Research Article

Role of Some Steroidogenic Hormones in Fish Reproduction

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Abstract

Some of the steroidal hormones like testosterone, estradiol, progestogens and corticosteroid play cascading effect on fish reproduction through direct or feedback mechanisms on reproduction. The process of steroidogenesis in the gonads initiates with the synthesis of pregnenolone from cholesterol and its subsequent conversion to progesterone and to androgens further aromatizing to estrogens. Reproductive activities in female fish generally start with low level of sex steroids which gradually increases reaching to the peak level at the time of vitellogenesis and which declines with concomitant increase in 17α, 20β-dihydroxy, 4-pregnen-3-one during the oocyte maturation and ovulation. Gamete maturation in fish reproduction process is regulated by a progestational steroid (the maturation-inducing hormone, MIH). The synthesis and feedback mechanism of these hormones were reported to differ from one species to another. It was also observed that these differences were also observed within sex and age groups of a species.

Keywords: Testosterone, estradiol, progestogens, corticosteroid, fish reproduction

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Introduction

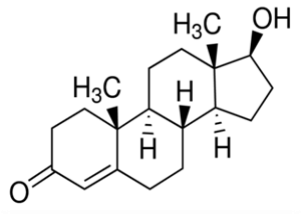
Role of steroidal hormone like testosterone, estradiol, progestogens and corticosteroid on fish reproduction are well recognised and explored. These hormones play a cascading effect through direct or feedback mechanisms on the reproductive functions in the fishes. Fish testes synthesize the androgenic hormones, testosterone (T), androstenedione and 11-ketotestosterone (11-KT) of which the role of T and 11-KT on spermatogenic process, gamete maturation, development of secondary sexual characters and induction of reproductive behaviour are well documented [1]. Testosterone especially 11-ketotestosterone has effect on spermatogenetic process like spermatogonial multiplication and spermatocyte formation in fishes. Steroidal hormones and their metabolites released in water act as sex pheromone in attracting opposite sex and affect sexual behaviour [2]. Testosterone is equally important in female specimens as precursor of estrogenic hormone biosynthesis influencing their female reproductive processes. Association of estrogenic hormones with reproductive cycle by means of coordinating the female reproductive efforts to yield maximum success is a classic model known for reproduction system wherein ova production, steroid hormones and sexual behaviors come together [3]. The 17β-estradiol (E2) produced from testosterone leads to the production of vitellogenin, a yolk pre-cursor, which are further deposited in the oocyte through vitellogenesis. Oocyte maturation, which occurs prior to ovulation, is a prerequisite for successful fertilization consisting of germinal vesicle breakdown (GVBD), chromosome condensation, meiotic spindle assembly and formation of the first polar body. Studies have revealed the regulation of oocyte maturation in fish by three mediators viz. gonadotropin (GTH; luteinizing hormone, LH), maturation-inducing hormone (MIH) and maturation-promoting factor (MPF) [4]. The progestogen, 17α, 20β-dihydroxy-4-pregnen-3-one (DHP) has been found to act as MIH in most of the fishes studied. Another groups of steroidal hormones, the corticosteroids, normally related to stress, plays a regulatory role in many important physiological processes and elevated plasma cortisol levels have been reported to have adverse impact on important for aquaculture traits such as growth, disease resistance, reproductive process etc.

Steroidogenic Process

Androgen: Testosterone

The process of steroidogenesis in the gonads initiates with the synthesis of pregnenolone from cholesterol and its subsequent conversion to progesterone and to androgens which are further aromatized to estrogens [5]. Borg [6] defined androgens as hormones that stimulate masculine traits, like differentiation of reproductive organs into the

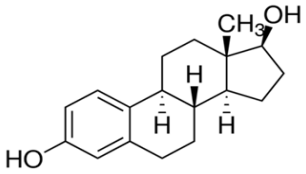
male direction, spermatogenesis, secondary sexual characters and reproductive behaviour. The hormonal pathway in most of the male teleost involves quiescence, spermatogenesis and spermiation [7]. The classical function of fish androgens such as testosterone (T) is to control the development and function of both male and female reproductive systems [8]. Androgen synthesis takes place in the Leydig cells stimulated by LH and FSH but the pattern is more complicated in fish due to cross-activation of FSH receptor by LH and the potent steroidogenic activity of both gonadotropins [5]. The type of androgen synthesized depends upon the species and developmental stage of the individual [9]. In most teleost, 11-KT and T is the main functional androgenic steroid hormone [1]. These hormones are also present in female even though the role of T in female has not been clear other than its effect in maintaining the release and surge of GtHs in *Cyprinus carpio* [10], goldfish [11], *Rutilus rutilus* [12] and Chinook salmon [13]. The specific function of T in fish as common precursor of 17β-estradiol in female and 11-KT in male with key physiological roles in gametogenesis [6, 14]. Testosterone level present both in female and in male increased during gonadal development in three species of sturgeon [15].



Testosterone

Estrogen: Estradiol

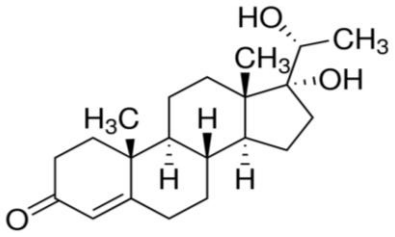
Reproductive success is always associated with timing the steroidal hormones with the reproductive cycles together with ova production and sexual behaviours to maximize success rate in order to coordinate the female reproductive process [3]. Reproductive activities in female fish generally start with a low level of sex steroids especially 17β-estradiol during previtellogenesis, which gradually increases reaching to the peak level at the time of vitellogenesis and declines with concomitant increase in DHP during the oocyte maturation and ovulation. Among the estrogens groups, 17β-estradiol (E2) controls the in female fish, while DHP controls the oocyte maturation, ovulation and spawning. Circulating E2 regulates the expression of vitellogenin (VTG) genes in the hepatocytes, which result in the synthesis of several closely related VTG proteins. Vitellogenin is a glycolipophosphoprotein containing about 20% lipid, mainly phospholipids, triglycerides and cholesterol. The source of proteins for chorion synthesis in the liver, follows a similar pattern under the stimulation of estradiol and are transported into the oocyte for the formation of the vitelline membrane or chorion [16, 17].



β-Estradiol

Gamete maturation is one of the most important stages in fish reproduction process regulated by a progestational steroid (the maturation-inducing hormone, MIH) besides two other mediators' viz. luteinising hormone (LH) and maturational promoting factor (MPF) [18-20]. In cyprinids, 17α, 20β-dihydroxy, 4-pregnen-3-one (DHP) is known as the main maturation-inducing hormone responsible for triggering final maturation of oocyte and resumption of meiosis after second meiotic arrest [21, 22]. It is known for the initiation of germ cell meiosis and follicular maturation and ovulation in a female while initiates the meiotic division of spermatogonia and controls the spermatozoa maturation and spermiation in male [23]. Immediately prior to oocyte maturation, there occurs a dramatic shift in the steroidogenic pathway from E2 to DHP in fish ovarian follicles. The type of steroid hormone produced by switching during ovarian development is likely to be primarily regulated by changes in the abundance of individual steroidogenic enzymes in developing ovarian follicles [4]. In the female, MIH activates MPF, triggering all changes associated with oocyte maturation and encompasses series of steps like germinal vesicle breakdown (GVBD), chromosome condensation and spindle formation. Similarly, in male, MIH activates the synthesis of T to 11-KT from interstitial cell and initiates spermatogenesis, sperm maturation. In induced spawn carp using pituitary extract, only a marginal decline in the level of circulating estradiol was noted during oocyte maturation simultaneous

with the dramatic surge of DHP followed by returned of estradiol concentration to the previous high level within a few hours [21].



17α, 20β-DHP

Synthesis and Feedback Mechanism

Many species including cyprinids, salmonids, silurids and perciforms have documented negative feedback by sex steroid [24-26]. However, there are also reports for a positive feedback by sex steroids in juvenile fish on LH content and release [27]. The mechanisms mediating these effects are likely to be extremely complex and can be caused by direct effects of steroids at the pituitary or the hypothalamic levels with both the regions containing a high density of estrogen and androgen receptors. This complexity is further increased by the well-known fact that the fish brain has a high capacity to convert aromatizable androgens into estrogens modulated by influencing the activity of the neuronal systems of sexual steroids [28]. Steroidal feedback released from gonads can regulate the production and release of FSH and LH although the effect (positive or negative) either varies with the gonadal phase of reproductive development operating indirectly through certain hypothalamic nuclei, or directly on the pituitary cells [23]. The presence of extra-pituitary gonadotropins from the oocytes of the gilthead sea bream [29]; brain of tilapia [30] and *Cichlasoma dimerus* [31]; testis and ovary of catfish [32] negated the control of reproduction by the restricted hypothalamus and pituitary endocrine.

Unbalanced production of androgen might limit the stimulation of germ cell proliferation at the testicular level arresting early puberty in male sea bass [33]. Ching-Fong and Mei-Ru [34] observed an increased level of sex steroids (T and E2) during the developmental stages and annual spawning cycle in adult male and juvenile common carp with higher level and early detection of T level in larval carp during the spawning season in juvenile fish. Roy *et al.,* [35] observed a significant changes in T level during the annual reproductive cycle of *Clarias batrachus* except post spawning phase whereas E2 show diurnal rhythm only during preparatory and pre-spawning phases. The plasma steroid level of T and E2 during different physiological gonadal changes and reproduction cycle shows specific alterations and high correlation in the cyprinid fish, the chub, *Leuciscus cephalus* [36], in both male and female of Indian major carp, *Labeo rohita* [37] and longspine scraper, *Capoeta trutta* (Heckel, 1843) [38]. Serum level of T and E2 in male and female giant sturgeon *Huso huso*, Russian sturgeon *Acipenser gueldenstaedtii* and stellate sturgeon *Acipenser stellatus* at different stages of gonadal maturity and after final maturation induced by hormonal treatment were found with distinct increased in serum steroid concentrations during gonadal development and high E2 levels in maturing female [15]. Endogenous E2 levels vary across the reproductive cycle in live-bearing poeciliid (*Xiphophorus nigrensis*) [39]. Ismail *et al.,* [40] investigated the annual gonadal hormonal profile of wild matured mahseer of 29 males and 23 female and observed correlated changes of reproductive hormones E2, T with the maturation of the ovary and testes. Berlinsky and Specker [41] reported a significant increased in serum T and E2 in wild striped bass, *Morone saxatilis* during the vitellogenic phase and DHP as the maturation-inducing hormone. Changes in gonadal development concentrations of plasma steroid hormones (T, E2, DHP) in male and female wild Mediterranean amberjack (*Seriola dumerili*) provided information on the relation between plasma sex steroid profiles and gonadal development for the first time in the species [42]. In *Cyprinus carpio carpio*, even though plasma T showed no significant differences at different stages of ovarian development, E2 decreased gradually during the same times and reached a minimum value at the spawning season with highest recorded at tertiary vitellogenesis stage while DHP occurred maximum level with oocyte maturation stage [43]. Plasma T and E2 can be used as secondary predictor index for the initiation and timing of spawning period whereas these hormones along with DHP correlate and indicates gonadal development of fish [44].

Corticosteroid in Fish Reproduction

In teleost, the corticosteroid is mainly synthesized in the inter-renal tissue embedded inside the anterior part of the kidney. Corticosteroids concentrations isolated from fish blood are depended based upon the species, sex and reproductive status [45]. As a determinant indicator of roles in fish reproduction, the plasma levels of corticosteroid

vary greatly throughout the reproductive cycle. In both sexes, some fish species exhibit a high surge in plasma cortisol levels during the pre-spawning or spawning period, like in the plaice, *Pleuronectes platessa* [46], two species of trout, *Salmo trutta* L. and *Salmo gairdneri* [47], rainbow trout, *Oncorhynchus mykiss* [48], perch, *Perca fluviatilis* [49] and masu salmon, *Oncorhynchus masou* [50] more often higher than the immature fishes which indicates its role in reproduction [45]. Seasonal changes in plasma cortisol levels in male rainbow trout suggest that the elevated plasma levels of cortisol may have certain physiological functions in the reproduction other than stresses [51]. Shankar and Kulkarni [52] reported an increased in serum cortisol level in the freshwater fish *Notopterus notopterus* during breeding phase and suggested the requirement of this hormone and the role it plays during ovarian growth and vitellogenesis.

Conclusion

The review incorporates information about steroidogenic changes associated with gonadal maturations and reproductive stages, which are species specific. Most of the studies were found to be carried out in a single age group and comparative studies on different age groups and sex were lacking for a single species. Hormonal validation was mostly carried out in blood plasma or serum samples and collective study on blood and target tissue are scanty. In addition, most of the studies were mainly focus on growth and breeding performance but information on hormonal profiling between different age groups and sex has been lacking. Hence, future study toward steroidal hormones in different age groups and sex of a species could be initiated for some commercially important species.

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