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REVIEWS IN Aquaculture

REVIEW

The farming and husbandry of *Colossoma macropomum*: From Amazonian waters to sustainable production

Alexandre Wagner Silva Hilsdorf[1] | Eric Hallerman[2] | Gustavo Moraes Ramos Valladão[3] | Micheli Zaminhan-Hassemer[1] | Diogo Teruo Hashimoto[4] | Jony Koji Dairiki[5,6] | Leonardo Susumu Takahashi[6,4] | Francielly Corrêa Albergaria[7] | Maria Emília de Sousa Gomes[7] | Rossana Luiza Leite Venturieri[8] | Renata Guimarães Moreira[9] | José Eurico Possebon Cyrino[10]

[1]Núcleo Integrado de Biotecnologia, Universidade de Mogi das Cruzes, Mogi das Cruzes, SP, Brazil

[2]Department of Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University Blacksburg, Virginia, USA

[3]Laboratório de Parasitologia e Patologia de Organismos Aquáticos, Universidade Nilton Lins, Manaus, AM, Brazil

[4]Centro de Aquicultura da, Universidade do Estado de São Paulo, Jaboticabal, SP, Brazil

[5]EMBRAPA Amazônia Ocidental, Manaus, AM, Brazil

[6]Departamento de Produção Animal, Faculdade de Ciências Agrárias e Tecnológicas, Universidade Estadual Paulista, Dracena, SP, Brazil

[7]Departamento de Ciência dos Alimentos, Universidade Federal de Lavras, Lavras, MG, Brazil

[8]Original Amazon Assessoria Empresarial Ltda., São Paulo, SP, Brazil

[9]Departamento de Fisiologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil

[10]Departamento de Zootecnia, Escola Superior de Agricultura Luiz de Queiroz, Universidade de São Paulo, Piracicaba, SP, Brazil

Correspondence
Alexandre Wagner Silva Hilsdorf, Núcleo Integrado de Biotecnologia, Universidade de Mogi das Cruzes, Mogi das Cruzes, SP, Brazil.
Email: wagner@umc.br

José Eurico Possebon Cyrino, Departamento de Zootecnia, Escola Superior de Agricultura Luiz de Queiroz, Universidade de São Paulo, Piracicaba, SP, Brazil.
Email: jepcyrino@usp.br

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Abstract

Within the rich diversity of South American freshwater fish, *Colossoma macropomum* (Characiformes: Serrasalmidae), known as tambaqui, cachama or blackfin pacu, can reach 30 kg, is a traditional product in regional fish markets and has drawn the attention of fish farmers since the 1930s. Considerable progress achieved in different fields of aquaculture science has contributed to the growth of tambaqui production. Tambaqui has proven suitable for both monoculture and polyculture systems, and for both extensive and intensive production systems aimed at achieving sustainable, higher productivity with minimal environmental impact. Studies of the reproductive anatomy and physiology of the species proved fundamental to development of techniques to boost commercial production, contributing to development of protocols for hormonally induced spawning and artificial propagation in the 1970s. Newly hatched larvae must be fed with live foods until they can be weaned to artificial feeds at about 100 mg weight. Despite its importance for aquaculture, only a few studies have reported components of quantitative genetic variance and parameters for weight at age, morphometric traits and disease resistance. Genomic tools currently available can be applied to detect variation relevant to performance and to accelerate the process of genetic improvement. While the species' feeding habit allows the use of diets

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containing 75%–85% plant protein, much more work needs to be done to optimize aquafeeds. Refinement of tambaqui production methods has the potential to significantly boost South American aquaculture. We recommend research on diets, genetic improvement and system optimization to spur further productivity and achieve sustainable tambaqui culture.

KEYWORDS
aquaculture, cachama, Characiformes, cultivation, gamitana, tambaqui

1 | HISTORICAL CONTEXT

Colossoma macropomum (Cuvier 1818) (Order Characiformes, Family Characidae) is the largest characin species in the Amazon and Orinoco river basins of South America. It is native to many South American countries, with distinct, regional common names, such as 'cachama' or 'morocoto' in Venezuela, 'cachama negra' or 'gamitana' in Colombia, 'paco' in Ecuador, 'gamitana' in Peru, 'pacu' in Bolivia, and 'tambaqui', 'bocó' or 'ruelo' (young forms) in Brazil. Termed 'black-finned pacu' in English, *C. macropomum* has been introduced into the United States, Mexico, China, Thailand and the Philippines for aquaculture purposes; feral populations have not become well established in these countries.[1-8]

C. macropomum, hereafter termed 'tambaqui', is a Neotropical (preferred temperature range, 25–34°C), potamodromous, benthopelagic, frugivorous-omnivorous fish often exceeding 1.0 m in total length and 30 kg (Figure 1). Ecologically, *C. macropomum* plays an important role in seed dispersal throughout the flooded forests of the Amazon basin. The reproductive behaviour of tambaqui is typical of most migratory characins. The adults feed in flooded, blackwater forests or floodplain lakes during the high-water season. With receding water levels, ripe 3- to 4-year-old fish migrate in large schools to spawn in whitewaters. The larvae, postlarvae and juveniles drift to nutrient-rich floodplain lakes until recruiting to the reproductive stage during the next spawning season.[1,3,9-11]

Tambaqui is a regionally important fishery resource, with commercial landings ranking among the top ten in the Amazon region's fish markets. Long a main species for local consumption and commercialization, extensive catches have been reported since the 19th century.[12,13] The flesh quality and high price of its products drew the attention of research groups in the early 1900s. The first records of domestication and farming of tambaqui date back to the 1930s, when R. von Ihering[14] advocated the husbandry of the species for aquaculture purposes.[15] In the early 1960s, research institutions in Brazil and neighbouring Amazon basin countries acknowledged tambaqui as a viable candidate for commercial fish farming.[16-18] In the early 1980s, the 'Red Regional de Entidades y Centros de Acuicultura de America Latina' (ie the Latin American Aquaculture Institutions and Research Centers Network) was established and sponsored technical workshops and symposia on tambaqui production. The very first meeting of the 'Grupo de Trabajo Tecnico—Cultivo de *Colossoma*' (Technical Working Group—Farming of *Colossoma*) was held at the then 'Centro de Pesquisa e Treinamento em Aquicultura' (Aquaculture Training and Research Center—CEPTA), Pirassununga in Sao Paulo state, Brazil, in 1988. The workshop was attended by delegates from Brazil, Colombia, Ecuador, Panama and Venezuela, and by Dr. Ulrich Saint-Paul, from Germany, an international expert in the farming and husbandry of *Colossoma*.[19,20] The proceedings of the workshop were likely the first compilation dedicated to farming of *Colossoma*.[21]

FIGURE 1 *Colossoma macropomum*—tambaqui (Source: Photo by Alexandre W.S. Hilsdorf)

The development of artificial propagation and hatchery techniques, and the consequent availability of tambaqui fingerlings on a regular, commercial basis during the 1980s consolidated tambaqui as a major aquaculture species. The species' (i) suitable response to induced spawning under hatchery conditions; (ii) adaptation to routine farming management; (iii) resilience under high stocking densities under grow-out conditions; (iv) unsurpassed growth rate (2–3 kg year^{-1}) in most warmwater (27 and 30°C) farming conditions; (v) resistance to low oxygen levels and poor water quality; (v) omnivorous feeding habit and readily acceptance of formulated aquafeeds; (vi) disease resistance; (vii) high market value and consumer acceptance; (viii) high added value for fishery products (ribs, loin and whole fish), and other biological and zootechnical characteristics soon boosted the popularity of tambaqui among fish farmers, turning the species into the most successful case of farming and husbandry of Neotropical characins.[19,22]

Data on fishery landings and aquaculture production of *Colossoma macropomum* lack precision, even those reported in

the FAO Fisheries and Aquaculture Global Production Statistics Database. The explanation is that the common name of *C. macropomum* in most Amazonian countries is 'cachama', but that common name may include other Amazonian characins, such as *Piaractus brachypomus*. In any case, Brazil is the most typical country regarding the farming of tambaqui. Statistics on landings and farm production of tambaqui in Brazil registered just 8.0 tonnes in 1994 and peaked at 139,000 tonnes in 2014. The total of fishery and aquaculture yield of native species decreased circa 4.5% since then, due to the rise of tilapia production; however, tambaqui and its hybrids still lead the farming and husbandry of native species, contributing 102,600 tonnes, a sizeable 19.7% of the total landings of freshwater farmed fish in the most recent reports (Figures 2 and 3).[23,24]

A multi-database search of Google Scholar, PubMed, Aquatic Science and Fisheries Abstracts (ASFA), and Biological Abstracts back to the 1960s recovered 914 references under the keyword '*Colossoma macropomum*', with reports heavily concentrated within the last two decades (Figure S1). Major research areas and themes on the farming and husbandry of tambaqui encompass the following: (i) physiology (22%), (ii) feeding and nutrition (21%), (iii) production and management (21%), (iv) diseases and health (9%), (v) reproduction and larviculture (8%), (vi) genetics and breeding (7%), (vii) ecology (6%), (ix) fish processing (4%), and (x) sociology and applied economics (2%). Reviews of tambaqui biology and farming have been published elsewhere.[3,9,19,20,22,25-28] Against this background, we update the state of knowledge of tambaqui aquaculture by assembling contributions from experts in areas extending from genetics to fish processing, so that the trajectory of *C. macropomum* farming and husbandry can be documented to foster the development of the species as a within the context of world aquaculture.

2 | FARMING AND PRODUCTION SYSTEMS

Description and characterization of tambaqui production systems date to the late 1970s and early 1980s (Supporting Information/Infographic 1). Lovshin,[29] Lovshin et al.[30,31] Honda et al.[32] Werder & Saint-Paul,[33,34] Goulding & Carvalho,[3] and Saint-Paul[19,20] reported findings on the species' biological characters and farming potential—growth rate, feeding habit, and reproductive behaviour—and the near-total dependence on fisheries to meet >95% of market demand in Manaus, Brazil. Neighbouring states supplied the remaining 5% of tambaqui products commercialized in the region. Economic development and population growth in the region led to increased market demand, with consequent overfishing that encouraged commercial farming of tambaqui. Increased demand for tambaqui also forced a shift in consumer purchasing habits, triggering the acceptance of so-called 'roelos', that is, juvenile tambaqui averaging 2~3 kg live weight produced in farming operations, as compared to full-grown, wild-caught fish, averaging in excess of 10 kg live weight usually available at northern Brazilian fish markets.[35-39] As a result, the supply of tambaqui products to Manaus, the largest regional marketing centre, shifted from the local fishery to farming operations in the neighbouring Brazilian states of Rondônia (RO), Acre (AC) and Roraima (RR).

Early trials on the farming and husbandry of tambaqui characterized the species as easily adaptable to farming conditions and to feeding on formulated aquafeeds.[19,20,34,40,41] Tambaqui proved a rather versatile fish and is now farmed in extensive, semi-intensive and intensive systems within Brazil, neighbouring South American countries such as Colombia, Peru and Venezuela,[35,42] Central America's Panama and Honduras[43,44] and even countries in Asia.[45] An increasing number of publications show growing interest in the

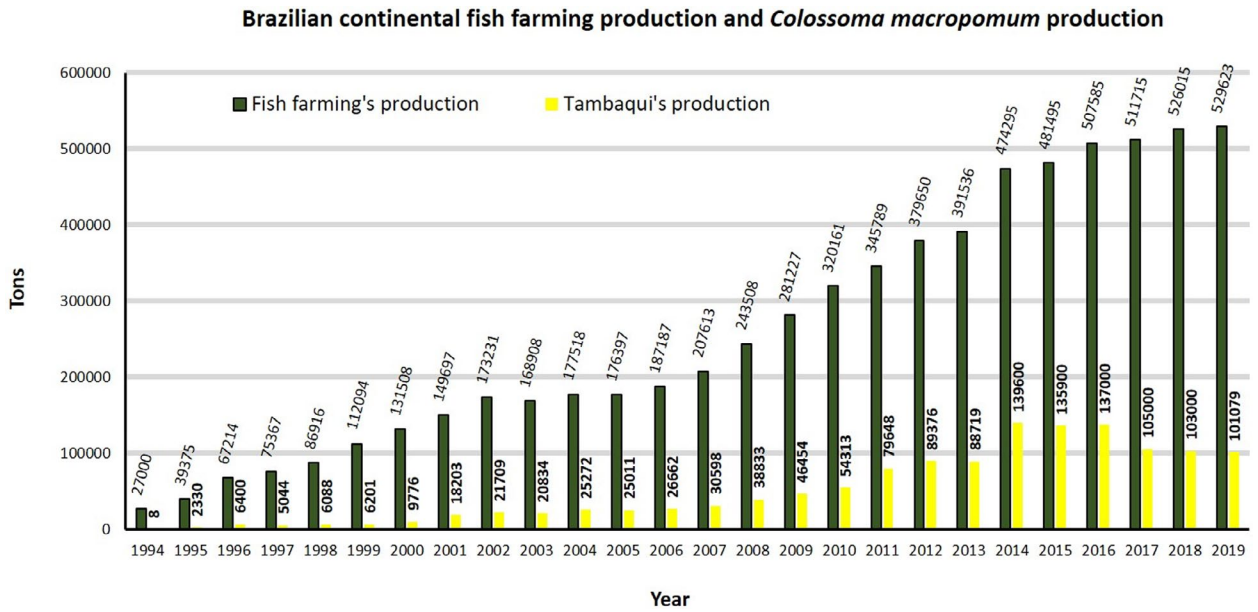

FIGURE 2 Continental fish farming production and *Colossoma macropomum* production in Brazil, 1994–2019. Statistical data adapted from IBGE (2020) and FAO-FIGIS (2020)

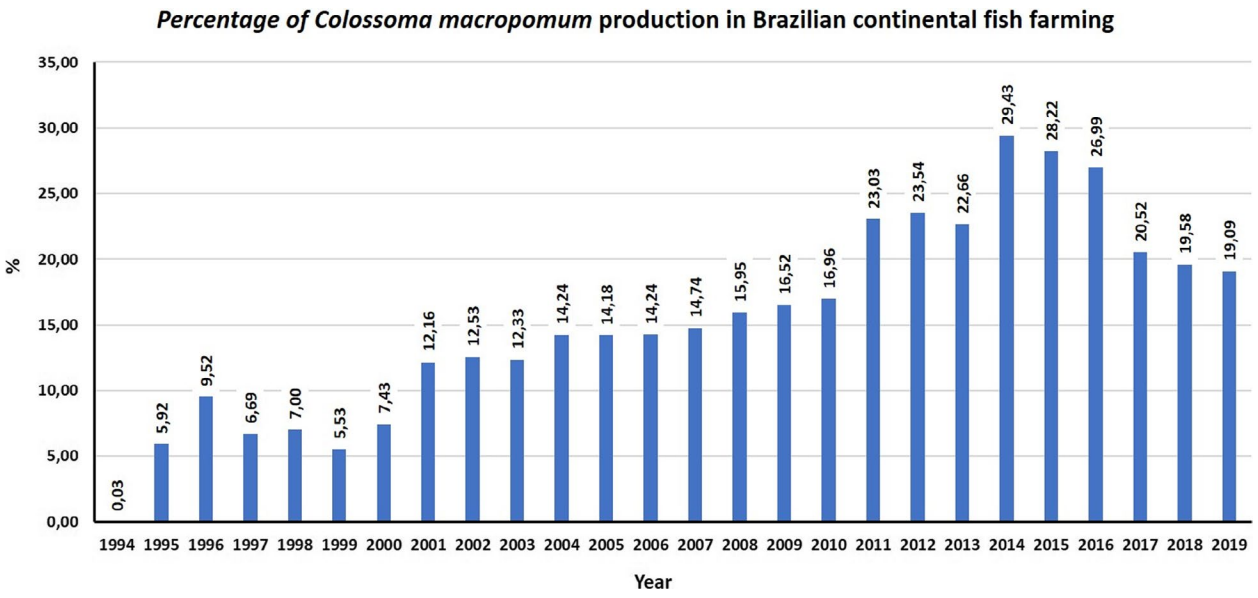

FIGURE 3 Per cent contribution of *Colossoma macropomum* to the landings of farmed freshwater fish in Brazil, 1994–2019. Statistical data adapted from IBGE (2020) and FAO-FIGIS (2020)

adaptation and development of the production systems in other regions (Figures S2 and S3).

From the very first attempts, tambaqui has proven suitable for both monoculture or polyculture systems, with attendant advantages and disadvantages. Peralta and Teichert-Coddington (1989),[43] for instance, reported that in comparison with Nile tilapia *Oreochromis niloticus*, tambaqui presents greater growth performance when raised in ponds. Teichert-Coddington[44] reported that polyculture with 75% tilapia and 25% tambaqui leads to increased overall fish productivity. Tambaqui also can be farmed successfully in polyculture with grass carp *Ctenopharyngodon idella*, catfish curimbatá *Prochilodus marggravii*, common carp *Cyprinus carpio*, the characid pirapitinga *Colossoma brachypomus*, and the cichlid silver (peacock) sunfish *Chaetobranchus semifasciatus*.[46-48] For some time, subsistence pig cum fish or integrated poultry fish farming of tambaqui, erroneously labelled extensive production systems because no formulated aquafeed was used, was encouraged or even enforced in some areas of the Brazilian Amazon.[49] However, as might be expected, several negative aspects of those integrated systems, such as deterioration of water quality and associated environmental and sanitary concerns, reduced yield and decreased the quality of the fishery products. While optimized management of production systems and nutrient balances might have addressed these issues, producers and would-be producers abandoned the integrated aquaculture approach.[50] Currently, polyculture of tambaqui and other benthopelagic species, such as freshwater prawn *Macrobrachium jelskii* and freshwater shrimp *Macrobrachium amazonicum*, is a developing trend.[51-56]

Farming tambaqui in ponds in a semi-intensive system depends upon utilization of the system's natural productivity—phytoplankton and zooplankton—as a primary food source, especially for fingerling and juvenile fish, followed by the use of supplementary aquafeeds in the grow-out phase. This farming system enables harvest of up to 10 tonnes of fish ha^{-1} $year^{-1}$; therefore, the economic feasibility of such systems is quite attractive.[36,37,57-63] The adoption of intensification practices, such as continuous or supplementary aeration, water renewal, use of complete, extruded, age(phase)-specific aquafeeds and correct feed management, although labour-intensive and prone to higher production costs, increases productivity and economic viability. However, intensification of the farming system brings higher economic risk to the activity and, unless the system is implemented and administered as an agribusiness, the investment might not prove profitable.[62,64,65]

The farming of fish in cages or other net enclosures in an intensive system allows use of almost any kind of water body for fish farming purposes, particularly large reservoirs, enabling the harvest of large quantities of quality fish.[66,67] Tambaqui has proven fit for cage farming. Defining the best stocking densities, volumes of net enclosures and cages, carrying capacities and best management practices for cage farming of tambaqui spurred multiple research efforts with good results.[35,38,50,68-71] However, the performance of tambaqui in raceways proved not comparable to those of semi-intensive and intensive pond or cage systems. A possible explanation is that tambaqui is native to lentic ecosystems and does not adapt well to raceways. Seemingly, growth rate and productivity of tambaqui are not negatively affected by slow water flow when farmed in irrigation channels, and the same is true for tambaqui hybrids farmed in recirculating aquaculture systems under moderate water flow rates.[36,72-76] For example, Silva et al.[77] reported that juvenile tambaqui (0.35 ± 0.10 g) performed rather well in a recirculating aquaculture system (RAS) with small, 28-L aquaria; thus, this study cannot be directly extrapolated to larger, commercial RAS. The production and yield of tambaqui in different farming systems are presented in Table 1.

TABLE 1 Production and yield of tambaqui in different farming systems

Farming system	Feeding and nutrition	Stocking density	Weight at stocking g	Weight at harvest g	Length of production cycle days	Fish yield kg/unit area or volume	Reference
Semi-intensive							
Earthen pond	Twice per day to apparent satiation	1 fish/m^3	90.4 ± 10.7	883.7	170	64.7/m^3	78
Earthen pond, static	Twice per day to apparent satiation	1 fish/m^2	121.8 ± 29.8	664.7 ± 148.3	150	0.66/m^2	75
Earthen pond, water renewal	Twice per day to apparent satiation	1 fish/m^2	115.8 ± 30.3	705.8 ± 192.4	150	0.71/m^2	75
Earthen pond (breeding phase)	NI	4 fish/m^2	2	286	120	0.8/m^2	79
Earthen pond (grow-out phase)	NI	0.31 fish/m^2	286	2,500	300	0.77/m^2	79
Earthen pond	Twice per day to apparent satiation	15 fish/m^2	0.4 ± 0.01	30.30 ± 4.63	56	0.45/m^2	80
Earthen pond (nursery phase)	Twice per day/% of BW	5 fish/m^3	4.82	163.78	182	0.02/m^2	41
Earthen pond (nursery phase) + greenhouse	Twice per day/% of BW	5 fish/m^3	4.82	167.22	182	0.82/m^2	41
Earthen pond (grow-out phase)	Twice per day/% of BW	1 fish/m^3	163.78	1,036.5	149	1.03/m^2	41
Earthen pond (grow-out phase)	Twice per day to apparent satiation	0.5 fish/m^2	55.3 ± 13.2	979 ± 244	210	0.41/m^2	60
Earthen pond, routine liming (grow-out phase)	Twice per day to apparent satiation	0.5 fish/m^2	55.3 ± 13.2	1.110 ± 28	210	0.53/m^2	60
Earthen pond; routine liming plus fertilization (grow-out phase)	Twice per day to apparent satiation	0.5 fish/m^2	55.3 ± 13.2	1.039 ± 38	210	0.50/m^2	60
Earthen pond	Twice per day/% of BW	0.4 fish/m^2	4.2	1,800	240	0.72/m^2	37
Earthen pond	Twice per day/% of BW	1 fish/m^2	30	698	111	0.70/m^2	37
Earthen pond	1–4 times per day/% of BW	0.32 fish/m^2	NI	3.100	356	1/m^2	36
Earthen pond	Once per day/% of BW	12 fish/m^2	11.7	298.1	225	0.35/m^2	57
Earthen pond	Once per day/% of BW	1 fish/m^2	33	426 ± 50	129	0.36/m^2	43
Earthen pond	NI	0.42 fish/m^2	42.7 ± 16.3	1,956.8 ± 440.2	356	0.78/m^2	65

(Continues)

TABLE 1 (Continued)

Farming system	Feeding and nutrition	Stocking density	Weight at stocking g	Weight at harvest g	Length of production cycle days	Fish yield kg/unit area or volume	Reference
Earthen pond + *M. amazonicum*	Twice per day to apparent satiation	3 fish/m^2	3.93 ± 1.63	50.0 ± 19.9	53	0.05/m^2	55
Earthen pond + *M. amazonicum* + *P. lineatus*	Twice per day to apparent satiation	3 fish/m^2	3.93 ± 1.63	39.0 ± 23.0	53	0.05/m^2	55
Earthen pond + *C. idella* + *P. marggravii*	Once per day/3% of BW	0.5 fish/m^2	75.15	491.5	164	0.20/m^3	46
Earthen pond + *C. semifasciatus*	3 times per day/% of BW	1 fish/m^2	24.0 ± 2.3	430.3 ± 56.0	160	0.81/m^2	48
Earthen pond + *C. semifasciatus* + *P. brachypomus*	3 times per day/% of BW	1 fish/m^2	26.6 ± 1.2	437.6 ± 103.0	160	0.40/m^2	48
Earthen pond + *O. niloticus*	Twice per day/% of BW	3 fish/m^2	0.8	269.9	182	0.13/m^2	44
Intensive							
Igarapé raceway[a]	Twice per day to apparent satiation	10 fish/m^3	86.2 ± 10.9	271.7	170	70/m^3	78
Supply channel	3 times per day/5% of BW	120 fish/m^3	15.30 ± 5.30	50.65 ± 3.25	45	6/m^3	74
Net pen (1 m^3)	3 times per day to apparent satiation	400 fish/m^3	0.24 ± 0.01	20.56 ± 1.33	60	8.22/m^3	69
Net pen (1 m^3)	Twice per day/5% of BW	34 fish/m^3	3 ± 0.18	427	240	14.5/m^3	50
Net pen (1 m^3)	3 times per day to apparent satiation	300 fish/m^3	3.89 ± 0.35	203.3 ± 36.7	60	4.15/m^3	70
Net pen (6 m^3)	3 times per day to apparent satiation	300 fish/m^3	3.89 ± 0.39	194.6 ± 33.3	60	3.86/m^3	70
Net pen (6 m^3)	Twice per day to apparent satiation	50 fish/m^3	55.0 ± 14.2	945.3	240	45.8/m^3	81
Net pen (1 m^3)	Twice per day to apparent satiation	40 fish/m^3	150.2 ± 32.7	486.2	120	18,6/m^3	38
Net pen (6.5 m^3)	1, 2 times per day/% of BW	150 fish/m^3	10.3	238.60	222	34/m^3	35
Earthen pond (aerated)	NI	0.42 fish/m^2	42.7 ± 16.3	1,949.6 ± 239	356	0.78/m^2	65
Earthen pond (aerated)	Twice per day	1.2 fish/m^2	70.24	903	180	0.97/m^2	64
Earthen pond (aerated)	1–3 times per day/% of BW	0.7 fish/m^2	160	2,620	300	1.85/m^2	37

TABLE 1 (Continued)

Farming system	Feeding and nutrition	Stocking density	Weight at stocking g	Weight at harvest g	Length of production cycle days	Fish yield kg/unit area or volume	Reference
Earthen pond (aerated)	Twice per day/% of BW	3 fish/m^2	1.8 ± 0.7	181 ± 27	171	0.53/m^2	56
Earthen pond (aerated) + *M. amazonicum*	Twice per day/% of BW	3 fish/m^2	1.8 ± 0.7	153 ± 34	171	0.43/m^2	56
Net pen (aerated) + *M. amazonicum*	Twice per day/% of BW	3 fish/m^2	1.8 ± 0.7	129 ± 36	171	0.30/m^2	56
Earthen pond (aerated + recirculated)	Once per day to apparent satiation	31.25 fish/m^3	40.65 ± 24	446.5 ± 10	192	12.13/m^2	73

Abbreviation: NI, no information.

[a]Channel-like raceways built up from 'Igarapés', which are shallow, black water, rapid Amazonian watercourses in the form of long arms of a river or major channel, running almost entirely under dense riparian vegetation.

Current tambaqui farming practices aim at higher productivity with minimal environmental impact, relying on mathematical models to support decision-making in farm management.[74,82,83] Intensive pond production of tambaqui is the most profitable system, but because it depends on intrinsic regional conditions—including weather, prices of agricultural inputs and market conditions, including the currency exchange rate—it may experience peaks and troughs in yield and profitability.[79,80,84] Pedroza Filho et al.[85] reported that cage farming of tambaqui is on the rise in the northern Brazilian states of Tocantins (TO), Pará (PA) and Mato Grosso (MT), where large, multiple-use, nearly pristine reservoirs, which may yield quality fish (notably devoid of off-flavour), are readily available for fish culture operations. However, logistic hurdles are yet to be overcome to advance the cage farming system to the state of pond farming, especially regarding economic feasibility.

Steady growth of productivity stirred interest in tambaqui production, encouraging research on transport of juvenile fish, physiology of cultured fish and health management, especially research on emerging, stress-related parasitic and bacterial diseases affecting intensively farmed stocks.[86] Widespread parasitic diseases are regarded as the leading cause of decreasing production and harvest, mainly in the northern region, causing stagnation of the species' national production (see the Diseases section below).[87-104]

Characterizing the production system of tambaqui requires considering aspects inherent to regional climatic differences and the high degree of adaptability of tambaqui, which, with the exception of southern-most regions of South America, can be produced at commercial scale with technical-economic feasibility. Such aspects led tambaqui to place second in the ranking of national production and first position among native fish, contributing significantly to the development of Brazilian aquaculture. Notwithstanding, the goal of intensifying farming systems while achieving sustainability guides research on tambaqui production. This will depend upon effective aquaculture extension to support improvement of farm management practices, changing the traditional mindset of many growers, as well as further application of aquaculture economics and sustainability assessments. The ultimate aim is to maintain supply to the domestic market with subsequent opening of external markets, touting the valuable quality and organoleptic characteristics products of the species.

3 | REPRODUCTION AND HATCHERY

Tambaqui is a migratory characin (Supporting Information/Infographic 2). In nature, female tambaqui are sexually mature at 4 to 5 years of age at 58 cm total length.[1] During the reproductive period, adults leave floodplains, streams, and lakes, assembling in large schools that head towards spawning areas in the main river channels. Spawning season peaks at the beginning of the flood period in the so-called 'white, nutrient-rich water rivers'.[105-107] Tambaqui has a synchronic ovarian development, is a group-spawning species and does not provide parental care. The larvae are carried by the current

for four to 15 days, covering 400 m to 1,300 km, drifting to floodplain lakes where the young spend the juvenile phase.[107,108]

Induced spawning and artificial propagation of tambaqui date back to the 1970s, with the first studies by researchers from the Departamento Nacional de Obras Contra a Seca (National Bureau of Actions Against Drought—DNOCS).[109] Since then, several manuals and field guides have been published, on topics ranging from broodstock formation and maintenance to commercial breeding.[22,27,110-113] Confined males reach puberty before females and may present testicular development at 5 months of age, while females begin oogenesis at 7 months; males and females reach sexual maturity in 3 and 4 years, respectively, at a total weight of 3–6 kg.[114,115] Campos Baca[63] reports that some government aquaculture hatcheries in Brazil may use broodfish for 12 years, while in Iquitos, Peru, for instance, broodfish are used for a maximum of 4 years. The difference in practice may reflect geographic differences; in Peru, which is mostly in the Amazon basin, one can easily capture broodstock, while many aquaculture regions of Brazil are far from the Rio Negro system where broodfish are most often captured. In any case, broodfish present better spawning performance at ages 4–7 years, at a body mass of 3–7 kg.

3.1 | Broodstock maintenance

Consensus is yet to be established regarding hatchery operations and management and biological parameters relevant to reproduction of tambaqui in confinement. As a rule, broodfish are usually selected from production ponds and grown to maturity in dedicated tanks or ponds under natural conditions, a procedure not well advised from a genetic management standpoint. In the event of recurrent propagation of a limited number of females and males followed by grow-out and reproduction of their progeny, the chance for inbreeding increases markedly (see the Genetics, Genomics and Breeding section).

Tambaqui is reared in warm waters in which low dissolved oxygen content is common, so monitoring stocking density of broodstock is key to successful hatchery operations. However, there is once again no consensus on ideal stocking density for broodstock maintenance and development, and most farms operate using specific, locally defined procedures. Most aquaculture centres in Peru work using a stocking density of 200–400 g broodfish m^{-2} in monoculture systems. However, on some farms, this load is reduced to 90 g m^{-2} (Iquitos, Peru), 66 g m^{-2} (southeast Brazil) or 50 g m^{-2} (northeast Brazil), but exceptionally in Venezuela, stocking density of tambaqui broodfish can be as high as 700 g m^{-2}.[63] Woynarovich & van Anrooy[27] recommend stocking 10- to 15 3.0-kg broodfish into a 1000-m^2 pond. Streit et al.[113] recommend stocking one fish of up to 3 kg live weight per 5 m^2, reducing stocking density of larger fish to one fish per 10 m^2.

Given that tambaqui is a migratory fish, reproduction under captive conditions requires artificial induction to achieve final maturation and spawning with use of hormonal administration.[27,116,117] Broodstock selection methods are similar among hatcheries. The choice of females suitable for hormonal induction is based on external maturation characteristics, such as dilated and bulging belly, hyperaemic genital papilla, and ovarian biopsy; choice of males is assessed by semen fluidity, checked by light pressure on the urogenital papilla.[113,116]

3.2 | Induced spawning and artificial propagation

Reproduction of fish is controlled by the hypothalamus-pituitary-gonadal (HPG) hormonal axis and modulated by environmental factors such as temperature, precipitation and photoperiod.[118,119] Hypothalamic neurons synthesize and release neurohormones—gonadotrophin-releasing hormone (GnRH), gonadotrophin inhibitory hormone (GnIH) and dopamine (inhibitory), among others. These hormones modulate the production of gonadotrophins in adenohypophyseal cells.[120] The gonadotrophins, follicle-stimulating hormone (FSH) and luteinizing hormone (LH) are distributed via the bloodstream, reach the testicles and ovaries and control gonadal steroidogenesis.[121]

Once the HPG axis of fish was characterized, multiple protocols were tested and proven suitable for use as inducing agents promoting teleost reproduction.[122] Human chorionic gonadotrophin (hCG), carp pituitary extract (CPE) and commercial GnRH preparations (Ovopel®, Ovaprim® and buserelin acetate, among others) each have specific dosage and latency times. Inducing agents are diluted in a liquid vehicle (usually saline solution, 0.6%) and injected intramuscularly at the base of the dorsal fin or, more commonly, intraperitoneally at the base of the pectoral or pelvic fin of broodfish. The most common and widely used inducing agent at tambaqui farms is CPE—carp pituitary glands commercially dehydrated, macerated and diluted in saline solution. The doses are applied according to fish body mass, usually in two doses: one preparatory and the other decisive.[27,113,116,123] Chellappa et al.[124] used CPE and hCG to induce spawning of tambaqui and reported positive response to both treatments. However, per cent fertilization and hatching were higher for the CPE treatment (70% and 80%, respectively) than for the hCG treatment (50% and 60%, respectively), and the authors thus concluded that CPE is more effective than hCG for inducing final maturation and ovulation in tambaqui.

CPE and Ovaprim (sGnRHa) have comparable effects on the release and concentration of semen of tambaqui. Per cent ovulation is also similar for both treatments; however, the highest fertilization rate was reported for eggs from fish treated with CPE, an indication that Ovaprim effectively induces final maturation and spawning of tambaqui, but yields lower-quality eggs.[125] Comparing CPE and Ovopel® (18–20 μg of mGnRHa per pellet) protocols, Souza et al.[126] reported that spawning responses of females treated with the 0.2 or 0.4 pellets of Ovopel® were, respectively, 100.0% and 62.5%, while treatment with CPE yielded 87.5% response, with no statistically significant difference among

treatments. However, Ovopel® promoted faster spawning, calculated as an accumulated thermic unit (ATU – average water temperature × number of hours from induction until spawning), than CPE treatment, with similar mass of oocytes released, fertility and hatching. Ovopel® is also used to increase milt release in tambaqui cryopreservation programmes.[127] Woynarovich & Van Anrooy[27] present similar, detailed protocols for Ovopel® and CPE. Table 2 lists and summarizes protocols and common inducers for final maturation and spawning of tambaqui.

Induced spawning and artificial propagation of tambaqui also can be accomplished by use of buserelin acetate, which yields spawning percentage, egg mass, ovulation and fertilization similar to those of CPE. However, ATU and the number of egg releases were higher for females treated with buserelin acetate than CPE.[138] Positive results from use of buserelin acetate to induce spawning of tambaqui also were reported by Almeida et al.[140] who monitored embryonic and larval development. Despite the various inducing agents available and experimentally demonstrated to induce spawning of tambaqui, CPE is still most commonly used because it is easily obtained and stored, easily handled (including calculation of dose) and proven effective. The widely used CPE protocol is based upon that previously established for carps, that is for females, 5.5 mg kg^{-1} of CPE (pituitary glands macerated and diluted in 0.7%–0.9% saline) and applied in two doses (0.5 mg and 5.0 mg kg^{-1}), at a 12-h interval; and for males, 2.5 mg kg^{-1} CPE in a single dose.[113] The CPE protocol for tambaqui also can stimulate successive spawns with viable eggs 75 days after the first induction.[150]

3.3 | Fertilization and incubation

Particular induced spawning agents have specific administration intervals and ATU to effectively induce gametic maturation and spawning. The ATU varies with water temperature and estimates the moment at which the gametes will be ready for fertilization (in degree-hours, varying by inducing agent; Table 2). Ova and semen are obtained with the aid of abdominal massage (extrusion) and collected into separate containers. The concentration of tambaqui semen varies from 8.5×10^9 sperm cells ml^{-1} (Streit et al.[113]) to 19×10^9 sperm cells ml^{-1} (Leite et al.[130]), which is high compared to other freshwater teleosts. Males release reasonable semen volumes (2.0~50 ml kg^{-1}) and can be stripped more than once, provided that stripping is done gently (Woynarovich & Van Anrooy[27]; see Cryopreservation section for additional material). Female tambaqui may produce as much as 5~20% body mass in eggs, that is at least a few hundred grams,[27] averaging 1,200~1,500 ova g^{-1} egg mass.[113,130]

Embryonic development begins upon fertilization by the spermatozoa; as soon as spermatozoa enters the micropyle, the fertilized egg starts the hydration process and gradual closing of the micropyle.[153] The hydration period varies among teleosts, ordinarily as a function of (final) egg size. Fertilization of tambaqui gametes is usually carried out in containers (most often, plastic bowls) where oocytes and semen are mixed dry, with water added shortly afterwards. A high percentage of fertilization is achieved when 1.0 ml of semen is added to 80 g of egg mass (circa 95,000 oocytes).[113] Regarding the spermatozoa/oocytes ratio, a high fertilization rate is reached with around 100,000 spermatozoa per oocyte.[130] Fertilized, hydrated eggs are transferred to conical, continuous flow, 60~200-L fibreglass incubation jars at a rate of 2 ± 0.5 g (2,000 ± 500 eggs) per litre. Tambaqui eggs have high dissolved oxygen requirements, so the stocking density of eggs should be carefully monitored. It is advisable that the volume of incubation jars does not exceed 40–200 L, with a water flow of 2~3 complete exchanges per hour.[27] The flow velocity during incubation should be divided into three parts: in the first third, from 1 to 2 L/min; in the second third, from 3 to 4 L/min; and in the final third, from 5 to 6 L/min.[113] The incubation period varies with water temperature, from 17.8 h (at 26°C) to 12.8 h (at 29°C),[27] embryonic development takes about 14–18 h at a temperature of 25–29°C, and hatching can occur around 12 h after incubation begins.[154] The entire artificial reproduction process for tambaqui is detailed by Woynarovich & Van Anrooy[27] and Streit et al.[113] Environmental, nutritional and other factors affect gamete quality.[153]

3.4 | Larviculture

Larval development of teleost fish begins upon hatching and ends with resorption of the yolk sac, opening of the mouth and onset of exogenous feeding. During this period, in addition to opening of the mouth, many events occur synchronously, including inflation of the swim bladder, eye pigmentation, fin development and flexion of the notochord. Cultured tambaqui larvae open the mouth about 36 h after hatch and can begin to feed on filtered zooplankton.[154,155] The lighting system used during larviculture can affect tambaqui larvae's capacity to capture prey.[156] There are many procedures and strategies to optimize tambaqui larval rearing, ranging from production in fertilized ponds to maintenance in laboratory tanks with recirculating water.[27,133,154,156-162]

Tambaqui larvae must be fed with live feed until they can be weaned to artificial feeds at about 100 mg[161] Usually, the live food consists of plankton or brine shrimp *Artemia salina*. Plankton can be collected from fertilized ponds and can be offered directly or selected by size. Pedreira et al.[154] grew tambaqui larvae through 20 days under the following dietary treatments: plankton; plankton + ration; size-selected plankton (using 350 and 1000 μm meshes); selected plankton + ration; and ration. The feed was given twice daily, *ad libitum*. The authors observed that treatments using live food resulted in more rapid larval growth. The addition of ration to the live food also improved growth performance, although the authors did not recommend ration as the sole food source through the first days of life. They concluded that the use of live food plus ration from the third day of exogenous feeding yielded higher survival and growth of tambaqui larvae.

Tambaqui larval development may be affected by nutrition during larviculture, although information is still limited, showing mainly that decapsulated *Artemia salina* cysts are more efficient than inert feeds

TABLE 2 Induction of final maturation and spawning of *Colossoma macropomum*

Inducer	Sex	Total dose	No. Injections	Interval between doses (h)	Water temperature °C	Hour-degrees for extrusion	Reference
CPE	M	0,5 mg/kg BW (0.25 + 0.25)	2	6			128
	F	3 mg/kg BW (0.25 + 0.25 + 0.25 + 0.75 + 1.5)	5	0–24–24–6–6			
CPE	M	0.75 mg/kg BW	1		27.5	240	129
	F	5.5 mg/kg BW (0.5 + 5.0)	2	12			
CPE	M	2.5 mg/kg BW	1		28.05	215	113
	F	5.5 mg/kg BW (0.5 + 5.0)	2	12			
CPE	M	2.5 mg/kg BW	1		27	243	130
	F	5.5 mg/kg BW (0.5 + 5.0)	2	12			
CPE	M	1.5 mg/kg BW (0.5 + 1.0)	2	12			131
CPE	M	3.0 mg/kg BW (0.5 + 2.5) (≤5 kg) 3.5 mg/kg BW (0.5 + 3.0) (≥6 kg)	2	12–14 or 18–22	26–29 24–26 29	260 270–290 230–250	27
	F	5.5 mg/kg BW (0.5 + 5.0) (≤5 kg) 6.0 mg/kg BW (0.5 + 5.5) (≥6 kg)	2	12–14 or 18–22			
Ovopel	M	0.84 pellet/kg BW (0.14 + 0.7) (≤5 kg) 0,94 pellet/kg BW (0.14 + 8.0) (≥6 kg)	2	12–14 or 18–22			
	F	1.54 pellet/kg BW (0.14 + 1.4) (≤5 kg) 1.74 pellet/kg BW (0.14 + 1.6) (≥6 kg)	2	12–14 or 18–22			
CPE	M	2.75 mg/kg BW (0.25 + 2.5)	2	8	27.5	330	132
CPE	M	2.5 mg/kg BW (0.25 + 2.25)	2	14			133
	F	5.0 mg/kg BW (0.5 + 4.5)	2	20			
CPE	M	2.5 mg/kg BW	1	12	27–29	180–220	134
	F	5.5 mg/kg BW (0.5 + 5.0)	2				
CPE	F	5.5 mg/kg BW (0.5 + 5.0)	2	12	27	243	135
CPE	F	5.5 mg/kg BW (0.5 + 5.0)	2	12	28	252	136
CPE	M	2.5 mg/kg BW	1	12		210	39
	F	5.5 mg/kg BW (0.5 + 5.0)	2				
CPE	M	3 mg/kg BW	1	8–12			124
	F	5.0 mg/kg BW (0.5 + 4.5)	2				
hCG	M	10 UI/g BW	1	18–24			
	F	30 UI/g BW (12 + 18)	2				
CPE	F	5.5 mg/kg BW (0.5 + 5.0)	2	12	28±2		137
CPE	M	1.5 mg/kg BW	1				125
	F	5.0 mg/kg BW	2	12			
Ovaprim	M	0.5 ml/kg BW	1				
	F	0.5 ml/kg BW					
Buserelin acetate	F	0.5 ml/kg BW	1				138
CPE		5.5 mg/kg BW (0.5 + 5.0)	2	12			
CPE	M	1.0 mg/kg BW	1			275	139
	F	5.5 mg/kg BW (0.5 + 5.0)	2	12			
Ovopel	F	0.2 pellet/kg BW	1			417.4	126
	F	0.4 pellet/kg BW	1			412.3	
CPE	F	5.5 mg/kg BW (0.5 + 5.0)	2	12		268.9	

TABLE 2 (Continued)

Inducer	Sex	Total dose	No. Injections	Interval between doses (h)	Water temperature °C	Hour-degrees for extrusion	Reference
Buserelin acetate	M	0.08 µl/kg	1				140
	F	0.7 µl/kg (0.20 + 0.50).	2	7.5			
CPE	M	2.0 mg/kg BW	1	.			141
CPE	M	1.5 mg/kg BW	1				142
CPE	M	2.75 mg/kg BW (0.25 + 2.5)	2	8			143
CPE	M	2.0 mg/kg BW	1				144
CPE	M	1.0 mg/kg BW	1				145
CPE	M	2.0 mg/kg BW	1				146
	F	5.5 mg/kg BW (0.5 + 5.0)	2				
CPE	M	1.5 mg/kg BW (0.5 + 1.0)	2	12			147
Ovopel	M	0.7 mg /kg BW	1				127
CPE	M	2.75 mg/kg BW (0.25 + 2.5)	2	8			148
CPE	M	2.0 mg/kg BW	1				149
CPE	M	2.5 mg/kg BW	1			240	150
CPE	M	1.5 mg/kg BW	1			240	151
	F	6.6 mg/kg BW (0.6) + (6.0 + 5 ml synthetic prostaglandin)	2	12			
CPE	M	2.5 mg/kg BW	1				152
	F	5.5 mg/kg BW	2				

Abbreviations: CPE, carp pituitary extract; hCG, human chorionic gonadotrophin.

for promoting larval growth.[140] Due to the ease of purchase and regular supply, *Artemia salina* nauplii are widely used in larval fish culture, especially when producing large quantities of larvae. However, it is a high-cost input, and hence, it is important to establish the most cost-efficient feeding regime for promoting growth of tambaqui larvae. Sevilla & Gunther[161] studied the relationship between growth, feed utilization and feed ration during the first 15 feeding days for tambaqui larvae fed with *Artemia* nauplii. Maintenance, optimum and maximum feeding rations (1.23; 5.48 and 27.2% body weight/day, dry feed, respectively) and feed conversion ratios (0.4 and 0.78 optimum and maximum, respectively) were determined. They observed that at maximum feeding, the larvae grew 2.6 times faster that at optimum feeding, but the feeding costs increased 1.94 times. Depending on the cost structure at a particular hatchery, the most efficient production strategy can be designed to minimize the combined costs.[161]

Although *Artemia salina* nauplii are successfully used in tambaqui larviculture, they are saltwater crustaceans and have a limited lifetime in fresh water, which can be increased with the use of water with low salinity.[162] Santos et al.[163] working in recirculation systems (RAS) studied stocking densities of tambaqui larvae in slightly saline water (2.01 ± 0.41 g salt/L), and concluded that culture of *C. macropomum* larvae can be carried out successfully at stocking densities of up to 50 larvae/L during the first 30 days of rearing in slightly saline water in RAS.

3.5 | New technologies

The importance of tambaqui for Brazilian aquaculture has led to numerous studies on the anatomy and physiology of the species, which proved fundamental for the development of techniques to boost commercial production. Studies of gonadal morphology,[115,142,143,164,165] action of steroid hormones during the reproductive cycle in captive animals,[115,164] embryonic development,[140] sexual differentiation[166] and molecular markers for germ cells,[167] among others, made significant contributions to the development of techniques such as cryopreservation of tambaqui semen for use in induced spawning.

In the past decade, many studies have developed protocols for tambaqui semen cryopreservation, including evaluation of semen characteristics (volume, motility, sperm count), diluents, cryoprotectants, storage containers, and semen quality pre- and post-freezing, among other aspects,[132,144-147,149,168-174] and a general protocol for the cryopreservation of tambaqui semen was then established.[148] Cryopreservation has been used to establish germplasm banks to maintain and conserve tambaqui genetic resources.[175] Reviews of cryopreservation of semen of Brazilian freshwater fish, including tambaqui, have been published by Viveiros & Godinho[176] and Garcia et al.[177] Although protocols for cryopreservation of tambaqui semen are established, those for embryos and oocytes still lack good results.[178] A cooling protocol for tambaqui embryos kept

up to 8 h at 2°C has been suggested for embryos at the stages of blastospore closure (8 h post-fertilization) and appearance of the optical vesicle (13 h post-fertilization).[139]

Tambaqui farmers are interested in the possibility of producing monosex populations. Tambaqui females are on average 16% heavier than males at harvest[115]; hence, rearing all-female stocks can be more profitable. Effective feminization of tambaqui is achieved by feeding 30-day post-hatch larvae (14 mm total length) a diet supplemented with 120 mg oestradiol (E_2) per kg of feed for 6 weeks.[179] However, an economic evaluation and consumer perception of hormone use in aquaculture operations must be considered before relying on sex-reversal techniques for improvement of routine commercial production.

Because triploid individuals are sterile and exhibit more rapid growth in many teleost species, triploidization via chromosome set manipulation has been evaluated for tambaqui.[180] Triploidy induction using thermal shocks was successful, with higher hatching and triploid induction rates for heat shock (41°C for 2 min) than for cold shock (6°C for 10 min); however, the protocols must be improved to increase the percentage of triploidy.[151]

3.6 | Perspectives on advances regarding tambaqui production

Tambaqui is probably the best-studied native South American aquaculture species, with many reported studies and published papers. However, it is essential to reflect on how much this research has resulted in practical techniques to boost culture of this species. Concerning reproduction and larviculture, it seems that little progress has been made since the beginning of induced spawning and artificial propagation of tambaqui in the early 1970s through the late 1980[109,110]; the techniques and procedures used today are practically the same. The early[110,111,123] and most recent production manuals[27] need to be revised to incorporate recent technical advances regarding tambaqui reproduction. This is because most tambaqui hatcheries still work in a traditional fashion to induce artificial reproduction. However, new technologies—such as sperm cryopreservation, sex control, altering the time of sexual maturation, induced sterilization, use of gonadotrophin-releasing hormone analogs, broodstock pit-tagging or monitoring of pedigree to avoid inbred crossings—have not been assimilated into practice by hatchery managers.

Although detailed manipulation of the HPG axis is known for many cultured fish, that is not true for tambaqui, noting that the most commonly used spawn-inducing agent used by fish farmers is still CPE. Although commercial protocols for use of GnRH (Ovopel®, Ovaprim and buserelin acetate) are in use by a few fish farms, it is necessary to standardize protocols so that they can be more broadly applied across the industry. Detailed analyses of use of these protocols on the production of viable larvae and the associated costs should be carried out. The formation, selection and maintenance of broodstocks are neglected at most fish farms, and available broodstock management protocols do not adequately address these issues. There is a lack of studies on protocols and optimized conditions for capturing and maintaining high-performance broodstocks (genetics, feed management and nutrition, space, water quality, etc.) focusing on industrial production. As a rule, most fish farmers choose broodfish from among the grow-out stock even without performance evaluation. As a result, many producers do not know how many reproductive cycles a particular male or female broodfish has had and its fry production recorded. Repeated selection of animals that did not respond positively to previous attempts at induced spawning is very common. This lack of control results in low reproductive performance and the need to maintain an exceedingly large number of broodstock. Likewise, it is necessary to update and standardize protocols for tambaqui larviculture, supported by studies on larval physiology and the development and implementation of specific nutritional protocols.

Among biotechnological approaches, those on cryopreservation of tambaqui semen have received most attention by researchers. These protocols still need standardization, and there is still a long way for the semen preserved and maintained in germplasm banks to be applied routinely at fish farms.[177] The biotechnological approach should apply knowledge of the genetic characteristics of tambaqui broodstock, which is still incipient. Research with feminization and triploidy is limited, and there is still no technology developed for practical use by tambaqui farmers.

While the amount of research carried out on tambaqui is commendable, it is still insufficient to make its culture predictable, profitable and resilient to varying conditions. Most research results never went beyond laboratory scale and are so do not meet the demands of the industry. This core of scientific information needs to be made available to producers so that a more sustainable and profitable tambaqui industry can be realized. Efforts in this direction are being made by researchers from the Brazilian Agricultural Research Corporation (EMBRAPA), and a qualitative leap in the development of protocols for application in fish farming of this species is expected in the coming years. In addition, efforts are needed to transfer these technologies and make them accessible to producers. Likewise, it is necessary to involve several sectors, including fish farms, to support and adopt new technologies and train their technicians with a focus on technical and sustainable industrial production.

4 | GENETICS, GENOMICS AND SELECTIVE BREEDING

4.1 | From cytogenetic to DNA studies

The genetic studies of the so-called 'round characins' date back to the 1980s when cytogenetic characterization of tambaqui (*C. macropomum*), pacu (*Piaractus messopotamicus*) (previously *Colossoma mitrei*) and their interspecific hybrids was reported by Almeida-Toledo et al.[181,182] (Supporting Information/Infographic 3). This cytogenetic study followed the first attempt to produce an interspecific hybrid

between tambaqui and pacu.[183] The development of this hybrid, named 'tambacu', was aimed at combining the high growth rate of tambaqui and the low temperature tolerance of pacu. Similarly, the interspecific cross between two Amazonian characins, tambaqui and pirapitinga (*Piaractus brachypomus*), named 'tambatinga', was aimed at yielding better-performance offspring.[184-187] As the hybrids, a 'secondary farmed type',[188] started being produced in aquaculture, additional cytogenetic investigations were undertaken to understand the biological response and behaviour of chromosomes during mitosis and meiosis.[189-192]

The characterization of wild relatives and confined farmed types of tambaqui using isozymes started during the 1990s. Leitão[193] used nine isozyme systems to assess the genetic variability of wild and confined populations.[194] With the passing of time, screening of DNA-based molecular markers led to advances in understanding of intra- and inter-population genetic variation.[195] As nuclear DNA markers such as microsatellites were developed for tambaqui,[196-199] new studies of genetic variability within and among tambaqui populations were reported. Three studies were published regarding levels of genetic variability within and genetic structure among wild populations of tambaqui across the Amazon basin, two using partial sequences of the mitochondrial DNA D-loop region and another using microsatellite markers. Using mtDNA, Santos et al.[133] suggested that that tambaqui forms a panmictic population along the Solimoões-Amazon River channel. On the contrary, Farias et al.[200] reported significant genetic differentiation ($\varphi_{CT} = 0.1209$, $p < 0.001$) between tambaqui populations in the main Amazon basin and in Bolivian subbasins on either side of the Madeira River rapids. A microsatellite-based assessment of landings at three important tambaqui fishery landing ports (Tefé, Manaus and Santarém) showed reasonable mean genetic diversity (expected heterozygosity, $H_e = 0.79$ and allelic richness, $A_R = 8.6$), with populations showing a pattern of high gene flow associated with the lack of genetic structure.[201] Results of these three studies showed no signature of genetic structure between populations sampled within the Amazon basin with either maternally inherited mitochondrial DNA or biparentally inherited microsatellites, suggesting that tambaqui form a panmictic population throughout the Amazon basin.

These results may be driven by the semi-migratory reproductive behaviour and feeding dispersal of the species. However, these studies cannot be entirely conclusive because the concept of 'population' should consider both ecological and demographic paradigms.[202] Therefore, spawning assemblages should be sampled before mixing at feeding areas, and quantitative criteria and markers with broader genomic coverage, such as single nucleotide polymorphisms (SNPs), should be applied to reveal genetic structure at smaller geographic scales and to assess genomic signatures of local adaptation.[203] The use of wild tambaqui by local artisanal fisheries and as a raw genetic material for selective breeding programmes depends on the long-term conservation of the wild genetic resources Hilsdorf and Hallerman,[204] which in turn depends on ongoing and continuing genetic characterization of wild populations throughout its distribution.

When the farming and husbandry of tambaqui started drawing attention outside the Amazon region, broodfish were translocated to other warm Brazilian regions. Thus, propagation of this 'primary farmed type' (Mair & Lucente[188]) has been established to produce fingerlings for local tambaqui farming. The genetic diversity of captive populations maintained in public and private hatcheries was assessed using multiple molecular markers, including random amplified polymorphic DNA (RAPD),[192,205,206] mitochondrial DNA,[207-209] inter-simple sequence repeat (ISSR),[210] microsatellite[208,211-215] and SNP[216] markers. Altogether, it was shown that the genetic resources of farmed tambaqui broodstock in the Amazon region and across other South American regions underwent loss of genetic diversity, which can be attributed to the lack of effective breeding management and founder effects resulting from the species' high fecundity and small number of broodstock utilized.

4.2 | Selective breeding and genomics

A better understanding of the genetic diversity of wild and captive populations and genetic parameter estimation for aquaculturally important traits are needed for planning an effective selective breeding programme. Despite the importance of tambaqui for South American aquaculture, only a few studies have reported components of variance and genetic parameters for weight at age and morphometric traits. Studying individuals from different fish farms having various degrees of domestication, Mello et al.[217] showed high estimates *a posteriori* of mean heritability (h^2) for body weight (0.44 and 0.42) and for daily weight gain (0.49 and 0.40) at 12 and 24 months, respectively. Using groups sourced from another commercial breeder, Perazza et al.[218] reported moderate-to-high heritability estimates of 0.26 at 221 days and 0.49 at 623 days for body weight, and 0.41 at 623 days for daily weight gain. This study also estimated parameters for a new trait of interest for industrial fish processing, loin eye area (LEA), with $h^2 = 0.39$. These outcomes show significant potential for selective breeding programmes to yield large genetic gains and improved performance.[219,220] Attempts to develop genetically superior strains for farming purposes have been implemented[221]; however, the advances in understanding of quantitative genetics have not markedly affected commercial tambaqui production, which still relies on non-selectively bred, captively propagated broodstock. Genetically improved strains are not yet commercially available.

Genomics is an interdisciplinary field that uses the tools of molecular genetics and bioinformatics to achieve advances in the understanding of the structure and function of genomes. Genomic tools currently available can address unknown issues of the tambaqui genome and accelerate the process of genetic improvement. For instance, the discovery of individuals lacking intermuscular bones at a fish farm in Brazil opened an avenue of new technological advances,[222] such as the use of ultrasound as a tool to detect animals lacking intermuscular bones and to measure LEA.[222,223] Subsequent studies constructed the first high-resolution genetic linkage map of

a Neotropical fish species using genotyping by sequencing (GBS),[224] followed by another high-density genetic linkage map for association analysis of sex-linked QTLs[225] and a genome-wide association study (GWAS) to seek the molecular mechanism underlying lack of intermuscular bones in tambaqui.[226]

Recent studies, including two genome assemblies, have contributed to our understanding of the tambaqui genome. Machado et al.[227] used RNA-seq technology to generate an extensive liver transcriptome of tambaqui. The authors reported and annotated a total of 43,098 transcripts, which will address issues concerning different facets of tambaqui farming. Ferraz et al.[228] presented a draft genome assembly for tambaqui and demonstrated its utility for studies of nutritional physiology. The authors focused on metabolism of long-chain (C20–24) polyunsaturated fatty acids (LC-PUFA) that are physiologically important nutrients for vertebrates. Previous studies had shown that tambaqui has all the desaturase and elongase enzymes needed to convert C18 polyunsaturated fatty acids into LC-PUFA. Elongation of very-long-chain fatty acid 4 (elovl4) proteins, which participate in the biosynthesis of very-long-chain (>C24) saturated fatty acids (VLC-SFA) and very-long-chain polyunsaturated fatty acids (VLC-PUFA), had not been characterized. Hence, the authors investigated the repertoire and function of two fatty acid elongation genes, *elovl4a* and *elovl4b*. *Elovl4a* and *elovl4b* have open reading frames of 948 and 912 base pairs, encoding putative proteins of 315 and 303 amino acids, respectively. Functional characterization in yeast showed that both elovl4 enzymes have activity towards all the PUFA substrates assayed (18:3n-3, 18:2n-6, 18:4n-3, 18:3n-6, 20:5n-3, 20:4n-6, 22:5n-3, 22:4n-6 and 22:6n-3), producing elongated products of up to C36. Moreover, both elovl4 enzymes were able to elongate 22:5n-3 to 24:5n-3, a key elongation step required for the synthesis of docosahexaenoic acid. Other transcriptome investigations are being applied to understand molecular signals leading to sex differentiation in tambaqui (Lobo et al.[166]) and differential patterns of expression of *Rex6* retrotransposable elements in samples from clear and blackwaters of Amazon rivers, which may help further understanding of insertion and selection sequences in the genome of tambaqui.[229] In addition, microRNA characterization of tambaqui was carried out to understand the role of these endogenous non-coding riboregulators of gene expression regarding the physiology and expression of traits of aquaculture interest.[230] Future climate change scenarios predicted by global models may directly affect the long-term survival of wild fish populations and the productivity of farmed stocks. Next-generation sequencing (NGS) tools have made possible studies of the transcriptome, that is the sequences of all messenger RNA molecules, termed RNA-seq, in tissues of fish exposed to extreme climate scenarios and to thereby observe differentially expressed genes. Fé-Gonçalves et al.[231,232] used RNA-seq to show that differentially expressed genes revealed signatures of local thermal adaptation, which will promote understanding of molecular processes putatively underlying responses to climate change, and identified candidate genes for use in marker-assisted selection (MAS).

The growth of tambaqui production has drawn the attention to several potential disease issues in farming operations (see section below on Diseases). As most farmed tambaqui stocks come from unselected stocks, there is unexplored potential for selecting tambaqui for resistance to diseases caused by key pathogens and parasites, as has been shown, for example, for farmed.[233] The first step to initiate a breeding experiment is to assess whether the targeted trait has phenotypic variation and is heritable, and then to determine how it can be included as a breeding objective. However, unlike growth that is easily measured as weight at age, selective breeding for disease resistance is challenging and complex, given that it is rather difficult to acquire precise and informative disease resistance measurements or related data via controlled challenge experiments or by taking advantage of uncontrolled field outbreaks. Moreover, to avoid compromising biosecurity within the breeding nucleus, fish breeding programmes use disease databases built up from performance of relatives of the selection candidates, as opposed to selection for growth that uses records from the candidates themselves.[234]

Several studies estimating genetic parameters of tambaqui resistance to bacteria and parasites have been published to date. Ariede et al.[235] carried out a challenge assay with pathogenic *Aeromonas hydrophila* inoculated intraperitoneally into 576 individuals from 18 full-sib families and registered binary survival (BS) and time of death (TD) within the population. The experiment also assessed whether resistance to *A. hydrophila* is correlated with growth performance in the juvenile phase. Results showed high phenotypic variation, as BS and TD differed considerably among families (BS = 26%–89% and TD = 10.7–69.2 h). Genetic parameter estimates showed moderate values for heritability for BS (0.17 ± 0.06) and TD (0.23 ± 0.09). Genetic correlations between resistance to *A. hydrophila* and growth of juvenile of tambaqui did not differ significantly from zero. The authors thus found significant genetic variation for *A. hydrophila* resistance under moderate genetic control; therefore, selection of superior genotypes is a feasible approach for reducing the impact of this disease in tambaqui culture.

An innovative protocol for evaluating resistance against the parasite *Ichthyophthirius multifiliis* (ich) was developed by Lira et al.[236] using thermal oscillations to imitate the primary stressor that naturally precedes outbreaks of this pathogen in tambaqui. Using an experimental cohabitation challenge, the traits evaluated were survival status (SS) and time of death (TD) of fish presenting clinical signs of ich infestation. Total cumulative survival rate differed significantly among families (16–100%). TD varied from 217 to 254 h post-cohabitation, a clear sign of significant phenotypic variation for resistance against the parasite. The quantitative genetic analysis demonstrated high values for heritability of SS (0.46 ± 0.09) and TD (0.60 ± 0.18). Overall, the genetic estimates suggest that these traits are under strong genetic influence and should respond to selection, which represents a sustainable and effective approach to decrease mortality and improve the production of tambaqui.

Reviews of the literature have shown that heritability for disease resistance in fish tends to vary from moderate to high, which demonstrates the potential of improving this trait by selective

breeding.[237,238] Hence, disease challenge experiments to evaluate the genetic basis of resistance of tambaqui to other pathogens, such as *Neoechinorhynchus buttnerae* and *Flavobacterium columnare*, would be useful. Results of such assessments would address whether resistance is specific to each disease or general, whether disease resistance is correlated with growth rate, and how disease resistance can be included in a selective breeding programme for tambaqui.

The main hurdles to including disease resistance traits in selective breeding programmes are the high cost of routine disease challenge assays for phenotypic characterization and the difficulty in obtaining data from relatives of the selected candidates, because animals evaluated in disease challenge need to be sacrificed because of biosecurity issues to avoid contamination of the breeding nucleus. This practice decreases the genetic progress for each generation due to the lower accuracy of estimated breeding values (EBVs) when using only sib information instead of the selection candidates themselves.[239] Therefore, marker-assisted selection (MAS) or genomic selection (GS) become fundamental approaches to disease resistance selection programmes, as recently reported for several aquaculture species.[240] However, initial studies to understand the genetic architecture or building knowledge of underlying quantitative trait loci (QTL) associated with disease resistance traits in tambaqui are still needed, particularly genome-wide association studies (GWAS) assessing numerous molecular markers. Therefore, the application of MAS to select candidates based on whether they bear favourable alleles close to large-effect QTL, or using GS to obtain higher prediction accuracy of breeding values for candidates which is based on marker effects estimated in a training population evaluated for both phenotypes and genotypes, is promising approaches.[241]

In total, genetic findings on tambaqui follow the advances of molecular techniques over the years. New approaches take advantage of available DNA technologies for long-read sequencing, designated 'third-generation sequencers'. These new technologies, such as the PacBio sequencer and Nanopore Sequencer, can yield genome assemblies of unprecedented quality.[242] A few draft Neotropical fish genomes have become available, such as those for *Astyanax mexicanus*,[243] *Arapaima gigas*[244,245] and *Pygocentrus nattereri*.[246] A high-quality genome assembly and annotation for tambaqui was assembled with PacBio reads and scaffolded with the high-density genetic map,[224] yielding a highly contiguous assembly; it then was submitted to NCBI for annotation, where it passed all quality checks and subsequently was made available in a genome data viewer for this species.[247] Added to this was the development of a multispecies SNP array, the Affymetrix SerraSNP array, for two serrasalmid species (*Piaractus mesopotamicus* and *Colossoma macropomum*) with validation of 74.17% (n = 21,963) and 71.25% (n = 21,072) of polymorphic SNP variants for the respective species.[248]

Despite the sizeable harvests of farmed tambaqui in Brazil, this represents less than what would be realized by use of a selectively bred strain with better performance, larger LEA, no intermuscular bones, improved disease resistance and other valued traits. Therefore, to achieve international standing as a commodity food, the sector needs to produce fingerlings from highly productive tambaqui strains developed by classical methods of selective breeding and genome-based selection methods to fast-track genetic improvement of this species, conserving wild populations as raw genetic resources for use in further genetic improvement.[249]

5 | NUTRITION AND FEEDING

Tambaqui is an omnivorous fish, feeding mainly on fruits and seeds from the riparian forest but also on snails, shrimps, insects and small fish[2,250] (Supporting Information/Infographic 4). Because of its distinctive molariform teeth, tambaqui is well adapted to crumble and ingest seeds and fruits from the jauari (*Astrocarium jauari*) and the belly spurge (*Hevea spruceana*, a rubber tree) throughout the rise of river waters in seasonally flooded forests.[1,251,252] Tambaqui also have branchial gill rakers adapted to rather efficient filtering of zooplankton.[3]

Farmed fish thrive on diets with adequate, balanced macronutrients and energy content, and tambaqui is no exception.[253] Proteins make up to 65–75% of farmed animals' dry weight, being the primary nutrients in their diets.[254-256] The first studies on the dietary protein requirement of tambaqui were carried out by Macedo,[257,258] which comprises pioneering research on nutritional requirements of the Neotropical round characins. The dietary protein requirement of juvenile tambaqui for optimized growth performance is 22% crude protein (CP) for fish ranging from 5 to 30 g, and 17% for fish ranging from 20 to 300 g live weight. Further studies have defined dietary CP requirement of tambaqui, with results ranging from 25 to 50 (see Table 3).[259-265]

Vieira et al.[266] reported highest growth performance under farm conditions for juvenile tambaqui (2.05~9.06 g) fed diets containing 32% CP. A recent study reported higher growth performance and reduced excretion of nitrogen metabolites for juvenile tambaqui (2~20 g) fed diets containing 30% CP,[267] and maximized growth rate for juvenile tambaqui (6.5~74.6 g) fed diets containing 29% digestible protein.[268]

Tambaqui feeding behaviour allows the species to be farmed using diets containing 75–85% plant protein. However, the inclusion of plant protein in aquafeed formulation and use depends on many variables, such as macronutrient proportions, amino acid composition, animal age and strain, water temperature and content of dietary non-protein energy sources.[254,269,270] Rodrigues[271] reported that results of studies on dietary protein requirements of fish between 1979 and 2012 showed significant divergences, which results not only from the virtual lack of knowledge on biological and nutritional value of the non-protein energy sources and the energy-to-protein ratios of diets but possibly also from the role of genetic variability-driven responses (Tave[272]), given that tambaqui has been used in intensive farming systems for no more than a few decades, selective breeding programmes for the species are still few, and no solid results have been reported to date. Further, experimental conditions evolved markedly within this period, which

TABLE 3 Dietary protein requirements with dietary energy levels for tambaqui (*Colossoma macropomum*)

Weight range[a] (g)	Protein requirement g kg^{-1}	Energy level[d] kcal kg^{-1}	Energy-to-protein ratio [h] kcal g^{-1}	Reference
2.0–9.0	320[b]	—	—	266
2–2	300[b]	4070–4286[f]	13.6–14.3:1	267
0.44–30.6	316[b]	3000[e]	9.5:1	264
1–50	481[b]	4585[e]	9.4:1	260
6.7–59.8	250/750[b]	2700[e]	10.8–3.6:1	262
6.5–174.5	290[c]	3300–3324[f]	11.4–11.5:1	268
30–145	300[b]	2700[e]	9.0:1	259
30–250	250[b]	3100[g]	12.4:1	261
46–75	300[b]	3860–4040[f]	12.9–13.5:1	265
50–100	360[b]	3407[e]	9.5: 1	263

[a]Weight range = approx. initial and final weights of fish.
[b]Crude protein.
[c]Digestible protein.
[d]Energy levels of diets.
[e]Digestible energy.
[f]Gross energy values.
[g]Metabolizable energy values.
[h]Calculated.

may have affected the results of trials. This uncertainly emphasizes the importance of continuing studies on nutrition for the species, especially regarding selection of feed ingredients based upon results of digestibility trials.

Considering that fish do not have specific dietary protein requirements, but rather need a balanced pool of dietary essential amino acids,[254,255] experimental trials based upon the concept of ideal protein[273] or, as currently redefined, the essential nitrogen concept are fundamental for the advancement of knowledge on the nutrition and feeding of tambaqui. In this regard, Lima et al.[274] reported that it is possible to reduce dietary protein contents from 32 to 24.5% if the diet of postlarvae tambaqui (0.44 g) is supplemented with a balanced pool of essential amino acids. In the same line of research, Marchão et al.[275] reported that juvenile tambaqui (22.9 g) require 1.58% dietary lysine, that is diets containing 5.7% lysine within the crude protein. Bonfim et al.[276] recommended 0.323% of digestible tryptophan in diet for the maximum deposition of body protein.

Energy is not a nutrient by definition, but it plays a key role in fish nutrition because of its biochemical and physiological importance to maintenance, growth and reproduction of animals.[277,278] The determination of the optimal dietary energy level and its correlation with dietary protein content is fundamental for optimizing practical fish nutrition and feed management, given that dietary energy deficiency can lead to use of protein as energy source.[279,280] On the contrary, excess dietary energy reduces feed consumption and, consequently, ingestion of nutrients.[255] In a review on nutritional requirements of tambaqui, Guimarães & Martins[281] pointed out that the species has great ability to use various non-protein energy sources and a tendency to increase body fat deposition. While a protein sparing effect driven by manipulation of dietary energy sources, mainly carbohydrates, is well documented for many fish, it has not been demonstrated for tambaqui.

Understanding of metabolic interactions between proteins, lipids and carbohydrates is key to evaluating the dietary lipid requirement of fish. That is, the dietary lipid requirement and use by fish depend on the content and quality of other dietary macronutrients, and no clear, precise definition of tambaqui's dietary lipid requirements is available. However, Camargo et al.[282] reported a linear response to increasing levels of dietary, metabolizable energy (2,850–3,300 kcal EM kg^{-1}) on growth performance of juvenile tambaqui (30.17 g), suggesting the highest values, 12.50–13.75 kcal EM g^{-1}, as the dietary energy requirement of the species. Oliveira et al.[283] reported a protein requirement of 30% crude protein (CP) and an energy-to-protein ratio around 9.0 kcal DE g CP^{-1} for juvenile tambaqui (1.0–125.0 g live weight).

Even though only a few studies report specific, dietary fatty acid requirements of tambaqui, such studies highlight that total lipid and fatty acid composition varies greatly between wild and farmed fish and that dietary fatty acids play a key role in growth, flesh quality and disease resistance of the species.[281,283] For instance, tambaqui fed varying dietary linoleic-to-linoleic acid (LA/ALA) ratios had no significant effects on growth, but significantly influenced carcass fatty acid deposition.[284] This study also reported that tambaqui can elongate and desaturate linoleic acid (LA, 18:2n-6) and linoleic acid (ALA, 18:3n-3) to their corresponding long-chain polyunsaturated fatty acids, such as arachidonic acid (ARA, 20n:4-6), eicosapentaenoic acid (EP, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3),

as has been reported for most freshwater fish. Results of a recent molecular study demonstrated that tambaqui express all desaturase and elongase activities (ie *fads2*, *elol5* and *elovl2*) required to convert LA and ALA to ARA, EPA and DHA.[228,285] Thus, the NRC[255] recommendations of supplying 5–20 g LNA kg^{-1} diet (based on total lipid content) and the importance of n-6 fatty acids in the nutrition and feeding of Neotropical fish species such as tambaqui are supported.

Non-protein feed ingredients rich in carbohydrates and lipids can be used to increase dietary energy content, attaining optimal energy-to-protein ratio.[286] Because of the importance of balance between these dietary macronutrients in fish production and metabolic pathways, de Almeida et al.[287] and Sandre et al.[288] evaluated, respectively, dietary protein-to-lipid and carbohydrate-to-lipid ratios for tambaqui and demonstrated that the species exhibits highest survival and growth when fed diets containing carbohydrate levels close to 40–46%.

Optimized productivity, maximization of profits and reduction in environmental impacts of commercial fish farming rely on the knowledge of coefficients of digestibility of ingredients used in formulation of fish diets, and tambaqui is no exception.[255,289,290] Buzollo et al.[291] studied the apparent digestibility coefficient (ADC) of protein and energy of ingredients ordinarily used to formulate commercial diets for tambaqui and reported that corn gluten has high apparent digestibility coefficients for crude protein (ADC_{CP}) (98.09%) and gross energy (ADC_{GE}) (96.91%). Corn meal (94.5%) and wheat bran (86.08%) presented the highest ADC_{CP} of all dietary energy sources. Regarding dietary lipid sources, corn oil (95.7%), fish oil (93.61%), soya bean oil (93.31%) and corn meal (88.70%) presented the highest ADC_{GE}. Tambaqui juveniles efficiently use the amino acids of protein and energy-rich ingredients. Corn meal and wheat bran presented high ADCs for total amino acids, 95 and 92%, respectively. Regarding dietary protein sources, corn gluten meal and soya bean meal presented the highest ADCs for tambaqui, 97.6 and 96.6%, respectively (Table 4).[292]

The natural foods of tambaqui are very rich in vitamins and minerals, and tambaqui farming is prevalent in regions with waters of high primary productivity. This may suggest why studies on dietary requirements of minerals and vitamins of tambaqui are scarce; that is, no dietary vitamin or mineral deficiency signs have been reported for pond-farmed tambaqui. Oliveira et al.[283] and Guimarães & Martins[281] reviewed reported information on vitamin and mineral requirements of tambaqui, but such reports are based on few studies. As for most teleosts, most studies target ascorbic acid requirements.[293] Chagas & Val,[294] for instance, evaluated the effect of L-ascorbic acid on the productive performance and haematological parameters of juvenile tambaqui and reported that 100 mg kg^{-1} was sufficient to maximize production and maintain homeostasis. Aride et al[295] studied the relationship between acid ascorbic and iron in diets for tambaqui and reported that the supplementation of acid ascorbic improved haematological parameters and tissue absorption of iron and that iron deficiency resulted in highly predictable anaemia. Sousa[296] tested increasing digestible phosphorus levels in diets for small juvenile tambaqui (0.51 g) and recommended inclusion of 0.71% P in diets, which corresponds to an estimated level of 1.04% of total dietary P.

The search for alternative feed ingredients, which can support higher performance and reduce production costs, is a major constraint for the fish feed industry, especially in the Amazon region. The use of locally available feed ingredients can improve diet (feed) efficiency and boost economic viability for farming and husbandry of tambaqui.[252] Most studies on alternative dietary feed ingredients for tambaqui evaluated only the chemical composition and substitution of conventional by alternative ingredients focusing on the animals' production. However, the evaluation of the digestibility coefficients of ingredients, independently of origin and nutritional contribution, is fundamental for enabling use of alternative ingredients in aquafeeds. In that regard, Silva et al.[297] evaluated the ADC of palm kernel (*Elaeis guineenses*) meal by-product for tambaqui in two weight classes, 4.4 and 115.2 g, and reported an ADC_{CP} of 63.29%. Silva et al.[298] determined the ADC of whole banana meal in diets for tambaqui (100.3 g) and reported ADC above 90% for protein, gross energy and dry matter with the inclusion of up to 8% of the ingredient in the diet (Tables 5 and 6).

The steady growth of aquaculture production in Brazil has encouraged feed mills to manufacture species-specific diets for the farming and husbandry of native species. However, despite the high number of feed mills producing fish feeds,[306] most formulated and processed diets claim to meet 'round characins' feeding and nutritional requirements, including tambaqui and pacu—*Piaractus mesopotamicus*—and their reciprocal hybrids. Only one brand is commercially available and labelled as specifically formulated for tambaqui. Despite the benefits to tambaqui production resulting from availability of manufactured diets, the feed formulae are usually kept as proprietary information by feed companies, making difficult the comparison of performance of fish on a nutrient content meeting requirements–based approach.

Feeding and nutrition are the major costs associated with farming of any fish. From the very first attempts to study nutritional requirements of tambaqui 40 years ago, studies on the nutrition of the species targeted dietary protein requirement of fingerlings and juveniles, and the results were not consistent. As of the early 2000s, studies on amino acid requirements have gained emphasis, but are still incipient. Trials on the use of feed additives, such as digestive enzymes, digestibility and use of alternative feedstuffs, have been carried out, but information on physiological mechanisms underlying nutrient absorption and use remains scarce at best. Tambaqui has peculiar feeding habits and nutritional requirements, so additional, targeted investigations are needed to develop cost-effective diets for each life stage to increase the economic viability and sustainable development of tambaqui farming.

TABLE 4 Apparent digestibility coefficients of essential and non-essential amino acids of dietary protein sources for tambaqui (adapted from Nascimento et al.[292])

	Apparent digestibility coefficients (%)								
Amino acid	Corn gluten meal	Soya bean meal	Poultry by-product meal	Fish meal (salmon processing residue)	Fish meal (tilapia processing residue)	Wheat gluten meal	Feather meal	Cottonseed meal	Alcohol yeast
Essential amino acids									
Arginine	99.1	99.2	80.2	81.6	92.2	51.3	69.1	81.3	53.8
Histidine	98.3	95.8	99.8	99.8	84.0	99.1	85.3	85.3	89.7
Isoleucine	98.8	97.1	93.3	93.8	84.7	95.4	88.6	84.4	69.4
Leucine	99.9	97.2	93.6	90.9	87.0	94.9	87.2	84.6	73.5
Lysine	93.5	94.5	91.4	92.9	85.9	65.4	78.7	67.2	72.3
Methionine	99.5	95.1	97.6	90.3	89.8	99.6	83.4	91.9	86.2
Phenylalanine	99.9	98.2	91.5	90.3	85.5	93.9	85.8	87.0	71.9
Tryptophan	81.2	94.2	92.8	84.8	85.4	92.1	72.2	90.8	72.5
Threonine	99.4	98.1	77.9	84.7	82.5	60.2	82.1	44.9	44.4
Valine	99.3	97.0	87.1	87.5	84.5	88.6	88.7	77.4	50.7
Average	96.9	96.6	90.5	89.7	86.1	84.0	82.1	79.5	68.4
Non-essential amino acids									
Aspartic acid	99.9	99.5	96.9	96.2	92.4	76.3	81.1	86.7	76.2
Glutamic acid	99.8	98.9	95.2	96.1	94.6	99.1	86.9	91.4	74.4
Alanine	99.9	97.0	98.7	99.3	90.3	99.4	99.9	99.6	99.8
Cystine	91.3	90.9	97.1	94.3	83.9	87.9	81.3	72.1	85.1
Glycine	90.3	93.9	87.2	90.0	86.5	55.3	85.6	83.6	71.3
Serine	99.5	96.2	99.9	99.4	85.1	97.3	85.5	75.9	63.3
Proline	99.8	97.9	89.4	93.9	86.8	95.1	86.0	73.0	73.1
Tyrosine	99.0	98.2	93.5	93.5	85.2	73.3	87.8	81.4	70.3
Arginine	99.1	99.2	80.2	81.6	92.2	51.3	69.1	81.3	53.8
Average	98.5	96.6	94.7	95.3	88.1	85.1	86.9	83.0	76.7

TABLE 5 Digestibility coefficient of selected feed ingredients for tambaqui (*Colossoma macropomum*)

Ingredient	ADC_{CP} %	DP %	ADC_{GE} %	DE kcal kg^{-1}	References
Protein, animal origin					
Blood meal	57.7	42.3	67.4	3257	270
Feather meal	84.1	64.1	77.2	4363	293
Meat and bone meal	88.6	33.9	83.9	2538	270
Poultry by-product meal	86.0	56.6	83.8	4191	293
Salmon meal	87.2	57.9	81.0	3558	293
Tilapia processing residue meal	78.4	47.2	70.2	3000	293
Energy, animal origin					
Fish oil	—	—	93.6	8722	293
Protein, vegetable origin					293
Alcohol yeast	63.17	22.9	46.2	1996	293
Cottonseed meal					293
Soya bean meal	95.0	45.10	76.8	3205	293
Soya bean whole, toasted	92.0	34.1	91.4	4973	270
Soya bean whole, raw	68.8	27.6	92.7	4715	270
Wheat gluten meal	93.9	75.6	78.2	4000	293
Plant ingredients	85.7		56.5		
Broken rice	71.21	58.3	85.5	3210	293
Common bean residue	66.3	13.4	46.6	1929	293
Corn	94.5	7.71	88.7	3432	293
Corn oil	—	—	95.7	9011	293
Mesquite meal	26.7	2.6	40.2	1612	299
Pasta by-product	95.7	14.1	84.6	2735	299
Sorghum	71.9	6.6	81.1	3190	293
Soya bean oil	—	—	93.3	8751	293
Wheat bran	86.0	14.2	68.2	2653	293
Whole banana meal	97.9	—	98.6	—	253

Abbreviations: ADC_{CP}, apparent digestibility coefficient for crude protein; ADC_{GE}, apparent digestibility coefficient for gross energy; DP, digestible protein; DE, digestible energy.

TABLE 6 Alternative feedstuffs tested for tambaqui (*Colossoma macropomum*)

Alternative feedstuff	Average initial weight (g)	Level of inclusion (%)	Replaced ingredient	Reference
Licuri meal (*Syagrus coronata*)[a]	3.1	100%	Corn	300
Cowpea (*Vigna unguiculata*)	10.0	25%	—	305
Cassava (*Manihot esculenta*)	10.6	15 or 45%	—	301
Pejibaye (*Bactris gasipaes*) meal[a]	32.4	100%	Corn meal	302
Babassu (*Attalea speciosa*) meal	24.0	12%	—	303
Leucaena leaf (*Leucaena leucocephala*) meal	41.1	24%	—	304

[a]Percentage of replacement.

6 | DISEASES AND HEALTH MANAGEMENT

Most pathogens affecting tambaqui farming operations have been found in wild specimens collected from Amazonian lakes and rivers.[307-309] (Supporting Information/Infographic 5). Nevertheless, outbreaks of acute mortality associated with pathogens have not been reported for wild tambaqui populations. This section discusses the pathogen-host relationship and the impact of prevalent parasitic and bacterial diseases of tambaqui in farming environments.

6.1 | Parasites

6.1.1 | Neoechinorhynchus buttnerae

The acanthocephalan *Neoechinorhynchus buttnerae* is regarded as the most relevant pathogen of farmed tambaqui.[310,311] The life cycle of this parasite involves the presence of an intermediate host (zooplankton) and a definitive host (tambaqui).[312] Outbreaks of this parasite do not cause sizeable mortalities, but do cause economic losses to farming,[313,314] because parasitized fish continue to feed normally, but nutrients are sequestered and used by the helminth, hampering feed conversion rate and growth of the fish. The parasitized tambaqui does not show change in behaviour or evident clinical signs, but disease diagnosis is simple and easy for *N. buttnerae*, as it is a macroparasite detectable by the naked eye inside the fish intestine, so routine health monitoring at the fish farm is necessary. Critical control points for the prevention of acanthocephalosis at tambaqui farms are as follows: (i) acquisition of acanthocephalan-free fish with a sanitary certification; (ii) a water source free of tambaqui, which is the natural host for this acanthocephalan; and (iii) implementation of careful preventive measures between production cycles by drying and disinfecting the ponds.

Recent *in vitro* studies have reported the potential of natural plant extracts[315] organic acids, essential oils[316] and oleoresins[317] to kill the acanthocephalan, and *in vivo* studies have shown that a commercial phytobiotic[318] and plant essential oils[319] have reduced the burden of parasitism at different levels. Recent *in vitro* studies have reported the potential of natural plant extracts,[315] organic acids, essential oils[316] and oleoresins[317] to kill the acanthocephalan, and *in vivo* studies have shown that a commercial phytobiotic[318] and plant essential oils[319] have reduced the burden of parasitism at different levels. However, there is still no consensus on the effectiveness of acanthocephalosis control in farmed tambaqui based only on fish medication, mainly because it is a disease caused by infected zooplankton that are dispersed three-dimensionally throughout the farming environment, making disease prevalence and relapse imminent if preventive measures are not in effect.

6.1.2 | Ichthyophthirius multifiliis

The ciliated protozoan *Ichthyophthirius multifiliis* is among most important parasites of farmed fish, causing massive mortality in farming operations worldwide,[320,321] including tambaqui farms.[157] Predisposing factors for mortality have long been known, including stress due to sudden environmental changes, especially water temperature, which lead to failure of the fish immune system.[320] This parasite is relevant to tambaqui farming mainly when it is farmed outside of its environmental comfort zone, that is a region of stable, warm climate. During health monitoring of 20 fish farms in the Amazon region between 2018 and 2020, no *I. multifiliis* outbreaks were reported at tambaqui farms (G.R.M. Valladão, Laboratório de Parasitologia e Patologia de Organismos Aquáticos, Universidade Nilton Lins, Manaus, Brazil; unpublished data). In contrast, a study carried out at the same time period reported the importance of ichthyophthiriasis in tambaqui farmed outside the Amazon region.[236]

Ichthyophthiriasis, or white spot disease (of fish), is characterized by high morbidity and mortality rates, and is the leading cause of fish death related to respiratory collapse. However, it is also common to find secondary systemic bacterial infections in intensely parasitized fish. Several molecules have been studied in different fish for treatment of this parasite.[26,322] However, fish farmers and professionals have not been able to apply recommended treatments to ponds because of the lack of registration of medications for aquaculture purposes. Nonetheless, late diagnosis at fish farms hampers the effectiveness of chemical treatments. Therefore, white spot disease is a seasonal and regional concern for the tambaqui farming industry, given the low resistance of the species to ichthyophthiriasis in regions with broad thermal variation or abrupt change of seasons. Effective, innovative prevention and control strategies for this tambaqui parasite are an immediate need.

6.2 | Monogenoidea

Monogenoid parasites plague almost all marine and freshwater farmed fish worldwide, wild and farmed tambaqui included, especially in Brazil and Peru.[323-328] Monogeneans mainly affect tambaqui gills, which is problematic because respiratory collapse is the main cause of fish mortality caused by parasites. The prevalence of monogeneans in tambaqui farming environments is close to 100% Godoi et al.,[329] and the intensity of parasitism varies with environmental factors. Warmwater fish farming generally is carried out under low dissolved oxygen contents, and the host-parasite relationship may vary greatly with water temperature, parasite load and management practices. Thus, fish having even a light gill parasite infestation may be prone to mortality due to respiratory collapse.

In one of the few studies associating the impact of climate change with tambaqui diseases, Costa & Val[330] reported that the rate of parasitism by monogeneans rapidly increased in the extreme climate change scenario; rise in temperature and carbon dioxide is predicted to affect the monogenean-tambaqui relationship. Recent studies report promising effects of different treatment protocols against monogenean infection in tambaqui.[331-333] However, none of the treatments has reached the market as a registered product for the species.

6.2.1 | Perulernaea gamitanae

The crustacean *Perulernaea gamitanae* (Lernaeidae) was described for the first time parasitizing wild tambaqui in the Amazon River near Iquitos, Peru.[309] *P. gamitanae* shows high host specificity to tambaqui and its hybrids.[334-336] and high specificity of the

infection site to the oral and opercular cavities. This parasitosis does not affect feed consumption or growth performance of affected fish, but decreases the post-harvest quality of fish products, which present haemorrhagic areas in the oral cavity and adjacent region.[337] Tambaqui is commercialized as whole fish or in halves ('bandas') with heads (see section on Processing methods). Therefore, the presence of macroscopic parasites and lesions in the product displeases consumers. Treatment of crustacean parasites in aquaculture is usually carried out using pesticides, for example diflubenzuron.[338,339] However, the impact of use of such molecules on fish health and the consumer is little known, and therefore, pesticide use is not advisable. Removal of heads of fish at processing is the only strategy to sell tambaqui infected by *P. gamitanae* because this parasite occurs only in the oral cavity and is not zoonotic, thereby not affecting food safety. Nonetheless, additional studies are needed to better understand the pathogenesis of infestation and to develop prevention strategies.

6.3 | Myxozoans

This group of parasites, which is diverse and well known because they cause outbreaks throughout global aquaculture, includes the genera *Myxobolus* sp., *Myxidium* sp., *Sphaerospora* sp. and *Henneguya* sp.[340] Myxosporeans have been routinely detected in both wild and farmed tambaqui.[341-343] However, little is known regarding harmful effects of parasitism by myxosporeans and how these parasites cause mortality in South American fish. Videira et al.[343] detected a severe infection by myxosporeans at a tambaqui farm during a mortality outbreak; however, the parasites were not proven as the causative agent of mortality. Between the years 2018 and 2020, numerous myxosporeans have been detected on farms during monitoring of tambaqui health without a history of mortality, clinical signs or behavioural changes (G.M.R. Valladão, G.R.M. Valladão, Laboratório de Parasitologia e Patologia de Organismos Aquáticos, Universidade Nilton Lins, Manaus, Brazil; unpublished data). Therefore, studies on the pathogenicity of myxosporeans are to determine which species of this vast group of parasites are relevant to tambaqui and to provide the basis for prevention and control methods.

6.4 | Bacteria

6.4.1 | Flavobacterium columnare

Flavobacterium columnare causes the common columnaris disease of several farmed fish worldwide[344] and has been isolated from farmed tambaqui presenting whitish, integumentary lesions.[345,346] Although *F. columnaris* had proven to be one of the most relevant and harmful diseases for tambaqui, associated with mortality outbreaks after transport or handling of young fish, only recently has the Koch postulate been fulfilled for this species.[347] After complaints from producers and analysis of tambaqui mortality outbreaks in recent years (2018 to 2020; G.M.R. Valladão, Laboratório de Parasitologia e Patologia de Organismos Aquáticos, Universidade Nilton Lins, Manaus, Brazil; unpublished data), the stress of handling young fish associated with the loss of scales caused by seines is recognized as a factor predisposing them to columnaris disease outbreaks up to 96 h after transport. Effective prevention strategies, such as adding 0.8% sodium chloride to transport water, are thus necessary to control columnaris infection.[347] On the contrary, addition of antibiotics or chemotherapeutants to transport water has not been shown effective to prevent columnaris disease and mortality. To date, there are no vaccines nor commercial treatments registered for the control of bacteriosis in general in tambaqui farming operations, a problem that needs to be addressed.

6.5 | Motile Aeromonads

The occurrence of haemorrhagic septicaemia caused by several *Aeromonas* species is common in farmed fish worldwide,[348-350] including tambaqui.[351] However, few studies of the pathogenesis of different *Aeromonas* species in tambaqui are available. Recently, Gallani et al.[351] fulfilled Koch's postulates for *A. hydrophila* isolated from the kidney of infected tambaqui. The same postulates were applied to the other two aeromonads, *A. jandaei* and *A. caviae*, isolated from infected tambaqui, corroborating that haemorrhagic septicaemia spreads among healthy fish.[347] Indeed, several aeromonads (*A. dhakensis*, *A. caviae*, *A. veronii*, *A. hydrophila* and *A. jandaei*) with pathogenic potential were isolated from tambaqui gills and described by Fernando-Ramos et al.[352] Aeromonads are opportunistic bacteria ordinarily found in the aquatic environment and soil; hence, stressful management of fish, poor environmental quality and primary diseases are predisposing factors for haemorrhagic septicaemia. Tambaqui infected by *A. hydrophila* can present darkened skin, ulcers, haemorrhage, lethargy, hypo/anorexia and different degrees of mortality at different life stages.[351] While several synthetic and natural disinfectants and antibiotics show promise for controlling this bacteriosis (Gallani et al.[351]), there are no registered products available on the market for prevention (eg a vaccine) or specific treatment for tambaqui.

In summary, the production of tambaqui can be affected by important pathogens, many of which are already known around the world. However, treatment of diseases is one of the least-developed areas of tambaqui culture, which calls for attention from the veterinary pharmaceutical industry and regulatory agencies in producer countries. Based on considerations of the pathogen-host relationship, climate change and anthropogenic changes in the aquatic environment can affect the natural response of tambaqui to pathogens, which can contribute to occurrence of outbreaks and emergence of new diseases. Prevention and control based on safe, effective methods still need to be developed for the main pathogens of tambaqui. Moreover, successful selective breeding programmes, especially those that incorporate genomic data, likely can result in cumulative and permanent improvement

of pathogen resistance in tambaqui, similar to other cases in model and aquaculture species.[233,241,353]

7 | PROCESSING METHODS

Tambaqui is traditionally commercialized as a whole, fresh or frozen product, and has high acceptance by the consumer market.[76] (Supporting Information/Infographic 6). Even in markets outside the Amazon basin, tambaqui products attract consumer interest because of its high quality and unique gastronomic qualities. Over recent decades, many studies have contributed to post-harvest processing technologies for tambaqui. During the 1980s and 1990s, studies focused on evaluating the chemical composition of whole tambaqui, fillet, ribs, mid-sagittal plane cut with head, processing of by-products, and mechanically separated meat (MSM), also called 'fish pulp'.

Castelo et al.[40] assessed the chemical and physical-chemical characteristics of abdominal fat and compared them with those of intramuscular fat. Palmitic, oleic and stearic acids were the primary fatty acids found, which varied quantitatively and qualitatively according to the time of year when slaughter took place. The authors also found a substantial increase in saturated fatty acids after deodorization and the development of rancidity. The abdominal fat was thermally unstable and that the deodorization process led to the destruction of natural antioxidants. Comparing abdominal fat with soya bean oil used in the frying of potato chips, sensory evaluation and consumer acceptance did not show a statistical difference, indicating the potential use of deodorized tambaqui abdominal cavity fat for cooking purposes. Ortíz & Bello[354] evaluated the composition and stability of tambaqui fatty acids in mechanically separated meat (MSM) during frozen storage. At highest concentration was palmitic acid observed, followed by oleic acid. Further, tambaqui MSM is rich in omega-6 polyunsaturated fatty acids (linoleic and arachidonic) content. The fatty acids were affected by storage temperature, with the highest values of free fatty acids observed at 4 months of storage at −10°C. The authors stressed that MSM is a sustainable and profitable way of using processing waste, yielding nutritional quality equivalent to red meat. However, further studies would be needed to ensure its stability. During storage, losses in the functionality of proteins, enzymatic and bacterial deterioration, and formation of various volatile compounds may occur, which can cause oxidative rancidity, among other problems.

Aguiar[355] assessed the nutritional composition of regional Amazon foods to help regional diet development. Raw tambaqui fillet presented 66.3% moisture, 24.8% protein, 3.1% ash, 5.8% lipids and 151.4 kcal/100 g of energy. Whole tambaqui presented 72.7% moisture, 19% protein, 1.4% ash, 6.9% lipids and 138.10 kcal/100 g of energy. Izquierdo et al.[356] showed that all essential amino acids are present in the meat of tambaqui. The main minerals found were phosphorus, calcium, and, to a lesser extent, iron. These authors reinforced the point that the nutritional composition of tambaqui products may vary depending on the fish's diet, sex, habitat, age and size.

These first investigations of tambaqui fillet and carcass nutritional values during the 1980s to the 2000s focused on the tambaqui originating from fisheries, and to a lesser extent from cultivation commercialized mostly at the regional market. As tambaqui farming expanded and other markets were opened, new tambaqui product conservation technologies were investigated. Almeida et al.[357] evaluated the useful life of tambaqui preserved on ice, performing a sensory analysis of raw and cooked fish over time. Raw fish retained superior quality (Class A) for 22 days. If cooked, products remained Class A for 31 days. Both raw and cooked products remained in sound quality (Class B) for up to 40 days. At 43 days, both achieved 'quality of current consumption', and at 49 days, they were considered putrid. These outcomes certified that tambaqui can be conserved and traded for 40 days after slaughter if kept between layers of ice. The pH and the total volatile nitrogenous bases (N-BVT) of the muscle increased with the storage time, showing these parameters to be adequate indices to determine product quality. The authors pointed out that the variation in useful life span would also depend on capture and storage conditions.

The studies so far focused on conservation of tambaqui products *in natura* on ice for quick post-harvest commercialization. However, increased demand for tambaqui products led to search for new tambaqui products. For instance, Izquierdo et al.[358] and Sleder et al.[359] developed sausages using mixtures of tambaqui MSM. The authors found that the higher the proportion of mechanically separated meat, the greater the fat content and, concomitantly, the greater the amount of essential fatty acids. In the sensory evaluation, the formulation containing the highest amount of tambaqui MSM was the most accepted, evidencing the possibility of using tambaqui processing residue to develop new products.

In addition, other value-added tambaqui products became strategic for market expansion. Cartonilho & Jesus[360] evaluated different cuts of tambaqui, such as ribs, loin, and steak, stored frozen at −25°C in polyethylene packages for 180 days. The yields obtained were 19.6% for ribs, 27.7% for the loin, and 16.4% for steak. The loin and steaks cuts were classified as low fat, and the rib cut as semi-fat, according to the classification proposed by Ref. 361 Thiobarbituric acid reactive substances (TBARs) values increased over the storage period and showed higher lipid oxidation in the fatter cut (rib). Thus, only lowering the storage temperature was not enough to prevent the process of lipid oxidation from developing, suggesting that storage in vacuum packaging could be an alternative. Bearing in mind full use of tambaqui processing residues, Leitão[362] developed a method to obtain flour from the skin. This by-product was nutritionally evaluated for use in food products. Bread, toasts and cookies were made with 10% tambaqui skin flour to replace wheat flour to increase these foods' protein content and were well accepted.

Mechanically separated meat from tambaqui was used by Kato et al.[363] to prepare nutritious rice, pasta, salad and pie. The authors evaluated the acceptance of these products by students at a primary school to supply part of the students' daily nutritional needs

and to favour the formation of good eating habits by students, with economic valuation of local ingredients. The results showed high acceptance rates (57.5–94.4%), demonstrating that mechanically separated meat of tambaqui is an efficient way to incorporate fish into school meals. The authors also emphasized the need for the implementation of nutritional education programmes aimed at incorporation of fish products.

Increasing consumer demand for healthy and ready-to-eat products opened opportunities to develop new tambaqui products to boost consumption and enter new markets. The *sous vide* technique (controlled cooking under vacuum, resulting in a ready-to-eat product) has shown great potential. Ramos et al.[364] evaluated quality parameters of *sous vide* products of tambaqui raised in cages. Tambaqui raw material was prepared using basil sauce and 5% sodium lactate treated under pasteurization in a water bath at 65°C for 12.5 min, followed by rapid cooling in water at 0°C and storage under refrigeration. Results showed that *sous vide* preparation of tambaqui reduced coliforms at 45°C and psychrotrophic microorganisms, extending product shelf life.

Currently, the perception of consumers regarding animal farming has been changing. Concern about animal welfare regarding pre-slaughter and slaughter practices is an emerging issue. There is need for studies on pre-slaughter procedures, which could directly interfere with rigour mortis and increase the fish product's shelf life. Mendes et al.[366] evaluated the advantages of recovery from pre-slaughter stress in tambaqui. The fish were placed into ponds to recover from the stress of transportation for 48 h, and then were slaughtered by asphyxia and hypothermia. Analysis after slaughter showed that N-BVT content and pH were higher in fish slaughtered by asphyxiation. Sensory analyses indicated that quality of fish products slaughtered just after transport was lower than that for fish that recovered from pre-slaughter stress. Thus, post-transport recovery contributes to preserving the freshness and quality of tambaqui slaughtered on an industrial scale. Further study would be needed, however, to determine the economic viability of this recommendation.

There has been a trend of seeking complete utilization of all residues from fish processing. Thus, use of tambaqui waste has be explored to add value to so-called 'low-value products'. Silva et al.[367] carried out a trial using head, skin and bones to extract collagen. The process yielded high-quality gelatine, a valuable multifunctional ingredient used in foods, pharmaceuticals, cosmetics and photographic films. This process turns out to be a profitable and environmental-friendly process for utilizing tambaqui processing residues.

The nutritional quality of fish products has aroused concerns for consumers, leading to changes in production practices mainly associated with fish feeding. Cortegano et al.[368] assessed the effect of supplementing the ration with *Schizochytrium* sp. microalgae flour on the composition and fatty acid content of tambaqui meat, comparing them with those obtained when using a non-supplemented ration. The authors observed no difference in the gross composition of fish meat. However, there was an increase in long-chain polyunsaturated fatty acid content from the omega-3 series, docosahexaenoic acid (DHA) from 14.81 to 38.60 mg/g, and an increase in the omega-3: omega-6 ratio from 0.16 to 0.51 in fish meat. This study showed the possibility of marketing a sustainability-oriented product with greater nutritional value.

The search for healthier and less-formulated foods has contributed to the commercialization of fish fillets due to their high nutritional value and easier preparation. However, shorter shelf life is a major disadvantage when compared to other meats. Thus, Vieira et al.,[369] aiming to minimize microbial deterioration in chilled tambaqui fillets, studied the application of an edible chitosan coating and clove essential oil for the ability to reduce growth of pathogenic agents (*Escherichia coli* 0157: H7, *Listeria monocytogenes*, *Salmonela enteritidis*, *Staphylococcus aureus* and *Pseudomonas aerugom*). The results showed that the coating exerted an antimicrobial effect, proving more effective against *L. monocytogenes* and *S. aureus*, increasing the useful life of chilled tambaqui fillets and making this a potential alternative to improve the safety of aquaculture products and, consequently, expand the market.

Over the past 40 years, tambaqui products have been studied progressively, characterized for chemical composition, quality, conservation and diversification of derived products. The challenges for building relevant and systematic knowledge about tambaqui processing are many.[370] Therefore, further investigation is needed on: (i) best pre-slaughter management and slaughter methods, which will be pivotal to obtaining highest-quality meat and derived products; (ii) standardization of tambaqui cuts, which is strategic to attract consumer fidelity; (iii) development of loin deboning techniques or even generating intermuscular bone-free loin strain by selective breeding (see the Genetics, genomics and selective breeding section) to add value to this favoured cut; (iv) developing packaging systems for advancing microbial food safety and longer shelf life; and (v) continuous assessment of the consumer market and preferences to support development of new products. Tambaqui has the potential to become an international fish commodity due to its excellent culture performance and its potential for the production of various processed by-products, suggesting following of the marketing path adopted by the poultry industry.

8 | CONCLUDING REMARKS

South American aquaculture is dominated by production of non-native species. However, the native tambaqui has the potential to make an even more significant contribution to regional aquaculture production. Most production has taken place in extensive or semi-intensive systems, and can be intensified by more widespread adoption of intensive pond systems and use of cages in reservoirs. While induced spawning protocols have been developed, larviculture systems can be improved to grow the supply of high-quality seed stocks. Methods for production of all-female monosex stocks would be valued by farmers. Because this is a newly domesticated fish with a large geographic range, tambaqui presumably harbours considerable quantitative genetic variation for valued traits, including growth

rate, morphometric traits, and parasite and disease resistance. Yet, quantitative genetic and molecular tools have not been systematically applied to breeding, an omission that we regard as worthy of further and sustained investment. Applied nutrition studies will contribute to the development of high-quality and cost-effective aquafeeds. Improved health management will decrease losses, especially as production intensifies. Improved processing and storage techniques will better maintain product quality through the marketing chain. Development of new value-added tambaqui products will create new market opportunities.

While targeted advancements are needed in these scientific and technical areas, considerable effort must be allocated to effective technical outreach and aquaculture extension so that advancements will be more readily adopted by farmers. This critical task is incumbent upon regional agricultural universities and ministries of agriculture.

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ORCID

Alexandre Wagner Silva Hilsdorf https://orcid.org/0000-0001-9565-8072
Eric Hallerman https://orcid.org/0000-0002-5839-858X
Gustavo Moraes Ramos Valladão https://orcid.org/0000-0002-3875-6247
Micheli Zaminhan-Hassemer https://orcid.org/0000-0001-5879-9132
Diogo Teruo Hashimoto https://orcid.org/0000-0002-8808-2498
Jony Koji Dairiki https://orcid.org/0000-0002-1899-6657
Leonardo Susumu Takahashi https://orcid.org/0000-0002-5820-188X
Francielly Corrêa Albergaria https://orcid.org/0000-0001-5641-2889
Maria Emília de Sousa Gomes https://orcid.org/0000-0002-2338-2684
Rossana Luiza Leite Venturieri https://orcid.org/0000-0002-3050-8310
Renata Guimarães Moreira https://orcid.org/0000-0001-8139-1776
José Eurico Possebon Cyrino https://orcid.org/0000-0002-8942-0102

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