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The effects of different photoperiods on body growth, gonadal growth and hypothalamic monoamine content in juvenile *Oreochromis niloticus* (Linnaeus, 1757).

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ABSTRACT

The effects of different photoperiods (12/12; 24/0 and 0/24 Light/Dark) on body growth, gonadal development and monoamine concentration.in the hypothalamus of male and female tilapia, *Oreochromis niloticus,* were studied. Standard body length and total weight were similar in male and female maintained under different photoperiods. The gonadosomatic index (GSI) was higher in female maintained under 0/24 conditions than in 12/12. The concentration of norepinephrine (NE) in the hypothalamus of males kept at 0/24, was higher than the male kept under 12/12 and 24/0. The content of dopamine (DA) in the hypothalamus of males at 24/0 was higher than in all other treated animals. The concentration of serotonin (5-HT) in the hypothalamus of male and female *O. niloticus* showed no statistical differences. The highest DA/NE relationship was observed in males maintained under 24/0 light/dark condition. The 5-HIAA/5-HT ratio in males kept under 24/0 light/dark condition was significantly lower than those maintained at 12/12 and 0/24. The present results suggest that there are sex differences in the neuroendocrine mechanisms regulating gonadal growth in *O. niloticus,* as well as in the participation of the light/dark conditions.

Key words: photoperiod, gonadal development, catecholamines, *Oreochromis niloticus.*

RESUMEN

Se estudio el efecto de tres condiciones de fotoperiodo (12/12; 24/0 y 0/24 l/o) sobre el crecimiento en longitud patrón, peso total, desarrollo gonadal y concentración de monoáminas en el hipotálamo de *Oreochromis niloticus*. Los resultados muestran que no existe diferencia en el crecimiento de la tilapia cuando se somete a diferentes fotoperiodos. Sin embargo, el índice gonadosomático de las hembras expuestas a condiciones de obscuridad continua fue mayor que para aquellas que se encontraban en fotoperiodo de 12/12. La concentración de NE en el hipotálamo de los machos sometidos a obscuridad continua son mayores que para el resto de los peces en otros fotoperiodos. La concentración de DA y la relación DA/NE alcanzó su máximo valor en las tilapias expuestas a condiciones de luz continua. La concentración de 5-HT en el hipotálamo de hembras y machos de *O. niloticus*, no presentó diferencias significativas. La relación 5-HIAA/5-HT en los machos mantenidos bajo condiciones 24/0 l/o fué significativamente menor que la de los animales expuestos a 12/12 y 0/24. Finalmente, los resultados apoyan que existe diferencia sexual y por exposición a los diferentes fotoperiodos en el mecanismo neuroendócrino que regula la maduración sexual de la tilapia.

Palabras clave: Fotoperiodo, desarrollo gonadal, catecolaminas, *Oreochromis niloticus*.

INTRODUCTION

The Nile tilapia, *Oreochromis niloticus*, is the most important species on account of its fast growth rate, adaptability to a wide range of culture conditions and high consumer acceptability. Many of the problems associated with tilapia farming stem from the exceptional mode of reproduction. In addition to being mouth-brooders, these fish mature precociously under certain conditions and energy is derived from growth into reproduction. The reproductive cycles of females within a breeding group are not synchronized, even though each fish may breed up to 12 times in a year (Macintosh and Little, 1995) (Anonymous, 1994).

There is evidence that the monoaminergic system in fishes as in mammals plays a role in the regulation of gonadotropin secretion and gonadal development. Norepinephrine (NE) has been consistently shown to stimulate luteinizing hormone (LH) secretion. Serotonin (5-HT) and dopamine (DA) may play a stimulatory or inhibitory role in the regulation of LH secretion, depending on the steroid environment, while all evidence indicates that g-amino-butyric acid (GABA) plays an inhibitory role (Peter *et al.,* 1991, Kordon *et al.,* 1994).

In teleosts, NE, DA and 5-HT are the most important neurotransmitters regulating gonadotropin secretion (Guerrero *et al.,* 1990; Trudeau *et al.,* 1993a; Senthilkumaran and Joy, 1995). Respect to GtH-I, had been observed that is structurally and functionally comparable to mammalian follicle-stimulating hormone and is the predominant GtH found in the pituitary and blood of fishes whose gonads are undergoing active growth and gametogenesis. In contrast, GtH-II appears similar to luteinizing hormone, predominating during time of final gonadal maturation and spawning.

Studies on the control of gonadotropin secretion in teleosts have shown that GtH-II release is regulated by monoamines in both a stimulatory as well as an inhibitory way (Chang and Peter, 1984; Peter *et al.*, 1986; Somoza and Peter, 1991). NE and 5-HT stimulates GtH-II release, while DA has been shown inhibitory effects. According to Peter *et al.*, (1991), DA has inhibitory effects on gonadotropin secretion by acting directly on gonadotrophs, as well as on gonadotropin-releasing hormone (GnRH) release in the goldfish.

In adult female tilapia hybrids (*Tilapia nilotica* X *Tilapia aurea*) (= *Oreochromis niloticus* X *Oreochromis aureus)* the blockade of dopamine-receptors by pimozide administration did not affect the spontaneous release of inmunoreactive tilapia gonadotropin. The same effect was observed by dopamine depletion induced by reserpine administration. When the dopamine-receptor blockade was followed by the administration of GnRH analogue, the response of the pituitary was considerably augmented and prolonged. Based in their results, the authors conclude that "The fact that reserpine or pimozide can augment the response to the GnRHa is consistent with the hypothesis that a certain catecholamine (probably dopamine) is involved in a gonadotropin-release inhibiting activity in this fish" (Gissis *et al.,* 1988).

Somoza and Peter (1991) demonstrated that 5-HT has a stimulatory effect on gonadotropin secretion and inhibits growth hormone (GH) secretion from goldfish pituitary fragments *in vitro.*

GABA has a stimulatory effect on the secretion of gonadotropin in goldfish (Kah *et al.,* 1991). Such action is not exerted at the level of the gonadotrophs apparently, but may be mediated by direct or indirect GABA influences on GnRH secretion.

Neuropeptides have also been included into the mechanism regulating gonadotropin secretion in teleosts. Neuropeptide Y (NPY) stimulate GtH-II release from dispersed goldfish pituitary cells in static culture, indicating a direct action on gonadotrophs (Peter *et al.,* 1991).

Photoperiod plays a role in the modulation of the mechanisms regulating gonadal functions in several vertebrates (Hoar, 1969; Peter, 1981). Studies on the influence of the light/dark period on fish growth have frequently resulted in variable, complex and confusing data. This could be explained by the multiple ways by which light acts, and by its interaction with other environmental factors, particularly temperature (Okuzawa *et al.*, 1989).

In the minnow, *Phoxinus phoxinus,* maintained under controlled laboratory conditions, a rapid increase in the photoperiod from 8 to 16 h resulted in a greater stimulation of vitellogenesis than when the photoperiod was gradually increased (Scott, 1979). In the rainbow trout, *Salmo gairdneri* (= *Oncorhynchus mykiss*), a decreasing photoperiod is more effective in stimulating gametogenesis than a constant short photoperiod (Billard *et al.*, 1981), while Skarphedinsson *et al.,* (1982) described that long photoperiods stimulate gonadal development.

To our knowledge, there is little information on the interaction of the monoaminergic systems and photoperiod in the regulation of gonadal recrudescence in fish. The pourpose of present study was to analyze the effects of different photoperiods on growth, gonadal recrudescence, monoaminergic concentration and their turnover rate in the hypothalamus of *Oreochromis niloticus*.

MATERIALS AND METHODS

The fish *Oreochromis niloticus* L. were obtained from "El Rodeo", a fish farm in the state of Morelos, Mexico (latitude 18°45′ N, longitude 99°20′ W, at an altitude of 1100 msnm).

The fry (length 1.3 cm and 0.4 g body weight), were transported to the laboratory in polyethylene bags with aeration. The fish were acclimated in 30 liters aquariums (8 animals by aquarium) with aeration, at 25°C on a natural photoperiod for 1 week after they arrived in the laboratory. Fish were fed daily to satiation with trout pellets (50% protein). The experiments were conducted during the months October, November and December.

When the animals were 30 days old, and had a standard length of 1.5 cm and 0.5 g body weight, they were randomly assigned to one of the experimental conditions. Because at this age external differences between males and females are not observed, a gender classification of the animals was not intended. The fish were maintained for three months in:

A. 12 h light/12 h dark condition (lights on from 08:00 to 20:00 h) (control group).

B. 24 h light condition, and

C. 24 h dark condition.

Photoperiod was set with a 40W daylight fluorescent lamp connected to an electric timer; water temperatures were maintained to the nearest 1.0°C by either a thermostatically regulated heater. Circulating filtered water was used in all aquarium.

Autopsy procedure. At the end of the experiment, the fish were measured for standard length (S.L.) to the nearest mm and weighed (gross weight) to the nearest g, and sacrificed by decapitation, between 10:00 and 13:00 h. The hypothalami were immediately removed, dissected and kept at -70°C until the content of catecholamines was measured by High Performance Liquid Chromatography (HPLC). The gonads were removed and weighed, and the gonadosomatic index (GSI=gonadal weight/body weight x 100) was calculated.

To know the GSI and catecholaminergic values at the beginning of the experiment, groups of 30-day old male and female tilapia of a standard length of 1.5 cm and 0.5 g body weight, were sacrificed and processed as experimental animals.

Monoamine determination. The hypothalamus of each animal was weighed and homogenized on ice in 300 μl of HPLC grade 0.1 M perchloric acid (Sigma, St. Louis. MO). After centrifugation at 12,000 rpm, at -4 °C for 30 min, the supernatant was filtered through a 0.22-μm pore diameter filter (Millipore, S. A.) and aliquots (30 μl) were directly injected in to the HPLC system. The HPLC system used was a L-250 solvent delivery pump (Perkin Elmer Co, Norwalk, CT, USA) a six-port injection valve (7125 model, Rheodyne, Cotati, CA, USA) with a 20 μl loop. Separation of catecholamines was achieved using Pecocil C18 10-μm cartridges (18 cm x 5 mm I.D.) from Perking Elmer. The detection system consisted of an amperometric detector Model LC-4C (Bioanalytical systems Inc., West Lafayatte, IN, USA) with a dual glassy carbon working electrode and a integrator PE model 1020 (Perkin Elmer Co., Norwalk, CT, USA). The operation potential was set at +0.85 V against the $Ag/AgCl_2$ reference electrode, and the detector sensibility was 10 nA. Mobile phase was prepared according to Domínguez-González, (1998). The flow rate was set at 1.2 ml/min. The standards for norepinephrine ((-)-Artenerol free base), 4-Hydroxy-3-MetoxyphenylGlycol (MHPG), 3-Hydroxy Tiramine hidroxyindole (DA), 3,4-Dihydroxy-phenyl acetic Acid (DOPAC), serotonin and 5-hydroxyindole -3-acetic acid (5-HIAA), were obtained from Sigma (St. Louis. MO). The stock solutions were prepared in 0.1N-perchloric acid, and the working solutions were prepared fresh every day. Assay sensitivity for each compound was 100 pg. The concentrations of the biogenic amines were expressed as ng/mg fresh tissue weight. The equipment was calibrated by the external standard method, using the chromatogram peak's area resulting from the three calibration points (2.0, 1.0 and 0.5 ng), the results were fitted by ordinary least squares regression and the values of coefficient of determination obtained were at least 0.95 for each substance. The values of the biologic samples were within the range of calibration.

The 5-HIAA/5-HT ratio was taken into account as a expression of amine turnover, or as an expression of the activity of the serotoninergic neurone suggested by Shannon *et al.,* (1986) and Kerdelhué *et al.,* (1989). The DA/NE ratio was used as an index of DA conversion to NE (Guerrero *et al.*, 1990).

Sex differences in body weight and standard length, gonadal weight, monoaminergic concentration and turnover rate expressed as mean ± SEM, were analyzed by Kruskal-Wallis test. A $p \leq 0.05$ was accepted as significative.

RESULTS

In 30 days old animals acclimated under natural conditions, the hypothalamic NE concentration in males was

Table 1. Standard length, body weight, GSI and concentration of norepinephrine, dopamine, serotonin (mean ± SEM) of *Oreochromis niloticus* males and females at 30 days old.

Sex	n	Standard lenght (cm)	Body weight (g)	NE (ng/mg tissue)	DA (ng/mg tissue)	5-HT (ng/mg tissue)	GSI
Males	5	1.5±0.1	0.5±0.0	2.4±0.31	0.5±0.09	2.0±0.34	0.25±0.03
Females	5	1.5±0.1	0.5±0.0	1.3±0.32*	0.4±0.09	1.1±0.34	0.25±0.03

*$p < 0.05$ vs. males

higher than in females. Significative differences in standard length, body weigth, DA and 5-HT concentrations and GSI between males and females animals, were not observed (Table 1).

In control group (12/12 l/d conditions), the GSI increased twice in males and three times in females, in comparison with those animals killed at the begining of the experiment. Such increment in gonadal index was accomplished without changes in monoamines concentrations in the hypothalamus of the males, while in the females a significant increase in NE and 5-HT hypothalamic concentrations, were observed (Tables 1 and 2).

No significative differences in body weight, standard body length and gonadal weight were observed between male and female tilapias kept in light/dark photoperiods. In comparison with control fish kept under 12/12 light/dark condition~~s,~~ the GSI in fish kept under 0/24 or 24/0 l/d conditions was higher; significative differences were observed only in those animals maintained under 0/24 l/d conditions, (Table 2). The GSI was not affected by the photoperiod in males.

The concentration of NE in the hypothalamus of males kept at 0/24, was higher than in males under 12/12 and 24/0 conditions, while the concentration of DA was higher in animals kept at 24/0. Significative differences in 5-HT were not observed (Table 3). The levels of MHPG and DOPAC were below the sensitivity level of the method (100 pg).

Significative differences in NE, DA and 5-HT concentration in the hypothalamus of females tilapia, were not observed (Table 3).

The DA/NE relationship was always higher in male than in female animals, and the highest relationship was observed in males maintained under 24/0 light/dark regimen (Table 3).

The 5-HIAA/5-HT ratio in males maintained in a 24/0 l/d conditions was significantly lower than males at 12/12 or 0/24 l/d (Fig. 1).

DISCUSSION

The differences in the GSI observed in males between the begining and the end of the experiment was accomplished

Table 2. Standard length, body weight, gonadal weight and GSI (mean ± SEM) of *Oreochromis niloticus* males and females kept in different photoperiod regimens for three months.

Light/dark	Sex	n	Standard length (cm)	Body weight (g)	Gonadal weight (mg)	GSI
12/12	males	23	7.68±0.33	15.1±1.78	66±14	0.45±0.11
24/0	males	23	7.18±0.43	12.8±2.08	96±31	0.48±0.09
0/24	males	19	7.23±0.43	14.0±2.16	74±18	0.42±0.07
12/12	females	11	6.70±0.65	10.2±2.83	184±119	0.81±0.39
24/0	females	8	7.01±0.62	11.9±2.67	293±111	1.69±0.53
0/24	females	12	6.79±0.40	10.8±1.73	409±126	2.84±0.77*

* $p<0.01$ vs. females kept to 12/12

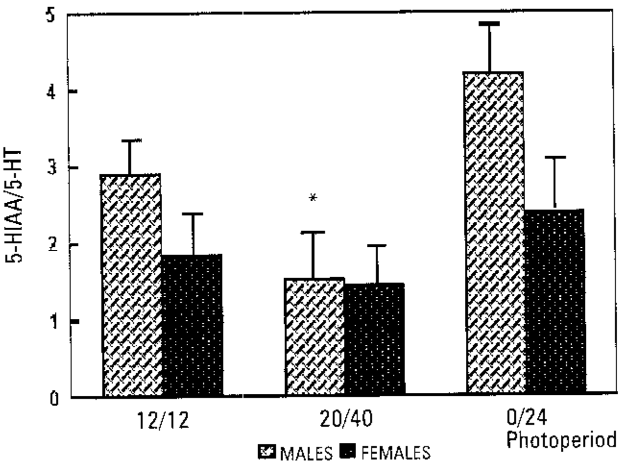
Table 3. Concentration of norepinephrine, dopamine, serotonin and DA/NE (mean ± SEM) in the hypothalamus of *Oreochromis niloticus* maintained at different photoperiod regimens for three months.

Light/dark	Sex	n	Norepinephrine ng/mg tissue	Dopamine ng/mg tissue	Serotonin ng/mg tissue	DA/NE (%)
12/12	males	22	2.60±0.43	0.55±0.19	2.51±0.46	0.34±0.12
24/0	males	21	2.60±0.52	2.20±0.31*	2.69±0.46	2.33±1.13 +
0/24	males	19	4.62±0.72 ◆	0.70±0.20	1.96±0.37	0.28±0.14
12/12	females	9	4.10±1.23	0.53±0.20	2.08±0.67	0.10±0.02
24/0	females	6	2.93±0.96	0.27±0.11	2.31±0.74	0.14±0.04
0/24	females	12	4.95±0.95	0.57±0.19	2.40±0.68	0.15±0.04

◆$p<0.05$ vs. 12/12 and 24/0; * $p < 0.05$ vs. 12/12 and 0/24; + $p < 0.1$ vs. 12/12 and 0/24

without changes in monoamines in the hypothalamus, while in the female the same response included a high increase in NE and 5-HT concentrations. Such sex differences could be explained by disparities in the neuroendocrine mechanisms regulating gonadotropin secretion. Such differences have been described in mammals, but to our knowledge there is not information in fishes (Kordon *et al.*, 1994).

In vertebrates, including fish, the temperature and photoperiod are the most important factors regulating reproductive activity. In most spring and summer spawners, increasing water temperature induces vitellogenesis and spawning, while shortening of day-length is important for maturation in autumn and winter spawners (Peter and Crim, 1979; Lam, 1983; Okuzawa *et al.*, 1989). Photothermal conditions have been reported to influence the contents and activity of monoamines and monoamine oxidase (MAO) activity in *C. punctatus* (Khan and Joy, 1988) and hypothalamic serotonin and monoamine oxidase (MAO) activity in *Carassius auratus* (Olcese and de Vlaming, 1980).



* $p < 0.05$ vs 12/12 and 0/24

Fig. 1. The activity of serotonin neurons in males and females (mean ± SEM) in the hypothalamus of *Oreochromis niloticus* maintained at different photoperiod regimens for three months. (* $p < 0.05$ vs. 12/12 and 0/24).

There is evidence that during the spawning period the tilapia´s males built the nest in the bank of the lagoons, where there is more light available, while the females remain the depth. The sex differences in the increment of gonadal development observed in males and females maintained under external light/dark conditions, could be explained by the unknown changes that the animals present when they are in natural conditions.

In the present study, the concentration of catecholamines measured in the hypothalamus of *Oreochromis niloticus* were similar to those measured in *Cyprinus carpio* (Abo and Hanke, 1981), *Heteropneustes fossilis* (Senthilkumaran and Joy, 1993, 1995), *Oncorhynchus mykiss* (Saligaut *et al.*, 1992), *Pygocentrus notatus* (Guerrero *et al.*, 1990).

The present results differ from those reported by Guerrero *et al.*, (1990) in *Pygocentrus notatus;* Chang and Peter (1984), Trudeau *et al.*, (1993b) in *Carassius auratus*, and Senthilkumaran and Joy, (1993) in *Heteropneustes fossilis*, who described changes in catecholaminergic concentration in the hypothalamus related to gonadal development. Such differences could be explained on the basis of the disparity in reproductive periods between *Oreochromis niloticus*, a precocious reproducer, and *Carassius auratus, Pygocentrus notatus* and *Heteropneustes fossilis*, which have an annual reproductive cycle (Chang and Peter 1984; Guerrero, *et al.*, 1990; Trudeau *et al.*, 1993b and Senthilkumaran and Joy, 1993).

In male tilapia, significant changes in the GSI compared with the start group were not evident, however the concentration of NE and 5-HT in the hypothalamus increased significantly. This lack of response of the male gonad can not be explained by a lack of gonadotropin receptors in the testis, since human chorionic gonadotropin (hCG) administration (30 IU) induced a significant increase in the weight of the gonads (unpublished observation). It is possible, therefore, that at this age the male hypothalamic-pituitary complex is not able to increase GnRH secretion following the increase in NE and 5-HT concentration. Besides, when the males were maintained under conditions of continuos light the DA concentration was highest, however, their metabolite was not register, this results suggests that the dopaminergic neurons activity is lower and that DA/NE ratio is higher in 24/0 than in 12/12 and 0/24 conditions (Table 3) on one hand, and the norepinephrine and serotonin concentration could be play a combined effect with dopamine. Other factors, possibly endogenous, may play a role during this period to influence gonadal growth. This results are supported by De Leeuw *et al.* (1985), in African catfish who suggested that a possible mechanism for sex steroid negative feedback on the brain-pituitary axis is that estrogens are converted to catecholestrogens, which then in turn compete with dopamine for catechol-O-methyl-transferase (COMT), leading to decreased dopamine degradation and increased inhibitory effects on GtH-II secretion.

The effects of the photoperiods observed in present study may be mediated by neurotransmitters other than catecholamines, such as NPY, catecholestrogen, GABA. Peng *et al.*, (1993) demonstrated that in the goldfish, the gNPY stimulates both GH and GtH-II secretions both *in vitro* and *in vivo*. De Leeuw *et al.*, (1987) have suggested a possible mechanism for sex steroid negative feedback on the brain-pituitary axis by which estrogen is converted to catecholestrogens which in turn compete with DA for catechol-o-methyltransferase, leading to a decrease in DA degradation, increasing it is inhibitory effects on GtH-II secretion.

According to Guerrero *et al.* (1990), a decrease in amine concentration reflects an increase in neurotransmission; while an increase in amine level indicates lower neural activity. Then, the increase in DA content with DOPAC concentration below the sensitivity of the method, observed in the hypothalamus of male tilapias kept under 24/0, may indicate a decrease in dopaminergic transmission at this age and this conditions. The present results show that there are sex differences in the response of tilapia to various photoperiods on GSI and gonadal weight, being females more sensitive. Such sex differences do not seem to be related to catecholaminergic and serotoninergic hypothalamic systems, since the DA/NE relationship and serotoninergic ratio were similar in females in the spite of the photoperiods. However in males both neural parameters showed significant differences in concentrations under the various regimens, without effects on gonadal development.

DA has inhibitory effects on gonadotropin secretion by acting directly on gonadotrophs. This effect on GtH-II release is effective within seconds of the exposure of pituitary cells to DA or the non-specific DA-agonist apomorphine (Peter *et al.*, 1986; Peter *et al.*, 1991). Besides, GtH-II secretion is also under the control of an inhibitory hormone (Peter *et al.* 1988), this release-inhibitory hormone, which is also produced in the hypothalamus, has been identified as dopamine. Treatment with antagonists of dopamine, like pimozide or domperidone, together with injections of LHRHa, leads to an enhanced release of GtH when compared with LHRHa alone, thus allowing for the dosage of LHRHa and the risks of excessive stimulation to be minimized (Bromage, 1995).

In conclusion, the present results suggest that there are sex differences in the neuroendocrine mechanisms regulating gonadal growth in *Oreochromis niloticus*, as well as in the participation of the light/dark conditions, being females more sensitive.

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