

**MORPHOLOGICAL, BEHAVIOURAL, AND ENERGETIC  
MECHANISMS OF CANNIBALISM IN JUVENILE BARRAMUNDI  
(*Lates calcarifer*): A LITERATURE SYNTHESIS WITH FIELD-BASED  
HATCHERY PERSPECTIVE**

Mekanisme Morfologis, Perilaku, dan Energetik Kanibalisme pada Benih Kakap Putih  
(*Lates calcarifer*): Sintesis Literatur dengan Perspektif Hatchery Berbasis Lapangan

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(Received March 11<sup>th</sup> 2026; Accepted April 11<sup>th</sup> 2026)

**ABSTRACT**

Cannibalism is a major constraint in juvenile barramundi (*Lates calcarifer*) hatchery production, particularly during the nursery phase when size heterogeneity, feeding competition, and predator-prey encounters increase. This article synthesizes published evidence and field-based hatchery perspectives to explain the morphological, behavioural, and energetic mechanisms underlying cannibalism and their implications for hatchery management. The synthesis focused on four domains: morphological limitation, prey-size vulnerability, energetic profitability, and nursery management factors, including grading, stocking density, and feeding frequency. The findings indicate that cannibalism is initiated mainly by size heterogeneity, where smaller juveniles become vulnerable when their body size allows capture and ingestion by larger conspecifics. Morphological constraints determine the physical feasibility of ingestion, whereas capture success, escape response, and handling time influence prey vulnerability. Energetic evidence further explains cannibalism persistence because cannibalistic individuals may gain growth advantages that intensify cohort size disparity. Therefore, cannibalism control should integrate early size monitoring, preventive grading, shooter removal, density regulation, and increased feeding frequency. This synthesis provides a practical framework for improving juvenile survival and nursery efficiency in tropical barramundi hatcheries.

**Keywords:** Bioenergetic Profitability, Cannibalism, Hatchery Management, Juvenile Barramundi, Prey-Size Vulnerability

**ABSTRAK**

Kanibalisme merupakan kendala utama dalam produksi benih kakap putih (*Lates calcarifer*), terutama pada fase pendederan ketika heterogenitas ukuran, kompetisi pakan, dan interaksi

predator–mangsa meningkat. Artikel ini mensintesis bukti ilmiah dan perspektif berbasis praktik pembenihan untuk menjelaskan mekanisme morfologis, perilaku, dan energetik yang mendasari kanibalisme serta implikasinya bagi manajemen pembenihan. Sintesis difokuskan pada empat domain, yaitu keterbatasan morfologis, kerentanan mangsa berbasis ukuran, profitabilitas energi, dan faktor manajemen pendederan, termasuk grading, kepadatan tebar, dan frekuensi pemberian pakan. Hasil sintesis menunjukkan bahwa kanibalisme terutama dipicu oleh heterogenitas ukuran, ketika benih kecil menjadi rentan karena ukuran tubuhnya memungkinkan untuk ditangkap dan ditelan oleh individu yang lebih besar. Keterbatasan morfologis menentukan kemungkinan fisik penelanan, sedangkan keberhasilan tangkap, respons pelarian, dan waktu penanganan memengaruhi kerentanan mangsa. Bukti energetik menjelaskan persistensi kanibalisme karena individu kanibal dapat memperoleh keunggulan pertumbuhan yang memperbesar ketimpangan ukuran kohort. Oleh karena itu, pengendalian kanibalisme perlu mengintegrasikan pemantauan ukuran dini, grading preventif, pemisahan ikan shooter, pengaturan kepadatan, dan peningkatan frekuensi pakan. Sintesis ini memberikan kerangka praktis untuk meningkatkan sintasan benih dan efisiensi pendederan kakap putih di pembenihan tropis.

**Kata Kunci:** Kanibalisme, Kakap Putih Juvenil, Kerentanan Ukuran Mangsa, Manajemen Hatchery, Profitabilitas Bioenergetik

## INTRODUCTION

Barramundi or Asian seabass (*Lates calcarifer*) is an economically important carnivorous fish species widely cultured in tropical and subtropical aquaculture systems. Its high market value, broad environmental tolerance, and suitability for hatchery-based seed production have made this species an important marine and brackishwater aquaculture commodity in the Indo-Pacific region. However, the expansion of barramundi aquaculture depends strongly on the stability of seed production during the larval and juvenile nursery phases. At these stages, mortality, size heterogeneity, feeding transition, and cohort management remain major constraints that can reduce seed availability and production efficiency. A recent bibliometric synthesis of *L. calcarifer* aquaculture also indicates that global research has increasingly shifted toward hatchery technology, functional feed, disease resistance, genetic improvement, and sustainable production systems, highlighting the need to connect biological mechanisms with practical hatchery management (Lesmana *et al.*, 2025b). Hatchery-oriented studies have emphasized that larval and juvenile performance is closely associated with feeding strategy, nutrition, weaning success, and early rearing management, all of which influence survival and size uniformity during nursery culture (Lesmana, *et al.*, 2025a; Safiin *et al.*, 2022).

One of the most persistent biological constraints in the nursery production of carnivorous fish is intracohort cannibalism, defined as predation among individuals of the same cohort. Cannibalism is particularly problematic in cultured fish because captive environments restrict spatial separation between predators and vulnerable prey, while high density, uneven food access, and rapid growth variation may increase encounters between large and small individuals. In larviculture and juvenile rearing systems, cannibalism may result not only in direct mortality through ingestion, but also in injury, stress, suffocation, infection, and progressive size heterogeneity. Similar patterns have been documented in other cultured fish larvae, where sibling cannibalism is associated with ontogeny, prey selectivity, bioenergetic gain, and progressive size heterogeneity. Therefore, cannibalism is not merely an aggressive behavioural event, but a complex biological and management problem that directly affects survival rate, production efficiency, and economic performance in hatchery operations (Baras & Jobling, 2002; Duk *et al.*, 2017; Hecht & Pienaar, 1993; Kestemont *et al.*, 2003).

In barramundi, cannibalism is strongly associated with size-dependent predation during the juvenile phase. Larger juveniles may prey upon smaller conspecifics when the size difference is sufficient to allow capture, handling, and ingestion. This phenomenon is especially important because barramundi naturally exhibits carnivorous and piscivorous tendencies, and under hatchery conditions, small differences in growth rate may rapidly create vulnerable size classes within a cohort. Previous field-based work in Indonesian hatchery conditions showed that cannibalism and cohort mismanagement remain important contributors to reduced larval and juvenile survival, particularly when size disparity develops and grading is not sufficiently synchronized with growth variation (Lesmana, Effendi, Suharman, Putra, et al., 2025). This evidence indicates that cannibalism control in barramundi hatcheries requires not only sufficient feeding, but also a mechanistic understanding of why some individuals become cannibals and why some prey sizes are more vulnerable than others.

Morphological limitation is one of the primary mechanisms determining whether cannibalism can occur in juvenile barramundi. Complete cannibalism requires the predator to ingest the whole prey, and this process is constrained by the relationship between the mouth dimension of the cannibal and the body depth of the prey, a principle also reported in morphometric prediction studies on other cultured carnivorous fish (Hseu et al., 2003; Ribeiro & Qin, 2013). Ribeiro and Qin (2013) demonstrated that the risk of cannibalism in barramundi is strongly regulated by gape-related morphology, allometric growth, and the relative size difference between cannibal and prey. Their experimental observations showed that barramundi could become cannibals when the initial prey size was less than 50% of the cannibal's body length, while fish did not become cannibals when prey exceeded 58% of their size. More importantly, experienced cannibals were able to ingest conspecific prey up to approximately 78–72% of their own total length, indicating that the morphological capacity of cannibalistic individuals may exceed predictions based solely on average mouth dimensions.

The behavioural mechanism of cannibalism provides another important explanation for prey vulnerability in juvenile barramundi. Although large prey may contain more biomass, they are not always the most profitable prey because they require longer handling time, present greater escape ability, and reduce capture success. Ribeiro and Qin (2015) showed that juvenile barramundi cannibals selected smaller prey even when they were morphologically capable of ingesting larger individuals. Their behavioural analysis indicated that handling time increased with prey size, whereas capture success decreased as prey and cannibal size increased. Interestingly, cannibals attacked prey of different sizes at relatively similar rates but ingested smaller prey more often, suggesting that prey size selection was largely passive and mediated by prey vulnerability rather than fully determined by active predator choice (Ribeiro & Qin, 2015). This behavioural evidence is important for hatchery management because it explains why the smallest individuals in a cohort are disproportionately removed during cannibalistic episodes.

Energetic profitability further explains why cannibalism may persist once it begins in juvenile barramundi populations. From an optimal foraging perspective, predators are expected to benefit from prey that provide the highest energy return relative to the effort required for capture and handling. In barramundi, conspecific prey may provide a highly digestible and energetically efficient food source for fast-growing cannibals. Ribeiro and Qin (2016) reported that barramundi fed conspecific prey showed better feed conversion efficiency, apparent digestibility, and growth performance than siblings fed formulated diets. Although formulated feed remains essential in hatchery production, this evidence suggests that artificial feeding alone may not fully eliminate cannibalism when vulnerable prey are present within the same cohort. The growth advantage obtained by cannibals may intensify size heterogeneity and create a feedback loop in which larger individuals continue to find smaller conspecifics as profitable prey (Ribeiro & Qin, 2016).

The interaction between stocking density, feeding frequency, and size heterogeneity is also central to the dynamics of cannibalism in hatchery systems. High stocking density may increase encounter rates between potential cannibals and smaller prey, while low feeding frequency may intensify hunger, competition, and aggressive interactions. Ribeiro *et al.* (2015) found that high feeding frequency and low stocking density reduced size dispersion and delayed or suppressed cannibalism in juvenile barramundi. Similarly, studies on cultured predatory fish have shown that growth heterogeneity and cannibalism are influenced by both intrinsic factors, such as developmental variation and individual growth capacity, and extrinsic factors, such as feeding regime, density, light, shelter availability, and environmental complexity (Duk *et al.*, 2017; Kestemont *et al.*, 2003; J. G. Qin *et al.*, 2004). These findings support the view that cannibalism control requires an integrated management approach rather than a single intervention.

Despite the availability of experimental studies on barramundi cannibalism, their practical translation into hatchery decision-making remains limited, particularly for tropical aquaculture systems in Indonesia. Most mechanistic studies have been conducted under controlled experimental settings, whereas hatchery operations often face practical constraints such as limited labour for frequent grading, variable seed quality, asynchronous growth, uneven feed acceptance, and differences in tank management. Therefore, a synthesis that connects morphological thresholds, prey-size vulnerability, energetic profitability, stocking density, feeding frequency, and field-based hatchery practice is needed to produce recommendations that are scientifically grounded and operationally applicable.

Based on this background, this article aims to synthesize the morphological, behavioural, and energetic mechanisms underlying cannibalism in juvenile barramundi and to interpret their implications for hatchery management. The article is positioned as a literature synthesis supported by field-based hatchery perspective, rather than as a fully replicated experimental study. The synthesis is expected to provide a practical framework for improving cannibalism control, juvenile survival, and nursery efficiency in Indonesian barramundi hatchery systems.

## RESEARCH METHODS

### Study Design

This article was designed as a narrative literature synthesis supported by a field-based hatchery perspective. The study did not aim to present a replicated experimental trial, but to synthesize mechanistic evidence on cannibalism in juvenile barramundi (*Lates calcarifer*) and interpret its practical relevance for hatchery management under Indonesian aquaculture conditions. This design was selected because field observations provided operational context, while the available quantitative field data were not sufficiently comprehensive to support a complete experimental analysis of morphological, behavioural, and bioenergetic variables. Therefore, the article integrates published experimental evidence with descriptive hatchery-based interpretation to formulate an applied framework for cannibalism control during the juvenile nursery phase.

### Literature Search Strategy

The literature search was conducted to identify scientific publications addressing cannibalism, size heterogeneity, prey-size selection, morphological constraints, energetic profitability, stocking density, feeding frequency, and hatchery management in barramundi and other cultured predatory fish. Literature was searched through Google Scholar, ScienceDirect, SpringerLink, PubMed Central, PLOS ONE, ResearchGate, Garuda, and national journal portals. The search emphasized peer-reviewed journal articles, doctoral thesis material, and national accredited aquaculture publications relevant to cannibalism mechanisms and hatchery management. The literature search covered publications from 1993 to 2025, with priority given

to barramundi-specific studies and recent studies on fish cannibalism mitigation. Search terms were developed by combining species-related, mechanism-related, and management-related keywords, as presented in Table 1. After screening titles, abstracts, and full texts, 13 sources were considered relevant and used in the synthesis.

Table 1. Literature Search Strategy Used for the Synthesis

Search Component	Keywords and Search Terms	Main Purpose
Species focus	“barramundi”, “Asian seabass”, “ <i>Lates calcarifer</i> ”	To identify studies specifically addressing the target species
Cannibalism mechanism	“cannibalism”, “intra-cohort cannibalism”, “size-dependent cannibalism”, “cannibalistic behaviour”	To identify literature on cannibalism dynamics in fish
Morphological mechanism	“gape limitation”, “mouth width”, “body depth”, “morphological constraint”, “prey size”	To identify evidence on physical constraints of prey ingestion
Behavioural mechanism	“prey size selection”, “capture success”, “handling time”, “escape response”, “predatory behaviour”	To identify studies explaining predator–prey behavioural interaction
Energetic mechanism	“bioenergetics”, “energy profitability”, “growth advantage”, “feed conversion”, “formulated diet”	To identify studies explaining energetic benefits of cannibalism
Hatchery management	“feeding frequency”, “stocking density”, “grading”, “nursery management”, “larval survival”	To identify practical interventions for reducing cannibalism

### Eligibility Criteria and Source Selection

Scientific sources were selected based on relevance to the objectives of the article. A publication was included when it met at least one of the following criteria: it examined cannibalism in barramundi; it described morphological constraints related to prey ingestion; it evaluated prey size selection, capture success, handling time, or predator–prey behaviour; it discussed energetic profitability or growth advantage of cannibals; or it provided evidence on stocking density, feeding frequency, grading, or hatchery management in cultured fish. Studies on other carnivorous or piscivorous fish species were included only when they provided broader conceptual support for mechanisms also relevant to barramundi.

Publications were excluded when they did not address cannibalism, hatchery management, juvenile fish rearing, or predator–prey mechanisms. Non-scientific web articles, unverified technical reports, and sources without sufficient methodological clarity were not used as primary evidence. When multiple sources reported similar findings, priority was given to studies with clear experimental design, peer-reviewed publication status, direct relevance to *Lates calcarifer*, and strong linkage to hatchery management implications.

The core mechanistic evidence was derived mainly from the series of studies by Ribeiro and colleagues, which investigated size-dependent cannibalism, prey size selection, bioenergetics, stocking density, and feeding frequency in juvenile barramundi. These sources were selected as the primary mechanistic basis because they directly examined *Lates calcarifer* and provided an integrated explanation of cannibalism through morphology, behaviour, energy allocation, and rearing management.

## Data Extraction from Literature

Information was extracted from selected sources using a thematic approach. The extracted information included study objective, fish species, developmental stage, experimental or observational design, key variables, major findings, and hatchery management implications. For barramundi-specific studies, particular attention was given to size thresholds, prey-to-predator size ratio, mouth dimension, prey body depth, capture success, handling time, energy profitability, growth advantage, feeding frequency, stocking density, and grading relevance.

The extracted evidence was grouped into four mechanistic domains. The first domain was morphological limitation, which focused on the relationship between mouth dimensions of the cannibal and body depth of the prey. The second domain was behavioural vulnerability, which included attack rate, prey size selection, capture success, handling time, and escape response. The third domain was energetic profitability, which included energy gain, feed conversion efficiency, apparent digestibility, and growth advantage of cannibals. The fourth domain was hatchery management, which included grading, feeding frequency, stocking density, and size heterogeneity control.

Table 2. Data Extraction Framework for Literature Synthesis

Mechanistic Domain	Variables or Information Extracted	Interpretation Focus
Morphological limitation	Predator total length, prey total length, mouth width, gape capacity, prey body depth, prey-to-predator size ratio	Determining physical feasibility of cannibalism and critical size thresholds
Behavioural vulnerability	Attack rate, capture success, handling time, escape response, prey size selection	Explaining why smaller prey are more vulnerable and more frequently ingested
Energetic profitability	Prey energy value, handling effort, feed conversion efficiency, digestibility, growth advantage	Explaining persistence of cannibalism and superior growth of cannibals
Hatchery management	Feeding frequency, stocking density, grading interval, size distribution, survival, mortality	Translating biological mechanisms into practical nursery management actions
Indonesian hatchery relevance	Field condition, practical grading, feeding practice, size heterogeneity, observed cannibalism risk	Contextualizing literature evidence for tropical hatchery operations

## Field-Based Hatchery Observation

The field-based component was derived from hatchery observations conducted during barramundi nursery activities at the Marine Aquaculture Fisheries Center, Batam, Indonesia, from August to October 2025. The observation focused on practical conditions related to cannibalism risk, including size heterogeneity, feeding management, grading practice, juvenile behaviour, and general nursery operation. This component was not designed as a controlled experiment and was therefore not analysed as a replicated quantitative trial. Instead, it served as contextual evidence to interpret whether mechanisms reported in the literature were relevant to practical hatchery conditions in Indonesia.

During the field observation, attention was directed to several operational indicators commonly associated with cannibalism risk. These included the emergence of larger

individuals within the same cohort, the presence of smaller and slower-growing fish, visible size disparity, feeding competition, injury or missing fish, and the timing of grading. These indicators were selected because previous mechanistic studies have shown that cannibalism in barramundi is strongly associated with size heterogeneity, prey vulnerability, feeding opportunity, and density-related encounter between large and small individuals.

The field-based information was recorded descriptively rather than experimentally. Observational notes were used to describe hatchery context, practical management conditions, and the relevance of published evidence for Indonesian hatchery practice. No unsupported numerical claim from the field observation was used as primary experimental evidence. Quantitative values reported in the article, such as critical size thresholds, prey size preference, and effects of feeding frequency or stocking density, were attributed to previous published studies rather than to the field observation.

### **Integration of Literature Synthesis and Field Observation**

The integration process was conducted by linking each mechanistic domain from the literature with practical hatchery observations. Morphological evidence was interpreted in relation to grading and size separation. Behavioural evidence was interpreted in relation to prey vulnerability and early detection of high-risk size groups. Energetic evidence was interpreted in relation to the persistence of cannibalism after larger individuals begin consuming conspecific prey. Management evidence was interpreted in relation to feeding frequency, stocking density, and routine monitoring in the nursery phase.

The synthesis followed a cause–mechanism–management logic. First, the biological cause of cannibalism was identified through size heterogeneity and prey vulnerability. Second, the mechanism was explained through morphology, behaviour, and energetics. Third, the management implication was formulated based on how hatchery interventions can reduce prey vulnerability and interrupt the progression of cannibalism. This logic was used to ensure that the Results and Discussion section remained directly connected to the methodological framework and did not present literature findings as primary experimental data.

Table 3. Integration Matrix Between Mechanistic Evidence and Hatchery Interpretation

Evidence Domain	Mechanistic Explanation	Hatchery Interpretation
Morphology	Cannibalism occurs when prey size and body depth remain within the ingestive capacity of larger individuals	Grading should prevent smaller juveniles from becoming vulnerable prey for larger siblings
Behaviour	Smaller prey are more likely to be captured and ingested due to lower escape ability and shorter handling time	The smallest individuals should be separated or protected before predation becomes intense
Energetics	Cannibalism may provide growth advantage through efficient energy conversion and high nutritional value of conspecific prey	Once cannibals emerge, size heterogeneity may increase rapidly and require immediate intervention
Feeding regime	Higher feeding frequency can reduce hunger motivation and competition	Feeding should be distributed more frequently during the nursery phase

Evidence Domain	Mechanistic Explanation	Hatchery Interpretation
Stocking density	High density increases encounter rate and competition among juveniles	Stocking density should be adjusted according to fish size, grading interval, and tank condition
Field observation	Practical hatchery conditions often involve asynchronous growth and operational limitations	Management recommendations must be realistic for production-scale hatchery practice

### Quality Control and Analytical Approach

The synthesis was conducted using a qualitative narrative approach rather than quantitative meta-analysis. This approach was appropriate because the selected studies varied in experimental design, fish size, rearing system, measured variables, and management context. Instead of combining numerical data statistically, the analysis focused on identifying consistent biological patterns and management implications across studies.

To improve transparency and reduce interpretive bias, the synthesis emphasized evidence that was directly relevant to juvenile barramundi. Findings from non-barramundi species were used only as supporting evidence when they helped explain general mechanisms of cannibalism in cultured predatory fish. Claims were organized according to the strength of evidence. Direct barramundi studies were treated as primary evidence, while broader fish cannibalism studies were treated as conceptual support.

No new statistical analysis was performed because the article did not generate a comprehensive primary dataset. The field-based component was analysed descriptively to support interpretation rather than to test hypotheses. Therefore, numerical values and statistical claims presented in this article were attributed only to the published studies from which they were derived.

### Ethical and Academic Positioning

This article was prepared with attention to academic integrity. Data and numerical findings from previous studies were not presented as original field data. The field observation was used only as contextual information to support the relevance of the literature synthesis for hatchery practice. All mechanistic findings derived from published studies were cited appropriately using author–year citation format.

Because the field component was observational and did not involve controlled experimental manipulation, invasive procedures, or deliberate exposure of fish to experimental predation beyond normal hatchery observation, formal animal experimental analysis was not included. However, the interpretation of hatchery management emphasized fish welfare by recommending practices that reduce injury, stress, predation, and mortality among juveniles.

### Methodological Limitation

The main methodological limitation of this article is that the field-based component was descriptive and did not provide new experimental validation of cannibalism mechanisms under Indonesian hatchery conditions. Therefore, the synthesis should be interpreted as an applied mechanistic review rather than as a controlled experimental study.

## RESULT

Table 4. Key Literature Sources Included in the Synthesis

Source	Species or Scope	Study Type	Main Contribution to the Synthesis
Hecht & Pienaar (1993)	Cultured fish larvae	Review	Foundational concept of cannibalism and its implications in fish larviculture
Baras & Jobling (2002)	Cultured fish	Review	Dynamics of intracohort cannibalism, size heterogeneity, and growth depensation
Kestemont et al. (2003)	Predatory fish larvae	Experimental/ review synthesis	Biotic and abiotic influences on size heterogeneity, competition, and cannibalism
Qin et al. (2004)	Juvenile barramundi	Experimental study	Use of refuges and low light to reduce cannibalism
Ribeiro & Qin (2013)	Juvenile barramundi	Morphological experiment	Size-dependent cannibalism and gape-related threshold
Ribeiro & Qin (2015)	Juvenile barramundi	Behavioural experiment	Prey size selection, capture success, and handling time
Ribeiro & Qin (2016)	Juvenile barramundi	Bioenergetic experiment	Growth advantage of cannibals over fish fed formulated diet
Ribeiro et al. (2015)	Juvenile barramundi	Hatchery management experiment	Effects of stocking density and feeding frequency on cannibalism
Duk et al. (2017)	Cultured freshwater fish	Review	Mitigation methods for intracohort cannibalism
Lesmana et al. (2025)	Barramundi hatchery	National hatchery study	Indonesian hatchery context for cannibalism management

### Evidence Profile of the Literature Synthesis and Field-Based Observation

The literature synthesis identified four major mechanistic domains explaining cannibalism in juvenile barramundi (*Lates calcarifer*): morphological limitation, prey-size-dependent behavioural vulnerability, energetic profitability, and hatchery management factors. The synthesis was based on 13 selected sources, including barramundi-specific experimental studies, broader reviews on intracohort cannibalism in cultured fish, and national hatchery-related publications. The strongest species-specific evidence was derived from experimental studies on juvenile barramundi that examined size-dependent cannibalism, prey-size selection, bioenergetics, stocking density, and feeding frequency. Supporting evidence from other cultured predatory fish was used to interpret general patterns related to size heterogeneity, growth depensation, feeding competition, and environmental management.

The field-based observation component provided practical context for interpreting the relevance of these mechanisms in Indonesian hatchery systems. Because the field information was not obtained through a fully replicated experimental design, it was not treated as a primary quantitative dataset. Instead, it was used to identify hatchery-relevant indicators of cannibalism risk, such as size heterogeneity, emergence of larger individuals, vulnerability of smaller juveniles, grading needs, feeding synchronization, and nursery management constraints.

Table 5. Summary of Evidence Domains Used in the Synthesis

Evidence Domain	Main Synthesized Finding	Hatchery Relevance
Morphological limitation	Cannibalism is constrained by the relationship between cannibal mouth dimensions and prey body depth	Determines safe size thresholds and grading urgency
Behavioural vulnerability	Smaller prey are more frequently ingested because they are easier to capture and handle	Identifies vulnerable size groups within the cohort
Energetic profitability	Cannibalistic feeding may provide growth advantage over formulated diet alone	Explains persistence of cannibalism after large individuals emerge
Feeding frequency	Higher feeding frequency can reduce food competition and delay cannibalism	Supports more frequent feeding during nursery culture
Stocking density	Higher density may increase encounter rates and size heterogeneity	Supports density adjustment and post-grading management
Field hatchery context	Practical hatchery conditions often involve asynchronous growth and limited grading windows	Provides operational relevance for Indonesian hatchery practice

### **Morphological Mechanisms of Cannibalism**

The synthesis showed that cannibalism in juvenile barramundi is strongly size-dependent and morphologically constrained. The critical mechanism is the relationship between the mouth dimension of a larger fish and the body depth of a smaller conspecific. When the prey body depth remains within the ingestive capacity of the predator, complete cannibalism becomes physically possible. Conversely, when prey body depth exceeds the effective mouth opening of the predator, the likelihood of successful ingestion declines.

The most important threshold identified from barramundi-specific evidence is that the emergence of cannibalism may occur when smaller fish are less than 50% of the body length of larger individuals. However, once a fish becomes an experienced cannibal, its ability to ingest conspecific prey may exceed simple predictions based on average mouth dimensions. Previous experimental evidence indicates that experienced cannibals may ingest prey reaching approximately 72–78% of their own total length, depending on cannibal size and mouth extension capacity (Ribeiro & Qin, 2013).

This finding highlights the distinction between two practical thresholds. The first is the threshold for the emergence of cannibalism, which is associated with small fish falling below approximately half the size of larger individuals. The second is the upper ingestion capacity of experienced cannibals, which may be much higher than the initial emergence threshold. For hatchery management, the first threshold is more important for prevention, whereas the second threshold is important after cannibals have already emerged within the population.

### **Behavioural Vulnerability and Prey Size Selection**

The synthesis also showed that cannibalism in juvenile barramundi is not determined only by whether prey can be swallowed. Behavioural vulnerability plays a central role in determining which prey are actually captured and ingested. Smaller prey are generally more vulnerable because they have lower escape capacity, shorter handling time, and higher

probability of successful capture. Larger prey may provide more biomass, but they are more difficult to subdue, handle, and ingest.

Evidence from prey-size selection studies indicates that juvenile barramundi cannibals tend to consume smaller prey even when larger prey are morphologically ingestible, primarily because smaller prey provide higher capture success and shorter handling time (Ribeiro & Qin, 2015). In practical terms, the most vulnerable individuals in a hatchery tank are not simply the smallest fish in absolute size, but those whose relative size makes them easy to capture, handle, and ingest by the larger fish present in the same cohort.

The behavioural synthesis further suggests that barramundi cannibals may attack prey of different size classes, but successful ingestion occurs more frequently in smaller prey. This means that observed attack frequency alone is not sufficient to assess cannibalism risk. A more meaningful risk indicator is the combination of prey size, capture success, escape response, and handling time. In hatchery practice, this supports the need to identify and separate the smallest size fraction before they become highly vulnerable to larger conspecifics.

### **Energetic Profitability and Growth Advantage**

The energetic synthesis indicates that cannibalism may persist because it provides a biological advantage to cannibalistic individuals. Conspecific prey may represent a highly digestible and nutritionally efficient food source for carnivorous juveniles. Compared with formulated feed alone, prey-based feeding can support superior growth in cannibalistic individuals through improved feed conversion efficiency, apparent digestibility, and allocation of consumed energy to growth.

This mechanism is particularly important because Ribeiro & Qin (2016) showed that juvenile barramundi feeding on conspecific prey may achieve better growth performance and feed conversion efficiency than siblings fed formulated diet alone. This growth advantage widens the size gap within the population and increases the number of individuals that become vulnerable prey. Thus, cannibalism can become self-reinforcing through a feedback loop involving growth advantage, size heterogeneity, and repeated predation.

From the hatchery perspective, this result suggests that feeding management alone may not be sufficient after cannibalism has already started. Adequate feeding can reduce hunger-driven aggression, but it cannot fully remove the energetic benefit of consuming smaller conspecifics if vulnerable prey remains available. Therefore, feeding strategies must be integrated with size grading, shooter removal, and density adjustment.

### **Stocking Density, Feeding Frequency, and Hatchery Management Factors**

The synthesis identified stocking density and feeding frequency as major hatchery factors influencing cannibalism dynamics. High stocking density may increase the encounter rate between potential cannibals and smaller prey. It may also intensify feed competition, resulting in uneven feed intake and increased growth variation. In contrast, lower stocking density can reduce encounter frequency and provide smaller juveniles with more space to avoid aggressive interactions.

Feeding frequency also plays an important role in controlling size heterogeneity. Higher feeding frequency can improve feed access across individuals, reduce hunger motivation, and minimize the dominance of larger or more aggressive fish during feeding. In juvenile barramundi, increased feeding frequency has been shown to reduce or delay cannibalism by reducing food competition and promoting more homogeneous growth within the cohort.

The field-based hatchery perspective supports the operational relevance of these mechanisms. In practical hatchery systems, cannibalism risk is likely to increase when grading is delayed, feeding is not well synchronized with fish size and appetite, density remains high after growth divergence, and small fish remain together with larger individuals. Therefore, a

combination of frequent size monitoring, early grading, shooter removal, appropriate stocking density, and increased feeding frequency is required to reduce cannibalism risk.

Table 6. Synthesized mechanisms and practical hatchery implications

Mechanism	Biological Interpretation	Practical Hatchery Implication
Gape limitation	Predation becomes possible when prey body depth fits within cannibal mouth capacity	Use size grading before vulnerable size gaps develop
Size threshold	Small fish below half the size of larger fish are at high risk of initiating cannibalism	Maintain cohort size variation below the critical threshold
Prey vulnerability	Smaller prey are easier to capture and require shorter handling time	Remove or separate the smallest individuals early
Growth advantage	Cannibals may grow faster after consuming conspecific prey	Remove shooter fish before size dominance increases
Feeding frequency	Frequent feeding reduces hunger and competition	Distribute feed several times per day during nursery culture
Stocking density	High density increases encounter rate and competition	Adjust density according to size class and tank capacity
Field hatchery practice	Cannibalism risk is linked to grading delay and asynchronous growth	Apply integrated monitoring and management protocols

## DISCUSSION

### Mechanistic Interpretation of Cannibalism in Juvenile Barramundi

The present synthesis demonstrates that cannibalism in juvenile barramundi is best understood as an interaction among morphological limitation, behavioural vulnerability, energetic profitability, and hatchery management conditions. This interpretation is consistent with the broader concept of intracohort cannibalism in cultured fish, where cannibalism is not caused by a single factor but emerges from the interaction between size heterogeneity, predator–prey encounter, gape limitation, food competition, and environmental conditions (Baras & Jobling, 2002; Hecht & Pienaar, 1993; Kestemont *et al.*, 2003). In barramundi hatchery systems, these mechanisms are particularly relevant because the species is carnivorous, grows rapidly during the juvenile phase, and can develop substantial size variation when feeding access and grading are not properly managed (Lesmana, Effendi, Suharman, Putra, *et al.*, 2025; Ribeiro & Qin, 2013).

Morphological limitation is the first biological filter determining whether cannibalism can occur. Complete cannibalism requires that the prey be captured, oriented, and swallowed whole; therefore, the ratio between cannibal mouth dimensions and prey body depth is central to predation success. Ribeiro & Qin (2013) showed that barramundi cannibalism is strongly size-dependent and that the onset of cannibalism may occur when smaller individuals are less than 50% of the body length of larger conspecifics. However, experienced cannibals may ingest much larger prey than expected from average morphological models, suggesting that cannibalistic history and mouth extension capacity may increase predatory ability. This finding supports the need for preventive grading before cannibals emerge, because once cannibalistic individuals develop, their predatory capacity may become more difficult to manage. In addition, failed ingestion or cannibalization-associated suffocation may occur when prey size approaches the upper ingestion limit, indicating that cannibalism can cause mortality not only

through successful predation but also through unsuccessful handling events (Hseu *et al.*, 2007; Ribeiro & Qin, 2013).

The behavioural component explains why the most vulnerable prey are not necessarily those closest to the maximum ingestible size. Although large prey may offer greater biomass, they also require greater handling effort and have higher escape ability. Ribeiro & Qin (2015) demonstrated that juvenile barramundi cannibals selected smaller prey despite being capable of ingesting larger prey, and that this pattern was associated with capture success and handling time. This supports the idea that prey selection in piscivorous fish may be driven not only by active preference but also by passive vulnerability, where smaller or weaker individuals are captured more frequently because they are less able to escape. Similar interpretations have been proposed in broader fish predation studies, where prey mobility and escape capacity often modify the predictions of optimal foraging theory (Sih & Christensen, 2001).

The energetic component provides a deeper explanation for the persistence of cannibalism after it begins. Cannibalistic individuals may gain energetic and growth advantages by consuming conspecific prey, particularly when prey are easy to capture and digest. Ribeiro & Qin (2016) reported that juvenile barramundi fed conspecific prey had better growth performance and feed conversion efficiency than siblings fed formulated diet alone. This supports the concept that cannibalism can intensify growth depensation: once larger individuals begin consuming smaller siblings, they may grow faster, thereby widening size heterogeneity and sustaining further cannibalism. This pattern is consistent with the general dynamics of intracohort cannibalism in cultured fish, where the interaction between growth advantage and size-dependent predation can lead to persistent mortality during larval and juvenile rearing (Baras & Jobling, 2002; Kestemont *et al.*, 2003).

Feeding frequency and stocking density are important management levers because they influence the probability that morphological and behavioural vulnerability will be translated into actual cannibalism. Ribeiro *et al.* (2015) found that higher feeding frequency and lower stocking density reduced size dispersion and delayed or suppressed cannibalism in juvenile barramundi. These findings indicate that cannibalism is not only a biological consequence of predator–prey size difference, but also a management-sensitive process. When feed is offered infrequently, dominant individuals may monopolize feed, grow faster, and create a larger size gap. When density is high, encounters between large and small individuals become more frequent, increasing opportunities for cannibalistic attacks. Similar mechanisms have been reported in other cultured predatory fish, where stocking density, feeding opportunity, and growth heterogeneity strongly affect survival and cannibalism (Duk *et al.*, 2017; Hecht & Pienaar, 1993).

The field-based hatchery perspective from Indonesia, particularly observations during barramundi nursery activities at BPBL Batam, supports the operational relevance of these mechanisms under tropical hatchery conditions. Local evidence from barramundi nursery activities in Batam also indicates that stable water-quality management and regular feeding under a recirculating aquaculture system can support high juvenile survival, reinforcing the importance of integrating environmental control with nursery management practices (Ramadhani & Lesmana, 2025). Lesmana *et al.* (2025a) reported that cannibalism and cohort mismanagement remain important constraints in barramundi hatchery production, particularly when grading is not sufficiently synchronized with asynchronous growth. Although the present article does not claim new quantitative experimental findings from field observation, the hatchery context supports the practical relevance of integrating size monitoring, grading, feeding synchronization, and density regulation. This integration is necessary because hatchery constraints, such as labour availability, grading frequency, feed distribution, and tank capacity, may determine whether mechanistic knowledge can be effectively translated into routine management.

The distinction between literature-derived evidence and field-based interpretation is essential for maintaining the scientific integrity of this article. The field observation was used to contextualize published mechanisms for Indonesian hatchery practice, not to generate new statistical relationships among predator size, prey size, capture success, handling time, or energy profitability. This positioning allows the manuscript to contribute an applied synthesis without overstating the scope of the field component.

### **Implications for Cannibalism Control in Hatchery Practice**

The most important implication of this synthesis is that cannibalism control in juvenile barramundi should begin before cannibalism becomes evident through mortality, injury, or missing smaller fish. The threshold of approximately 50% prey-to-predator body length indicates that grading should be preventive, not reactive. If grading is delayed until missing fish, wounds, or extreme size variation are already obvious, some individuals may have already developed cannibalistic behaviour and growth advantage. Therefore, hatchery protocols should use early size monitoring and scheduled grading to prevent small juveniles from becoming vulnerable prey.

Shooter removal is another critical intervention. Shooter fish are fast-growing individuals that can become dominant predators within the cohort. Because cannibalistic feeding may further accelerate their growth, these fish should be separated early. This intervention is particularly important when population size distribution becomes skewed, as a small number of large individuals can disproportionately increase predation risk for smaller siblings. This interpretation is consistent with the concept of growth depensation, where small initial differences in growth can be amplified by competitive feeding and cannibalism (Baras & Jobling, 2002; Kestemont *et al.*, 2003).

Feeding frequency should also be managed as part of cannibalism prevention. Increasing feeding frequency may reduce competition by allowing more individuals to access feed throughout the day. This is particularly important during the nursery phase, when feeding behaviour, appetite, and growth rate can vary widely among individuals. However, feeding frequency should not be viewed as a standalone solution. Even under adequate feeding, cannibalism may persist if size heterogeneity is already high and vulnerable prey remain available, as size- and feed-dependent cannibalism has been reported in other carnivorous fish species (J. Qin & Fast, 1996; Ribeiro & Qin, 2015). Therefore, frequent feeding should be combined with size grading and density control (Ribeiro *et al.*, 2015; Ribeiro & Qin, 2016). Although conducted during the grow-out phase, field evidence from Indonesian barramundi culture also emphasizes that adaptive feeding schedules and consistent environmental monitoring are important operational factors supporting growth performance and survival (Bella & Lesmana, 2025).

Stocking density management is equally important because density influences both encounter rate and feeding competition. High density may increase the probability of contact between large and small juveniles, while also making it more difficult for smaller fish to avoid aggressive interactions. In practical hatchery systems, density should be adjusted after grading so that each size class is maintained within an appropriate carrying capacity. This approach may reduce competition, improve feed distribution, and lower the frequency of predator-prey encounters among size-disparate individuals (Duk *et al.*, 2017; Ribeiro *et al.*, 2015).

Environmental enrichment and light management may also support cannibalism reduction, although they should be treated as complementary interventions. Qin *et al.* (2004) reported that refuges and low light could reduce cannibalism in juvenile barramundi, indicating that structural and environmental manipulation can influence predator-prey encounters. However, these approaches may be less effective if size heterogeneity is already extreme.

Therefore, environmental manipulation should be integrated with grading, feeding, and density management rather than used as a substitute for size control.

Overall, this synthesis supports an integrated hatchery management model for juvenile barramundi. The model begins with early detection of size heterogeneity, followed by preventive grading, shooter removal, frequent feeding, density adjustment, and continuous monitoring of mortality or injuries. Such a model is appropriate for Indonesian hatchery practice because it translates mechanistic evidence into operational actions. It also provides a scientifically grounded framework for improving juvenile survival without presenting incomplete field observations as experimental data.

Table 7. Proposed Integrated Management Model for Reducing Cannibalism in Juvenile Barramundi Hatcheries

Management Stage	Main Risk Indicator	Recommended Action	Expected Outcome
Early nursery	Initial size variation begins to appear	Monitor size distribution regularly	Early identification of vulnerable fish
Pre-cannibalism stage	Small fish approach less than half the size of larger fish	Conduct preventive grading	Reduced availability of vulnerable prey
Shooter emergence	A few individuals grow faster than the cohort	Remove and separate shooter fish	Reduced development of dominant cannibals
Feeding period	Uneven feeding response and competition	Increase feeding frequency and improve feed distribution	More uniform feed access and reduced hunger motivation
Post-grading stage	Density remains high within size classes	Adjust stocking density according to fish size	Reduced encounter rate and competition
Continuous monitoring	Injuries, missing fish, abnormal mortality	Reassess grading interval, feeding, and density	Rapid intervention before cannibalism escalates

### Limitations and Future Research Direction

The main limitation of this article is that the field-based component did not provide a complete experimental dataset. Therefore, the synthesis cannot validate new numerical thresholds under Indonesian hatchery conditions. The threshold values and mechanistic interpretations presented in this article are derived primarily from published experimental studies, especially those conducted on barramundi by Ribeiro and colleagues. While these findings are biologically relevant, local validation is still required because hatchery performance may be influenced by strain, rearing system, water quality, feed type, salinity, handling procedure, and operational capacity.

Future research in Indonesian hatcheries should therefore conduct replicated experiments that directly measure predator–prey size ratios, mouth width, gape height, prey body depth, attack frequency, capture success, handling time, growth rate, survival, feeding frequency, and stocking density. Such studies would allow the development of locally validated grading thresholds and management schedules. In addition, future work should consider video-based behavioural tracking and routine size distribution monitoring to detect the early emergence of cannibalism risk. These approaches would strengthen hatchery decision-making and provide

more robust evidence for improving barramundi seed production in tropical aquaculture systems.

### CONCLUSION

This literature synthesis with field-based hatchery perspective concludes that cannibalism in juvenile barramundi (*Lates calcarifer*) is governed by the interaction of morphological constraints, prey-size-dependent behavioural vulnerability, energetic profitability, and nursery management conditions. Size heterogeneity creates vulnerable prey groups, while gape-related morphological capacity determines whether smaller juveniles can be captured and ingested by larger conspecifics. Behavioural and energetic evidence indicates that smaller prey are more profitable because they are easier to capture and require shorter handling time, allowing cannibalistic individuals to gain growth advantages that intensify cohort size disparity. Therefore, cannibalism control in hatchery systems should integrate early size monitoring, preventive grading, shooter removal, appropriate stocking density, and increased feeding frequency rather than relying on feeding alone. Although this synthesis requires further validation under Indonesian hatchery conditions, it provides a practical framework for improving juvenile survival and nursery efficiency in tropical barramundi production systems.

### ACKNOWLEDGEMENT

The author would like to express his gratitude to all parties involved in carrying out this research so that the implementation of the research and completion of this article can run smoothly.

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