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CONDIÇÕES AMBIENTAIS E MORFOLÓGICAS NA MODULAÇÃO DO
CANIBALISMO EM LARVAS DE *Brycon amazonicus*

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Junho, 2025



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Tese apresentada ao Programa de Pós-Graduação em Zoologia, da Universidade Federal do Amazonas/Instituto Nacional de Pesquisas da Amazônia, como parte dos requisitos para obtenção do título de Doutor em Zoologia.

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“Entregue o seu caminho ao Senhor;
confie nele, e ele agirá.” (Salmos 37:5)

Resumo

Esta tese avaliou como condições ambientais e morfológicas modulam o canibalismo em larvas de matrinxã, *Brycon amazonicus*, espécie nativa da Amazônia com elevada relevância ecológica e econômica para a piscicultura regional. A pesquisa foi estruturada em três capítulos complementares. No primeiro, realizou-se uma revisão integrativa comparativa sobre o canibalismo e o comportamento agressivo em espécies cultivadas de *Brycon*, evidenciando que o conhecimento disponível é concentrado em poucas espécies, principalmente *B. amazonicus*, e que o período inicial de alimentação exógena constitui uma janela crítica para a ocorrência de interações canibais. No segundo capítulo, foi desenvolvido um modelo morfométrico preditivo para estimar o tamanho máximo de presas coespecíficas que larvas de *B. amazonicus* são capazes de ingerir, com base na relação entre comprimento total, altura corporal e abertura máxima da boca. O modelo indicou que as larvas canibais podem ingerir presas entre 92 e 106% de seu próprio comprimento total, demonstrando elevada capacidade predatória durante a ontogenia inicial e ausência de uma limitação morfológica evidente no intervalo analisado. No terceiro capítulo, avaliou-se o efeito de diferentes espectros de luz sobre a ontogenia, a sobrevivência, o cortisol corporal e a predação intraespecífica em *B. amazonicus*. A condição de escuro retardou o desenvolvimento de algumas estruturas morfológicas, mas aumentou a sobrevivência e reduziu o estresse, enquanto a luz vermelha esteve associada à maior mortalidade. Em conjunto, os resultados indicam que o canibalismo em *B. amazonicus* deve ser compreendido como um processo ontogenético, morfológicamente favorecido e ambientalmente modulável. Assim, práticas como o manejo adequado da primeira alimentação, a compatibilização do tamanho das presas, a classificação por tamanho e o controle da luminosidade podem contribuir para reduzir perdas na larvicultura, melhorar o bem-estar dos animais e fortalecer sistemas de produção mais sustentáveis na Amazônia.

Palavras-chave: *Brycon amazonicus*; canibalismo, larvicultura, modelo preditivo, espectro de luz.

Abstract

This thesis evaluated how environmental and morphological conditions modulate cannibalism in *Brycon amazonicus* larvae, a native Amazonian species with high ecological and economic relevance for regional aquaculture. The research was organized into three complementary chapters. The first chapter presents an integrative comparative review of cannibalism and aggressive behavior in cultured *Brycon* species, showing that available evidence is concentrated in a small number of species, especially *B. amazonicus*, and that the onset of exogenous feeding is a critical window for cannibalistic interactions. The second chapter develops a morphometric predictive model to estimate the maximum size of conspecific prey that *B. amazonicus* larvae are able to ingest, based on the relationship among total length, body depth and maximum mouth opening. The model indicated that cannibal larvae can ingest prey ranging from 92 to 106% of their own total length, demonstrating high predatory capacity during early ontogeny and no evident morphological limitation within the analyzed interval. The third chapter evaluated the effect of different light spectra on ontogeny, survival, body cortisol and intraspecific predation in *B. amazonicus*. Darkness delayed the development of some morphological structures, but increased survival and reduced stress, whereas red light was associated with higher mortality. Overall, the findings indicate that cannibalism in *B. amazonicus* should be understood as an ontogeny-driven, morphologically favored and environmentally modulated process. Therefore, strategies such as appropriate first-feeding management, prey-size compatibility, size grading and light control may reduce larviculture losses, improve animal welfare and support more sustainable production systems in the Amazon.

Key-words: *Brycon amazonicus*, cannibalism, larviculture, predictive model, light spectrum.

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Introdução Geral

O canibalismo em peixes é uma interação intraespecífica complexa, com implicações ecológicas, comportamentais e produtivas, especialmente durante as fases iniciais do desenvolvimento. Esse fenômeno está associado à dinâmica de competição, à disponibilidade de alimento, à formação de hierarquias de tamanho e ao rápido avanço ontogenético, sendo frequentemente registrado em larvas e juvenis de espécies cultivadas (Kestemont et al. 2003). Em peixes predadores ou com alta plasticidade alimentar, o canibalismo pode ocorrer quando há sobreposição entre capacidade de captura, abertura bucal, tamanho corporal da presa e oportunidade de encontro entre indivíduos coespecíficos (Baras e Jobling 2002; Duk et al. 2017). Por isso, sua ocorrência tende a ser mais intensa nos primeiros estágios de vida, quando pequenas diferenças de tamanho podem se converter rapidamente em vantagens predatórias (Baras 2000; Souza et al. 2014; Ribeiro e Portella 2020; Ribeiro e Portella 2021).

No contexto neotropical, o gênero *Brycon*, pertencente à família Bryconidae, reúne espécies de ampla relevância ecológica e socioeconômica. Segundo Lima (2017), o gênero possui 44 espécies descritas, das quais 22 ocorrem em corpos d'água da América do Sul cis-andina. Em condições de cultivo, diferentes espécies de *Brycon* apresentam registros de canibalismo intracoorte ou comportamento agressivo, como observado em *Brycon amazonicus* (Leonardo et al. 2008), *Brycon sinuensis* (Atencio-García et al. 2003; Jiménez-Velásquez et al. 2021) e *Brycon sp.* (Coraspe-Amaral et al. 2012). Embora os registros em ambiente natural sejam menos evidentes para o gênero, o canibalismo é reconhecido em outros teleósteos como parte de processos de competição, mudança ontogenética de habitat e estruturação populacional (Foster et al. 1988; Persson et al. 2000; Ocampo et al. 2011).

Em sistemas de criação, o canibalismo representa um dos principais entraves para a larvicultura de peixes, pois pode elevar rapidamente a mortalidade, ampliar a heterogeneidade de tamanho e comprometer a previsibilidade dos lotes. Além das perdas diretas por predação intraespecífica, ataques e perseguições podem provocar lesões, aumentar a susceptibilidade a patógenos, induzir respostas de estresse e reduzir a eficiência alimentar e o crescimento (Cutts et al. 1998; Huntingford et al. 2006). O comportamento agressivo, ainda que não seja sinônimo de canibalismo, pode atuar como indicador de instabilidade social e de aumento da probabilidade de interações predatórias, sobretudo quando associado à limitação alimentar, à densidade inadequada ou à elevada variação de tamanho entre indivíduos (Vøllestad e Quinn 2003; Kestemont et al. 2003).

Entre os mecanismos bióticos envolvidos nesse processo, destacam-se o crescimento alométrico, a heterogeneidade corporal e a relação morfológica entre predador e presa. Em espécies com desenvolvimento larval acelerado, pequenas diferenças no crescimento de estruturas como boca, cabeça e corpo podem favorecer a captura e a ingestão de presas coespecíficas (Baras 2000; Baras et al. 2000;

Ribeiro e Portella 2020; Ribeiro e Portella 2021). Assim, compreender o tamanho máximo da presa que pode ser ingerida por um indivíduo canibal é essencial para interpretar a dinâmica das interações intracoorte e para propor medidas práticas de manejo, como a oferta de alimento compatível com a fase de desenvolvimento e a classificação dos lotes por tamanho (Baras e Jobling 2002; Ribeiro e Qin 2015).

A relação entre o tamanho do predador e o tamanho da presa constitui um eixo central para o estudo do canibalismo, pois a ingestão geralmente só é possível quando a abertura bucal do canibal supera a altura corporal da presa (Juanes 1994). Nesse sentido, análises morfométricas permitem estimar limites de captura e ingestão a partir de medidas como comprimento total, altura corporal e abertura máxima da boca. Modelos preditivos baseados nessas relações vêm sendo utilizados para determinar a faixa de tamanho de presas que pode ser consumida por peixes canibais, contribuindo para o planejamento de estratégias de manejo mais precisas em larvicultura e alevinagem (Parazo et al. 1991; Sakakura e Tsukamoto 1996; Hseu et al. 2003; Ribeiro e Portella 2020).

Além dos fatores morfológicos, variáveis ambientais modulam a frequência e a intensidade das interações agressivas e canibais. A luminosidade, em especial, é um fator abiótico de fácil manipulação em sistemas de cultivo e pode influenciar diretamente a atividade locomotora, a capacidade visual, a detecção de presas, o desenvolvimento ontogenético e as respostas fisiológicas ao estresse. Esse fator compreende dimensões como fotoperíodo, intensidade e espectro de luz, que afetam crescimento, sobrevivência, características morfométricas e marcadores hormonais, incluindo cortisol e melatonina (Falcón et al. 2010; Navarro e Navarro 2012; Navarro et al. 2014; Villamizar et al. 2014; Shibata et al. 2019; Blanco et al. 2020; Septriani et al. 2021; Lopes et al. 2023). Estudos também demonstram que a luz pode alterar o comportamento agressivo e o canibalismo em peixes, reforçando sua importância como ferramenta de manejo em fases iniciais de criação (Mukai et al. 2013; Lopes et al. 2018).

Apesar desse avanço, ainda são escassas as abordagens que integram, em uma mesma perspectiva, o efeito de condições ambientais e limitações morfométricas sobre a relação predador-presa em larvas de peixes tropicais. Essa lacuna é particularmente relevante porque o canibalismo não resulta de um único fator isolado, mas da interação entre ontogenia, disponibilidade alimentar, variação de tamanho, capacidade morfológica de ingestão, densidade, luminosidade e estresse. Dessa forma, a combinação entre revisão integrativa, modelagem morfométrica e experimentação ambiental pode ampliar a compreensão dos mecanismos que sustentam o canibalismo e favorecer recomendações mais aplicáveis à produção aquícola (Hseu et al. 2003; Ribeiro e Qin 2015; Roy et al. 2020; Ribeiro e Portella 2020; Ribeiro e Portella 2021).

A espécie *Brycon amazonicus*, conhecida regionalmente como matrinxã, é nativa da Amazônia e ocorre ao longo do sistema Solimões-Amazonas, seus afluentes e a bacia do rio Orinoco (Lima 2017). Trata-se de uma espécie onívora bentopelágica (Izel et al. 2004), associada a ambientes de águas

brancas, claras e pretas, incluindo lagos e rios amazônicos (Goulding et al. 1988; Ferreira 1993). Também apresenta comportamento diurno e realiza migrações reprodutivas no início do período de inundação, formando cardumes em direção a áreas favoráveis à desova (Lima e Araujo-Lima 2004; Granado-Lorencio et al. 2005; Soares et al. 2008). Além de sua relevância ecológica, a espécie possui importância econômica para a região Norte do Brasil, sendo considerada promissora para a piscicultura amazônica (Urbinati et al. 2014; Zaniboni-Filho et al. 2016). Entretanto, a elevada incidência de canibalismo durante a larvicultura compromete a sobrevivência, o bem-estar e a padronização dos lotes, limitando o avanço produtivo da espécie (Bernardino et al. 1993; Leonardo et al. 2008).

Diante desse cenário, esta tese parte da premissa de que o canibalismo em larvas de *B. amazonicus* é um processo ontogenético, favorecido por características morfológicas e modulável por condições ambientais. Essa abordagem permite considerar, de forma integrada, a revisão do conhecimento disponível para espécies de *Brycon*, a estimativa morfométrica do tamanho máximo de presas coespecíficas e o efeito de diferentes espectros de luz sobre desenvolvimento, sobrevivência, estresse e predação intraespecífica. Assim, busca-se avançar da descrição do fenômeno para a identificação de pontos críticos de manejo que possam reduzir perdas durante a fase larval.

De modo geral, esta tese teve como objetivo avaliar a modulação do canibalismo em larvas de *Brycon amazonicus* a partir da integração entre condições ambientais e morfológicas, com ênfase nas relações predador-presa, no desenvolvimento ontogenético e no efeito da luminosidade. Com isso, pretende-se fornecer informações que possam subsidiar práticas de manejo aplicáveis à larvicultura, à conservação e ao aprimoramento de sistemas produtivos de matrinxã na Amazônia.

Assim, os resultados obtidos estão apresentados em três capítulos:

Capítulo 1: Cannibalism in cultured *Brycon* species (Bryconidae): advances, knowledge gaps, and management perspectives.

Capítulo 2: Morphometric prediction of maximum cannibal-prey size for larvae of matrinxã, *Brycon amazonicus* (Spix and Agassiz, 1829).

Capítulo 3: Light wavelength affects ontogeny, survival and intra-specific predation in larvae of matrinxã, *Brycon amazonicus*.

Capítulo 1_

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Cannibalism in cultured *Brycon* species (Bryconidae): advances, knowledge gaps, and management perspectives

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Declarations

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Abstract

Cannibalism remains one of the main biological bottlenecks in *Brycon* aquaculture because it can trigger rapid mortality, size heterogeneity, and unstable larval performance during the earliest phases of culture. This study is an integrative comparative review based on a systematic literature search and qualitative comparative narrative synthesis of published evidence on cannibalism and aggressive behavior in cultured *Brycon* species. The 37 included studies were reorganized into three comparative evidence tables covering biotic, abiotic, and mixed-factor drivers. Available evidence is taxonomically and ontogenetically uneven, being concentrated in a small subset of species, especially *Brycon amazonicus*, which represents the largest proportional share of both larval and juvenile records and limits genus-level generalization. Across studies, cannibalism usually begins very early, often around the onset of exogenous feeding and frequently within the first 22-36 h after hatching, although the exact timing depends on species, ontogeny, and rearing context. Feeding management emerges as the most consistent practical control point: adequate live prey, compatible prey size, and balanced predator: prey ratios tend to reduce cannibalism and improve survival. Abiotic factors such as density, light, temperature, salinity, turbidity, and biofloc conditions also modulate encounter rates, stress, activity, and growth, but their effects are strongly stage dependent and species specific. Physiological and neuroendocrine approaches, including triiodothyronine, tryptophan, melatonin, and serotonergic manipulation, show mixed and context-dependent outcomes and should therefore be interpreted as complementary rather than primary control tools. Overall, the literature supports integrated hatchery management centered on the first-feeding window, while highlighting major gaps for most *Brycon* species, especially the need for broader species coverage and ontogeny-based thresholds linking mouth development, prey size, density, and cannibalism risk.

Keywords: Cannibalism; Aggressive behavior; *Brycon*; Larviculture; Environmental management; Aquaculture.

Introduction

Cannibalism is a widespread phenomenon in cultured fishes, particularly during early life stages, and can be broadly described as either type I cannibalism (partial consumption, often starting with fins or tail) or type II cannibalism (complete ingestion of conspecifics). In larviculture and nursery phases, cannibalism can rapidly become a major source of mortality and size heterogeneity, affecting survival, growth trajectories, welfare, and ultimately production efficiency. Because cannibalism is shaped by both intrinsic drivers (e.g., ontogeny, mouth gape, feeding capacity, behavioral phenotypes) and extrinsic drivers (e.g., density, light environment, temperature, water turbidity, and feeding regimes), mitigation strategies are rarely one-size-fits-all and often show strong species- and stage-specific responses (Baras et al. 2000a, 2000b; Atencio-Garcia et al. 2010; Leonardo et al. 2008).

Multiple mechanistic hypotheses have been proposed to explain cannibalism in fishes, including food limitation or poor prey availability, opportunistic predation under high encounter rates (often promoted by high density), size-structured dominance hierarchies, behavioral syndromes (consistent aggressiveness among individuals), and adaptive trade-offs where consuming conspecifics increases growth and survival probability during narrow developmental windows. In practice, these mechanisms can overlap and are often mediated by functional morphology (e.g., gape size, digestive capacity) and sensory ecology (e.g., light and turbidity conditions) (Atencio-Garcia et al. 2010).

The Neotropical genus *Brycon* (Bryconidae) currently includes 44 recognized species distributed from southern Mexico to the La Plata basin, with clear ecological relevance and long-standing socioeconomic importance for capture fisheries and aquaculture (Lima 2017). In South American hatcheries, *Brycon amazonicus* (matrinxa) is frequently highlighted as a species with pronounced aggressive behavior and high levels of cannibalism during larval rearing, making early survival a persistent bottleneck. Importantly, although cannibalism is a recurrent theme in *Brycon* larviculture, the currently available evidence is not evenly distributed across the genus: published records concentrate on a small subset of species, which raises the need to clearly distinguish general patterns from species-specific outcomes (Leonardo et al. 2008; Atencio-Garcia et al. 2010).

Evidence indicates that cannibalism in *Brycon* can emerge very early in development, often around the onset of exogenous feeding and coinciding with rapid changes in morphology and sensory capabilities. For example, in *B. amazonicus* larviculture, aggression and cannibalism have been reported within the first three days after hatching under particular conditions. Across other *Brycon* species, early cannibalism has also been reported within the first day post-hatching, emphasizing the relevance of aligning feeding and husbandry protocols with age-specific functional capacity (Baras et al. 2000b; Atencio-Garcia et al. 2010).

Despite the practical relevance of cannibalism control, existing studies in *Brycon* are dispersed across different husbandry conditions, response metrics, and experimental designs, frequently reported with limited cross-study comparability (e.g., high temperature or high density without explicit values). This lack of standardized reporting hinders synthesis and prevents the identification of thresholds that can be translated into actionable hatchery recommendations (Ferreira et al. 2020; Carvalho et al. 2024).

This manuscript presents an integrative comparative review of cannibalism and aggressive behavior in *Brycon* species under culture conditions, with emphasis on larviculture and nursery phases. Our aims were to (i) identify which *Brycon* species and developmental stages have documented cannibalism or aggression under culture conditions, (ii) compare the main biotic, abiotic, and mixed drivers reported across studies, and (iii) derive practical management implications and research priorities, particularly those related to ontogeny, functional morphology, and first-feeding dynamics. By organizing the evidence around ontogeny, functional morphology, feeding compatibility, environmental modulation, and social interactions, this review also proposes a practical framework for interpreting cannibalism in *Brycon* as a management-sensitive process rather than as a fixed species trait.

Methodology

Review design and reporting

We conducted an integrative comparative review, consistent with the integrative review approach proposed by Whitemore and Knafl (2005) and informed by the comparative method of Ragin (1987). The review was based on a systematic literature search and a qualitative comparative narrative synthesis to examine scientific evidence on cannibalism and aggressive behavior in *Brycon* species, with emphasis on larviculture and nursery production contexts. This design was chosen because the literature is taxonomically restricted, methodologically heterogeneous, and dominated by qualitative and stage-specific outcomes that do not support formal meta-analysis. To improve transparency, literature identification, screening, eligibility assessment, and inclusion were documented following PRISMA 2020 guidance for reporting review flow processes (Page et al. 2021).

Information sources and search strategy

We searched Scopus (Elsevier), Web of Science Core Collection, and SciELO for peer-reviewed journal articles on cannibalism and aggressive behavior in *Brycon*. Google Scholar was explored only as a supplementary source for citation chasing and title checking, but it did not contribute additional records retained in the screened dataset. Search descriptors were defined from the thematic axes repeatedly represented in the original *Brycon* literature: feeding management, chemical modulators,

body-size heterogeneity and predator-prey relationships, water temperature, stocking density, luminosity, salinity, turbidity, and biofloc-related rearing conditions (Gomes et al. 2000; Souza et al. 2014; Lopes et al. 2018; Barros et al. 2019; Oliveira et al. 2020; Izel-Silva et al. 2024). Searches were conducted in English, Portuguese, and Spanish.

The search strategy combined taxonomic, outcome, and management-related descriptors, with syntax adapted to each database. The core logic joined *Brycon* terms (e.g., '*Brycon*', '*Brycon amazonicus*', '*Brycon orbignyanus*', '*Brycon moorei*', '*Brycon sinuensis*') with outcome terms ('cannibalism', 'aggressive behavior', 'aggress*', 'intra-cohort predation', 'size heterogeneity') and context/intervention terms ('larviculture', 'larvae', 'juveniles', 'stocking density', 'temperature', 'light', 'photoperiod', 'salinity', 'turbidity', 'biofloc', 'melatonin', 'tryptophan', and 'triiodothyronine/T3'). Searches were restricted to the 2000-2025 period, and document-type filters for journal articles were applied when available in the database interface.

Database-specific search strings were recorded to improve reproducibility. The following core strings were used and adapted to each interface: Scopus: TITLE-ABS-KEY (*Brycon* AND (cannibalism OR cannibal* OR aggress* OR "aggressive behavior" OR "intra-cohort predation" OR "size heterogeneity")) AND (larviculture OR larvae OR juvenile* OR "stocking density" OR temperature OR light OR photoperiod OR salinity OR turbidity OR biofloc OR melatonin OR tryptophan OR triiodothyronine OR T3)). Web of Science Core Collection: TS=(*Brycon* AND (cannibalism OR cannibal* OR aggress* OR "aggressive behavior" OR "intra-cohort predation" OR "size heterogeneity")) AND (larviculture OR larvae OR juvenile* OR "stocking density" OR temperature OR light OR photoperiod OR salinity OR turbidity OR biofloc OR melatonin OR tryptophan OR triiodothyronine OR T3)). SciELO: (*Brycon*) AND (cannibalism OR cannibalismo OR agresividad OR agressividade OR aggression OR "aggressive behavior" OR larviculture OR larvicultura). The final database search was conducted on 31 December 2025.

Eligibility criteria

We included peer-reviewed journal articles published between 2000 and 2025 (English, Portuguese, or Spanish) that addressed cannibalism and/or aggressive behavior in *Brycon* species and reported at least one biotic, abiotic, or mixed factor relevant to cannibalism risk, aggressive interactions, or their management under culture conditions. Direct evidence included studies that measured cannibalism incidence, mortality attributable to cannibalism, attack frequency, or explicitly defined aggressive behavior. Indirect but relevant evidence included studies on ontogeny, morphometry, or physiological modulation only when the analytical link to cannibalism or aggression was explicit in the study objectives, results, or interpretation.

We excluded grey literature (e.g., theses, dissertations, conference abstracts, technical reports), narrative opinion pieces without primary data, and studies focused solely on taxonomy, reproduction, migration, or induced breeding without linking outcomes to aggression or cannibalism. Review papers and broader conceptual sources retained in the manuscript were used only for conceptual framing and were not counted as primary evidence in the comparative tables. We also excluded purely descriptive developmental or ultrastructural studies when they did not provide a direct analytical bridge to cannibalism, aggressive behavior, or management interpretation.

Screening and study selection

Records exported from each database were compiled in a reference sheet and deduplicated primarily by DOI and title, with additional manual removal of obvious multilingual duplicates. The selection process was conducted in two stages: (i) title and abstract screening to remove records clearly unrelated to Brycon or to cannibalism/aggressive behavior and (ii) full-text eligibility assessment for potentially relevant articles. Screening and eligibility decisions should be verified by at least two reviewers before submission; disagreements should be resolved by consensus or by consultation with a senior author. Reasons for exclusion at the eligibility stage were documented and grouped by recurrent motives. The identification, screening, eligibility, and inclusion steps are summarized in a PRISMA 2020 flow diagram (Figure 1) adapted for the present integrative narrative review from Page et al. (2021).

After database-specific filtering, 90 records were identified through database searches (Web of Science = 36; Scopus = 41; SciELO = 13). After removing 29 duplicate records, 61 unique records remained for screening. During the title and abstract screening phase, 18 records were excluded, resulting in 43 reports sought for retrieval and assessed for eligibility. At this stage, 6 reports were excluded for specific reasons: 4 due to no explicit cannibalism/aggressiveness outcome and 2 due to a descriptive developmental or ultrastructural focus without explicit linkage to review outcomes. Consequently, 37 studies were included in the final review.

Data extraction and coding

For each eligible study, we extracted: species, life stage (larvae/juveniles), culture context, onset timing (e.g., hours after hatching), experimental or husbandry conditions (e.g., larvae/L, fish/m³ or biomass when available, temperature, photoperiod and light intensity, salinity or salt concentration, turbidity type, total suspended solids in biofloc systems), feeding protocol (prey type and size, feeding frequency, predator-prey ratios), and outcome metrics (cannibalism incidence/type, survival, growth,

stress indicators when reported). Species-level nomenclature and genus-level diversity were checked against Lima (2017) and related taxonomic sources cited in the original manuscript. Where studies reported only qualitative descriptors (e.g., 'high' density), this limitation was explicitly noted.

Data synthesis

Evidence was synthesized qualitatively using a comparative narrative approach. Findings were organized into three evidence domains: biotic factors, abiotic factors, and mixed-factor studies. Within these domains, studies were compared according to life stage, culture context, factor or intervention tested, values reported, observed direction of effect, and practical takeaway. When possible, we coded the direction of effect on cannibalism or aggression as increase, decrease, or no clear effect, while also noting when the response appeared stage dependent, species specific, or primarily associated with performance rather than direct behavioral control. To make the qualitative synthesis more transparent, each factor was interpreted according to the consistency of the reported direction of effect, the number of species and life stages represented, and whether the outcome was direct cannibalism, aggressive behavior, survival, growth, or an indirect physiological/morphometric proxy.

Methodological limitations

Because the available literature differs substantially in species coverage, experimental design, response metrics, and reporting quality, we did not conduct a formal risk-of-bias assessment or meta-analysis. Instead, we prioritized transparent extraction of reported values, explicit distinction between direct and indirect behavioral evidence, and careful interpretation of stage- and species-specific responses. Accordingly, the PRISMA diagram should be interpreted as a transparent record-selection framework for an integrative comparative review rather than as a full systematic-review audit of every potentially retrievable report. This choice limits the inferential strength of the review: the conclusions should be interpreted as a qualitative evidence synthesis and not as pooled quantitative estimates of effect size. Management recommendations are therefore framed as conditional and stage-specific rather than universal thresholds.

Results

Available evidence shows that cannibalism under culture conditions has been documented for only a limited subset of *Brycon* species, despite the broader diversity of the genus, which currently includes 44 recognized species (Lima 2017). Reports are concentrated in *B. amazonicus*, *B. insignis*, *B. moorei*, *B. orbignyanus*, *B. orthotaenia*, *B. sinuensis*, and *B. gouldingi*, which reinforces the need to

avoid extrapolating findings indiscriminately across all *Brycon* species (Baras et al. 2000a, b; Pedreira et al. 2008; Atencio-Garcia et al. 2010; Leonardo et al. 2008). This imbalance is also evident when the included evidence is expressed in percentage terms by species and life stage (Figure 3), showing that *B. amazonicus* represents the largest proportional share of both larval and juvenile records, whereas the remaining species occupy much smaller fractions of the available literature.

Across the available studies, cannibalism emerges very early in development, often around the onset of exogenous feeding and, in some species, even before complete yolk-sac absorption. This timing indicates that ontogenetic transitions, mouth development, prey size compatibility, and the first-feeding window are central to understanding both risk and control (Baras et al. 2000b; Atencio-Garcia et al. 2010).

The temporal distribution of the included studies was irregular when expressed in percentage terms, but the literature became visibly more concentrated in the most recent decade, indicating increased attention to cannibalism, aggressive behavior, and associated biotic, abiotic, and mixed factors in *Brycon* (Figure 2). Taken together, Figures 2 and 3 show that the recent expansion of publications has not eliminated the strong taxonomic concentration of the evidence base, which remains centered mainly on *B. amazonicus* and on early life stages.

Accordingly, the evidence base is organized into three complementary tables, which form the empirical backbone of the Results section rather than independent appendices. Table 1 summarizes studies in which cannibalism or aggression is mainly linked to biotic mechanisms, including ontogeny, mouth and head development, prey availability, predator: prey ratio, food restriction, body-size heterogeneity, social status, and physiological or nutritional modulation. Table 2 groups environmental drivers such as tank background, light intensity and wavelength, temperature, salinity, density, and biofloc conditions. Table 3 then integrates experiments where biological and environmental variables act together, showing that many hatchery outcomes depend on factor combinations rather than isolated treatments.

Comparative synthesis

Across studies, and consistent with the concentration of evidence summarized in Figures 2 and 3 and Tables 1-3, feeding management is the most consistent practical leverage point. Adequate live prey supply, suitable prey size, and balanced predator: prey ratios repeatedly reduce encounter-driven attacks and improve survival during the earliest feeding window. This pattern appears across multiple species and remains the most transferable practical message currently supported by the literature.

The patterns presented in Table 1 therefore support the interpretation that the first-feeding

window is the main biotic control point. Studies on *B. moorei*, *B. sinuensis*, *B. orthotaenia*, *B. orbignyianus*, and *B. amazonicus* converge in showing that cannibalism risk rises when rapid mouth development, insufficient or unsuitable prey, food restriction, or cohort asymmetry occur during early ontogeny. In contrast, nutritional or endocrine modulators may reduce aggression in juveniles, but their evidence is more context-specific and less directly transferable to larval cannibalism control.

Size heterogeneity interacts directly with cannibalism risk because mouth gape, body depth, and relative prey size determine which conspecifics can be attacked and ingested. For that reason, first feeding, prey dimensions, and size grading should be interpreted jointly rather than as isolated management variables. Morphometric thresholds are especially valuable because they help explain why the same cohort can rapidly shift from coexistence to active cannibalism.

Abiotic controls are important, but their effects are not uniform across studies. Density, temperature, light, salinity, and system characteristics influence encounter rates, activity, stress, visibility, and growth, yet the direction and magnitude of those effects depend strongly on species, developmental stage, and rearing context. These variables should therefore be interpreted as modulators rather than universal solutions.

Light management illustrates this context dependence clearly: low-intensity light can reduce aggressive behavior and improve survival in *Brycon amazonicus* larvae, whereas cannibalism may persist under darkness in other species. Likewise, density or temperature manipulations may reduce attacks in one ontogenetic window but compromise growth or performance in another. Practical recommendations should therefore be framed as conditional, not absolute.

Salinity manipulation, turbidity, refuge-related environmental complexity, and biofloc conditions may improve survival and reduce cannibalism in specific contexts, but these treatments can also generate trade-offs involving feeding efficiency, growth, solids accumulation, or water-quality management. Their value is greatest when behavioral endpoints are interpreted together with production outcomes rather than in isolation.

These findings are directly reflected in Table 2, where abiotic factors are not presented as universal anti-cannibalism solutions but as environmental filters that alter visibility, activity, stress, prey detection, and encounter probability. For instance, low light, selected light wavelengths, moderate salinity, and biofloc conditions can improve survival or reduce cannibalism under defined conditions, whereas dark backgrounds, unsuitable spectral environments, or unmanaged solids may reduce performance. Thus, Table 2 supports the conclusion that environmental manipulation should be calibrated to species, age, system type, and production target.

Chemical and physiological modulators, including triiodothyronine, tryptophan, melatonin, fluoxetine, and serotonergic pathways, show mixed evidence. Some interventions reduce aggressive

displays or alter neuroendocrine responses, but they do not consistently replace the benefits of well-timed feeding and husbandry control. Current evidence therefore supports these tools as complementary refinements rather than primary solutions.

Taken together, the literature indicates that *Brycon* cannibalism is best understood as the outcome of interacting ontogenetic, social, and environmental processes concentrated around the first-feeding period. This integrative perspective is more consistent with the available evidence than any single-factor explanation. A practical interpretation of the evidence is that hatchery protocols should prioritize four linked control points: timely first feeding, prey-size compatibility, reduction of extreme size divergence, and environmental modulation of encounter rates and visibility.

The mixed-factor evidence in Table 3 bridges the biotic and abiotic tables and helps explain why some responses appear contradictory when factors are examined separately. Interactions such as density x temperature, photoperiod x diet, farming system x live food, and arena novelty x endocrine status show that cannibalism and aggression depend on how feeding opportunity, developmental timing, stress physiology, and the physical environment combine. This link justifies treating management recommendations as integrated protocols rather than isolated prescriptions.

Aggressive behavior is not interchangeable with cannibalism

An important conceptual distinction emerges from the reviewed studies: aggressive behavior and cannibalism are related but not equivalent outcomes. Some experiments measure direct cannibalism, mortality, or ingestion of conspecifics, whereas others quantify aggressive displays such as chasing, biting, dominance interactions, mirror responses, or neuroendocrine changes associated with agonistic encounters.

This distinction matters because a factor that reduces aggressive display does not necessarily eliminate cannibalism risk, and a factor that improves survival does not automatically reveal the behavioral mechanism responsible for that outcome. Accordingly, studies on aggression were retained in this review when they informed plausible mechanisms linked to cannibalism risk, especially in *Brycon amazonicus*, but they should not be interpreted as direct evidence of cannibalism control unless such control was explicitly measured.

This distinction also clarifies how Tables 1-3 should be interpreted: rows based on attack frequency, mirror response, endocrine markers, or social challenge inform mechanisms of aggression, whereas rows reporting cannibalism mortality, ingestion of conspecifics, or survival during the cannibalistic window provide more direct evidence for hatchery control. Separating these endpoints prevents overstatement of aggression studies as proof of cannibalism suppression.

Future *Brycon* studies would benefit from jointly reporting aggressive interactions, cannibalism incidence, survival, growth, and morphometric thresholds within the same experimental framework. That integration would allow researchers to test when aggression functions as a precursor, correlate, or independent process relative to cannibalism.

Research priorities and reporting standards

For future experimental studies, minimum reporting should include species, strain or broodstock origin when available, hours after hatching, mouth dimensions, prey dimensions, density as both individuals and biomass when possible, tank size and background, light intensity and spectrum, temperature, salinity, turbidity or total suspended solids, feeding frequency, and explicit separation of cannibalism, aggression, survival, and growth endpoints.

The organization of Tables 1-3 also makes these reporting gaps visible. Several studies provide clear species, timing, density, light, or feeding values, whereas others use qualitative descriptions or emphasize performance endpoints without measuring cannibalism and aggression together. Future studies should therefore be designed so that each table domain can be connected in the same experiment, allowing direct comparison among biotic drivers, abiotic modulators, and their combined effects.

The literature reveals important methodological gaps that should guide future work. Most studies focus on *Brycon amazonicus*, which limits transferability to the rest of the genus. Many papers still lack exact ontogenetic descriptors, explicit units, standardized cannibalism metrics, prey-size measurements, or sufficiently detailed environmental reporting to support cross-study comparison. Future studies should therefore prioritize broader species coverage, standardized reporting of hours after hatching, mouth dimensions, prey dimensions, density expressed both as individuals and biomass, light intensity and spectrum, and parallel measurement of behavior and production endpoints.

Conclusion

1. Under culture conditions, documented cannibalism and aggression in *Brycon* are concentrated in a limited number of species, with the empirical evidence strongly dominated by *Brycon amazonicus* and, proportionally, by early life-stage studies.

2. Cannibalism generally begins very early, often around first feeding, which makes ontogeny, mouth development, prey-size compatibility, and early cohort structure central to management.

3. Feeding management remains the strongest practical control point, especially adequate live prey supply, suitable prey size, and prevention of rapid size divergence within the cohort.

4. Abiotic factors such as density, light, temperature, salinity, and biofloc conditions influence

cannibalism through stage- and species-specific pathways and should therefore be reported with explicit values, units, and ontogenetic context.

5. Physiological and endocrine modulators can complement hatchery management, but current evidence does not support their use as standalone solutions for controlling cannibalism.

6. Future studies should expand species coverage and life-stage balance beyond *B. amazonicus* and adopt standardized reporting that integrates behavior, survival, growth, and morphometric thresholds so that ontogeny-based recommendations can be translated into robust hatchery protocols. Overall, the evidence indicates that cannibalism in cultured *Brycon* is best understood as an ontogeny-driven and management-sensitive process, in which functional morphology, prey availability, social structure, and environmental conditions interact during a narrow early-life window.

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Table 1. Biotic factors reported in studies on cannibalism, aggressive behavior, ontogeny, feeding, and physiological modulation in cultured *Brycon* species (n = 22 studies).

Factor	Species / stage	Values reported	Observed direction	Practical takeaway	Key reference(s)
Onset of sibling cannibalism / prey-size selectivity	<i>Brycon moorei</i> / larvae to early juveniles	Cannibalism began at 21 h after hatching; complete cannibalism by ~3 days; larval period to ~144 h; 27.0 ± 0.5 °C; 12L:12D	Increase in cannibalism very early in ontogeny	Very early first-feeding management is critical; delay favors severe intracohort cannibalism	(Baras et al. 2000)
Head-skeleton ontogeny related to feeding/cannibalism capacity	<i>Brycon moorei</i> / larvae	Hatching at ~15 h after fertilization; 27 ± 1.5 °C; 12L:12D; live Artemia from 24 h after hatching	Developmental progression toward predatory/cannibalistic capacity	Mouth and head development should be considered when defining first-feeding timing	(Vandewalle et al. 2005)
Egg immersion in triiodothyronine (T3)	<i>Brycon cephalus</i> / larvae	0, 0.01, 0.05, 0.1 ppm T3; egg exposure 15 min; cannibalism monitored 36–72 h post-hatch	No clear reduction in cannibalism	T3 exposure alone is not a reliable practical tool to suppress cannibalism	(Leonardo et al. 2008)
Social interaction / social status	<i>Brycon amazonicus</i> / juveniles	Dominance interaction monitored up to 6 h; aggression increased markedly by the 5th hour	Agonistic interaction increased stress/immune disturbance	Social instability quickly produces physiological costs; stocking and social management matter	(Ferraz and Gomes 2009)
Individual growth trajectories linked to aggression	<i>Brycon moorei</i> / juveniles	Isolated rearing until 36 DAH; 27 ± 0.5 °C; 12L:12D; final heterogeneity up to 22.42–39.44 mm TL	Aggressive behavior associated with divergent growth trajectories	Growth heterogeneity is linked to behavioral divergence	(Baras and Lucas 2010)
Morphological and behavioral larval development	<i>Brycon orbignyanus</i> / larvae	0–172 h after hatching; at 28 h AH larvae ~6.25 ± 0.13 mm SL already showed structures enabling exogenous feeding	Transition to active predation early in larval life	First-feeding protocols must match rapid acquisition of predatory ability	(Maciel et al. 2010)
Predator:prey ratio at first feeding	<i>Brycon sinuensis</i> / larvae	Ratios 0:1, 1:1, 2:1, 4:1 using <i>Prochilodus magdalenae</i> larvae;	Higher prey supply reduced cannibalism and	Early supply of suitable live prey is one of the strongest anti-	(Atencio-Garcia et al. 2010)

Factor	Species / stage	Values reported	Observed direction	Practical takeaway	Key reference(s)
		28.6–28.8 °C	improved larviculture outcome	cannibalism tools	
Probiotic bioencapsulated in Artemia	<i>Brycon amazonicus</i> / larvae	0, 2.5, 5.0, 7.5, 10.0, 12.5 g/L probiotic in Artemia bioencapsulation	No influence on cannibalism	Probiotic use may support culture, but should not be expected to control cannibalism by itself	(Dias et al. 2011)
Dietary L-tryptophan	<i>Brycon amazonicus</i> / juveniles	0.47%, 0.94%, 1.88%, 3.76% TRP for 7 days; resident-intruder test	Reduced aggressiveness	TRP is a promising nutritional modulator of aggression in juveniles	(Wolkers et al. 2011)
Early development and onset of cannibalism	<i>Brycon orthotaenia</i> / embryos/larvae	Fertilization rate 50.0 ± 5.5% at 24 °C; embryogenesis finished in 21 h 30 min; mouth opening on day 3	Cannibalism appears very early after mouth opening	The third day post-hatch is a critical window for management intervention	(Gomes et al. 2011)
Egg exposure to T3	<i>Brycon amazonicus</i> / larvae	0, 0.01, 0.05, 0.1 mg/L T3; higher larval weight in 0.05 and 0.1 mg/L; ~25.2 ± 2.8 °C	Improved biomass/growth, but no strong evidence of cannibalism suppression	T3 may enhance larviculture performance, but not necessarily solve cannibalism	(Leonardo et al. 2013)
Hatching time	<i>Brycon amazonicus</i> / larvae	Behavioral comparison among larvae with different hatching timing	Hatching time influenced aggressiveness/activity	Temporal heterogeneity within a cohort can amplify behavioral asymmetry	(Souza et al. 2014)
Social challenge / monoamines	<i>Brycon amazonicus</i> / juveniles	Social challenge in isolated resident fish at 28 °C; cortisol and hypothalamic monoamines measured after fight	Aggression/social challenge increased cortisol and hypothalamic monoamines	Behavioral assays should be interpreted jointly with neuroendocrine status	(Wolkers et al. 2015)
Fluoxetine immersion	<i>Brycon amazonicus</i> / juveniles	Acute immersion treatment; aggression assessed by bites, chases, and latency to first attack	Increased aggressiveness after acute fluoxetine	Serotonergic manipulation can enhance, not only suppress, aggression depending on protocol	(Wolkers et al. 2016)
Mirror test versus real	<i>Brycon amazonicus</i> /	Mirror trial n=7 vs real trial n=7; 20-	Mirror elicited aggression, but	Mirror tests are useful, but do not	(Serra et al. 2015)

Factor	Species / stage	Values reported	Observed direction	Practical takeaway	Key reference(s)
opponent	juveniles	min trials at 28 °C; mirror cortisol 84.2 ± 13.8 ng/mL vs real 77.2 ± 16.9 ng/mL	less locomotion and lower aggression intensity than real opponent	fully reproduce real agonistic interaction	(Serra et al. 2017)
Time course of aggressive behavior under dietary TRP	<i>Brycon amazonicus</i> / juveniles	TRP-supplemented diets; body mass ~107.8 ± 14.9 g	TRP dampened early-phase aggression	Nutritional modulation may affect intensity and time course of aggression	(Wolkers et al. 2013)
Body size heterogeneity	<i>Brycon amazonicus</i> / larvae	Homogeneous vs heterogeneous groups; observations at 12, 24, 36, 48, 60, 72 HAH	Aggressiveness was higher in homogeneous groups	Size structure within the cohort affects aggression; complete homogeneity may not reduce conflict	(Carvalho et al. 2018)
Melatonin	<i>Brycon amazonicus</i> / juveniles	0, 1, 10 µmol/L melatonin; fish isolated for 96 h, then mirror test	Melatonin reduced aggressiveness	Hormonal modulation is a promising tool to mitigate social stress and aggression	(Amaral et al. 2020)
Food restriction	<i>Brycon orbignyanus</i> / larvae	Restriction periods of 0, 2, 4, 6, 8, 10 days; density 15 larvae/L	Food restriction impaired performance and feeding behavior	Prolonged fasting is detrimental in early larviculture and should be avoided	(Melo et al. 2020)
Embryogenesis and larval development / onset of cannibalism	<i>Brycon orthotaenia</i> / embryos and larvae	Embryogenesis lasted 15 h at 27 °C; mouth opening at 13 h AH; cannibalism observed at 29 h AH	Cannibalism began very early	The first day after hatching is a critical window for intervention	(Floresta-Oliveira et al. 2020)
First feeding with cladocerans	<i>Brycon sinuensis</i> / larvae	<i>Moina minuta</i> , <i>Macrothrix elegans</i> , Mix, or forage larvae; 20 prey mL ⁻¹ for cladocerans; prey:predator ratio 2:1 for forage larvae; 50 larvae/L	<i>Moina minuta</i> yielded highest survival and lowest cannibalism mortality	Appropriate cladocerans can replace more costly live prey and help control cannibalism	(Jiménez-Velásquez et al. 2021)
Morphometric limitation / maximum prey size	<i>Brycon amazonicus</i> / larvae	Cannibals could ingest prey from 92 to 106% of their own TL; based on body depth and maximum mouth opening	Rapid growth and size heterogeneity favored conditions for cannibalism	Size structure and morphometric relationships are central to understanding cannibalism risk	(Muller et al. 2025b)

Table 2. Abiotic factors reported in studies on cannibalism, aggressive behavior, survival, growth, and environmental modulation in cultured *Brycon* species (n=10 studies).

Factor	Species / stage	Values reported	Observed direction	Practical takeaway	Key reference(s)
Tank color	<i>Brycon orthotaenia</i> / larvae	White, light blue, light green, brown, black; 10-day larviculture; $\sim 26 \pm 0.6$ °C; black tank survival 28.7%	Dark tanks worsened performance	Avoid dark tank colors during the cannibalistic phase; lighter backgrounds are safer	(Pedreira et al. 2008)
Aquarium color	<i>Brycon sp.</i> / larvae	White, green, blue, brown, black aquaria; 15-day larviculture; blue tank survival 66.25% and cannibalism 17.08%	Blue background increased cannibalism and reduced survival	Aquarium/tank background color directly affects larval outcome and should be standardized	(Costa et al. 2013)
Water salinity	<i>Brycon vonoi</i> / larvae	Salinities 0, 2, 4, 6‰; best at 2‰ with 52.5% survival and 0.49 g biomass; freshwater survival only 6.6%	Moderate salinization improved survival and biomass	Slight salinization can be used as a practical anti-stress/production strategy	(Coraspe-Amaral et al. 2017)
Light intensity	<i>Brycon amazonicus</i> / larvae	17 ± 3 lx, 204 ± 12.17 lx, 1613.33 ± 499.03 lx; groups of three larvae at 12 HAH	Lower light reduced aggressive interactions and locomotor activity	Light manipulation is a strong practical tool to reduce larval aggression	(Lopes et al. 2018)
Light intensity across larval stages	<i>Brycon amazonicus</i> / larvae	10–72 HAH, 72–168 HAH, 168–288 HAH; low ~ 20 lx, intermediate ~ 200 lx, high $\sim 2,000$ lx	Low light increased survival and favored performance	Reduced illumination is broadly beneficial during early larval rearing	(Muller et al. 2019)
Water temperature	<i>Brycon amazonicus</i> / juveniles	24.33 ± 0.33 °C, 29.49 ± 0.43 °C, 34.48 ± 0.56 °C; isolated fish, 8 days	Higher temperature reduced aggressive interactions	Temperature can be manipulated to reduce aggression in juveniles within tolerated limits	(Ferreira et al. 2020)
Common salt (NaCl)	<i>Brycon amazonicus</i> /	Study tested salt use to modulate	Salt use affected	Ionic manipulation of	(Oliveira et al. 2020)

	larvae	larval aggressiveness; sodium chloride discussed as stress-reducing additive	aggressiveness in larvae	water can be used during aggressive larval phases	
Biofloc system / TSS concentration	<i>Brycon amazonicus</i> / larvae	Clear water vs BFT with TSS <200, 200–350, 350–500 mg/L; density 10 larvae/L; evaluations at 5 and 10 days	Biofloc systems increased survival; TSS 200–350 mg/L particularly reduced cannibalism	BFT is a strong alternative to reduce cannibalism and improve larval productivity	(Izel-Silva et al. 2024)
Stocking density in biofloc	<i>Brycon amazonicus</i> / juveniles	50, 140, 230, 320, 410 fish m ⁻³ for 61 days	Survival remained >90% at densities >230 fish m ⁻³ ; quadratic effect on growth	Juveniles can be efficiently reared in BFT at about 291–293 fish m ⁻³ , with solids and alkalinity control	(Silva et al. 2024)
Light wavelength	<i>Brycon amazonicus</i> / larvae	Darkness, white, red, blue, green; exposure from 6–50 HAH; 200 larvae/L	Darkness increased survival and reduced stress/predation; red light increased mortality	Spectral manipulation is highly relevant; darkness is especially useful during the critical larval period	(Muller et al., 2025a)

Table 3. Mixed-factor studies combining biological, environmental, endocrine, or husbandry variables relevant to cannibalism and aggressive behavior in cultured *Brycon* species (n = 5 studies).

Factor	Species / stage	Values reported	Observed direction	Practical takeaway	Key reference(s)
Arena novelty × cortisol manipulation	<i>Brycon amazonicus</i> / juveniles	Familiar vs novel arena; hydrocortisone treatment; 28 °C; 06:00–18:00 photoperiod	Arena novelty impaired cortisol-related increase in aggression	Environmental context changes the behavioral effect of endocrine state	(Serra et al. 2015)

Embryonic and larval development / temperature-sensitive timing	<i>Brycon amazonicus</i> / embryos/larvae	Dry egg diameter 1.28 ± 0.19 mm; perivitelline space 0.56 ± 0.3 mm; cannibalism started at 34 h AF; yolk absorption >90% until 50 h AF	Rapid development associated with very early cannibalism	Temperature-sensitive developmental timing must be considered in hatchery schedules	(Nakauth et al. 2016)
Stocking density × temperature	<i>Brycon amazonicus</i> / larvae	After 72 HAH, 20, 40, 60 larvae/L combined with 24.09 ± 0.15 °C and 28.33 ± 0.12 °C	Lower temperature reduced aggression, but also reduced growth	There is a trade-off between behavioral control and performance	(Barros et al. 2019)
Photoperiod × diet	<i>Brycon orbignyanus</i> / larvae	12L:12D and 24L:0D; Artemia nauplii vs formulated microdiet; 10 days	Artemia + 24 h light reduced cannibalism and improved survival	Photoperiod and diet interact strongly; both must be optimized together	(Silva Souza et al. 2022)
Farming system × live food	<i>Brycon amazonicus</i> / larvae	Semi-intensive mesocosm/green water, clear water with Artemia, <i>Dendrocephalus brasiliensis</i> , mix, and swimming-exercise versions	System and live food changed growth and nutritional profile	Larviculture outcome depends on the combination of system and live food	(Arbeláez-Rojas and Melão, 2023)

Figure captions

Figure 1. PRISMA 2020 flow diagram adapted for the present integrative narrative review, showing identification, screening, eligibility assessment, exclusion reasons, and inclusion of studies on cannibalism and aggressive behavior in *Brycon*.

Figure 2. Temporal distribution (%) of the 37 studies included in the review, showing annual publication frequency on cannibalism, aggressive behavior, and related biotic, abiotic, and mixed factors in *Brycon* between 2000 and 2025.

Figure 3. Relative distribution (%) of the included studies by *Brycon* species and life stage (larvae, juveniles, and total), highlighting the predominance of *Brycon amazonicus* and the uneven taxonomic and ontogenetic coverage of the evidence base.

Figure 1.

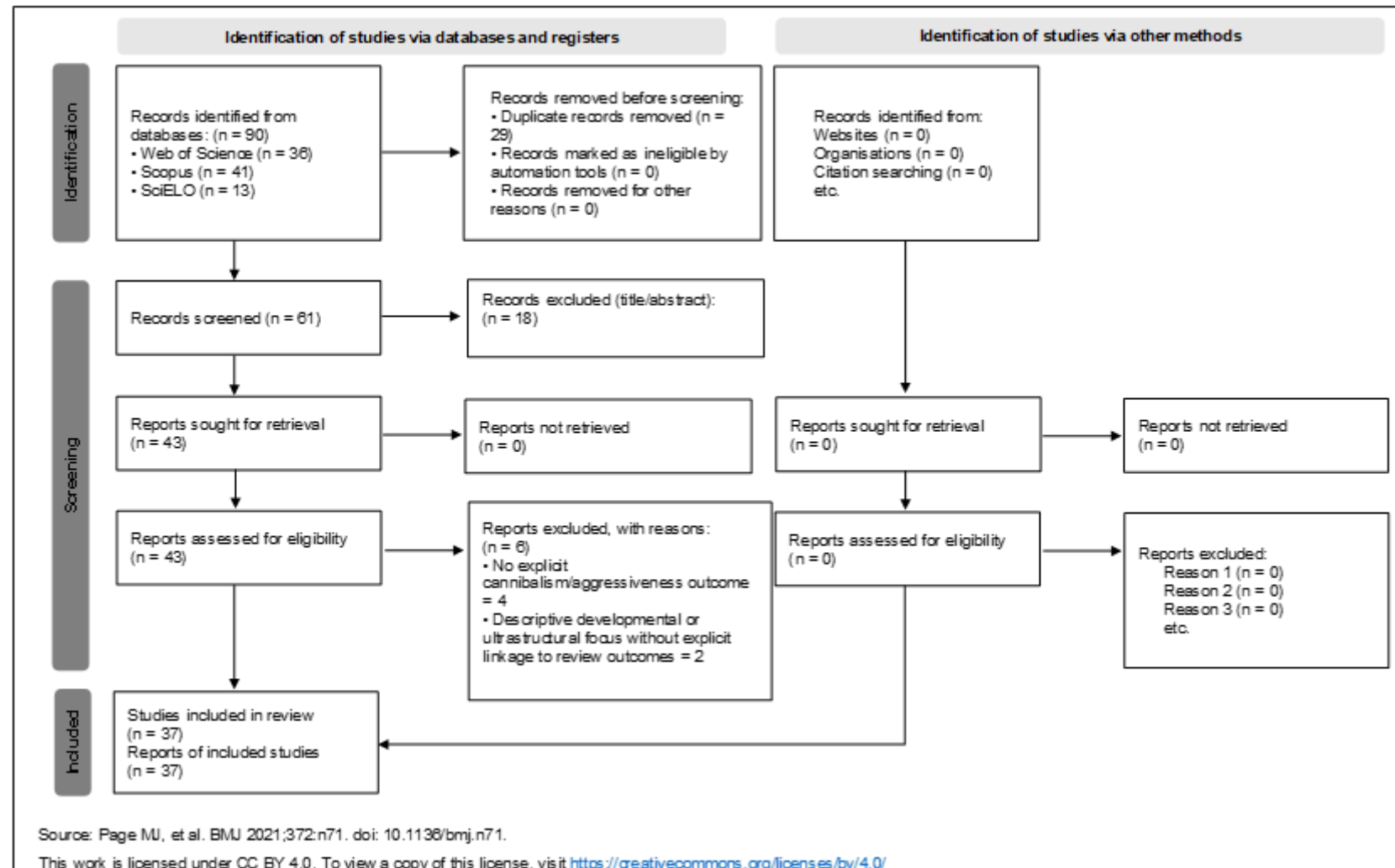


Figure 2.

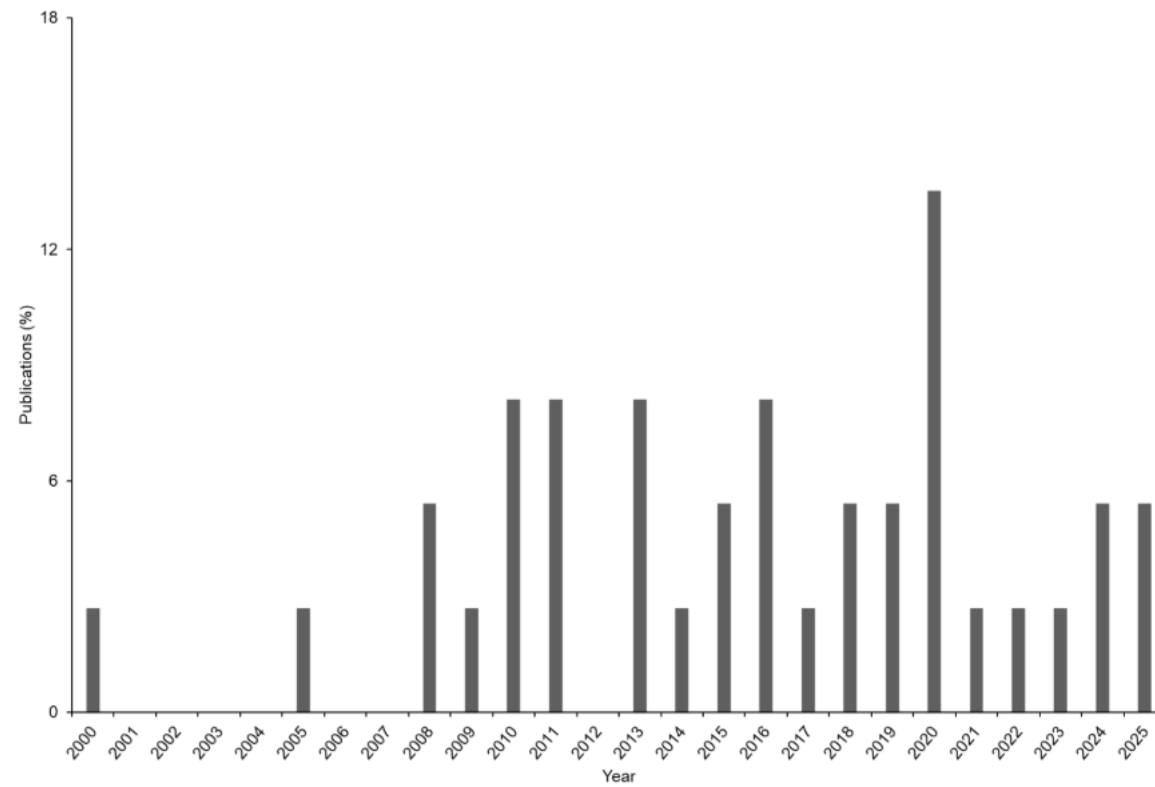
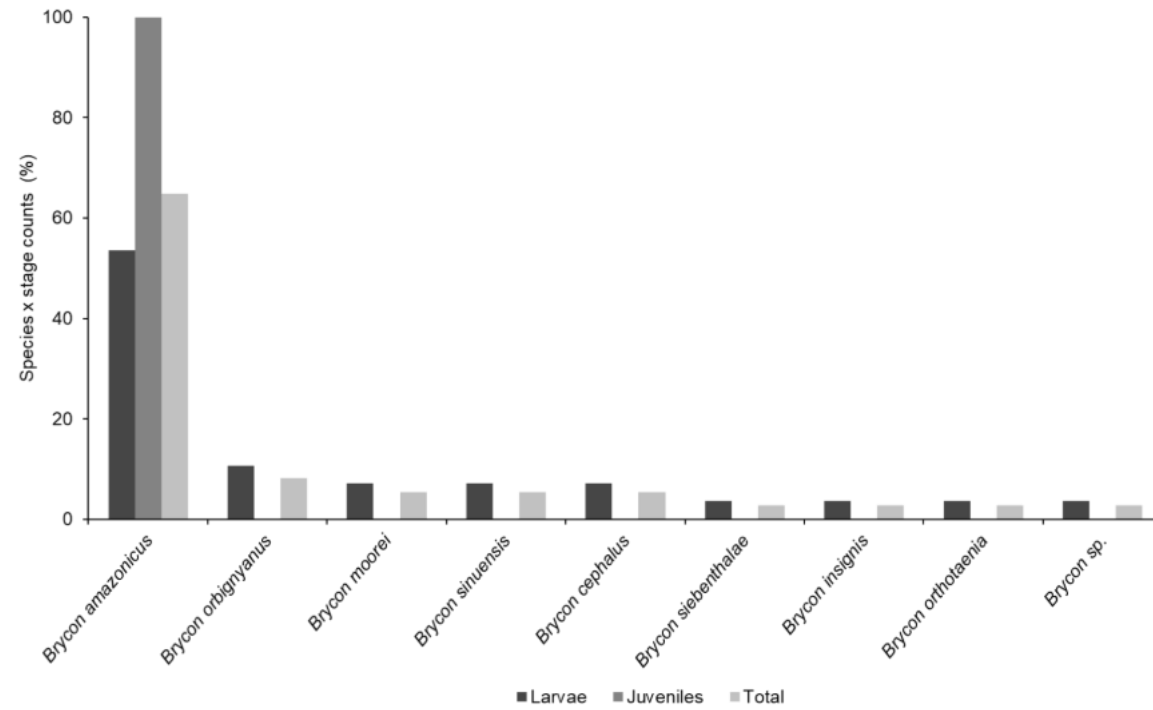


Figure 3.



Capítulo 2

Manuscrito publicado no periódico Brazilian Journal of Biology em 09 de junho de 2025 (Anexo).

Morphometric prediction of maximum cannibal-prey size for larvae of matrinxã, *Brycon amazonicus* (Spix and Agassiz, 1829)

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Figures: 1, 2 and 3

Table: 1

Short title: Morphometric predicting cannibalism in *Brycon amazonicus* larvae

Abstract

Cannibalism among fish is an interaction affecting both intra- and interspecific relationships in aquatic environments. It is related to the size and developmental stage, with prey size determined by morphometric measurements. In general, cannibalism only occurs when the predator's mouth width is greater than the prey's body depth. In this way, understanding these limitations during ontogenetic development is important, as it significantly influences the dynamics of cannibalism. This study aimed to evaluate the maximum size of conspecific prey that the larvae of matrinxã (*Brycon amazonicus*) are morphologically able to ingest. For this, the morphometric measurements of body depth (BD) and maximum mouth opening (MMO) in relation to the total length (TL) of the larvae were considered. BD and MMO showed negative allometric growth. The maximum prey size was expressed as a proportion of the size of the cannibal, which shows that cannibals can ingest prey from 92 to 106% of the TL_{cannibal} . Therefore, the mathematical model of maximum cannibal-prey size for *B. amazonicus* shows rapid growth, possibly due to heterogeneous growth that, in turn, can increase the display of aggressive behavior, and it is not possible to determine a predatory morphological limitation. Studies with longer observation periods, focusing on predator-prey interaction and capture time, should be conducted to reduce cannibalism and increase survival and growth. Reducing cannibalism in *B. amazonicus* is essential for advancing the production of this economically and ecologically important species in the Amazon region.

Keywords: Cannibalism, morphological limitations, predictive model, prey size.

Introduction

Cannibalism in fish is a complex interaction that permeates intra- and interspecific relationships in aquatic environments (Kestemont et al. 2003). This behavior is especially evident during early life stages (Baras et al. 2005a; Ribeiro and Portella, 2021). Cannibalism is intrinsically related to the size and developmental stage of fish (Kestemont et al. 2003), with prey size influenced by both the predator's and prey's morphometric characteristics (Parazo et al. 1991). This relationship is especially notable in omnivorous and carnivorous species (Neumann et al. 2018; Ribeiro and Portella, 2020), where cannibalism serves as an adaptive strategy to enhance survival and population growth (Atencio-García and Zaniboni-Filho, 2006).

Allometric and heterogeneous growth are key modulators of cannibalism, particularly in species with rapid body growth (Baras et al. 2005b; Ribeiro and Portella, 2020). This uneven growth pattern creates size disparities within populations, promoting cannibalism as a mechanism to regulate competition and optimize resource utilization (Kestemont et al. 2003). In this context, the size of both predator and prey directly affects the dynamics of cannibalism (Juanes, 1994). To study the maximum prey size in cannibalistic fish species, it is essential to understand the allometric growth of body structures, such as the mouth, and how this relates to the predator's morphological limitations, growth, and survival (Baras and Jobling, 2002; Ribeiro and Qin, 2015). This is supported by the fact that, in most fish species, prey size tends to increase as the predator grows (Scharf et al. 2000; Arranz et al. 2019).

Studying morphometric relationships is important for developing an effective size grading program, as it relies on understanding allometric growth and the predator's morphological limitations in relation to its prey (Hseu et al. 2003; Ribeiro and Portella, 2020). Predictive models based on mathematical equations are often used to estimate the maximum prey size that cannibals can consume. These models are built using data from direct observations of cannibals and their prey (Sakakura and Tsukamoto, 1996) as well as morphological measurements (Qin and Fast, 1996).

In general, the maximum size of prey is closely linked to the growth and development of fish (Baras et al. 2005a). As fish mature, their ability to catch prey improves, and their food preferences shift, which affects the size of the prey they target (Neumann et al. 2018). Understanding these relationships is essential for studying population dynamics and ecology, particularly in species that exhibit cannibalism. This knowledge helps in applying effective management strategies in both natural habitats and aquaculture (Ribeiro and Qin, 2015; Ribeiro and Portella, 2020).

Negative or positive allometric growth is linked to the ability of fish to select and capture prey, and is common in many cannibalistic teleost species. The size of the prey is important for these fish, offering advantages in competition, food efficiency, and survival, as well as increasing opportunities for

cannibalism and early growth (Baras et al. 2005a; Ribeiro and Qin, 2015). This disproportionate growth, especially in mouth size, enables cannibalistic fish to consume prey larger than themselves, which helps them thrive and maintain cannibalistic behavior (Dörner et al. 2007).

Studying morphometric relationships between physical traits is crucial for predicting cannibalism risk and managing this behavior in different cannibalistic fish species, such as *Lates calcarifer* (Ribeiro and Qin, 2013), *Salminus brasiliensis* (Ribeiro and Portella, 2020) and *Pseudoplatystoma reticulatum* (Ribeiro and Portella, 2021). The predator-prey size ratio, for example, is a key measure of the largest prey a predator can consume, making it a useful tool for size grading (Qin and Fast, 1996; Xi et al. 2017).

Mathematical models based on morphometric relationships offer a predictive tool for understanding cannibalism dynamics during fish development (Ribeiro and Portella, 2020; Ribeiro and Portella, 2021). These models help predict growth under specific conditions, optimize resource use, and identify key moments for size-based classification, improving survival rates. They also demonstrate that applying these models reduces cannibalism and aggression, leading to more sustainable and cost-effective aquaculture practices (Hseu et al. 2003; Ribeiro and Qin, 2013).

Understanding these relationships benefits both aquaculture and ecological studies. Cannibalism, as a survival strategy, affects population structure and trophic interactions in natural environments (Rudolf, 2007; Pereira et al., 2017). Therefore, morphometric models are essential for both aquaculture and species conservation, highlighting the need for further research in this field.

Matrinxã (*Brycon amazonicus*), native to the Amazon region and found along the Solimões-Amazonas and Orinoco River basins (Lima, 2017), is of great economic importance in Amazon fish farming (IBGE, 2022). However, cannibalism during larviculture poses significant production challenges, compromising fish growth, survival, and overall production expansion in the region (Bernardino et al., 1993). Cannibalism in matrinxã larvae *B. amazonicus* shows distinct predatory behaviors, with type II cannibalism (complete consumption) being dominant among conspecifics (Izel-Silva et al. 2024). Leonardo et al. (2008) describe two attack patterns: head-to-tail and tail-to-head. Cannibalism occurs in 50-60% of larvae, with predatory larvae showing differences in weight and length, giving them a nutritional advantage that supports growth. This behavior also creates size variation within groups, leading to high size variation coefficients at different developmental stages (Carvalho et al. 2018).

Several studies have explored ways to reduce cannibalism and improve the survival and performance of *B. amazonicus* larvae. These include adjusting stocking densities, water temperature (Barros et al. 2019), light intensity (Lopes et al. 2018; Muller et al. 2019), salinity (Oliveira et al. 2020), water turbidity, providing refuges (Cornélio et al. 2021), and using biofloc technology (Izel-Silva et al.

2024). Such adjustments can increase survival rates to an average of 79% (Carvalho et al. 2018; Barros et al. 2019; Oliveira et al. 2020; Cornélio et al. 2021; Muller et al. 2019; Izel-Silva et al. 2024). However, little is known about the species' predatory morphometric limitations during ontogeny, when cannibalism is most common, particularly between 12 to 72 hours after hatching (Souza et al. 2014). While Leonardo et al. (2008) describe some predatory characteristics of cannibalism, studies on the morphological limitations driving this behavior are lacking. Understanding these limitations is essential, as they significantly affect cannibalism dynamics in fish (Baras and Jobling, 2002).

We evaluated the maximum size of prey that matrinxã larvae can ingest based on morphometric relationships of body depth (BD), maximum mouth opening (MMO), and total length (TL). Using these relationships, we developed a predictive model for the maximum prey size during the developmental stage when cannibalism is most prevalent (e.g., 24 to 74 hours after hatching). Additionally, the equations were used to analyze the allometric growth of body structures (BD, MMO) in relation to TL. This approach helps to understand the morphometric dynamics between cannibals and their prey, providing insights for management strategies to control cannibalism during larviculture. These findings can contribute to creating protocols for fish production and support fish farming and restocking programs for the species in Amazonian aquatic environments.

Methods

Study area and ethical approval

The experiment was carried out at the fish farming station of the Experimental Farm at the Federal University of Amazonas - FAEXP/UFAM, Manaus, Brazil, (2° 38' 39" S, 60° 03' 11" W), and was conducted according to the ethical principles of the National Council for Animal Experimentation Control (CONCEA). Approval for the study was granted by the Ethics Commission on the Use of Animals (CEUA-UFAM), under process No. 066/2018.

The larvae were obtained via induced reproduction of three males (1.600 ± 0.50 g and 39.33 ± 3.11 cm) and three females (2.130 ± 0.37 g and 41.33 ± 2.11 cm) with the use of crude extract of carp pituitary, according to the adjusted protocol of Romagosa et al. (2001). After extrusion, the oocytes were fertilized and stored in 90 L incubators with constant water renewal and density of 1 g of eggs per L of water (Souza et al. 2014).

Experimental design

A total of 3.600 larvae at 24 hours after hatching (HAH) were randomly allocated in three 300 L tanks (1.200 larvae per tank) at an average stocking density of 12 larvae/L (e.g., Jomori et al. 2013) in an indoor system with 10% renewal of the water volume once a day. The larvae were fed with

commercial feed mix (40% crude protein) and zooplankton (Cladocera, *Moina micrura*; 1.000 organisms/larvae), which was divided into eight daily meals, adapted from Jomori et al. (2013). The zooplankton used for feeding came from the nurseries of the fish farming station, which were then isolated and maintained in the Plankton Laboratory (FAEXP/UFAM) for large-scale production.

The physical and chemical parameters of the water were monitored by means of digital thermometer (Minipa MV-363), digital oximeter (HI 9146), digital pH meter (pH-221) and a colorimetric kit (Labcon test). The mean values of temperature (26.43 ± 0.16 °C), dissolved oxygen (6.46 ± 0.04 mg/L), pH (7.39 ± 0.04) and non-ionized ammonia (0.006 ± 0.001 mg/L) were maintained at adequate levels for the species (Gomes et al. 2000). The light intensity was monitored with the aid of a portable digital lux meter (model LD 240) and maintained at 367.33 ± 17.11 lx, which is considered adequate for controlling aggressive behavior (Lopes et al. 2018) and promoting growth (Muller et al. 2019) in *B. amazonicus* larvae. The photoperiod was set at 12 hours of light and 12 hours of dark, as this environmental factor also affects behavioral and growth parameters in fish (Biswas et al. 2008).

Predictive model

A total of 180 larvae from 24 to 74 HAH (5.20 to 9.49 mm in total length) were collected periodically every 10 hours (30 larvae for each time point) from the maintenance tanks with the aid of a hand net. Then, these larvae were killed via an overdose of anesthetic (eugenol at 5 µL/L) and fixed in 4% buffered formaldehyde, as performed by Souza et al. (2014) and Muller et al. (2019). The fixed larvae were photographed under a stereomicroscope (Bioptika L20) and, later, processed using ImageJ32 software, version 1.50i.

The morphometric measurements obtained were those of total length (TL, mm), body depth (BD, mm) and maximum mouth opening (MMO, mm). The TL was measured from the distance between the rostral extremity of the head and the caudal extremity of the embryonic fin of the larvae; BD was the distance between the dorsal and ventral extremities of the body, as described by Nakatani et al. (2001) (Figure 1). The MMO was calculated using the equation below, as proposed by Shirota (1970): $D = \sqrt{2 \times A \times B}$.

With the morphometric data of the absolute values of BD, MMO and TL (mm), it was possible to elaborate the equations from the linear regression models and apply them in the mathematical equation described below (see Results section). In addition, they were also used to estimate allometric growth, i.e., the relative growth of body structures (BD, MMO) in relation to TL (% of total length), as performed by Ribeiro and Portella (2020).

These models assume that cannibalism only occurs when the predator's mouth size (i.e. mouth width, MW) is greater than the prey's body depth (BD) (Ribeiro and Portella, 2020). In this research, the

models for predicting the maximum prey size considered the maximum mouth opening (MMO) at an angle of 90°, resulting in the equation proposed by Shirota (1970).

Data analysis

Total length (TL, mm), body depth (BD, mm) and maximum mouth opening (MMO, mm) were compared among time points (HAH) using Kruskal-Wallis, followed by the LSD test for multiple comparisons. Morphometric measurements of BD and MMO were regressed with TL to generate simple linear regression equations for monitoring allometric growth during the experiment. An analysis of covariance (ANCOVA) was used to test the homogeneity of the regression slopes of the BD and MMO, using the TL (mm) as a covariate. These regressions were applied in the mathematical formula of morphological limitation of cannibalism ($BD_{prey}=MMO_{cannibal}$), used to estimate the maximum size of prey (Qin and Fast, 1996; Ribeiro and Portella, 2020), considering the interval of the range of total length of the larvae during the experiment. Statistical analyses were conducted using the Statistica software (StatSoft, version 10). Statistical significance was defined as $p<0.05$.

Results

During the observed larval stage, the statistical values of the regressions fit into linear models (Table 1). Morphometric measurements of TL (Kruskal-Wallis, $X^2 = 78.40$; $p = 0.001$), BD (Kruskal-Wallis, $X^2 = 49.85$; $p = 0.001$), and MMO (Kruskal-Wallis, $X^2 = 49.20$; $p = 0.000$) have increased from 34 to 54 HAH (Figure 2(a) and 2(b)). The BD and MMO variables in relation to the TL% of the matrinxã larvae showed negative allometric growth (Figure 2(c)). BD showed higher growth in relation to MMO for TL% (ANCOVA, $df= 158$; $F= 607.356$; $p<0.001$).

Assuming that a cannibal could only swallow prey if the prey BD_{prey} is equal to or smaller than the $MMO_{cannibal}$, a predictive model was devised to predict the maximum prey size that cannibalistic individuals of *B. amazonicus* are morphologically capable of ingesting. The maximum prey size was expressed as a proportion of $TL_{cannibal}$, resulting in the equation: $TL_{prey}= 1.2243 TL_{cannibal} - 1.5698$, and this demonstrated that predation capacity varies according to ontogenetic development. Thus, it is possible to observe that cannibalistic larvae of 5.20 mm in length have the maximum physical capacity to ingest conspecific prey of 92% of their TL. As the cannibals develop, the negative allometric growth of body structures favors their predatory capacity, leading to the possibility of ingestion of conspecific prey larger than their own body length (106% TL) (Figure 3).

Discussion

The rapid body development observed in *Brycon amazonicus* (Nakauth et al. 2016; Neumann et

al. 2018) may be directly related to the negative allometric growth described in this study. This characteristic is also observed for other species of fish such as *Lophiosilurus alexandri* (Guimarães-Cruz et al. 2014), *Oryzias profundicola* (Nursyahrhan et al. 2022), *Tor tambra* (Muchlisin et al. 2015), *Rasbora tawarensis* and *Poropuntius tawarensis* (Muchlisin et al. 2010).

In cases in which fish have negative allometric growth, which includes *Brycon amazonicus*, certain body parts do not grow in proportion to the overall increase in fish size. This can lead to situations in which larger individuals within a population may exhibit cannibalistic behavior towards smaller ones, taking advantage of the difference in size to attack them (Lahnsteiner and Kletzl, 2018). This negative allometric growth can be attributed to the environmental conditions or to the specific morphological characteristics of each species (Nursyahrhan et al. 2022). In addition, it is suggested that the negative allometric growth of body structures are directly related to their predation function. This morphological adaptation allows cannibals to achieve flexibility in the size of the prey they can ingest. This idea applied to *B. amazonicus* is supported by Van Snik et al. (1997) where larvae of *Cyprinus carpio* and *Clarias gariepinus* adjust their structural growth to better adjust to specific requirement, which in their case includes the ingestion of relatively large prey. Sepúlveda-Quiroz et al. (2022) also described the relationship between morphology and fish behavior, since *Atractosteus tropicus* adjust their physical characteristics to facilitate cannibalism in specific environments. This comparison underlines the idea that negative allometry in *B. amazonicus* structures is not just a result of growth, but a targeted ontogenetic adaptation that amplifies predation strategies throughout development.

The presence of cannibalistic behavior in fish is also often associated with heterogeneous growth within a population. Fish that exhibit cannibalistic behavior may exhibit accelerated growth compared to their potential prey, leading to size discrepancies that further promote cannibalism (Barron et al. 2013; Ribeiro and Qin, 2015). These characteristics of differential growth are frequently observed in several species of fish that exhibit cannibalism, which suggests the predominance of these behaviors in aquatic environments. This study provides important information into cannibalism in *B. amazonicus* larvae over a short period (24 to 74 hours post-hatching), but a longer observation period would help better understand how cannibalistic behavior changes as larvae grow (Ribeiro and Portella, 2020). Since cannibalism may vary with development, future research should extend the observation time to capture how growth differences affect the intensity and progression of cannibalism. This would allow for a clearer understanding of the limits of cannibalism as larvae mature. This phenomenon is a consequence of allometric growth, in which parts of the fish's body grow at different rates, resulting in significant variations in size and shape (Baras et al. 2005b; Barron et al. 2013; Ribeiro and Qin, 2015; Ribeiro and Portella, 2020; Ribeiro and Portella, 2021).

Some studies indicate that fish that belong to the genus *Brycon* have high rates of cannibalism in

the larval stage (Baras and Lucas, 2010; Jiménez-Velásquez et al. 2021), which may be related to the observed negative allometric growth. In fact, after hatching, the growth of the larvae of *Brycon nattereri* (Maria et al. 2017), for example, was lower than what is observed for *Brycon orbignyanus* (Nogueira et al. 2014), suggesting a potential negative allometric growth pattern. Allometric growth of head length in relation to total length was also observed in *B. orbignyanus*, from hatching to metamorphosis, indicating the presence of negative allometric growth (Nogueira et al. 2014). These studies collectively provide evidence of negative allometric growth of larvae of the genus *Brycon*, and these results are similar to those described for *B. amazonicus*.

According to Nakauth et al. (2016) and Neumann et al. (2018), the body changes described for *Brycon amazonicus* are directly related to the appearance of swimming and digestive structures and the capture of food or prey. These factors, in turn, can significantly influence the ingestion dynamics of the maximum prey size for matrinxã. For example, Leite and Araujo-Lima (2002) found that, in a natural environment, matrinxã larvae prey on medium and large individuals, and this may be associated with the size of the mouth and the anatomy of the digestive tract, which may allow the ingestion of prey of considerable size.

Through these morphometric relationships for *B. amazonicus* applied in the predictive model of maximum size selection in the cannibal-prey relationship, it was possible to observe that the BD showed greater growth in relation to MMO, within the size range analyzed in the present study. The predictive model of maximum prey size offers useful information into the predation capacity of *B. amazonicus* larvae, but its application for managing cannibalism in aquaculture is not well explored. One approach could be using the model to create strategies for separating batches by size, reducing size differences within groups and lowering cannibalism rates (Qin and Fast, 1996; Xi et al. 2017). Additionally, it could help optimize feeding strategies by providing larvae with appropriately sized food to minimize cannibalistic behavior. These strategies could improve production efficiency in controlled farming environments. Similar results were obtained for other fish species, such as *Brycon moorei* (Baras et al. 2005a), *Epinephelus lanceolatus* (Hseu et al. 2004) and *Heterobranchus longifilis* (Baras, 2005). This trend favors the increase in predatory morphological capacity as cannibals grow, leading to the possibility of ingestion of conspecific prey of body length greater than their own body. This characteristic may be related to the fact that individuals develop jaw musculature due to the plasticity of the oral apparatus, allowing them to open their mouths to a greater extent to ingest larger prey (Vandewalle et al. 2005).

Brycon amazonicus opens its mouth very frequently, which contributes to the strengthening of the mandible (Souza et al. 2014) and, consequently, aids predation. Herbing (2001) points out that this movement is an important mechanism in the development of skeletal and muscular structures involved

in the capture of food. Furthermore, Souza et al. (2014) suggest that the intense mandibular movement precedes cannibalism and may explain the increased aggressiveness in matrinxã larvae. A similar pattern was observed by Leite and Araújo-Lima (2002) via positive morphometric relationships and diameter/size of prey for *B. amazonicus* in a natural environment.

Using the predictive model of maximum prey size, it was possible to show that matrinxã larvae are capable of ingesting prey larger than their TL, and this was also observed in *Brycon moorei* in rearing systems (Vandewalle et al. 2005). This relationship is highlighted by Arranz et al. (2019) who cite the existence of a direct linear correlation between prey and predator size in fish. In this context, the dynamics of cannibalism up to 72 HAH in larvae of *Brycon moorei* and *B. amazonicus* indicate that successful attacks begin with larger larvae attacking smaller larvae. These interactions can lead to the death of both the larvae or more larvae involved, since larvae that have the same TL or a smaller TL end up dying with the prey in their mouths (Baras et al. 2005a; Leonardo et al. 2008). The morphological changes observed in TL, BD, and MMO over time points are adjusted for cannibalistic behavior. Specifically, the negative allometric growth of these structures suggests an ontogenetic specialization that favors cannibalism. Sepúlveda-Quiroz et al. (2022) showed that predation behavior and preferences may be conditioned by physical characteristics that facilitate the ingestion of larger prey. Thus, responses in *B. amazonicus*, such as the ability to ingest prey up to 106% of its length, reflect a morphological evolution that supports specific attack and predation behaviors.

Given the above, we considered that the description of the negative allometric growth of body structures and the predictive model of the maximum size in the cannibal-prey ratio for *B. amazonicus* are of great importance for the species, since these characteristics show rapid growth and high predation capacity. This may end up triggering the heterogeneity of body size within the group and, consequently, increase cannibalism and mortality of larvae, and it is not possible to determine a predatory morphological limitation for the observation period of this study.

Further studies are needed to validate the cannibal-prey predictive model, focusing on prey capture, ingestion capacity, and energy gain (Gill and Hart, 1994; Juanes, 1994). The results indicate that matrinxã larvae can capture larger, energy-rich prey, but the time spent on capture and ingestion also impacts cannibalism dynamics. Environmental factors, such as light intensity (Lopes et al. 2018; Muller et al. 2019) and temperature (Barros et al. 2019), must be studied to understand their influence on cannibalistic behavior. These factors could affect the model's effectiveness under different farming conditions. Additionally, research on how food items influence cannibalism and reduce aggression is crucial for developing control strategies, which are essential for improving *B. amazonicus* production in the Amazon region.

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Figure Captions

Figure 1. Representation of morphometric measurements of *Brycon amazonicus*: BD = body depth; TL = total length; MMO = maximum mouth opening; A = maxillary length and B = mandible length.

Figure 2. (a) Mean ($\pm$ standard error) of the total length (TL) of *B. amazonicus* larvae in each time point; (b) Mean ($\pm$ standard error) of the body depth (BD) and maximum mouth opening (MMO) of *B. amazonicus* larvae in each time point; (c) Morphological variation of BD (●) and MMO (●), in relation to TL(%). Each symbol represents individually estimated values (n= 180). The dotted lines represent the mean of the body parts (BD and MMO), respectively, in relation to TL%.

Figure 3. Maximum size of conspecific prey for matrinxã (*Brycon amazonicus*). Prey size is expressed in % of TL_{cannibal}. The dotted regression line includes the predictive model developed with the values of body depth (BD) and maximum mouth opening (MMO). The symbol (●) shows the size of the cannibal and the line shows the maximum size of the prey that can be ingested.

Table 1. Relationship between the body parts (BD, MMO and TL) of the matrinxã (*Brycon amazonicus*) larvae. The absolute values (mm) were used to estimate the regression equations (n=180) for the construction of the cannibal-prey predictive model.

Range TL (mm)	Variables	Equations	R ²	df	F	P value
5.20-9.49	BD x TL	BD = 0.1067 (0.004) TL + 0.8622 (0.035)	0.7754	158	545.342	<0.001
	MMO x TL	MMO = 0.1308 TL (0.007) + 0.6947 (0.055)	0.6788	158	333.943	<0.001

TL: total length (mm); BD: body depth (mm); MMO: maximum mouth opening (mm). ANOVA p<0.05. The values in parentheses in the equations are the standard errors of the coefficient.

Figure 1

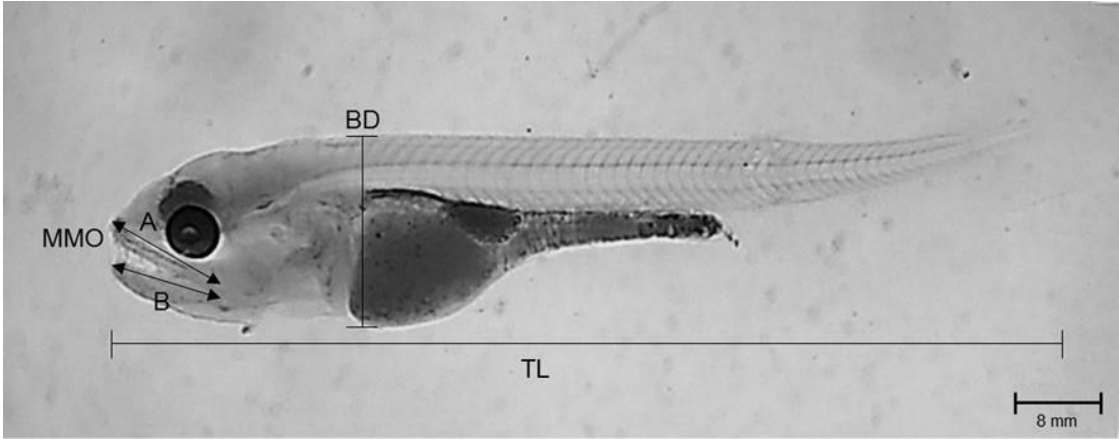


Figure 2

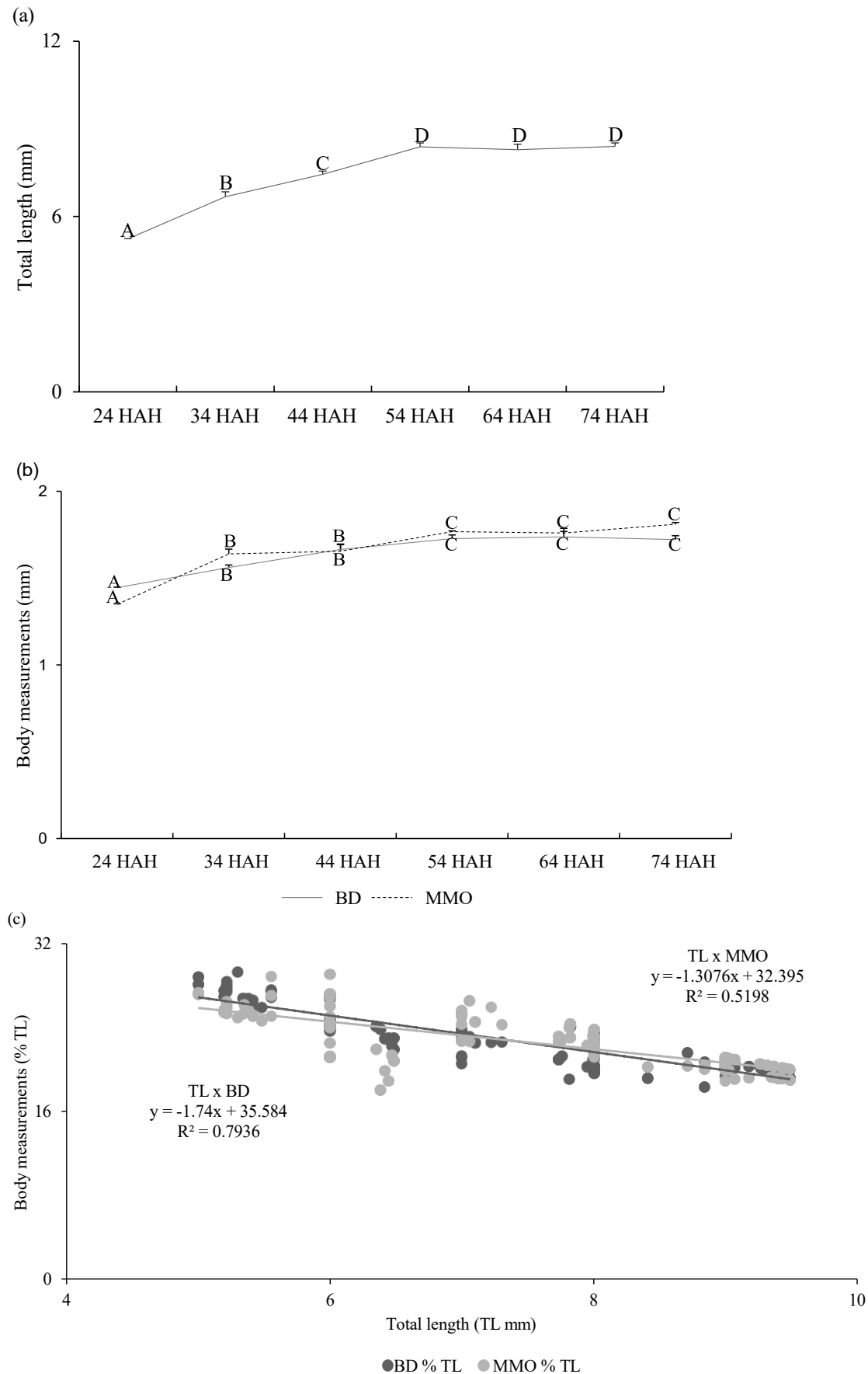
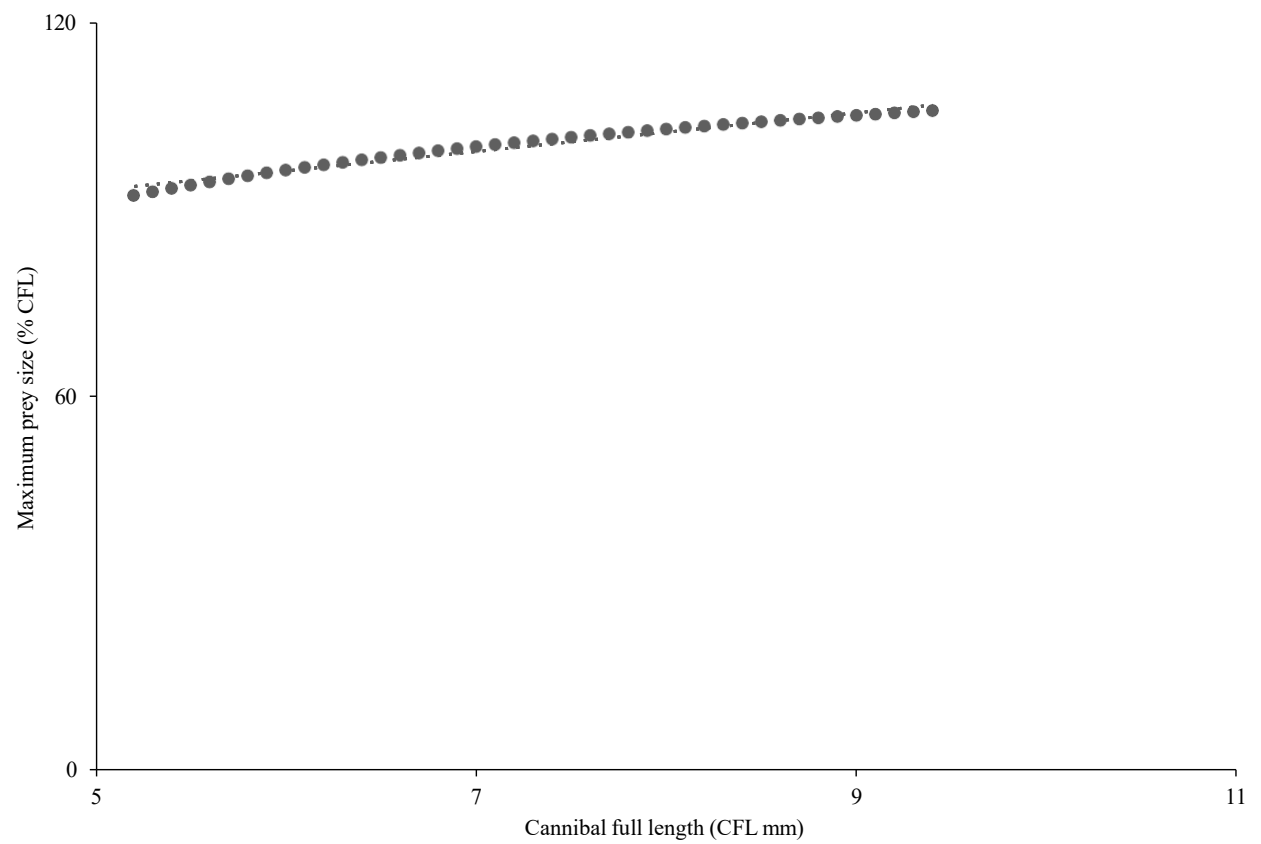


Figure 3



Capítulo 3

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Light wavelength affects ontogeny, survival and intra-specific predation in larvae of matrinxã, *Brycon amazonicus*

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Abstract

The light spectrum influences fish physiology and behaviour. This study assessed the effects of light on development, survival and intraspecific predation in matrixTM larvae (*Brycon amazonicus*). Larvae (6–50 HAH, 200 larvae/L) were exposed to darkness, white, red, blue or green light. Darkness resulted in slower development but higher survival and lower stress, whereas red light increased mortality. Darkness delayed morphological changes linked to aggression and cannibalism, improving survival. Dark conditions optimized growth by reducing aggressive interactions. Light manipulation during *B. amazonicus* rearing enhances larval welfare and supports sustainable Amazonian aquaculture.

Keywords: Darkness, growth, larviculture, light spectrum.

Underwater light, with its varying wavelengths, significantly influences fish (Merighe et al., 2004; Migaud et al., 2007). Light spectra affect growth and survival (Alba et al., 2022; Kaewpranee et al., 2022; Martins et al., 2024; Sierra-Flores et al., 2016; Villamizar et al., 2009; Wu et al., 2021; Zheng et al., 2024). For example, darkness enhances survival, weight and length in *Clarias gariepinus* (Mukai et al., 2013; Padhi et al., 2022) and development in *Anguilla anguilla* (Politis et al., 2014). White light promotes *Trachinotus blochii* growth (Mapunda et al., 2021), whereas blue light improves weight gain (Martins et al., 2024) and *Dicentrarchus labrax* development (Villamizar et al., 2009). Blue and green lights enhance growth and survival in *Gadus morhua* and *Scophthalmus maximus* (Sierra-Flores et al., 2016), as well as larval development in *Danio rerio* (Septriani et al., 2021). Red light increases aggression in *Argyrosomus japonicus* (Timmer & Magellan, 2011), whereas darkness reduces cannibalism in *C. gariepinus* (Mukai et al., 2013). Further, light colour modulates stress responses (Mommensen et al., 1999; Volpato & Barreto, 2001). For instance, white and purple lights reduce *T. blochii* cortisol (Mapunda et al., 2021), whereas red light exacerbates stress in *Micropterus salmoides* and *Pseudopleuronectes yokohamae* (Shibata et al., 2019; Zheng et al., 2024). Darkness stimulates melatonin, reducing aggression in *Salmo salar* (Porter et al., 2001) and *Salmo gairdneri* (Max & Menaker, 1992).

Light spectra's impact on predator–prey dynamics, particularly concerning morphology, is crucial for fish management (Baras et al., 2000; Hseu et al., 2003; Ribeiro & Portella, 2020; Ribeiro & Qin, 2015; Roy et al., 2020). Understanding cannibal growth and morphological limitations relative to prey is key (Hseu et al., 2003; Ribeiro & Portella, 2020), including how predation skills and prey size preferences change with growth (Neumann et al., 2018; Ribeiro & Portella, 2020). These predator–prey relationships are vital for ecological and population dynamics, especially in cannibalistic species (Ribeiro & Portella, 2020; Ribeiro & Qin, 2015). Predictive models using morphology estimate maximum prey size (Muller et al., 2025; Parazo et al., 1991; Ribeiro & Portella, 2020). Although light affects larval development, performance, hormones, aggression and cannibalism, its influence on tropical freshwater species like matrinxã (*Brycon amazonicus*) is understudied. Native to the Amazon and Orinoco (Lima, 2017), matrinxã is a key South American aquaculture species (SIDRA-IBGE, 2022), valued for its traits and market appeal (Urbinati et al., 2014; Zaniboni Filho et al., 2016). Larval cannibalism, however, hinders its production, impacting growth, welfare, survival and expansion (Leonardo et al., 2008).

Studies on *B. amazonicus* larviculture have explored reduction in cannibalism through

various factors: stocking density, temperature (Barros et al., 2019), size-grading (Carvalho et al., 2018), light intensity (Lopes et al., 2018; Muller et al., 2019), salinity (Oliveira et al., 2020), turbidity, refuge (Cornélio et al., 2021), biofloc (Izel-Silva et al., 2024) and morphology (Muller et al., 2025). However, light colour's effects on *B. amazonicus* growth, stress and cannibalism (peaking at 12–72 h after hatching; Souza et al., 2014) remain unstudied. *B. amazonicus* naturally spawns in turbid, low-light floodplains, optimizing early development (Junk, 1997). This study hypothesizes that darkness slows development, reduces stress, aggression and cannibalism, increasing larval survival. Darkness may also affect vision, food capture (Neumann et al., 2018; Sampaio-Nakauth et al., 2016) and cannibalistic size relationships. Therefore, darkness may improve performance of *B. amazonicus* and reduce mortality, similar to other species (Mukai et al., 2013; Padhi et al., 2022; Porter et al., 2001). This research evaluated the effect of different light wavelength on ontogeny, survival, body cortisol and predator–prey ratio in *B. amazonicus* larvae. These results may improve fish hatchery protocols and restocking programmes in the Amazon.

The experiment was conducted at the fish farming station of the experimental farm of the Federal University of Amazonas (UFAM), Manaus, Brazil, following ethical principles approved by the UFAM Ethics Commission (no. 019/2019). Matrinxã larvae were obtained from induced reproduction using carp pituitary extract (Romagosa et al., 2001). Fertilized oocytes were incubated at 1 g eggs/L in 90-L incubators with constant water renewal (Souza et al., 2014). To assess light spectrum effects on matrinxã larvae, we used a methodology reported by Villamizar et al. (2009) and Sampaio-Nakauth et al. (2016) tailored to the specific needs of this study. Larvae at 6 h after hatching (HAH) were stocked at 200 larvae/L (Alvarez-González et al., 2001) in isolated 20-L trays (56.5 × 14.5 × 38 cm) without feeding until 48 HAH. Treatments included 24-h illumination with white (367–1057 nm), blue (435–500 nm), green (500–565 nm), or red (641–718 nm) light, as well as a dark condition (four replicates each). The experiment lasted 44 h after stocking.

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To create the spectral conditions of the experiment, light-emitting diode (LED) lamps in the form of a flexible adhesive tape were used, which had silicone protection to avoid damage to the lighting. Each lamp was installed and fixed approximately 25 cm above the surface of the water. The lamps were powered by a 12-volt and 3-ampere source that was connected to a 110-volt socket and allowed us to adjust the light intensity to 100 ± 17.11 lx, monitored with the aid of luxmeter (MINIPA, LD 240). The experimental units had water renewal of 50% (by siphoning) after 24 h. The physical and Chemical parameters of the water were monitored by means of a multiparameter measuring probe (ASKO, AK88), and ammonia was measured by means of a freshwater colorimetric kit (Alfakit). The mean values of temperature (26.8 ± 0.05 °C), dissolved oxygen (6.58 ± 0.04 mg/L), pH (7.49 ± 0.05) and non-ionized ammonia (0.006 ± 0.001 mg/L) were maintained at adequate levels for the species (Romagosa et al., 2001).

The observations of the structures of the larvae of *matrinxã* were analysed at 6, 12, 18, 24, 30, 36, 42 and 48 HAH, following Sampaio-Nakauth et al. (2016) and Neumann et al. (2018). Fourteen structures were considered: oral cleft delineation, oral cavity delineation, teeth, olfactory cavity, retinal pigmentation, operculum, gill arches, otoliths, yolk sac, body pigmentation, swim bladder, fin membranes, fin formation and gastrointestinal tract. Three larvae were collected from each replicate (per treatment), and the average of the values of the parameters analysed was calculated. Thus, four replicates were considered per treatment. Ontogenetic development was assessed as not applicable (NA), absent (A), or present (P), with presence further categorized as low (-), intermediate (0), or high (+). Morphometric measurements (mm) included total length (TL), body depth (BD), oral cleft delineation (DOC), and maximum mouth opening (MMO) (Nakatani et al., 2001). MMO was calculated as $D = \sqrt{2 \times A \times B}$ (Shirota, 1970), where A is maxilla length and B is mandible length. Yolk sac volume (μ L) was calculated as $V = (\pi/6) \times L \times h^2$ (Blaxter, 1969), where L is yolk sac length and h is height.

Matrinxã larvae were fixed in 4% formalin (n = 12 for each treatment and time) following Villamizar et al. (2009) and Sampaio-Nakauth et al. (2016). From the preserved animals, body weight (BW) was measured using a high-precision analytical balance, and the

TL was determined from stereomicroscopic images processed using ImageJ. Survival rate at 50 HAH was calculated as $S(\%) = (Nf/Ni) \times 100$ (Hirt-Chabbert et al., 2014). Body cortisol was measured from pooled samples ($n = 50$ per experimental unit at 40 HAH) stored in liquid nitrogen (Canavello et al., 2011; Oliveira et al., 2020) using an ELISA kit validated for fish larvae (Canavello et al., 2011; Oliveira et al., 2020; Velasco Santamaría & Cruz Casallas, 2007). Maximum prey size was predicted using the equation $TL_{prey} = 1.2258 \times TL_{cannibal} + 1.5698$ (Muller et al., 2025) based on total length intervals from morphometric analyses. This model, developed according to Ribeiro and Portella (2020) and Shirota (1970), was validated for this experiment.

Data were checked for outliers, normality (Shapiro–Wilk) and homogeneity (F max). BW, TL, BD, vitellus volume (VV), DOC and MMO were compared between treatments using Kruskal–Wallis and Dunn's post hoc tests. These variables were compared over time in each treatment using the Friedman test, followed by a post hoc test. Maximum prey size, survival and body cortisol were compared using one-way analysis of variance (ANOVA) and Tukey's test. Statistical analyses were performed using the SPSS software (version 20.0, IBM). All analyses followed Zar (1997), with $\alpha \leq 0.05$ for significance.

Developmental observations were made across different light conditions. In darkness, oral cleft, gill arches, otoliths, yolk sac and fin membranes appeared at 6 HAH; retinal pigmentation at 12 HAH; teeth, olfactory cavity, operculum and gastrointestinal tract at 18 HAH; body pigmentation and fin formation at 24 HAH; and swim bladder at 36 HAH. White light conditions showed oral cleft, olfactory cavity, retinal pigmentation, gill arches, otoliths, yolk sac and fin membranes at 6 HAH; teeth and operculum at 12 HAH; body pigmentation, fin delimitation and gastrointestinal tract at 18 HAH; and swim bladder at 42 HAH. Red light development mirrored white light, with swim bladder appearing at 42 HAH. Blue light showed similar development, with body pigmentation at 24 HAH and swim bladder at 42 HAH. Green light also followed this pattern, with swim bladder at 42 HAH. Dark-reared larvae lacked olfactory cavities and retinal pigmentation at 6 HAH. At 12 HAH, they lacked buccal delineation, teeth and olfactory cavities and opercula (also absent in red light larvae). Fin delimitation was absent in dark-reared larvae, and body pigmentation was absent in dark- and blue-light larvae. Dark-reared larvae showed earlier swim bladder visibility (Table 1).

BW and TL varied significantly between period at each treatment (Friedman's test, $\chi^2 > 49.45$, $p < 0.001$; Figure 1a,b). BW increased at 30 HAH in dark- and blue-light larvae, whereas TL was higher at 24 HAH (blue light) and 30 HAH (dark and green light). BW and

TL also differed between colours at each period (Kruskal–Wallis test, $\chi^2 > 10.44$, $p < 0.034$). Dark-reared larvae showed the lowest BW and TL at 6, 12, 18, 42 and 48 HAH. Differences in BD varied significantly between light treatments, with darkness decreasing BD at 42 HAH (Friedman's test, $\chi^2 = 34.10$, $p < 0.001$; Figure 1c). Darkness showed the highest BD at 12 HAH, and blue light from 30 to 48 HAH (Friedman's test, $\chi^2 > 26.32$, $p < 0.001$). VV decreased across all treatments (Friedman's test, $\chi^2 > 12.43$, $p < 0.014$; Figure 1d). The DOC and MMO increased across all treatments (Friedman's, $\chi^2 > 16.21$, $p < 0.001$; Figure 1e,f). Dark-reared larvae had smaller DOC at 6 and 18 HAH (Friedman's, $\chi^2 = 24.00$, $p < 0.001$). Blue light led to larger MMO at 30, 42 and 48 HAH (Friedman's test, $\chi^2 = 39.84$, $p < 0.001$), whereas red light and darkness showed the lowest MMO (Kruskal–Wallis test, $\chi^2 > 13.92$, $p < 0.003$). Survival was highest in darkness and lowest under red light (ANOVA, $F = 277.76$, $p < 0.001$; Figure 1g). Dark-reared larvae had a higher predicted maximum prey size (ANOVA, $F = 21.3$, $p < 0.001$; Figure 1h). Cortisol was lowest in darkness and highest under white and blue light (ANOVA, $F = 36.67$, $p < 0.001$; Figure 1i).

This study evaluated light spectrum effects on *matrinxã* larval development, growth, survival, cortisol and predator–prey relationships. Dark-reared larvae showed slowest development but highest survival and lowest stress. Red light resulted in lowest survival, increased cortisol and reduced maximum prey size. This is the first report on light spectrum effects in *Brycon*, highlighting its influence on this Amazonian species. Darkness delayed olfactory cavity, retinal pigmentation, teeth, operculum and swim bladder development, indicating light's role in these processes (Villamizar et al., 2011). Light regulates physiology, including circadian rhythms (Lopes et al., 2022, 2023), and activates growth-related hormonal and cellular mechanisms (Villamizar et al., 2011). Similar to *D. rerio* (Kazimi & Cahill, 1999), darkness delayed but did not prevent *matrinxã* development, with delayed olfactory development, reduced retinal pigmentation and smaller oral clefts.

Darkness reduced *B. amazonicus* visual acuity, minimizing cannibalism and increasing survival. As visual predators, these larvae rely on light for feeding (Neumann et al., 2018; Sampaio-Nakauth et al., 2016). Reduced light likely decreased visual and chemical stimuli, lessening aggression and improving survival, as in *C. gariepinus* (Mukai et al., 2013). This is possible despite small dark larvae would have been able to eat prey that is closer to their body size, as predicted for *Salminus brasiliensis* (Ribeiro & Portella, 2020) and *B. amazonicus* (Muller, personal observation). Although weight and length increased across all treatments, reflecting rapid development (Neumann et al., 2018; Sampaio-Nakauth et al., 2016),

darkreared larvae showed lower weight and size, indicating slower growth due to delayed ontogeny. This may be due to faster yolk reserve depletion in light, affecting metabolism and growth, similar to *Sarda sarda*, *Thunnus thynnus* (Blanco-Vives et al., 2010) and *Solea senegalensis* (Blanco et al., 2017).

Darkness enhances larval fish survival, as observed in *B. amazonicus* and other species (Arambam et al., 2020; Mukai et al., 2013). It stimulates melatonin, reducing aggression and increasing survival (Oliveira & Gonçalves, 2008; Porter et al., 2001), while decreasing cannibalism (Mukai et al., 2013; Paramanik et al., 2014). Lower locomotion in *B. amazonicus* under low light reduces encounters and enhances survival (Lopes et al., 2018; Muller et al., 2019), similar to *S. brasiliensis* and *Pseudoplatystoma corruscans* (Campagnolo & Nuñez, 2008; Schütz & Nuñez, 2007). Darkness increases maximum prey size ($97.49 \pm 1.04\%$), as limited visibility favours larger prey capture (Gaeta et al., 2018; Sánchez-Hernández & Cobo, 2015), a behaviour seen in *Salmo trutta*, *Pomoxis nigromaculatus* and *M. salmoides* (Gaeta et al., 2018; Sánchez-Hernández & Cobo, 2015). These findings demonstrate how darkness influences prey selection and survival in predatory fish.

In addition to increasing survival, larvae kept in the dark had lower body cortisol levels. According to Wendelaar Bonga (1997), the hypothalamic–pituitary–interrenal (HPI) axis is responsible for the production and secretion of corticosteroids and is activated in fish by stressors. This pathway is also activated in the early stages of Fish development (De Jesus & Hirano, 1992; Tsalafouta et al., 2014) When the synthesis and body levels of cortisol are detected in matrinxã larvae (Oliveira et al., 2020). Thus, the different light spectra acted as stressors for *B. amazonicus* and were intense in the larvae under red and green light. Red light also caused a higher mortality rate, indicating that this spectrum can negatively affect the welfare condition of matrinxã larvae. Furthermore, when the larvae of the genus *Brycon* possess a pigmented retina, this indicates that photosensitive cells are present, for example, the cones, which are the structures responsible for the detection of colours (David-Ruales et al., 2024; Gomes et al., 2013; Junior et al., 2021; Sampaio-Nakauth et al., 2016).

Different light colours influenced the ontogenetic development, growth and survival of *B. amazonicus* larvae, impacting both biological and aquaculture aspects. Constant darkness delayed the appearance of certain morphological structures, reducing aggressiveness and cannibalism, leading to higher survival rates. This is linked to their reliance on light for regulating physiological and behavioural processes. Despite delayed development, larvae in darkness efficiently utilized endogenous reserves, ensuring initial growth. For aquaculture,

dark environments may optimize the interplay of growth and survival of matrinxã larvae. Manipulating light conditions can enhance larval welfare and productive efficiency, supporting sustainable Amazonian aquaculture development.

Author Contributions

Reinaldo Luzeiro Muller: Writing – original draft; methodology; investigation; formal analysis. **Ana Carolyny Cerdeira Lopes:** Methodology; investigation; formal analysis. **Bruno Olivetti de Mattos:** Writing – review and editing; validation; supervision; project administration; conceptualization. **Francisco Javier Sánchez-Vázquez:** Writing – review and editing; conceptualization. **Thaís Billalba Carvalho:** Writing – review and editing; validation; supervision; project administration; funding acquisition; conceptualization.

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Conflict of Interest Statement

The authors declare that there are no competing interests.

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Figure captions

Figure 1. Mean ($\pm$ standard error) of body weight (mg; A), total length (mm; B), body depth (mm; C), vitellus volume (μ L; D), delineation of oral cleft (mm; E), maximum mouth opening (mm; F), survival (%; G), maximum prey size (%_TLcannibal; H), and body cortisol (ng/mL; I) for *matrinxã* larvae submitted to experimental treatments (dark, white, red, blue and green light). Lowercase letters indicate statistical differences between treatments ($p < 0.05$). Different uppercase letters indicate differences between observation periods for each treatment ($p < 0.05$).

Table 1. Morphological structures of *Brycon amazonicus* larvae observed at different hours after hatching (HAH) for each experimental treatment (dark, white, red, blue and green light).

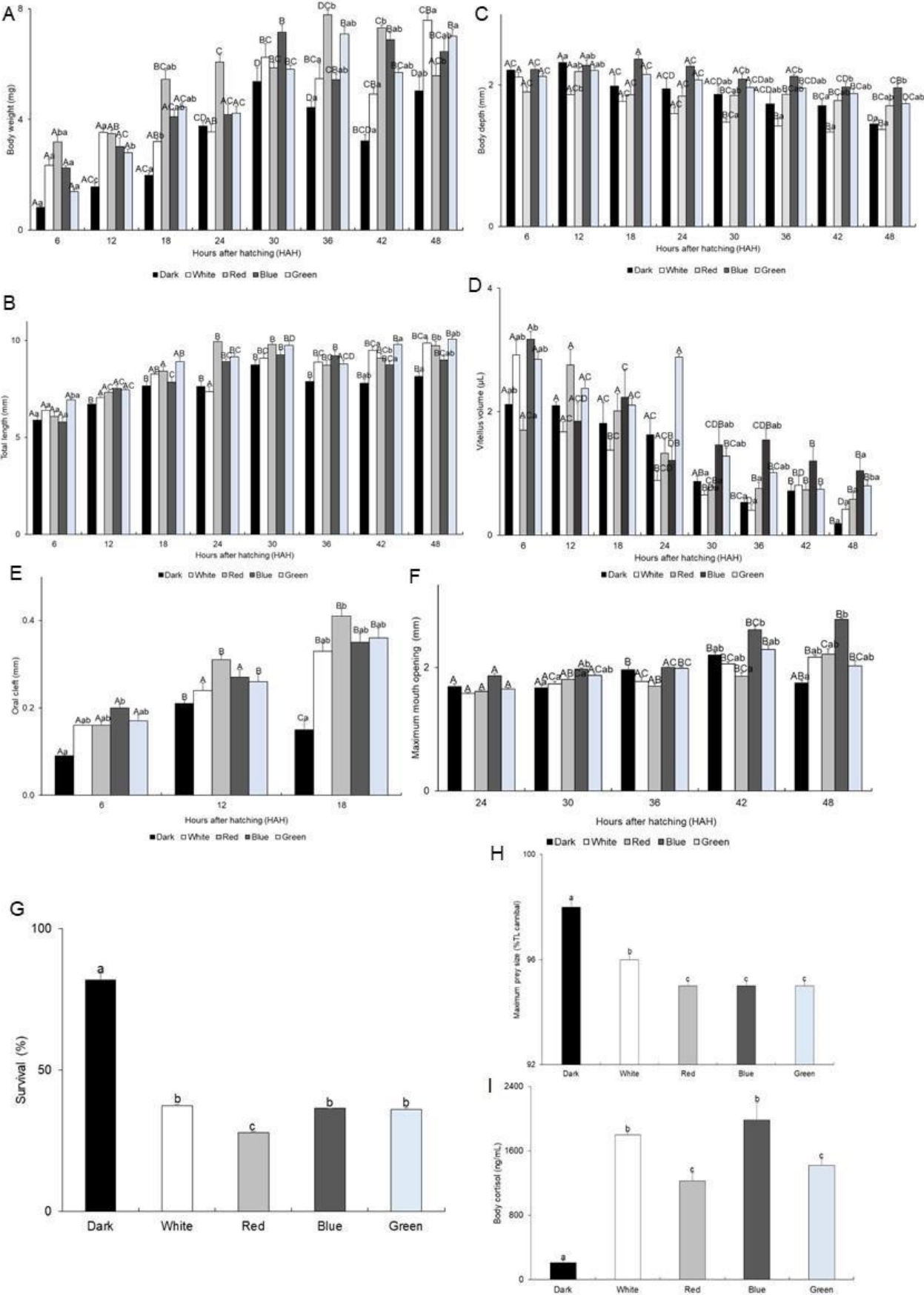
Morphological characteristic	Observation period																			
	6 HAH					12 HAH					18 HAH					24 HAH				
	Dark	White	Red	Blue	Green	Dark	White	Red	Blue	Green	Dark	White	Red	Blue	Green	Dark	White	Red	Blue	Green
Delineation of oral cleft	P	P	P	P	P	P	P	P	P	P	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Buccal delineation	A	A	A	A	A	A	P-	P-	P-	P-	P-	P0	P0	P0	P0	P0+	P+	P+	P+	P+
Teeth	A	A	A	A	A	A	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Olfactory cavity	A	P	P	P	P	A	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Retinal pigmentation	A	P-0	P-	P-0	P-0	P-	P0+	P-	P-0+	P0+	P0+	P0+	P+	P-0+	P+	P-0	P0+	P-0	P-0+	P+
Operculum	A	A	A	A	A	A	P-	A	P-	P-	P-	P-	P-	P-	P-	P-0	P0	P0	P-0	P0
Gill arches	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Otoliths	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Yolk sac	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P0	P+	P+	P+	P+	P+	P+	P+	P+	P+
Body pigmentation	A	A	A	A	A	A	A	A	A	A	A	P-	P-	A	P-	P-	P-	P-	P-	P-
Swim bladder	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
Fin membranes	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Fin formation	A	A	A	A	A	A	A	A	A	A	A	P-	P-	P-	P-	P-	P-	P-	P-	P-
Gastrointestinal tract	A	A	A	A	A	A	A	A	A	A	P-	P-	P-	P-	P-	P-0	P-	P-	P-0	P-

Table 1. Continuation

Morphological characteristic	Observation period																			
	30 HAH					36 HAH					42 HAH					48				
	HAH					HAH					HAH					HAH				
	Dark	White	Red	Blue	Green	Dark	White	Red	Blue	Green	Dark	White	Red	Blue	Green	Dark	White	Red	Blue	Green
Delineation of oral cleft	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Buccal delineation	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+
Teeth	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Olfactory cavity	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Retinal pigmentation	P-0	P0+	P-0+	P0+	P0+	P-0+	P0+	P0+	P0+	P0+	P0+	P+	P+	P0+	P+	P+	P+	P+	P+	P+
Operculum	P-0	P0	P0	P+	P+	P0+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+
Gill arches	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Otoliths	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Yolk sac	P+	P+	P+	P+	P+	P0	P+	P0	P0	P0	P0	P0	P0	P0	P0	P-	P-	P-	P-	P0
Body pigmentation	P-	P-	P-	P-	P-	P-	P-	P-	P-	P-	P-	P-	P-	P-	P-	P0	P0	P0	P-0	P0
Swim bladder	A	A	A	A	A	P	A	A	A	A	P	P	P	P	P	P	P	P	P	P
Fin membranes	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Fin formation	P-0	P-	P0	P0	P0	P0	P0	P0+	P0	P0	P0	P0	P0	P0	P0	P0	P0	P0	P0	P0
Gastrointestinal tract	P-0	P-	P0	P-0	P0	P-	P0+	P+	P0	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+	P+

Does not apply (NA), absence (A) and presence (P). For presence (P), intensity was considered in three categories: lower (-), Intermediate (0) and higher (+)

Figure 1.



Considerações Finais

A presente tese demonstrou que o canibalismo em larvas de *Brycon amazonicus* não deve ser interpretado como um evento isolado ou exclusivamente comportamental, mas como um processo ontogenético, morfológicamente favorecido e ambientalmente modulável. A integração entre revisão do conhecimento, modelagem morfométrica e experimentação com espectros de luz permitiu compreender de forma mais ampla como fatores bióticos e abióticos interagem durante a fase larval, período em que pequenas diferenças no desenvolvimento podem resultar em perdas expressivas por predação intraespecífica.

O Capítulo 1 evidenciou que o canibalismo e o comportamento agressivo em espécies cultivadas de *Brycon* são temas relevantes, porém ainda concentrados em poucos táxons e fases de desenvolvimento. A literatura indica que a primeira alimentação, a compatibilidade entre tamanho da presa e do predador, a densidade, a heterogeneidade corporal, a luminosidade, a salinidade, a temperatura, a turbidez e os sistemas de criação atuam como moduladores do risco de canibalismo. Essa síntese reforça que as recomendações de manejo devem ser formuladas de maneira integrada, considerando espécie, estágio ontogenético e condições de cultivo, e não como soluções universais aplicáveis a todos os contextos.

O Capítulo 2 mostrou que as larvas de *B. amazonicus* apresentam elevada capacidade morfológica de predação ainda nas primeiras horas de desenvolvimento. A partir das relações entre comprimento total, altura corporal e abertura máxima da boca, o modelo preditivo indicou que indivíduos canibais podem ingerir presas coespecíficas com tamanho equivalente a 92-106% do seu próprio comprimento total. Esse resultado sugere que, no intervalo ontogenético avaliado, não há uma limitação morfológica clara que impeça a ingestão de presas de tamanho semelhante ao do canibal. Portanto, a classificação por tamanho, a redução da heterogeneidade extrema e a oferta de alimento compatível com a capacidade de captura das larvas tornam-se estratégias fundamentais para reduzir a ocorrência de canibalismo.

O Capítulo 3 demonstrou que a luminosidade interfere diretamente no desenvolvimento, na sobrevivência, no estresse e na predação intraespecífica de larvas de *B. amazonicus*. A condição de escuro retardou o aparecimento de algumas estruturas morfológicas, mas proporcionou maior sobrevivência e menores níveis de cortisol, indicando redução do estresse e das interações predatórias. Por outro lado, a luz vermelha foi associada à maior mortalidade, enquanto outros espectros luminosos também alteraram variáveis morfométricas e fisiológicas. Esses resultados indicam que o manejo da luz, especialmente durante as fases iniciais de maior risco, pode ser utilizado como ferramenta prática para melhorar o bem-estar larval e a eficiência produtiva.

Em conjunto, os achados da tese apontam que a redução do canibalismo em *B. amazonicus* depende da combinação de medidas de manejo. Entre elas, destacam-se o controle rigoroso da janela de primeira alimentação, o fornecimento de presas ou alimento em tamanho adequado, o monitoramento da heterogeneidade corporal, a classificação de lotes quando necessária, a adequação da densidade de estocagem e a manipulação do ambiente luminoso. Essas ações podem contribuir para aumentar a sobrevivência, reduzir o estresse, melhorar a uniformidade dos lotes e tornar a larvicultura da matrinxã mais previsível e eficiente.

Do ponto de vista científico, esta tese contribui ao articular três dimensões complementares do problema: a dimensão comparativa, ao organizar o conhecimento sobre o canibalismo em *Brycon*; a dimensão morfológica, ao estimar a capacidade máxima de ingestão de presas por larvas de *B. amazonicus*; e a dimensão ambiental, ao demonstrar que o espectro de luz altera respostas ontogenéticas, fisiológicas e comportamentais. Essa integração amplia a compreensão sobre os mecanismos que sustentam o canibalismo em peixes tropicais e oferece uma base para novos estudos com enfoque experimental e aplicado.

Apesar dos avanços alcançados, algumas limitações devem ser consideradas. Os experimentos foram conduzidos em condições controladas, o que permite isolar fatores específicos, mas pode não reproduzir integralmente a complexidade de ambientes naturais ou de sistemas comerciais de larga escala. Além disso, a extrapolação dos resultados para outras espécies de *Brycon* deve ser feita com cautela, uma vez que a literatura disponível ainda é taxonomicamente desigual. Estudos futuros devem testar a aplicação dos modelos morfométricos em diferentes densidades, regimes alimentares, sistemas de criação e condições ambientais, além de avaliar por períodos mais longos a relação entre crescimento, comportamento, estresse e sobrevivência.

Conclui-se que a modulação do canibalismo em larvas de *Brycon amazonicus* depende da interação entre ontogenia, morfologia e ambiente. Ao demonstrar que larvas dessa espécie possuem elevada capacidade de ingestão de presas coespecíficas e que a condição luminosa pode alterar a sobrevivência e o estresse, esta tese oferece contribuições teóricas e práticas para o manejo da matrinxã. Os resultados podem auxiliar a formulação de protocolos de larvicultura mais eficientes, favorecer a conservação e o uso sustentável de espécies amazônicas e apoiar o desenvolvimento de uma aquicultura regional mais produtiva, responsável e adaptada às particularidades biológicas dos peixes tropicais.

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ANEXOS

Original Article

Morphometric prediction of maximum cannibal-prey size for larvae of matrinxã, *Brycon amazonicus* (Spix and Agassiz, 1829)

Predição morfométrica do tamanho máximo cannibal-presa para larvas de matrinxã, *Brycon amazonicus* (Spix e Agassiz, 1829)

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Abstract

Cannibalism among fish is an interaction affecting both intra- and interspecific relationships in aquatic environments. It is related to the size and developmental stage, with prey size determined by morphometric measurements. In general, cannibalism only occurs when the predator's mouth width is greater than the prey's body depth. In this way, understanding these limitations during ontogenetic development is important, as it significantly influences the dynamics of cannibalism. This study aimed to evaluate the maximum size of conspecific prey that the larvae of matrinxã (*Brycon amazonicus*) are morphologically able to ingest. For this, the morphometric measurements of body depth (BD) and maximum mouth opening (MMO) in relation to the total length (TL) of the larvae were considered. BD and MMO showed negative allometric growth. The maximum prey size was expressed as a proportion of the size of the cannibal, which shows that cannibals can ingest prey from 92 to 106% of the TLcannibal. Therefore, the mathematical model of maximum cannibal-prey size for *B. amazonicus* shows rapid growth, possibly due to heterogeneous growth that, in turn, can increase the display of aggressive behavior, and it is not possible to determine a predatory morphological limitation. Studies with longer observation periods, focusing on predator-prey interaction and capture time, should be conducted to reduce cannibalism and increase survival and growth. Reducing cannibalism in *B. amazonicus* is essential for advancing the production of this economically and ecologically important species in the Amazon region.

Keywords: cannibalism, morphological limitations, predictive model, prey size.

Resumo

O canibalismo entre peixes é uma interação que afeta tanto as relações intra quanto interespecíficas em ambientes aquáticos. Está relacionado ao tamanho e estágio de desenvolvimento, com o tamanho da presa determinado por medidas morfométricas. Em geral, o canibalismo só ocorre quando a largura da boca do predador é maior que a profundidade corporal da presa. Dessa forma, entender essas limitações durante o desenvolvimento ontogenético é importante, pois influencia significativamente na dinâmica do canibalismo. Este estudo teve como objetivo avaliar o tamanho máximo de presas coespecíficas que as larvas de matrinxã (*Brycon amazonicus*) são morfologicamente capazes de ingerir. Para isso, foram consideradas as medidas morfométricas de profundidade corporal (PC) e abertura máxima da boca (AMB) em relação ao comprimento total (CT) das larvas. PC e AMB apresentaram crescimento alométrico negativo. O tamanho máximo da presa foi expresso como uma proporção do tamanho do canibal, o que mostra que os canibais podem ingerir presas de 92 a 106% do TLcanibal. Portanto, o modelo matemático de tamanho máximo canibal-presa para *B. amazonicus* mostra rápido crescimento, possivelmente devido ao crescimento heterogêneo que, por sua vez, pode aumentar a exibição de comportamento agressivo, e não é possível determinar uma limitação morfológica predatória. Estudos com períodos de observação mais longos, com foco na interação predador-presa e tempo de captura, devem ser conduzidos para reduzir o canibalismo e aumentar a sobrevivência e o crescimento. A redução do canibalismo em *B. amazonicus* é essencial para o avanço da produção desta espécie econômica e ecologicamente importante na região Amazônica.

Palavras-chave: canibalismo, limitações morfológicas, modelo preditivo, tamanho da presa.

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Light wavelength affects ontogeny, survival and intraspecific predation in larvae of matrinxã, *Brycon amazonicus*

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Abstract

The light spectrum influences fish physiology and behaviour. This study assessed the effects of light on development, survival and intraspecific predation in matrinxã larvae (*Brycon amazonicus*). Larvae (6–50 HAH, 200 larvae/L) were exposed to darkness, white, red, blue or green light. Darkness resulted in slower development but higher survival and lower stress, whereas red light increased mortality. Darkness delayed morphological changes linked to aggression and cannibalism, improving survival. Dark conditions optimized growth by reducing aggressive interactions. Light manipulation during *B. amazonicus* rearing enhances larval welfare and supports sustainable Amazonian aquaculture.

KEYWORDS

darkness, growth, larviculture, light spectrum

Underwater light, with its varying wavelengths, significantly influences fish (Merighe et al., 2004; Migaud et al., 2007). Light spectra affect growth and survival (Alba et al., 2022; Kaewpranee et al., 2022; Martins et al., 2024; Sierra-Flores et al., 2016; Villamizar et al., 2009; Wu et al., 2021; Zheng et al., 2024). For example, darkness enhances survival, weight and length in *Clarias gariepinus* (Mukai et al., 2013; Padhi et al., 2022) and development in *Anguilla anguilla* (Politis et al., 2014). White light promotes *Trachinotus blochii* growth (Mapunda et al., 2021), whereas blue light improves weight gain (Martins et al., 2024) and *Dicentrarchus labrax* development (Villamizar et al., 2009). Blue and green lights enhance growth and survival in *Gadus morhua* and *Scophthalmus maximus* (Sierra-Flores et al., 2016), as well as larval development in *Danio rerio* (Septiani et al., 2021). Red light increases aggression in *Argyrosomus japonicus* (Timmer &

Magellan, 2011), whereas darkness reduces cannibalism in *C. gariepinus* (Mukai et al., 2013). Further, light colour modulates stress responses (Mommsen et al., 1999; Volpato & Barreto, 2001). For instance, white and purple lights reduce *T. blochii* cortisol (Mapunda et al., 2021), whereas red light exacerbates stress in *Micropterus salmoides* and *Pseudopleuronectes yokohamae* (Shibata et al., 2019; Zheng et al., 2024). Darkness stimulates melatonin, reducing aggression in *Salmo salar* (Porter et al., 2001) and *Salmo gairdneri* (Max & Menaker, 1992).

Light spectra's impact on predator–prey dynamics, particularly concerning morphology, is crucial for fish management (Baras et al., 2000; Hseu et al., 2003; Ribeiro & Portella, 2020; Ribeiro & Qin, 2015; Roy et al., 2020). Understanding cannibal growth and morphological limitations relative to prey is key (Hseu et al., 2003;