A review on cobia, *Rachycentron canadum*, aquaculture

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Abstract
Cobia, *Rachycentron canadum*, is an important species for aquaculture worldwide. Production technology from egg to market was established in the early 1990s and continues to be perfected to this day. This species exhibits extraordinary scope for growth and can reach between 4 and 8 kg in 1 year, with females growing almost twice as fast and large as males. Despite continuous progress in maturation, spawning, larval rearing, fingerling production, nutrition, health management, genetics, and growout technology, overall cobia aquaculture production worldwide has been slow in the last decade. One of the biggest challenges remains the development of practical commercial feeds that are ecologically and economically efficient for this species. Feed conversion ratios are still very high, ranging from 2.0 to 3.0:1. In addition to nutritional challenges, diseases such as *Photobacterium*, *Amyloodinium ocellatus*, and *Brooklynella hostilis* continue to impact cobia aquaculture production worldwide. Genetics and breeding programs for cobia are still at their infancy. We report on current status of cobia...
breeding efforts as well as on advances on developing female monosex populations to exploit the sexually dimorphic growth in this species. Nutrition, health, and genetics will be the greatest drivers to improve overall performance and increases in production of the cobia aquaculture industry.

**KEYWORDS**
breeding, cobia, hatchery, overview, production

1 | INTRODUCTION AND BACKGROUND

Cobia, *Rachycentron canadum*, is an important marine fish species for commercial aquaculture throughout their distribution range in tropical and subtropical regions around the world. This species has historically received considerable attention from researchers, and there have been hundreds of scientific and technical publications on various aspects of their biology, ecology, physiology, fisheries, nutrition, genetics, and aquaculture in general. We review progress and limitations of cobia aquaculture worldwide and report the latest technological and scientific advances in the field.

1.1 | Overview of historical information to current status of knowledge

The earliest documented account on cobia available is from 1766, by Alexander Garden in Carl Linnaeus’s *Systema Naturae*, where it described cobia as *Gasterosteus canadus* (Daugherty & Benetti, 2017). Since then, there have been a growing body of literature covering all aspects of this fish. All research of the species in the 19th century and up to the mid-20th century covered wild populations of cobia detailing their habitat, distribution, and parasitism on the species by other organisms in both the Atlantic Ocean and the Pacific Ocean. It was not until the 1960s that the first documented observations were published exploring and describing an important biological trait associated with aquaculture viability: the courtship behavior and biological traits associated with spawning of wild cobia. The first accounts of cobia culturing techniques were recorded in the 1970s, yet the majority of the published literature remained focused on wild fish distributions, parasitism, population dynamics, fisheries, and habitat descriptions. Shaffer and Nakamura (1989) thoroughly reviewed their biological information.

By the late 1990s, another important milestone in the aquaculture of cobia was published exploring aspects in the culture of the species on Hsiao Liu Chio Island in the waters of Southeast China (Chang et al., 1997). The beginning of the 21st century marked a turning point in cobia research with several studies exploring various aspects of their nutritional requirements, fish health, genetics, larviculture, growout, and the impacts of culturing cobia on water quality and the environment. Of the now 530+ publications on the species, approximately 70 were published before the 21st century, and recent research activities have been dominated by nutrition (>200), fish health (>280), and culture of the species (>150) within the 21st century. Estrada, Yasumaru, Tacon, and Lemos (2016) produced an annotated bibliography of the species from 1967 to 2015, highlighting research on broodstock management, larviculture, nutrition, health, biology, fisheries, and aquaculture. The University of Miami Aquaculture Program maintains a bibliographic reference list of cobia literature as well (Daugherty & Benetti, 2017).

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salmon, *Salmo salar*; Japanese flounder, *Paralichthys olivaceus*; sea bream, *Sparus aurata*; and sea bass, *Dicentrachus labrax*. Cobia have been cultured at experimental, demonstration, and commercial feasibility levels in Asian countries (Taiwan, China, Vietnam, and others), Australia, United States mainland, Puerto Rico, Dominican Republic, Martinique, the Bahamas, Cuba, Mexico, Belize, Panama, Colombia, Ecuador, Chile, Denmark, and Saudi Arabia. The majority of cobia hatcheries and farms in these countries were no longer in production in 2020. The rigorous, difficult protocols and demands of culturing this species prevented most operations to expand to commercial levels. An analysis of the global situation points to the fact that, despite expectations, the environmental and nutritional requirements of cobia could not be met in the early attempts in most of those countries. Likewise, several U.S. academic/state/federal research facilities have had difficulty maintaining their own spawning broodstock with consistent production to justify the cost of maintenance, and the commercialization of hatchery technology and production has limited access to eggs and larvae to many researchers that would otherwise continue cobia work. Despite continuous progress in maturation, spawning, larval rearing, fingerling production, nutrition, health management, genetics, and growout technology, overall cobia aquaculture production worldwide has been slow and nearly plateaued in the last decade. Cobia production in China, Taiwan, Panama, and Vietnam—the most important producing countries—is estimated to have been 53,000 m.t. in 2020, an increase of only 3% from the previous year. Since 2010, production in these countries has fluctuated around levels of 40 to 50,000 m.t. (Figure 1; Tveterås et al., 2019).

In recent years, published research into cobia aquaculture has become more narrowly focused and less prolific, likely due to the proliferation of private companies involved in cobia aquaculture and their attempts to preserve their own proprietary knowledge. Still, there are certain topics that have received significant academic attention including fish health and disease mitigation, nutrition, and food quality. Significantly, there have also been a limited number of forays into the development of more efficient, high-growth production models which have yielded encouraging results.

From a fish health perspective, characterization techniques of the effects of *Streptococcus* spp. and *Vibrio* spp. have received particular attention because of their proliferation in cage culture (Maekawa, Wang, & Chen, 2019; Ramachandra et al., 2020; Rameshkumar et al., 2017). Some attempts at developing reliable vaccination protocols against these particular pathogens have been reported with limited effectiveness (Eto et al., 2019; Nguyen et al., 2018; Nguyen, Nguyen, Wang, Wang, & Chen, 2020). Effects of endocarditis and *Photobacterium* spp. infections have also been quantified, demonstrating negative impacts on the overall aquaculture performance (Tran, Chen, Chaung, & Cheng, 2019; Tran, Lee, Guo, & Cheng, 2018; Warren et al., 2017). In one theoretical model, Lee et al. (2020) demonstrated the compounding negative effects of a heat wave and harmful algal bloom in cage-culture cobia, highlighting the emerging dangers of climate change on the tropical aquaculture industry.

![Figure 1](image-url)  
**FIGURE 1** World cobia, *Rachycentron canadum*, estimated production data.  
*Source: Tveterås, Jory, and Nystoyl (2019)*
Cobia’s greatest asset is also its main drawback for aquaculture. Although this species has been successfully cultured using traditional cages and ponds in Asia, these systems present clear environmental limitations. This, along with high production costs required for high energy, high-protein diets, in part explains the slow rate of global production expansion. Precisely because of its very fast growth rates, this species demands exceedingly high environmental and nutritional conditions to thrive. Their physiological, nutritional, and environmental requirements by far exceed those of other commercially raised marine fish and are very difficult to meet. Although the potential clearly exists, the commercial failure of several cobia farms located in near shore, coastal areas, as well as land-based ponds and RAS in the Americas over the years, indicates that it is difficult to raise this species under conditions other than those presented in the offshore environment—where highly dissolved oxygen concentrations, stronger currents, and greater depths increase the carrying capacity of the sites. To this end, it is not a coincidence that the only large operating cobia farm in the Americas is Open Blue Sea Farms (OBSF) in Panama. It is located in an exposed, high-energy site offshore, providing the adequate environmental conditions for this species. OBSF operates under these conditions utilizing submerged offshore cages, However, raising fish under these conditions requires advanced technologies that are automated, complex, and expensive to establish and operate. Hence, cobia produced offshore must be sold at high prices to compensate for the high production costs, thus limiting its demand in a highly competitive white fish market. These drawbacks are limiting cobia aquaculture expansion to the industrial level.

1.2 | Artificial propagation and closed-cycle aquaculture technology

Several authors have studied and published extensively on most aspects related to cobia biology and aquaculture (Arnold, Kaiser, & Holt, 2002; Benetti et al., 2003, 2006; Holt, Kaiser, & Faulk, 2007; Kaiser & Holt, 2005). Research and development efforts have been directed to the growth, reproduction, and artificial propagation of this species. Following the success of cobia aquaculture in Taiwan (Liao, 2003; Liao et al., 2004; Su, Chien, & Liao, 2000), the technology for raising cobia from egg to market has been well understood in the Western hemisphere as well. It was anticipated that the prospects for large-scale commercial aquaculture of this species in the Americas and the Caribbean were extraordinary (Benetti et al., 2007). Benetti, Orhun, et al. (2008), Benetti, Sardenberg, et al. (2008), Benetti et al. (2010), and Stieglitz et al. (2012) reported on most aspects related to cobia hatchery and closed-cycle aquaculture technology. These authors reported on successful capture, transport, acclimation, broodstock maintenance, maturation, and conditioned year-round volitional spawning of large numbers of high-quality eggs with high fertilization. Cobia year-round spawning has been shown possible through the control and manipulation of water parameters (Stieglitz, Benetti, Hoenig, et al., 2012). The maturation systems used for conditioning broodstock cobia to volitionally spawn have been described by Benetti, Sardenberg, et al. (2008) and Stieglitz, Benetti, Hoenig, et al. (2012). In summary, selected breeders are maintained on a strict feed regimen of high-quality sardine, squid, and shrimp, along with a custom maturation stimulator and conditioner consisting of Algamac MADMAC-MS, Astaxanthin, Lecithin, Taurine, and Vitamin/Mineral Premix. Maintaining fish at an appropriate sex ratio of 2:1 (female to male) reduces stress due to competition between males, allowing for female ovulation and hydration without being aggressively chased. Optimal temperatures for natural spawning are between 27 and 30°C. Another component believed to reduce stress and improve spawning consistency is maintaining “cleaning stations” inside the maturation tanks. These structures are stocked with neon gobies, Oceanops ocellatus, which are efficient at cleaning ectoparasites from the gills and skin of a variety of broodstock marine fish (Zimmerman et al., 2001). At the University of Miami Experimental Hatchery (UMEH), cobia broodstock continue to be held in 50–80 m³ semi-RAS (recirculating aquaculture system) tanks with temperature control to allow for conditioned spawning on and off season. UMEH facilities have and continue to produce fertilized cobia eggs at commercial scale quality, volume, and consistency since the early 2000s. Using this technology, we have obtained over 270 spawning events during the last 5 years, averaging five volitional spawning events per month. During this time period, cobia broodstock have produced over 1.4 million eggs per spawning event, with
an average of 2.5 L of fertilized eggs and fertilization rate above 80%. These quantities of high-quality eggs are sufficient to support the development of commercial growout activities (Benetti et al., 2020).

Benetti, Orhun, et al. (2008) and Benetti, Sardenberg, et al. (2008) also reported larval husbandry protocols consistently yielding 5–35% survival rates through the graded fingerlings stages, as well as the production of hundreds of thousands of juveniles that were used to develop commercial aquaculture of this species. Nursery and growout performance along with survival rates and feed conversion ratios (FCRs) were also reported for offshore submerged cage systems in the Caribbean by Benetti et al. (2010), and in RAS in Northern Chile by Díaz-Muñoz et al. (2019). These authors reported extremely fast growth rates for this species in cages (4–6 kg) and in RAS (4 kg) in 12 months from eggs, respectively, corroborating previous accounts for this species in the wild (Shaffer & Nakamura, 1989). A direct comparison of the growth rates of cobia and mutton snapper, *Lutjanus analis*, in cages studied by the authors showed that, at 45 days post hatch, cobia juvenile averaged 5.5 g and 11.5 cm, whereas the mutton snapper averaged 0.2 g and 2 cm. After being stocked in cages and raised for 10–12 months to harvest size, the cobia ranged in size from 4 to 6 kg and the snapper from 0.4 to 0.6 kg (Benetti et al., 2002; Benetti, O’Hanlon, et al., 2010). Mutton snapper represents an appropriate species for comparison since their growth rates are similar to many other species occurring in the habitat and distribution of cobia. Stocking densities and temperature are crucial determinants for the overall aquaculture performance of this species. Within our experience, considering existing and empirical data as well as anecdotal evidence, rates of growth, survival, and FCRs of cobia seems to be inversely proportional to stocking densities. Also it is noteworthy that the environmental footprint of cobia aquaculture in a commercial offshore cage farm located off the Atlantic Coast of Panama was studied and reported by Welch et al. (2019), who found no significant or lasting cumulative impact on the benthic and the water column surrounding the farm.

1.3 | Physiology, metabolism, and energetics

Over the years, research has been conducted on cobia metabolism and energetics. Feeley, Benetti, and Ault (2007) studied the oxygen uptake and rates of nitrogen excretion in early life stages of cobia. This study reported high oxygen consumption and ammonia excretion, which were expected for a species of such fast growth rates, particularly during the early life stages. Watson and Holt (2010) developed a complete energy budget for juvenile cobia, concluding that cobia’s rapid growth rates during the juvenile stages derive from high energy intake and oxygen consumption rates and high feed efficiency. Prior to those studies, Sun, Chen, and Wang (2006) and Chen et al. (2009) studied the effect of temperature and salinity on growth and energy budget of cobia juveniles and found that a modal distribution is observed within the range of 20–35°C and 20–35 ppt, respectively, with increasing efficiency up to 30°C and 30 ppt, decreasing afterwards. Salinity has been shown to impact the growth and physiological responses of cobia in captivity (Antony, Reddy, Sudhagar, Vungurala, & Roy, 2020), and there have been a number of studies that have documented salinity impacts on various endpoints, such as growth and survival, in this species (Atwood, Young, Tomasso, & Smith, 2004; Chen et al., 2009; Denson, Stuart, Smith, Weirlch, & Segars, 2003; Resley, Webb Jr, & Holt, 2006; Santos et al., 2014). In general, cobia are tolerant of a wide range of salinities, and such tolerance can offer a number of advantages from an aquaculture perspective. With the growth of the cobia aquaculture industry in the past few decades, commercial-scale production hatcheries are sometimes located in areas distant from growout sites. In such scenarios, cobia seedstock (i.e., fingerlings) must be shipped using air freight in live-transport boxes over a period of 18–30 hr. Research aimed at optimizing the shipping process for juvenile cobia has indicated that transport biomass, corresponding to the number of live fish, within shipping boxes can be significantly increased by reducing water salinity during such extended air-freight shipments (Stieglitz, Benetti, & Serafy, 2012). Much of the salinity-related physiological research with cobia has centered on juvenile-stage fish, and there is not much information available on salinity impacts in larger life stages. However, given the fact that wild cobia are routinely encountered in estuarine areas, such a wide range of salinity tolerance may extend throughout the entire lifecycle of the species. The metabolism and swimming energetics of cobia have also been investigated in an effort to optimize
production methodologies for this species (Stieglitz et al., unpublished) as well as to assess the impacts of crude oil exposure on cardiac function and aerobic capacity (Nelson et al., 2017). To assist in determining optimal conditions for raising them in land-based RAS (hatchery and nursery stages) and offshore cages by OBSF in Panama, significant ongoing efforts are being made in research on nutrition, energetics, and the swimming performance of juveniles and adult cobia at UMEH.

2 | BREEDING PROGRAM

Modern genetic tools for cobia breeding are in the process of being implemented or are under development. Using a genotyping by sequencing approach (GBS), a single nucleotide polymorphism (SNP) marker was identified and has now been validated and is routinely used to predict genetic sex in cobia. Cobia is a species where there is no clear sexual dimorphism for identifying sex. In addition, a low-density (<200 SNPs) panel has been designed that allows assignment of progeny to parents and sorting of families in breeding programs. This panel has also been used for more sophisticated breeding applications including genomic selection. Mapping of the full cobia genome is underway as a collaborative effort among James Cook University, Beijing Genomics Institute (BGI), the University of Chile, and OBSF. The results of the cobia genome sequence will produce major improvement in the genomic resources available for cobia and development of larger SNP panels (>2000 SNPs) that can be used for genome wide-association studies for important traits such as disease resistance and improved genomic selection approaches. These studies are ongoing.

Initial progress on genetic gains in desired traits of cobia for aquaculture has been limited to a basic breeding program utilized at UMEH aimed at domesticating the stock to create independence from natural stocks. Research started several years ago by initially collecting and maintaining wild fish from different collection sites in the Gulf of Mexico and the Atlantic Ocean in southern Florida. The fish were not initially genotyped, yet it was assumed that they belonged to two different populations. Males from one group of fish were crossbred with females from another group and their best performing offspring were subsequently successfully bred to capitalize on acquired desirable traits toward domestication, particularly growth, disease resistance, and survival. We have produced first generation (F1s) and second generation (F2s) over the years and are currently working on a third generation (F3) of selectively bred broodstock that have been identified as producers of high-quality offspring. The cobia breeding program at UMEH is funded by OBSF. UMEH is currently expanding this collaboration with the Center for Aquaculture Technologies (CAT) to conduct genotypic analysis of cobia aiming at determining fish fitness, that is, individuals or families that perform better in terms of quality of spawns at the hatchery and in terms of growth, survival, and FCR at the farm. Low-density SNP panel genotypes will be used to track performance of groups of fish with high growout performance and identify their parental origin. This can be used to identify superior broodstock based on performance of known progeny.

At OBSF, collaborative work has led to the successful deployment of a family-based breeding program. The low-density SNP panel is used to assign progeny measured from commercial production conditions to source broodstock families, allowing assembly of tanks of superior broodstock based on evaluation of performance of progeny. In the same manner, poor performing broodstock can be removed from the breeding population. In addition, the low-density SNP panel has been used to build a genomic selection model. This allows implementation of genomic selection using very large training populations from commercial production conditions and data collected from processing the fish. In this sense, phenotypic information such as growth, fillet yield, and carcass traits can be incorporated into selection. A facet of this approach includes collecting data on disease resistance from true commercial production conditions, a program which was launched in the last year. Additionally, a medium-density (MD) array (>2000 SNPs) is being evaluated in order to improve the accuracy and thus rate of genetic gain from genomic selection.

Finally, efforts are underway to select for improved ability in cobia to convert feed to biomass or FCR. This trait is difficult to measure directly in individual fish, and individual measurements are needed to make rapid genetic
improvements in FCR. Overall, a general design using both phenotypic measurements through the whole production process and genotype screening of both the training and testing population will lead to further genetic gains, which address the core objectives of the breeding program. It is still the beginning of the path of utilizing modern genetics to improve cobia aquaculture production, and adjustments will be made along the road as new findings come to light.

2.1 | Sexual size dimorphism and monosex production

The primary trend in cobia research in recent years is addressing knowledge gaps associated with their commercial production, biology, nutrition, food safety, and the leveraging of molecular techniques and genomics for enhancing genetic traits, particularly growth, aiming at improving the aquaculture performance of the species. Dutney, Elizur, and Lee (2017) first quantified the apparent sexually dimorphic growth (females growing faster than males) and simultaneously described the first intersex individuals for the species. The following year, Molina et al. (2018) expanded this analysis to include the implications for the creation of monosex culture, which has been utilized to great effect in numerous finfish species cultured throughout the world. Cobia clearly show sexual size dimorphism (SSD) as adults, with females being significantly larger than males (Molina et al., 2018). Females are known to grow faster and larger than males, both in the wild (Shaffer & Nakamura, 1989) and in captivity (Benetti, O’Hanlon, et al., 2010; Díaz-Muñoz et al., 2019). Indeed, previous OBF R&D trials showed that, on average, females were shown to grow 30% bigger than males in the same period of time under same culture conditions. Morphological sexual dimorphism can be the result of ecological, functional, or adaptive selection. Hence, attempts have been made toward developing techniques to increase both the biotechnological and specifically the growth potential of this species by producing an all-female population. To this end, Molina et al. (2018) conducted morphological analyses in cobia juveniles aged 139 days (4.6 months), using geometric morphometrics—a multivariate method of analyzing and describing shape change. Interestingly, the authors reported that sexual shape dimorphism (SShD) in female cobia is expressed by elongated bodies and distance between pectoral and anal fins, pointing to fecundity-related morphological adaptations. The results indicate a high index of early sex determination during the juvenile stages, demonstrating the possibility of developing routine protocols that can be applied to increase this species production (Molina et al., 2018).

We have recently conducted attempts to develop neomales as a starting point to produce an all-female population with promising results. This economically significant sexually dimorphic trait available for optimization through gender manipulation is a method utilized in commercial aquaculture (Lokman & Symonds, 2014). Both direct and indirect gender manipulation require an understanding on the labile period, effective ways to gender reverse, and identification of ways to isolate the genotypic gender to effectively produce monosex cohorts. To date, none of this has been isolated in cobia. Using a series of increasing doses and duration of hormone exposures during the previously identified labile period, the gender ratio of a cohort of cobia was reversed to 70% male.

Following the identification of the labile period and effective hormonal gender reversal, a method to identify the genotypic gender of a cobia was next needed for monosex production. To this end, 10 male and 10 female F2 cobia 453 ± 75 g were prepared following technique described by Costa, Cioffi, Bertollo, and Molina (2013). After tissue sampling, each individual fish was necropsied, and gender was identified following Babatunde et al. (2018). Cell suspensions were photographed using an Olympus BX51 epifluorescence microscope coupled to an Olympus DP73 digital image capture system, using CellSens Standard 1.8.1 software (Olympus). Images were cropped and aligned to orient and position male and female karyotypes in sequence for analysis. Each male and female cell preparations showed the same number, and same karyotype morphology, making it ineffective for identifying genetic gender. Indeed, only roughly 15% of perciform species exhibit morphologically distinct chromosomes between the genders. The remaining 85% species do not possess distinct sex chromosomes (Galetti, Aguilar, & Molina, 2000). The general karyotype of cobia follows the basal perciforms’ karyotype, with a
diploid number of 48 (Costa et al., 2013; Costa, Cioffi, Bertollo, & Molina, 2015; Jacobina et al., 2011). No publications to date have attempted comparing male and female cobia cytogenetic results.

Many genetic tools have been used to find specific differences between groups. Groups can be categorized as species, populations, or genders. There is minimal genomic information available for cobia; sequencing technologies were employed to read fragmented DNA sequences and use single-nucleotide differences for analysis. There do exist various cobia research areas in the field of genetics looking into stock enhancement for a genetically distinct subpopulation (Darden et al., 2014), modeling to forecast genetic impacts of net pen failures (Darden et al., 2017), and evaluation of stock structure and boundaries (Perkinson et al., 2019). These research areas and genetic tools, although dealing specifically with wild populations, can be applied to aquaculture practices such as parentage analysis, broodstock breeding programs, and identification of improved production traits.

Production of sequencing data for cobia followed Wagner et al. (2017). A total of 40 cobia of known gender from 12 different families were selected for sequencing. Several GBS data analysis pipelines are available for sequence data processing and marker identification (Bradbury et al., 2007; Catchen, Amores, Hohenlohe, Cresko, & Postlethwait, 2011; Melo, Bartaula, & Hale, 2016). Each has its own strengths in sequence data handling and marker identification (Mastretta-Yanes et al., 2015). To this end, sequencing data pipelines were implemented to ensure that all suitable genetic markers were identified using GBS. This wide range of analysis tools identified several putative sex markers. Interestingly, the SNPs identified by the Stacks (Catchen et al., 2011) and UNEAK (Bradbury et al., 2007) bioinformatics pipelines genotyped all females as homozygous at the loci of interest, while males were mixed (either heterozygous or homozygous) at those sites. In processing complex GBS data bioinformatics, pipelines such as Stacks (Catchen et al., 2011), UNEAK (Bradbury et al., 2007), and GBS-SNP-CROP (Melo et al., 2016) are utilized to isolate and attribute association between loci and traits in large sets of highly repetitive sequencing data.

Using these methods, a genotypic female was gender reversed and produced sperm at UMEH in collaboration with OBSF. A small portion of the gonad, which constituted 7% of the total gonadal mass, contained both male and female germ cells. The small sample of the spermatozoa was used to test motility and the spermatozoa responded normally to seawater. Milt was then preserved in liquid nitrogen using commercial practices. To investigate post-thaw activation rate, a series of thaw trials were conducted. This process included a number of activation trials using previously frozen neomale milt. The remaining spermatozoa are now preserved for future use and production of both monosex cohorts and future neomales. Results are still preliminary and these efforts are ongoing. However, this is, to our knowledge, the first known instance of a neomale production in cobia.

3 | NUTRITION

Conversely, much work has been done and a vast amount of literature is available on cobia nutrition. Craig, Schwarz, and McLean (2006), Fraser and Davies (2009), and Rodríguez-González, Miguez-Lozano, Llopis-Belenguer, and Balbuena (2015) thoroughly examined the main nutritional studies conducted with this species. Although their nutritional requirements have been extensively studied, to date most practical diets used for commercial aquaculture of this species still need to be optimized. It is particularly important to determine the digestibility of ingredients used in their formulations for their different life stages in order to completely fulfill the exceedingly high energetic and overall nutritional needs of this species. Nutrition studies on cobia have been limited to juveniles (5–50 g), which are of much lower sizes than fish near or at harvest size (4–8 kg). The difference in nutritional requirement between juvenile and market-size cobia, even if minimal, would have an important commercial impact. This is because the vast majority of the feeds (>80%) are used when the fish are of large size (>2 to 4–8 kg). Such impact will be mostly felt on the protein and lipid levels, which are the two dietary components with the highest volume in all formulations. The more precisely a diet can meet nutritional requirements of the target fish size, the more economic benefits will be incurred with increased growth, FCR, and survival along with decreasing waste excretion, lowering environmental impact in aquatic systems.
Even though the nutritional principles are similar for all animals, the amounts of the required nutrients vary broadly among species. There are ~40 essential nutrients in fish diets, which can be categorized in five groups: proteins, lipids, carbohydrates, vitamins, and minerals. Based on the premises that nutrition is a key component for the welfare and successful development of any species, and that cobia exhibits high nutritional requirements, we will review each of these groups separately, summarizing the most important studies conducted by a number of authors worldwide (Table 1).

3.1 Protein and amino acids

The first published article to determine protein requirements in cobia was that of Chou, Su, and Chen (2001). The authors determined, by means of a regression analysis, a protein requirement of 44.5% for the juvenile stages. Craig et al. (2006) carried out a factorial study with two levels of crude protein (40 and 50%) and three levels of lipids (6, 12, and 18%) in juvenile cobia (7.4 g). The authors found significant differences in feed efficiency of cobia fed with the lowest level of protein. However, when they used slightly larger size cobia (49.3 g), there were no significant differences in feed efficiency due to the level of protein. Nonetheless, it is well known that the nutritional value of a high protein diet is influenced by the composition of its amino acids. For this reason, the choice of a protein to be used in practical diet formulations should be based on its digestible amino acid profile and the quantitative amino acid requirements. Publications on cobia amino acid requirements are limited, and only 3 of the 10 amino acids considered essential have been investigated. Zhao et al. (2006) determined the methionine requirements in juvenile cobia. The authors established that to obtain the maximum growth and the lowest feed conversion ratio, the methionine requirement is 1.19% (dry diet) in the presence of 0.67% cysteine; this corresponds to 2.64% dry weight of the dietary protein. Based on the straight broken-line analysis of weight gain ratio against dietary methionine levels, Chi et al. (2020) estimated the optimal dietary methionine requirement for juvenile cobia to be 12.4 g/kg (26.9 g/kg dietary protein). A diet with the optimal level of methionine induces fish growth and is associated with increased IGF-I (the expression of insulin-like growth factor) and TOR (rapamycin [TOR] genes). Zhou, Wu, Chi, and Yang (2007) determined the nutritional requirement of lysine for juvenile cobia. The results of lysine requirement were 2.33% dry diet and 5.30% of dietary protein. The values of methionine and lysine are consistent with the requirement values of other commercially important farmed fish species. Ren, Ai, and Mai (2014) studied the dietary requirement of arginine in juvenile cobia. Based on specific growth rate and feed efficiency ratio, the optimal dietary arginine requirements of juvenile cobia were estimated to be 2.85% of the diet (6.20% of dietary protein) and 2.82% of the diet (6.13% of dietary protein), respectively, using second-order polynomial regression analysis. Watson, Barrows, and Place (2014) state that cobia have a greatly diminished capacity for the biosynthesis of taurine due to the high concentrations in their natural prey and thus may require supplemental taurine in artificial diets for culture. Salze, McLean, and Craig (2012), Salze, Craig, Smith, Smith, and Mclean (2011), and Lunger et al. (2007) demonstrated the critical importance of supplemental taurine in diets for cobia larvae and juveniles to incur improved survival, development, growth, and feed efficiency. Salze and Davis (2015) carried out a review on taurine supplementation and importance and state that several studies described marked improvement in growth and survival of larvae and juveniles when feeding taurine-supplemented feeds. With the available literature on cobia, it appears that taurine can be considered essential as they lack proper physiological pathways to synthesize it. Watson, Barrows, and Place (2014) evaluated taurine supplementation added to a traditional fishmeal-based formulation with juvenile cobia. These investigators indicated that increasing dietary taurine in a diet containing 34.5% fish meal resulted in significantly increased taurine levels in fillet, liver, and plasma, but did not significantly affect growth or production characteristics in cobia. Finally, Watson, Barrows, and Place (2014) evaluated taurine supplementation added to a traditional fishmeal-based formulation with juvenile cobia. These investigators indicated that increasing dietary taurine in a diet containing 34.5% fish meal resulted in significantly increased taurine levels in fillet, liver, and plasma, but did not significantly affect growth or production characteristics in cobia.
| Reference                        | Objective                                                                 | Results                                                                                                                                 |
|---------------------------------|---------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------|
| Chou et al. (2004)              | Substituting fishmeal with soybean meal.                                  | On the basis of growth, a quadratic regression analysis shows an optimum replacement of 16.9%.                                       |
| Zhou, Tan, Mai, and Liu (2004)  | Optimum level of fishmeal protein replacement with defatted soybean meal. | On the basis of weight gain, a quadratic regression analysis shows an optimum replacement of 189.2 g/kg.                               |
| Hsu and Chen (2005)             | Effects of partially substituting fishmeal with four soybean products.    | Increasing replacement of SBM and fermented SBM from 20 to 40% performed comparatively better than other diets.                         |
| Haung and Liao (2005)           | Effect of rapeseed as a protein source to partially replace fish meal on the growth of cobia. | The optimal level of rapeseed replacement was determined to be 10%.                                                                     |
| Wang, Wu, Xie, and Yu (2005)    | Optimal dietary soybean–fish meal ratio.                                 | Optimal dietary soybean–fish meal ratio was 1:1.8 in the basal diet (20% SBM).                                                        |
| Lungar, McLean, Gaylord, and Craig (2007) | Use of a yeast-based, certified organic protein source as a replacement for fish meal. | Growth and feed conversion ratio of diet with 25% dietary protein from yeast-based protein was equal to the control diet (100% FM). |
| Salze, McLean, Battle, Schwarz, and Craig (2010) | Use of soy protein concentrate and novel ingredients in the total elimination of fish meal and fish oil. | Diet formulated with soy protein concentrate (SPC), marine worm meal, nucleotide-rich yeast extract protein, and mannan oligosaccharide (MOS) had the best weight gain and feed efficiency with no mortality or negative impact on muscle and liver composition. |
| Saadiah, Abol-Munafi, and Utama (2011) | Use of local poultry by-product meal (PBM) for the replacement of fishmeal. | PBM could replace 100% of dietary fishmeal without adversely affecting the growth performance. An optimal replacement level of ~60% was recommended for better growth performance and efficient feed utilization. |
| Trushenski et al. (2011)        | Effect of replacing dietary fish oil with soybean oil on production performance and fillet lipid and fatty acid composition. | Soybean oil can replace a substantial amount of dietary fish oil, but aggressive replacement of fish oil may result in fatty acid deficiencies that can be amended with alternative sources of nutrients. |
| Zhou, Zhao, Li, Wang, and Wang (2011) | The potential use of poultry by-product meal (PBM) as a partial replacement of fish meal protein. | On the basis on protein efficiency ratio, a quadratic regression analysis shows an optimum replacement of 30.75%.          |
| Luo et al. (2012)               | Effects of dietary rapeseed meal (RM) levels on feed intake, growth, survival, digestion, and protein metabolism in relation to gene expression. | Protein from RM could substitute 125 g/kg fish meal protein without influencing the growth, feed utilization and protein metabolism. Higher substitution levels induced negative influences on feed intake, growth, and hepatic IGF-1 expression level. |
| Luo et al. (2013)               | Effects of dietary corn gluten meal (CGM) levels on fish growth, whole body composition, and protein metabolism. | 52.5% of FM protein could be replaced by CGM without significant influences on growth, feed utilization, and protein metabolism. |
3.2 | Lipids

For juvenile cobia, the lipid requirement was estimated at 5.76% (Chou et al., 2001). In another study, Wang, Liu, et al. (2005) used three isoproteic diets (47% protein) with three levels of lipids (5, 15, and 25% dry matter). The authors did not observe significant differences in growth between the cobia (7.7 g) fed diets containing 5% and 15% lipids. However, cobia fed a diet containing 25% lipids had a significant reduction in daily consumption, suggesting that lipid levels above 15% reduce growth due to a decrease in consumption. Cobia require both eicosapentaenoic (EPA) and docosahexaenoic (DHA) acids to meet dietary n-3 long chain polyunsaturated fatty acid (LC-PUFA) demand. Soybean oil supplemented with DHA is an effective alternative to fish oil in juvenile cobia diets (Trushenski, Schwarz, Bergman, Rombenso, and Delbos (2012). These authors found that the dietary n-3 LC-PUFA requirement of juvenile cobia can be largely satisfied by DHA, and that EPA can be present in trace amounts.

3.3 | Carbohydrates

Because commercial cobia feeds contain starch and cereal products, research on carbohydrate requirements is of great importance. Schwarz, Mowry, McLean, and Craig (2007) suggest that cobia can use up to 360 g/kg of dietary starch from low molecular weight carbohydrates such as dextrin. Webb Jr., Rawlinson, and Holt (2010) determined that cobia could use carbohydrates up to a level of 340 g/kg (dry diet) with an optimal protein–energy ratio of approximately 34 mg protein kJ⁻¹ metabolizable energy, respectively, corrected for analyzed protein content. Cui, Zhou, Liang, Yang, and Zhao (2010) found that juvenile cobia fed diets formulated with wheat starch or dextrin showed significantly improved weight gain, specific growth rate, and protein efficiency ratio when compared to the other diets containing glucose, sucrose, maltose, or corn starch. Finally, Ren, Ai, Mai, Ma, and Wang (2011) estimated that to achieve optimal specific growth rate and feed efficiency ratio for juvenile cobia, a dietary starch supplementation of 21.1 and 18.0%, respectively, is required. These levels are similar to those published by Webb Jr. et al. (2010) when commercial diets for cobia (17–20%) were used.
3.4 | Vitamins and minerals

Although very small amounts of supplemented vitamins are required in the diets, they are essential nutrients necessary for the growth, health, and reproduction of organisms. Mai et al. (2009) determined the choline requirements in juvenile cobia. The requirement for best weight gain, determined by broken-line analysis, was 696 mg/kg of diet in the form of choline chloride. Liu et al. (2010) investigated vitamin B₆ requirements in juvenile cobia. Specific growth rate had an improved trend with the increase of dietary vitamin B₆ from 0.22 to 3.87 mg/kg, but levels higher than 3.87 mg/kg had no significant differences. With a broken-line model for specific growth rate, a requirement of vitamin B₆ between 3.09 and 3.26 mg/kg was recommended by Liu et al. (2010). In addition, Wang, Xie, and Wu (2006) estimated an optimal supplementation of vitamin E, vitamin C, choline, and inositol to be 45, 750, 3,000, and 400 mg/kg, respectively, for juvenile cobia. Zhou et al. (2013) examined the effects of vitamin E on growth, lipid peroxidation, and nonspecific immune responses in juvenile cobia. Specific growth rate, protein efficiency ratio, feed efficiency, and survival improved with the increase of dietary vitamin E. According to a second-order polynomial regression of weight gain and lysozyme, the dietary vitamin E requirement is 78–111 mg/kg. Regarding minerals, Liu et al. (2013) investigated the dietary manganese requirement for juvenile cobia and found that the dietary level significantly influenced survival, specific growth rate, feed efficiency ratio, and the concentration of manganese in whole body, vertebra, and liver. A broken-line regression of specific growth rate indicates that manganese concentration in whole body and vertebra and the manganese requirements of juvenile cobia are of 21.72, 22.38, and 24.93 mg/kg diet in the form of manganese sulfate, respectively. Xu, Dong, and Liu (2007) determined, through a broken-line regression, that a minimum requirement for dietary zinc for juvenile cobia is 42.86 mg/kg. There was no significant difference in feed conversion rate as a factor of supplemented zinc, but survival, weight gain rate, serum alkaline phosphatase, and zinc concentration in tissue and serum increased with the increasing dietary zinc levels. Yang et al. (2010), through a survival and weight gain study, recommended an optimum supplemental level of 200 mg/kg diet for iron and 110 mg/kg for zinc in diets for juvenile cobia.

3.5 | Fishmeal replacement

There have been numerous studies conducted on fishmeal (FM) replacement in juvenile cobia diets (Table 1). Although many studies focused on juvenile stages of this species, investigations using fish of larger size are rare. Suarez et al. (2013) reported that an FM replacement study with significant commercial impact was conducted to evaluate the aquaculture performance of larger size cobia weighing between 1.8 and 3.2 kg. The soy-based products used as FM replacement were de-hulled SBM, solvent extracted SBM, and a novel non-GMO variety of SBM (produced by Navita Premium Feed Ingredients). Suarez et al. (2013) reported that up to 80% FM could be replaced in larger size cobia, attaining a “Fish-In-Fish-Out” (FIFO) ratio of 1.3, without compromising growth performance or health. The ability to replace such high amount of FM indicates that developing more cost-effective and environmentally sustainable diets for all stages of the production cycle of cobia is possible without compromising health or growth rates of this species at larger sizes (Suarez et al., 2013). This study is among a number of studies investigating the value of incorporating alternative ingredients and by-products from processing into other food sources to enhance protein quantities and nutrient levels (Calixto et al., 2020; Fagundes, Rocha, & Salas-Mellado, 2018; Shirahigue et al., 2018; Sukeri, Sampath Kumar, Shaik, & Sarbon, 2021). Some of the relevant related studies summarized in Table 1 corroborate the need for additional research on cobia at all stages of the production cycle.

Besides nutrition, rearing density and salinity have also been shown to significantly impact the growth, physiological responses, and flesh composition of cobia in captivity (Antony et al., 2020; Silva, Trushenski, Schwarz, & Cavalli, 2020). Finally, as the cobia global aquaculture industry expands, there has been a concerted effort to explore the effects of harvesting, processing, and handling practices on the quality of the product that is being delivered to
the market (Baldi et al., 2018; Fogaça et al., 2017; Gonçalves & Santos, 2018; Remya, Mohan, Venkateshwarlu, Sivaraman, & Ravishankar, 2017).

4 | CONCLUSIONS AND RECOMMENDATIONS

Being commercially ready, the potential for continuously expanding cobia aquaculture industry worldwide, including in the United States, is enormous. As production technologies have improved over time, the research needs have evolved and are now centered on addressing the remaining knowledge gaps that exist for this species. In recent years, published research into cobia aquaculture has become more narrowly focused and less prolific, likely due to the proliferation of private companies and their attempts to preserve their own proprietary knowledge. Still, there are certain topics that have received significant academic attention, including fish health and disease mitigation, nutrition, and market product quality. Unfortunately, there have been a limited number of forays into the development of more efficient, high-growth production models, which have yielded encouraging results.

There is a continued need for cobia research in all aspects of production, including nutrition, physiology, biology, food safety, genetics, systems engineering, and animal health and welfare. Focusing on these areas will be essential to improve successful culture of cobia on a commercially viable basis. Under these broad fields, new tools are becoming available to assist producers to improve results of cobia performance from hatchery to harvest. For example, nutrigenomics and functional feeds can and should be used to enhance their immune systems, and microbiome control is key. Bacteriophages, probiotics, prebiotics, eubiotics, organic acids, essential oils, beta-glucans, monoglycerides, and nucleotides can all assist producers in gaining control over the organisms and the systems. It is recommended that further studies should be carried out in the following lines of cobia nutrition research: (a) determination of the nutritional requirements at different ages; (b) investigation of amino acids, vitamins, and minerals requirements; (c) supplementation of the existing information on digestibility and energy balance of protein ingredients of animal and vegetable origin; (d) replacement of fishmeal and fish oil in finishing diets; (e) monitoring and safeguarding the quality of commercial feed to prevent oxidation, reduce the use of low-quality ingredients, and improve transportation and storage conditions; and, (f) implementation of better feeding management practices. Finally, with regard to nutrition, we reiterate that these studies were conducted during very short periods of time in juvenile cobia, a stage characterized by very efficient FCR (1:1) and exponential growth. Hence, since 80% of the feed cost goes in the 1.5–4.5 kg stage, the commercial applications of most cobia nutritional studies are of limited value. OBSF and the University of Miami are currently conducting performance, digestibility, and nutritional studies on fish above 2 kg, to obtain data in the critical period of growth and where most inefficiencies are found and need refinement.

In conclusion, with so many favorable biological attributes, the prospects and potential of expanding cobia aquaculture to an industrial level clearly remain. Nutrition, health, animal welfare, and genetics will be the greatest drivers to improve overall performance of cobia aquaculture. Continuously expanding on the breeding program efforts will be crucial, as well as on perfecting neomas for a monosex, all-female population.

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