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Reproductive characteristics of Keudawah (*Rasbora arundinata* (Lumbantobing, 2014)), a native species of Krueng Lanca River, Nagan Raya District, Aceh, Indonesia

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Abstract. *Abdan M, Sulistiono, Kamal MM, Mashar A, Butet NA. 2025. Reproductive characteristics of Keudawah (*Rasbora arundinata, *Lumbantobing 2014), a native species of Krueng Lanca River, Nagan Raya District, Aceh, Indonesia. Biodiversitas 26: 1461-1473.* Keudawah (*Rasbora arundinata* (Lumbantobing, 2014)) is a freshwater fish native to Indonesia, particularly found in the waters of Nagan Raya. Understanding its reproductive biology is crucial for developing sustainable management and conservation strategies. Given this importance, this study aimed to assess the spawning season, sex ratio, Gonadal Maturity Stage (GMS), size at first gonadal maturity (LM_{50}), and fecundity of *R. arundinata* in the Krueng Lanca River, Aceh Province, Indonesia. Sampling was conducted from January to December 2023 at six stations selected based on habitat characteristics and local fishermen's recommendations. Fish were caught using gill nets with mesh sizes of 0.5 and 1.0 inches, as well as throw nets with a 6-meter diameter and a 0.5-inch mesh size during monthly sampling. The collected specimens were measured for total length and weighed, after which their gonads were analyzed to determine maturity stage, Gonadosomatic Index (GSI), and fecundity. The size at first gonadal maturity (LM50) was estimated using the Spearman-Karber method. A total of 2,225 specimens were collected, comprising 1,162 males and 1,063 females, with size distributions ranging from 34 to 121 mm (males) and 46 to 135 mm (females). The length-weight relationship is expressed as $W = 8.17E\text{-}05L^{2.55}$ ($R^2 = 0.88$), while in females, it follows the equation $W = 8.17E\text{-}05L^{2.11}$ ($R^2 = 0.89$). The results indicated that the sex ratio was slightly male-biased, averaging 1.09:1 (M:F). The LM_{50} was estimated at 86.98 mm for males, with a Gonadosomatic Index (GSI) of 6.96%-9.10%, and 94.77 mm for females, with a GSI of 10.30%-12.61%. Fecundity of *R. arundinata* ranged from 1,156 to 2,090 oocytes. The findings suggest that *R. arundinata* exhibits year-round reproductive activity, with peak spawning occurring in April and September. These insights are valuable for conservation planning and provide a foundation for future aquaculture development.

Keywords: Conservation management, fecundity, *Keudawah*, *Rasbora arundinata*, reproductive biology, spawning season

INTRODUCTION

Rasbora, a genus in the family Danionidae, is widely distributed across Asia, including Southern China, Southeast Asia, and Indonesia Kottelat (2013). It plays a vital role in freshwater ecosystems by regulating plankton and small invertebrate populations, contributing to the aquatic nutrient cycle (Kakade 2017). Of the 83 known Rasbora species, 56 have been identified in Indonesia (Eschmeyer 2025), yet many species, particularly those with restricted distributions, remain poorly documented. These fish inhabit diverse freshwater habitats, including rivers, lakes, and wetlands, many of which face increasing threats from pollution, habitat fragmentation, and land-use changes (Rahmi et al. 2021; Haryani 2022). Conservation efforts are essential to safeguarding these ecosystems, which support freshwater biodiversity and ecological stability (Marinović and Đuretanović 2024). Further research and conservation strategies are needed to ensure the survival of Rasbora species, particularly those at risk due to anthropogenic pressures (Suryani et al. 2019).

Several *Rasbora* species have been recorded in Aceh Province, including *Rasbora tawarensis* in Lake Laut Tawar (Muchlisin 2013), *Rasbora klutuensis* in the Kluet River, *Rasbora nodulosa* in Tripa waters, and *Rasbora truncata* in the Alas River (Lumbantobing 2010). *Rasbora arundinata* (Lumbantobing 2014), locally known as Keudawah, was identified in 2014 and is exclusively distributed in southwestern Aceh, making it highly susceptible to localized threats and necessitating targeted conservation efforts. Given its restricted range, reliance on specific freshwater habitats, and sensitivity to environmental changes, *R. arundinata* has the potential to serve as a bioindicator for assessing aquatic ecosystem health (Muchlisin et al. 2018; Santos and Ferreira 2020). Reports confirm its presence in the Tripa Jaya, Kluet, and Alas rivers, which flow into the Indian Ocean (Lumbantobing 2014). In Nagan Raya, *R. arundinata* holds ecological and economic significance, serving as a food source and a commercially valuable species supporting local fisheries. Market prices range from IDR 50,000 to 120,000 per kilogram, providing a stable income for fishers and traders. However, increasing exploitation, habitat degradation, and land-use changes have placed additional pressures on its population. Deforestation and land conversion have also affected other freshwater species, such as Naleh (*Barbonymus* spp.), which share similar ecological niches with *R. arundinata* (Abdan and Sulistiono 2023). These challenges highlight the need for sustainable management strategies to balance conservation efforts with economic interests.

Previous studies indicate that habitat destruction, primarily due to deforestation, disrupts freshwater ecosystems, affecting fish metabolism, reproduction, growth, and trophic interactions (Cheng et al. 2015; Fugère et al. 2018; Cantera et al. 2023). Small-scale mining also threatens these habitats by degrading water quality and endangering vulnerable species like *R. arundinata* (Damseth et al. 2024). Currently classified as Data Deficient (DD) on the IUCN Red List, *R. arundinata* lacks sufficient data for proper conservation assessment (Lumbantobing 2019). Deforestation and land-use changes have been shown to disrupt natural fish reproductive cycles (Chu et al. 2015; Da Silva Reis et al. 2022). Research on fish reproduction is essential for understanding reproductive capacity, which supports evidence-based management strategies for population sustainability (Baumgartner et al. 2016; AbouelFadl et al. 2024). Additionally, external factors such as temperature, water flow, and seasonal variation significantly influence reproductive success, impacting population dynamics and conservation priorities (Kumar et al. 2022; Jewell et al. 2024).

To date, research on *R. arundinata* has primarily focused on its morphological validation (Lumbantobing 2014) and fundamental ecological parameters, such as length-weight relationships (Abdan et al. 2024). However, critical aspects of reproductive biology remain unexplored, creating a significant knowledge gap that hinders effective population management and conservation planning. Understanding reproductive traits, including gonadal maturation, fecundity, and spawning periodicity, is essential for elucidating the species' life cycle and developing targeted, evidence-based management strategies for conservation biologists and policymakers. Given the ecological and socio-economic importance of *R. arundinata* as a protein source and a key component of local fisheries, further research is necessary, particularly on population dynamics and reproductive biology. Previous studies Muchlisin (2014) and Sunarni and Maturbongs (2018) have emphasized the role of reproductive data in assessing reproductive capacity and population sustainability. Therefore, this study aimed to analyze the reproductive characteristics of *R. arundinata* in the waters of Krueng Lanca, Nagan Raya District, Aceh Province, Indonesia, to contribute to broader conservation initiatives for freshwater biodiversity in the region.

MATERIALS AND METHODS

Study area

The research was conducted in Krueng Lanca, Nagan Raya District, Aceh Province, Indonesia (Figure 1), over a 12-month period from January to December 2023. Six research stations were selected to represent the diverse habitat characteristics of the *R. arundinata* area. These stations were chosen based on their ecological features, including variations in water depth, flow rate, and substrate composition, with additional input from the local fishermen familiar with the area.

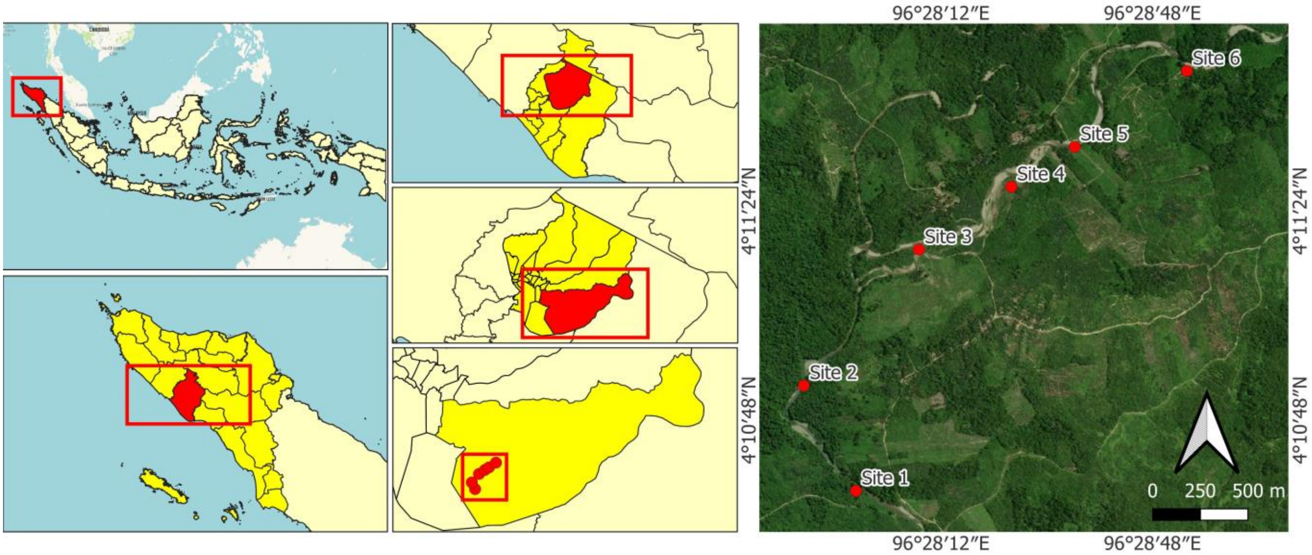


Figure 1. The sampling sites of *Rasbora arundinata* were located in Krueng Lanca, Nagan Raya District, Aceh Province, Indonesia. The geographical coordinates for each site were as follows: Site 1 (96°27'56.985"E, 4°10'35.988"N), Site 2 (96°27'48.109"E, 4°10'53.74"N), Site 3 (96°28'8.24"E, 4°11'17.33"N) Site 4 (96°28'23.97"E, 4°11'28.14"N), Site 5 (96°28'34.76"E, 4°11'35.03"N), and Site 6 (96°28'53.88"E, 4°11'48.10"N)

Station 1 featured fast-flowing water with a rocky substrate and a depth of <50 cm. Station 2 had moderate flow with a sandy substrate and a depth of <50-100 cm. Stations 3 and 4, located near community gold mining and palm oil plantations, had moderate flow with sandy and rocky substrates and a depth of <50 cm. Station 5 had a mix of sand, and gravel, with deeper pools (80-100 cm) and shaded riverbanks. Station 6 featured a sandy-muddy substrate, abundant leaf litter, and deep pools (>100 cm), with dense vegetation along the riverbanks. Each station was systematically surveyed to ensure comprehensive coverage of the habitat's spatial and temporal dynamics. The collected fish specimens were then analyzed at Laboratory Mina Mandiri, Nagan Raya District for general biometric and reproductive assessments, while histological analyses of gonadal tissue were conducted at the Aquaculture Laboratory, IPB University to examine the microscopic structure of reproductive organs. The geographical locations of the research stations are presented in Figure 1.

Procedures

Fish sampling and preservation

R. arundinata were collected monthly from January to December 2023, during each sampling visit, using gill nets with mesh sizes of 0.5, and 1.0 inches, as well as throw nets with a 6 m diameter and 0.5 inch mesh size. Gill nets were set for one hour, covering the entire water area. A variety of net sizes were used to ensure the capture of individuals across all size classes. After the nets were set, fish were driven or guided toward the nets to increase capture efficiency. The average monthly catch was 98 males and 88 females. Following collection, the samples were preserved in a 10% formalin solution to maintain tissue integrity for subsequent analyses.

Morphological measurements included Total Length (TL), body weight, and gonad weight, which were recorded using a digital caliper (±0.01 mm accuracy) and an analytical balance (±0.001 g accuracy). Sex identification was performed through dissection to determine the Gonadal Maturity Stages (GMS). Gonadal maturity was assessed using both morphological and histological approaches. Morphologically, the gonads were evaluated based on their shape, size, color, and degree of development, providing a macroscopic perspective on maturity.

Fecundity was estimated for individuals at gonadal maturity stages (TKG) III and IV by weighing the gonads and extrapolating the total number of mature oocytes. Egg diameter measurements were conducted at all gonadal maturity stages (TKG I-IV) to assess developmental progression. Measurements were performed using a stereo microscope at 4×10 magnification, with eggs placed on a glass slide for observation. A total of 50 oocytes from each gonad section (anterior, middle, and posterior) were measured at each stage using an ocular micrometer to determine the mean egg diameter.

Histological analysis involved preparing slides stained with hematoxylin and eosin to observe the phases of oocyte and spermatocyte development in greater detail. Gonads were sectioned transversely into anterior, middle, and posterior portions, with multiple thin sections (4-6 µm) taken from each region. These sections were mounted on glass slides, stained, and examined under a light microscope at 10× and 40× magnifications. For each individual, at least three sections per gonadal region were evaluated to ensure a comprehensive assessment of reproductive status.

Data analysis

Growth pattern and sex ratio

The fish growth pattern was calculated using the Linear Allometric Model based on Effendie (1979), with the formula:

$$W = aL^b$$

Where:
W : Fish weight
L : Fish length
a : Constant
b : Allometric coefficient describing body proportion

The sex ratio was analyzed to determine the proportion of males and females in the population. The ratio of males to females was calculated according to Effendi (2002) using the following formula:

$$P_j = \frac{A}{B} \times 100$$

Where:
P_j : Proportion of the species (male/female)
A : Number of individuals of a particular sex (male/female)
B : Total number of fish individuals (male + female)

Gonadal Maturity Stage (GMS)

The gonadal maturity stage in *R. arundinata* was identified using both morphological and histological approaches. Morphologically, the maturity stage was determined by assessing the shape, color, size, and weight of the gonads, as well as the developmental stage of the gonadal contents. Key parameters such as gonad size and morphological characteristics were evaluated following the guidelines provided by Mote et al. (2014) (Table 1). Histological analysis provided further insight into gonadal development of *R. arundinata.* The process of oogenesis was examined following the methodology outlined by Efizon et al. (2021), and spermatogenesis was assessed based on the approach described by Yang et al. (2024). These combined methods ensured a comprehensive evaluation of the reproductive status of *R. arundinata.*

Size at first gonadal maturity (Lm_{50})

The Spearman-Karber Method was used to estimate the average size of fish reaching gonadal Maturity (M), as outlined by Williams et al. (2008). The formula is as follows:

$$\mathrm{Log\ M} = \left[xk + \left(\frac{x}{2}\right)\right] - \left(x \sum p_i\right)$$

Table 1. The stages of fish gonadal maturity according to Mote et al. (2014)

GMS	Male	Female
I	The testes are threadlike, short, clear, and transparent, not extending to the front end of the abdominal cavity	The ovary is threadlike, extends to the abdomen, and has a clear, smooth surface
II	The testes do not reach the front end of the abdominal cavity, are larger, milky white in color, and have a more defined shape compared to grade I	The ovary measures up to the front end of the abdominal cavity, fills less than one-tenth of it, is clear white, and contains small oocyte granules
III	The testes do not reach the front end of the abdominal cavity but fill half of it, with a milky white appearance	The ovary measures up to the anterior end of the abdominal cavity, fills less than one-tenth of the cavity, is clear white, and contains small oocyte granules—the size of the ovary to the front end. The ovary fills half the abdominal cavity. The eggs begin to be visible, and the ovary is yellowish
IV	The testes do not reach the anterior end of the abdominal cavity. They become more extensive and milkier white, filling most of the abdominal cavity	The ovary measures up to the front end of the abdominal cavity. The color becomes yellower and darker with a larger filling of the abdominal cavity. The eggs are visible and separated from one another
V	The size of the testicle does not reach the anterior end of the abdominal cavity, and the testicle deflates at the posterior end	The size of the gonads extends to the front end of the abdominal cavity, with greenish-yellow residual eggs throughout the ovary. The ovary is deflated at the posterior end as the eggs have been expelled during spawning

A 95% confidence interval was applied, and the final value of M was obtain by taking the antilog of M. M = antilog M:

$$\text{antilog m (M)} = m \pm 1{,}96\sqrt{x^2 \sum \frac{pixqi}{ni\text{-}1}}$$

In this equation, xk represents the fish size at the last interval with a maturation probability of less than 1, x/2 serves as a correction for size distribution, and $x \sum p_i$ indicates the total probability of mature fish across all size intervals. The final value of M is obtained by taking the antilogarithm of log M, converting it back to the original scale. The 95% confidence interval is determined using m as the mean of log M, a 1.96 factor for normal distribution, and x^2 along with $\sum \frac{pixqi}{ni\text{-}1}$ to calculate the standard deviation based on the probability of maturation and non-maturation in each size class.

Gonadosomatic Index (GSI)

The Gonadosomatic Index (GSI) was calculated following Effendi (2002) using the formula:

$$GSI = \frac{gw}{bw} \times 100$$

Where:
GSI : Gonadosomatic Index
gw : Gonad weight (g)
bw : Total fish body weight (g)

Fecundity

Fish egg fecundity was calculated based on Effendi (2002) using the formula:

$$F = \frac{G.V.X}{Q}$$

Where:
F : Fecundity (number of eggs)
G : Total gonad weight (g)
V : Dilution volume (mL)
X : Number of eggs in 1 mL
Q : Sample egg weight (g)

Regression exponential using the least squares method was applied to assess the relationship between egg Fecundity (F) and three variables: body Weight (W), body Length (L), and gonad Weight (G). The regression equations were formulated as follows:

$$F = aX^b$$

Where:
F : Fecundity (oocyte count)
X : Independent variable (W, L, or G)
a : Intercept
b : Regression coefficient

Model fit was evaluated using the coefficient of determination Microsoft excel.

Egg diameter

Egg diameter was calculated by referring to Omar (2010) using the formula:

$$D = \sqrt{Dh.Dv}$$

Where:
D : Actual egg diameter
D_h : Horizontal egg diameter
D_v : Vertical egg diameter

RESULTS AND DISCUSSION

Fish collection, growth pettern and sex rasio

A total of 2,225 *R. arundinata* individuals, comprising 1,162 males and 1,063 females, were collected from Krueng Lanca waters. The total length of males ranged from 34 to 121 mm, whereas that of females ranged from 46 to 135 mm (Figure 2). The length-weight relationship of *R. arundinata* for both males and females exhibits a negative allometric growth pattern, as indicated by the growth exponent (b) value of less than 3. In male fish, the length-weight relationship can be expressed by the equation $W = 8.17E\text{-}05L^{2.55}$ ($R^2 = 0.88$), while in females, it follows the equation $W = 8.17E\text{-}05L^{2.11}$ ($R^2 = 0.89$) (Figure 3).

The annual sex ratio of *R. arundinata* was 1:0.91, the spatial and temporal analysis of the sex ratio revealed significant variations across stations and periods. Spatially, the lowest ratio was observed at ST3, while the highest was recorded at ST5. Ratios below 1 at ST1-ST3 indicated female dominance, whereas ratios above 1 at ST4-ST5 indicated male dominance (Figure 4.A). Temporally, males consistently outnumbered females, with sex ratios ranging from 0.96 to 1.18 and an overall male-to-female ratio of 1.09:1 (Figure 4.B). These findings suggest that sex ratio dynamics are influenced by both spatial and temporal factors, driven by ecological and behavioral mechanisms.

The monthly fluctuations in the male-to-female ratio were highest in September and lowest in June, indicating temporal variability in population dynamics. Previous studies have reported varying sex ratios in closely related species and in other cyprinids. For example, one study Rosadi et al. (2016) reported a sex ratio of 3:1 in *R. argyrotaenia* from the South Kalimantan River, whereas another study Iriansyah et al. (2016) reported a ratio of 2:1 in *Rasbora lateristriata* from the Borito River, South Kalimantan. The sex ratio observed in the Krueng Lanca waters was comparatively lower than that reported in these studies, suggesting environmental and ecological differences between the regions. Similarly, (Magalhães et al. 2022) documented a sex ratio of 1.1:1 in zebrafish (*Danionidae*) in Brazil, which closely aligns with the findings of the present study. In contrast, a previous study Rambe et al. (2023) reported a sex ratio of 1:2 for *Rasbora spilotaenia* in North Sumatra, emphasizing that interspecific and regional variations are substantial.

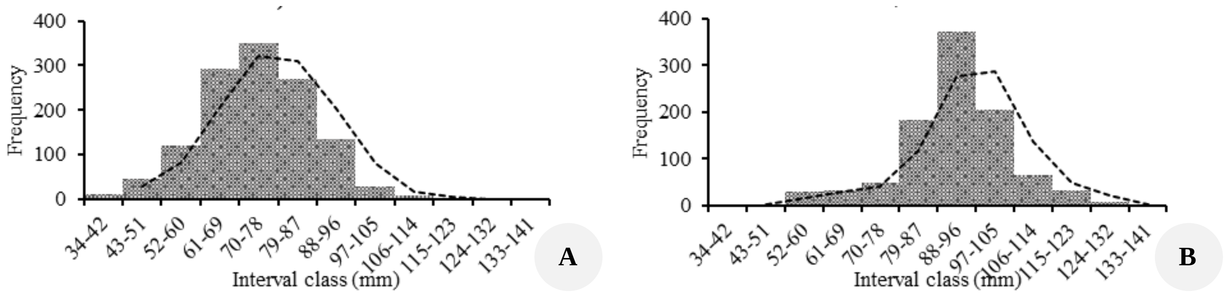


Figure 2. Length distribution of *Rasbora arundinata*: A. Males; B. Females caught in Krueng Lanca, Nagan Raya District, Aceh, Indonesia

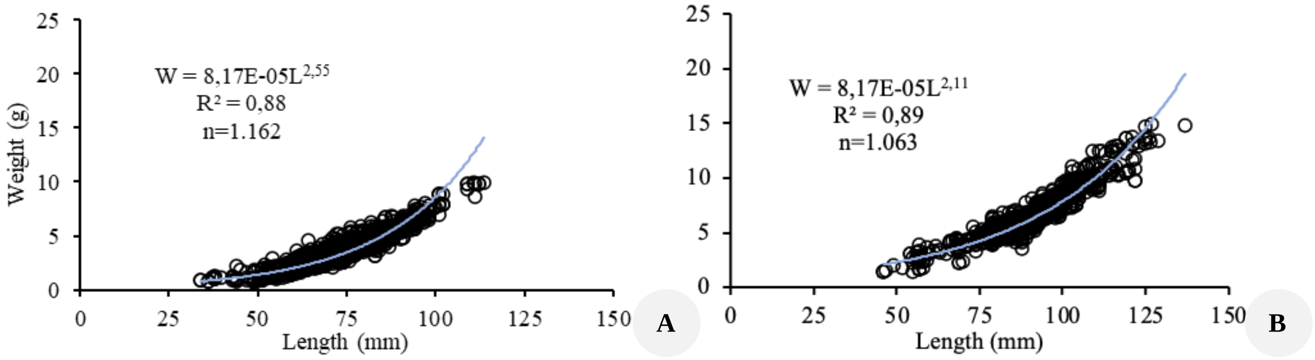


Figure 3. Total body length-weight relationship of *Rasbora arundinata*: A. Males; B. Females caught in Krueng Lanca, Nagan Raya District, Aceh, Indonesia

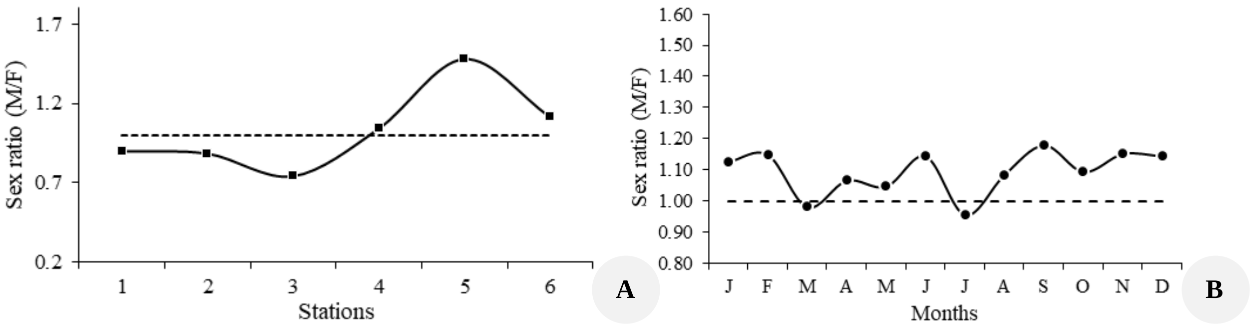


Figure 4. The sex ratio (M/F) of *Rasbora arundinata*: A. Spatial; B. Temporal distribution in Krueng Lanca, Nagan Raya District, Aceh, Indonesia. Note: J: January; F: February; M: March; A: April; M: May; J: June; J: July; A: August; S: September; O: October; N: November; D: December

The observed differences in the sex ratios may have resulted from various biological and environmental factors. Some cyprinid fish exhibit competitive behavior among males during spawning, leading to skewed ratios. According to Chadijah et al. (2022), intense male competition during spawning can result in higher survival and reproductive success among dominant males, thereby increasing their proportion in the population. Furthermore, the smaller body size of males compared to females, as noted in many cyprinids, may increase male vulnerability to predation and fishing, thus affecting the sex ratio (Jayadi et al. 2016). Crowley and Labonne (2021) proposed that environmental conditions and population imbalances could drive variations in sex ratios among freshwater fishes.

Conservation biology highlights the significance of a balanced sex ratio for maintaining sustainable fish populations, ideally 1:1 (Agustini et al. 2023; Li 2024). However, sex ratios are influenced by multiple environmental and genetic factors, such as water temperature and pH (Verma et al. 2024), level of fish adaptation to their habitat (Sulistiono 2012), and gonadal maturity (Abdalla et al. 2020). Additionally, external pressures, including predation, natural mortality, and human activities such as overfishing, affect these ratios (Koyakomanda et al. 2019; Maina et al. 2019; Nisa et al. 2023).

Environmental degradation in the Krueng Lanca area may affect the sex ratio and population dynamics of *R. arundinata*. Harmful fishing practices, such as the use of poison (tuba) and electrofishing, along with land conversion and mining activities that cause river siltation, have been observed (Batubara et al. 2019; Abdan et al. 2024). These practices degrade habitats and disrupt the reproductive cycle by reducing the availability of suitable spawning grounds, increasing egg and larval mortality, and causing physiological stress that affects gonadal development. Abdan and Sulistiono (2023) reported that environmental degradation in the surrounding area contributed to low sex ratios observed in cyprinid populations, including *Barbonymus* sp., in the Krueng Lanca waters, suggesting a potential impact on *R. arundinata* as well.

Gonadal Maturity Stages (GMS) and size of first mature gonads (Lm_{50})

The Gonadal Maturity Stage (GMS) of *R. arundinata* peaked during two distinct periods, March-April and August-September, with the highest reproductive activity occurring in March-April (Figure 5).

These findings indicated the presence of two spawning seasons within a year. The first size at gonadal maturity (Lm_{50}) was recorded at GMS stages 3 and 4, with males reaching maturity at a total length of 86.98 mm and females reaching 94.77 mm (Figure 6). This suggests that males attain gonadal maturity earlier than females, reflecting potential differences in reproductive strategies and energy allocation between sexes.

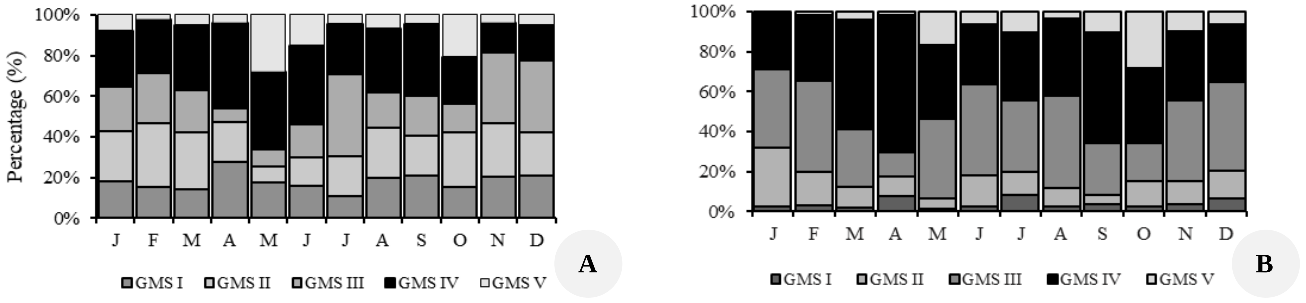


Figure 5. Gonadal Maturity Stage (GMS) of *Rasbora arundinata*: A. Male; B. Female, based on the observation time

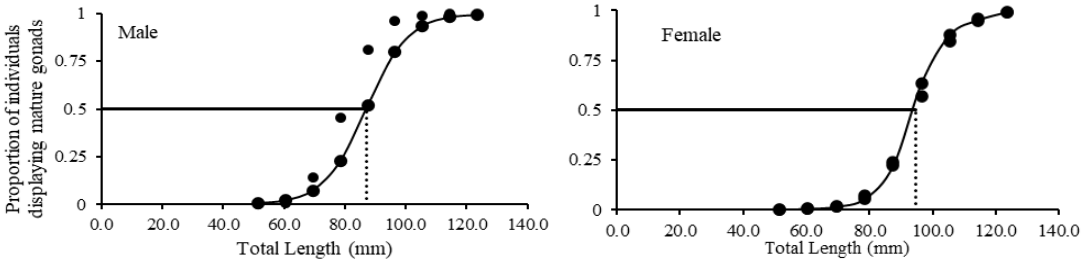


Figure 6. Size at first gonadal maturity (Lm_{50}) (95% confidence interval) of *Rasbora arundinata*. Males mature at a smaller size (86.98 mm) compared to females (94.77 mm), indicating sexual dimorphism in growth and maturation patternsof *R. arundinata* caught in Kreung Lanca River, Nagan Raya District

The spawning season of *R. arundinata* in Krueng Lanca was estimated to occur throughout the year, which is consistent with multiple spawning strategies. Monthly variations in the percentage of fish with mature gonads reinforced this finding, with the highest peaks in gonadal maturity occurring in April and September. Similar patterns have been reported for other species, such as *R. argyrotaenia*, in the rainforests of Brunei Darussalam, where year-round spawning was observed (Kahar et al. 2023). Another study Muchlisin et al. (2010) of *R. tawarensis* identified three annual spawning peaks, with the highest peak occurring in September. This consistent pattern of multiple spawning events underscores the adaptability of *R. arundinata* to environmental conditions that favor prolonged reproductive windows.

Comparisons with other related species further validated these findings. For instance, *R. lateristriata* primarily spawns from April to August (Djumanto and Setyawan 2009), whereas *R. argyrotaenia* spawns from September to December (Rosadi et al. 2014). Similarly, *R. philippina*, an endemic species, spawns in early and late April, and mid-March (Genovia et al. 2023). These studies suggest that *Rasbora* species exhibit diverse spawning behaviors, with variations driven by both environmental and intrinsic factors.

In *R. arundinata*, peak spawning activity is estimated to occur twice a year, coinciding with April and September. The earlier maturation of males compared to females, evident from the Lm_{50} values of 86.98 mm for males and 94.77 mm for females, reflected the trends observed in other fish species. For instance, in Lake Matano, South Sulawesi, *Telmatherina prognatha* (Kottelat, 1991), and *Telmatherina antoniae* (Kottelat, 1991), males mature earlier than females (Chadijah et al. 2022; Agustini et al. 2023). *Barbonymus* sp. in the waters of the Nagan Raya District (Efizon et al. 2021; Abdan and Sulistiono 2023) showed similar trends. This early maturity in males may be attributed to their reproductive roles, in which earlier maturity increases their chances of successfully competing for mates.

The timing of spawning in fish is affected by various environmental factors, including food availability, water temperature, and suitable spawning locations, as well as intrinsic factors, such as genetics (Haryono et al. 2014; Chattopadhyay and Chattoraj 2017). Additionally, abiotic factors, such as water discharge and rainfall, along with biotic factors, such as biomass, average weight, prior spawning experience, and habitat conditions, play significant roles in determining spawning timing (Sinnatamby et al. 2018; Manangkalangi et al. 2020; Endo et al. 2021; Davies et al. 2023). These factors collectively contribute to the reproductive success and adaptive strategies of fish populations in dynamic aquatic ecosystems.

Gonadal histology

Histological analysis (Table 2) highlights that the gonadal development of *R. arundinata* closely aligns with the typical gametogenesis process observed in teleost fish. In male gonads, the progression of spermatogenesis is distinctly visible, starting from Spermatogonia (Spg), moving through primary Spermatocytes (Sp), secondary Spermatocytes (Ss), Spermatids (Sd), and culminating in mature Spermatozoa (Sz) (Schulz et al. 2024; Yang et al. 2024). The cellular distribution follows an asynchronous development pattern, a hallmark of fish with repeated reproductive cycles (Domínguez et al. 2024). The absence of Spermatozoa in certain tubules (Sz(-)) suggests the presence of regeneration phases within the reproductive cycle, providing long-term flexibility and ensuring sustained reproduction (Jin et al. 2024). This asynchronous development is crucial for continuous sperm production throughout the spawning season, which may facilitate *R. arundinata* in adapting to varying environmental conditions, such as mate availability and variations in spawning conditions (Ilyasova et al. 2022).

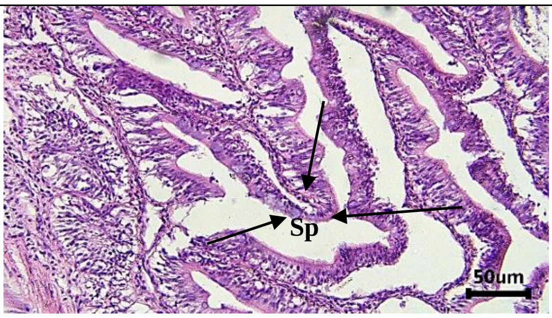
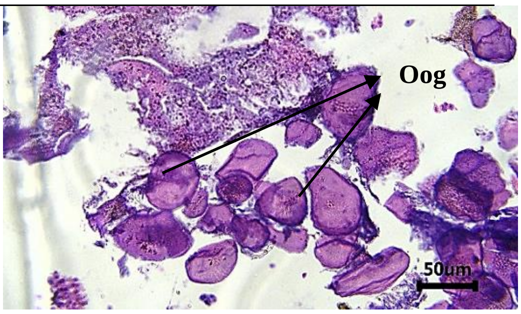
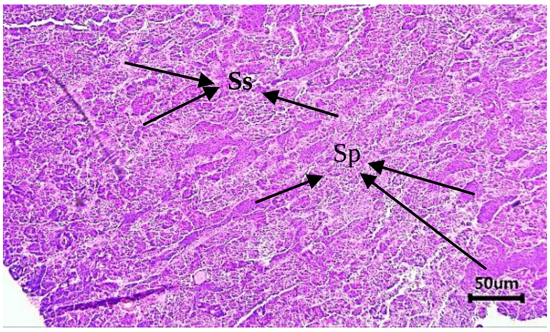
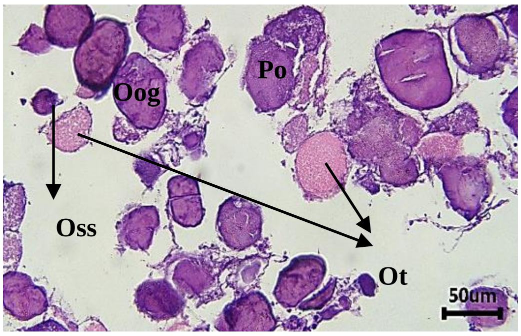
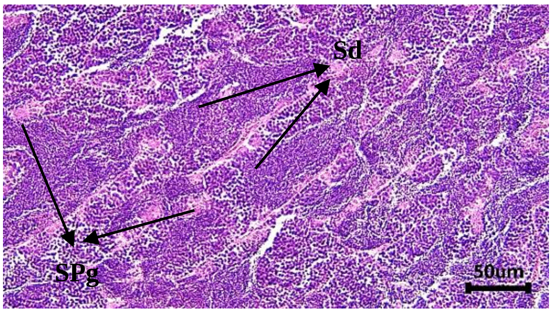
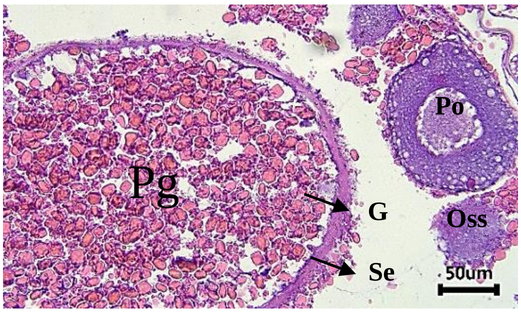
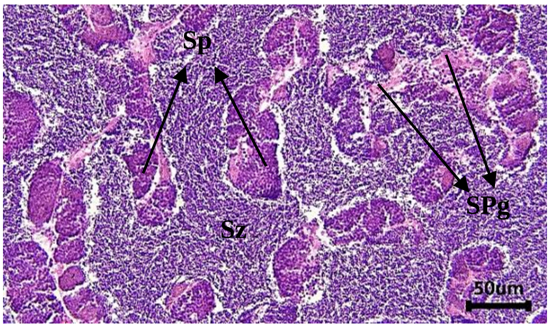
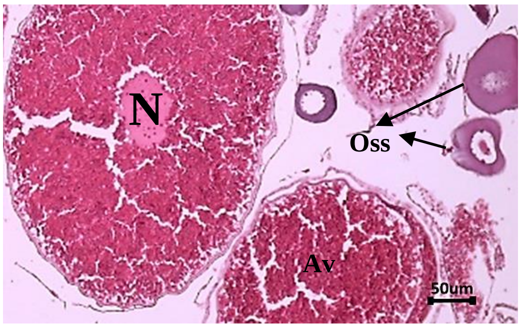
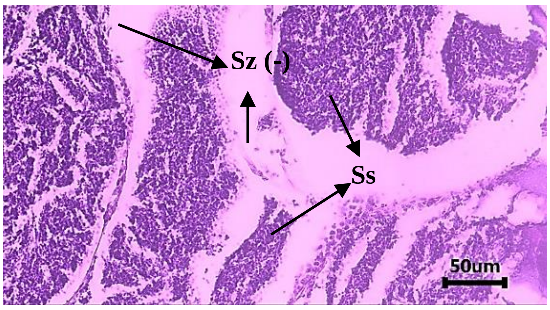
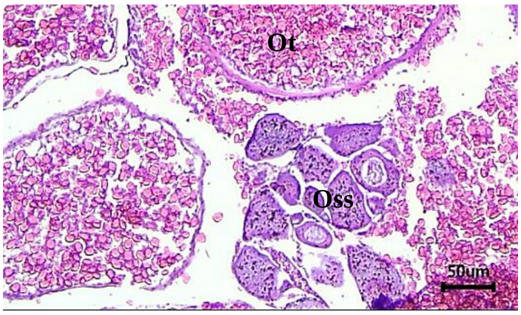
In female gonads, oogenesis unfolds in a structured sequence, beginning with Oogonia (Oog), transitioning to Primary oocytes (Po), Secondary oocytes (Oss), and ultimately developing into mature oocytes or Ootids (Ot). The presence of oocytes undergoing Advanced vitellogenesis (Av) indicates the active deposition of Protein granules (Pg), which act as vital energy reserves for embryonic development post-fertilization (Hara et al. 2016; Jiang et al. 2021). The Granulosa layer (G) and Surface epithelium (Se) play key roles by providing structural support and serving as sources of hormones that regulate oocyte growth and maturation (Eppig and Handel 2012). Distinct Nuclei (N) in mature oocytes demonstrate their readiness for fertilization and indicate the successful completion of the vitellogenesis process (Carnevali et al. 2019).

The gametogenesis pattern in *R. arundinata* reflects an efficient and adaptive reproductive strategy. In males, the ability to produce sperm continuously ensures reproductive success in habitats with high ecological variability, such as rivers and estuaries. These environments, often subject to fluctuations in factors like temperature, salinity, and mate availability, can influence spawning dynamics (Baldé et al. 2019; Elisio et al. 2024). Continuous sperm production reduces the risk of reproductive failure caused by mismatched spawning timing (Li et al. 2021).

In females, oocyte development represents a significant energy investment during vitellogenesis. This process, which involves the synthesis of yolk proteins in the liver and their subsequent storage in oocytes, is essential for the reproductive success of oviparous fish (Mahalingam and Santhanam 2023). The accumulation of protein granules supports embryonic development and equips the species to survive in variable environments. Research suggests that oocytes with optimal yolk reserves are more likely to develop into healthy larvae, ultimately securing long-term reproductive success (De Almeida et al. 2023).

Additionally, the granulosa layer and surface epithelium emphasize the complexity of female reproductive regulation in fish. Apart from offering mechanical protection to oocytes, the granulosa layer plays a critical role in hormone production, particularly estradiol, which facilitates both vitellogenesis and oocyte development. Effective hormonal regulation is a cornerstone of successful oogenesis and, by extension, overall reproductive success (Mokhtar 2024).

Table 2. Histology results of gonad development of *Rasbora arundinata* during observation (Arrows indicate the different gonadal cell types at various stages of development)

GMS	Males	Females
I		
II		
III		
IV		
V		

Notes: Description: In males: Sp: Primary spermatozoa; Ss: Secondary spermatozoa; Sd: Spermatide; Spg: Spermatogenia; and Sz(-): Spermatozoa excluded; While in females: Oog: Oogenia; Po: Primary oocyte; Oss: Secondary oocyte; Ot: Ootide; Pg: Protein granules; G: Granulosa layer; Se: Surface epithelium; Av: Advanced vitellogenic; N: Nucleus

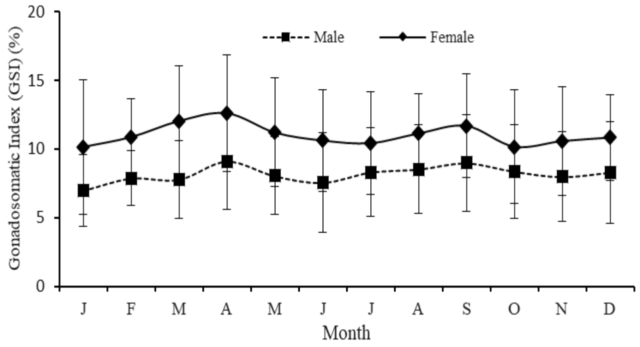


Figure 8. Gonadosomatic Index (GSI) of *Rasbora arundinata* caught in Kreung Lanca River, Nagan Raya District, Aceh, Indonesia

Gonadosomatic Index (GSI)

The Gonadosomatic Index (GSI) of *R. arundinata* displayed distinct seasonal patterns, with male GSI values ranging from 6.96% to 9.10% and female GSI values ranging from 10.30% to 12.61%. The highest GSI values for both sexes were recorded in April, indicating a peak in reproductive activity, whereas the lowest male GSI value (6.96%) was observed in June (Figure 8). In contrast, female GSI values gradually increased from January to April, reaching a peak of 12.61%, followed by a stable phase, and a secondary peak in September. These patterns suggest that April is a critical period for reproductive activity in both the sexes, with September serving as the secondary spawning period.

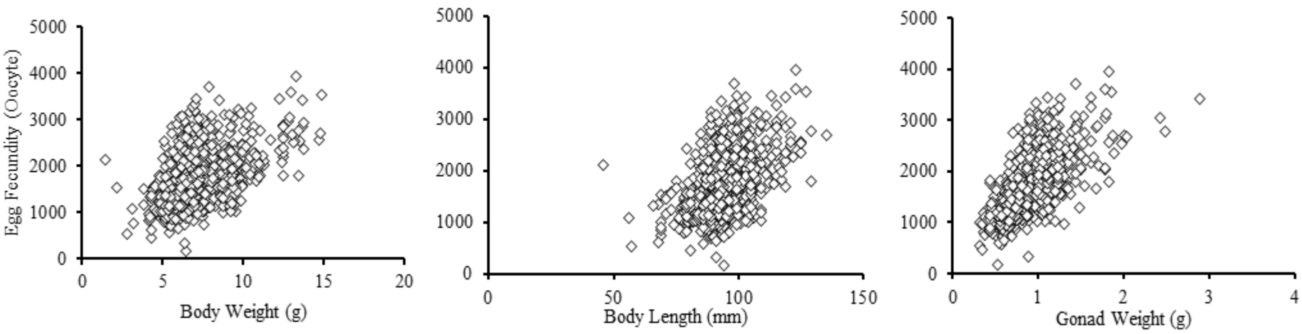
Males maintain gonadal readiness for multiple spawning events, whereas females require substantial energy reserves for oocyte development, resulting in higher GSI values. This observation aligns with the findings of Muchlisin et al. (2010) for *R. tawarensis*, where male GSI ranged from 4.94% to 8.56%, and female GSI ranged from 6.65% to 18.16% in Lake Laut Tawar, Aceh, Indonesia. The highest GSI values in both species were observed in March and September, indicating a similar seasonal pattern in *R. arundinata.*

The GSI patterns observed in *R. arundinata* differed from those reported by Kumar (2015) for *Rasbora daniconius* in the Shahdol District, MP, India, where the highest GSI values occurred in July and August. These differences highlight the influence of environmental and ecological conditions on species-specific reproductive cycles. Demin et al. (2020) emphasized that variations in GSI peaks can occur among closely related species owing to differences in species, location, and ecological factors. For instance, populations of *Cyprinus carpio* subsp. *communis* and *Carassius carassius* (Linnaeus, 1758) at various locations in Lake Dal, Kashmir exhibit different GSI peaks depending on their geographic location (Waheed et al. 2023). Similarly, *Tenualosa ilisha* (Hamilton, 1822) displays significant variability in GSI patterns across habitats (Ahammad et al. 2021).

The GSI patterns observed in *R. arundinata* further highlight adaptive reproductive strategies aimed at optimizing reproductive success. The April peak potentially coincided with favorable environmental conditions, such as increased food availability and suitable water temperatures, which are essential for spawning and larval survival. However, the specific food sources available during this period and the optimal temperature range for reproduction in this species have not been experimentally determined. The secondary peak in September might represent a strategic adjustment to environmental cues, thereby ensuring a second reproductive opportunity throughout the year.

Fecundity analysis and oocyte diameter

The fecundity of *R. arundinata* exhibited significant variation throughout the year, with oocyte counts ranging from 1,156 to 2,090. The highest fecundity peaks were recorded in April and again in September to October, while the lowest was observed in January. These seasonal patterns reflect the species' reproductive strategy and align with the two primary spawning peaks identified in the Gonadosomatic Index (GSI) analysis. A similar pattern was observed in *R. lateristriata* from the Ngrancah River, where environmental factors such as water temperature and food availability influenced reproductive timing (Djumanto et al. 2008). This suggests that *R. arundinata* may also rely on environmental cues to regulate its spawning cycles.



A B C

Figure 9. Relationship between fecundity: A. Body weight (W); B. Body length (L); and C. Gonad weight (G) of *Rasbora arundinata* caught in Kreung Lanca River, Nagan Raya District, Aceh, Indonesia

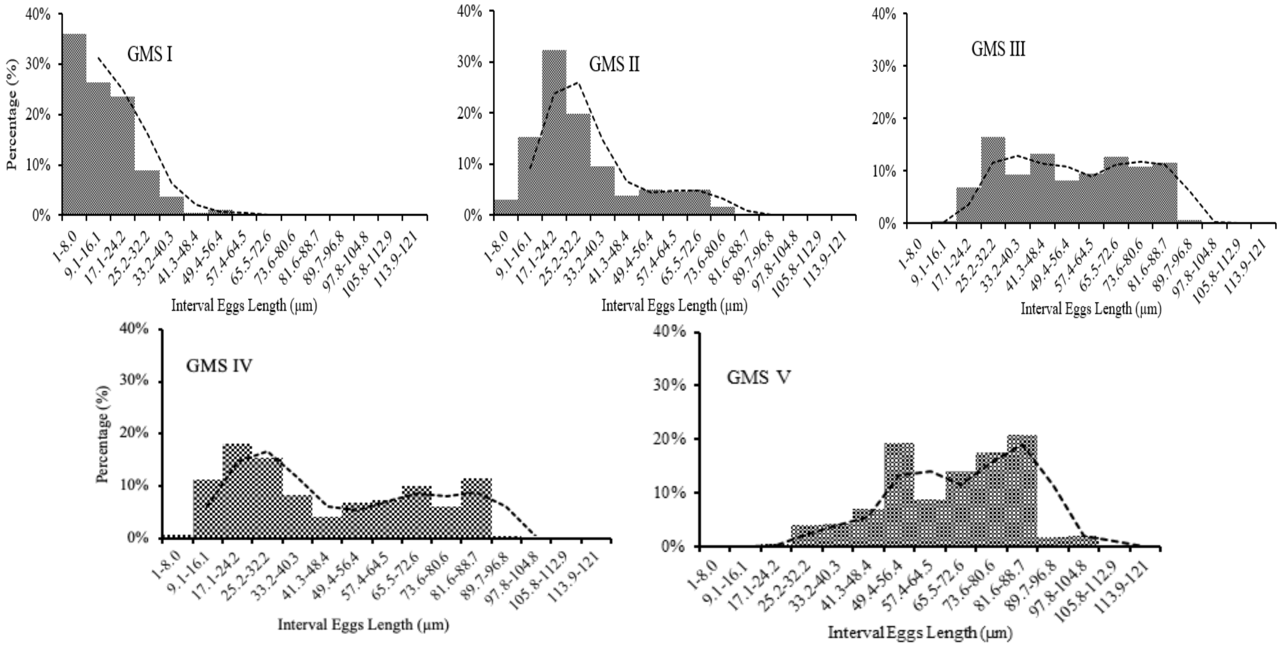


Figure 10. Oocyte size distributions of *Rasbora arundinata* caught in Kreung Lanca River, Nagan Raya District, Aceh, Indonesia

To gain deeper insights into the reproductive potential of *R. arundinata*, the relationships between fecundity and key biological parameters—body weight, total length, and gonad weight—were analyzed. The results showed no significant correlation between fecundity and body weight ($F = 420.15W^{0.687}$, $R^2 = 0.25$) (Figure 9.A) or total length ($F = 1.4835L^{1.5368}$, $R^2 = 0.24$) (Figure 9.B). However, fecundity exhibited a stronger correlation with gonad weight ($F = 1817.3G^{0.7589,}$ $R^2=0.47$) (Figure 9.C), indicating that gonad weight is a more reliable predictor of fecundity. Despite this, the considerable variability observed in the model suggests that additional external and internal factors influence fecundity, reflecting the complexity of the reproductive process in this species.

The weak correlation between fecundity and body weight or total length in *R. arundinata* contrasts with findings in other species. For instance, *Rasbora rubrodorsalis* in Sieo River, Roi Et Province, Northeast Thailand, demonstrated a stronger correlation between fecundity and body dimensions (Kulabtong et al. 2018). Similarly, Oboh and Omoigberale (2014) reported that fecundity in *Parachanna obscura* (Günther, 1861) was associated with length and weight, albeit with a weak correlation. Comparable trends were observed in channel catfish (Su et al. 2016); *Betta* sp. reared under laboratory conditions (Fasya and Mufidah 2022); and *Barbonymus balleroides* (Valenciennes, 1842) domesticated from the Cirata Reservoir, Java (Kusmini et al. 2018).

The variability in fecundity among these species highlights the influence of environmental conditions and ecological adaptations. Timothy and Ekpe (2018) emphasized that fecundity can differ significantly between habitats due to variations in food availability, water quality, and environmental factors such as rainfall and water flow. These external factors directly affect reproductive success by altering the nutritional state and spawning readiness of the fish. Additionally, factors such as feeding habits, physiological health, and water quality influence fertility levels (Pratama et al. 2019). Internal factors, including genetics, age, and fish size, also play a pivotal role in determining fecundity, as suggested by De Souza Andrade et al. (2015) and Chang and Chen (2020). Even within the same species, differences in environmental conditions, habitat structures, and food resource availability can lead to significant variations in fecundity across different populations (Chen et al. 2022).

Oocyte development

The oocyte diameter of *R. arundinata* exhibited significant variability across different gonadal maturity stages, ranging from 1 to 108 µm, as depicted in Figure 10. This variation reflects the sequential growth and maturation of oocytes, aligning with the physiological changes associated with reproductive readiness (Lin et al. 2022). The observation of larger oocytes in advanced maturity stages supports the notion that the species follows a synchronized reproductive strategy, closely linked to environmental and biological cues.

Moreover, advanced stages of oocyte development coincided temporally with the peak reproductive activity observed in March-April and September. This temporal alignment suggests a well-defined spawning periodicity, likely adapted to optimize fertilization success and larval survival. These findings are consistent with previous studies that have highlighted the seasonal reproductive patterns in similar aquatic species, where oocyte maturation peaks correspond with optimal ecological conditions (Genovia et al. 2023).

In conclusion, *R. arundinata* demonstrated an adaptive reproductive strategy with year-round spawning capability and two primary reproductive peaks in April and September. The observed variations in oocyte size, high fecundity, and relatively balanced sex ratio indicate an efficient and environmentally responsive reproductive strategy. These findings not only enhance our understanding of the reproductive dynamics of the species but also highlight the importance of evidence-based conservation efforts to safeguard *R. arundinata* populations from escalating ecosystem threats. Based on this study, conservation and management initiatives should be prioritized during the peak reproductive periods in April and September. Implementing measures, such as fishing restrictions during these months, can help protect species during spawning. Furthermore, habitat rehabilitation efforts in the months leading to reproductive peaks, specifically from February to March and July to August, could improve environmental conditions for successful spawning and larval survival. Strengthening regulations against harmful fishing practices, such as the use of toxins or electrofishing, is essential for ensuring the sustainability of *R. arundinata* populations. A strategically designed conservation approach can enhance the health of aquatic ecosystems and livelihoods of local communities.

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