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ADVANCES IN REPRODUCTIVE ENDOCRINOLOGY ON TELEOST CLARIAS BATRACHUS (LINNAEUS)

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ABSTRACT:

Reproductive system in teleost Clarias batrachus (Linnaeus) is orchestrated by complex network of nervous, endocrine system and environmental factors during gonadal growth as well as recrudescence. Lot of new information on the molecular mechanism of gonadal development have been obtained over several decades which are evident from significant number of scientific publications pertaining to reproductive biology and neuroendocrine research in catfish. This review aims to synthesize key findings and compile highly relevant aspects on how catfish can offer insight into fundamental mechanisms of all the areas of reproduction and its neuroendocrine regulation, from gametogenesis to spawning including seasonal reproductive cycle. In addition, the state-of-knowledge surrounding gonadal development and neuroendocrine control of gonadal sex differentiation in catfish are comprehensively summarized in comparison with other fish models. As endocrine system regulates gonadal development, growth, and reproduction, hence, fish endocrinology has been the focus of various studies for basic understanding of these physiological events and for advances in aquaculture. Over the decades, many fish species have been used to study various aspects of endocrinology in vivo. Several genome editing and transgenesis studies have also been done to understand the complexity of endocrine functions and regulation in fish. This review summarizes the present knowledge and key evidence on catfish being used as research models for studying fish endocrinology. To begin with, key evidence of neuroendocrine control of gonadal development and sex determination/differentiation are discussed followed by understanding of steroidogenic regulation in catfish. Key findings on how catfish models have been used to understand gene regulation and function using gene knock

out/transient gene knock down through short interfering RNA (siRNA) are listed. Furthermore, wherever necessary the research findings from catfish models were compared with other teleostean counterparts for comprehensive review of literature.

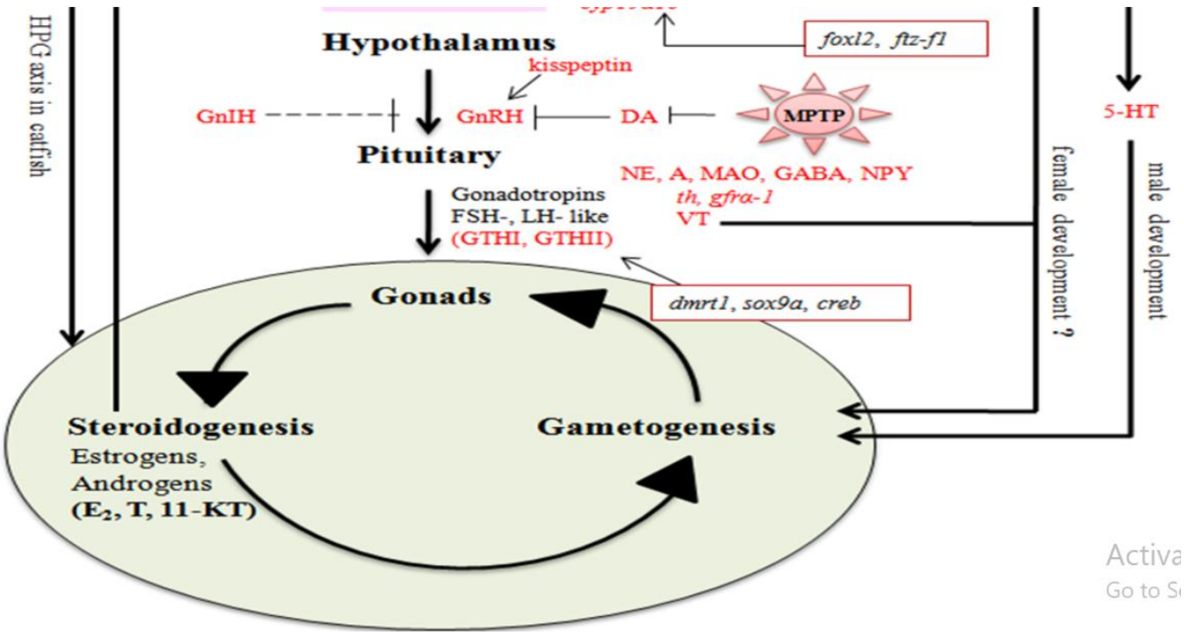
INTRODUCTION:

GTH, a glycoprotein hormone, stimulates gonadal maturation and development in most of the vertebrates. In many t teleost Clarias batrachus (Linnaeus) , two types of GTHs, GTH-I (FSH- like) and GTH-II (LH-like) have been characterized [26,27,28,29,30] which are equipotent in stimulating E2 production, hence, stimulating steroid synthesis, although localized in separate cells. However, in primitive teleosts such as eel [31,32] and catfish [33,34,35], only a single GTH (GTH-II) has been characterized which is known to regulate the entire process of gonadal development. The possibilities implicating about the absence of FSH-like GTH-I in catfish has been attributed by Joy [36]. The African catfish FSH-R responded clearly to the highly purified African catfish LH when expressed in a mammalian cell line [37] and the channel catfish FSH-R responded to human chorionic gonadotropin (hCG) although the response was weaker than when challenged with human FSH [38,39].

Furthermore, GnRH's role in the stimulation of LH synthesis in catfish has been reviewed by Schulz et al. In line with this, it has been reported that the pituitary gonadotrophs are known to be activated strongly during initiation of spermatogenesis in the African catfish, Clarias gariepinus [41].

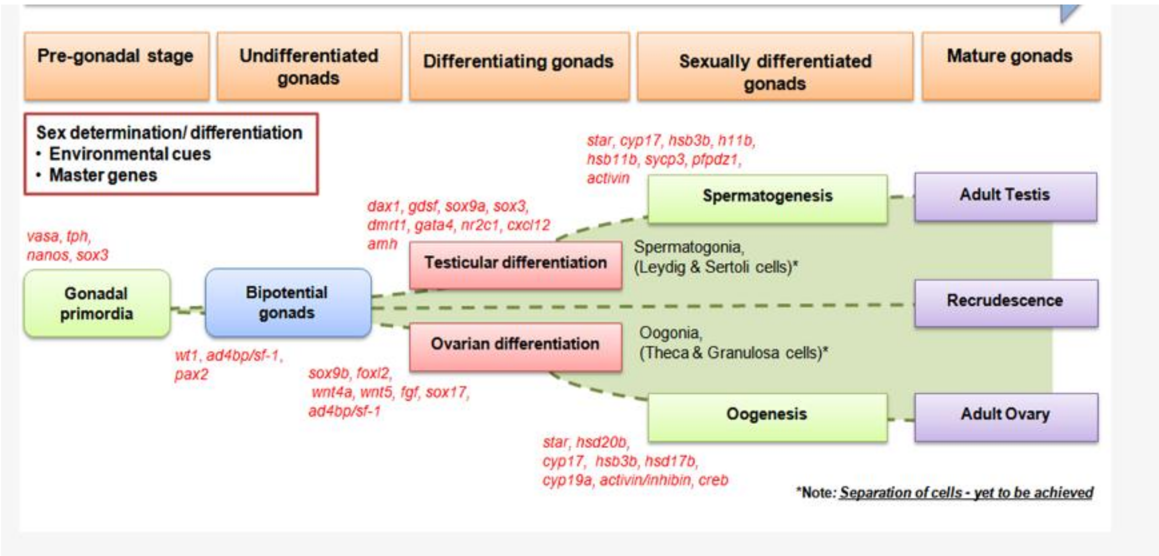
In addition, seasonal cyclicity of GTH-II has been demonstrated in various catfish species with standardized protocols as well as comparison with nuclear E2 receptor binding [42,43]. However, since there is no distinction of GTH-I and GTH-II, it is referred as GTH-II or LH in these catfish species.

DISCUSSION:



Studies on pubertal development have been conducted in various fish species including in teleost Clarias batrachus suggesting that sex steroids regulate the development of the HHG axis in teleost. Furthermore, its correlation with testicular function has been reviewed by Blázquez and Trudeau [91]. Gonadectomy during later stages of gonadal recrudescence increases LH secretion in several teleost including the African catfish and the Indian catfish which can be restored by treatment with testosterone/E2]. Ovarian aromatase, cyp19a1a, is known to be involved in conversion of androgens to estrogens and is also known for its role in sex reversal [96]. However, teleost also produce brain aromatase, encoded by cyp19a1b which synthesize high amounts of neuroestrogens [97] plausibly along with the action of its related transcription factors such as ftzf1 and foxl2 [98] as seen in catfish, leading to "Brain sex differentiation". In teleost, most of the earlier reports tend to suggest that gonadal sex differentiation drives brain sex differentiation which has been reviewed extensively by Senthilkumaran et al. [99]. Nevertheless, the influence of brain serotonergic system on gonadal sex development in catfish is well demonstrated indicating the existence of "Brain sex differentiation" in teleosts including catfish. However, yet the brain sex changes are questioned as a "consequence" or "cause" to gonadal sex determination/differentiation [44,47,89].

Additionally, teleost models including in teleost Clarias batrachus have been used extensively to study neurotoxicity [100] and neuroendocrine disruption [101]. Neurotoxicity studies are important to identify promising neuroprotective agents for example, ascorbic acid for Al-induced neurotoxicity which was demonstrated using C. gariepinus [102]. In line with this, Mamta and Senthilkumaran [67] used 1-methyl-1,2,3,6-tetrahydropyridine (MPTP), to demonstrate the interaction of GDNF and DA-ergic system in catfish brain. In addition, controlled release of sex steroids using osmotic pump altered brain GnRH1 and CA-ergic system dimorphically in the African catfish providing insights into the reproductive toxicity of sex steroid analogues during gonadal recrudescence [103]. The schematic representation on neuroendocrine control of reproduction in catfish has been depicted in the



Several genes/factors have been identified in teleost implicating their crucial roles in gametogenesis and gonadal steroidogenesis and most of which are regulated directly/indirectly by pituitary GTHs [137]. Steroidogenesis starts with rate-limiting transport of cholesterol into mitochondria [192] mediated by steroidogenic acute regulatory protein (StAR). StAR gene has been identified and characterized in teleosts, including rainbow trout, the African catfish and medaka [193,194,195]. Enzyme, cyp11a1, is involved in the conversion of cholesterol to pregnenolone, which thereby initiates the whole process of steroidogenesis including production of active steroids like 17α,20β-DP, T, 11-KT and E2 [168,196] via action of several steroidogenic enzymes genes which have been well identified and characterized in many teleost including catfish together with their associated transcription factors as evident from promoter motif analysis of the steroidogenic enzymes which has been reviewed in detail by Rajakumar and Senthilkumaran [169].

In addition to these, over a decade, next generation sequencing (NGS) techniques has been widely utilized for the identification of sex-related candidate genes and genetic markers using catfish models including red tail catfish [197]; These studies have provided a valuable genomic resource for further investigating the genetic basis of sex determination/differentiation and would aid in understanding more about sex-controlled breeding in catfish with a scope to extend this information to other teleost species.

CONCLUSION:

However, in recent years, the field of reverse genetics has been evolving widely with the development of novel genome editing technologies, such as RNA interference (RNAi), zinc finger nucleases (ZFN) and plasmids, morpholinos, Morpholinos, on the other hand, provide better specificity than RNAi (siRNA/shRNA/esiRNA) by decreasing the possibility of catastrophic off-target antisense effects [219], and has been widely used for studies in zebrafish and goldfish [217,218]. However, use of these technologies in catfish model has not been explored due to year long duration for development to maturation. Nevertheless, future studies need to be performed on this line to obtain novel information. In many animal models including catfish, RNA knockdown can be achieved more feasibly using siRNA, shRNA or esiRNA. In this line, In addition, Senthilkumaran [168] compared mammalian and piscine oocyte maturation with a note on sperm maturation citing the involvement of hsd20b vis-à-vis 17α,20β-DP in addition to T and 11-KT [140,222

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