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Review

Digestive Physiology, Nutrition and Feeding of *Arapaima gigas*: A Review

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Abstract: The *Arapaima gigas*, a native fish species in the Amazon basin, presents particular biological and zootechnical characteristics, along with substantial economic value, that make it a promising candidate for its production within intensive aquaculture systems. To date, different studies have been conducted to (a) increase the understanding of its digestive physiology in relation to feeding habits, (b) determine its nutritional requirements at different developmental stages, (c) assess the potential use of alternative ingredients in diets, and (d) elucidate its feeding behavior patterns in captivity to improve feeding strategies. However, important gaps still remain in the available information related to the above-mentioned aspects that compromise the formulation of efficient and balanced aquafeeds used in the different production phases of this species. This article provides a comprehensive review of the current state of knowledge regarding digestive physiology, nutritional requirements and feeding strategies of *A. gigas* with the main objective of identifying areas that require further research for application in developing suitable and sustainable feeds for the species.

Keywords: enzymatic activity; diets; digestibility; feeding strategies; nutritional requirements; neotropical fish

Key Contribution: This review paper provides a comprehensive review of the current state of knowledge regarding digestive physiology; advancements in nutrition and feeding strategies developed over the past two decades in *Arapaima gigas*.

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1. Introduction

Arapaima gigas, a native species of the Amazon River basin, holds the distinction of being the world's largest freshwater fish. Its suitability for aquaculture is underscored by a range of favorable traits, including rapid growth, ease of adaptation to commercial aquafeeds, good meat quality, high fillet yield without intramuscular bones, strong market demand and widespread consumer acceptance [1–5]. The aquaculture of *A. gigas* plays a vital role in mitigating various negative impacts in some Amazonian regions, these include the reduction in wild fish populations, primarily due to overfishing in rivers, the expansion of agricultural land, and other human activities negatively affecting natural resources. Despite their interesting biological and zootechnical features, the production of *A. gigas* under intensive systems remains at an early stage of development, primarily due to the number of limitations that hinder its commercial advancement [4]. One main constraint pertains to the limited knowledge still existing on the fundamental and applied aspects of the digestive physiology of the species, as well as on its nutritional requirements in captivity. Although in recent years several studies have contributed valuable information on aspects like the functional characterization of the gastrointestinal tract, the determination of optimal protein and energy levels, the formulation of feed rations, and the assessment of ingredient digestibility in *A. gigas* [6–9], there remain substantial gaps in knowledge regarding other aspects of digestive physiology relevant to nutrition. These include some basic issues related to the biochemistry of the digestive tract or the nutritional requirements for lipids, carbohydrates, vitamins, and minerals, as well as practical applications of such knowledge to the formulation of feed rations, the incorporation of functional additives and the use of non-conventional ingredients. In this regard, it is worthwhile to note that a comprehensive understanding of digestive mechanisms and effective nutritional management is essential to formulate efficient aquafeeds capable of meeting the species' diverse nutritional needs throughout its life stages [10,11].

Considering all the above-mentioned information, the primary objective of this paper is to offer an up-to-date review of existing information on critical aspects concerning the digestion and feeding of *A. gigas*. Additionally, it aims to identify areas that warrant further investigation, with the ultimate goal of contributing to the establishment of strategies for the sustainable development of the species in commercial aquaculture.

2. Literature Review Methodology

Systematic research of scientific articles and technical papers published in English, Spanish and Portuguese was carried out in Google Scholar, Scielo, ScienceDirect, Scopus, Springer Link and Wiley Online Library databases using the Preferred Reporting Items for Systemic Reviews and Meta Analyses (PRISMA). A flowchart of the PRISMA method applied is detailed in Figure 1.

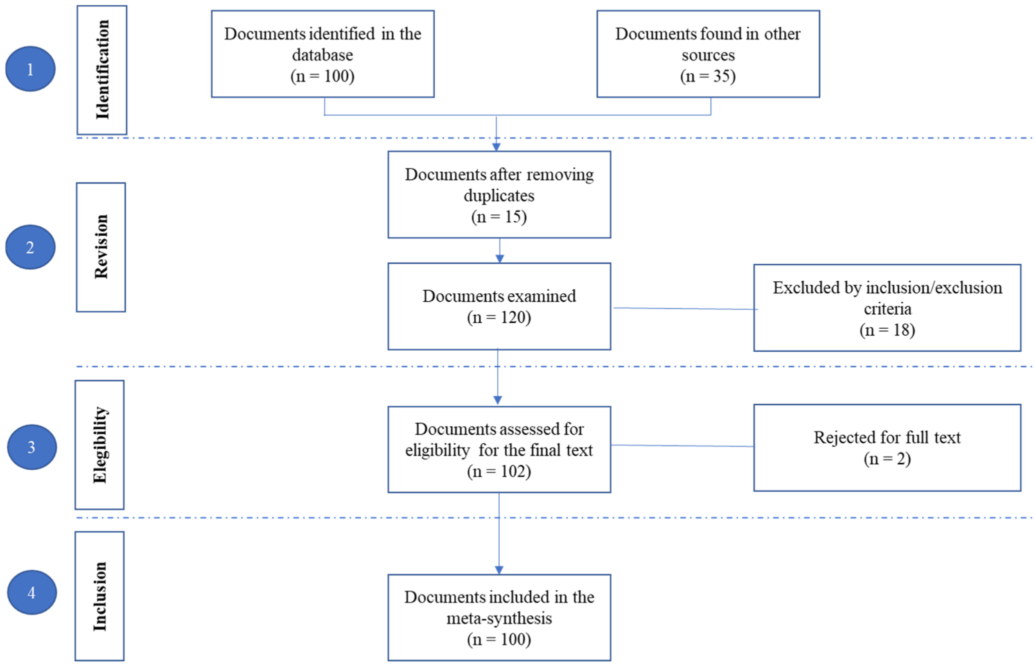

Figure 1. PRISMA flowchart for literature searches and article inclusion.

The words "*Arapaima*, diets, feed, nutritional requirements, enzymes, digestibility and culture" were used in the bibliographic search. The search was carried out from January to March 2023, with a time horizon of 2002–2022. Inclusion and exclusion criteria were used to process the information obtained. All articles or documents related to the species, nutritional physiology and feeding were considered, with the main exclusion criteria referring to documents that did not focus on the particular aspects of digestive physiology applied to the nutrition and feeding of the species. A total of 100 articles, research works, and technical documents were finally considered and organized into five categories: general review of species, digestive physiology, nutrition and nutritional requirements, digestibility, and feeding strategies. After categorizing the documents, the information was reviewed and analyzed with the aim of systematizing and identifying the gaps in knowledge still existing in the aspects studied.

3. General Aspects of the Species

3.1. Distribution and Habitat

Arapaima gigas is a native teleost native in the South American Amazon basin, which can reach a length of up to 3 m and body weight of 200 kg [12–14], and is considered the largest freshwater fish species. Commonly called "paiche" in Peru and Ecuador, it is also known as "pirarucu" in Brazil, "warapaima" in Colombia and "arapaima" or "de-chi" in Guyana [14–16]. The taxonomic classification of this species, according to Bezerra et al. [17], is as follows:

Division: Teleostei,
Subdivision: Osteoglossoporma,
Order: Osteoglossiformes,
Family: Arapamidae (Osteoglossidae),
Sub-family: Heterotidinae,
Genus: Arapaima,
Species: *Arapaima gigas* (Cuvier 1829) (Figure 2).

Figure 2. The *Arapaima gigas*, a native fish species in the Amazon basin.

Species of the genus *Arapaima* have been traced back to the Cretaceous and Tertiary Amazon periods and likely evolved from primitive bony fish [18,19]. Although traditionally regarded as a monotypic genus, *Arapaima* was recently considered to be composed of more than one species [20]. A distinctive characteristic of the Osteoglossiformes order, to which *A. gigas* belongs, is the ossification (hardening) of the tongue, which is made up of fine villi-form lingual teeth [18–21]. This bony tongue enables the crushing of food, thus functioning as an accessory organ of the gastrointestinal tract [21,22]. *A. gigas* is considered a tropical habitat species, thriving in water bodies with consistent temperatures ranging from 24 to 26 °C year-round [23]. It is naturally distributed in the sub-basins of the Amazon, Tocantins-Araguaia and Essequibo rivers, Brazil, Ecuador, Colombia, Peru, and the rivers of Guyana [24–26] (Figure 3). Over time, it has been introduced to the Bolivian Amazon [15,27]. At present, this species can also be found in Central America, North America and even Asia, including China, Indonesia, the Philippines, Malaysia, Singapore, and Thailand [28–31].

The preferred habitats of *A. gigas* are the low-gradient aquatic environments of the Amazon River and its tributaries, mostly lakes, in addition to connecting channels during seasons of low water levels [12,32]. These environments are characterized by low water flow, high depth, turbidity, abundant floating and emerging macro phytic vegetation, which in some cases, can cover the entire body of water, and frequent hypoxic conditions [12,33]. This species can also be found in shallow areas in slow flowing rivers [17,34].

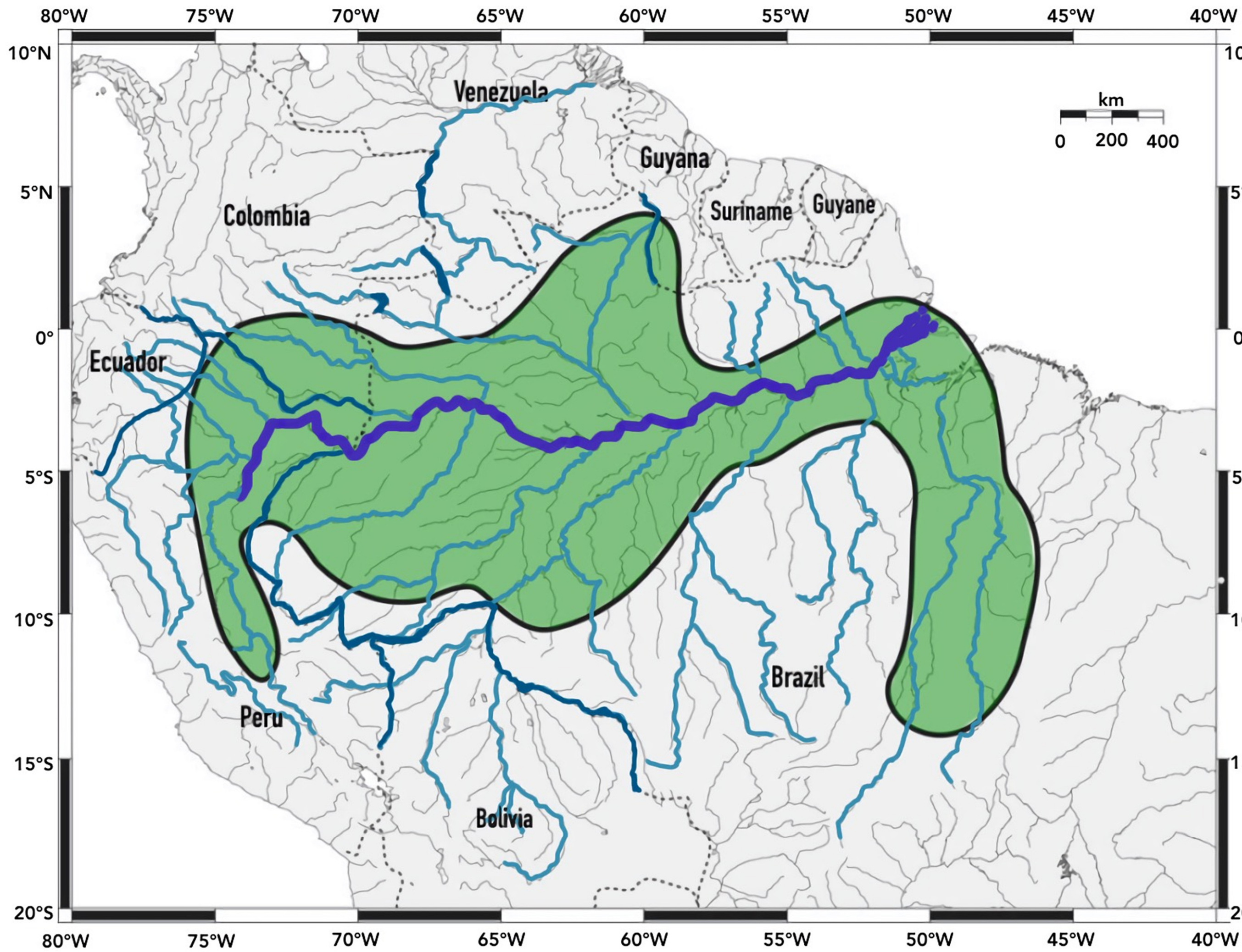

Figure 3. Map of the approximate natural distribution of *A. gigas* in South America [35]. "Reproduced with permission from Hrbek et al., Animal Conservation; published by John Wiley & Sons, 2005".

3.2. Feeding Habits

As a carnivorous species, *A. gigas* has a natural diet that primarily consists of small fish, crustaceans, mollusks and insects [19,33]. During the early stages, particularly as fry, it primarily consumes plankton, later transitioning to insects. In the juvenile stage, the diet mainly consists of small fish and microcrustaceans, but when they reach the adult stage, they feed exclusively on fish, crabs and prawns [19,36]. Studies suggest that there is no particular "prey target—size" [19]. *A. gigas* captures its prey through rapid movement of the head, often accompanied by a tail whip, producing a distinct high-pitched noise. This movement, involving the opercula lids, expels water taken in during the strike [37]. Fish prefer to feed during dawn or dusk, although they may also feed during the day. When temperatures rise, they seek refuge among aquatic vegetation to avoid intense sunlight, often remaining stationary at the water's bottom but emerging periodically to the water's surface to breathe atmospheric oxygen [38].

3.3. Culture and Production Cycle

A. gigas is well known for its excellent meat quality, high fillet yield (up to 50%) and remarkable rapid growth, which is unique among freshwater fish species, reaching up to 10 kg in a single year [4,13,39]. Consequently, the interest in cultivating this species has emerged over the past two decades [40–42]. The worldwide production of *A. gigas* was

2113 tons in 2022, with Brazil (2028 t) and Peru (85 t) being the two main producers [43,44] (Table 1).

Table 1. Production of *A. gigas* in Brazil and Peru 2003–2022 (in tons) [43,44].

Year	Brazil	Peru
2013	2301	94
2014	11,763	55
2015	8389	135
2016	1266	142
2017	1259	218
2018	1832	295
2019	1893	86
2020	1886	99
2021	2137	81
2022	2028	85

The remarkable growth in production in 2014 was due to various factors such as incentives granted by government authorities, investment by aquaculture companies and increased supply of fry [45,46].

A. gigas is typically farmed in earthen ponds, although floating cages are also utilized. Culture in land-based ponds involves from one to three well-defined production phases: pre-growth, growth, and final fattening. However, the specific stages may vary based on the size of the fingerlings at the beginning of fry-rearing and pre-growth processes. In some fish farms, particularly in Peru, where the emphasis is put on fingerling growth, only two main production stages are recognized: initial and final fattening [38]. Nevertheless, an increasingly popular approach is direct fattening, which involves seeding fingerlings previously conditioned to commercial aquafeed (typically above 15 cm in size) in ponds for final harvesting in a single production system.

Following the description made by Chu-Koo et al. [38], the fry-rearing stage begins with the capture of individuals from breeding ponds when they reach a minimum size of 2 cm. During this phase, fry initially consume zooplankton, followed by Artemia nauplii and a gradual transition to a balanced diet as a part of a feed training protocol. This phase typically lasts between 17 and 32 days, depending on the specific protocol used, and concludes when the fish reach sizes ranging from 7 to 8 cm [38]. Moving into the pre-growth stage, fingerlings, with sizes between 8 and 15 cm, continue their adaptation to balanced aquafeed and initiate their development towards the fattening stage. This last phase takes place during a period of 2 months in earthen ponds or other suitable culture facilities typically measuring between 300 and 500 m^2. During this time, the fish reach weights between 150 and 200 g and sizes ranging from 24 to 30 cm [38]. In the initial fattening phase, juveniles from this pre-growth stage are stocked in ponds measuring 500 m^2 at a density of 1 to 1.5 fish per m^2. This phase lasts approximately 3 months or until the fish reach 2 kg in weight; they are then selected and transferred to the final growth phase in which fish are stocked at a density of 0.25 individuals per m^2, typically in ponds ranging from 1000 to 2000 m^2 in size. During this stage, *A. gigas* can reach a weight of 10 to 12 kg after approximately 8 months or other weights dictated by market demand [38]. The life cycle and development of *A. gigas* from the larval stage to breeding and the production process from purchase and seeding of fingerlings to final harvesting are summarized in Figures 4 and 5.

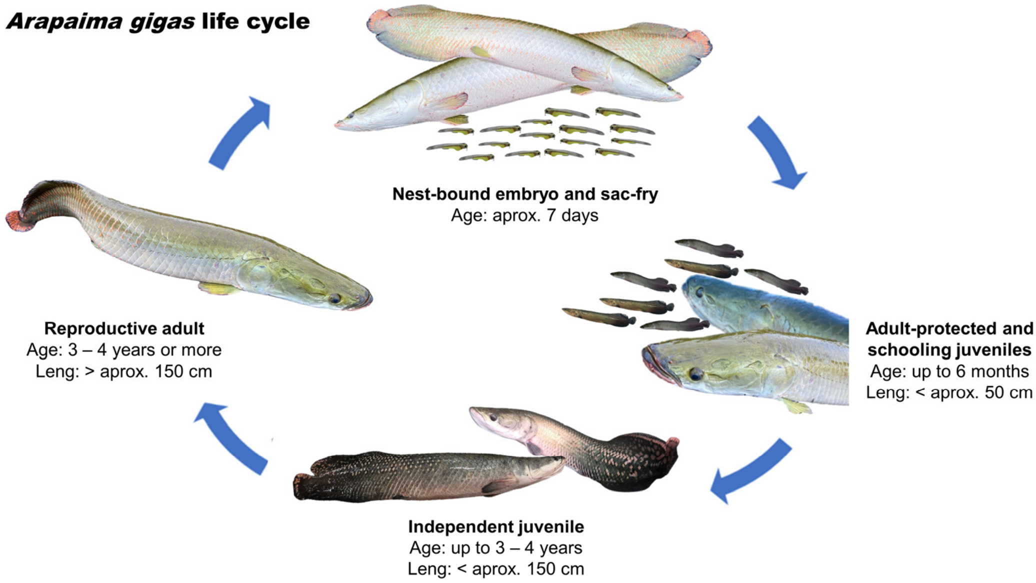

Figure 4. Life cycle of *Arapaima gigas* can be divided into four main stages: (1) nest-bound embryo and sac fry, (2) adult-protected, schooling juveniles, (3) independent juveniles, and (4) reproductive adults [47].

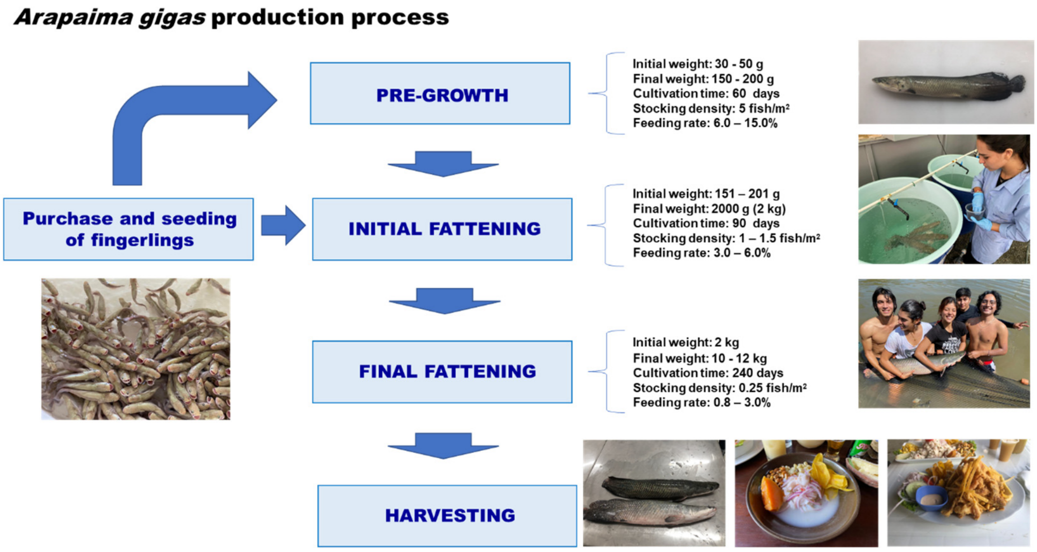

Figure 5. *Arapaima gigas* production stages: purchase and seeding of fingerlings, pre-growth, initial fattening, final fattening and harvesting.

3.4. Rearing Conditions

Optimal water quality conditions are crucial to ensure the optimal growth of *A. gigas*, and hence, it is essential to monitor parameters such as water temperature and pH in the culture units. It is worth noting that *A. gigas* is dependent on aerial respiration, obtaining most of the oxygen through its swim bladder [4,13,39]. This adaptation allows the species to inhabit waters with low levels of dissolved oxygen, providing an advantage over fish species that primarily breathe through the gills [1,10]. *A. gigas* can survive even in environments with levels of dissolved oxygen below 2 mg/L [48]. Despite its reliance on aerial respiration, this species still excretes CO_2 through the gills, needing low levels of this gas in the water for an effective exchange. For this reason, levels of CO_2 above 20 mg/L, particularly in juveniles, can increase stress and adversely affect health. *A. gigas* also exhibits notable tolerance to high concentrations of total ammonium; it has been shown that levels ranging from 0.8 to 2.4 mg/L do not significantly affect the development of the species in culture units [39]. Table 2 provides detailed information on some of the optimal water parameters for the culture of *A. gigas*.

Table 2. Suitable water quality ranges for the production of *A. gigas* [38,39].

Parameters	Stage: Fingerling		Stage: Fattening	
	Permissible Range	**Optimal Range**	**Permissible Range**	**Optimal Range**
Temperature (°C)	26.0–30.0	27.0–28.0	25.0–31.0	27.0–29.0
Dissolved oxygen (mg/L)	4.0–7.0	>5.0	4.0–7.0	>5.0
Ammonium (mg/L)	<0.05	<0.02	<0.05	<0.02
Nitrites (mg/L)	<0.05	absent	<0.05	absent
pH	6.0–8.0	6.0–7.0	5.0–8.0	6.5–7.0
Total alkalinity (mg/L $CaCO_3$)	>30.0	-	>20.0	-
Total hardness (mg/L $CaCO_3$)	>30.0	-	>20.0	-
Transparency (cm)	30.0–60.0	-	30.0–60.0	-
Carbon dioxide (mg/L)	<20.0	-	<20.0	-

Regarding the water requirement for the culture of *A. gigas*, there are no studies on the subject. It is known that the evolutionary aspect of the respiration of *A. gigas*, gill respiration and accessory respiration through the vascularized swim bladder, allows it to develop in environments with low levels of dissolved oxygen, characteristic of Amazonian waters [37]. This presumes a low water requirement for the culture of this species in conventional systems.

Considering an earthen pond of 10,000 m^2 and an average depth of 1.5 m, the volume of water in the culture enclosure is 15,000 m^3, which is necessary to obtain a biomass of 10,000 kg of *A. gigas* of 10 kg average market weight in 16 months of culture [38,39]. To ensure adequate fish development, a continuous daily replacement of 5–10% of volume of water is recommended [49], estimating a water requirement of 37.5–73.5 m^3/tons (1.30–2.55 L/min/tons). Furthermore, de Sousa et al. [50] determined the greywater footprint value to produce *A. gigas* at 64.51 m^3/tons, indicating the sustainability of the cultivation of this species from an environmental point of view.

4. Nutritional Requirements

Conducting experimental work with this species is inherently challenging for several reasons—mainly the limited availability of laboratories equipped with suitable facilities and experimental systems for maintaining fish of large sizes and the considerable cost associated with using *A. gigas* as biological material. Considering that nutritional requirements can vary depending on factors such as the size or stage of the species, the nutritional quality of protein sources in the diet, the production system, the experimental conditions and environmental factors, there is an increasing need to complement the existing research with information on nutrition requirements at different stages of development. Within this context, available studies have primarily focused on determining optimal levels of protein, energy and the energy/protein ratios.

4.1. Protein and Amino Acids

Different studies have assessed the requirements of crude protein (CP) in *A. gigas*, with values ranging between 30% and 56% of the diet, depending on the age/size of the individuals. Nevertheless, several other parameters may influence those values, like the type of rearing facility (floating cage, earthen pond), the duration of the experiment (from 4 weeks to 12 months) or the feeding system used (Table 3). In small juveniles of less than 100 g, some studies suggest optimal levels of around 50% CP for achieving the best weight gain [51,52], while others concluded that the best growth was achieved using diets containing 40% and 45% protein [53]. In a recent work conducted by Casado del Castillo et al. [54], the authors demonstrated that fish fed diets ranging from 44% to

48% protein exhibited the best growth and protein efficiency, while diets including 52% CP induced stress, affecting hemoglobin concentration and increasing oxygen demand. The levels of CP can be reduced as fish grow up; in juveniles of 120 g, Ituassú et al. [11] determined an optimal CP level of 48.6%, although they found that feed conversion and protein efficiency indices were not affected by reducing protein levels up to 33%. Juveniles of around 500–650 g present a requirement of around 40–45% CP [55,56]. On the other hand, protein requirements for fish of a higher size, over 1.5 to 4.0 kg seem to be around 36% [8,42].

Both practical information obtained from producers of commercial feeds and technical documents for rearing of *A. gigas* have established protein levels of 50% to 55% for the pre-starting stage (fish between 12 and 15 cm and weighing less than 15 g), 48% to 50% for the starting stage (fish larger than 16 cm and weighing between 15 and 20 g), 45% for the growing stage (fish in the juvenile stage, between 300 and 500 g), and 40% for the fattening stage (fish larger than 1000 g until harvest) [39,57].

Table 3. Optimal protein levels determined at different sizes and experimental conditions for *A. gigas*.

Initial Weight (g)	Optimal Protein (%)	Diet	Evaluated Parameters	Facility	References
40.72	53.76	Pelletized	WG	Fiberglass tank for 6 weeks	[52]
54.00	50.00	Pelletized	CF, FCR, SGR	Floating cage	[51]
68.75	44.00–45.80	Pelletized	FCR, PER, WG	Fiberglass conical tank 75 days	[54]
86.84	40.00	Extruded	FL, LG, FW, WG	Rectangular cement tank for 84 days	[53]
120.60	48.60	Extruded	FCR, SGR, WG	Floating cage for 45 days	[11]
133.00	40.00	Extruded	FB	Earthen pond for 12 months	[58]
500.00	40.00	Extruded	FCR, WG	Earthen pond for 110 days	[55]
654.44	44.53	Extruded	FCR, WG	Self-feeding system for 28 days (nutritional challenge)	[56]
1573.30	56.30	Pelletized	Not determined	Self-feeding system for 23 days (nutritional challenge)	[42]
2000.00	36.00	Extruded	FCR, WG	Tank system for 18 weeks	[8]
2025.00	37.40	Extruded	PER	Floating cage for 88 days	[59]

Adapted from López-Vásquez [60] and Guevara-Gutiérrez [61]. Abbreviations: CF, condition factor; FB, final biomass; FCR, feed conversion rate; FL, final length; FW, final weight; LG, length gain; SGR, specific growth rate; PER, protein efficiency rate; WG, weight gain.

Regarding the essential amino acid requirements for *A. gigas*, only two studies have been conducted based on the essential amino acid composition found in muscle tissue (Table 4).

Table 4. Estimated essential amino acid requirement (as % of dietary protein) of *A. gigas* based on the amino acid profile of muscle tissue following Rodrigues et al. [62] and Orosco-Napan [63].

Weight	1.66 kg		10.49 kg		0.94 kg
Environment	Natural	Controlled	Natural	Controlled	Controlled
Arginine	3.66	3.93	3.72	3.74	6.77
Histidine	1.14	1.26	1.09	1.12	1.03
Isoleucine	2.74	2.48	3.02	2.96	2.47
Leucine	5.25	5.00	5.31	5.40	3.11
Lysine	6.10	6.03	5.95	6.03	5.00
Methionine	1.80	1.81	1.81	1.81	Not determinated
Methionine + Cysteine	2.53	2.70	2.36	2.42	2.16
Phenylalanine	2.73	2.75	2.64	2.66	Not determinated
Phenylalanine + Tyrosine	4.65	4.76	4.46	4.42	4.16
Threonine	2.68	2.72	2.65	2.62	1.39
Tryptophan	0.54	0.49	0.55	0.53	0.43
Valine	2.90	2.79	3.06	2.93	2.21

Rodrigues et al. [62] estimated amino acid requirements by the analysis of muscle composition in specimens sampled in the wild and in farms considering two size classes (1.66 ± 0.22 kg and 10.49 ± 1.07 kg, respectively). The estimated essential amino acid requirements were very similar between both groups, despite the differences in the muscle amino acid profile. Their results suggest that the highest estimated requirements for *A. gigas* should be for leucine, phenylalanine + tyrosine, arginine, and valine, mainly. In a different study, developed using juvenile specimens with an average weight of nearly 1 kg, the amino acids with the highest estimated requirements were arginine, phenylalanine + tyrosine, leucine and isoleucine [63]. Both studies report close estimated requirements for the amino acids, except for arginine, leucine, lysine and threonine, with marked differences probably due to the calculation methodology used by the authors. On the other hand, in the few studies existing about the requirements of functional amino acids, Ramos et al. [64] determined that the inclusion of 1.02% of glutamine in the diets of juvenile pirarucu (82.12 g) improved growth performance and influenced intestinal villi height and activity of important digestive enzymes, favoring nutrient digestion and absorption. Glutamine plays a role as a regulator of essential metabolic pathways and has the potential to enhance the nutrition of neotropical carnivorous fish [65,66].

4.2. Lipids and Carbohydrates

No specific research has been found on lipid requirements in *A gigas*, but this information is important because carnivorous fish can digest unsaturated lipids more easily than long-chain saturated lipids (C18:0) due to the interference of saturated fatty acids with total digestibility [67,68]. During the initial stages, a level of around 20% of total lipids in diets with 4000 kcal DE is recommended [69], with this amount ensuring an adequate energy/protein ratio (from 10 to 11 kcal DE/g CP) and optimal utilization of dietary protein. de Mattos et al. [42], after subjecting juvenile *A. gigas* to nutritional challenges in self-feeding systems, observed that fish set their target lipid intake at 19.5% of the diet. In contrast, some technical studies consider optimal lipid levels between 8% and 12% for the different stages of production [57]. Lipid levels in commercial diets are also highly variable, ranging from 9% to 12% for the pre-starter stage, 8% to 12% for the starter stage, 8% to 10% for the grower stage, and 7% to 10% for the fattening stage, respectively (Table 5).

Requirements of carbohydrates are scarcely studied in this species. The available information suggests that the species has a reduced ability to use dietary carbohydrates [70]. In contrast, the previously mentioned study by de Mattos et al. [42], determined that juvenile specimens set their target carbohydrate intake at 24.2% when subjected to nutritional challenges in self-feeding systems.

Table 5. Requirements of the main nutrients for *A. gigas* according to culture stage (in g/100 g diet) [57].

Nutrient	Fry/Fingerling	Grower	Juvenile/Finisher	Broodstock
Protein	55	45	40	35
Lipid	12	12	10	8
Fiber	<2	<3	<4	<5
Ash	<10	<9	<9	<7

4.3. Energy and Protein:Energy Ratio

López-Vásquez [60] evaluated the effects of two protein levels (40% and 44%) and two digestible energy (DE) levels (4.0 and 4.4 Mcal/kg feed) in fingerlings weighing 12.42 g. After 42 days of evaluation, the best results of weight gain and feed conversion factor were obtained with diets containing 44% protein and 4 Mcal/kg digestible energy. In bigger juvenile fish of around 170 g, Vergara et al. [71] analyzed the effects of five levels of digestible energy in the diet (4.4, 4.6, 4.8, 5.0, and 5.2 Mcal/kg) and they found the optimal response when using 4.80 Mcal/kg feed. In another study, conducted with juveniles of nearly 350 g, Guevara-Gutiérrez [61] concluded that diets with 50% CP and 8.5 kcal DE/g CP showed better values of feed efficiency. However, with a ratio of 10 kcal DE/g CP and the same protein level, improvements were observed in gross body energy and body lipids. Table 6 summarizes the optimal energy and energy:protein ratio values obtained in different studies.

Ono et al. [68] conducted experiments with juvenile *A. gigas* (96.8 ± 2.3 g) to evaluate the digestibility of four diets with different energy-to-protein ratios (11, 10.1, 9, and 8 kcal DE/g CP) and two lipid sources (soybean oil and poultry fat). The diets with ratios of 11 and 10.1 kcal/g exhibited the best apparent digestibility coefficients for dry matter (DM) (68.3 ± 0.9%), CP (73.4 ± 2.6%), lipids (98.8 ± 0.5%), and gross energy (GE) (74.5 ± 0.9%). This suggests that the energy-to-protein ratio significantly influences diet digestibility. Regarding the lipid sources, the diet including soybean oil showed the better digestibility of the lipid fraction (98.5 ± 0.5%) when compared to that including poultry fat, which suggests that *A. gigas* digests better unsaturated than saturated fats.

Table 6. Optimal energy/protein ratios for different sizes of *A. gigas*.

Initial Weight (g)	Optimal Energy	Energy/Protein Ratio	References
12.42	4.0 Mcal DE/kg	9.0 Mcal/kg	[60]
169.81	4.8 Mcal DE/kg	9.0 Mcal/kg	[71]
345.7	-	8.5 kcal/g	[61]

4.4. Micronutrients

There is a lack of information on vitamin and mineral requirements for *A. gigas*, and the only available studies evaluated the use of vitamins C and E at levels that may be well above such requirements. In this sense, de Menezes et al. [72] conducted an evaluation of the efficacy of dietary supplementation with either vitamin C, vitamin E or both in juvenile fish of around 500 g maintained in cages and fed with diets containing 40% CP. After a 45-day trial period, their findings indicated that the inclusion of 800 mg/kg of vitamin C, as well as the combination of 800 mg/kg of vitamin C and 500 mg/kg of vitamin E, led to increased weight gain and improved survival rates. Nevertheless, in a similar study developed by the same research group, using smaller fish of about 115 g, weight gain and survival rates remained unaffected by the amounts of vitamin C and E when included at levels of 500, 800, and 1200 mg/kg during a 2-month experimental period [73].

5. Digestive Physiology

5.1. Morphology of the Gastrointestinal Tract

The morphology of the fish digestive tract has evolved to ensure that the processes of ingestion, digestion, and nutrient absorption are well adapted to the feeding habits of each species. Therefore, the development of species-specific feeds and suitable feeding strategies must consider not only feeding habits but also the anatomical and morphophysiological features of their digestive systems [74]. In this regard, a number of studies have explored different aspects of the ontogeny, morphology and histology of the gastrointestinal tract of *A. gigas* in the larval stages, [75–77]. Ruíz-Tafur et al. [76] observed that newly hatched *A. gigas* larvae lacked a mouth and any vestiges of a digestive tract, with the yolk sac accounting for 82.8% of total body mass, but the buco-pharyngeal cavity appeared approximately 48 h after hatching (HAH). Notably, as reported by the authors, the larvae began ascending to the water's surface at around 103 HAH, or approximately 4.3 days post-hatching. This timeframe suggests a high degree of independence in swimming activity, the ability to breathe atmospheric oxygen and the capability to capture and ingest exogenous food.

Saavedra and Collado [78] report that *A. gigas* larvae emerge on the surface of ponds once the yolk sac has been completely reabsorbed and they typically begin to feed on plankton around the fifth or sixth day post-hatching. Chu-Koo et al. [38] suggest that the digestive system is fully developed and ready for the digestion of complex exogenous foods when fry reach a length of approximately 1.7 to 2.0 cm and rise to the surface. In contrast, Ruíz-Tafur et al. [77] observed that the fish exhibit a fully developed digestive tract and initiate exogenous feeding at 146 HAH, while the yolk sac is almost entirely absorbed by 194 HAH.

de Alcântara et al. [28] conducted a study on the morphological and histochemical development of the gastrointestinal tract of larvae at the initial stage of swimming towards the water surface. At this stage, the larvae, with a weight of 0.05 $\pm$ 0.01 g and a length of 2.21 $\pm$ 0.06 cm, present an open mouth and anus, no yolk sac, well-developed digestive organs, fully formed gastric glands, and a folded intestinal tract with functional brush border. From days 11 to 14, the concentration of gastric glands and thickness of the stomach's muscular layer increases. Subsequently, during days 14 to 20, the larvae present a more complex intestinal tract. Based on their observations, the authors suggest that *A. gigas* larvae can be effectively fed on inert diets when they reach a size of approximately 2.0 cm. The morphology of the digestive tract gradually changes with growth, showing typical morphological and histological features described in other carnivorous fish [76].

The esophagus is characterized by a short, straight muscular tube with deep longitudinal folds of mucosa. It also presents a fan-shaped dilation at the beginning and continues with a marked reduction in lumen in the medial portion, thus enabling distension during the ingestion of large foods [75]; this elasticity is a common feature in predatory fish. The mucosa and submucosa contain dense and thick connective tissue, which serves to protect the integrity of the esophageal wall against sudden distension during prey ingestion. The stomach of *A. gigas* is a "J" shaped muscle sac characterized by its muscular and distensible nature [75,76]. This configuration has also been described in other species with carnivorous and omnivorous feeding habits [79–81]. The stomach of *A. gigas* is divided into three regions: cardiac, with a lighter aspect, fundus portion, with few folds in the mucosa, and pyloric, with deeper folds [75]. However, Rodrigues and Cargnin-Ferreira [76] identified only two regions, the "body" (proximal and glandular region, with folded mucosa) and the "pylorus" (distal and glandular region, relatively more muscular with shallower folds). The substantial volume of the stomach, along with the presence of deep longitudinal folds and a well-developed muscular tunica, facilitates distension and allows for the storage of large quantities of food [82].

The intestine of *A. gigas* is a relatively short tube, with an intestinal length:total length ratio close to 1.0. Near the beginning of the intestine, two pyloric caeca can be observed, while the rectum is identified by its flattened shape [76]. The midgut begins as a wide tube that gradually decreases in diameter, and after, widens again [76]. The intestinal mucosa presents complex and transversely oriented folds, which supposedly optimize the processes of digestion and nutrient absorption, compensating for the relatively short length of the intestinal tract [76] (Figure 6). The liver is a single organ, and the pancreas is diffusely located within it. These exocrine glands are situated in the mesentery, near the pyloric caeca, and in the initial portion of the intestine [76].

Figure 6. Illustrative figure of the gastrointestinal tract of juvenile paiche (*Arapaima gigas*).

5.2. Digestive Biochemistry

It is well-known that the activity of digestive enzymes in fish varies depending on factors such as the composition of the feed offered, the feeding conditions, and the metabolic adaptations in response to feeding schedules. Studies assessing the activity of digestive enzymes have been focused on the ability of *A. gigas* to modulate its digestive processes in response to diet changes. The enzymatic digestion in *A. gigas* is mainly mediated by acid and alkaline proteases, lipases and amylases [83,84]. From the beginning of feeding, specimens of *A. gigas* with an average weight of 1.5 g present proteases, lipases and amylases; their activity is influenced by the type of live prey supplied and also increases as a response to the requirements of digesting commercial feeds [85]. Regardless of the type of food supplied, the proteolytic activity (around 25 and 60 IU/mg protein for acidic and alkaline protease) is higher than the lipolytic (less than 25 IU/mg protein) and amylolytic activity (less than 0.010 IU/mg protein) [85]. In the juvenile stage, the enzymatic activity becomes more evident depending on the characteristics of the diets supplied. Lima et al. [86] determined the activities of alkaline proteases (11.29 ± 2.60 U/mg), lipases (8.22 ± 0.79 U/mg) and amylases (16.76 ± 1.36 U/mg) in specimens with 65.2 ± 0.4 g and improved such activities with the use of exogenous enzyme complexes.

Luz et al. [87] working with juveniles (132.07 ± 3.12 g) fed on extruded diets (45% CP) including sodium butyrate and described an increase in enzyme activities, including amylase (1.26 IU), lipase (5.92 IU), and nonspecific alkaline protease (2.63 IU). Also, Maraví-Aguilar [88] found improved activity in digestive enzymes of juvenile *A. gigas* (127.5 ± 28.41 g) cultured in the biofloc system, with significantly higher expression of lipases (1.60 U/mg protein) and amylases (0.04 U/mg protein). The authors suggested that the observed increase in lipases and amylases could be attributed to the contribution of exogenous enzymes from microorganisms associated with the bioflocs. In a study by Pedrosa et al. [89] with juveniles weighing 500.0 ± 50.9 g maintained in a recirculation system, different feeding strategies related to feed intake were tested but no significant differences were observed in enzymatic activities of protease, amylase, and lipase. It is suggested that those fish have evolved to maintain a full set of digestive enzymes, enabling them to utilize all available food efficiently, despite the energy cost of their production [90].

In relation to alkaline proteases, studies have identified one type of trypsin in the pyloric ceca and dipeptidases throughout the intestinal tube. This trypsin is characterized by its high activity and stability in a wide range of pH (from 6.0 to 11.5, with maximum activity at pH 9.0), thermostability (22 to 55° C, with maximum activity at 65 °C), and activity at high salt concentrations (up to 45%, *w*/*v*) [91]. Revilla-Aguirre [92] studied the expression of dipeptidase in various parts of the digestive tract (anterior segment, middle segment, and pyloric caeca segments) demonstrating that it was influenced by the type of diet; the fish that were fed forage fish exhibited higher enzyme activity, showing increases of 19%, 16%, and 10% in these respective segments.

A. gigas presents low amylase activity [70,93]. Enzymatic hydrolysis of starch was observed in juvenile specimens (131.34 ± 3.29 g) when fed with different vegetable ingredients, showing surface erosion of starch granules eliminated with feces [94]. Revilla-Aguirre [92] reported that maltase activity increased by 33.5% to 42.6% in intestinal segments in fish fed diets with 43% CP provided by plant ingredients. This indicates that *A. gigas*, being a carnivorous species, exhibits a slight modulation and adaptation of enzymes in response to a diet that primarily contains plant ingredients.

5.3. Functional Parameters of the Gastrointestinal Tract

No information could be found regarding key aspects of the functionality of the gastrointestinal tract of *A. gigas*, such as changes in the postprandial pH at the stomach and intestine or gastrointestinal transit rates.

6. Feed Management

Feeding represents the largest expense in intensive production systems, especially in carnivorous fish farming, primarily due to the high cost of protein ingredients required by those species [95]. To establish efficient feed management strategies, it is essential to establish suitable feeding protocols based on accurate measurements of feed intake and feeding frequencies, which can result in improved growth of cultured organisms, reducing feed wastage, and ultimately, maximizing profitability [96,97]. In the case of *A. gigas*, several studies have been conducted to determine optimal feed management practices [7].

6.1. Feeding Rate

Studies on determining the feeding rate specifically for *A. gigas* are limited. The available information is typically found in technical documents or extension guides. As reported by Rodrigues et al. [98], *A. gigas* exhibits a feeding rate variation ranging from 10.0% to 0.8% relative to the fish size (Table 7).

Oliveira-Tenazoa and Delgado Vargas [99] evaluated the effects of three feeding rates (5%, 10%, and 15% live weight/day) on the growth of juvenile *A. gigas* of less than 5 g using a diet containing 50% CP. At the end of the 80-day experimental period, the 10% feeding rate demonstrated superior performance in terms of final weight, final length, weight gain and length increment. In another study by Cardoso [100], feeding rates ranging from 4% to 8% of live weight were evaluated in fish with an average weight of 480 g raised in pens and fed on diets containing 40% CP. The results showed no significant differences in performance among the various feeding rates after 60 days of experimentation, and hence, the authors recommended a feeding rate equal to or below 4% of live weight due to its cost-effectiveness. These amounts may be even lower when using self-feeding systems. de Mattos et al. [41] found that juvenile *A. gigas*, with an average weight of 310 g, fed diets containing 45% CP exhibited a daily feed consumption rate of approximately 2.35% of their body weight. After 30 days of experimentation, fish nearly doubled their initial weight and achieved a feed conversion rate of approximately one. In another similar study carried out with bigger fish of nearly 650 g, authors observed a daily feed consumption representing 2.14% of body weight, and similar results in weight gain and feed efficiency after 28 days of culture [56].

Table 7. Feeding rates (g feed/100 g live fish) proposed by different authors for different sizes of *A. gigas*.

Average Weight (g)	Ono and Campos [48], Rodrigues et al. [98]		Aquatech's Feed Chart	
	Minimum	**Maximum**	**Minimum**	**Maximum**
5–10	6.0	10.0	10.0	12.0
10–20	4.5	6.0	7.0	10.0
20–50	3.7	4.5	7.0	10.0
50–100	3.3	3.7	4.5	7.0
100–700	2.4	3.3	3.5	4.5
700–1500	1.9	2.4	2.5	3.5
1500–4000	1.5	1.9	1.5	2.5
4000–8000	1.1	1.5	1.0	1.5
8000–12,000	0.8	1.1	0.5	1.0

6.2. Feeding Frequency and Feeding Time

In aquaculture feed management, feeding frequency holds significant importance as it directly impacts feed intake, digestion, absorption, and consequently, production efficiency and profitability of the culture [101,102]. The appropriate feeding frequency is species-specific, contingent upon feeding behavior and gut transit rates [5,103]. Furthermore, it can vary based on developmental stage [104,105] and growth conditions [106]. It is crucial to carefully consider feed supply because unsuitable feeding frequencies can potentially increase foraging and aggressive behavior in fish, leading to elevated energy expenditure. This, in turn, may alter growth and feed efficiency [103]. In addition, low feeding frequencies in some species may reduce the available energy for fish growth [107].

A number of studies have been conducted to determine the optimal feeding frequency in *A. gigas*; however, the results remain inconclusive (Table 8). There are variations even among fish at similar developmental stages, with no discernible trend according to growth.

In the previously mentioned study related to feeding rates conducted on fry below 5 g, by Oliveira Tenazoa and Delgado Vargas [99], the authors also evaluated the effect of two feeding frequencies (4 and 6 times/day), and they did not report significant differences on specific growth rate, feed conversion, and condition factor or survival.

Similarly, Medeiros et al. [108] assessed the performance of fingerlings weighing 30 g using feeding frequencies of two, three, and four times/day with diets containing 40% CP and a feeding rate of 5% in an open water circulation system. After a 15-day evaluation, there was no discernible influence of feeding frequency on final weight, weight gain, or feed conversion. The authors suggested that the absence of differences might be attributed to the relatively short experimental period. However, from an economic perspective, feeding twice a day at this cultivation stage would be more advantageous as it requires less labor [108]. Pozo–Reyes [109] tested three feeding frequencies (2, 4, and 6 times/day) in fingerlings weighing nearly 90 g raised in cages within earthen ponds and at a feeding rate of 8% on a commercial diet with 45% CP. After 56 days of experimentation, fish fed 6 times/day exhibited superior length gain, but other parameters such as weight gain, specific growth rate, feed conversion, condition factor and survival were not affected by feeding frequency.

Rodrigues et al. [110] suggested that feeding frequency for fish weighing 80 g should be between three and four times/day. Their recommendation was based on observations that this feeding frequency resulted in higher feed consumption, greater muscle growth, and increased body fat. They also noted that fish fed only once a day exhibited hyperphagic behavior. Such behavior is commonly observed in fish subjected to food deprivation or low feeding frequency, as documented in previous studies [111,112]. Silva-Espín [113] (2016) conducted research on specimens weighing 240 g and used commercial trout feed with 50% CP. They examined three different feeding frequencies: three, five, and seven times/day. After 6 months of experimentation, it was found that feeding seven times/day had a more favorable impact on weight gain and length increase. A higher feeding frequency in fish of this size may result in more efficient feed utilization by the animals and generate less waste.

Table 8. Feeding frequencies (meals/day) proposed by different authors.

Initial Weight (g)	Optimal Feeding Frequency (Meals/Day)	Diet Used	Evaluated Parameters	Experimental Condition	References
5	6	Commercial trout extruded (50% CP)	FL, FW, LG, WG	Circular tank system with continuous water flow for 80 days (T: 27.9–29.0 °C)	[99]
30	2	Commercial feed (45% CP)	SGR	Open water circulation system for 15 days	[108]
78	6	Commercial feed (45% CP)	LG	Cage system inserted in earthen ponds for 56 days (T: 29.1 °C)	[109]
80	3–4	Mixture of two commercial extruded (41.8% CP)	FW, SGR, WG	Circular tank system with continuous water flow for 63 days (T: 26.1 °C)	[113]
240	7	Extruded	LG, WG	Aquarium system for 13 months (T: 25.0–28.0 °C)	[108]
500	2	Extruded	Fish exhibited no differences for FI, FL, FCR, FW, and SGR	Recirculation systems for 8 weeks and different feeding strategies evaluated (T: 28.0–30.0 °C)	[89]
1000	2	Commercial extruded (40% CP)	FW, WG	Cage system inserted in ponds for 45 days	[112]

Pedrosa et al. [89] evaluated various feeding strategies in juveniles weighing 500 g in a recirculation system. These strategies included feeding to apparent satiety two and three times/day, feeding at a rate of 2% of body weight, and self-feeding, using diets with 40% protein. They found no significant differences between the treatments after 8 weeks, indicating that the evaluated feeding strategies did not compromise animal growth, biochemical parameters, or digestive enzymes. Similar results were reported by Gandra et al. [112] when they tested feeding strategies in juveniles weighing more than 1 kg. They used a commercial extruded diet with 40% CP and fed the fish at apparent satiety, either once or twice a day, or every other day. Their findings indicated that animals fed twice a day achieved higher weight gain and final weight after 45 days of the trial.

Considering the aforementioned, practical feeding frequency recommendations typically range from four times/day for the early stages of growth to one time/day for the final or finishing stages, as detailed in Table 9.

Table 9. Feeding frequency and pellet size for *A. gigas* according to weight following Ono and Campos [48] and Rodrigues et al. [98].

Average Weight (g)	Feeding Frequency	Pellet Size (mm)
5–10	4	0.8–1.0
10–20	4	1.5–1.7
20–50	4	1.7–2.5
50–100	3	2.5
100–700	3	4.0
700–1500	3	6.0
1500–4000	2	8.0
4000–8000	2	10.0
8000–12,000	1	10.0–15.0

To date, there have been very few studies aimed at identifying the preferential timing of food intake by *A. gigas* and the influence of different feeding shifts on its productive performance. Only three studies were found related to verifying daily food consumption and feeding behavior in specimens weighing between 318 and 1500 g [41,42,114]. The results consistently show that juvenile *A. gigas* exhibit a diurnal feeding habit in accordance with their period of normal activity.

Crescêncio et al. [114] examined feeding periods and their impact on the growth of juvenile specimens weighing 318 g. Fish were subjected to diurnal (feeding from 9 a.m. to 3 p.m.), nocturnal (feeding from 9 p.m. to 3 a.m.), and continuous (feeding at 9 a.m., 3 p.m., 9 p.m., and 3 a.m.) feeding schedules. They observed that fish fed continuously exhibited better weight gain, biomass gain, specific growth rate, and total consumption. However, fish fed during the day and at night showed similar weight gain. In the previously mentioned studies carried out by de Mattos et al. [41,42] using a self-feeding system, results indicated that fish displayed a strict diurnal feeding pattern, with approximately 70–90% of their daily feeding activity occurring during the day. The observed differences in the feeding behavior of *A. gigas* could be explained by the feeding protocol used in the experiments (fixed feeding vs. feeding by choice). The diurnal feeding behavior of *A. gigas* has also been observed in other carnivorous fish [42].

7. Type of Ingredients and Their Digestibility

As with any other fish species, the intensive culture of *A. gigas* requires the use of a balanced diet. Although there are some specific feeds commercially available for this species, in practice, most producers in Peru and Brazil use rainbow trout feeds or general formulations for carnivorous fish, respectively. The more common ingredients used in commercial diets for *A. gigas* are fishmeal, soybean meal, maize meal, rice, wheat middlings, fish oil and soybean oil, with some of them occasionally including beef meal, maize protein concentrates and maize gluten.

In the case of the Peruvian Amazonia, agro-industrial by-products or cereals such as rice or ground maize are easily accessible, while more conventional ingredients such as fishmeal and fish oil come from the coast and soybean is imported—both at a high cost. Thus, there is a strong interest in reducing such dependence by developing feeds based on local ingredients in such a region. Nevertheless, there has been limited research into the utilization of non-traditional ingredients in the diets of *A. gigas*.

Some studies have explored the incorporation in diets of animal byproducts generated from the meat and fish industry, as well as some locally produced plant-based ingredients. For example, it has been demonstrated that the inclusion of blood meal and poultry by-product meal in diets for fingerlings of 5–35 g at levels of up to 9% and 15%, respectively, improved production parameters [115,116]. Also, it has been demonstrated that the proportion of fishmeal in the diet could be reduced by up to 30%, being replaced by poultry by-product meal and meat-and-bone meal without causing any adverse effects on production performance and feed intake in juveniles of 5 g [117].

Regarding the use of vegetable sources, soybean meal can be included in diets for *A. gigas* larvae (25–235 g) without compromising zootechnical performance and fish welfare, even with a 30% reduction in fish meal [118,119]. The inclusion of 5% sunflower cake resulted in good growth in juveniles around 430 g [120]. The good results in growth and feed efficiency obtained by Ribeiro [115] in diets for 10 g fry using a combination of chestnut residues with dehydrated blood, meat and bone meal and pork fat suggest that there is great potential to explore the use of alternative ingredients in feeds for this species. In this sense, detailed information on digestibility coefficients for common and alternative ingredients in *A. gigas* is required and results obtained in different experiments carried out to date are resumed in Table 10.

Sources from marine origin presented apparent digestibility coefficients above 75%, with fishmeal being the higher values (89.2% for DM, 97.6% for protein and 89.1% for GE) [121]. Terrestrial animal sources, with the exception of blood meal, present a wide range of ADC values above 70%. Poultry by-product meal has the best digestibility (93.5% for DM, 90.3% for protein and 85.7% for GE) [121], followed by meat and bone meal (70.8% for DM, 89.4% for protein and 75.4% for GE) [121] and hydrolyzed feather meal (79.5% for DM, 79.7% for protein and 91.1% for GE) [122].

Sources of plant origin present a greater variability in their ADCs due to their diversity of types and processing methods. With the exception of soybean meal, oilseed meals and their processed products showed digestibilities higher than 70%, as in the case of soybean meal (79.0% for DM, 92.4% for protein and 83.7% for GE) [122] and soybean protein concentrate (71.6% for DM, 96.9% for protein and 65.9% for GE) [123], respectively. Although cereals such as corn or broken rice showed intermediate digestibility values, results suggest that these ingredients are well-utilized by *A. gigas*, exceeding the typical range of 70 to 75%. Wheat bran presented the lowest digestibility in the reported studies (<70%) [6,93], probably due to its high contents in fiber [6]. In relation to local inputs in the Amazon region, digestibility tests with raw sacha inchi cake (*Plukenetia volubilis* Linneo) and palm kernel cake (*Elaeais guineensis* Jacq) presented ADC values higher than 80%, both for DM, protein and GE [124,125]. These results suggest that raw sacha inchi and palm kernel cake have the potential to be used in *A. gigas* diets during the juvenile stage, as well as other local inputs that require research.

Table 10. Apparent digestibility coefficients (ADC) of dry matter, gross energy and protein from different animal and plant sources in the diets of "paiche" (*A. gigas*).

Ingredients in Experimental Diets	ADC Dry Matter (%)	ADC Protein (%)	ADC Gross Energy (%)	Fish Weight (g)	Reference
		Marine sources			
Fish by-product meal	72.3	77.2	76.1	204.45	[122]
Fish meal	89.2	97.6	89.1	235.00	[121]
Salmon by-product meal	83.6	83.9	75.6	204.45	[122]
		Terrestrial animal sources			
Blood meal	42.1	38.6	56.0	204.45	[122]
Feather meal	79.5	80.4	83.3	235.00	[121]
Hydrolyzed feather meal	79.5	79.7	91.1	204.45	[122]
Meat and bone meal	62.4	72.0	70.1	204.45	[122]
Meat and bone meal	70.8	89.4	75.4	235.00	[121]
Poultry by-product meal	100.6	83.6	85.7	204.45	[122]
Poultry by-product meal	93.5	90.3	96.2	235.00	[121]
Poultry fat	63.9	65.7	69.0	96.80	[68]
		Plant sources			
Broken rice	81.1	80.2	68.5	131.34	[93]
Corn	70.2	64.4	77.7	131.34	[93]
Corn	76.4	93.4	40.1	235.00	[6]
Corn gluten feed [1]	65.9	77.1	63.9	204.45	[122]
Corn gluten meal [2]	102.4	93.5	87.8	204.45	[122]
Corn gluten meal [2]	61.2	74.2	59.8	235.00	[121]
Corn starch	70.7	90.9	47.9	235.00	[6]
Defatted rice bran	76.5	67.1	56.7	131.34	[93]
Low-tannin sorghum	77.7	65.9	54.9	131.34	[93]
Palm kernel cake	89.0	96.2	89.8	322.69	[125]
Rice bran	46.2	68.2	42.2	235.00	[6]
Sacha inchi cake	83.0	86.4	84.9	180.00	[124]
Soybean meal	61.4	80.8	71.3	279.22	[126]
Soybean meal	76.7	83.8	58.0	235.00	[121]
Soybean meal	79.0	92.4	83.7	204.45	[122]
Soybean oil	65.3	68.5	70.6	96.80	[68]
Soy protein concentrate	71.6	96.9	65.9	217.68	[123]
Wheat bran	77.3	54.7	57.6	131.34	[93]
Wheat bran	45.1	68.6	47.4	235.00	[6]

[1] Byproduct of the wet milling process with 20–25% CP. [2] Byproduct of the wet milling process, rich in protein and low in fiber.

8. Use of Functional Feed Additives

To date, only a limited number of studies have explored the use of functional feed additives, such as amino acids, peptides, nucleotides or enzyme complexes in diets for *A. gigas*, which yield diverse results. For this reason, there is a need for further research in this area in order to obtain a better understanding of their potential benefits.

Several studies have demonstrated the positive effects of including exogenous enzymes in diets for *A. gigas* on productive performance and nutrient digestibility. Cavero [93], working with specimens weighing 6.6 ± 0.5 g, analyzed the effects of including proteases, lipases, and amylases at proportions of 0.1%, 0.2%, and 0.4% in commercial diets containing 45% CP over a period of 37 days. Diets containing exogenous proteases and lipases led to improvements in final weight, weight gain, and feed conversion when compared to the control diet. However, the addition of amylase did not result in any significant improvement in these parameters.

The addition of enzymes to the diet was evaluated in the work of Bordinhon [70] and aimed to increase the low digestibility of the carbohydrate fraction of raw wheat meal. The author obtained an improvement in the digestibility coefficient, which was maximized with diets containing cooked wheat meal and supplemented with exogenous amylase. Alcântara [127] evaluated the addition of lipase and protease in diets with partial substitution of poultry viscera meal and meat and bone meal and concluded that there was no increase in the apparent digestibility coefficients of nutrients in the diets, nor in the digestibility of these alternative ingredients. In contrast, Lima et al. [86] evaluated the effects of including an enzyme complex (Allzyme® SSF®, USA) at different concentrations (0.25, 0.50, 0.75, and 1 g/kg) in 40% CP extruded diets for fish with an average weight of 65.2 ± 0.4 g. After a 30-day experiment, the inclusion of the enzyme complex led to an increase in the apparent digestibility of CP, GE, and DM, as well as an increase in liver glycogen and total protein content in the liver and intestine. The higher accumulation of DM, GE, and body fat indicated weight gain in fish treated with the enzyme complex.

Calderón-Espinoza [128] evaluated the inclusion of two nutritional supplements based on peptides and nucleotides (2% Fish 40® and 2% Fish 75®) in fry weighing 2.3 g, measuring 7.3 cm and fed diets with 40% CP. After 45 days of evaluation, it was concluded that the inclusion of these additives had no effect on growth improvement or economic performance. However, they partially affected the water chemistry parameters by increasing carbon dioxide and alkalinity levels. The use of fish protein hydrolysates has also been evaluated in *A. gigas*. Ribeiro et al. [9] analyzed the effect of including different inclusion levels (0, 4, 8, 12, 16, and 20%) of this functional additive derived from tilapia waste in diets for juveniles with an average weight of 91.4 ± 2.7 g. After an experimental period of 8 weeks, growth parameters were not significantly affected by the inclusion of the hydrolysate, suggesting that it can be safely used up to an inclusion level of 20%.

Regarding the use of probiotics, in a study conducted by do Vale Pereira et al. [129], the effects of feeding diets containing two indigenous bacterial strains, Lactococcus lactis subsp. lactis (1×10^9 CFU/mL) and Enterococcus faecium (1×10^9 CFU/mL), previously isolated from the gastrointestinal tract of *A. gigas* [130], were analyzed in juveniles with an average weight of 58.86 ± 10.25 g. After 21 days of feeding, the study observed that both bacterial strains could positively influence haematoimmunological parameters, modulate the gut microbiota and increase antimicrobial capacity in the gut. This finding suggests that the use of specific probiotics could be beneficial for the production of *A. gigas*.

9. Final Considerations

One major obstacle to the development of an intensive culture of *A. gigas* is the incomplete validation of technological packages, which encompass various aspects of fish farming, including different aspects of its nutrition. While Amazonian aquaculture has the potential for dynamic growth, it faces significant challenges related to technological validation and production costs of fish feeds, since they contribute to increased production expenses, making large-scale production less economically viable. Addressing these challenges will be crucial for the sustainable development of aquaculture in the region.

Within this context, the present review is an attempt to present current knowledge on both basic and applied aspects of the nutrition and feeding of *A. gigas*, as well as to identify those aspects still requiring further research. It is concluded that there is a lack of information regarding aspects such as times for gastric emptying and gut transit rates, postprandial pH variation and its influence on digestive biochemistry. Also, the modulation of enzyme activity by *A. gigas* is not yet fully understood, so further studies are needed to identify patterns of enzyme production as a response to feeding in the stomach and intestine.

The lack of comprehensive knowledge regarding the digestive physiology of *A. gigas* also limits the proper determination of nutritional requirements and suitable feeding practices. Although there is general information on the suitable dietary levels of protein, lipids and carbohydrates, there is a need for more accurate and detailed information considering different growth stages, production systems and environmental conditions.

The inclusion of carbohydrates and the determination of the appropriate level are key to reducing feed costs, but this is still not well known. Also, little is known about the suitable levels of inclusion of micro-ingredients such as vitamins and minerals in *A. gigas*.

Regarding feeding practices, the studies present inconclusive results, making it imperative to determine the optimal feed dosage to supply the appropriate amount of nutrients efficiently. Additionally, there is a need to assess the digestibility of non-traditional ingredients and to understand how this species utilizes such ingredients metabolically. All those knowledge gaps make it difficult to formulate and produce well-balanced and efficient feeds that can adequately meet the species' metabolic needs, which are summarized in Table 11.

Table 11. Knowledge gaps on the nutritional physiology and feeding strategies of *A. gigas*.

Aspects	Comments
Gastrointestinal functionality	Further studies are required to comprehend the variations in postprandial gastrointestinal pH, gastric emptying, and gut transit rates. This will aid in understanding the physiological responses of *A. gigas* to feed intake.
Digestive enzymes	The modulation of enzymes in *A. gigas* during postprandial digestion is not yet known. This information is necessary to identify the peaks of enzyme expression in the stomach and intestines.
Protein and amino acids	Research on this subject has primarily focused on individuals from the juvenile stage onwards. However, there is a need to determine the nutritional requirements of protein and essential amino acids for the early stages. The ideal protein method for estimating amino acid requirements is unreliable, so research for the estimation of these nutrients should focus on dose-response methods. Additionally, further studies are required to include other variables that affect protein and amino acid requirements, such as production systems, nutritional challenges, and environmental conditions.
Energy and P:E ratio	To date, few studies have been conducted on the subject. It is necessary to determine the E/P ratio for different sizes of *A. gigas*, taking into account the various stages of production.
Lipids and fatty acids	The use of dose–response methodology, considered appropriate for determining nutritional requirements in fish, has not been employed to determine lipid levels. The available information is provided in technical documents for extension purposes, and in some cases, the recommended levels are only applicable to certain stages of the species.
Carbohydrates	The carbohydrate levels in *A. gigas* have not been determined using the dose–response methodology. Further studies are needed to observe the protein-sparing effect in this species and determine the maximum levels of inclusion in the diet.
Vitamins	Only the effects of two vitamins have been studied. Therefore, further research is necessary to determine the requirements for a larger number of vitamins. This will enable the formulation of vitamin premixes that can be included directly in the feed.
Feeding rates	Producers make use of information that is available in technical extension manuals or information provided by the aquafeed company. Scientific information is currently only available for four specific sizes of *A. gigas*. To ensure efficient use of the provided feed, further studies on a larger range of sizes and culture stages are necessary.
Feeding frequencies	Producers make use of information that is available in technical extension manuals or information provided by the aquafeed company. The studies conducted have reported varying results for the same stages of *A. gigas*, indicating inconclusiveness. Further studies are necessary, with adjustments made to the experimental design, to determine the optimal feed supply for the day.
Feeding time	The studies focus solely on certain sizes of *A. gigas*. It is necessary to determine the optimal feeding time for the various sizes involved in the species' production cycle to ensure optimal feed intake and nutrient utilization throughout the culture.
Use of alternative ingredients	Although some non-traditional inputs have been evaluated, further research is required to assess the effects of including local inputs, particularly waste generated by economic activity, such as beer bran, fish, poultry, livestock, and agro-industrial waste. Additionally, aspects such as nutritional quality, price, and availability of these inputs should be taken into consideration.
Functional additives	The focus of studies on functional additives has mainly been on improving the palatability of aquafeeds with a higher content of plant inputs or enhancing the absorption of nutrients. However, it is important to consider the effects of other functional additives such as acidifiers, gut conditioners, and phytases, which could improve the bioavailability of nutrients provided by aquafeed inputs.
Digestibility of ingredients	Analyses of digestibility mainly focus on the DM digestibility of ingredients and/or feed, rather than the digestibility of N and P. This would enable an understanding of *A. gigas'* ability to access the nutrients provided and could lead to the use of pre-digestive treatments or additives to enhance aquafeed-ingredient digestibility.

Given the factors discussed in this article, it is crucial to undertake further research into the nutritional aspects of *A. gigas*. These studies should encompass various developmental stages and involve longer experimental periods. It is also essential that the experimental conditions closely resemble the characteristics of field conditions. By conducting such research, it will be possible to establish sustainable feeding strategies that will contribute to the responsible and environmentally friendly development of the aquaculture of this species.

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