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Impact of shifting abiotic factors in aquaculture on fish breeding and reproduction: a review

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Abstract

The reproductive success of fish is intricately linked to environmental factors, which regulate the hypothalamic-pituitary–gonadal (HPG) axis and influence gonadal development, gamete production, and spawning. Key environmental parameters such as photoperiod, temperature, pH, alkalinity, hardness, dissolved oxygen (DO), turbidity, and nitrogenous compounds (ammonia, nitrate, nitrite) play critical roles in fish reproduction. These factors significantly impact reproductive functions, including gonadal growth and maturation, gamete cell development, hatching rates, and larval survival. Unfortunately, hatchery experts and fish farmers often overlook these parameters, leading to suboptimal seed production and lower-quality fish stocks.

This review discusses the various environmental parameters and their effects on gonadal development and reproductive performance in fish particularly at the molecular level. Understanding these factors can help researchers differentiate the impact of environmental variables from other influences like feed quality and genetic factors, ultimately leading to better management practices in fish breeding and seed production.

Keywords Environment, Gene, Temperature, Breeding, Fish

Introduction

The sex is determined during the embryonic development which is mostly controlled by genetic factors [31, 69]. After sex determination, the gonads are developed like higher animals which produce gametes through the reproduction process. Reproduction is one of the most significant parts of fish biology and enables a species to continue to exist and sustain their population [83, 84]. Mostly fish reproduce sexually resulting in the mixing of genes of the two sexes. The reproduction pattern in fish is diverse like most of them have external or internal fertilization and are annual breeders or produce seeds throughout the year. In order to categorize guilds or ways that bony fish reproduce, Balon [8] divided the species into three main groups: non-guarders, guarders, and bearers.

Fish reproductive cycles are regulated and synchronized by the environmental factors. The common factors include photoperiod, temperature, nutrition, social status, lunar cycle, turbidity, etc. [90]. The environmental factors affect the hypothalamic-pituitary–gonadal axis (HPG) axis which in turn controls the production of hormones necessary for the gonadal development and gamete production [16].

Due to population growth and the exploitation of natural stocks, there has been a shift towards aquaculture production in controlled environments such as ponds

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and tanks. Fish culture primarily relies on high-quality seeds, which depend on the availability of well-grown brooders, typically produced in broodstock ponds. Broodstock is the most critical component in hatcheries since future production hinges on their quality gametes [109]. Environmental factors in the broodstock pond are crucial, and even slight deviations can negatively impact the growth, development, and gamete production of brooders. This, in turn, affects seed production, labor, time, and financial resources. This review discusses the significance of environmental factors in the development of gonads and reproduction in fish, as well as the negative impact on the reproductive process when these factors deviate from normal levels.

Review of literature

In compiling this review, the authors utilized a diverse array of reputable databases and search platforms to gather pertinent literature. The primary sources included Google Scholar, PubMed, bioRxiv, the Directory of Open Access Journals (DOAJ), ScienceDirect, PLOS ONE, MDPI journals, and Frontiers journals. These platforms provided a comprehensive collection of peer-reviewed articles and preprints relevant to the study.

The literature reviewed spans several decades, with a few publications dating from 1972 to 1979. However, the majority of the data originates from studies conducted between 1990 and the present, ensuring that the review encompasses both foundational and contemporary research findings.

To identify relevant studies, the authors employed a series of targeted keywords during their searches. These included combinations such as "fish and physicochemical parameters of water," "fish reproduction and physicochemical parameters of water," "fish gonads and physicochemical parameters of water," "HPG axis and physicochemical parameters of water," "gene expression and physicochemical parameters of water," "photoperiod and fish gonad," "physicochemical parameters of water and gonadal gene expression," "fish reproduction and photoperiod," "fish reproduction and temperature," "fish reproduction and pH," "fish reproduction and alkalinity," "fish reproduction and hardness," "fish reproduction and dissolved oxygen," "fish reproduction and turbidity," "ammonia, nitrate, and nitrite and fish reproduction," "fish reproduction and handling stress," "nutrition and fish reproduction," "toxicants and fish reproduction," and similar combinations focusing on fish gonadal development. This comprehensive keyword strategy ensured the inclusion of a wide range of studies pertinent to the environmental factors affecting fish reproduction and gonadal development.

Photoperiod

Photoperiod is widely considered the main environmental factor influencing puberty in fish [138]. Photoperiod directly affects the reproductive and aggressive behaviours via the HPG axis [45]. Photoperiod stimulates the brain to secrete neuropeptides like Gonadotropin releasing hormone (GnRH), gonadotropin-inhibitory hormone (GnIH), kisspeptins, etc.) and neurohormones (mainly melatonin, dopamine (DA), and serotonin) that stimulate or inhibit the gonadotrophins from brain that have direct effect on the development of gonads and gamete production [15, 63].

In Chub Mackerel (*Scomber japonicus*), extending the photoperiod and increasing light wavelength raised testosterone and 17β-estradiol levels [23] Similarly, in rainbow trout, (*Oncorhynchus mykiss*), a longer photoperiod promoted ovulation and spermatogenesis, which correlated with increased plasma levels of 17β-estradiol and testosterone in female salmon [9].

It has been found that lower photoperiod can delay gonadal maturation and reproduction timing in many fish species [10]. The change in the normal photoperiod can influence the reproductive behaviour and gonadal development in fish [41]. In some fish species, the longer photoperiod resulted in regression of gonadal growth [66, 104]. It is found that alteration in photoperiod releases the hormone melatonin which is the negative regulator of the HPG axis, thereby affecting the gonadal maturation [57]. In zebrafish (*Danio rerio*) changes in the photoperiod led to a disruption in the synchronization of clock genes, which are associated with tumour formation in the ovary [145]. The effect of photoperiod on the reproductive physiology is shown in Fig. 1.

The physiological response to photomanipulation, including its effects on reproduction, varies widely depending on species, photoperiod, duration of exposure, developmental stage, and culture conditions. While photomanipulation benefits some species, it may have adverse effects on others. Further, adjusting photoperiod in aquaculture is crucial, as improper settings can alter reproduction. Experiments on new species are necessary to prevent losses. Further research is needed to understand how photoperiod and internal factors like melatonin, stress, and gene expression affect fish growth and reproduction.

Temperature

Temperature plays a crucial role in timing gamete maturation and spawning, allowing reproductive cycles to adapt to local and short-term thermal variations [91, 127]. It is considered to be a major environmental cue controlling reproduction in cyprinids [95]. Water

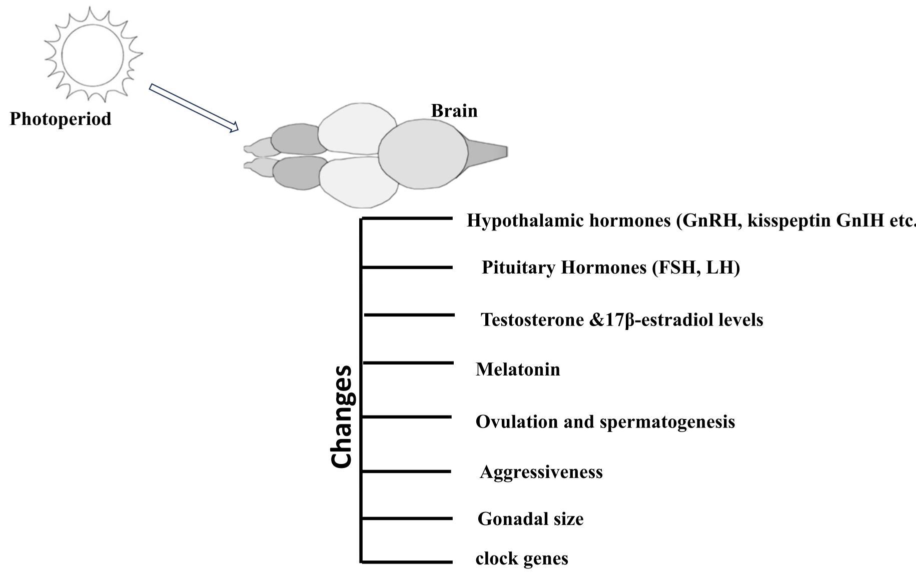

Fig. 1 Effect of photoperiod on different reproductive responses in fish

temperature influences physiological processes like endocrine regulation, energy and material allocation [121]. It also impacts the induction of oogenesis, vitellogenesis, and the final stages of reproduction, including maturation, ovulation, and oviposition [131]. Temperature has been found to have direct effects on gamete quantity and quality in captive and wild broodstocks as well as the final ripening of eggs [17]. In Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*), elevated temperature inhibited ovulation, reduced fertility and egg survival [44, 91], similarly in rainbow trout and Red seabream (*Pagrus major*) it decreased the fertility, larval survival, and reproductive output [64, 92]. In Wolffish (*Anarhichus lupus*), reductions in fertility, egg and larval survival were recorded with the increase in the temperatures [125]. In sea bass, elevated temperatures induce male sex reversal [94]. In brown trout (*Salmo trutta*), high temperatures reduce the phospholipids and free fatty acid deposition in fish eggs as well as reduce the egg osmoregulation process [61]. Furthermore, it was found that in rainbow trout males, the increased temperatures affect spermatogenesis by affecting the androgen levels [4]. The effect of temperature on the reproductive output in different fishes is presented in Fig. 2.

It is found that a reduced temperature increases dopamine secretion which has inhibitory activity on GnRH and therefore on gonadotrophins while an increase in the temperature inhibits the aromatase gene (Cyp19) which is the main enzyme required for the conversion of testosterone to estradiol thereby affecting the gonadal development, vitellogenesis and egg development in fish [91]. Evidence also shows that elevated temperature increases

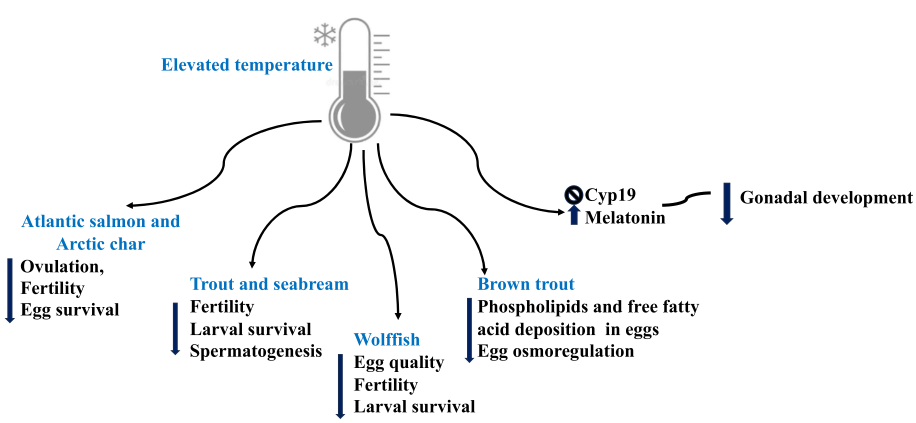

Fig. 2 Effect of elevated temperature on different reproductive responses in fish

melatonin secretion and therefore affects the hypothalamic and gonadal hormones [76].

pH

The pH scale measures the acidity or basicity of water, reflecting its hydrogen ion concentration [141]. Specifically, pH is defined as the negative logarithm of the molar hydrogen ion concentration (-log [H+]). For proper growth and development of fish, the water pH should be in the range of 6.0 to 9.0 and the deviation could have fatal effects on the animal [86]. Problems in physiology particularly the growth of species [147] and ion regulation disturbance are the common problems associated with the deviation in pH [29]. The disturbance could lead to the collapse of the circulatory system and ultimately cause the death of organisms [129].

Research on the effect of pH deviation on reproductive behaviour has been conducted on numerous fish species. In acidic pH, a very low or almost nil hatching rate was observed in some of the migratory fish [47, 103]. In characin, *Astyanax lacustris*, acidic pH decreased the yolk content in eggs, and induced deformities in the chorion and the hatched larvae [33]. In salmonids, the weakly acidic water (5.8–6.4) inhibited the digging and upstream behaviour [54]. pH below 7 or 7.8 does not activate the sperm of rainbow trout, so this deviation could greatly influence the hatching of eggs in this species in captivity [55]. In flathead minnows (*Pimphalus promelas*) and brook trout (*Salvelinus fontinalis*), low pH was found to affect fecundity, egg fertility, and reproductive survival [75, 79]. At pH 5.5 and pH 6.5, the sex ratio was found to be biased towards females in West African cichlid fish, (*Pelvicachromis pulcher*) while the shift is towards the male production at pH 5.5 [102]. The reason according to the study of Reddon and Hurd, [102] could be due to a reduction in the expression of the aromatase gene at low pH which results in the formation of more males in this species. Javanese medaka (*Oryzias javanicus*) exposed to pH levels between 6 and 7 had the lowest mortality rates, and also showed an increase in egg production and hatchability [107]. Acidification delays the spawning and causes ovarian atresia in salmonids by inhibiting vitellogenesis and ovulation [80, 119, 120]. Similarly, Weiner et al. [136] reported reduced development, hatching, and yolk-sac absorption in eggs from acid-exposed female rainbow trout. Again, in the same species, low pH impacts oocyte maturation and acid stress was found to affect the hormonal mechanisms that control the final maturation of fish gametocytes [53]. In the study, it was speculated that acid stress might have caused chromosomal damage during meiosis in gametogenesis, due to abnormal changes in sex hormones resulting in poor reproductive activity. In general, the deviation in the pH could have serious consequences on the reproductive system and breeding of fish ranging from gonadal development to the fertilization and post-fertilization processes. The effect of different pH levels on the reproductive parameters of different fish species is presented in Table 1.

Alkalinity

Alkalinity represents the total concentration of negatively charged ions, particularly carbonate and bicarbonate, that neutralize hydrogen ions in natural waters [1]. Water with high alkalinity possess stronger buffering capabilities with levels between 60–150 mg/L $CaCO_3$, but no less than 20 mg/L [140]. Alkalinity fluctuations can cause stress to fish, leading to hormonal imbalances that may hinder gonad development and reduce egg and sperm production [78]. Fluctuations in alkalinity can result in decreased dissolved oxygen (DO) levels and increased waste buildup, creating poor water conditions that stress fish and negatively impact their reproductive health and gonad development.

Table 1 Effect of different pH levels on the reproductive parameters of different fish species

Species	pH	Effect
Prochilodus lineatus	acidic	Poor hatching rate
Astyanax lacustris,	acidic	decreased yolk content in eggs, deformities in chorion and the hatched larvae
Oncorhynchus nerka, *trutta, Salvelinus leucomaenis*	Weakly acidic	digging and upstream behaviour
O. mykiss	< 7–7.8	influence hatching of eggs
In flathead minnows (*Pimphalus promelas*) and brook trout (*Salvelinus fontinalis*),	acidic	Affect fecundity, egg fertility and reproductive survival
Pelvicachromis pulcher	5.5 and 6.5	female sex reversal
Salmonids	acidic	delayed the spawning and cause ovarian atresia by inhibiting vitellogenesis and ovulation
Female *O. mykiss*	acidic	Reduced hatching, and yolk-sac absorption in eggs

Medaka (*Oryzias latipes*) exposed to high alkalinity, significantly reduce the fecundity, impair ovarian development and declines the reproductive parameters (fertilization rate and hatching rate of eggs) with severe effect on embryonic and reproductive stages [142]. In another study by Yao et al. [143], the alkalinity stress downregulated the genes involved in reproduction such as gonadotrophin, GnRH, estrogen-regulated gene, mitogen-activated protein kinase, corticotropin-releasing hormone binding protein in Medaka.

Hardness

Hardness measures the total concentration of divalent salts in water, primarily calcium and magnesium. Calcium, is essential for bone and scale formation in fish and plays a crucial role in osmoregulation and normal physiological functions. The ideal calcium hardness range is 75 to 200 mg/L CaCO3 [140].

Variations in water hardness can influence ion availability, leading to physiological stress that may adversely affect the reproductive parameters such as gonadosomatic index and hormone levels, ultimately impacting successful reproduction and growth in aquaculture settings. The ionic composition of the water, influenced by hardness, affects the permeability of egg membranes and the viability of the eggs. Inappropriate hardness levels may reduce fertilization success and hinder embryonic development. Water hardness can also influence sperm motility, with certain hardness levels being more conducive to successful fertilization. For example, excessively soft water may negatively affect sperm motility and viability.

In Guppy (*Poecilia reticulata*) and Siamese fighting fish (*Betta splendens*), the effect of hardness on growth and reproductive potential was evaluated after exposure to different concentrations of $CaCO_3$ [59]. In *P. reticulata,* higher water hardness increased reproductive output,including fecundity and gonadosomatic index. However in *B. splendens,* it adversely affected the reproductive potential including the hatchability and nest formation suggesting that the hardness effects of hardness on fish depends on the species.

Water hardness exceeding 120 ppm has been shown to severely impact gonadal development and maturity in angelfish (*Pterophyllum scalare*). Similarly in Rosy barb (*Barbus conchonius*) and Tiger barb (*B. tetrazona*), increased hardness suppress the gonadal maturation [101]. Additionally, studies indicate that high calcium levels in water can accumulate on the surface of *B. splendens* eggs, obstructing water absorption into the perivitelline space, leading to dehydration and egg shrinkage [46].

Ofor and Udah [87] investigated the fertilization and hatching rates in African catfish (*Clarias gariepinus*) and sampa (*Heterobranchus longifilis*) under varying water hardness. It was found that while fertilization rates in *C. gariepinus* were not significantly affected by higher hardness levels, fertilization and hatching rates in *H. longifilis* were severely impacted.

In Channel catfish (*Ictalurus punctatus*) low-calcium hardness water (4.7 mg/L CaCO3) decreased the hatching rates [116]. Similarly in Rhamdia quelen eggs, hard water had a negative impact on hatchability [115]. In zebrafish, increased hardness (>63 mg/L) reduced the hatchability and larval survival [22]. In Rare Minnows (*Gobiocypris rarus*), the higher water hardness decreased the egg size and adversely affected the hatching rate [67].

DO

DO levels in aquatic environments can be a limiting factor due to lower oxygen availability compared to terrestrial habitats as well as the higher energy demands required for oxygen extraction [58]. In fish ponds, inadequate DO can negatively impact fish growth and reproduction, making it essential to maintain a minimum concentration of 5 mg/L at all times [1]. Oxygen levels below the threshold create hypoxia and low levels of DO can adversely affect gonadal development, fertility, and spawning success, ultimately impacting the reproductive health and population sustainability of fish species [68]. Therefore, maintaining ideal DO levels is crucial to ensuring effective reproduction and the growth of healthy progeny.. DO levels in ponds are influenced by several factors including water temperature, which affects oxygen solubility,the presence of aquatic plants and algae, which produce oxygen through photosynthesis but also consume it during respiration; and the decomposition of organic matter which depletes oxygen as bacteria break down organic materials. Hypoxia alters the hormone levels involved in gonad development and reproduction leading to delayed gonadal development, reduced spawning success, altered sperm motility, and compromised fertilization, hatching rates, and larval survival [106].

In Greenland halibut (*Reinhardtius hippoglossoides*), severe hypoxic conditions significantly affected the embryonic development and egg hatching rate [74]. In Koi carp, (*Cyprinus carpio*), a DO level of 0.8 −1 mg/L over 1- 3 months disrupted steroidogenesis, a crucial process for steroid hormone formation [11]. Goldfish (*Carassius auratus*) exposed to low DO levels (0.8 mg/L) for 8 weeks exhibited reduced vitellogenin levels in the blood, poor egg growth in females, and lower 11-KT production, ultimately halting spermatogenesis and sperm motility [12]. In Gulf killifish (*Fundulus grandis),* low DO level (1.34 mg/L) led to impaired steroidogenesis and reduced gonadal growth [62]. Brooders of pacu (*Piaractus brachypomus*) exposed to DO level of 2.0–4.5 mg

/L of experienced a reduction in male and female steroid hormones, along with delayed ovulation [30]. In zebrafish, hypoxia downregulated the expression of genes involved in the HPG axis pathway, negatively impacting spermatogenesis [70, 113]. In male carp (*C. carpio*), 12 weeks of hypoxia (1 mg/L DO) significantly reduced sperm motility, indicating impaired sperm quality [139]. Similarly, Atlantic croaker (*Micropogonias undulatus*) exhibited testicular damage and reduced sperm motility following 4 weeks of hypoxia (1.7 mg/L DO) [122]. Oxidative stress resulting from hypoxia (1 mg/L DO) is believed to contribute to reproductive impairment in fish. In tambaqui (*Colossoma macropomum*), hypoxia induced oxidative stress, lead to a shorter sperm motility duration and reduced sperm count [20]. Table 2 presents the effects of DO levels on reproductive parameters across different fish species. Overall, chronic hypoxia disrupts reproductive processes in fish by impairing steroidogenesis, gamete quality, fertilization, and embryogenesis, often resulting in developmental malformations. The impact varies depending on the severity and duration of hypoxia. Studies suggest that hypoxia acts as an endocrine disruptor, impairing the HPG axis and inhibiting gonadal development in fish.

Turbidity

Turbidity in water refers to the reduced ability to transmit light which limits photosynthesis. It results from factors like suspended clay particles, plankton, particulate organic matter, and pigments from decomposing organic matter. Bhatnagar et al. (14) suggest that a an ideal turbidity range for fish health is 30–80 cm while 15–40 cm is suitable for intensive culture systems,. However levels below 12 cm can cause stress.

Suspended solid particles or high phytoplankton abundance are the primary causes of turbidity in water [126]. This immediately reduces light intensity, scatters light, alters the water's light spectrum, and changes the contrast between objects and their surroundings [128]. These optical changes affect the schooling behaviour, communication, and predator–prey interactions in fishes [146].

High turbidity levels can impede sunlight penetration, which is crucial for aquatic plant growth and overall ecosystem health,. This in turn may reduce food availability for fish during critical breeding periods [135]. A decrease in food resources can negatively impact fish growth and reproductive success, as studies have linked increased turbidity to lower reproductive outcomes and impaired gonad development in various aquatic species [135]. Additionally, research suggests that suspended particles from high turbidity can disrupt fish endocrine functions, leading to reduced fecundity and developmental anomalies during reproduction. This further underscores the negative effects of poor water quality on fish physiology, development, and survival across life stages [19, 82].

The impact of suspended solids and sediment on the reproductive behavior of warmwater fish varies depending on the season, spawning location, and specific spawning behaviours of the species [81].

In rainbow trout, turbidity negatively affects egg fertilisation rates [137] and in giant gourami (*Osphronemus goramy*), turbidity levels exceeding 200 NTU (Nephelometric Turbidity unit), resulted in no spawning [118].

Melanin-based pigmentation can also be affected by turbidity, which may interfere with visual communication sexual selection in fish [28]. In Spotted gar (*Lepisosteus oculatus*), turbidity levels of approximately 5 NTU reduced egg hatching rates [48].

Overall, high turbidity negatively affects egg fertilization and hatching rates while also disrupting hormonal levels crucial for gonadal development in fish. Therefore, maintaining optimal turbidity levels is essential for the healthy development of brooders.

Table 2 Effect of DO levels on the reproductive parameters of different fish species

Species	DO level	Effect
Reinhardtius hippoglossoides	hypoxia	affect embryonic development and hatching rate of eggs
Cyprinus carpio	0.8 –1 mg/L	disrupted the process of steroidogenesis
Carassius auratus	0.8 mg/L	reduction of vitellogenin in blood, poor egg growth in females and lesser 11-KT production, defective spermatogenesis and poor sperm motility in male
Fundulus grandis	1.34 mg/L	poor steroidogenesis and gonadal growth
Piaractus brachypomus	2.0–4.5 mg	reduced the male and female steroid hormones
Danio rerio	Hypoxia	Decreased the gene expression levels involved in HPG axis pathway, affected the spermatogenesis
Male *C. carpio*	1 mg/L DO	Reduced sperm motility
Micropogonias undulates	1.7 mg/L DO	testicular damage and reduced sperm motility
Colossoma macropomum	hypoxia	reduced sperm motility time and number

Ammonia, nitrate and nitrite

Ammonia, produced from fish metabolism and bacterial decomposition of organic matter, exists in two forms: toxic unionized ammonia (NH_3) and less harmful ionized ammonia (NH4+). Together these are referred as "total ammonia." Toxic NH_3 levels for fish pond range from 0.1 to 0.6 mg/L, with a safe limit below 0.02 ppm [72, 110]. Nitrite, produced by Nitrosomonas bacteria during nitrification, is highly toxic to fish, as it converts haemoglobin into methaemoglobin, impairing respiration and damage organs. Safe nitrite levels should remain below 0.02 ppm, while lethal effects occur above 1.0 ppm. The ideal level in any aquatic system is zero [14]. Nitrate, produced by Nitrobacter bacteria from nitrite, is generally harmless to fish, at levels between 0 to 200 ppm though, marine species are more sensitive to nitrate toxicity [73].

High concentrations of nitrogenous compounds can create toxic conditions, impair gamete quality and reduce fertilization rates, posing significant challenges for fish populations in polluted ecosystems [93]. Prolonged NH_3 exposure weakens a fish's ability to regulate the internal ammonia levels. While many species detoxify ammonia by converting it to glutamine, glutamate, or urea, extended exposure weakens this mechanism week, eventually leading to ammonia toxicity [77].

In Nile Tilapia *(Oreochromis niloticus)* high ammonia content in water reduced the gonadotrophin hormones -Follicle stimulating hormone (FSH) and Luteinizing hormone (LH), which are essential for gonad development and spawning. Additionally ammonia concentrations of at 0.5–0.6 mg/L concentration lowered fertilization and hatching rate in the species [38, 114]. Schilling [112] investigated nitrate and ammonia toxicity in zebrafish reproduction finding that ammonia has greater toxicity than nitrate. This was evident through alterations in the gene expression related to steroidogenic pathway and follicle development, leading to reduced egg production. In flathead minnows, exposure to 0.06 mg/L NH_3 significantly reduced fecundity, with a 29% decrease in cumulative egg production after a 20 days [6]. Goldfish exposed to high ammonia levels (50 mg/L) for 48 h inhibited oocyte maturation, induced ovarian damage, and increased oxidative stress, leading to excessive ROS accumulation, ovarian apoptosis, and impaired steroid synthesis, ultimately harming reproductive performance [98]. In this study, the genes such as CYP11a1, 3βHSD, and CYP19a2 were significantly downregulated thereby disturbing the steroidogenic pathway.. In zebrafish, prolonged exposure to *Microcystis aeruginosa* and ammonia disrupted the endocrine-reproductive system. *M. aeruginosa* exposure led to reduced body weight, increased GSI, and changes in ovarian oocyte proportions, with ammonia amplifying these effects. Both stressors disrupted hormone homeostasis by altering hypothalamic-pituitary–gonadal-liver (HPG)L axis [88]. In common carp, high ammonia concentrations significantly reduced GSI, decreased the yolk vesicles and mature oocytes counts, and inhibited spermatogenesis [52].

Flathead minnows exposed to nitrate showed increased 11-KT and vitellogenin levels in males, while vitellogenin levels were significantly females elevated in compared to controls. this suggest nitrate may disrupt steroid hormone synthesis and metabolism [56].

Plasma testosterone levels in Atlantic salmon exposed to 10.3 mg/L nitrate increased non-monotonically [43]. Daily nitrate injections over seven-days in walking catfish (*Clarias batrachus*) led to a reduced blood and testicular testosterone levels [34]. In Eastern mosquitofish (*Gambusia holbrooki),* nitrate exposure increased testicular weight and gonopodium length but decreased muscle 11-ketotestosterone, sperm count, pregnancy rates, and embryo mass [37]. Siberian sturgeon (*Acipenser baerii*) exposed to 57 mg/L nitrate displayed increased plasma testosterone, 11-ketotestosterone, and estradiol levels [49].

Lin and his coworkers [65] studied nitrite exposure in adult male zebrafish and found severe testicular damage, including disrupted seminiferous epithelium, expanded intercellular gaps, and suppressed growth. It also lowered the gonadosomatic index and significantly reduced testosterone and estrogen levels by downregulating key genes in the hypothalamus-pituitary–gonadal-liver axis (HPGL-axis), including gnrh2, lhβ, androgen receptor (ar), and lhr.

Ciji et al. [24] reported that nitrite exposure impaired testosterone and estradiol synthesis in juvenile *Labeo rohita*.

Nitrate and nitrite impact steroidogenesis and reproductive function through a number of interrelated processes. Nitrate and nitrite act as substrates for Nitric oxide (NO) which then binds to heme-containing proteins and cytochrome P450 enzymes, including aromatase to inhibit their activity [42]. NO also promotes S-nitrosylation of key enzymes such as CYP11A, CYP17, and CYP19A1, inactivating them and reducing steroidogenesis [35, 117]. S-nitrosylation can also inactivate steroidogenic factor-1 (SF-1), which regulates critical steroidogenic enzymes such as CYP11A, CYP17, CYP21, and StAR (steroidogenic acute regulatory protein)et al. [35, 60]. The effect of ammonia, nitrate and nitrite on the reproductive parameters in various fish species are summarised in Table 3.

In general, ammonia, nitrate, and nitrite are highly toxic to fish reproductive system. These compounds disrupt normal gonadal and germ cell development, reduce

Table 3 Effect of Ammonia, nitrate and nitrite on the reproductive parameters of different fish species

Type	Fish	Concentration	Effect
Ammonia	*Oreochromis niloticus*	0.5–0.6 mg/L	Decreased FSH and LH level, fertilization and hatching rate
Ammonia	*Danio rerio*	4.5 mg/L	Alterations in genes involved in steroidogenic pathway and reduction in egg production
Ammonia	*Pimephales promelas*	0.06 mg/L	Reduction in fecundity
Ammonia	*Carassius auratus*	50 mg/L	affected oocyte maturation, induced ovarian damage, and increased oxidative stress, leading to excessive ROS accumulation, ovarian apoptosis, and impaired steroid synthesis
Ammonia	*Cyprinus carpio*	5, 10 and 20 mg/L	reduced GSI, decreased the number of yolk vesicles and mature oocytes, and inhibited spermatogenesis
Nitrate	*P. promelas*	56.5 mg/L	Increased 11-KT and vitellogenin levels
Nitrate	*Salmo salar*	10.3 mg/L	Increased testosterone non-monotonically
Nitrate	*Acipenser baerii*	57 mg/L	increased levels of plasma testosterone, 11-ketotestosterone, and estradiol
Nitrite	*D. rerio*	0, 3, 30 μg/L and 0, 2, 20 mg/L	severe effects in the testicles, such as damaged seminiferous epithelium, expanded intercellular gaps, and growth suppression
Nitrite	*Labeo rohita*	2.0 mg/L	impaired the synthesis of both testosterone and estradiol

reproductive output, and alter behavior, leading to poor hatching success and lower larval survival rates.

Handling stress

When fish experience stress, they undergo a primary neuro-hormonal reaction that triggers the release of corticosteroids and catecholamines [71]. This leads to physiological changes, known as secondary consequences. Studies have shown that stress and elevated cortisol levels, inhibit gonadal development, sex steroid production and gonadotropin secretion in salmonids [32].

Fish captured for breeding weather from wild or hatcheries are often subjected to handling and confinement stress particularly after receiving exogenous hormone treatments. Even domesticated stocks regularly face stress from routine husbandry practices [92]. Elevated cortisol levels from handling stress reduce plasma levels of gonadal steroids such as testosterone and 17β-estradiol, while also increasing the occurrence of ovarian atresia in various species [89, 97].

Insnapper (*Pagrus auratus*) capture and handling stress disrupts their endocrine system and reduces the effectiveness of hormone induced treatments. This stress impairs the ovulatory response, impacting reproductive outcomes [26].

In tilapia, *Oreochromis mossambicus*, handling stress significantly increased the cortisol level compared to undisturbed fish [40]. Oocyte atresia was more common in wild-caught red gurnards and also the plasma estradiol levels were decreased [25].

Wild Cohu (*Oncorhynchus kisutch)* and Chinook salmon (*Oncorhynchus tschawytscha*) showed significantly higher plasma cortisol levels after handling compared to hatchery raised fish [108].

In farmed snapper (*P. auratus*), capture and handling stress increased the plasma cortisol levels while decreasing steroid hormonal levels including estradiol and testosterone [27].

Male brown trout exposed to chronic confinement for one month followed by one hour of acute handling stress, showed a significant decline in plasma levels of 11KT and testosterone [96]. The effects of handling stress on gonadal physiology are illustrated in Fig. 3.

To mitigate handling stress in broodstock fish should be kept undisturbed in tanks following hormone injections or transfers. This allows their stress hormone levels, particularly cortisol, to return to baseline. Immediate use of fish for induced breeding or transport after hormonal injections should be avoided, as elevated cortisol levels can negatively impact reproductive performance.

Nutrition

Broodstock nutrition plays a vital role in fish farming, significantly influencing reproductive success, egg quality, and the healthy development of larvae. An adequate intake of macronutrients, along with essential vitamins and minerals, is critical in supporting the complex physiological processes involved in spawning and egg formation.

Diet and food availability, or in the case of aquaculture, the feed regime, directly impact on growth, size, and energy reserves [50]. Physiological processes such as smoltification and maturation are highly energy-demanding, requiring an organism to reach a specific energy threshold to proceed [123]. There is a genetically defined lipid (energy) threshold that must be surpassed for sexual maturation to occur [123]. The relationship between energy availability and maturation

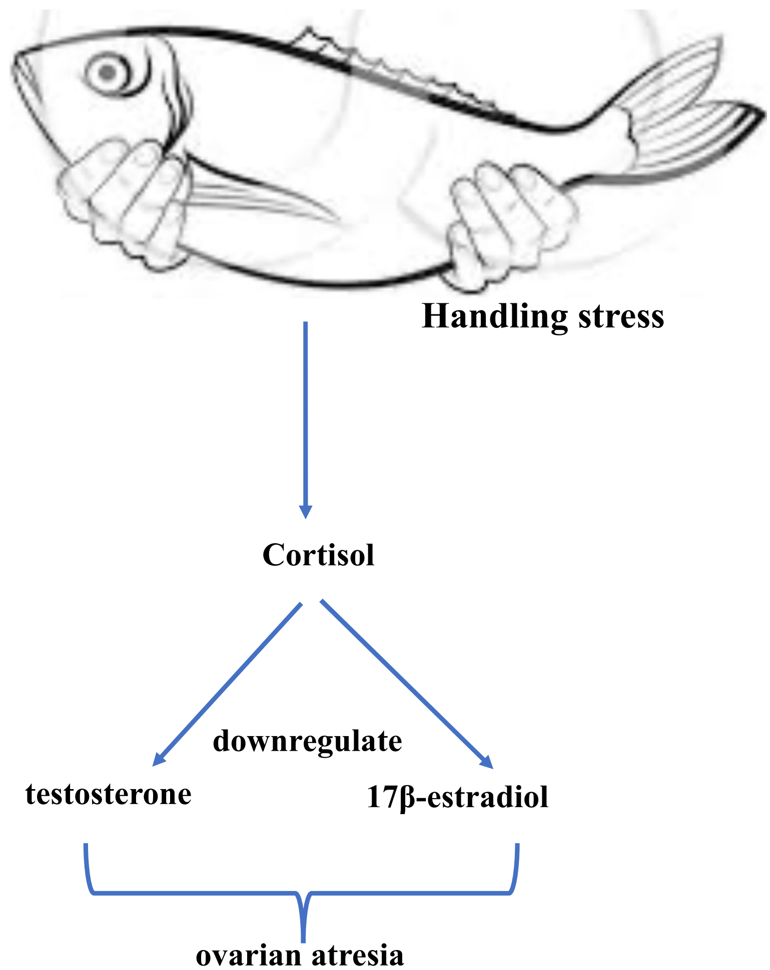

Fig. 3 Effect of handling stress on steroid hormones and gonad development

can be explored by altering feeding regimes to limit energy intake. For example, Rowe and Thorpe [105] demonstrated that reducing food availability during the spring months in juvenile Atlantic salmon can suppress maturation. In rabbit fish (*Siganus guttatus*), increasing dietary lipid content in diet (12–18%) in the broodstock has been shown to enhance fecundity and improve hatching rates [36]. Food restriction can significantly impact spawning success, with reduced feeding rates inhibiting gonadal maturation in various fish species. This effect has been observed in goldfish [111], European seabass (*Dicentrachus labrax*, [21], and male Atlantic salmon [13]. In gilthead seabream (*Sparus aurata* and other sparid species, fecundity significantly increased with dietary n-3 HUFA levels up to 1.6% [39, 132]. Increasing dietary α-tocopherol levels up to 125 mg/kg improved fecundity and egg viability in gilthead seabream. Additionally, supplementing 0.1% tryptophan, a serotonin precursor, in the diet of ayu (*Plecoglossus altivelis*) significantly elevated serum testosterone levels, advancing spermiation in males and inducing maturation in females [3]. A deficiency of ascorbic acid in diet negatively affects sperm concentration, motility and the spawning period. Improved egg quality in European seabass has been linked to a higher content of total n-3 fatty acids in fish fed a pelleted diet enriched with high-quality fish oil [85]. Studies on red seabream have shown that dietary phospholipids enhance egg quality [133]. These benefits are attributed to their role in stabilizing free radicals [134] and their importance during larval development, as they are preferentially catabolized after hatching and before first feeding [99].

Overall, nutrition plays a crucial role in all stages of reproduction, from gamete development to final spawning. Nutritional deficiencies in the diet can have serious consequences on reproductive success, affecting fertility, egg quality, and larval survival.

Other stressors having negative influence on breeding and reproduction of fish

The global population increase has led to a rise in the production of toxic substances, both intentionally and unintentionally. These toxicants eventually enter water bodies, where they accumulate in living organisms across all trophic levels through food chain. Common pollutants released into water bodies include heavy metals, which originate from both natural sources and human activities, such as agricultural fertilizers and pesticides containing these metals [5, 130]. Heavy metals can also be introduced into water bodies through construction activities, including the buildings and roads and infrastructure where these metals are frequently used [7]. Another major source of water contamination is pesticides which are widely used in agriculture and industry. These chemicals enter aquatic environments through surface runoff or atmospheric deposition [2]. An emerging class of toxicants with significant negative impact on aquatic organisms is nanoparticles particularly metallic in nature such as iron, gold and silver. These are extensively used in medical and engineering applications leading to their release into aquatic ecosystems [18].

One of the most concerning environmental issues today is microplastic pollution., which results from the breakdown of larger plastics through biological, chemical, and physical processes such as solar radiation, heat, and water. These fragments have severe effects on the physiology of aquatic organisms, particularly their reproduction, including in fish [51].

Many toxicants released into water bodies disrupt the reproductive systems of fish. These substances, known as endocrine disruptors, interfere with the reproductive hormone production by affecting the hypothalamic-pituitary–gonadal (HPG) axis. Some toxicants also accumulate directly in the gonads, impairing their function [100, 124, 144].

Conclusion

This review provides a comprehensive information on how environmental factors influence reproduction and breeding in fish. Often, fish farmers or breeders may lack awareness of how external conditions affect breeding success. By carefully compiling data from various sources, this review serves as a valuable resource on the relationship between environmental parameters and fish breeding. This information can be valuable for fish researchers studying the effects of various agents on breeding and reproduction. External variables, such as environmental factors, can significantly influence results, and it is crucial to control these parameters during the experimental period to ensure accurate findings.

Ideal levels for fish reproduction

Maintain photoperiod based on species, temperature within optimal ranges, pH 6.0–9.0, alkalinity 60–150 mg/L $CaCO_3$, hardness 75–200 mg/L $CaCO_3$, dissolved oxygen $\geq$ 5 mg/L, turbidity 30–80 cm, ammonia < 0.02 ppm, nitrite < 0.02 ppm, nitrate 0–200 ppm, and minimize exposure to heavy metals, pesticides, nanoparticles, and microplastics, which disrupt the HPG axis and impair reproduction. Reduce handling stress and ensure balanced nutrition for optimal gamete development, spawning, and larval survival.

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Authors' contributions
Irfan Ahmad Bhat: Conceptualization, Methodology, Writing - Original Draft. Mohd Ashraf Rather: Visualization, Investigation. Irfan Ahmad: Writing- Reviewing and Editing. Irshad Ahmad: Visualization, Investigation. Mir Ishfaq Nazir Resources and Writing- Reviewing and Editing. Hussna: Writing- Reviewing and Editing.

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References

1. Wolf-Gladrow DA, Zeebe RE, Klaas C, Körtzinger A, Dickson AG. Total alkalinity: The explicit conservative expression and its application to biogeochemical processes. Mar Chem. 2007;106(1–2):287–300.
2. Adla K, Dejan K, Neira D, Dragana Š. Chapter 9 - Degradation of ecosystems and loss of ecosystem services. Editor(s): Joana C. Prata, Ana Isabel Ribeiro, Teresa Rocha-Santos. One Health, Academic Press. 2022, pp. 281-327, ISBN 9780128227947.
3. Akiyama T, Shiraaishi M, Yamamoto T, Unuma T. Effect of dietary tryptophan on maturation of ayu Plecoglossus altiÕelis. Fish Sci. 1996;62 Ž5:776–82.
4. Alavi SM, Cosson J. Sperm motility in fishes. I. Effects of temperature and pH: a review. Cell Biol Int. 2005;29:101–10.
5. Alengebawy A, Abdelkhalek ST, Qureshi SR, Wang MQ. Heavy metals and pesticides toxicity in agricultural soil and plants: Ecological risks and human health implications. Toxics. 2021;9(3): 42.
6. Armstrong BM, Lazorchak JM, Murphy CA, Haring HJ, Jensen KM, Smith ME. Determining the effects of ammonia on fathead minnow (Pimephales promelas) reproduction. Sci Total Environ. 2012;420:127–33.

7. Aziz KHH, Mustafa FS, Omer KM, Hama S, Hamarawf RF, Rahman KO. Heavy metal pollution in the aquatic environment: efficient and low-cost removal approaches to eliminate their toxicity: a review. RSC Adv. 2023;13(26):17595–610.
8. Balon EK. Reproductive guilds of fishes: a proposal and definition. J Fish Res Board Can. 1975;32:821–64.
9. Bani A, Tabarsa M, Falahatkar B, Banan A. Effects of different photoperiods on growth, stress and haematological parameters in juvenile great sturgeon *Huso huso*. Aquac Res. 2009;40:1899–907.
10. Ben Ammar I, Milla S, Ledoré Y, Teletchea F, Fontaine P. Constant long photoperiod inhibits the onset of the reproductive cycle in roach females and males. Fish Physiol Biochem. 2020;46:89–102.
11. Bera A, Chadha NK, Dasgupta S, Chakravarty S, Sawant PB. Hypoxia-mediated inhibition of cholesterol synthesis leads to disruption of nocturnal sex steroidogenesis in the gonad of koi carp, Cyprinus carpio. Fish Physiol Biochem. 2020;46(6):2421–35.
12. Bera A, Sawant PB, Dasgupta S, Chadha NK, Sawant BT, Pal AK. Diel cyclic hypoxia alters plasma lipid dynamics and impairs reproduction in goldfish (Carassius auratus). Fish Physiol Biochem. 2017;43(6):1677–88.
13. Berglund I. Effects of spring temperature and feeding regime on sexual maturation in Atlantic salmon ŽSalmo salar L.. male parr. In: Goetz, F.W., Thomas, P. ŽEds.., Reproductive Physiology of Fish. Fish Symp. 95, Austin, 1995. pp. 170–172.
14. Bhatnagar A, Jana SN, Garg SK, Patra BC, Singh G, Barman UK. Water quality management in aquaculture, In: Course manual of summer-school on development of sustainable aquaculture technology in fresh and saline waters, CCS Haryana Agricultural, Hisar (India). 2004. pp 203- 210.
15. Biran, J., Levavi-Sivan, B., 2018. Endocrine control of reproduction, fish. In: Encycl. Reprod, vol. 6. 2nd ed. p. 362–368.
16. Blanton ML, Specker JL. The hypothalamic-pituitary-thyroid (HPT) axis in fish and its role in fish development and reproduction. Crit Rev Toxicol. 2007;37(1–2):97–115.
17. Brown NP, Shields RJ, Bromage NR. The influence of water temperature on spawning patterns and egg quality in the Atlantic halibut (Hippoglossus hippoglossus L.). Aquaculture. 2006;261(3):993–1002.
18. Bundschuh M, Englert D, Rosenfeldt RR, Bundschuh R, Feckler A, Lüderwald S, et al. Nanoparticles transported from aquatic to terrestrial ecosystems via emerging aquatic insects compromise subsidy quality. Sci Rep. 2019;9(1):15676.
19. Carnevali O, Santangeli S, Forner-Piquer I, Basili D, Maradonna F. Endocrine-disrupting chemicals in aquatic environment: what are the risks for fish gametes? Fish Physiol Biochem. 2018;44:1561–76.
20. Castro JS, Braz-Mota S, Campos DF, Souza SS, Val AL. High temperature, ph, and hypoxia cause oxidative stress and impair the spermatic performance of the Amazon fish *Colossoma macropomum*. Front Physiol. 2020;11:772.
21. Cerda J, Carrillo M, Zanuy S, Ramos J. Effect of food ration on estrogen and vitellogenin plasma levels, fecundity and larval survival in captive sea bass, Dicentrarchus labrax: preliminary observations. Aquat Living Resour. 1994;7:255–6.
22. Chanu TI, Rawat KD, Sharma A, Das A, Devi BN. Effects of water hardness on egg hatchability and larval survival of aquarium fish. Danio rerio J Aquac. 2010;18:1–7.
23. Choi YJ, Park SGNR, Jo AH, Kim JH. Physiological Effect of Extended Photoperiod and Green Wavelength on the Pituitary Hormone, Sex Hormone and Stress Response in Chub Mackerel. Scomber Japonicus Fishes. 2023;8(2):77.
24. Ciji A, Sahu NP, Pal AK, Akhtar MS. Nitrite-induced alterations in sex steroids and thyroid hormones of Labeo rohita juveniles: effects of dietary vitamin E and ltryptophan. Fish Physiol Biochem. 2013;39:1297–307.
25. Clearwater SJ, Pankhurst NW. The response to capture and confinement stress of plasma cortisol, plasma sex steroids and vitellogenic oocytes in the marine teleost, red gurnard. J Fish Biol. 1997;50(2):429–41.
26. Cleary JJ, Battaglene SC, Pankhurst NW. Capture and handling stress affects the endocrine and ovulatory response to exogenous hormone treatment in snapper, Pagrus auratus (Bloch & Schneider). Aquac Res. 2002;33(11):829–38.
27. Cleary JJ, Pankhurst NW, Battaglene SC. The effect of capture and handling stress on plasma steroid levels and gonadal condition in wild and farmed snapper Pagrus auratus (Sparidae). J World Aquaculture Soc. 2000;31(4):558–69.
28. Côte J, Pilisi C, Morisseau O, Veyssière C, Perrault A, Jean S, et al. Water turbidity affects melanin-based coloration in the gudgeon: a reciprocal transplant experiment. Biol J Linnean Soc. 2019;128(2):451–9.
29. Cott DM, Lucas MC, Wilson RW. The effect of high pH on ion balance, nitrogen excretion and behavior in freshwater fish from an eutrophic lake: a laboratory and field study. Aquat Toxicol. 2005;73(1):31–43.
30. Dabrowski K, Rinchard J, Ottobre JS, Alcantara F, Padilla P, Ciereszko A, De Jesus MJ, Kohler CC. Effect of oxygen saturation in water on reproductive performances of Pacu Piaractus brachypomus. J World Aquaculture Soc. 2003;34(4):441–9.
31. Devlin RH, Nagahama Y. Sex determination and sex differentiation in fish: an overview of genetic, physiological and environmental influences. Aquaculture. 2002;208:191–364.
32. Donaldson, E.M., 1990. Reproductive indices as measures of the effects of environmental stressors in fish. In: S.M. Adam (Editor), Biological Indicators of Stress in Fish. Proceedings, American Fishery Society Symposium 8, pp. 109–122.
33. Dos Santos JA, Soares CM, Bialetzki A. Effects of pH on the incubation and early development of fish species with different reproductive strategies. Aquat Toxicol. 2020;219: 105382.
34. Dubey N, Lal B. Seasonality in expression and distribution of nitric oxide syn- thase isoforms in the testis of the catfish, Clarias batrachus: Role of nitric oxide in testosterone production. Comp Biochem Physiol C-Toxicol Pharmacol. 2010;151:286–93.
35. Ducsay CA, Myers DA. eNOS activation and NO function: differential control of steroidogenesis by nitric oxide and its adaptation with hypoxia. J Endocrinol. 2011;210(3):259–69.
36. Duray M, Kohno H, Pascual F. The effect of lipid enriched broodstock diets on spawning and on egg and larval quality of hatchery-bred rabbitfish ŽSiganus guttatus. Philipp Sci. 1994;31:42–57.
37. Edwards TM, Guillette LJ Jr. Reproductive characteristics of male mosquitofish (Gambusia holbrooki) from nitrate-contaminated springs in Florida. Aquat Toxicol. 2007;85(1):40–7.
38. El-Greisy ZAEB, Ahmed NAM. Effect of prolonged ammonia toxicity on fertilized eggs, hatchability and size of newly hatched larvae of Nile tilapia, Oreochromis niloticus. Egypt J Aquat Res. 2016;42(2):215–22.
39. Fernandez-Palacios H, Izquierdo MS, Robaina L, Valencia A, Salhi M, Vergara J. Effect of ny3 HUFA level in broodstock diets on egg quality of gilthead seabream ŽSparus aurata L. Aquaculture. 1995;132:325–37.
40. Foo JTW, Lam TJ. Serum cortisol response to handling stress and the effect of cortisol implantation on testosterone level in the tilapia. Oreochromis Mossambicus Aquac. 1993;115(1–2):145–58.
41. Foss A, Siikavuopio SI, Imsland AK. Effects of altered photoperiod regimes during winter on growth and gonadosomatic index in Arctic charr (Salvelinus alpinus) reared in freshwater. Aquac Res. 2020;51(4):1365–71.
42. Franke A, Stochel G, Suzuki N, Higuchi T, Okuzono K, van Eldik R. Mechanistic Studies on the Binding of Nitric Oxide to a Synthetic Heme– Thiolate Complex Relevant to Cytochrome P450. J Am Chem Soc. 2005;127(15):5360–75.
43. Freitag AR, Thayer LR, Leonetti C, Stapleton HM, Hamlin HJ. Effects of elevated nitrate on endocrine function in Atlantic salmon, *Salmo salar*. Aquaculture. 2015;436:8–12.
44. Gillet C, Breton B. LH secretion and ovulation following exposure of Arctic charr to different temperature and photoperiod regimes: Responsiveness of females to a gonadotropin-releasing hor- mone analogue and a dopamine antagonist. Gen Comp Endocrinol. 2009;162:210–8.
45. Gonçalves-de-Freitas E, Carvalho TB, Oliveira RF. Photoperiod modulation of aggressive behavior is independent of androgens in a tropical cichlid fish. Gen Comp Endocrinol. 2014;207:41–9.
46. Gonzal AC, Aralar EV, Pavico JM. The effects of water hardness on the hatching and viability of silver carp (Hypophthalmichthys molitrix) eggs. Aquaculture. 1987;64(2):111–8.
47. Gosmann MA. Incubação dos ovos e larvicultura de piava (Leporinus obtusidens): efeito do pH. Dissertação de Mestrado em Aquicultura-Programa de Pós graduação em Aquicultura, centro de Ciências Agrarias. Universidade Federal de Santa Catarina; 2012.

48. Gray SM, Chapman LJ, Mandrak NE. Turbidity reduces hatching success in threatened spotted gar (*Lepisosteus oculatus*). Environ Biol Fishes. 2012;94:689–94.
49. Hamlin HJ, Moore BC, Edwards TM, Larkin IL, Boggs A, High WJ, et al. Nitrate-induced elevations in circulating sex steroid concentrations in female Siberian sturgeon (Acipenser baeri) in commercial aquaculture. Aquaculture. 2008;281(1–4):118–25.
50. Handeland SO, Imsland AK, Stefansson SO. The effect of temperature and fish size on growth, feed intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon post-smolts. Aquaculture.2008;283(1-4):36–42.
51. Hassan I, Sethupathi S, Bashir MJ, Munusamy Y, Chan CW. A systematic review of microplastics occurrence, characteristics, identification techniques and removal methods in ASEAN and its future prospects. J Environ Chem Eng. 2024;12(2):112305.
52. Hussein SY, Kelany AM. A study on the effect of ammonia on the maturation of gonads in common carp (Cyprinus carpio) L., 1758. Assiut Vet Med J. 1995;33(65):51–72.
53. Ikuta K, Kitamura S. Effects of low pH exposure of adult salmonids on gametogenesis and embryo development. Water Air Soil Pollut. 1995;85:327–32.
54. Ikuta K, Suzuki Y, Kitamura S. Effects of low pH on the reproductive behavior of salmonid fishes. Fish Physiol Biochem. 2003;28:407–10.
55. Ingermann RL, Holcomb M, Zuccarelli MD, Kanuga MK, Cloud JG. Initiation of motility by steelhead (*Oncorhynchus mykiss*) sperm: membrane ion exchangers and pH sensitivity. Comp Biochem Physiol A Physiol. 2008;151:651–6.
56. Kellock KA, Moore AP, Bringolf RB. Chronic nitrate exposure alters reproductive physiology in fathead minnows. Environ Pollut. 2018;232:322–8.
57. Kim JH, Park JW, Jin YH, Kim DJ, Kwon YJ. Effect of melatonin on GnIH precursor gene expression in Nile tilapia. Oreochromis niloticus Biol Rhythm Res. 2017;49(3):1–13.
58. Kramer DL. Dissolved oxygen and fish behavior. Environ Biol Fishes. 1987;18:81–92.
59. Krishnakumar A, Patrick Anton ES, Jayawardena UA. Water hardness influenced variations in reproductive potential of two freshwater fish species; Poecilia reticulata and Betta splendens. BMC Res Notes. 2020;13:1–6.
60. Kröncke KD. Zinc finger proteins as molecular targets for nitric oxide-mediated gene regulation. Antioxid Redox Signal. 2001;3(4):565–75.
61. Lahnsteiner F, Leitner S. Effect of temperature on gametogenesis and gamete quality in brown trout, Salmo trutta. J Exp Zool A Ecol Genet Physiol. 2013;319(3):138–48. https://doi.org/10.1002/jez.1779. Epub 2013 Jan 11.
62. Landry CA, Steele SL, Manning S, Cheek AO. Long term hypoxia suppresses reproductive capacity in the estuarine fish, Fundulus grandis. Comp Biochem Physiol - A Mol Integr Physiol. 2007;148(2):317–23.
63. Lee CH, Hur SW, Kim BH, Soyano K, Lee YD. Induced maturation and fertilized egg production of the red-spotted grouper, *Epinephelus akaara*, using adaptive physiology of photoperiod and water temperature. Aquac Res. 2020;51:2084–90.
64. Lim B-S, Kagawa H, Gen K, Okuzawa K. Effects of water temperature on the gonadal development and expression of stero- idogenic enzymes in the gonad of juvenile red seabream, Pagrus major. Fish Physiol Biochem. 2003;28:161–2. https://doi.org/10.1023/B:FISH.0000030511.73742.35.
65. Lin W, Guo H, Li Y, Wang L, Zhang D, Hou J, et al. Single and combined exposure of microcystin-LR and nitrite results in reproductive endocrine disruption via hypothalamic-pituitary-gonadal-liver axis. Chemosphere. 2018;211:1137–46.
66. Liu Y, Li X, Xu GF, Bai SY, Zhang YQ, Gu W, Mou ZB. Effect of photoperiod manipulation on the growth performance of juvenile lenok, Brachymystax lenok (Pallas, 1773). J Appl Ichthyol. 2015;31:120–4.
67. Luo S, Wu B, Xiong X, Wang J. Effects of total hardness and calcium: magnesium ratio of water during early stages of rare minnows (Gobiocypris rarus). Comp Med. 2016;66(3):181–7.
68. Malcolm IA, Youngson AF, Soulsby C. Survival of salmonid eggs in a degraded gravel-bed stream: effects of groundwater– surface water interactions. Riv Res Appl. 2003;19:303–16.
69. Martinez P, Vin˜as, A. M., Sa´nchez, L., D´ıaz, N., Ribas, L. and Piferrer, F. Genetic architecture of sex determination in fish: applications to sex ratio control in aquaculture. Front Genet. 2014;5:340.
70. Martinovic D, Villeneuve DL, Kahl MD, Blake LS, Brodin JD, Ankley GT. Hypoxia alters gene expression in the gonads of zebrafish (Danio rerio). Aquat Toxicol. 2009;95(4):258–72.
71. Mazeaud MM, Mazeaud F, Adrenergic responses to stress in fish. In: A.D. Pick- ering (Editor), Stress and fish. Academic Press, London. 1981. pp. 49-75.
72. Meade JW. Allowable ammonia for fish culture. Progressive Fish Cult. 1985;47:135–45.
73. Meck Norm. Pond water chemistry, San Diego, Koi Club, http://users.vcnet.com/rrenshaw/h2oquality.html. 1996. Revised on July 31, 1996.
74. Mejri S, Tremblay R, Lambert Y, Audet C. Influence of different levels of dissolved oxygen on the success of Greenland halibut (Reinhardtius hippoglossoides) egg hatching and embryonic development. Mar Biol. 2012;159:1693–701.
75. Menendez R. Chronic effects of reduced pH on brook trout (Salvelinus fontinalis). J Fish Board Canada. 1976;33(1):118–23.
76. Migaud H, Davie A, Taylor JF. Current knowledge on the photoneuroendocrine regulation of reproduction in temperate fish spe- cies. J Fish Biol. 2010;76:27–68.
77. Miller DH, Jensen KM, Villeneuve DL, Kahl MD, Makynen EA, Durhan EJ, Ankley GT. Linkage of biochemical responses to population-level effects: A case study with vitellogenin in the fathead minnow (*Pimephales promelas*). Environ Toxicol Chem: Int J. 2007;26(3):521–7.
78. Mota VC, Martins CI, Eding EH, Canário AV, Verreth JA. Cortisol and testosterone accumulation in a low pH recirculating aquaculture system for rainbow trout (Oncorhynchus mykiss). Aquac Res. 2017;48(7):3579–88.
79. Mount DI. Chronic effect of low pH on fathead minnow survival, growth and reproduction. Water Res. 1973;7(7):987–93.
80. Mount DR, Ingersoll CG, Gulley DD, Fernandez JD, LaPoint TW, Bergman HL. Effect of long-term exposure to acid, aluminum, and low calcium on adult brook trout (Salvelinus fontinalis). 1. Survival, growth, fecundity, and progeny survival. Can J Fish Aquat Sci. 1988;45(9):1623–32.
81. Muncy RJ. Effects of suspended solids and sediment of reproduction and early life of warmwater fishes: a review. 1979.
82. Murl Rolland R. Ecoepidemiology of the effects of pollution on reproduction and survival of early life stages in teleost. Fish Fish. 2000;1(1):41–72.
83. Nagahama Y, Yamashita M. Regulation of oocyte maturation in fish. Develop GrowthDiffer. 2008;50:195–219.
84. Nagahama Y, Yoshikuni M, Yarnashita M, Tokumoto T, Katsu Y. Regulation of oocyte growth and maturation. Curr Top Dev Biol. 1995;30:103–45.
85. Navas JM, Trush M, Ramos J, Bruce M, Carrillo M, Zanuy S, Bromage N. The effect of seasonal alteration in the lipid composition of broodstock diets on egg quality in the European sea bass ŽDicentrarchus labrax. Proc. V Int. Symp. Rep. Physiol. Fish. Austin, TX, 2–8 July 1995. 1996. pp. 108- 110.
86. Oba ET, Mariano WS, Santos LRB. Estresse em peixes cultivados: agravantes e atenuantes para o manejo rentável. In: Tavares-Dias M, editor. Manejo e sanidade de peixes em cultivo. Amapá: Embrapa; 2009. p. 226–247.
87. Ofor CO, Udeh H. Effect of water hardness on fertilisation and hatching success of Clarias gariepinus (Burchell, 1822) and Heterobranchus longifilis Valenciennes, 1840 eggs fertilised with C. gariepinus sperm. Asian Fish Sci. 2012;25:270–7.
88. Ou-Yang K, Zhang Q, Wang L, Yang H, He Y, Li D, Li L. New insights into endocrine reproductive toxicity of Microcystis aeruginosa combined with ammonia exposure in zebrafish. Environ Pollut. 2024;342:123021.
89. Pankhurst NW. Stress inhibition of reproductive endocrine processes in a natural population of the spiny. 2001.
90. Pankhurst NW, Porter MJR. Cold and dark or warm and light: variations on the theme of environmental control of reproduction. Fish Physiol Biochem. 2003;28:385–9.
91. Pankhurst NW, King HR. Temperature and salmonid reproduction: implications for aquaculture. J Fish Biol. 2010;76(1):69–85.
92. Pankhurst NW, Thomas PM. Maintenance at elevated temperature delays the steroidogenic and ovulatory responsiveness of rainbow

trout Oncorhynchus mykiss to luteinizing hormone releasing hormone analogue. Aquaculture. 1998;166:163–77.
93. Paul I, Panigrahi AK, Datta S. Influence of nitrogen cycle bacteria on nitrogen mineralisation, water quality and productivity of freshwater fish pond: a review. Asian Fish Sci. 2020;33(2):145–60.
94. Paullada-Salmerón JA, Loentgen GH, Cowan ME, Aliaga-Guerrero M, Rendón- Unceta MC, Muñoz-Cueto JA. Developmental changes and day–night ex- pression of the gonadotropin-inhibitory hormone system in the European sea bass: effects of rearing temperature. Comp Biochem Physiol A. 2017;206:54–62.
95. Peter RE, Yu KL. Neuroendocrine regulation of ovulation in fishes: basic and applied aspects. Rev Fish Biol Fish. 1997;7:173–97.
96. Pickering AD, Pottinger TG, Carragher J, Sumpter JP. The effects of acute and chronic stress on the levels of reproductive hor- mones in the plasma of mature male brown trout, Salrno trutta L. Gen Comp Endocrinol. 1987;68:249–59.
97. Pottinger TG, Yeoman WE, Carrick TR. Plasma cortisol and 17b-oestradiol levels in roach exposed to acute and chronic stress. J Fish Biol. 1999;54:525±532.
98. Qi, Q., Zhang, C., Xu, R., Lv, C., Xue, Y., Wang, P.,et al. (2024). High Ammonia Nitrogen-Induced Reproductive Toxicity in Goldfish (Carassius auratus) Mature Ovary. Aquaculture Research, 2024(1), 9577902.
99. Rainuzzo JR, Reitan KI, Olsen Y. The significance of lipids at early stages of marine fish: a review. Aquaculture. 1997;155:105–18.
100. Ramsden C. The effects of manufactured nanoparticles on fish physiology, reproduction and behaviour. Thesis, Univerity of Polymouth. 2012. https://doi.org/10.24382/4464.
101. Rathinam K. Influence of certain environmental factors on growth and breeding of ornamental fishes. B.F.Sc., Thesis submitted to Tamil Nadu Veterinary and Animal Sciences University, Tuticorin. 1993. pp. 18–27.
102. Reddon AR, Hurd PL. Water pH during early development influences sex ratio and male morph in a West African cichlid fish. Pelvicachromis pulcher Zoology. 2013;116(3):139–43.
103. Reynalte-Tataje DA, Baldisserotto B, Zaniboni-Filho E. The effect of water pH on the incubation and larvicultura of curimbatá Prochilodus lineatus (Valenciennes, 1837) (Characiformes: Prochilodontidae). Neotrop Ichthyol. 2015;13(1):179–86.
104. Rodríguez L, Zanuy S, Carrillo M. Influence of daylength on the age at first maturity and somatic growth in male sea bass (Dicentrarchus labrax, L.). Aquaculture. 2001;196:159–175.
105. Rowe DK, Thorpe JE. Suppression of maturation in male Atlantic salmon. Aquaculture. 1990;86(2-3):291–313.
106. Saha N, Koner D, Sharma R. Environmental hypoxia: A threat to the gonadal development and reproduction in bony fishes. Aquac Fish. 2022;7(5):572–82.
107. Salleh AFM, Azmai MNA, Nasruddin NS, Zulkifli SZ, Yusuff FM, Ibrahim WNW, Ismail A. Water pH effects on survival, reproductive performances, and ultrastructure of gonads, gills, and skins of the Javanese medaka (Oryzias javanicus). Turkish J Vet Anim Sci. 2017;41(4):471–81.
108. Salonius K, Iwama GK. Effects of early rearing environment on stress response, immune function, and disease resistance in juvenile coho (Oncorhynchus kisutch) and chinook salmon (O. tshawytscha). Can J Fish Aquat Sci. 1993;50(4):759–66.
109. Samad MA, Hossain MT, Rahman BMS. Present status of broodstock management at carp hatcheries in Jessore. J Bangladesh Agric Univ. 2013;11(2):349–58.
110. Santhosh B, Singh NP. Guidelines for water quality management for fish culture in Tripura, ICAR Research Complex for NEH Region, Tripura Center, Publication no.29. 2007.
111. Sasayama Y. Effect of starvation and unilateral castration in male goldfish, Carassius auratus, and a desigh of bioassay for fish gonadotropin using starved goldfish. Bull Fac Fish Hokkaido Univ. 1972;22:267–83.
112. Schilling C. Mechanisms of reproductive inhibition in zebrafish (Danio rerio) exposed to ethinylestradiol, nitrate and ammonia (Doctoral dissertation, University of Guelph), Ontario, Canada. 2015.
113. Shang EHH, Yu RMK, Wu RSS. Hypoxia affects sex differentiation and development leading to a male-dominated population in zebrafish (Danio rerio). Environ Sci Technol. 2006;40(9):3118–22.
114. Shokr EA. Effect of ammonia stress on growth, hematological, biochemical, and reproductive hormones parameters. Abbassa Int J Aqua. 2019;12(1):111–30.
115. Silva LVF, Golombieski JI, Baldisserotto B. Incubation of silver catfish, Rhamdia quelen (Pimelodidae), eggs at different calcium and magnesium concentrations. Aquaculture. 2003;228:279–87.
116. Small BC, Wolters WR, Bate TD. Identification of a calcium-critical period during channel catfish embryo development. J World Aquac Soc. 2004;35:291–5.
117. Snyder GD, Holmes RW, Bates JN, Van Voorhis BJ. Nitric oxide inhibits aromatase activity: mechanisms of action. J Steroid Biochem Mol Biol. 1996;58(1):63–9.
118. Sularto S, Listiyowati N, Gunadi B. The influence of water turbidity on the spawning success of giant gourami Osphronemus goramy Lacepède, 1801. In E3S Web of Conferences (Vol. 442, p. 02036). EDP Sciences. 2023.
119. Tam WH, Payson PD. Effects of chronic exposure to sublethal pH on growth, egg production, and ovulation in brook trout, Salvelinus fontinalis. Can J Fish Aquat Sci. 1986;43(2):275–80.
120. Tam WH, Fryer JN, Valentine B, Roy RJJ. Reduction in oocyte production and gonadotrope activity, and plasma levels of estrogens and vitellogenin, in brook trout exposed to low environmental pH. Can J Zool. 1990;68(12):2468–76.
121. Taranger GL, Carrillo M, Schulz RW, Fontaine P, Zanuy S, Felip A, Weltzien FA, Dufour S, Karlsen Ø, Norberg B, Andersson E, Hansen T. Control of puberty in farmed fish. Gen Comp Endocr. 2010;165:483–515.
122. Thomas P, Rahman MS. Chronic hypoxia impairs gamete maturation in Atlantic croaker induced by progestins through nongenomic mechanisms resulting in reduced reproductive success. Environ Sci Technol. 2009;43(11):4175–80.
123. Thorpe JE. Maturation responses of salmonids to changing developmental opportunities. Mar Ecol.Prog Se. 2007;335:285–8.
124. Tomza-Marciniak A, Witczak A. Distribution of endocrine-disrupting pesticides in water and fish from the Oder River, Poland. Acta Ichthyol Piscat. 2010;40:1–9.
125. Tveiten H, Solevå̊g SE, Johnsen HK. Holding temperature during the breeding season influences final maturation and egg quality in common wolffish. J Fish Biol. 2001;58:374–85.
126. Utne-Palm AC. Visual feeding of fish in a turbid environment: physical and behavioural aspects. Mar Freshw Behav Physiol. 2002;35(1-2):111–28.
127. Van Der Kraak G, Pankhurst NW. Temperature effects on the reproductive performance of fish. In: Wood CM, McDonald DG, editors. Global Warming: Implications for Freshwater and Marine Fish. Cambridge: Cambridge University Press; 1997. p. 159–76.
128. Van der Sluijs I, Gray SM, Amorim MC, Barber I, Candolin U, Hendry AP, Krahe R, Maan ME, Utne-Palm AC, Wagner HJ, Wong BB. Communication in troubled waters: responses of fish communication systems to changing environments. Evol Ecol. 2011;25:623–40.
129. Van Dijk PLM, Thillart GEEJM, Balm P. The influence of gradual acid/base status and plasma hormone levels in carp (Cyprinus carpio). J Fish Biol. 1993;42:661–71.
130. Vu CT, Lin C, Shern CC, Yeh G, Tran HT. Contamination, ecological risk and source apportionment of heavy metals in sediments and water of a contaminated river in Taiwan. Ecol Ind. 2017;82:32–42.
131. Wang N, Teletchea F, Kestemont P, Milla S, Fontaine P. Photothermal control of the reproductive cycle in temperate fishes. Rev Aquacult. 2010;2:209–22.
132. Watanabe T, Arakawa T, Kitajima C, Fujita S. Effect of nutritional quality of broodstock diets on reproduction of red sea bream. Nippon Suisan Gakkaishi. 1984;50 Ž3:495–501.
133. Watanabe T, Fujimura T, Lee MJ, Fukusho K, Satoh S, Takeuchi T. Effect of polar and nonpolar lipids from krill on quality of eggs of red seabream Pagrus major. Nippon Suisan Gakkaishi. 1991;57 Ž4:695–8.
134. Watanabe T, Kiron V. Broodstock management and nutritional approaches for quality offsprings in the Red Sea Bream. In: Bromage, N.R., Roberts, R.J. ŽEds.., Broodstock management and egg and larval quality. Cambridge Univ. Press, Cambridge. 1995. 424 pp.
135. Wei K, Cossey HL, Ulrich AC. Effects of calcium and aluminum on particle settling in an oil sands end pit lake. Mine Water Environ. 2021;40(4):1025–36.
136. Weiner GS, Schreck CB, Li HW. Effects of low pH on reproduction of rainbow trout. Trans Am Fish Soc. 1986;115(1):75–82.

137. Wojtczak M, Kowalski R, Dobosz S, Goryczko K, Kuźminski H, Glogowski J, Ciereszko A. Assessment of water turbidity for evaluation of rainbow trout (Oncorhynchus mykiss) egg quality. Aquaculture. 2004;242(1–4):617–24.
138. Worrall KL, Carter CG, Wilkinson RJ, Porter MJR. The effects of continuous photoperiod (24L: 0D) on growth of juvenile barramundi (Lates calcarifer). Aquacult Int. 2011;19:1075–82.
139. Wu RSS, Zhou BS, Randall DJ, Woo NYS, Lam PKS. Aquatic hypoxia is an endocrine disruptor and impairs fish reproduction. Environ Sci Technol. 2003;37(6):1137–41.
140. Wurts WA. Alkalinity and hardness in production ponds. World Aquac-Baton rouge-. 2002;33(1):16–7.
141. Wurts WA, Durborow RM. Interactions of pH, carbon dioxide, alkalinity and hardness in fish ponds. 1992.
142. Yao ZL, Lai QF, Zhou K, Rizalita RE, Wang H. Developmental biology of medaka fish (Oryzias latipes) exposed to alkalinity stress. J Appl Ichthyol. 2010;26(3):397–402.
143. Yao ZL, Wang H, Chen L, Zhou K, Ying CQ, Lai QF. Transcriptomic profiles of Japanese medaka (*Oryzias latipes*) in response to alkalinity stress. Genet Mol Res. 2012;11(3):2200–46.
144. Yi, J., Ma, Y., Ruan, J., You, S., Ma, J., Yu, H., ... & Sun, D. (2024). The invisible threat: Assessing the reproductive and transgenerational impacts of micro-and nanoplastics on fish. *Environment International*, 108432.
145. Yumnamcha T, Khan ZA, Rajiv C, Devi SD, Mondal G, Sanjita Devi H, et al. Interaction of melatonin and gonadotropin-inhibitory hormone on the zebrafish brain-pituitary-reproductive axis. Mol Reprod Dev. 2017;84:389–400.
146. Žák J, Šuhajová P. The effect of water turbidity on prey consumption and female feeding patterns in African turquoise killifish. Ecol Freshwater Fish. 2024;33(3):e12774.
147. Zweig RD, Morton JD, Stewart MM. Source Water Quality for Aquaculture. Washington: World Bank; 1999.

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