

Review

Review on Gilthead Seabream (*Sparus aurata*) Aquaculture: Life Cycle, Growth, Aquaculture Practices and Challenges

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Abstract: Over the years, the gilthead seabream (*Sparus aurata*), a prominent species in Mediterranean aquaculture with an increasing production volume and aquafarming technologies, has become an important research focus. The accumulation of knowledge via several studies during the past decades on their functional and biological characteristics has significantly improved the aquacultural aspects, namely their reproductive success, survival, and growth. Despite the remarkable progress in the aquaculture industry, hatchery conditions are still far from ideal, resulting in frequent challenges at the beginning of intensive culture, entailing significant economic losses. Given its increasing importance and the persistent challenges faced in its aquacultural practices, a thorough review is essential to consolidate knowledge, and elucidate the intricate facets concerning its distribution, life cycle, growth dynamics, genetics, aquaculture methodologies, economic dimensions, and the challenges inherent to its cultivation.

Keywords: gilthead seabream; *Sparus aurata*; development; growth; larvae; aquaculture



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1. Introduction

During the past decade, aquaculture has been increasingly recognized for its cardinal contribution in fulfilling the demand for safe and healthy food for a world population that will reach nearly 10 billion by 2050 [1]. This acknowledgment is largely due to the exceptional productivity of freshwater and seawater species, namely gilthead seabream (*Sparus aurata*), blackspot seabream (*Pagellus bogaraveo*) [2,3], rainbow trout (*Oncorhynchus mykiss*) [4,5], and the African arowana (*Heterotis niloticus*) [6,7].

The gilthead seabream, one of the principal Mediterranean aquaculture species, ranks 33rd among the most reared fish, with an estimated annual production volume of 258,754 T/year. Its considerable economic potential is evident in its 2018 worldwide exports of 130,042 tons valued at USD 653 million, and imports of 100,584 tons valued at USD 532 million [8]. Thus, gilthead seabream stands out as a pivotal species in Mediterranean aquaculture, surpassing many others, and has become an important research topic over the years [1,9–13]. Better knowledge of their functional and biological characteristics and molecular pathways has significantly improved their aquacultural aspects, namely their reproductive success, survival, and growth [14–17]. Like most teleosts, gilthead seabream exhibits indeterminate growth, with muscle mass increasing via hyperplasia and hypertrophy [18], and the first marketable size of 300 to 500 g of pre-fattened fish takes between 18 and 24 months, depending on the rearing conditions [19].

Even though the gilthead seabream aquaculture industry has made remarkable progress, hatchery conditions are still far from ideal, resulting in frequent challenges and significant economic losses [20–23].

Therefore, our main purpose in the present review was to examine and elucidate the intricate facets concerning the gilthead seabream life cycle, growth dynamics, aquaculture methodologies, and attendant challenges.

2. Gilthead Seabream's Taxonomy and Habitat

The gilthead seabream (*Sparus aurata*), known as orata, is a unique species of the *Sparus* genus that has given the whole family of sparidae its name. It belongs to the superclass of ray-finned fishes, Actinopterygii, to the class of Osteichthyes, and the order of Perciformes (perch-like) [24].

Gilthead seabream is characterized by a silvery grey leaf-like body, recalling the shape of the glittering metallic tip of a spear, hence the name of the genus "Sparus" [24,25]. It has several other distinct characteristics, including a prominent black region at the lateral line's origin expanding on the opercle's higher margin. The head profile is regularly curved with a golden frontal band separating the two small eyes; hence, the nomenclature of the species is derived from the Latin term "auratus", signifying golden. It has a dorsal fin with 11 spines preceded by 13 to 14 soft rays, and an anal fin with 11 to 12 soft rays and 3 spines, a scaleless preopercle, and scaly cheeks [25].

In the wild, it inhabits in a small shoal or stays solitary, in sandy seabeds, seagrass beds, and the surf or breaker zone, frequently at depths of approximately 30 m, with adults occasionally observed as deep as 150 m. It is a sedentary eurythermal and euryhaline fish that can tolerate an ample range of temperatures and salinity and thus frequents estuaries and coastal waters [13,24]. The gilthead seabream adapts, adjusting its feeding habits based on the availability of resources in its habitat, as an opportunistic feeder [26]. Its diet consists of polychaetes, echinoderms, and teleosts but mainly bivalves and gastropods [26,27]. The occasional consumption of ascidians, algae, and bryozoans is also noted, emphasizing an omnivorous feeding strategy [27].

It is known as a conventional subtropical fish of the warm coastal waters distributed in the region spans from 62 degrees north latitude to 15 degrees north latitude and 7 degrees west longitude to 43 degrees east longitude, thus including the Black and Mediterranean seas, as well as the Eastern Atlantic Ocean. However, recent increasing capture records in England and Ireland have proven this species' distribution in the Celtic Sea and the English channel's cold waters [28].

3. Gilthead Seabream's Developmental Stages

The overall life cycle of gilthead seabream was reconstructed through in vivo observations. At 18.5 °C, the first cleavage division occurs around 1:15 h after fertilization (HPF). Later, at 1:45 h, 2 h, 2:30 h, 3 h, and 4:15 HPF, several cleavages in different planes upgrade the 2-cell zygote morphology to 4-, 8-, 16-, and 32-cell stages and morula, respectively. Then, the cleavages continue, the blastodisc begins to gain a ball-like shape, and the high blastula stage is reached at 6:00 HPF. The epiboly carry-on and the involution define the initiation of gastrulation at 10:00 HPF. The gastrula undergoes a variety of morphometric movements, and from 18:00 HPF, the embryo begins to increase in density, and the first 5–6 couples of somits and kupffer apparatus are observed two hours later. The appearance of the first pigmentation was recorded at 21:00 HPF [29]. Two days after fertilization, the zygotes hatch in the open sea between October and December in the Mediterranean, and the released larvae measure around 3 mm in length (Figure 1) [29,30]. The planktonic larval phase lasts around 50 days at 17–18 °C [13].

At hatching, the larvae of 21 somites were intermittent swimmers with a prominent head and a large yolk sac. The larvae of 15–18 days of age had their yolk sac contents completely resorbed and started to develop efficient guts with their associated glands: the opening of the mouth, the beginning of exogenous feeding, and the intestinal digestive activity. At this stage, the larvae could perform more regular swimming based on undulant body movements, searching for food. The axial muscle progressively acquired its complicated anatomical pattern [31,32]. At the pre-metamorphic stage, larvae aged 30–45 days

(about 5.5–8 mm long; 25 definitive somites) showed a pronounced development at the origin of the classic vertebrate bauplan and showed intestine maturation. Larvae aged 60–90 days represented true juveniles. The fry (about 14–20 mm long) was characterized by the development of gastric functionality, the loss of larval features, and the demonstration of the definitive anatomical organization of scales and rayed fins [31,32]. At this age, locomotion mainly relied on the caudal region propeller push, which explains the significant improvement in the fry swimming performances [31]. The fry of 150 days, measuring approximately 28 mm in length, exhibited a general anatomy and swimming behavior comparable to those of adult fish (Figure 1) [31].

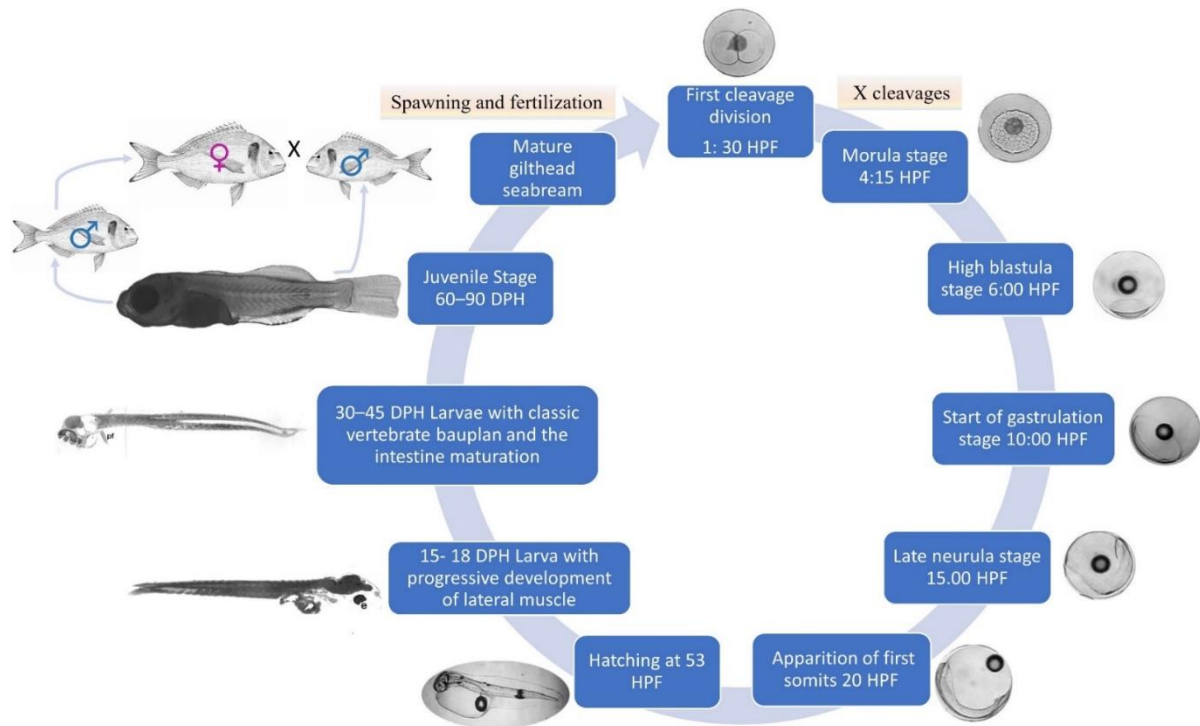


Figure 1. A reconstruction of gilthead seabream life cycle. Several cleavages in different planes upgrade the zygote morphology into a morula, and high blastula stage at 4:15, and 6 HPF, respectively. The epiboly continues, and the involution defines the gastrula (10 HPF), which undergoes a variety of morphometric movements at the origin of a dense larva. Two days after fertilization, zygotes hatch, and larvae develop functional guts and the classic vertebrate bauplan (15–45 DPH) progressively. Planktonic larvae lose their typical features, and a pronounced development is at the origin of a true juvenile (60–90 DPH). They undergo maturation as functional males within the first two years, transitioning into females when they reach over 30 cm in length. This figure was made using materials from [29,31,33].

The seabream exhibits protandrous hermaphroditism. Indeed, within the first two years, the members of this species undergo maturation as functional males, and then they transition into females when they reach over 30 cm in length [34,35]. As batch spawners, females with asynchronous ovarian development can lay between 20,000 and 80,000 eggs per spawning period of 24 h up to 3 months, with a normal fertilization ratio of 90 to 95% [13]. Several studies have assessed the influences of different factors, including the age of female broodstock and dietary $n - 3$ HUFA level, on spawning. Indeed, mature female gilthead seabream of 3 years showed a higher fertility and at least equal egg quality parameters compared to older females of 4–6 years of age [36]. Furthermore, a dietary intake of 1.6% $n - 3$ HUFA demonstrated a significant potential in enhancing the spawning quality in terms of fecundity, hatching, and larval survival [37]. During the male stage, the gonad has a non-functional dorsal ovarian area and ventral functional testes

with asynchronous spermatogenesis [38]. Considering the genetic identity between males and females, the morphological, behavioral differences, and sexual dimorphisms were explained by a sex-biased expression where genes are transcribed more or less in one sex than another [39,40].

4. Growth Characteristics and Requirements

Growth is an integrated physiological process in which the ingested energy is converted to biomass. In gilthead seabream, the efficacy of this conversion is regulated by the genetic growth potential of fish and various abiotic factors such as food quality and availability, temperature, photoperiod, and salinity [41–43]. Like most teleosts, it demonstrates indeterminate growth, with its muscle mass increasing via hyperplasia and hypertrophy throughout its lifespan [18,44,45]. As a long-lived species, its maximum reported growths are 57.5 cm/2500 g in a Mediterranean 12-year-old fish and 61.4 cm/3080.6 g in a Black Sea 14-year-old fish [46,47]. Depending on the aquaculture rearing conditions, 300 to 500 g commercial-sized fish production takes 18 to 24 months.

Gilthead seabream are ectotherms. Thus, the water temperature greatly influences their physiology and growth rate [48]. Although it is a eurythermal fish that can tolerate a wide range of temperatures, the ideal growth rate is observed between 25 and 30 °C [16].

Moreover, the photoperiod is one of the directive factors affecting growth since it triggers the endocrine system, namely the growth hormone levels [11,49]. Indeed, seabream reacts to long photoperiod treatments, redirecting the energy from gonadal to muscle tissue and fat in the abdominal cavity by suppressing sexual maturation or directly improving its food intake and feed conversion efficiency [49]. Gilthead seabream was one of the species in which the photoperiod's positive effects on larvae cultivation were already demonstrated by enhancing prey detection [50]. In other studies, however, the common practice of seabream rearing in continuous light has been suspected of interrupting the circadian rhythm alternation, affecting larval growth and raising the occurrence of skeletal abnormalities [11]. In young and adult seabream, long and constant photoperiods and permanent light have enhanced growth efficiency by delaying sexual maturity [50].

Gilthead seabream demonstrates euryhaline characteristics, allowing it to adeptly manage the variations in environmental salinity, which seems to have a minor effect on adult growth [51]. In seabream larvae, however, decreasing the daily dilution rate of water salinity induced significant rises in the specific growth rate (SGR), the average daily gain, and the protein, fat, and energy gains [52].

In addition to the physico-chemical parameters of the aquatic environment, the growth is affected by many other factors, including the genetic component, food availability, and dietary quality [42,49]. Table 1 summarizes the nutritional requirements of gilthead seabream.

The optimal dietary protein requirements of *Sparus aurata* are influenced by several factors, such as fish size, protein source quality, the quota of non-protein energy, and lipid levels in the diet (Table 1) [53–57]. Indeed, in their study conducted on gilthead seabream fingerlings of 2.1 g, Fountoulaki et al. investigated the potential of diets made of different protein levels ranging between 40 and 51% from fish meal in combination with three lipid levels of fish oil ranging from 11 to 21% and variable carbohydrate contents to enhance the support for fish performance parameters. Their findings postulate that the combination of 51% protein with 16% lipids, corresponding to an energy content of 22.2 kJ/g feed, is the best cost-effective diet for fish of this size when feeding is performed to satiation [55]. In another study, the most suitable lipidic diet for gilthead seabream of 75 ± 1.4 g, providing a protein-sparing effect, was 18% (Table 1) [54]. An insufficient amount of non-protein energy in the diet may induce the catabolism of the dietary proteins' supplying energy. Thus, to improve the efficacy of protein utilization and the protein-sparing effect, dietary supplementation of energy-yielding nutrients, mainly lipids, was a good alternative [54,58]. Still, the supply of dietary lipids more than the requirement can limit feed consumption, consequently reducing the amounts of protein and other essential nutrients [55].

The interaction between low dietary lipid and temperature changes was studied in groups of 30 gilthead seabream (67.50 ± 1.66 g) exposed to low-to-high and high-to-low temperature changes. This interaction was marked by improved feed intake, growth, and nutrient utilization [56]. Moreover, to ensure high growth and digestibility, juvenile seabream’s diets should include around 20% digestible carbohydrates [57].

Table 1. Nutritional requirements for gilthead seabream.

	Mongile et al., 2014 [54]	Fountoulaki et al., 2005 [55]		Pelusio et al., 2021 [56]		Basto-Silva et al., 2022 [59]
Average weight (g)	75	2.1	2.8	67.50 ± 1.66		9.10 ± 0.01
Experimental condition	27 ± 1 °C Recirculating flow of 16.6 L/min Water renewal: 5% daily Photoperiod: 12/12 DL Light intensity: 200 lx Dissolved oxygen: 100% saturation ad libitum	Open flow Feeding to satiation		Closed recirculating aquaculture system Oxygen level: 8.0 ± 1.0 mg/L Total ammonia nitrogen ≤ 0.1 mg L ⁻¹ , NO ₂ ≤ 0.2 mg/L NO ₃ ≤ 50 mg/L Salinity: 25–30 g/L		24 ± 1 °C Continuous flow: 6 L/min Dissolved oxygen: near saturation
		25 °C	10–14 °C	23.17 ± 1.11 °C to 17.34 ± 0.92 °C	17 °C to 23 °C	
Protein	46%	51%	46%			40
Lipids	18%	16–21%	21%	16%		-
Carbohydrate	-	-	-			20
Energy content of the feed	-	21	20			-

The awareness of the nutritional importance of vitamins, specifically vitamins C and E, has grown increasingly over the past decades. A study on gilthead seabream suggests that increasing dietary vitamin E levels associated with medium highly unsaturated fatty acids (HUFAs) enhanced larval total length growth [60].

Different minerals’ suitability and effects on gilthead seabream have been investigated in a few papers published in recent decades (Figure 2), though the mineral requirements of gilthead seabream are not yet fully understood. The publication trends for the query of gilthead seabream mineral requirements over time show an increased special interest during the past years. This particular interest increased after the challenges faced by aquaculture production, succeeding fish meal and oil substitution with plant meals and oil adoption. Indeed, the use of sustainable vegan ingredients, even if formulated to fulfill the protein and lipid requirements, affects the mineral composition of feeds, creating the need for additional mineral supplementation [61,62].

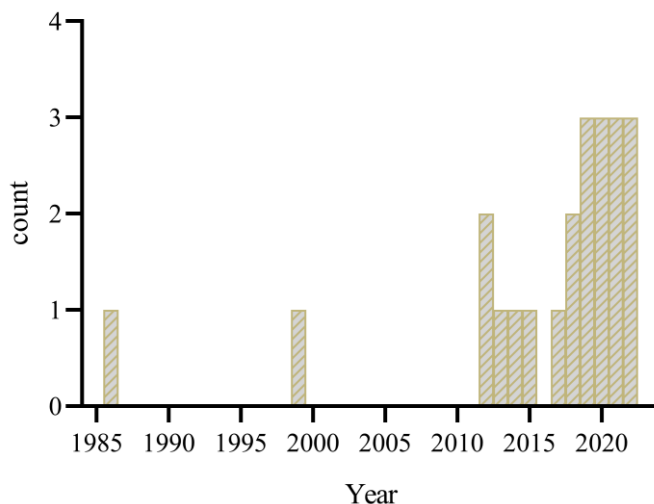


Figure 2. Publication trends over time for mineral + nutrition + sparus + aurata; obtained via PubMed analysis.

A study conducted on gilthead seabream larvae has proven the key roles of selenium (Se), zinc (Zn), and manganese (Mn) supplementation in good growth performance, bone mineralization, improving stress resistance, and preventing skeletal anomalies [61,63].

Indeed, zinc is an essential cofactor for several metabolic reactions, namely the regulation of oxidative stress, bone remodeling, and many other physiological processes.

Selenium is another key micronutrient also implicated in preventing oxidative stress and promoting bone formation (Table 2) [61].

The study of Domínguez et al. conducted on fingerlings of 25.5 ± 2.7 g that were fed with a plant-based diet and Zn and Se supplementation requirements for better growth and bone mineralization were evaluated with 150 mg/kg of zinc and 0.77 mg/kg of a basal plant-based diet [61]. Besides Zn and Se, the same study highlighted the requirement of adding a supply of 1.9 mg/kg of cobalt (Table 2) [61].

Manganese is one of the important minerals for gilthead seabream with bone mineralization and oxidative stress resistance properties [63,64]. In a study on fingerlings of 12.6 ± 1.5 g, the authors proved that 19 mg of manganese and 150 mg/kg of zinc per kilogram of diet cover the requirements in juvenile gilthead seabream (Table 2) [62,65].

Calcium (Ca), as the main element of fish bone, has a pivotal role in muscle contraction, nerve transmission, and acid–base equilibrium [66]. According to Izquierdo et al., gilthead seabream juveniles do not need Ca supplementation, and an optimum level of ≤ 7.6 g/kg diet could be covered by the basal dietary Ca levels in the diet (Table 2) [61].

Table 2. The mineral requirements for gilthead seabream.

	Manganese [62]	Zinc [61]	Selenium [61]	Cobalt [61]	Calcium [61]
Average weight (g)	12.6 ± 1.5		25.5 ± 2.7		
Experimental conditions	Temperature: 19.4 ± 0.4 °C Photoperiod: 12 h L/12 h D Diets high in vegetable ingredients (fish meal: 10%; fish oil: 6%)		Temperature: 19.4 ± 0.4 °C Photoperiod: 12 h L/12 h D Diets with low FM and FO levels		
Requirements	19	150 mg/kg	0.77 mg/kg	1.9 mg/kg	≤ 7.6 g/kg

Many studies have investigated the relationship between morphometric indices and physiological status for adult gilthead seabream and examined whether the use of feeds with different diets or additives affects the length–weight relationship [67].

The length–weight relationship for feeding with different protein levels (38%, 42%, and 45%) were estimated to be $W = 0.051 \times TL^{2.63}$, $W = 0.046 \times TL^{2.67}$, and $W = 0.046 \times TL^{2.68}$, respectively. These values favored a higher growth in length than in weight for the three experimental groups [67]. Those results are in concordance with the result reported for the Aegean Sea gilthead seabream populations during winter months, where the b values ranged from 2.736 to 2.737 [68,69] compared to 2.83 to 2.98 in the Mediterranean Sea [70,71]. The reason behind the negative allometric growth reported by the first study [67] could be explained by the gonadal development, during which fish need to reach the length of sexual development, while that of the Aegean Sea gilthead seabream was justified by the fish being caught in the winter when they were still in the spawning period [67–71]. Thus, the differences in the b value can result from various factors such as the length of the fish at initial maturity, age, gender, water temperature, and the amount of feed.

Larvae grow from 3 mm to 9 mm in about 30 days [25]. Larvae could be fed extremely small particles or inert food of live rotifers and artemia. Studies have proven that the values of growth performance of the gilthead seabream larvae were significantly increased by increasing the ratio of live food [72]. The preferences for food particles are related to the mouth opening, ranging between 50 and 250 μ m for 8 to 10 mm larvae, 180 and 400 μ m for 20 mm larvae, and 315 and 600 μ m for 25 mm juveniles [25].

5. Genetic Insights into Gilthead Seabream Populations

The gilthead seabream represents a crucial economic asset for Mediterranean aquaculture. Given its extensive ecological range, the genetic composition of natural populations and the possible existence of panmictic or subdivided populations have been largely studied. Those studies have revealed a heterogeneous degree of genetic differentiation among gilthead seabream through allozymes and microsatellites [73–75]. Indeed, in a study conducted on seven reared stocks of gilthead seabream *Sparus aurata*, and two wild populations, each of the five polymorphic microsatellite markers revealed 11 to 19 alleles [75]. Those findings remain to be inconclusive because of the limitations of the markers used. In more comprehensive and recent studies, the analyses of the different markers, including high-quality SNP, have identified three genetic clusters defined as East, West Mediterranean, and Atlantic. The first mentioned group could be subdivided, in turn, using the outlier markers, into Ionian/Adriatic and Aegean groups [74,76,77]. Supported by a genomic functional analysis, one of these investigations suggested that this differentiation was mainly due to differences in salinity [76].

Additionally, it was shown that the non-confined coastal lagoons restocking with fry of unknown origin, or the accidental escape of farmed fish, have contributed to intermingling all gilthead seabream genetic stocks [13].

These results provide a baseline for future reference in any management program of wild and farmed gilthead seabream, a first step to investigate the potential genetic impact of the aquaculture industry on wild populations [76,77]. These challenges, affecting both the wild population and the sustainability of gilthead seabream aquaculture, call for global legislation or international conventions to implement necessary measures in offshore farms and open lagoons, preventing the mixing of wild and aquaculture populations.

6. Breeding and Culture Practices

6.1. History

The early gilthead seabream culturing relied on the wild juveniles captured using “valli” and fish barriers, taking advantage of their natural migration from the sea into coastal lagoons [78]. Valli, the plural of valle, are portions of the aquatic ecosystem of 300 to 400 hectares, isolated artificially for the practice of fish culture. Such activity has considerably reduced the resources of the wild stocks and consequently limited the expansion of the activity, creating the need to develop intensive production practices [78]. Indeed, the large-scale production of fry was first achieved by the early 1980s’ copying technology that was previously developed for the cage rearing of salmonids in Northern Europe [79]. By the 1990s, the intensive production of commercial-sized fish in cages or ponds was significantly enhanced [78]. The accumulation of knowledge on reproduction techniques and larval nutritional and environmental requirements have allowed for the inflation of the scale of gilthead seabream production [78,79].

6.2. Production and Trade

Gilthead seabream is a valuable reared species in aquaculture, particularly in the Mediterranean Sea, with an increasing exploitation status in production volume and culture technologies. Intensive gilthead seabream production in the Mediterranean began in the early 1980s with the use of marine cages as well as recirculating aquaculture systems. In the late 1980s, this species’ production was 1800 tons (T), and in ten years only (1997), it reached 45,000 T [79]. In 2020, its production was estimated at 258,754 T, classifying this species 33rd among the most reared fish [1,8].

The leading six producers worldwide are Turkey, Greece, Egypt, Tunisia, Spain, and Italy, with 38.54%, 21.43%, 13.87%, 6.96%, 4.82%, and 2.84%, respectively, of the world’s gilthead seabream production [1]. Since 2000, the 50% increase in UE production was promoted mainly by a six-time multiplied production in Croatia and by a two-time multiplied production in Cyprus. In 2019, the EU27 produced 93,639 T, representing 36.19% of the world’s production [8].

Greece and Turkey are the largest exporters of gilthead seabream in the world, with 52,879 T and 52,516 T, respectively, while Italy is the largest importer with 34,912 T, followed by Portugal with 13,351 T [8].

The rapid growth of the seabream farming sector was correlated with the robustness and the plasticity of this species, in addition to the reliable supply of prime juveniles spawned under controlled conditions in hatcheries [13,17,79].

Several studies have indicated considerable economic potential for gilthead production, and its worldwide 130,042 T export was evaluated at USD 653 million, while the 100,584 T import in 2018 was evaluated at almost USD 532 million [8].

6.3. Gilthead Seabream Farming from Hatchery to Harvest

The intensive gilthead seabream production commences by collecting good-quality eggs derived from the mass spawning process of the selected broodstock. The selection standards used to identify adult fish as suitable breeders include a standard morphology and color, the absence of skeletal anomalies, an overall good well-being, natural behavior, the highest level of growth that fish can achieve within its age group, as well as newly estimated genetic parameters including those enhancing growth or disease resistance [17,78,80,81]. Breeders of various age groups may be conditioned by environmental manipulation such as adjustments of the photoperiod and temperature to induce sexual maturation [33].

For optimal broodstock reproductive performance, it is advisable to maintain a sex ratio of two males for every female.

Males are left to release sperm naturally or through stripping, while females can release eggs naturally or hormonally (5–20 mg/kg GnRH α (1) (D-Ala δ 6; Pro δ 9Net-mGnRH) at 15–17 °C [33,78]. The females' maturation stage should be confirmed by investigating the oocytes diameter, and only females with oocytes larger than 500 μ m in diameter (late vitellogenic stage) are selected [78].

In the gilthead seabream, as in other Sparidae, the buoyancy of spawned eggs serves as a key factor in hatcheries when assessing the potential of an egg batch to produce viable embryos. This relates to the fact that egg hydration during oocyte maturation and right after spawning is fundamental for its development and viability [82,83]. The loss of the buoyancy of eggs could be explained by a defect in their vitelline envelopes' components or differential concentrations of cathepsin D and L, which are proteolytic enzymes involved in yolk proteolytic processes, and the elevated osmotic pressure that is necessary for egg hydration, which induces excessive hydration [82,84].

The eggs are collected by a basic screen within the broodstock tank's outflow system. Only the floating eggs are collected and placed into conical incubating tanks in the dark for 36–48 h at 18–22 °C [82].

Before the estimated hatching time, water renovation should be raised to reach two full exchanges per hour, after which environmental parameters should be reset according to Table 3 [78,85].

Table 3. Main environmental parameter variations during gilthead seabream production cycle.

	Incubation	Hatching	Larval Stage	Fry Stage
Water temperature (°C)	15–17.5	15–17	15–20	20
Salinity (ppt)	35–38	35–38	35	30
Photoperiod (h)	-	16:8	16:8	14:10
Water renewal (time/day)	12	12	8–12	18

In gilthead seabream rearing, like in any aquaculture species, the primary goal of water renewal is to maintain optimal water quality, including dissolved oxygen levels, pH, dilute wastes, and ammonia, enhancing the well-being and growth of the fish while mitigating adverse effects on the nearby ecosystem.

The newly hatched larvae should be moved to a rearing tank, where they show a pronounced tendency to sink, conserving a uniform dispersion in the water body [78]. Directly after hatching, the digestive tract will still be incomplete, the mouth will be closed, and the eyes will not be pigmented yet. Throughout this phase, the larvae rely on their yolk sac [86]. Once the visual and digestive organs are fully developed, the larvae are involved in progressively active movements characterizing the first-feeding predatory position [86]. Thus, they can initiate their feeding on live prey from the third to the fourth day of hatching, initially consuming *Branchionus* spp. (Rotifers), and subsequently transitioning to Artemia (Brine shrimp) [87]. In addition, during the first 25 DPH, a microalgal culture, so-called green water, is added to tanks, where it is used to feed directly the rotifer and thus indirectly feed the larvae, or this may work as a water quality conditioner, holding the water quality attributes at optimum ranges, and as an immunological stimulus, minimizing bacteriological contamination and the nitrogen concentration [85,87,88]. The production of the “green water” involves the use of specific species, namely *Isochrysis galbana*, *Tetracelmis suecica*, *Nannochloropsis gadinota*, and *Nannochloropsis oculata*. These species are selected for their high protein contents, strong production capabilities, and lack of adverse side effects. Several key parameters significantly impact the growth and production rates of microalgae. These include the temperature and salinity levels, which should be maintained within the ranges of 18 °C to 24 °C and 20 and 35 ppt, respectively. Moreover, 1000 to 2000 lux’s light intensity ensures optimal algal growth. Furthermore, maintaining the pH level in the range of 7.5 to 8.5 is essential to encourage the algae’s desired growth and production rates [85].

Feeding on live microorganisms lasts between 40 and 50 days. During the first seven days, the larvae consume up to 20 million rotifers/m³ of rearing water volume daily along with 40 L (12 × 10⁶ cell/mL) of mature algal culture/m³ of rearing water volume. From the 8th to 12th days, the number of rotifers is increased by 20%, and between the 13th and 16th days, it is further increased by 40%. At 17 DPH, the quantity of rotifers should be increased to 60%, and the microalgal supplements should be decreased to 50%, adding 0.1 to 0.5 million Artemia AF [78]. This high prey density increases the likelihood of fish approaching and consuming microorganisms, thereby significantly improving their survival possibilities (Figure 3).

Starting from day 20, the algae and rotifers quantities are decreased to 10 L/m³ and 20 M/m³, respectively. This adjustment is in favor of an increased amount of artemia AF (0.5–1 million) and 0.3–0.6 M/m³ of artificially enriched artemia metanauplii and a small amount of inert feed acclimating the larva to the new food source [78]. From the 24th to the 27th day, the green water is gradually disregarded, the rotifers drop to 10 M/m³, the artemia AF increases further to 250–500% (1.5 M/m³), and large-size artemia EG or RH increase to 3 million. From day 28, the rotifers, artemia AF nauplii, and green water supply are suspended, and the fish are fed with artemia EG or RH (10 M/m³) and inert feed (15–20 g/m³). From the 34th to 39th day, the fish receive an increased quantity of EG or RH artemia (12 M/m³). Additionally, they are provided with 20 g/m³ of 80–200 µm medium-sized particles, plus 10 g/m³ of the larger 150–300 µm particles of inert food. Between the 40th and 43rd day, as the transition from the larval stage to the juvenile (fry) stage begins, it is advisable to boost the provision in EG or RH artemia and 150–300 µm inert feed, which align better with the larval requirements, to reach 16 M/m³ and 30 g/m³, respectively.

The feeding regimen should involve three daily distributions, commencing as soon as the lights are turned on, with a lapse time of 6 h, and concluding 4 h before lighting shutdown. At this stage, the fingerlings or juveniles of 2–5 g, assuming the adult aspect, could be moved to the weaning facilities [89]. The weaning stage is a true intensive rearing period where the biomass of the juveniles can reach up to 20 kg/m³ [19]. The feeding procedures and environmental parameters in this critical step are marked by the interruption of the live feed supply and the automatic distribution of dry feed. The environmental parameters in the weaning section are based on the protocol detailed in Table 3. The feeding protocol is founded on the use of dry feeds, while the freshly prepared moist food, totally consumed within the same day, represents a resource to supply

additional nutritional integrators and drugs. The live feed supply ends when the juveniles reach an age of sixty days, after which they are fed exclusively with dry compounded feed (Figure 3). When the fry reach a size of 2 to 5 g, they could be marketed to the fattening facilities [78].

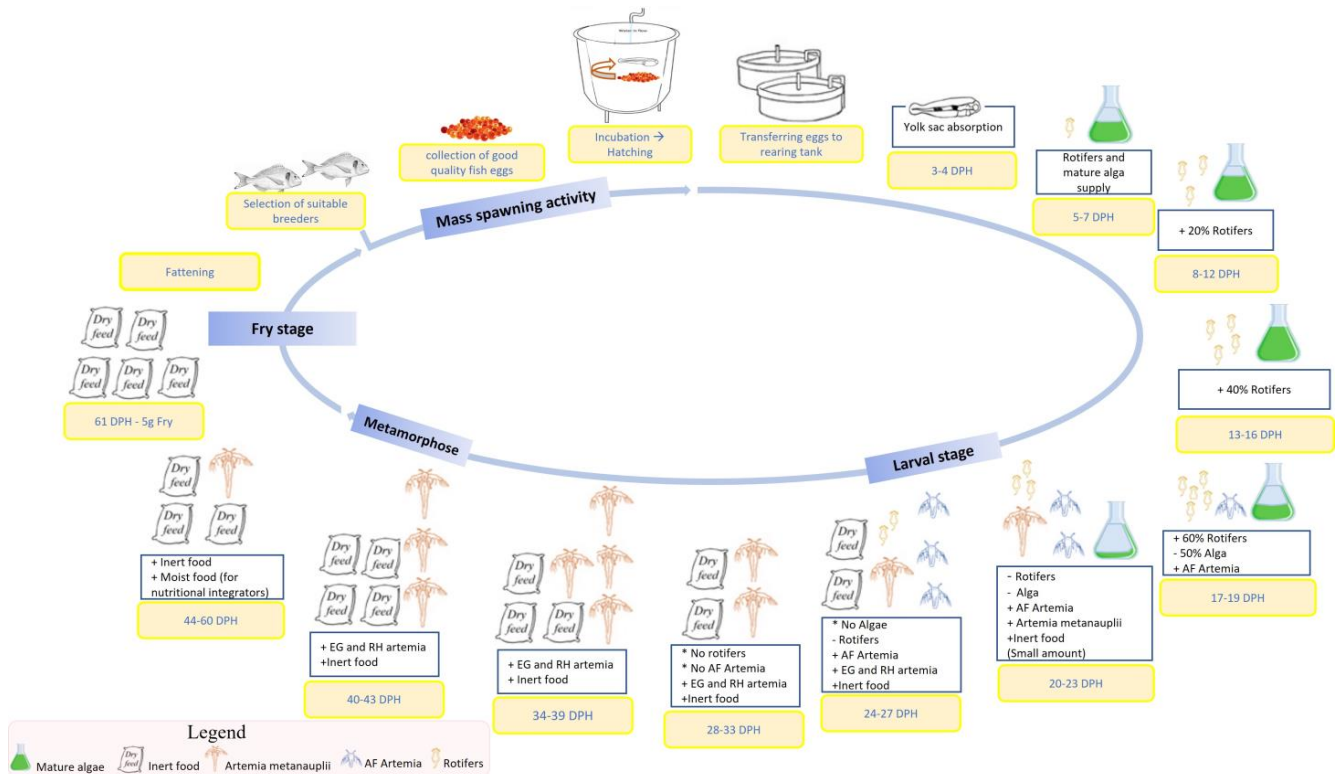


Figure 3. The production cycle of gilthead seabream.

Those dietary requirements are specific to a rearing density of 150 to 200 larvae per liter of larvae and 10–20 fry per liter at a temperature of 18 °C and a salinity of 35 to 37 ppt. Thus, variations in the rearing system and condition mean there are different requirements.

7. Aquaculture Challenges

Over the past twenty years, the gilthead seabream aquaculture industry has undergone a rapid development with impressive advancements in rearing methods, disease management, nutrition, and industrial hatcheries knowledge. As a maximal yield in growth success may come into reach, quite a few challenges emerge with respect to the overall quality of the fry. The quality of fish depends on morpho-anatomic and organoleptic features that should closely resemble those of wild fish, which is the quality reference for the consumer [20]. Various studies have reported the occurrence of morphological anomalies induced during the embryonic and post-embryonic stages, hindering the efficiency of the production cycle [11,14,20,22]. These abnormalities, affecting as much as 80% of the fingerling production, cause an enormous economic slump in the industry. They primarily affect the survival rates, growth, biological performance, and quality of fish, the consumers’ overall perceptions of fish, and thus, the cost-efficiency of marine fish aquaculture [90,91]. A notably higher prevalence of anatomical abnormalities can be noted in gilthead seabream produced in intensive aquaculture compared to wild-caught animals [20].

Although there have been advancements in rearing techniques, the hatchery conditions are still far from ideal. This may explain the fact that the most frequent abnormalities are recorded at the beginning of intensive gilthead seabream culture, long before osteological deformities are externally visible [20,92,93]. Skeletal abnormalities will only become visually identified once the fish reach a size of over 0.5 g. Fish carrying such deformities

must be detected and removed immediately since they will compete with the healthy fish for food and space [78]. Moreover, infectious disease outbreaks are another major threat to the aquaculture industry [94].

During the specific 17th workshop of the European Association of Fish Pathologists e.V. (EAFP), experts in the Mediterranean aquaculture of gilthead seabream established the baseline of sanitary issues. They reported that viral nervous necrosis (VNN), known as well as viral encephalopathy and retinopathy (VER), is the most pressing concern in Mediterranean aquaculture succeeded in terms of pathogenicity via bacterial and parasitological infectious diseases [95]. VNN or VER pathogenesis was associated with a vacuolation and necrosis of the nervous cells ensued by neurological damages, an increased mortality rate, and reduced growth [96]. It was believed that seabream possess resistance against VNN until redundant cases of high mortality attributed to the emergence of a new VNN strain was reported [97,98]. This has raised the necessity to characterize the Nodavirus species behind the loss of resistance in gilthead seabream and the possibility of undertaking preventive actions via selective breeding enhancement with resistance against NNV [99].

According to the EAFP, the second and third places go to bacterial and parasitological contagious diseases [95]. Despite the presence of vaccines and antibiotics, the proper management of bacterial pathogens like *Photobacterium damsela* subsp. *piscicida* and *V. anguillarum* remains a top priority. Among the parasitic diseases, however, the first importance was given to the gill flukes, which represent a major sanitary issue in the whole northern African production region and the Eastern and Western Mediterranean areas, resulting in high mortalities [95,100].

To overcome this issue, intensive selective breeding programs have been adopted for gilthead seabream under the Mediterranean mariculture, improving the growth performance [101], morphology [102], and the genetic resistance to pathogens [103] and preventing the impact of diseases [104]. Indeed, this highly valuable tool showed a high genetic gain of 12.5% in disease resistance per generation [105], namely the seabream resistance to pasteurellosis with a genomic heritability estimated by 0.32 [106] and a 5 to 29% increase in the growth rate per generation [107,108], creating genetically enhanced seeds. Still, the application of this approach is conditioned by sufficient genetic variability within the species [102].

The genomic selection tool employs genomic markers for estimating genetic relationships among individuals and evaluating their breeding potentials, thereby enhancing the efficiency of selective breeding and genetic improvement per generation [81].

8. Conclusions

In this review, we appraised the multifaceted realm of gilthead seabream aquaculture, analyzing its taxonomic, biological, and growth-related bibliographies. Through a systematic puzzle of its life cycle, growth characteristics, and genetic dynamics, we aimed to supply a profound understanding of the species' ecological and physiological requirements. Furthermore, by scrutinizing the breeding techniques, the complete production cycle, and culture practices, we exposed the elaborate processes and considerations involved in rearing gilthead seabream. This review also underlined the challenges that face the aquaculturists of seabream. Indeed, even though the accumulation of knowledge on gilthead seabream's functional and biological characteristics has significantly improved the aquacultural aspects, namely their reproductive success and survival, their hatchery conditions are still far from ideal, resulting in frequent challenges entailing significant economic losses. Thus, in-depth examinations of the molecular pathways behind those functional and biological characteristics (growth, skeletogenesis, and disease resistance) and the hatchery condition are needed.

In conclusion, we believe that an intricate balance between scientific understanding, the accumulation of knowledge, and practical application will shape the future of gilthead seabream aquaculture. Through dedicated research, new policies, and a commitment to

environmental stewardship, we can enhance an ecological industry that benefits both the ecosystem and the global demand for safe and healthy food.

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Abbreviations

Abbreviation	Meaning
DPH	Day post hatching
HPF	Hour post fertilization
HUFAs	Highly unsaturated fatty acids
SGR	Specific growth rate
Se	Selenium
Zn	Zinc
Mn	Manganese
Ca	Calcium
SNP	Single-nucleotide polymorphism
VER	Viral encephalopathy and retinopathy
VNN	Viral nervous necrosis
EAFP	European Association of Fish Pathologists

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