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Growth and Reproductive Development of Asian Seabass, *Lates calcarifer* in Small-Scale Aquaculture Farms in Malaysia

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ABSTRACT

Understanding the relationship between production management and protandrous hermaphroditism in farmed Asian seabass (*Lates calcarifer* Bloch 1790) is vital for optimising aquaculture efficiency. This study evaluated the growth performance and gonadal development of Asian seabass ($n = 112$) across six open and semi-closed small-scale farms in Peninsular Malaysia. With the exception of one farm population that displayed negative allometric growth ($b < 3$), fish growth was isometric ($b = 3$) across the remaining groups. Non-parametric Mann-Whitney U tests revealed that semi-closed systems achieved significantly higher performance metrics than open configurations, where the relative condition factor (K) was significantly elevated (median 1.30 vs. 1.18; W = 172, $p < 0.001$), as was the Specific Growth Rate (SGR, median 1.01 vs. 0.99 % day^{-1}; W = 279.5, $p = 0.046$). Multi-model information-theoretic selection (AIC_c) confirmed that farming practice models that combine enclosure method and water-source environment offered the highest predictive support (model weight, $W_t = 76\%$), outperforming models based on broad system (semi-closed vs. open) configurations alone. Histologically, ordinal logistic regression models revealed that water salinity environmentally drives sex reversal in the farmed fish. Holding total length constant, fish reared in low-salinity environments (≤ 25 ppt) exhibited 9.1 times higher odds of occupying advanced gonadal stages compared to high-salinity cohorts (> 25 ppt), significantly compressing both male-peak and female-transition size thresholds. Ultimately, these findings demonstrate that while semi-closed infrastructure accelerates daily growth velocity, small-scale farmers must prioritise matching specific culture methods to environmental salinity profiles to manage growth and sex reversal timelines effectively.

Keywords: Asian seabass, precocious maturation, protandrous hermaphroditism, salinity modulation, small-scale aquaculture

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INTRODUCTION

Optimising growth performance is a primary objective in aquaculture production. This is because faster growth shortens production cycles, which in turn increases biomass yield (Small et al., 2016). However, growth and reproduction are physiological processes that compete for energy resources. For example, increased allocation of energy towards reproductive development may reduce somatic growth, and rapid growth can also alter the timing of sexual maturation (Bogevik et al., 2014). In aquaculture, early or precocious sexual maturation is generally undesirable because energy is diverted from muscle deposition to gamete production. This would ultimately reduce growth efficiency and harvest quality (Felip et al., 2008; Taranger et al., 2010). Such processes are regulated through the hypothalamic-pituitary-gonadal (HPG) axis. In the HPG, nutritional status, body size, and growth rate influence endocrine signalling and the expression of genes involved in reproduction (Ding et al., 2026). Therefore, understanding how farming conditions influence these physiological processes is important for improving management practices in both grow-out and broodstock production.

The relationships between farming practices and the respective physiological responses are important in protandrous hermaphroditic species such as the Asian seabass (*Lates calcarifer* Bloch, 1790). As a catadromous species, Asian seabass generally matures first as a male in lower-salinity riverine habitats. The fish would then migrate to higher-salinity marine waters to undergo sex reversal to become functional females (Rossi et al., 2018). This reproductive plasticity enables the Asian seabass to be cultured across a wide range of salinities during the grow-out phase (Hassan et al., 2024; Yusof et al., 2024). Hatcheries can produce Asian seabass larvae at salinities of 33 ppt or higher (Young & AlMoutiri, 2022). However, the fish achieve optimal growth and feed conversion in brackish water between 5 and 15 ppt (Wijayanto et al., 2021; Yusof et al., 2024). Such environmental flexibility has contributed to the ubiquitous rearing practices of Asian seabass in both marine and inland aquaculture.

Small-scale aquaculture enterprises dominate Asian seabass farming in Malaysia and across Southeast Asia. Typically, these farms operate with limited infrastructure, scarce resources, and minimal environmental control (Abdullah et al., 2018). Most rely on either open or semi-closed production systems. Open systems, which mainly use floating cages in coastal or riverine waters, depend entirely on natural water exchange. While they require very little capital upfront, they leave fish vulnerable to wild environmental shifts, disease outbreaks, and sudden water quality drops (Venkatachalam et al., 2018). Alternatively, semi-closed systems like inland earthen ponds and flow-through tanks offer better control via active water treatment (Turlybek et al., 2025). However, the trade-off is financial, where running these systems demands higher operating costs and strict management to stop waste from accumulating (Rud et al., 2017). Because most smallholders cannot afford

these rigorous feeding programs or salinity controls, production performance varies wildly from farm to farm (Mohd Nor et al., 2019).

In Malaysia, Asian seabass remains a premier cultured brackishwater and marine finfish (Department of Fisheries Malaysia, 2024). Brackish water ponds drove the bulk of production volume in 2024, yielding 52,677.95 tonnes. This translated to a wholesale value of RM722.8 million and a retail value of RM837.5 million (Exchange rate: RM1 = USD0.22, December 2024). By contrast, floating cages produced a fraction of that volume at just 8,183.61 tonnes, yet their wholesale value per tonne was roughly 62% higher than pond-raised fish. This stark valuation gap points to a clear market premium for cage-cultured seabass, likely driven by superior fish quality and distinct production methods. The structural advantage of cage culture, namely constant water exchange, has long been linked to better growth rates and sharper feed conversion efficiency (Anil et al., 2010).

While small-scale Asian seabass farming is economically vital, we still know very little about how commercial culture systems influence growth and reproduction. Most data comes from controlled laboratory or hatchery trials focusing tightly on artificial spawning, sex differentiation, and endocrine regulation (Athauda et al., 2012; Donaldson, 1996; Harvey et al., 1985; Heidari et al., 2025; Ravi et al., 2014). How these biological processes play out in the unpredictable environments of commercial open and semi-closed farms remains a blind spot. Intensive culture pushes rapid somatic growth, which can accelerate male differentiation and trigger earlier sex reversal as compared to wild populations (Terence et al., 2021). This shifts the biological timeline. In practical terms, these shifts disrupt harvest size uniformity during grow-out and throw off the male-to-female ratio needed for sustainable broodstock management. Therefore, this study aimed to evaluate the growth performance and reproductive development of Asian seabass cultured in smallholder farms across Peninsular Malaysia. Mapping these relationships on active commercial farms is critical to upgrading production efficiency and securing long-term broodstock survival.

MATERIALS AND METHODS

Farm Practice Characterisation

Samples were collected from March to October 2023 at six small-scale commercial Asian seabass farms located in Peninsular Malaysia. All farms were located along the coastal regions bordering the Straits of Malacca or the South China Sea (Figure 1). The farms represented a range of aquaculture systems that differed in culture practices, environmental conditions, and farm management. The range of aquaculture systems reflects variations in local geographical settings and available resources. To systematically analyse the impact of these farming practices on biological outcomes, the operations were classified into two open and semi-closed infrastructure systems. Additionally, three distinct farming methods

were identified: cage culture, earthen ponds, and fibreglass tanks. The rearing environment was characterised based on water source as either river, sea, or inland.

The open system refers to full exchange of water in the natural environment where the fish are contained. On the other hand, the semi-closed system refers to culture settings in a confined area, where exchange of water is dependent on the weather and man-power availability. For open systems operation, fish are **r**eared in floating net cages positioned within coastal seas or large river estuaries characterised by continuous, natural water exchange. The surveyed open-system sites include Tanjung Dawai, Bagan Lalang, and Sungai Marang. As for the semi-closed systems operation, fish are reared within confined inland infrastructures, such as earthen ponds or fibreglass tanks, where water exchange is intermittent and dependent on localised weather conditions and manual labour. The surveyed semi-closed sites include Kelanang, Gelang Patah, and Rompin.

Ambient salinity profiles during the field visits remained unaugmented and unmitigated across all sites, ranging natively between 21 and 27 ppt. For predictive modelling purposes, these sites were further partitioned into two explicit environmental categories based on baseline salinity thresholds of the low salinity group (≤ 25 ppt, comprising Kelanang, Bagan Lalang, and Gelang Patah) and high salinity group (> 25 ppt, comprising Tanjung Dawai, Sungai Marang, and Rompin).

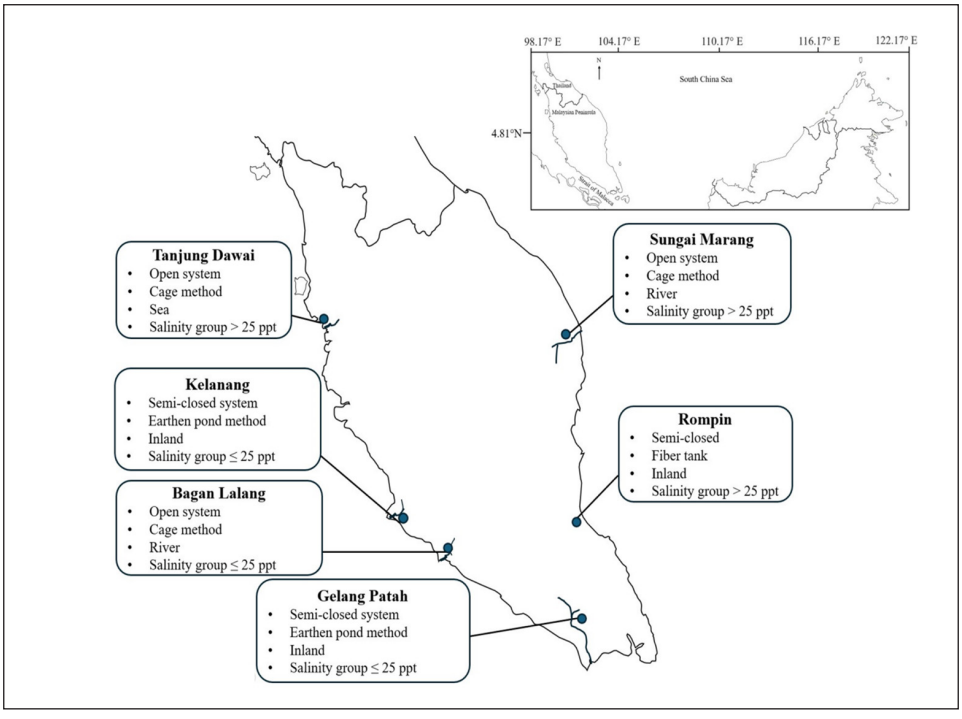

Figure 1. Sampling farms with their culture conditions

Fish Sampling and Biometric Growth Performance

Asian seabass was sampled (n = 112) from the six farms to obtain integrated biometric and histological profiling. At stocking, fingerlings had been introduced into their respective rearing systems at a standardised total length of approximately 5 inches. Because smallholding farmers did not maintain formal written historical registries, fish age (ranging from 5 to 42 months) was determined by calculating the duration between the farmer's recalled stocking date and the active sampling event. The fish were variably fed commercial pellet diets or available trash fish depending on age and individual farm resource constraints. Despite these differences, all farms followed a similar feeding schedule, with fish fed twice daily and feed rations adjusted according to fish body weight and culture duration. Variations in feeding practices among farms were considered an inherent limitation of this field-based study.

Individual fish ranged from 33 to 79 cm in total length (TL) and from 0.4 to 7.0 kg in body weight. We measured individual total lengths to the nearest 0.1 cm and recorded body weights to the nearest gram. From these metrics (Equations 1 to 4), we evaluated growth performance by calculating the length-weight relationship (LWR), relative condition factor (K), and specific growth rate (SGR).

- Length-weight relationship (LWR)

$$W = aL^b \quad [1]$$

- Logarithmic transformation to linear equation:

$$\log(W) = \log(a) + b \log(L) \quad [2]$$

where a denotes the intercept, and b denotes the allometric coefficient.

- Relative condition factor (K)

$$W = W_o/Wc \quad [3]$$

where W_o denotes observed body weight, and Wc denotes predicted body weight from the corresponding length-weight relationship.

- Specific growth rate (SGR, % day^{-1})

$$SGR = [(\ln W_2 - \ln W_1) / (T_2 - T_1)] \times 100 \quad [4]$$

where W_1 and W_2 are the initial and final body weights, respectively, and $(T_2 - T_1)$ is the culture duration in days. As stocking records were unavailable for all farms, an initial body weight of 100 g was assumed for all fish. Culture duration was estimated by converting the reported culture age from months to days using 30 days per month.

Microscopic Examination of Gonads

Following collection, fish were temporarily maintained in aerated 1,000-L holding tanks supplied with flow-through seawater until processing. Water temperature was maintained at 28-30 °C, salinity at 30-35 ppt, pH at 7.5-8.5, and dissolved oxygen above 6 mg/L. All procedures involving fish were conducted in accordance with the animal ethics guidelines approved by the Universiti Putra Malaysia Institutional Animal Care and Use Committee (UPM/IACUC/AUP-R010/2020).

Fish were euthanised by immersion in 200 mg/L clove oil solution (Sigma-Aldrich, CAS 8000-34-8). We confirmed death by verifying the absolute absence of reflex responses and opercular movement. Following that, we made a mid-ventral incision to expose the abdominal cavity, carefully harvesting the gonads with sterile instruments. To remove residual blood, we rinsed the excised tissues in 0.9% saline before fixing them in 10% neutral buffered formalin for 48 hours. The samples were then transferred to 70% ethanol for storage.

For histological processing, we cut the fixed gonads into roughly 2-cm sections and ran them through an automatic tissue processor on a standard 24-hour cycle. This sequence included dehydration via graded alcohol, xylene clearing, and final paraffin embedding. Finally, we sectioned the tissue blocks at 5-7 µm using a rotary microtome. Sectioned tissues were stained with hematoxylin and eosin (H&E) for microscopic evaluation.

Gonadal development was classified into four developmental stages following the modified criteria of Guiguen et al. (1994) and Terence et al. (2021). Stage 1 (Undifferentiated) comprised immature gonads showing no visible cellular differentiation. Stage 2 (Male) was characterised by an abundance of spermatogenic cells such as spermatocytes, spermatids, or mature spermatozoa in the absolute absence of advanced oocytes. Stage 3 (Intersex/ Transitional) displayed a mixture of both spermatogenic cells and developing primary or secondary oocytes. Lastly, Stage 4 (Female) was defined by the presence of secondary, vitellogenic, or hydrated oocytes with no remaining spermatogenic tissue.

Data Analysis

To check for data normality, we evaluated the skewness, kurtosis, and distribution of total length and body weight using Shapiro-Wilk tests alongside normal Q-Q plots. We also checked for homogeneity of variance across the farming sites using Levene's test before running any analysis of variance (ANOVA).

We modelled variations in the length-weight relationships among the farms using a General Linear Model (GLM). To test for divergence in regression slopes, we evaluated the interaction term between farm site and log-transformed total length via ANOVA, an approach functionally equivalent to an analysis of covariance (ANCOVA). For each farm, the estimated allometric coefficient (b) was further compared with the theoretical value for isometric growth ($b = 3$) using a two-tailed one-sample t-test. Failure to reject the null hypothesis (H_0: $b = 3$) indicates isometric growth, whereas significant deviations indicate either positive or negative allometric growth.

Variations in somatic parameters (total length and body weight) across the four ordinal stages of gonadal development were assessed via one-way ANOVA. Post-hoc comparisons were executed using Tukey's Honest Significant Difference (HSD) test, with the *a priori* significance level at $\alpha = 0.05$.

Relative condition factor, K and specific growth rate (SGR) were then evaluated for their differences across farms. Data normality was first assessed using the Shapiro-Wilk test. Both K and SGR data violated normality assumptions ($p < 0.001$), and transformations (log, square root, Box-Cox) failed to achieve normality (all $p < 0.05$). Therefore, non-parametric tests were employed. Differences in K and SGR between farming systems, i.e. open (Bagan Lalang, Marang and Tanjung Dawai) vs. semi-closed (Gelang Patah, Kelanang and Rompin) were compared using the Mann-Whitney U test. Comparisons among farming methods (cage, earthen pond, fibre tank; $n = 3$ groups) and environments (river, sea, inland; $n = 3$ groups) were not conducted due to insufficient sample sizes within several groups (e.g., only one farm representing cage-river system with n = 10, and one farm representing cage-sea system with n = 10), which would compromise statistical power and increase the risk of Type II errors. Additionally, the unequal distribution of samples across method and environment categories violated the assumptions of multi-group non-parametric tests. Therefore, analyses were restricted to comparisons between the two farming systems (open vs. semi-closed; n = 30 and n = 27, respectively), which provided adequate and balanced sample sizes for robust statistical inference. For comparisons across multiple farms, the Kruskal-Wallis test was used, followed by Dunn's post-hoc test with Bonferroni correction for pairwise comparisons. Effect sizes were calculated as eta-squared (η^2).

To determine which farm characteristics best explained variation in gonadal development, we executed model selection via an information-theoretic approach. This framework utilised Akaike's Information Criterion corrected for small sample sizes (AICc). Six candidate ordinal logistic regression models were developed using different combinations of three categorical predictors: culture method (cage, earthen pond, or fibre tank), rearing environment (river, sea, or inland), and farming system (open or semi-closed). Gonadal development stage was used as the ordinal response variable (undifferentiated = 1, male = 2, intersex = 3, and female = 4). Candidate models were compared using AICc, the

difference in AICc from the best-supported model (ΔAICc), and Akaike weights (AICcWt), which indicate the relative support for each model. Cumulative Akaike weights were also calculated to assess the overall importance of the candidate models. Log-likelihood values from each fitted model were used to calculate AICc.

Ordinal logistic regression (OLR) was then used to examine the relationship between fish size and gonadal development. Total length (TL) was included as the explanatory variable, while gonadal development stage was treated as the ordinal response. Body weight was excluded because it was highly correlated with total length (r = 0.94). This was confirmed by variance inflation factor (VIF) analysis, and excluding body weight reduced multicollinearity in the model.

A second OLR model was fitted using only grow-out fish (≤ 9 months old) to estimate the probability of precocious male differentiation under different rearing environments. To maintain statistical clarity, we used p exclusively for hypothesis testing significance levels and reserved $\hat{p}$ to signify the predicted probabilities output by the ordinal logistic regression models. All statistical analyses and graphical presentations were performed in RStudio (RStudio Team, 2020).

RESULTS

Fish Growth Performance

The length-weight relationship revealed variation in growth patterns among farms, with b values ranging from 2.12 to 3.59. Except for Bagan Lalang, all of the surveyed populations showed no significant deviation from the theoretical isometric value ($b = 3$), maintaining a proportional weight increase relative to length across the different farming systems. The only anomaly that occurred at Bagan Lalang showed that the fish exhibited distinct negative allometric growth ($b < 3$).

Growth patterns varied among the farming sites, with calculated b values spanning from 2.12 to 3.59 within the length-weight relationships. Most populations showed no meaningful deviation from the theoretical isometric value ($b = 3$), tracking a proportional increase in body weight alongside length across the different systems. The sole exception was Bagan Lalang, where the fish displayed distinct negative allometric growth ($b < 3$)

The general linear model accounted for 98.5% of the variation in log-transformed body weight ($R^2 = 0.9853$). Model residuals showed no significant deviation from normality (Shapiro-Wilk test: $W = 0.9835$, $p = 0.626$) and no evidence of heteroscedasticity based on the Breusch-Pagan test ($\chi^2 = 17.17$, $p = 0.103$). The ANCOVA revealed a significant log Total Length × farm interaction ($F_{5, 110} = 3.82$, $p = 0.006$), indicating that the growth exponent b in the power equation $W = aL^b$ varies among farms (Table 1). Post-hoc comparisons further revealed that only the Bagan Lalang-Marang slope contrast was significant ($p = 0.009$), with all other pairwise comparisons non-significant ($p > 0.05$).

The Mann-Whitney U tests revealed statistically significant differences in both relative condition factor (*K*) and specific growth rate (SGR) between open and semi-closed farming systems. For *K*, the median was 1.18 (interquartile range, IQR = 1.07-1.25) in open systems and 1.30 (IQR = 1.09-1.48) in semi-closed systems, respectively (W = 172, $p < 0.001$, r = 0.49). For SGR, the median was 0.99 (IQR = 0.49-1.14) in open systems and 1.01 (IQR = 0.93-1.16) in semi-closed systems, respectively (W = 279.5, $p = 0.046$, r = 0.27). Semi-closed systems exhibited higher central values and reduced variability for both parameters, as indicated by narrower IQR and smaller standard deviations. The effect size for *K* ($r = 0.49$) was nearly double that of SGR ($r = 0.27$), indicating a more pronounced system-related difference in condition factor than in growth rate.

Gonad Development by Means of Histological Examination

Microscopic examination showed clear differences in gonadal structure among the developmental stages. Histological examination of the male gonads revealed a clear dominance of spermatogenic cells arranged within distinct tubular structures, staining a vivid blue purple (Figure 2a). Staining intensity shifted dynamically with spermatogenic stages. Under 10× magnification, spermatocytes stood out as loosely organised circular profiles with clearly visible nuclei. In contrast, mature spermatozoa clustered tightly within the seminiferous tubules, and we noted a complete absence of oogonia in these male-stage tissues.

The intersex gonads presented a complex cellular mosaic, where male and female germ lines, including oogonia, previtellogenic oocytes, and vitellogenic oocytes, were observed at varying developmental depths, with the presence of atretic oocytes and residual spermatogenic cells (Figure 2b). We observed wide structural variation across this transitional cohort, ranging from gonads heavily anchored by spermatogenic tissue with sparse oocytes to specimens overflowing with oocytes alongside dying spermatogenic clusters.

Developing oocytes at secondary or advanced vitellogenic stages indicated fully developed female gonads. The ovaries displayed asynchronous development, showcasing multiple developmental phases simultaneously to give the tissue a signature pink-to-red appearance (Figure 2c). Follicular thickness and yolk accumulation increase as vitellogenic oocytes expand in size. Where atretic oocytes occurred, we identified them by their irregular boundaries, disrupted cellular layout, and depleted yolk volume.

All four stages of Asian seabass gonadal development were present within our sampled cohorts upon histological evaluation. Most individuals were classified as undifferentiated (66.1%), while the remaining cohort consisted of either males (17.9%), females (8.9%), or intersex individuals (7.1%). Fish collected from the Kelanang, Sungai Marang, and

Table 1

Descriptive statistics and growth performance metrics of Asian seabass sampled across six Malaysian aquaculture farms, where ± for b indicates mean and standard error, while for K and SGR indicate median and interquartile range (IQR)

Farm	n	Weight, g	Total length, cm	Age (Months)	b	a	Relative Condition Factor, K	SGR, % day^{-1}
Bagan Lalang	18	922 ± 290 ^{a}	45.0 ± 12.6^{a}	7	2.12 ± 0.24^{a}	0.33	1.22 ± 0.24	0.97 ± 0.26
Gelang Patah	20	3,940 ± 1,429 ^{b}	65.5 ± 7.9^{b}	30 - 42	2.89 ± 0.23^{ab}	0.02	1.29 ± 0.11	0.34 ± 0.04
Kelanang	14	601 ± 77 ^{a}	35.9 ± 1.2^{a}	5	3.28 ± 0.91 ^{ab}	0.00	1.21± 0.08	1.15 ± 0.09
Sungai Marang	20	1,460 ± 503 ^{a}	48.6 ± 4.4^{a}	7	3.59 ± 0.43 ^{b}	0.00	1.22 ± 0.15	1.25 ± 0.16
Rompin	20	1,750 ± 458 ^{a}	48.0 ± 4.6^{a}	9	2.82 ± 0.19 ^{ab}	0.03	1.55 ± 0.09	1.05 ± 0.10
Tanjung Dawai	20	565 ± 235 ^{a}	36.7 ± 4.5^{a}	6	2.85 ± 0.21 ^{ab}	0.02	1.10 ± 0.08	0.93 ± 0.18

Note. Values expressed with ± indicate the mean ± standard deviation. Coefficients a = intercept and b = slope of the log-transformed length-weight equation, K = relative condition factor, and SGR = specific growth rate. Different superscript letters for Weight, Total length and b indicate statistically significant differences between farms (one-way ANOVA $p < 0.05$) based on the Tukey-HSD post-hoc test

Tanjung Dawai farms were exclusively at the undifferentiated stage, whereas the other farms contained individuals representing multiple stages of gonadal development (Figure 3). The occurrence of different developmental stages within the same farm indicates variation in the timing of sexual differentiation among cultured fish.

Across the sampled population, our histological screening captured all four stages of gonadal development in the Asian seabass. Most individuals were undifferentiated (66.1%), with the remaining cohort consisting of males (17.9%), females (8.9%), and intersex variants (7.1%). Interestingly, sampling sites varied in maturity; fish from Kelanang, Sungai Marang, and Tanjung Dawai were entirely undifferentiated. By contrast, the remaining farms yielded mixed populations spanning multiple reproductive stages (Figure 3).

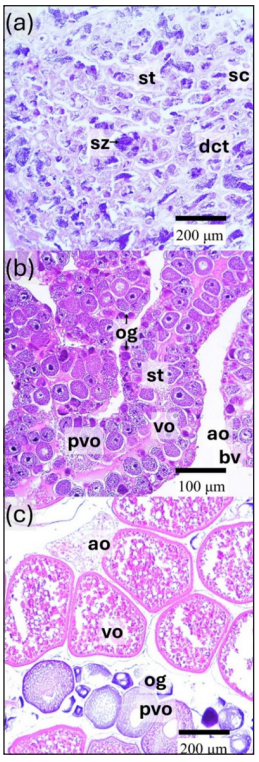

Figure 2. Histological sections of Asian seabass gonads stained with hematoxylin and eosin (H&E): (a) male (67 cm TL, 3.9 kg body weight), (b) intersex (56 cm TL, 2.4 kg body weight), and (c) female (72 cm TL, 4.6 kg body weight). All images were taken at 10× magnification. st = spermatids, sc = spermatocytes, sz = spermatozoa, pvo = previtellogenic oocytes, vo = vitellogenic oocytes, ao = atretic oocytes, og = oogonia, dct = dense connective tissue, and evo = early-stage vitellogenic oocyte

The relationship between somatic growth and gonadal development showed considerable variation among individuals. Across the sampled size range (56-79 cm TL and 2.2-7.0 kg body weight), fish of similar size were observed at different stages of gonadal development (Figure 4). Gonadal stages did not follow a consistent progression according to body size, as undifferentiated, male, intersex, and female individuals occurred across overlapping size ranges. For example, undifferentiated and intersex fish were both observed at 56 cm TL, while males occurred across a wide body weight range (2.4-7.0 kg). Similarly, fish with the same total length (e.g., 72 cm) were classified as either intersex or female based on histological examination.

Size Overlap and Correlation Analysis

Body size varied considerably among the different gonadal developmental stages. Male individuals (n = 20) ranged from 41.5 to 72 cm TL and 0.95 to 4.6 kg body weight. Intersex fish (n = 8) ranged from 56 to 73 cm TL and 2.2 to 4.8 kg, whereas females (n = 10) ranged from 62 to 79 cm TL and 2.8 to 7.0 kg.

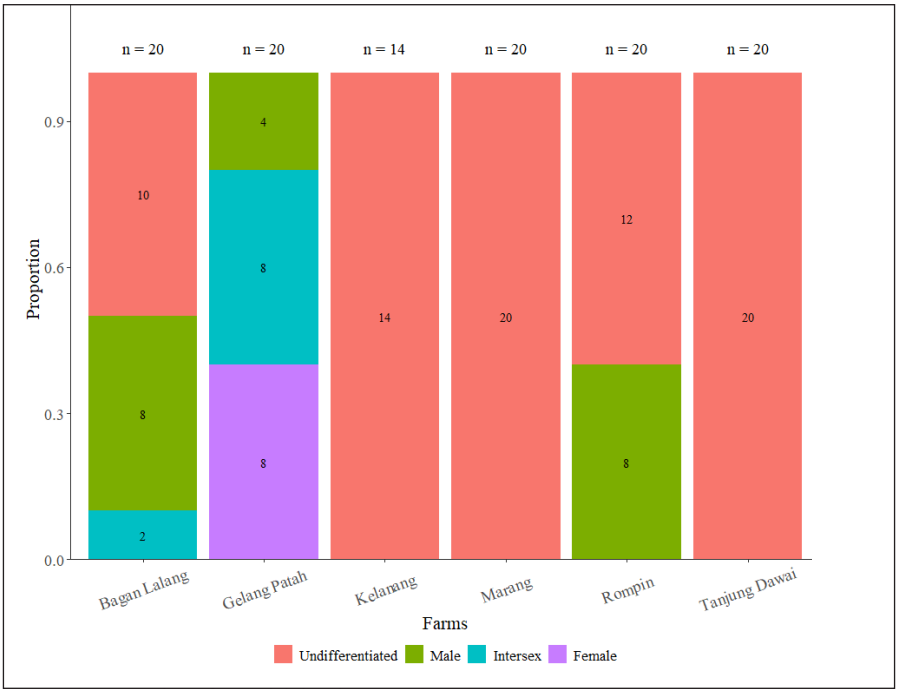

Figure 3. Proportion of gonadal developmental stages among Asian seabass sampled in this study. Numbers within each section of the stacked bars represent the number of individuals

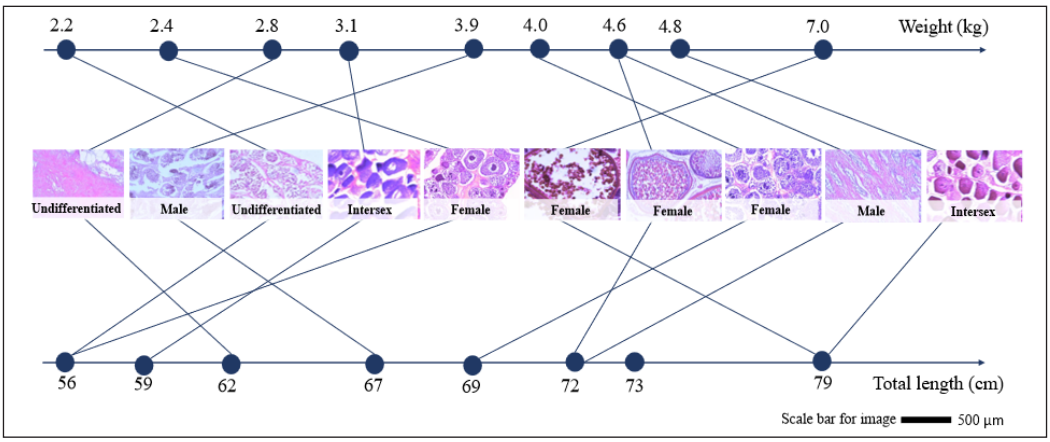

Figure 4. Relationship between gonadal developmental stages and body size (total length and body weight) of Asian seabass. Representative histological images at 20× magnification show variation in gonadal development among individuals of different size classes

A strong positive relationship between total length and body weight was observed within each farm, with Pearson's correlation coefficients exceeding 0.86 (Figure 5). Similar length-weight patterns were observed among farms, suggesting comparable somatic growth trends across the surveyed operations. When all samples were pooled, total length and body weight showed a strong correlation (r = 0.94), indicating that both measurements provided similar information regarding fish size.

One-way ANOVA showed significant differences in biometric characteristics among gonadal developmental stages. Intersex and female individuals were significantly larger than male and undifferentiated fish ($p < 0.01$; TL: $F_{3,33} = 13.75$; weight: $F_{3,33} = 10.42$) (Figure 6). A variance inflation factor (VIF) diagnostic confirmed strong collinearity between total length and body weight (VIF = 8.59), prompting us to retain only the former for subsequent regression modelling.

Ordinal Logistic Regression Models

The AICc-based model selection indicated that the combination of culture method and rearing environment provided the strongest support for explaining variation in gonadal development (ΔAICc = 0; Akaike weight = 0.26) (Table 2). Among the candidate models, those including rearing environment accounted for most of the model support, with a cumulative Akaike weight of 0.76. In contrast, models without rearing environment received substantially lower support (ΔAICc > 2). *Method* + *Environment* ranks as the top model (AICc = 108.78, ΔAICc = 0, weight = 0.26), followed by *Environment* alone (AICc = 108.88, ΔAICc = 0.1) and *System* + *Environment* (AICc = 108.88, ΔAICc = 0.1) rank joint second. All models have *K* values between 4 and 6 parameters, with similar log-likelihood scores ranging from -48.2 to -51.52. The ΔAICc differences between the top three models are less than 2, indicating they have substantial empirical support. Models containing *Environmen*t that records farming practices at sea, in the river and inland, consistently appear in the top three positions. Models without *Environment* show ΔAICc values exceeding 2, indicating considerably less support.

Exponentiating the logit coefficient values provided odds ratios (OR) that explain how the predictors vary with the response. Holding environmental salinity constant, fish exhibited a 1.2-times increase in the odds of shifting into advanced stages of gonadal development for every 1 cm increase in total length (OR = 1.2 ± 0.6 SE; Figure 7a). Conversely, when keeping total length constant, the gonads demonstrated 9.1 times higher odds of being in advanced developmental stages if the fish were cultured in a low-salinity environment (OR = 9.1 ± 1.0 SE).

The predicted probability ($\hat{p}$) curves indicated that while the likelihood of transitioning into a female increases with total length, the speed of this transition depends heavily on salinity (Figure 7b). Given the same TL, fish cultured in low salinity had a higher

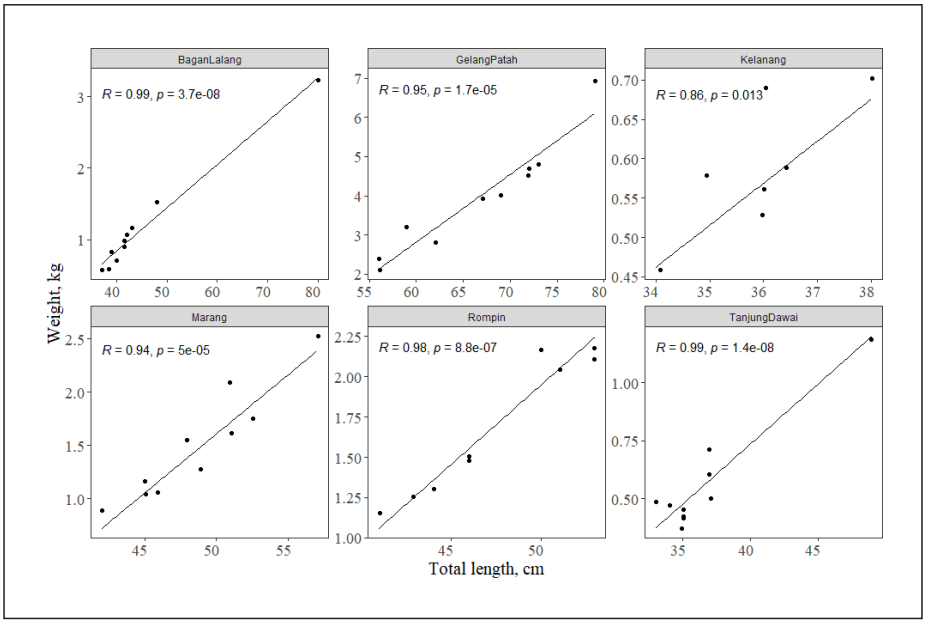

Figure 5. Pearson correlation between total length and body weight of Asian seabass sampled from each farm

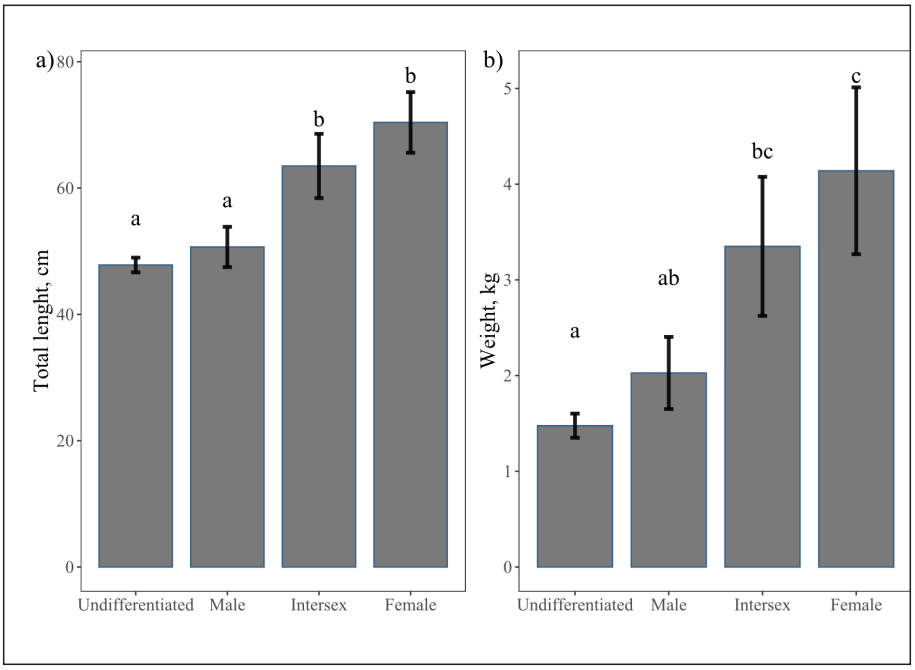

Figure 6. Comparison of Asian seabass size according to gonadal developmental stage: (a) total length and (b) body weight

Table 2
Corrected Akaike Information Criterion (AIC_c) model ranking of farm infrastructure effects on Asian seabass sex reversal

Model	K	AIC_c	ΔAIC_c	AIC_cW_t	Cumulative W_t	Log-likelihood
Method + Environment	6	108.78	0	0.26	0.26	-48.2
Environnment	5	108.88	0.1	0.25	0.51	-49.3
System + Environment	5	108.88	0.1	0.25	0.76	-49.3
Method	5	111.12	2.34	0.08	0.84	-50.43
System + Method	5	111.12	2.34	0.08	0.92	-50.43
System	4	111.22	2.44	0.08	1	-51.52

Note. K = number of estimated model parameters (including intercepts); AIC_c = Akaike Information Criterion corrected for small sample sizes; ΔAIC_c = difference in ΔAIC_c value relative to the top-ranked model; AIC_cW_t = Akaike model weight indicating relative predictive probability; Cumulative W_t = running sum of model weights within the candidate set; Log-likelihood = maximised log-likelihood value of the fitted regression function. System denotes structural infrastructure class (open vs. semi-closed), Method denotes rearing technique (cage, pond, or tank), and Environment denotes the baseline salinity classification (≤ 25ppt vs. > 25 ppt)

predicted probability ($\hat{p}$) of transitioning to an advanced gonadal stage than fish cultured in high salinity. For example, the gonads began to differentiate into functional males earlier when cultured in low salinity than high salinity, achieving a peak predicted probability of $\hat{p}$ = 0.60 at 52 cm TL compared to 61 cm TL, respectively. Similarly, the total length at which a fish crossed a $\hat{p}$ > 0.50 probability of becoming female was reached at approximately 73 cm TL under low salinity but was delayed until 82 cm TL under high salinity regimes.

Age-based regression models confirmed that fish also exhibited 1.2 times increase in the odds of occupying advanced stages of gonadal development for each additional month of age (OR = 1.2 ± 0.6 SE; Figure 8a). The probability curves showed that the likelihood of transitioning into a female increases steadily with age (Figure 8b). At 40 months of age, the probability of an individual developing as

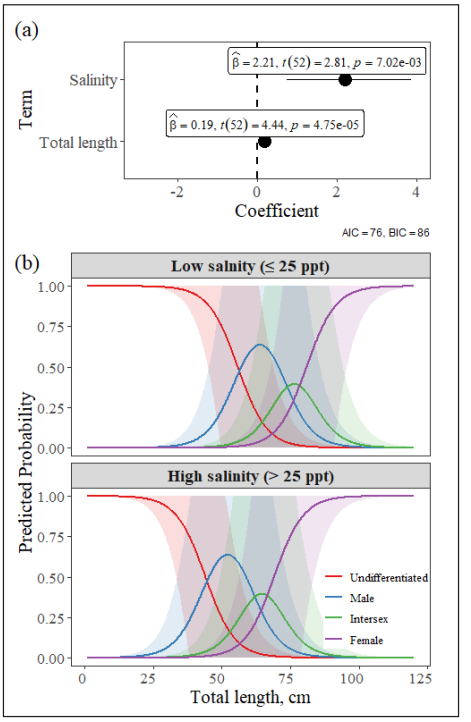

Figure 7. Predicted proportions and confidence intervals of (a) Parameter estimates and (b) respective predicted probability of Asian seabass sexually differentiated at varying gonad stages in low (≤ 25 ppt) and high (> 25 ppt) high range of salinity rearing environments

a female within the Gelang Patah cohort reached $\hat{p}$ = 0.75. By this 40-month threshold, the total probability of a fish possessing a differentiated gonad (male, intersex, or female) reached 100%. The active intersex transition window peaked at 34 months of age with a maximum predicted probability of $\hat{p}$ = 0.45 (Figure 8b). Prior to this transition, younger fish reached a $\hat{p}$ = 0.70 probability of functioning as males at approximately 20 months of age. As age progressed, the probability of being male at 22 months of age was maintained at $\hat{p}$ = 0.70. Following the 22-month milestone, the fish had a higher probability of entering the transition phase, which peaked at $\hat{p}$ = 0.45 at 36 months of age. The narrow age band and low overall probability curve for the intersex stage across the models confirm that this transitional stage is short-lived.

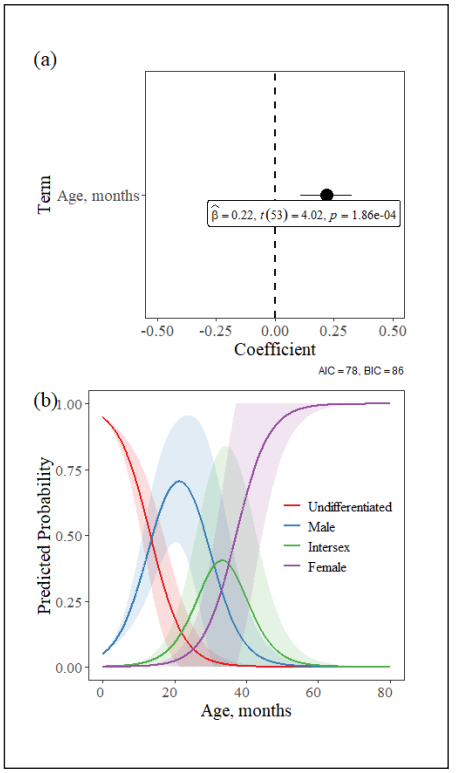

Figure 8. Predicted proportions and confidence intervals of (a) Parameter estimates and (b) respective predicted probability of Asian seabass sexually differentiated with age

For the condition factor model, the logit coefficient was not significant (p = 0.13), suggesting that *K* alone was not a strong predictor of gonadal development (Figure 9). Across the observed range of *K* values (0.6-1.7), the predicted proportion of undifferentiated fish gradually decreased, whereas the probabilities of male, intersex, and female stages showed only small increases. In contrast, the SGR model showed a significant relationship with gonadal development (p = 0.02). As SGR increased, the probability of undifferentiated fish decreased, accompanied by an increase in the probability of male development followed by higher probabilities of intersex and female stages at greater growth rates.

Model comparisons confirmed that both the condition factor (AIC = 119) and SGR (AIC = 115) frameworks offered substantially weaker predictive power. Their elevated AIC scores fell short of the superior total length (AIC = 76) and chronological age (AIC = 84) models. Our findings show that total length (as a measure of structural size) and chronological age are far more reliable predictors of gonadal development than condition factor or SGR.

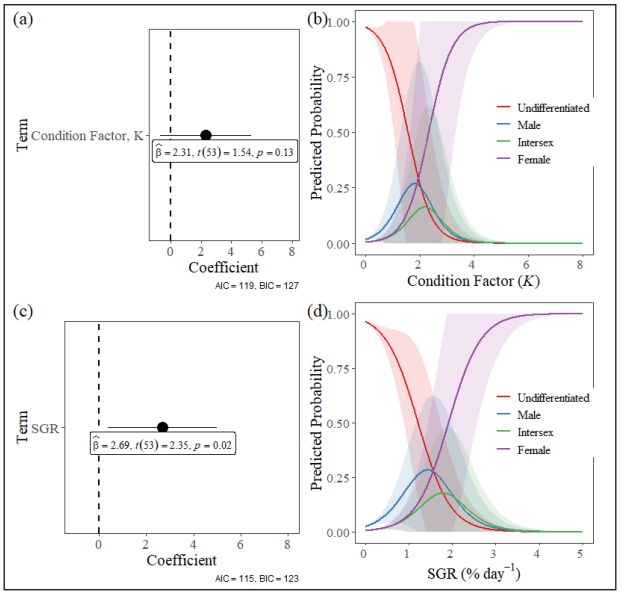

Figure 9. Predicted proportions and confidence intervals for (a) condition factor (K) parameter estimates, (b) predicted proportions based on K, (c) specific growth rate (SGR) parameter estimates, and (d) predicted proportions based on SGR

DISCUSSION

The length-weight relationship indicated predominantly isometric growth across the evaluated Asian seabass farming systems, except for Bagan Lalang, as fish from the farm showed negative allometric growth. The findings contrasted previous reports of positive allometric growth in Asian seabass under favourable culture conditions (Asres et al., 2023). Isometric growth reflects proportional increases in length and weight, which does not necessarily indicate poor growth performance (Che Abdullah & Md Zain, 2019). In terms of performance, all farms maintained favourable condition factors (K = 1.10-1.55) and SGR values (0.34-1.25% day^{-1}) that reflect good overall growth status.

The low b value at Bagan Lalang may be related to its younger age structure, where energy allocation may favour length increase before greater body mass accumulation (Froese, 2006). Given the protandrous hermaphroditic nature of Asian seabass, these variations in b exponents among the sites reflect localised differences in culture conditions alongside shifting ontogenetic and maturation stages (Sari et al, 2020; Kumar et al., 2016).

Cage culture is the dominant production system in Malaysia, followed by pond culture; each system presents different advantages and constraints. For example, a closed aquaculture system with salinity maintained between 20 and 36 ppt has been reported to achieve an optimal SGR of 8.74 ± 0.03 % day^{-1} (Hassan et al., 2024). However, previous studies have also shown that different culture systems produce comparable performance among fry, fingerlings (Sorphea et al., 2019), and grow-out fish (Szentes et al., 2012).

The present study also found that infrastructure type alone did not result in differences in growth patterns, as fish from all surveyed farms exhibited isometric growth. This suggests that cultured Asian seabass were able to maintain proportional increases in length and weight under different farming conditions. Similar growth patterns may reflect effective energy allocation towards maintaining body condition and adaptation to local culture environments (Dikou, 2023; Mitra et al., 2023; Zhang et al., 2023). In contrast, allometric growth patterns have been reported in some marine cage-cultured populations (Che-Zulkifli et al., 2023), where growth allocation may vary according to environmental conditions, age, and reproductive status (Athauda & Anderson, 2013). Juvenile fish frequently skew toward positive allometry during rapid physical expansion. Conversely, as fish mature, shifting metabolic priorities often redirect energy away from immediate mass gain, driving older individuals toward isometric or negative allometric growth patterns (Froese, 2006; Lupatsch et al., 2003).

Operational profitability in aquaculture relies heavily on optimising growth performance. In semi-closed earthen pond systems, growth rates often fluctuate due to shifting environmental variables, organic loading, algal blooms, and erratic oxygen levels. Managing these volatile dynamics requires daily control over pH, dissolved oxygen, and ambient ammonia (Abd El-Hack et al., 2022; Aljehani et al., 2023). Open cage systems benefit from continuous water exchange and natural oxygenation, which can support higher stocking densities, although these systems remain vulnerable to external environmental changes such as pollution and harmful algal blooms (Price et al., 2014; Soto et al., 2008).

Although feeding practices differed among farms, including the use of commercial pellets or trash fish depending on fish size and farm resources, all farms followed a similar feeding frequency of twice daily. Feed quantities were adjusted according to estimated fish biomass and culture duration. Differences in feed type among farms represent a limitation of this field survey; however, the consistency in feeding frequency may have reduced variation in feeding-related management practices among farms.

CONCLUSION

This study indicates that small-scale aquaculture systems in Malaysia can support stable growth patterns in Asian seabass (*Lates calcarifer*) but may also be associated with early onset of male differentiation during the grow-out phase. Condition factor (K) was comparable among culture systems, whereas fish reared in semi-closed systems exhibited higher specific growth rates than those cultured in open floating cages. However, ordinal logistic regression and AIC_c-based model selection proved that environmental salinity remains the primary driver of reproductive transitions. Holding body length constant, fish in low-salinity environments (≤ 25 ppt) exhibit 9.1 times higher odds of entering advanced gonadal stages, compressing the 50% female transition threshold down to 73 cm from 82

cm TL under high-salinity regimes (> 25 ppt). Consequently, grow-out operations utilising semi-closed systems must prioritise strategic water-source sourcing or timed high-salinity water intake to prevent premature maturation from diverting metabolic energy away from muscle production. Conversely, broodstock managers can leverage low-salinity configurations to accelerate female sex-reversal timelines. These operational applications optimise commercial farming predictability. However, future longitudinal research under controlled laboratory conditions is required to overcome unavoidable field constraints. Such limitations include unmonitored daily water chemistry parameters and limited late-stage sample sizes.

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