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Back to the basics: Neuroendocrine control of reproduction

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Abstract
Endocrine regulation is vital for the physiological activities of several organisms, including fish. Within aquatic habitats, characterized by volatile conditions, fish depend on a sophisticated endocrine system to uphold homeostasis, control reproduction, and react to environmental stimuli. This article delves into the intriguing realm of endocrine regulation in fish, providing insight into the hormones that control their behavior, growth, and reproduction. The endocrine system in fish has multiple glands, such as the pituitary gland, thyroid gland, and gonads, which collectively generate a wide range of hormones. These hormones function as chemical messengers, circulating through the bloodstream to certain tissues and organs, exerting an impact on physiological processes. The endocrine system plays a crucial role in regulating reproduction in fish, ensuring that spawning episodes are synchronized with environmental conditions. The hypothalamus-pituitary-gonad axis serves as a crucial regulatory route. Fish demonstrate extraordinary adaptations to effectively manage environmental problems through the regulation of their endocrine system. For instance, certain species possess the ability to adapt their physiological functions in accordance with alterations in salinity, temperature, or oxygen levels, thereby showcasing the adaptability of their hormone regulatory systems. The endocrine regulation in fish is a sophisticated and highly developed system that controls multiple aspects of their physiology, growth, and reproduction. Gaining a comprehensive understanding of the complexities of these hormonal interactions is crucial, not only for furthering our understanding of fish biology but also for effectively managing and preserving aquatic environments. As we explore further into the field of fish endocrinology, we gain important knowledge that aids in the sustainable control of fisheries and the conservation of aquatic biodiversity.

Keywords: Endocrine regulation, adaptations, hormonal interactions, hypothalamus-pituitary-gonad axis, environmental cues, behavior

Introduction
According to FAO (2022) [8], recently the worldwide fisheries industry has seen a notable change characterized by the decrease in capture fisheries and the rapid expansion of aquaculture. Capture fisheries, formerly the predominant supplier of seafood, are currently facing a multitude of issues. The depletion of fishery resources has been significantly caused by overfishing, pollution, inadequate management, and climate change. The reduction is apparent in the diminishing landings from marine capture fisheries (SOFIA). With the ongoing increase in the world population, these difficulties become more pronounced, exerting further strain on catch fisheries. However, this provides opportunities for the promotion of culture-based fisheries and aquaculture (Tacon, 2015) [21].

In order to realize the true genetical potential of the fishes in the Indian agro-climatic conditions the knowledge of the reproductive biology and the endocrine regulatory mechanism is pivotal. The breeding behavior of most teleost fishes is characterized by seasonality, with just a small number of species breeding continuously. Seasonal breeders exhibit significant variation in the timing of breeding throughout the year. Freshwater fish in the temperate zone reproduce during the spring and early summer, while salmonids and other species do so in the autumn. Some fish species, such as salmon, reproduce only once during their lifespan. The freshwater eel *Anguilla angulia* reproduces on a biennial basis, with a breeding cycle occurring every 10-14 years. Within the Indian subcontinent, a vast majority of freshwater fish engage in reproduction during the monsoon season, which is marked by exceptionally high quantities of

of rainfall.
The regulation of reproduction in fish through the endocrine system is a captivating and convoluted process that entails a sophisticated interaction between hormones, neurotransmitters, and neuropeptides. Gaining insight into these systems is essential for understanding the reproductive biology of fish. This article offers a comprehensive analysis of the fundamental elements implicated in the endocrine regulation of fish reproduction.

Sexual maturity

Sexual maturation in fish denotes the developmental phase in their life cycle during which they acquire the ability to reproduce (Sabraha *et* al., 2017; Palafox *et al.*, 2022) [17, 13]. The growth of gonads and the ability to produce viable gametes (sperm and eggs) are important components of their reproductive system. The attainment of sexual maturity in fish is subject to variation among species and is modulated by factors such as genetics, environmental conditions, and diet (Rahman and Samat, 2021) [14]. Assessing sexual maturity is crucial for the purposes of fisheries management and aquaculture activities. The L50, which represents the length at which 50% of the population reaches sexual maturity, is a crucial metric for evaluating the reproductive capacity of fish populations (Aruho *et al*., 2018) [3]. The measurement of this distance is a crucial factor in establishing laws on fishing techniques in order to guarantee the sustainable utilization of resources. Sexual maturity is influenced by factors such as age, rate of growth, and hormonal fluctuations (Palafox *et al.*, 2022) [13]. Scientists frequently examine the physiological and morphological alterations linked to sexual maturity in order to gain insights into the reproductive biology of various fish species.
The ovaries and testes undergo cyclic modifications throughout the reproductive cycle of fish, which coordinate the processes of gametogenesis and reproduction. Complex hormonal and neuroendocrine systems control these periodic shifts. There are three distinct phases to the ovarian cycle in fish: the previtellogenic, vitellogenic, and maturational phases that culminate in ovulation (Bhattacharya, 1992) [6]. The ovarian cycle and the development, growth, and reproduction of the gonadal organs are controlled by hormones such as gonadotropins (GtH) (Bhattacharya, 1992; Senthilkumaran & Kar, 2021) [6, 20]. Ovulation, oocyte development, and plasma and ovarian steroid hormone level fluctuations impact female fish (Sang *et al*., 2019) [18]. Once the ovaries and testicles have matured, hormonal regulation allows for the expression of secondary sex traits (Arcand and Benson, 1998) [2]. Processes including oocyte degradation, follicle atresia, and the subsequent formation of testicular tissue are involved in sex transition in some species, such as wrasse (Adolfi *et al*., 2023) [1]. These periodic shifts help keep the species going by coordinating mating and nesting cycles, which in turn helps gametes develop and mature.

Environmental Control of Reproduction

Fish endocrine regulation is greatly influenced by environmental stimuli (Fig. 1). The fish's endocrine system can be influenced by a range of stressors and environmental signals, which can have effects on growth, reproduction, and overall physiology (Won & Borski, 2013; Arcand and Benson, 1998; Weber *et al*., 2019;) [26, 2, 25].

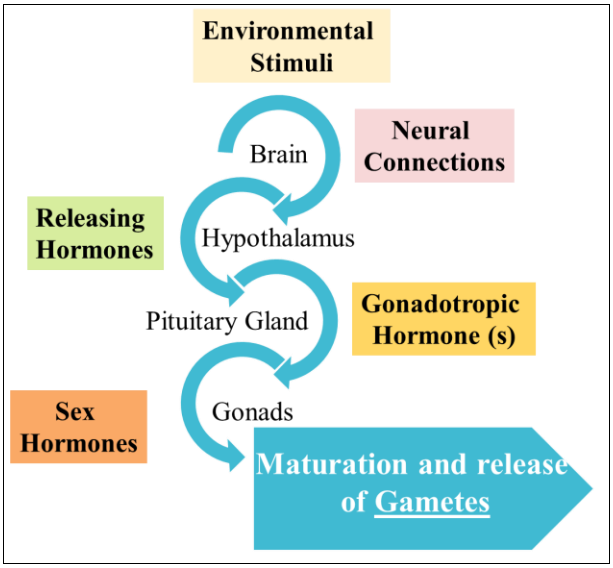

Fig 1: Effect of environmental cues on Endocrine Regulation

Neural events initiate the sequence, whereas subsequent connections are mediated by hormones. The environment provides stimuli, such as day length (photoperiod), temperature, and rainfall, which are detected by sensory receptors. These stimuli generate neural signals that travel to the hypothalamus, located at the base of the brain. In turn, the hypothalamus influences the pituitary gland by releasing chemical messengers called releasing hormones. Induce the pituitary gland to secrete hormones into the bloodstream that specifically target the gonads. The hormones responsible for this process are known as "gonadotropins" and they have a direct impact on the creation of sex steroids in the gonads.

Ovarian and Oocyte maturity stages

Fish ovarian maturation comprises a sequence of stages that can be classified according to macroscopic and histological features (Dihn *et al.*, 2022; Milton *et al.*, 2018; Farhana & Ohtomi 2013; Tan-Fermin & Pudadera, 1989) [7, 12, 9, 22]. Although there may be variations according on the fish species, a broad outline of the five stages is as follows:

1. Immature Stage

Marked by the presence of underdeveloped oocytes in the ovaries.
The ovaries exhibit a transparent or pale appearance.

2. Maturing Stage

Oocytes undergo maturation and morphogenesis.
The ovaries display enlarged dimensions and enhanced pigmentation.

3. Mature Stage

Oocytes attain their maximum size and get prepared for ovulation.
The ovaries are swollen and may exhibit a discernible pigmentation.

4. Spawning Stage

Ovulation takes place, resulting in the release of fully developed ova.
The ovaries may exhibit indications of partial or full depletion.

5. Post-spawning (spent) stage

Post-spawning stage: The ovaries undergo atrophy, resulting in decreased size and loss of firmness.

The vascular supply diminishes, resulting in a loss of color.
Following are the steps outlined offer a structural basis for comprehending the ever-changing process of ovarian maturation in fish, which is vital for their reproductive triumph (Selman *et al*., 1993) [19].
During stage I, oocytes are initially found in clusters with other oocytes (Stage IA) and later within a specific follicle (Stage IB), where they undergo significant expansion in size.
During stage II, oocytes can be identified by the presence of cortical alveoli of different sizes, and the vitelline envelope becomes more noticeable.
During stage III, known as vitellogenesis, oocytes begin to include yolk proteins.
Oocytes acquire the ability to undergo oocyte maturation *in vitro* in response to the steroid 17a, 20P-dihydroxy-4-pregnen-3-one (DHP).
During stage IV of oocyte maturation, the oocytes undergo a modest increase in size, become transparent, and their yolk transforms into a non-crystalline state as they complete their last meiotic maturation *in vivo* (and in response to DHP *in vitro*).
During stage V, eggs that are around 0.75 mm in size are released into the ovarian lumen and can be fertilized.

Endocrine Regulation of Oogenesis
Environmental and social stimuli are transmitted to various brain regions via sensory signals, which ultimately reach the hypothalamus. In the absence of the hypophyseal portal system, the nerve fibers of the hypothalamus that regulate the secretion and production of follicle-stimulating hormone (FSH) and luteinizing hormone (LH) are dispersed across the adenohypophysis. Dopamine, which is secreted by the hypothalamus, inhibits the release of LH. FSH and LH bind to their respective receptors in the genitals, which are referred to as FSH-R and LH-R.
In response, reproductive steroid hormones, specifically estradiol 17 (E2) in females, are secreted by the gonads. E2 promotes the development and growth of oogonia as well as the synthesis of egg material. In addition, progestogens include 17, 20-dihydroxy-4-pregnen-3-one (DHP), which aids in the maturation and ensuing expulsion of follicles during ovulation and the initiation of germ cell meiosis.
Following the conclusion of vitellogenesis, the embryo may exhibit a prolonged period of inactivity. Nevertheless, it commences the final maturation process, wherein meiosis is resumed, in reaction to pheromonal, environmental, or social signals. Whether or not dopaminergic inhibition is diminished, the process commences with an increase in gonadotropin-releasing hormone (GnRH). Following this, there is an increase in the level of luteinizing hormone (LH) in the bloodstream.
Upon ligation hormone (LH) binding to its receptors located on the granulosa cells, the ovarian follicle generates DHP (20β-S), which is a maturation-inducing steroid. This steroid initiates the maturation process. The binding of the MIS to its receptors located on the plasma membrane of the oocyte initiates the maturation-promoting factor (MPF) activation pathway. The MPF is a complex that is formed by the newly synthesized cyclin B and the pre-existing cdc2-kinase. GV migration, the process by which the germinal vesicle (GV) advances towards the animal pole, is a defining characteristic of oocyte maturation. In addition, the membrane of the GV undergoes disintegration during the GV breakdown phase (GVBD). The chromosomes then endure condensation, which culminates in the development of a spindle. Following this, the initial polar body is expelled, signifying the culmination of the preliminary meiotic division. Oocytes undergo water absorption and inflation throughout this phase. This is especially evident in marine organisms that lay ova in the pelagic zone. The pressure within the follicle increases, leading to the rupture of the follicular wall and the expulsion (ovulation) of the oocyte into the coelomic cavity or ovarian lumen. Meiosis is inhibited in metaphase II once more. The second meiotic division is delayed, and fertilization of the egg is a prerequisite for the expulsion of the second polar body.

Testicular Cycle
Testicular development in fish follows a sequence of five phases, characterized by noticeable changes in both structure and function (Bhat *et al.*, 2021; Dinh *et al.*, 2022; Truong *et al*., 2022) [5, 7, 24].

Indifferent Stage
At first, the gonadal primordium is undifferentiated and is called the indifferent stage. The gonad has the potential to differentiate into either ovaries or testes.

Differentiation Stage
The gonad undergoes differentiation into testicular tissue in response to genetic and hormonal signals.

Proliferation Stage
Germ cells undergo rapid cell division in the developing testicular tissue, resulting in their proliferation.

Maturation Stage
The testis undergoes maturation, during which germ cells undergo spermatogenesis, resulting in the creation of spermatozoa.

Regression Stage
In certain animals, the testis may undergo regression, reducing in size and activity, either after the reproductive season or in reaction to environmental stimuli, until the subsequent reproductive cycle.
These phases are essential for the reproductive success of fish, as they guarantee the creation of viable sperm for fertilization.

Endocrine Regulation of Spermatogenesis
Each phase of the biological process referred to as spermatogenesis is governed by a distinct set of hormones. The interstitial Leydig cells secrete E2, which regulates the process by which spermatogonia endure mitotic divisions to regenerate germ cells, in response to gonadotropic stimulation, primarily FSH. Spermatogonial stem-cell renewal factor (GSDF), alternatively referred to as gonadal soma-derived growth factor (SRF), is secreted by Sertoli cells upon E2 binding to their receptors. Mitotic proliferation of spermatogonia is induced by this factor. Observations of alterations in the expression of FSH and FSH-Rs in the testis of African catfish (*Clarias gariepinus*) revealed modifications in Sertoli cell proliferation and testicular growth. This indicates that FSH and androgens likely regulate the quantity of Sertoli cells in fish, just as they do in humans. Meiosis is the process by which a subset of spermatogonial germ cells in Japanese eels, in response to gonadotropic stimulation

(*Anguilla japonica*), transform from a cell renewal line to a cell proliferation line. Elevated levels of 11-KT are rapidly secreted from Leydig cells in response to gonadotropins, specifically follicle-stimulating hormone (FSH).

Numerous mediators, including AMH from the Sertoli cell line, insulin-like growth factor I (IGF-I), and activin B, are stimulated by this increase in 11-KT. 11-KT exerts its effect on this spermatogonial line via the positive mediators Activin B and IGF-I, as opposed to the negative mediator AMH. DHP, on the other hand, is an endogenous chemical produced by germ cells that stimulates meiotic division, culminating in the formation of spermatids. Germ cells are subject to both paracrine and autocrine effects induced by this chemical. Anti-DHP serum inhibited the DNA replication and meiosis stimulation induced by 11-KT in eel testes organ culture, demonstrating that DHP is essential for the initiation of meiosis. In addition, portions of the testes formed synaptonemal complexes, and DHP insertion stimulated two meiosis-specific markers, Spo11 and DMC1. The development of sperm into mature spermatozoa is an essential developmental stage. Carbonic anhydrase activation in spermatozoa is facilitated by DHP, which functions as a mediator and drives this maturation process directly. The seminal plasma experiences an increase in pH subsequent to the enzyme activation process. Sediment motility is enhanced due to the elevation in intra-sperm cAMP concentrations induced by the pH increase.

Table 1: Seasonal Spawners and their spawning seasons

Sl. No.	Initiation	Arrest	Species	Reference
1.	March	June	*Mystus seenghala*	Sathyanesan, 1962
2.	April	September	*Tor tor*	Rai, 1967 [15]
3.	June	September	*Clarias batrachus*	Lehri, 1968 [11]
4.	July	September	*Channa punctatus*	Belsare, 1962 [4]
5.	June	August	*Channa gachua*	Khanna and Sanwal, 1971 [10]
6.	April	August	*Rasbora daniconius*	Raizada, 1971 [16]
7.	October	December	*Suchizotharax richardsonii*	Bisht, 1972

Conclusion

- Ecological Health Monitoring: Fish reproduction acts as a biologically significant marker of endocrine disturbance, offering valuable information on the general well-being of aquatic ecosystems (Arcand-Hoy & Benson, 1998) [2].
- Comprehending compensatory growth mechanisms in fish is facilitated by studying their endocrine activity during metabolic phases, which in turn contributes to the improvement of aquaculture practices (Won & Borski, 2013) [26].
- Endocrine factors are crucial in regulating food intake and growth, which are essential for the correct development of organisms (Bertucci et al., 2019).
- Understanding the hormonal control of fish reproduction provides valuable insights into the fundamental mechanisms of hormonal regulation, which in turn helps in the effective management and protection of fisheries. The user's text consists of two references (Bhattacharya, 1992; Nagahamaya, 1994) [6].
- Thyroid hormone is linked to growth and development in numerous teleost species through endocrine regulation (Arcand-Hoy & Benson, 1998) [2].

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