$) in broodfish fed the cortisol-laden feed compared to those fed the control diet, 28·60 and 6·58 ng ml^{-1}, respectively (Table I.) Dietary F and resultant increased plasma F had significant negative effects on broodfish mass ($P = 0{\cdot}02$) and I_L ($P = 0{\cdot}01$) at the end of the experiment (Table I). Fish receiving dietary F also had significantly higher ($P < 0{\cdot}0001$) plasma glucose levels than those fish fed the control diet, 92·5 *v.* 39·9 mg dl^{-1}, respectively (Table I).

Ten days after the start of feeding experimental diets, the fish began spawning (two spawns in control ponds). The first spawn in a cortisol pond occurred 2 days later. Spawning continued for 10 weeks, and the experiment was ended when no spawns occurred in either treatment over a 7 day period. The relative frequency of spawning was similar between treatments (Fig. 1). The number of spawns per pond within treatments was variable over time; however, the total number of spawns from cortisol-fed channel catfish was 1·7 times greater than

TABLE I. Mean ± S.E. ($n = 3$ ponds) effect of dietary cortisol administration on channel catfish mass, hepato-somatic index* and plasma cortisol and glucose levels after 11 weeks

Treatment	Final mass (kg)	I_L	Plasma cortisol ($ng\,ml^{-1}$)	Plasma glucose ($mg\,dl^{-1}$)
Control	1527 ± 66	1·71 ± 0·07	6·58 ± 1·58	39·9 ± 2·0
Cortisol	1240 ± 24	1·24 ± 0·08	28·60 ± 0·61	92·5 ± 1·2
P	0·02	0·01	0·0003	<0·0001

*$I_L = 100$ (liver mass) (body mass)$^{-1}$.

those fed the control diet. On average, broodfish in ponds receiving the cortisol diet spawned 25·5 times compared to 12·3 spawns for those fish in control ponds ($P = 0{\cdot}10$; Table II). No effect was observed on egg production (Table II); with individual egg mass, fecundity and hatching success being similar ($P \geq 0{\cdot}27$) for both treatments.

DISCUSSION

Dietary administration of F has been shown to effectively alter physiology in channel catfish (Davis *et al.*, 1985, 2003) and rainbow trout (Barton *et al.*, 1987). As in those studies, dietary F administration in the present study resulted in decreased growth compared to the controls. These results are in agreement with earlier studies by Storer (1967), who observed decreased body masses in goldfish injected with 200 μg cortisol g^{-1} body mass per day, and Freeman & Idler (1973), who observed mass loss in salmonids which had been implanted with cortisol pellets. The resulting decrease in growth observed in the present study by feeding F further validates the use of dietary administration as an effective means of administering F, thus avoiding the added stresses of handling, injecting or implanting. This approach allowed for long-term exposure

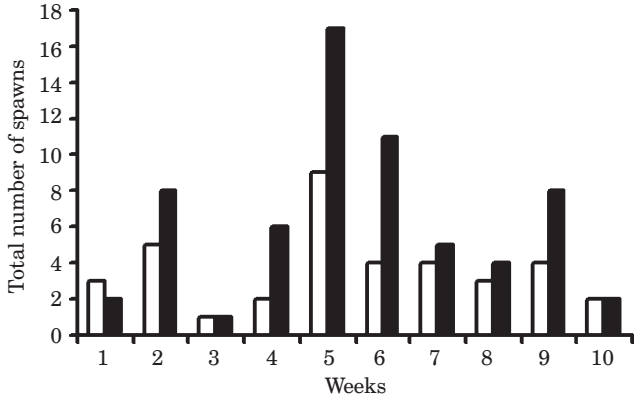

FIG. 1. Spawning frequency of channel catfish fed diets without (control; □) or with cortisol (■; 150 mg kg^{-1} feed) during the 10 week spawning season.

TABLE II. Mean ± S.E. ($n = 3$ ponds) effect of dietary cortisol administration for 11 weeks during the spawning season on channel catfish reproductive success

Treatment	Number of spawns	Individual egg mass (mg)	Fecundity	Hatching success (%)
Control	12·3 (44·0)[a] ± 0·9	26·1 ± 0·6	13 227 ± 243	43·3 ± 1·0
Cortisol	25·5 (91·1) ± 6·1	26·0 ± 0·9	13 136 ± 93	42·7 ± 0·3
P	0·10	0·27	0·75	0·60

[a]Number in parentheses represents mean spawns as a per cent of 28 female broodfish per pond.

and the ability to regulate plasma F concentrations without the effects of handling stress. One disadvantage of administering F in the feed is the inability to insure individual feed consumption. The low variability associated with plasma concentrations of F and glucose suggest all fish consumed the experimental diets in the present study.

Elevation of plasma F not only had a negative effect on somatic growth, but also resulted in decreased hepatic growth as well. The observed decrease in I_L is consistent with that reported by Davis *et al.* (1985) for channel catfish, and earlier studies with F-injected Japanese eels *Anguilla japonica* Temminck & Schlegel (Lidman *et al.*, 1979). Loss of liver mass might be explained by glycolytic effects of cortisol. Evidence that F affects glycogen mobilization has been observed following stress in other teleosts (Paxton *et al.*, 1984; Morales *et al.*, 1990; Trenzado *et al.*, 2003). This explanation is supported by the observed increase in circulating glucose.

While dietary F had significant negative effects on somatic and hepatic growth, it did not appear to negatively affect reproductive performance in this study. On the contrary, cortisol-fed channel catfish had an average of 47·1% more spawns than the control-fed fish, and there were no differences in egg quantity or quality, as determined by hatching success. Stress, however, has been shown to adversely affect reproductive performance, causing changes in fecundity, egg size and larval development (Billard *et al.*, 1981; Campbell *et al.*, 1994). Capture, confinement and handling stresses have been shown to inhibit ovulation in spawning snook *Centropomus undecimalis* (Bloch) (Wallace *et al.*, 1993) and increase oocyte atresia in red gurnard (Clearwater & Pankhurst, 1997). The association between stress, elevations in plasma F and concomitant depression of plasma T and E_2 levels in fishes (Pickering *et al.*, 1987; Carragher & Pankhurst, 1991) together with observations that exogenous F inhibits reproductive performance (Carragher *et al.*, 1989; Pottinger *et al.*, 1991; Foo & Lam, 1993) has led to the general assumption that F mediates the effects of stress on fish reproduction. Evidence in *H. fossilis* (Sundararaj & Goswami, 1977), goldfish, common carp and snapper (Pankhurst *et al.*, 1995) suggests otherwise. Treatment of follicles with F did not inhibit gonadotropin-induced steroidogenesis in these fishes, and in some cases actually augmented steroidogenesis.

Although the majority of available literature suggests physiological stress negatively affects reproductive processes in teleosts through modified endocrine

function (Pankhurst & Van Der Kraak, 1997), the correlation between modified stress, cortisol and reproductive success is not so clear. What little information is available is confounded by many factors, including differences in species, age, season and type and duration of stress or exogenous cortisol administration. For some species [*i.e. H. fossilis*, goldfish, common carp, yellow perch *Perca havescens* (Mitchill) and goby *Gillichthys mirabilis* Cooper] F appears to have no direct effect at the ovarian level (Sundararaj & Goswami, 1977), and may, as suggested by Pankhurst *et al.* (1995), be mediated by way of factors other than F (*i.e.* ACTH, endorphins and catecholamines).

Despite observed negative effects of F on somatic and hepatic growth in the present study, reproductive output was higher with no observable effects on the eggs or hatching success. It is tempting to speculate that F may be acting as a maturation-inducing agent in channel catfish, as it appears to in *H. fossilis*, but the actual role of F in channel catfish reproduction remains to be determined and merits further investigation. The results of this study demonstrate no causal effects of cortisol on reproductive dysfunction in channel catfish.

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References

Barton, B. A., Schreck, C. B. & Barton, L. D. (1987). Effects of chronic cortisol administration and daily acute stress on growth, physiological conditions, and stress responses in juvenile rainbow trout. *Diseases of Aquatic Organisms* **2,** 173–185.

Billard, R., Bry, C. & Gillet, C. (1981). Stress, environment, and reproduction in teleost fish. In *Stress and Fish* (Pickering, A. D., ed.), pp. 185–208. London: Academic Press.

Campbell, P. M., Pottinger, T. G. & Sumpter, J. P. (1994). Preliminary evidence that chronic confinement stress reduces the quality of gametes produced by brown and rainbow trout. *Aquaculture* **120,** 151–169.

Carragher, J. F. & Pankhurst, N. W. (1991). Sress and reproduction in a commercially important marine fish *Pagrus auratus* (Sparidae). In *Reproductive Physiology of Fish 1991* (Scott, A. P., Sumpter, J. P., Kime, D. E. & Rolfe, M. S., eds), pp. 253–255. Sheffield: FishSymp 91.

Carragher, J. F., Sumpter, J. P., Pottinger, T. G. & Pickering, A. D. (1989). The deleterious effects of cortisol implantation on reproductive function in two species of trout, *Salmo trutta* L. and *Salmo gairdneri* Richardson. *General and Comparative Endocrinology* **76,** 310–321.

Clearwater, S. J. & Pankhurst, N. W. (1997). The response to capture and confinement stress of plasma cortisol, plasma sex steroids and vitellogenic oocytes in the marine teleost, red gurnard. *Journal of Fish Biology* **50,** 429–441.

Cleary, J. J., Pankhurst, N. W. & Battaglene, S. C. (2000). The effect of capture and handling stress on plasma steroid levels and gonadal condition in wild and farmed snapper *Pagrus auratus* (Sparidae). *Journal of the World Aquaculture Society* **31,** 558–562.

Clemens, H. P. & Sneed, K. E. (1957). The spawning behavior of channel catfish *Ictalurus punctatus*. *Special Scientific Report-Fisheries No. 219*. Washington, DC: U.S. Fish and Wildlife Service.

Davis, K. B., Torrance, P., Parker, N. C. & Suttle, M. A. (1985). Growth, body composition and hepatic tyrosine aminotransferase activity in cortisol-fed channel catfish, *Ictalurus punctatus* Rafinesque. *Journal of Fish Biology* **27,** 177–184.

Davis, K. B., Griffin, B. R. & Gray, W. (2003). Effect of dietary cortisol on resistance to infection by Ichthyopthirius and mortality due to channel catfish virus. *Aquaculture* **218,** 121–130.

Foo, J. T. W. & Lam, T. J. (1993). Retardation of ovarian growth and depression of serum steroid levels in the tilapia, *Oreochromis mossambicus*, by cortisol implantation. *Aquaculture* **115,** 133–143.

Freeman, H. C. & Idler, D. R. (1973). Effects of corticosteroids on liver transaminases in two salmonids, the rainbow trout (*Salmo gairdnerii*) and the brook trout (*Salvelinus fontinalis*). *General and Comparative Endocrinology* **20,** 69–75.

Goswami, S. V., Lamba, V. J. & Sundararaj, B. I. (1985). Gonadotrophin-induced oocyte maturation in the catfish, *Heteropneustes fossilis* (Bloch), requires steroidogenesis in both interrenal and ovary. *General and Comparative Endocrinology* **57,** 53–63.

Lamba, V. J., Goswami, S. V. & Sundararaj, B. I. (1983). Circannual and circadian variations in plasma levels of steroids (cortisol, estradiol-17 beta, estrone, and testosterone) correlated with the annual gonadal cycle in the catfish, *Heteropneustes fossilis* (Bloch). *General and Comparative Endocrinology* **50,** 205–225.

Leatherland, J. F. (1999). Stress, cortisol and reproductive dysfunction in salmonids: fact or fallacy? *Bulletin of the European Association of Fish Pathologists* **19,** 254–257.

de Leeuw, R., Goos, H. J. T., Richter, C. J. J. & Eding, E. H. (1985). Pimozide-LHRHa-induced breeding of the African catfish, *Clarias gariepinus* (Burchell). *Aquaculture* **44,** 295–302.

Lidman, U., Dave, G., Johansson-Sjobeck, M.-L., Larsson, A. & Lewander, K. (1979). Metabolic effects of cortisol in the European eel, *Anguilla anguilla* (L.). *Comparative Biochemistry and Physiology* **63,** 339–344.

Manickam, P. & Joy, K. P. (1989). Induction of maturation and ovulation by pimozide-LHRH analogue treatment and resulting high quality egg production in the Asian catfish, *Clarias batrachus* (L.). *Aquaculture* **83,** 193–199.

de Montalembert, G., Jalabert, B. & Bry, C. (1978). Precocious induction of maturation and ovulation in northern pike (*Esox lucius*). *Annales de Biologie animale, Biochimie, Biophysique* **18,** 969–975.

Morales, A. E., García-Rejón, L. & De la Higuera, M. (1990). Influence of handling and/or anaesthesia on stress response in rainbow trout. Effects on liver primary metabolism. *Comparative Biochemistry and Physiology* **95A,** 87–93.

Pankhurst, N. W. (2001). Stress inhibition of reproductive endocrine processes in a natural population of the spiny damselfish *Acanthochromis polyacanthus*. *Marine and Freshwater Research* **52,** 753–761.

Pankhurst, N. W. & Van der Kraak, G. (1997). Effects of stress on reproduction and growth of fish. In *Fish Stress and Health in Aquaculture* (Iwama, G. K., Pickering, A. D., Sumpter, J. P. & Schreck, C. B., eds), pp. 73–93. Cambridge: Cambridge University Press.

Pankhurst, N. W. & Van der Kraak, G. (2000). Evidence that acute stress inhibits ovarian steroidogenesis in rainbow trout *in vivo*, through the action of cortisol. *General and Comparative Endocrinology* **117,** 225–237.

Pankhurst, N. W., Van der Kraak, G. & Peter, R. E. (1995). Evidence that the inhibitory effects of stress on reproduction in teleost fish are not mediated by the action of cortisol on ovarian steroidogenesis. *General and Comparative Endocrinology* **99,** 249–257.

Paxton, R., Gist, D. H. & Umminger, B. L. (1984). Serum cortiol levels in thermally-acclimated goldfish (*Carassius auratus*) and killifish (*Fundulus heteroclitus*): implications in control of hepatic glycogen metabolism. *Comparative Biochemistry and Physiology* **78B,** 813–816.

Pickering, A. D., Pottinger, T. G., Carragher, J. & Sumpter, J. P. (1987). The effects of acute and chronic stress on the levels of reproductive hormones in the plasma of mature male brown trout, *Salmo trutta* L. *General and Comparative Endocrinology* **68,** 249–259.

Pottinger, T. G., Campbell, P. M. & Sumpter, J. P. (1991). Stress-induced disruption of the salmon liver-gonad axis. In *Reproductive Physiology of Fish 1991* (Scott, A. P., Sumpter, J. P., Kime, D. E. & Rolfe, M. S., eds), pp. 114–116. Sheffield: FishSymp 91.

Schreck, C. B., Contreras-Sanchez, W. & Fitzpatrick, M. S. (2001). Effects of stress on fish reproduction, gamete quality, and progeny. *Aquaculture* **197,** 3–24.

Silverstein, J. T. & Small, B. C. (2004). Reproductive physiology. In *Biology and Culture of Channel Catfish* (Tucker, C. S. & Hargreaves, J., eds). Amsterdam: Elsevier Science Publishers (in press).

Silverstein, J. T., Bosworth, B. G. & Wolters, W. R. (1999). Evaluation of dual injection of lhrha and the dopamine receptor antagonist pimozide in cage spawning of channel catfish *Ictalurus punctatus*. *Journal of the World Aquaculture Society* **30,** 263–268.

Small, B. C. (2003). Anesthetic efficacy of metomidate and comparison of plasma cortisol responses to tricaine methanesulfonate, quinaldine and clove oil anesthetized channel catfish *Ictalurus punctatus*. *Aquaculture* **218,** 177–185.

Small, B. C. & Davis, K. B. (2002). Validation of a time-resolved fluoroimmunoassay for measuring plasma cortisol in channel catfish *Ictalurus punctatus*. *Journal of the World Aquaculture Society* **33,** 184–187.

Stacey, N. E., MacKenzie, D. S., Marchant, T. A., Kyle, A. L. & Peter, R. E. (1984). Endocrine changes during natural spawning in the white sucker, *Catostomus commersonii*. 1. Gonadotropin, growth hormone, and thyroid hormones. *General and Comparative Endocrinology* **56,** 333–348.

Storer, J. H. (1967). Starvation and the effects of cortisol in the goldfish (*Cariassius auratus* L.). *Comparative Biochemistry and Physiology* **20,** 939–948.

Sundararaj, B. I. & Goswami, S. V. (1977). Hormonal regulation of *in vivo* and *in vitro* oocyte maturation in the catfish, *Heteropneustes fossilis* (Bloch). *General and Comparative Endocrinology* **32,** 17–28.

Tharakan, B. & Joy, K. P. (1996). Effects of mammalian gonadotropin-releasing hormone analogue, pimozide, and the combination on plasma gonadotropin levels in different seasons and induction of ovulation in female catfish. *Journal of Fish Biology* **48,** 623–632.

Trenzado, C. E., Carrick, T. R. & Pottinger, T. G. (2003). Divergence of endocrine and metabolic responses to stress in two rainbow trout lines selected for differing cortisol responsiveness to stress. *General and Comparative Endocrinology* **133,** 332–340.

Wallace, R. A., Boyle, S. M., Grier, H. J., Selman, K. & Petrino, T. R. (1993). Preliminary observations on oocyte maturation and other aspects of reproductive biology in captive female snook, *Centropomus undecimalis*. *Aquaculture* **116,** 257–273.