

Growth Hormone Involvement in Growth, Oogenesis, Sex Determination and Differentiation in Russian Sturgeon (*Acipenser gueldenstaedtii*): An Integrative Review

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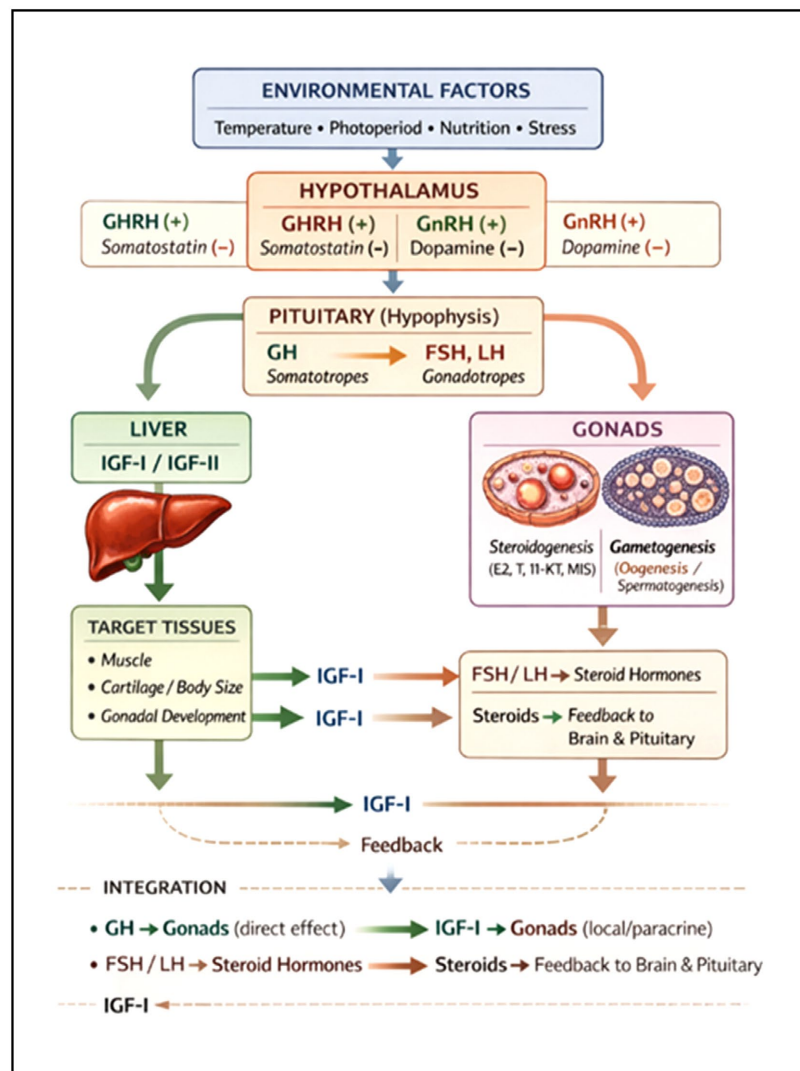


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Abstract

Growth hormone (GH) plays a pivotal integrative role in regulating growth, reproduction, sex determination, and differentiation in the Russian sturgeon (*Acipenser gueldenstaedtii*), a species of major economic importance for caviar production in aquaculture. This mini-review synthesizes current knowledge on the interaction between the somatotrophic axis (GH-IGF-I) and the brain-pituitary-gonadal (BPG) axis, highlighting their coordinated involvement across developmental stages. During early life stages (larvae and juveniles), growth is primarily influenced by environmental factors, and no clear sexual dimorphism is observed. However, following gonadal differentiation, pronounced sex-related growth differences emerge, with females exhibiting enhanced somatic growth and lipid accumulation associated with oogenesis and vitellogenesis, while males allocate energy predominantly to spermatogenesis. The review describes the endocrine regulation of oocyte development, including pre-vitellogenic growth, estradiol-induced hepatic vitellogenin synthesis, and final oocyte maturation triggered by luteinizing hormone (LH) and maturation-inducing steroids (MIS). In parallel, spermatogenesis is regulated by gonadotropins (FSH and LH), androgens, and local testicular factors, with additional modulation by the GH-IGF-I system. Furthermore, artificial fertilization is presented as a key aquaculture tool, linking endocrine control mechanisms to practical applications in broodstock management, larval production, and genetic improvement programs. Special emphasis is placed on early sex determination strategies, which are essential for optimizing caviar production efficiency. Overall, this mini-review highlights GH as a central regulator connecting growth, reproductive physiology, and aquaculture performance, providing a compre-

hensive framework for improving production strategies in Russian sturgeon.



Keywords

Growth Hormone (GH), Russian Sturgeon, Somatotrophic Axis (GH-IGF-I), Brain-Pituitary-Gonadal (BPG), Luteinizing Hormone (LH), Maturation-Inducing Steroids (MIS)

1. Introduction

Distribution and Importance

The Russian sturgeon (*Acipenser gueldenstaedtii*) is distributed in the Caspian, Black, and Azov Sea basins and migrates into freshwater rivers for reproduction. Due to population decline, aquaculture has become the primary source of production (Figure 1) (Bronzi et al., 2021).



Figure 1. Distribution of the Russian sturgeon (*Acipenser gueldenstaedtii*) across the Caspian, Black, and Azov Sea basins, including principal spawning rivers (Volga and Don), highlighting its ecological range and aquaculture importance.

2. Sex-Related Growth Variation in Russian Sturgeon (*Acipenser gueldenstaedtii*)

2.1. Introduction

Sexual growth dimorphism is a well-documented phenomenon in sturgeons, including the Russian sturgeon (*Acipenser gueldenstaedtii*), and plays a central role in aquaculture production systems (Bronzi et al., 2021). Due to severe population declines, aquaculture has become the primary source of sturgeon products, particularly caviar (Bronzi et al., 2021). Growth differences between males and females emerge progressively during development and are regulated by endocrine, genetic, and metabolic mechanisms (Havelka et al., 2022). In principle, many of the mechanisms described in the Russian sturgeon (*Acipenser gueldenstaedtii*) are also found in other sturgeon species, although with certain differences among species. In addition, kisspeptin signaling and the endocrine control of gametogenesis are mechanisms that have been identified both in Russian sturgeon and in other teleost fishes (Figure 2). However, the mechanisms of sex determination in sturgeons are still not sufficiently understood. This is mainly because sturgeons are very difficult species to study, the process of sex determination and differentiation is long and complex, and sturgeons are ancient evolutionary fish species with unique biological characteristics.

2.2. General Growth Pattern in Russian Sturgeon

Sexual maturity is defined as the stage at which mature sperm cells or mature oocytes ready for reproduction appear in the gonads. In Russian sturgeon, as in fishes in general, the age of sexual maturity is influenced both by the species and sex of the fish, as well as by environmental and aquaculture conditions such as temperature, nutrition, water quality, and growth rate.

Russian sturgeon is characterized by relatively slow growth, long lifespan, and

delayed sexual maturation compared to teleost fishes (Bemis, 1997; Chebanov & Billard, 2001). Males typically reach sexual maturity between 6-10 years, whereas females mature later, between 8-16 years, depending on environmental and nutritional conditions (Bemis, 1997; Chebanov & Billard, 2001). These life-history traits strongly influence the development of sex-related growth differences. Male Russian sturgeon exhibit slower growth rates compared to females and reach sexual maturity earlier, typically at 3 - 4 years of age, whereas females attain sexual maturity later, at approximately 7 - 8 years (Figure 3). These patterns are observed under optimal aquaculture conditions, particularly at water temperatures of 16°C - 18°C (Hurvitz et al., 2007).



Figure 2. Gonadotropic and somatotropic hormonal axes involvement in the regulation of sex-related growth variation in Russian sturgeon under aquaculture conditions.

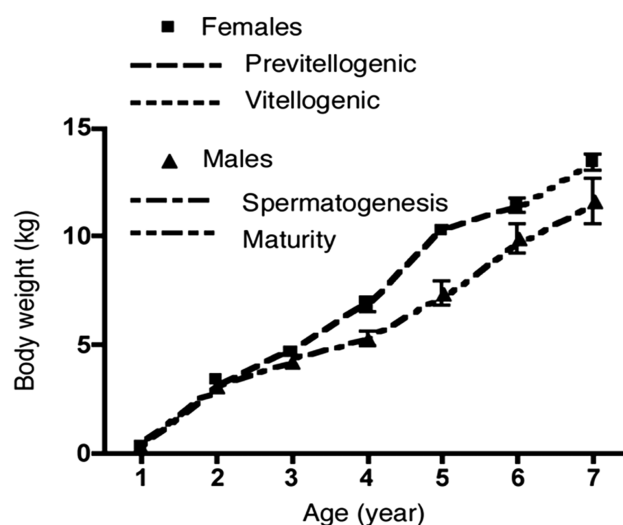


Figure 3. Growth and sex differentiation in male and female Russian sturgeon under aquaculture conditions in Dan water at 16°C - 18°C (Hurvitz et al., 2007).

3. Life Stages (Larvae-Juveniles-Adult)

3.1. Before Sex Differentiation

During early development, including larval and juvenile stages, no significant differences in growth rate or morphology are observed between males and females (**Figure 3**) (Havelka et al., 2022; Kuhl et al., 2021). Growth at this stage is primarily influenced by environmental factors such as temperature, feeding regime, and stocking density rather than sex (Chebanov & Galich, 2013). At this stage, sex cannot be distinguished phenotypically, and molecular markers are required for identification (Kuhl et al., 2021) (**Figure 4**).

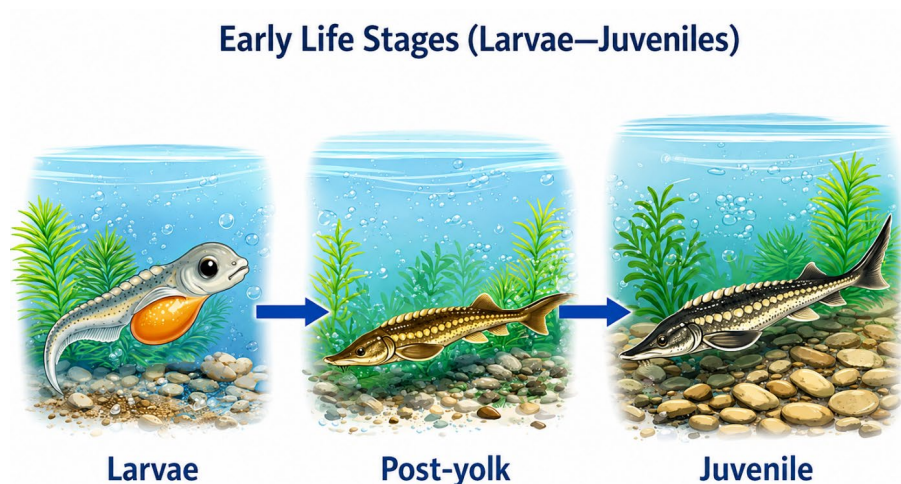


Figure 4. The first stages of Russian sturgeon development before differentiation into males and females.

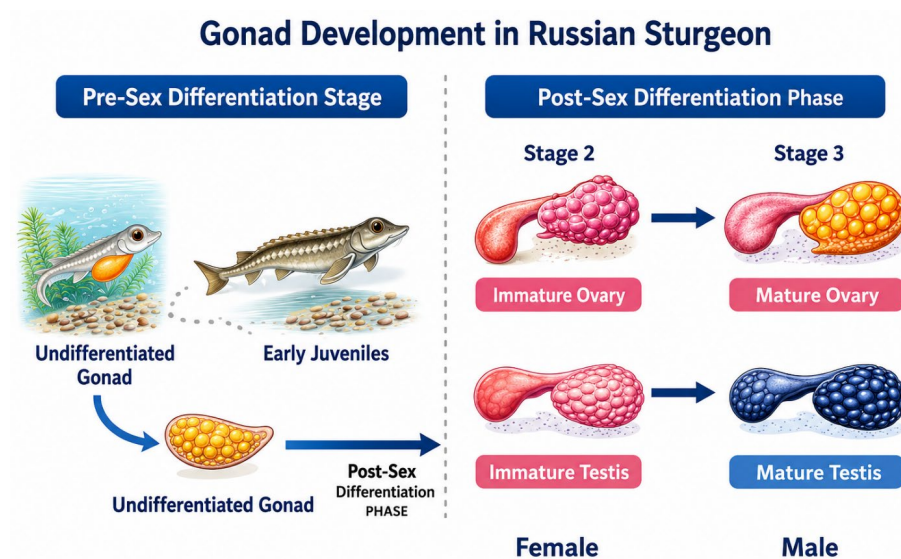


Figure 5. There are two main developmental phases: 1) a pre-sex differentiation stage (early life stages, including larvae and early juveniles), and 2) a post-sex differentiation stage, encompassing subsequent developmental phases (stages 2 and 3), during which sexual characteristics and growth differences between males and females become evident (**Figures 3-5**).

3.2. After Sex Diferntion

3.2.1. Intermediate Stage (Juveniles to Subadults)

Sexual growth divergence begins during the juvenile-to-subadult transition, coinciding with gonadal differentiation and activation of the brain-pituitary-gonadal (BPG) (Figure 5) axis (Billard & Lecointre, 2001; Havelka et al., 2022). Females begin to exhibit slightly higher somatic growth rates and increased lipid accumulation compared to males, reflecting early preparation for future reproductive investment (Bronzi et al., 2021).

3.2.2. Adult Stage (Sexual Maturity)-Females

At sexual maturity, females exhibit significantly greater body size and weight compared to males (Billard & Lecointre, 2001). This is largely due to energy allocation toward oogenesis and vitellogenesis, processes that require substantial lipid and protein reserves (Billard & Lecointre, 2001). The gonadosomatic index (GSI) in females can reach 20% - 30% of total body weight during the reproductive cycle (Chebanov & Billard, 2001).

A) Primary Growth Stage (Pre-vitellogenic oocyte). Small oocytes with a large nucleus (germinal vesicle). Cytoplasm basophilic, no yolk deposition. Surrounded by follicular cells. Controlled mainly by early gonadotropic signaling (FSH-like activity).

B) Early Vitellogenesis. Initiation of yolk deposition (vitellogenin uptake from liver). Appearance of lipid droplets and small yolk granules. Zona radiata begins to form. Strong involvement of: Estrogen (E2). Hepatic vitellogenin synthesis.

C) Late Vitellogenesis. Rapid accumulation of yolk globules. Oocyte increases dramatically in size.

Cytoplasm becomes filled with proteinaceous yolk + lipids. Follicular layers well developed: Theca, Granulosa. Regulated by: BPG axis (Brain-Pituitary-Gonad). GH-IGF system interaction (Figure 6).

Schematic illustration of kisspeptin (Kiss1 and Kiss2) regulation of oogenesis in Russian sturgeon (*Acipenser gueldenstaedtii*), showing the progression from previtellogenesis (early oocyte development) through vitellogenesis (yolk accumulation and growth) to final maturation (formation of mature, caviar-stage oocytes) (Figure 6 and Figure 7).

1) BPG Axis (Central Trigger). Hypothalamus → GnRH. Pituitary → LH surge. Ovary: Steroidogenesis activation. MIS ($17\alpha,20\beta$ -DHP-like) production. Direct effects: GVBD. Final oocyte maturation. 2) Hepatic Axis (Vitellogenesis → Substrate Supply). Estradiol (E2) → liver. Liver → Vitellogenin (VTG). Oocyte: Uptake of VTG → ● yolk granules. Final stage → coalescence + hydration. 3) Somatotrophic Axis (Growth Support) GH → liver → IGF-I. IGF-I: Promotes oocyte growth. Increases LH sensitivity. Enables maturation competence.

Endocrine regulation of final oogenesis and black caviar production is primarily mediated by the brain-pituitary-gonad (BPG) axis. Gonadotropin-releasing hormone (GnRH) from the hypothalamus stimulates the pituitary to release a surge of luteinizing hormone (LH), which acts as the principal trigger for final oocyte

maturation (**Figure 7**). The LH surge induces ovarian steroidogenesis, leading to the production of maturation-inducing steroids (MIS), such as $17\alpha,20\beta$ -dihydroxyprogesterone-like compounds in teleosts, which directly promote GVBD and oocyte maturation. In parallel, the hepatic axis plays a critical role during earlier vitellogenic stages by mediating estradiol (E2)-dependent synthesis of vitellogenin (VTG) in the liver, which is subsequently taken up by growing oocytes and deposited as yolk inclusions. These yolk reserves, visualized as yellow structures, later undergo coalescence during final maturation. Additionally, the somatotropic axis contributes to oocyte development through growth hormone (GH)-stimulated production of insulin-like growth factor I (IGF-I), which enhances oocyte growth, increases gonadotropin sensitivity, and supports the acquisition of maturation competence (Degani, 2022; Hurvitz, 2007; Yom Din, 2017). Growth hormone (GH) is involved in the reproductive system, but it does not act directly on sex determination and differentiation. Its effects are mainly mediated through the GH-IGF-I axis and through interactions with the brain-pituitary-gonadal (BPG) axis.

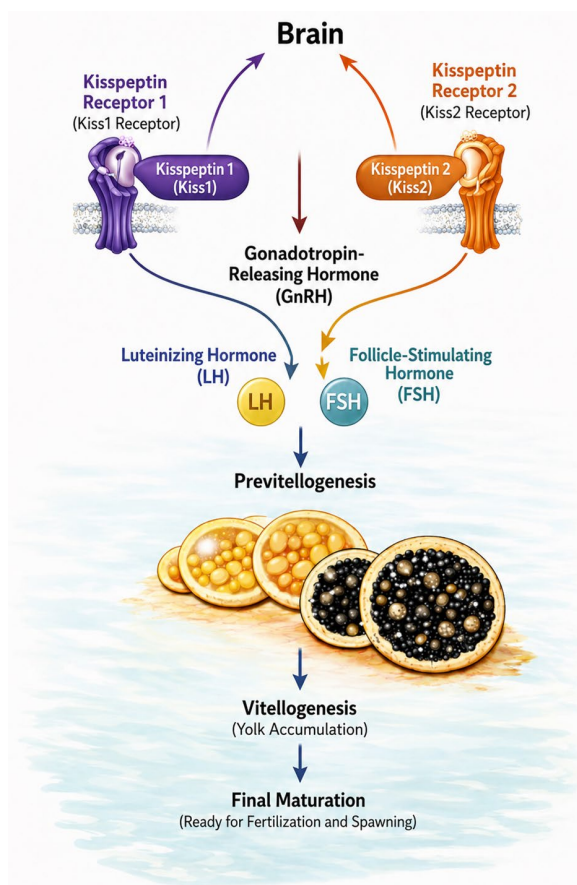


Figure 6. Schematic illustration of kisspeptin signaling (Kiss1 and Kiss2) and their receptors (Kiss1R and Kiss2R) regulating oogenesis in Russian sturgeon (*Acipenser gueldenstaedtii*). The figure shows the progression from previtellogenesis (early oocyte development) through vitellogenesis (yolk accumulation and oocyte growth) to final maturation, leading to the formation of mature, caviar-stage oocytes.

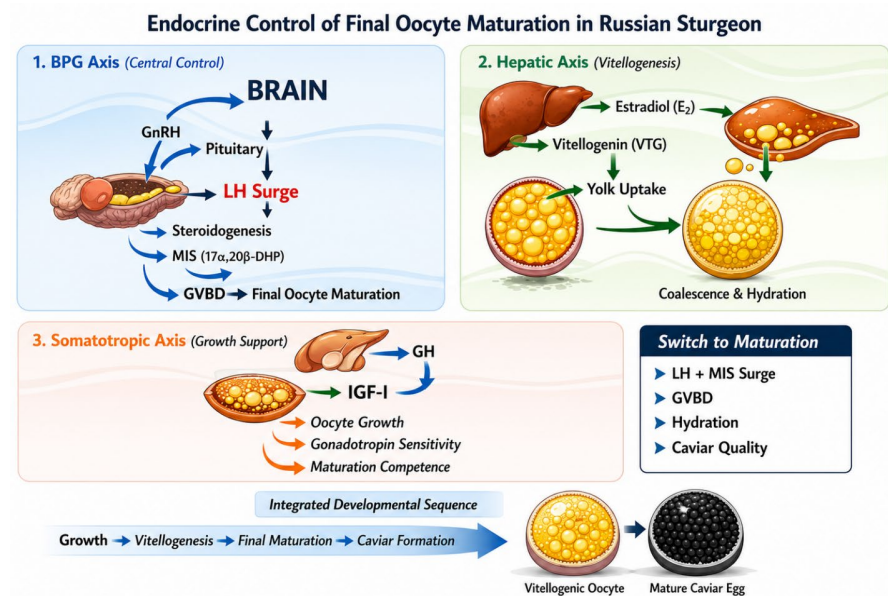


Figure 7. Endocrine regulation of final oocyte maturation in Russian sturgeon.

The integrated developmental progression from left to right—growth, vitellogenesis, final maturation, and caviar formation—reflects a tightly coordinated transition from gradual endocrine regulation dominated by estrogen-driven vitellogenesis to an acute, switch-like phase induced by the LH surge and MIS production. In this context, the transformation of dispersed yolk granules into a dense, dark, fully mature oocyte represents the culmination of endocrine, cellular, and biochemical processes that underlie the formation of high-quality black caviar.

3.2.3. Males

In contrast, males exhibit slower somatic growth after maturation and allocate energy primarily to spermatogenesis, which is energetically less demanding than oogenesis (Billard & Lecointre, 2001; Bronzi et al., 2021). Consequently, males remain smaller and have lower commercial value.

The testis exhibits a typical lobular (acinar) architecture characteristic of Acipenseridae, in which seminiferous lobules radiate from the efferent ducts and contain discrete germinal cysts. Spermatogenesis (Figure 8) proceeds in a centripetal gradient within each lobule. Spermatogonia (Type A and Type B) are located at the peripheral region adjacent to the basal lamina and undergo mitotic proliferation. These cells differentiate into primary and secondary spermatocytes, which undergo meiosis within Sertoli cell-bound cysts in the intermediate zone. Subsequent differentiation leads to the formation of spermatids, which undergo spermiogenesis characterized by nuclear condensation, flagellum development, and cytoplasmic reduction. Mature spermatozoa accumulate in the lumen of the lobules prior to release into the spermatic ducts. Sertoli cells envelop each cyst and provide structural and metabolic support for synchronized germ cell development. The interstitial compartment contains steroidogenic Leydig cells responsible for androgen production, primarily 11-ketotestosterone, which regulates sper-

matogenic progression. The overall organization reflects a cystic mode of spermatogenesis under endocrine control of the brain-pituitary-gonadal (BPG) axis (**Figure 9**).

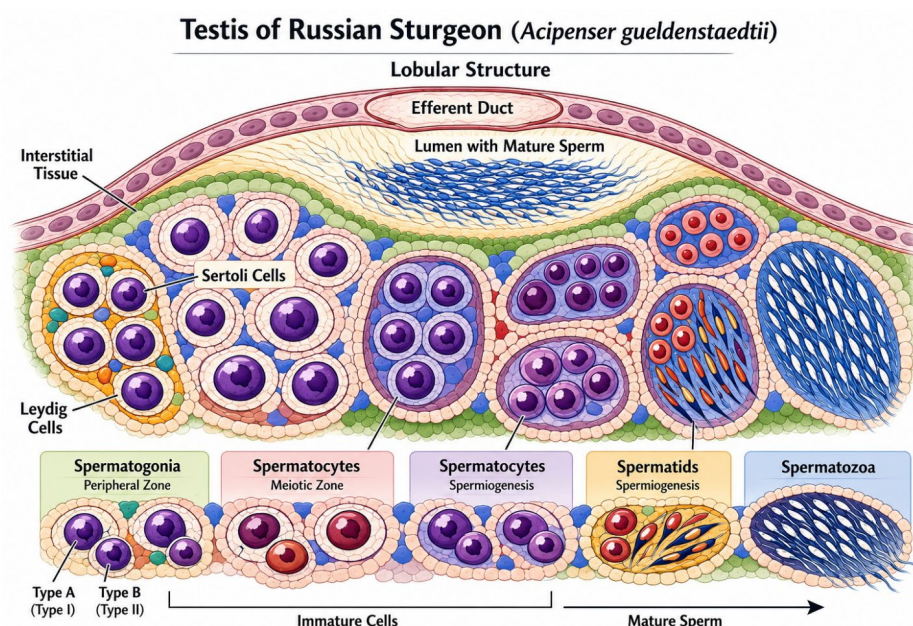
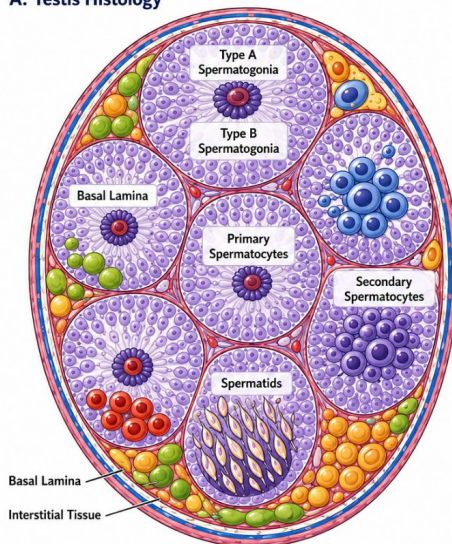


Figure 8. Histological organization and spermatogenesis in the testis of Russian sturgeon (*Acipenser gueldenstaedtii*).

Spermatogenesis and Endocrine Regulation in the Russian Sturgeon (*Acipenser gueldenstaedtii*)

A. Testis Histology



B. Hormonal Regulation of Spermatogenesis

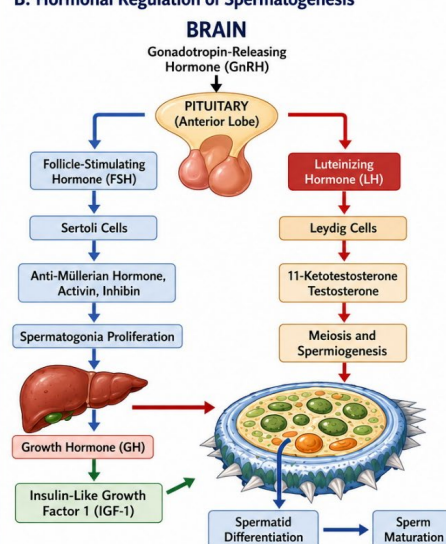


Figure 9. Endocrine regulation of spermatogenesis in the Russian sturgeon (*Acipenser gueldenstaedtii*). Testis histology (left). Lobular structure, Spermatogenic stages: Spermatogonia → Spermatocytes → Spermatids → Spermatozoa. Sertoli cells (cyst organization), Interstitial Leydig cells. B. Hormonal regulation (right). Brain (GnRH) → Pituitary (FSH, LH), FSH → Sertoli cells → early spermatogenesis, LH → Leydig cells → 11-KT & testosterone. GH → IGF-1 → supports differentiation and maturation. Local factors: AMH, Activin, Inhibin.

4. Artificial Fertilization in Russian Sturgeon (*Acipenser gueldenstaedtii*)

4.1. Artificial Fertilization (Controlled Reproduction)

Artificial fertilization (controlled reproduction) is a fundamental technique in sturgeon aquaculture, enabling the reliable production of larvae and significantly improving survival rates compared with natural spawning. This process replicates the species' natural reproductive cycle while allowing precise control under hatchery conditions. By carefully managing broodstock maturation, gamete collection, fertilization, and embryo incubation, hatcheries can ensure consistent offspring production, maintain genetic resources, and support both commercial aquaculture and conservation programs. Controlled reproduction has therefore become an essential tool for sustainable sturgeon farming and stock enhancement efforts worldwide (Figure 10).



Figure 10. Artificial fertilization in Russian sturgeon (*Acipenser gueldenstaedtii*).

4.2. Broodstock Selection and Conditioning

Mature broodstock (typically 6 - 12 years old in aquaculture conditions) are selected based on: Females: late vitellogenic or pre-ovulatory stage (oocytes ~2.8 - 3.2 mm, polarized nucleus) and Males: flowing milt with high motility (>70% - 80%). Fish are maintained under controlled: Temperature: 12°C - 18°C, Photoperiod: seasonal simulation. Nutrition: high-protein diets with lipid support. Final maturation depends on activation of the Brain-Pituitary-Gonadal (BPG) axis, particularly LH surge and maturation-inducing steroids (MIS).

4.3. Hormonal Induction of Ovulation and Permeation

Since natural spawning rarely occurs in captivity, hormonal stimulation is required. Common hormones: GnRH analogs (GnRHa) + dopamine antagonists. Artificial Fertilization in Russian sturgeon. Artificial fertilization (controlled reproduction) is the central technique in sturgeon aquaculture, enabling reliable production of larvae and ensuring high survival rates compared to natural spawning. The process mimics the natural reproductive cycle but is tightly regulated under hatchery conditions. Carp pituitary extract (CPE).

Artificial fertilization (controlled reproduction) represents the central technique in sturgeon aquaculture, enabling reliable larval production and significantly improving survival rates compared to natural spawning (Billard & Lecointre, 2001; Chebanov & Billard, 2001). This approach mimics the natural reproductive cycle but is conducted under strictly controlled hatchery conditions (Figure 10).

Broodstock selection and conditioning constitute the first critical step. Mature individuals, typically aged 6 - 12 years under aquaculture conditions, are selected based on reproductive readiness (Chebanov & Galich, 2013). Females are chosen at the late vitellogenic or pre-ovulatory stage, characterized by oocyte diameters of approximately 2.8 - 3.2 mm and a polarized nucleus, while males are selected based on the presence of freely flowing milt with high motility rates exceeding 70% - 80% (Billard et al., 1999). Broodstock are maintained under controlled environmental conditions, including water temperatures of 12°C - 18°C, seasonal photoperiod simulation, and nutritionally balanced diets rich in protein and lipids to support gametogenesis (Chebanov & Galich, 2013).

Hormonal induction of ovulation and spermiation is required because natural spawning rarely occurs in captivity (Billard & Lecointre, 2001). Commonly used hormonal treatments include gonadotropin-releasing hormone analogs (GnRHa) combined with dopamine antagonists, or carp pituitary extract (CPE) (Zohar & Mylonas, 2001). Females typically receive two injections (priming and resolving doses), whereas males receive a single lower-dose injection. Ovulation generally occurs within 12 - 20 hours following the final injection, depending on water temperature (Chebanov & Galich, 2013).

Gamete collection is performed by stripping. In females, eggs are obtained through gentle abdominal massage and collected into dry, clean containers to pre-

vent premature activation; contact with water must be avoided (Dettlaff et al., 1993). In males, milt is collected either by stripping or catheterization and stored short-term at 4°C. Contamination with water, urine, or feces must be avoided, as these factors significantly reduce sperm viability (Billard et al., 1999; Dettlaff et al., 1993).

Fertilization is conducted using the dry method. Eggs are placed in a dry container, sperm is added directly, and the mixture is gently stirred to ensure uniform contact. Activation is then initiated by the addition of water or an activation solution, with fertilization occurring within seconds to minutes (Billard et al., 1999; Dettlaff et al., 1993). Activation media may include freshwater or specialized solutions such as urea-NaCl mixtures.

Following fertilization, egg de-adhesion is required because sturgeon eggs are naturally adhesive, which can lead to clumping and hypoxia (Chebanov & Galich, 2013). De-adhesion treatments include clay suspensions, milk solutions, or tannic acid, applied for approximately 30 - 60 minutes under gentle agitation, resulting in non-adhesive eggs suitable for incubation (Dettlaff et al., 1993).

Incubation of fertilized eggs is carried out under controlled conditions, including temperatures of 14°C - 18°C, dissolved oxygen levels exceeding 7 mg/L, and continuous water flow. Common incubation systems include McDonald jars and vertical incubators (Chebanov & Galich, 2013). Embryonic development progresses through cleavage, gastrulation, and organogenesis, with hatching occurring after approximately 5 - 8 days, depending on temperature (Dettlaff et al., 1993).

The larval stage begins with yolk-sac larvae (prolarvae), which rely entirely on endogenous yolk reserves and do not require external feeding. After approximately 8 - 12 days, larvae initiate exogenous feeding and are transferred to rearing systems (Gisbert & Williot, 2002).

Several critical factors influence the success of artificial fertilization. Biological factors include egg quality and maturation stage, as well as sperm motility and concentration. Environmental factors encompass temperature stability, adequate oxygenation, and high water quality characterized by low ammonia levels. Technical factors involve precise timing between gamete stripping and fertilization, as well as effective egg de-adhesion procedures (Chebanov & Galich, 2013).

From both scientific and aquaculture perspectives, artificial fertilization is of paramount importance. It enables controlled breeding cycles, facilitates genetic management and selective breeding programs, and supports year-round production. Moreover, it underpins early sex determination programs, which are essential for optimizing caviar production (Fontana et al., 2020).

5. Conclusion

Growth hormone (GH) and the somatotrophic GH-IGF-I axis play a central integrative role in the regulation of growth, gonadal development, oogenesis, spermatogenesis, and reproductive performance in Russian sturgeon (*Acipenser guel-*

denstaedtii). This review highlights the close interaction between the somatotrophic axis and the brain-pituitary-gonadal (BPG) axis throughout the life cycle of the species, particularly under aquaculture conditions.

During early developmental stages, growth is primarily regulated by environmental conditions such as temperature, nutrition, and water quality, while sex differentiation remains phenotypically undetectable. Following gonadal differentiation, clear sexual dimorphism develops, with females exhibiting enhanced somatic growth, vitellogenesis, and lipid accumulation associated with black caviar production, whereas males allocate energy mainly to spermatogenesis.

The review further demonstrates that GH does not directly regulate sex determination and differentiation, but rather acts indirectly through the GH-IGF-I axis and through interactions with the BPG axis. In females, the coordinated activity of gonadotropins, estradiol, vitellogenin synthesis, and IGF-I signaling regulates oocyte growth and final maturation. In males, spermatogenesis is controlled by gonadotropins, androgens, Sertoli and Leydig cell activity, together with local and somatotrophic regulatory mechanisms.

Artificial fertilization represents a major technological application of endocrine regulation in sturgeon aquaculture. Controlled hormonal induction, gamete management, egg incubation, and larval production are essential for sustainable aquaculture and for improving caviar production efficiency. In addition, the development of molecular markers for early sex determination provides important opportunities for selective breeding and optimized broodstock management.

Overall, this integrative review emphasizes that the interaction between the GH-IGF-I system and reproductive endocrine pathways constitutes a major physiological framework underlying growth and reproduction in Russian sturgeon. A deeper understanding of these mechanisms will contribute both to basic knowledge of sturgeon reproductive biology and to the advancement of modern aquaculture practices, conservation programs, and sustainable caviar production.

Conflicts of Interest

The author declares no conflicts of interest regarding the publication of this paper.

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