

Genetic assessment of feed efficiency in the spotted Babylon *Babylonia areolata*

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ABSTRACT

The spotted Babylon (*Babylonia areolata*) is an emerging aquaculture species in China. Feed accounts for 40–60 % of the total expense of spotted Babylon rearing, making feed efficiency one of the most important traits for genetic improvement in this species. This study evaluated the growth and feed efficiency of 528 spotted Babylons from 22 families for 56 days, comprising two periods: the initial 1–28 days and days 29–56. The feed efficiency ratio (FER) and residual feed intake (RFI) displayed genetic correlations in both periods, with heritability values of 0.20 ± 0.077 and 0.14 ± 0.064 , respectively, indicating medium and low heritability, respectively. The RFI had a high genetic and phenotypic correlation with the daily feed intake (DFI), and the FER had a high genetic and phenotypic correlation with the specific growth rate (SGR) and a high genetic correlation with the DFI. A comparative experiment was conducted on 11 families under the group feeding mode. The results showed that there were no significant differences in feed efficiency, growth traits, or feeding traits between the two modes. The study established an evaluation method for determining the feed efficiency of the spotted Babylon using a single individual rearing mode and found that spotted Babylon feed efficiency exhibited good breeding potential.

1. Introduction

The spotted Babylon snail is an emerging aquaculture species in southern China (Fu et al., 2023). During the spotted Babylon rearing process, fish, cephalopods, and formulated diets are used as feed. Therefore, the feed cost is relatively high, accounting for 40–60 % of the total expense of spotted Babylon breeding. Moreover, due to the continuous decline of fishery resources, the price of mixed fish meal is rising. Therefore, increasing the feed efficiency of spotted Babylons could decrease breeding costs and improve the economic benefits of spotted Babylon aquaculture, while reducing the damage to fishery resources and the discharge of aquaculture waste. However, there is currently a lack of research on the feed efficiency of the spotted Babylon. In mollusks, in-depth research on the genetic control of feed efficiency has only been reported in the Pacific abalone (*Haliotis discus hannai*) (Yu et al., 2022).

The trait of feed efficiency is difficult to measure directly, as it requires the use of certain measurement indicators and evaluation

methods. The traditional indicators used to evaluate animal feed efficiency are the feed efficiency ratio (FER) (Crampton and Bell, 1946) and the feed conversion ratio (FCR) (Byerly, 1941). However, researchers have found that using these ratios to study the genetic characteristics of feed utilization efficiency has limitations because it is difficult to determine whether an increase in the FER is the result of a decrease in feed intake, an increase in weight gain, or both. In 1963, Koch and colleagues proposed the concept of residual feed intake (RFI) in their study of cattle (Koch et al., 1963). The RFI is defined as the proportion of feed intake that is not accounted for by the expected requirements for body weight maintenance and production. A low or negative RFI value stands for high feed efficiency, while a high or positive RFI value indicates low efficiency. Experts from the Animal Genetic Resources Committee of the Food and Agriculture Organization (FAO) of the United Nations also recommend the RFI as an indicator for evaluating animal feed efficiency traits (Zhang, 2010). This method has gradually been applied to the study of feed efficiency traits in aquatic organisms such as Nile tilapia (*Oreochromis niloticus*) and the shrimp *Litopenaeus*

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vannamei (de Verdal et al., 2017; Dai et al., 2017).

Regardless of which indicator is used to measure the feed efficiency, a feed efficiency estimate is urgently needed for the spotted Babylon. However, due to the labor-intensive evaluation methods utilized under general aquaculture conditions and the complex underwater environment of aquatic animals (de Verdal et al., 2017), including the breeding methods and feeding characteristics of spotted Babylons, it is difficult to accurately measure feed efficiency traits in spotted Babylon snails. In a study of *Pomacea canaliculata*, researchers placed fresh vegetables together with the snails for 24 h, then centrifuged and drained the remaining feed to determine the food intake and calculate the feed efficiency (Tamburi and Martín, 2009). In a study of *H. discus hannai*, researchers accurately evaluated the feed efficiency. Eighteen individuals from 36 sibling families were selected and placed in independent net bags, which allowed food residue to remain in the mesh bags and feces to be filtered into the water (Yu et al., 2022). In studies involving fish, glass beads made of specific materials are widely utilized in feed, and X-ray scanning can be performed on the tested individuals to determine their food intake (Kause et al., 2006; Maluwa et al., 2006). Although his method is simple and less labor intensive, it may cause stress to the fish and is therefore not conducive to further experiments and evaluation. Regarding the feed efficiency of spotted Babylons, some researchers have studied the effects of various factors on the feed efficiency of immature individuals, but there are limitations in evaluating feed efficiency on a group basis. Such methods cannot be used to identify individual differences (Chaitanawisuti and Kritsanapuntu, 1999; Chaitanawisuti et al., 2001; Chaitanawisuti et al., 2011a; Chaitanawisuti et al., 2011b; Xue et al., 2010; Zhang et al., 2009; Zhong et al., 2023). Therefore, in the design of an evaluation system, the feed selection and feeding device should allow for the evaluation of single individuals, and special attention should be paid to the separation of sand and residual feed while minimizing the loss of residual feed as much as possible.

Heritability refers to the ability of traits to be passed on to offspring, and evaluating the heritability of economic species is a prerequisite for the development of breeding programs for these species. In invertebrates, research has been conducted on abalone and shrimp, demonstrating that the heritability of RFI and FER is moderate to high (Yu et al., 2022; Dai et al., 2017).

Genetic correlations are important parameters in the study of quantitative traits. Such correlations are usually caused by gene polymorphism. Some traits may be positively correlated, while others may be negatively correlated. In the breeding process, when one trait is improved, corresponding attention should be paid to changes in other traits. Research on abalone, shrimp, fish, and terrestrial animals generally presents the assumption that the FER is strongly correlated with growth traits, while the RFI has a low correlation or no correlation with growth traits (Yu et al., 2022; Dai et al., 2017; Kolstad et al., 2004; Thodesen et al., 2001; Archer et al., 1997; Santana et al., 2014).

The individual feeding mode has become a major method utilized in the evaluation of animal feed efficiency due to its advantages, which include accurate evaluation and a lack of harm to the test animals. Many studies have suggested that under collective breeding conditions, it is necessary to overcome competitive pressure, thus requiring energy expenditure, while under individual breeding conditions, competition between animals can be eliminated (Jackson et al., 2003; Silverstein, 2006; Martins et al., 2006; Martins et al., 2011). However, researchers studying the Pacific abalone conducted a comparative experiment between individual and group farming modes and found that there was no significant difference in weight gain between the two modes. Furthermore, the feeding amounts consumed by abalone in the single farming experiment were significantly higher than in the group farming treatment. In addition, the feed intake exhibited a strong correlation in both modes (Spearman correlation coefficient = 0.856) (Yu et al., 2022). Therefore, it is necessary to conduct comparative experiments between individual and group farming modes to test the applicability of individual farming modes.

In the present study, the feed intake and other related indicators of spotted Babylon individuals were measured during two consecutive periods. This work calculated the heritability of feed efficiency as well as growth and feeding traits during these two periods and evaluated the correlation between genetics and phenotype. In addition, a preliminary evaluation was conducted on the possibility of extrapolating the individual feeding results of spotted Babylon to group feeding conditions.

2. Materials and methods

2.1. Experimental animals

On May 30, 2023, a total of 324 pairs of spotted Babylons were obtained from the Xiamen Institute of Oceanography and Fisheries, and egg laying began in early June. By December 1, 2023, a total of 37 families with over 50 siblings had been established. In January 2024, this study selected 22 whole-sibling families that had laid eggs from mid-to late June through early July of 2023 and settled to begin metamorphosis from the end of July through early August. Twenty-four individuals were collected from each family to evaluate the feed efficiency, with 528 individuals evaluated in total. The average shell length of the tested individuals was 2.9 ± 0.27 cm, and the average weight was 4.9 ± 1.3 g.

The 528 spotted Babylons were divided into four parallel groups, with 132 snails in each group, and placed in four pools measuring 118 cm (length) \times 240 cm (width) \times 47 cm (water depth). Each pool contained 132 breeding containers with a length of 19 cm, a width of 9.5 cm, a height of 35 cm, and a water depth of about 15 cm. The excess height was used to prevent the spotted Babylons from climbing out of the breeding containers. A 60-mesh net was used to ensure smooth water flow. The entire aquaculture system shared a circulating water system consisting of a water storage tank, a controllable temperature chiller, an oxygen supply pipeline, a seawater supply pipeline, two water pumps, an oxygen pump, a protein separator, a microfilter, and ultraviolet lamps. Feed was placed on a feeding platform to prevent sand from mixing with residual feed. In addition, there was a water spray hole above each of the four breeding containers, with a shared gas stone in the middle, to ensure that the dissolved oxygen content and water environment in each container were consistent (Fig. 1).

The 528 spotted Babylons were placed in individual breeding containers for 10 days. After the 10-day adaptation period, the spotted Babylons underwent a 56-day feed efficiency evaluation. Feed was prepared in advance before the start of the experiment. The feed used in this experiment was obtained from the carcasses of the same batch of Chinese squid (*Uroteuthis (Photololigo) sinensis*) to ensure that it contained equal nutritional contents. During the experiment, feed was provided at a rate of 30–50 % of the spotted Babylons' body weights every 2 days to ensure that leftover food remained after each feeding, and the weight of the residual feed was recorded. If the feed was completely consumed, the next feeding amount was increased to ensure that the spotted Babylons could eat to satiation. About 2–4 h after feeding, spotted Babylons drill back into the sand. Therefore, feed should be recovered as soon as possible to minimize the impacts of physical disintegration and microorganisms on the quality of residual feed. Subsequently, 30 feed control groups were set up for each feeding to measure the moisture content of the feed. Any remaining feed was gently rinsed with fresh water to remove salt and small amounts of sand that may have been present. The residual feed was collected in a partition box, and its position in the grid of the partition box corresponded to the position of the spotted Babylon in the pool. The feed was then frozen and stored at -20 °C in a refrigerator. The residual feed was dried and weighed every 28 days. During the experiment, 50 % of the water was changed daily, and on the day of feeding, the water was changed after the residual feed was collected. In addition, the temperature was controlled at 23.5 ± 1.0 °C; the salinity was 32.2 ± 0.6 ‰; the pH was 8.1 ± 0.1 , and the dissolved oxygen was 8.75 ± 0.2 mg/L.

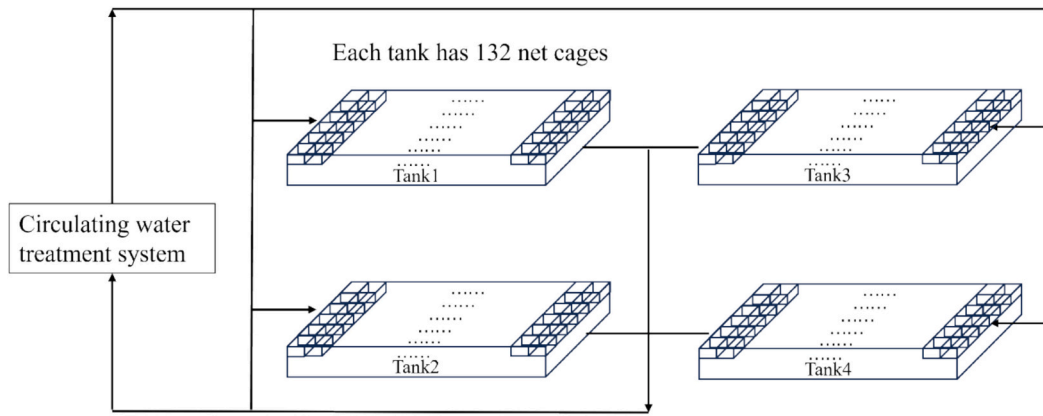


Fig. 1. Measurement system for the feed efficiency of *Babylonia areolata*.

To investigate whether the growth characteristics, feeding habits, and feed efficiency of the spotted Babylon under the individual feeding mode were consistent with the group feeding mode, 11 families containing a large number of individuals were selected from the 22 families mentioned above, with 36 spotted Babylons selected from each family. The spotted Babylons were divided into three pools, with 12 individuals in each pool, and placed in a large net basket. The area of the net basket was 12 times that of the nets used for the evaluation of single individuals at $57 \times 38 \times 35$ cm. The sand content was also 12 times the individual amount and the same source was utilized to ensure that properties such as the particle size and thickness remained consistent. Similarly, the above three pools were placed in the same circulating water system to ensure that insulation and other conditions were consistent. In addition, the experiment also ensured that there was no significant difference in the initial average weight of experimental snails between the two modes.

2.2. Data collection and analysis

In the evaluation experiment of the individual feed efficiency of spotted Babylons, the body weight (BW), shell length (SL), and shell width (SW) were measured on days 0, 28, and 56 and recorded as BW_0 , BW_1 , and BW_2 , respectively; SL_0 , SL_1 , and SL_2 , respectively; and SW_0 , SW_1 , and SW_2 , respectively. The weight gain was calculated as the body growth (BG) of snails for days 1–28, days 29–56, and the entire evaluation period ($BG_1 = BW_1 - BW_0$, $BG_2 = BW_2 - BW_1$). This study also calculated the shell length growth (SLG), ($SLG_1 = SL_1 - SL_0$, $SLG_2 = SL_2 - SL_1$, $SLG = SL_2 - SL_0$), shell width growth (SWG, $SWG_1 = SW_1 - SW_0$, $SWG_2 = SW_2 - SW_1$, $SWG = SW_2 - SW_0$), and specific growth rate (SGR, $SGR_1 = 100 \times (\ln BW_1 - \ln BW_0)/28$, $SGR_2 = 100 \times (\ln BW_2 - \ln BW_1)/28$, $SGR = 100 \times (\ln BW_2 - \ln BW_0)/56$). In addition, the weight gain rate (WGR, $WGR_1 = (BW_1 - BW_0)/BW_0$, $WGR_2 = (BW_2 - BW_1)/BW_1$, $WGR = (BW_2 - BW_0)/BW_0$) was calculated.

The total amount of squid meat fed to each snail was multiplied by (1 – moisture content) minus the corresponding remaining dry feed to obtain the feed intake for each spotted Babylon. The feed intake rates of spotted Babylons on days 1–28 and 29–56 were recorded as FI_1 and FI_2 , respectively. Therefore, the FERs on days 1–28, 29–56, and 1–56 were determined as $FER_1 = WG_1/FI_1$, $FER_2 = WG_2/FI_2$, and $FER = \text{weight gain/feed intake}$, respectively. The FCRs on days 1–28, 29–56, and 1–56 were $FCR_1 = FI_1/WG_1$, $FCR_2 = FI_2/WG_2$, and $FCR = FI/WG$ respectively. To calculate the RFI, a multivariate nonlinear model was employed (daily feed intake (DFI) = $b_1 \times MW^{b_2} + b_3 \times ADG + e$) (Dai et al., 2017). In the equation, the metabolic weight ($MW = (BW \text{ start} + BW \text{ end})/2$), average daily gain (ADG, $BG/56$), and DFI (feed intake/56) are calculated based on the WG and feed intake; b_1 , b_2 , and b_3 are partial regression coefficients; and e is the error term equal to RFI. The RFI values for days 1–28 and 29–56 were recorded as the RFI_1 and RFI_2 ,

respectively. The calculation of the above parameters was completed in R 4.1.3.

In the comparative experiment between individual and group feeding, the evaluation methods utilized to assess various traits of spotted Babylons were the same as those described above. In addition, the trait values of each individual under group breeding conditions were represented by the group averages. The group breeding model can only obtain the mean values of various traits. In addition, at the end of each breeding experiment, preliminary screening was conducted on data such as the BG and feed intake to exclude negative values and outliers close to zero, which indicated an abnormal condition.

2.3. Estimation of genetic parameters

The statistical description and Spearman correlation analysis of all phenotype data were completed using SPSS.27 software, and the trait data were tested for normality distribution. The variance components of SGR, DFI, FER, and RFI were estimated with the ASReml-R V4 software package using the pedigree-based best linear unbiased prediction (BLUP) method (Butler et al., 2009). The fixed effects included gender, age, tank, and initial weight. The model is as follows:

$$y = Xb + Zu + e, \quad (1)$$

where y is the phenotype vector for different traits (SGR, DFI, FER, and RFI); b is a fixed-effect vector containing four factors (different aquaculture systems, age, sex, and initial weight); and X and Z are correlation matrices for fixed and random effects, respectively. The variable u is the random-effects factor vector, which is assumed to follow $\sim N(0, A\sigma_g^2)$, where A is the relationship matrix constructed from the pedigree and σ_g^2 is the additive genetic variance. The residual vector e assumes that $\sim N(0, I\sigma_e^2)$, where I is the identity matrix and σ_e^2 is the residual variance. The narrow-sense heritability (h^2) was computed based on the additive genetic variance and the total phenotypic variance using the following formula:

$$h^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2}. \quad (2)$$

The phenotypic (r_p) and genetic correlations (r_g) between different traits within each period and between the same trait recorded during two periods were estimated using a bivariate model. The equations are as follows (Falconer and Mackay, 1990):

$$r_{p(m,n)} = \frac{\sigma_{p(m,n)}}{\sqrt{\sigma_{p(m)}^2 * \sigma_{p(n)}^2}}, \quad r_{g(m,n)} = \frac{\sigma_{g(m,n)}}{\sqrt{\sigma_{g(m)}^2 * \sigma_{g(n)}^2}}, \quad (3)$$

where $\sigma_{p(m,n)}$ and $\sigma_{g(m,n)}$ are the phenotypic and genetic covariance between two traits (m, n), respectively, and $\sigma_{p_p}^2$ and $\sigma_{g_g}^2$ are the phenotypic

Table 1
Descriptive statistics of feed efficiency, growth traits, and feed intake during days 1–28, 29–56, and 1–56.

Period	Trait	N	Max	Min	Mean	SD	CV
Feed efficiency traits							
Days 1–28	RFI1 (g/day)	523	0.014	−0.018	0.00	0.0049	–
	FER1	523	2.59	0.26	1.31	0.32	25
	FCR1	523	2.70	0.39	0.82	0.26	32
Days 29–56	RFI2 (g/day)	524	0.018	−0.022	0.00	0.0067	–
	FER2	524	2.69	0.68	1.48	0.31	21
	FCR2	524	1.48	0.37	0.71	0.16	23
Days 1–56	RFI (g/day)	524	0.011	−0.015	0.00	0.0044	–
	FER	524	2.62	0.51	1.40	0.25	18
	FCR	524	1.96	0.38	0.74	0.18	21
Growth traits and feed intake							
Days 1–28	SGR1 (g)	523	2.50	0.13	1.04	0.33	32
	WGR (%)	523	1.01	0.04	0.34	0.13	37
	SLG1 (mm)	523	7.49	0.27	2.61	0.92	35
	SWG1 (mm)	523	5.12	0.17	1.93	0.96	50
Days 29–56	FI1 (g)	523	1.72	0.64	1.20	0.17	14
	SGR2 (g)	524	2.25	0.33	1.11	0.27	24
	WGR (%)	524	0.88	0.10	0.37	0.10	28
	SLG2 (mm)	524	7.10	0.48	3.56	0.88	25
	SWG2 (mm)	524	4.51	0.03	1.55	0.72	46
Days 1–56	FI2 (g)	524	2.23	0.8	1.56	0.22	14
	SGR (g)	524	1.93	0.26	1.07	0.26	25
	WGR (%)	524	1.94	0.16	0.84	0.28	33
	SLG (mm)	524	11.19	1.18	6.17	1.47	24
	SWG (mm)	524	6.76	0.48	3.49	1.25	36
	FI (g)	524	3.61	1.66	2.76	0.33	12

RFI: residual feed intake; FER: feed efficiency ratio; FCR: feed conversion ratio; SGR: special growth rate; WGR: weight gain rate; SLG: shell length growth; SWG: shell width growth; FI: feed intake; Max: maximum of the trait estimates; Min: minimum of the trait estimates; Mean: means of the trait estimates; SD: standard deviations of the trait estimates; CV: coefficient of variation for the trait estimates (%).

and genetic variances of traits *m* and *n*, respectively.

3. Results

3.1. Survival rate

After 10 days of temporary care and 56 days of individual evaluation, only one snail died, and three to four snails provided abnormal data, with a total of 523–524 snails available for subsequent analysis.

In the comparative experiment of different breeding modes, 255 out of 256 snails survived in the single breeding mode; out of the 352 snails in the group farming mode, 350 survived, for a survival rate of over 99 %. The traits obtained from the evaluation could thus be employed in subsequent analyses.

3.2. Descriptive statistics of growth, feed intake, and feed efficiency values

The evaluation under individual breeding mode was divided into two periods: days 1–28 and days 29–56. The WGRs in the first and second periods were 32.2 % and 36.7 %, respectively, with a total WGR of 84.3 %, indicating significant growth. There was significant variation in the SGR, SLG, and SWG values, but the variation during the second period decreased compared to the first period, while the mean value increased. The variation in feed intake was relatively small, and the variation in the two periods was relatively stable, with a significant increase in the mean. After testing, both the RFI and FER were normally distributed during the two periods and throughout the entire evaluation cycle. The mean FER values during days 1–28 and 29–56 were 1.31 and 1.48, respectively, ranging from 0.26–2.59 and 0.68–2.69, respectively, exhibiting an upward trend. The average value throughout the evaluation cycle was 1.40, ranging from 0.51 to 2.62; the coefficient of variation in the second period decreased compared to the first period. The RFI ranged from −0.018–0.014 and from −0.022–0.018 in first and second periods, respectively. The WGRs for the first and second stages were 34 % and 37 %, respectively (Table 1). The FER and RFI traits followed a normal distribution (Fig. 2).

3.3. Genetic parameters

In the two feeding periods, SGR displayed moderate heritability, with values of 0.21 ± 0.081 and 0.34 ± 0.107 for days 1–28 and days 29–56, respectively. The DFI values were 0.19 ± 0.078 and 0.41 ± 0.119 , indicating low and high heritability for days 1–28 and days 29–56, respectively. The FER and RFI exhibited low heritability in the two periods, while throughout the entire evaluation cycle, the heritability of FER was 0.20 ± 0.077 , indicating moderate heritability. The RFI was 0.14 ± 0.064 , indicating low heritability. In addition, throughout the entire evaluation cycle, the ratio of shell length/shell width indicated high heritability (Table 2).

The RFI and DFI, as well as the FER and SGR, exhibited a highly positive correlation during both periods and throughout the entire evaluation cycle. The phenotypic correlation between the RFI and DFI was 0.774 ± 0.019 , while the genetic correlation was 0.893 ± 0.076 ; the phenotypic correlation between the FER and SGR was 0.815 ± 0.016 , and the genetic correlation was 0.983 ± 0.030 . For days 1–28, days 29–56, and the entire evaluation cycle, the RFI and SGR exhibited extremely weak phenotypic correlations (-0.035 ± 0.047 , -0.020 ± 0.053 , and 0.008 ± 0.054 , respectively) and high genetic correlations (0.698 ± 0.355 , 0.622 ± 0.223 , and 0.626 ± 0.216 , respectively). The same relationship was also observed between the FER and the DFI. There was a moderate to high phenotypic correlation between the DFI and SGR, with values of 0.507 ± 0.036 , 0.430 ± 0.047 , and 0.598 ± 0.038 for days 1–28, days 29–56, and the entire evaluation cycle, respectively. There was also a high genetic correlation, with values of 0.902 ± 0.098 , 0.869 ± 0.087 , and 0.905 ± 0.059 for days 1–28, days 29–56, and the entire evaluation cycle, respectively (Table 3).

Analysis of the correlations between the SGR, DFI, FER, and RFI in the two periods revealed that in terms of phenotypic correlation, the DFI exhibited a moderate positive correlation of 0.339 ± 0.048 during the two periods, while other traits displayed lower positive correlations of 0.154 ± 0.053 for the SGR, 0.171 ± 0.045 for the FER, and 0.108 ± 0.045 for the RFI. In terms of genetic correlations, FER had a moderate to high positive correlation of 0.578 ± 0.277 , while the other traits

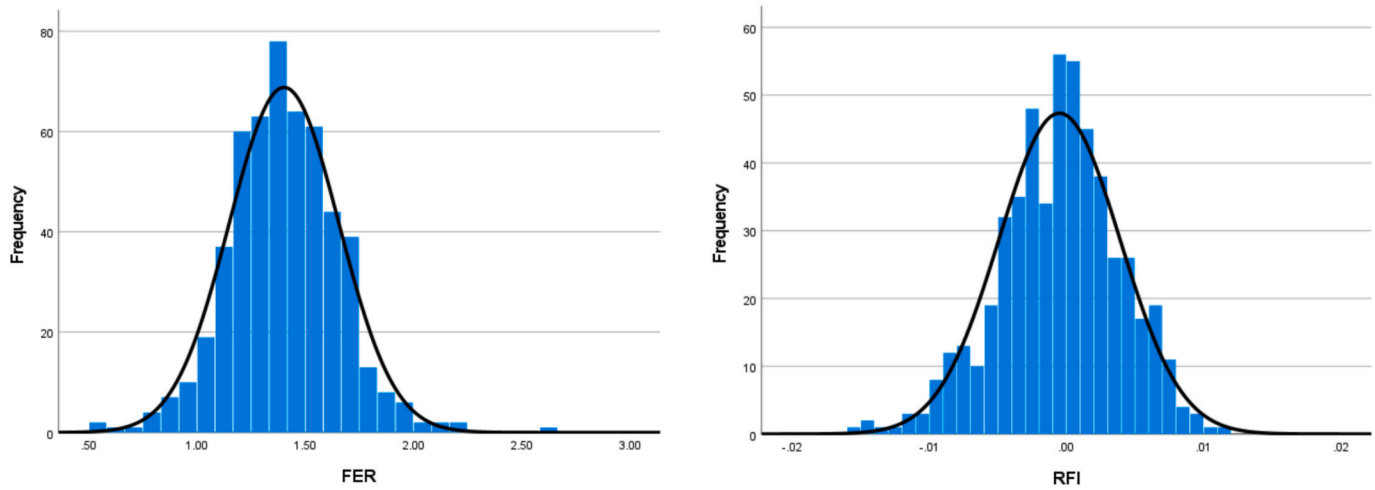


Fig. 2. Normal distributions of the feed efficiency ratio (FER) and residual feed intake (RFI).

Table 2
Estimates of variance components and heritability for the main growth traits and feed efficiency traits.

Period	Traits	Variance components			Heritability (Mean ± SE)
		σ_a^2	σ_c^2	σ_p^2	h^2
Days 1–28	ADG1	5.61E–05	1.93E–04	2.49E–04	0.23 ± 0.085
	SGR1	1.30E–02	4.98E–02	6.29E–02	0.21 ± 0.081
	DFI1	6.61E–06	2.73E–05	3.39E–05	0.19 ± 0.078
	FER1	9.13E–03	9.22E–02	1.01E–01	0.09 ± 0.052
	FCR1	8.69E–03	7.39E–03	8.25E–02	0.11 ± 0.080
	RFI1	1.22E–06	2.19E–05	2.31E–05	0.05 ± 0.042
	ADG2	1.70E–04	1.98E–04	3.68E–04	0.46 ± 0.128
Days 29–56	SGR2	1.40E–02	2.74E–02	4.14E–02	0.34 ± 0.107
	DFI2	2.42E–05	3.53E–05	5.95E–05	0.41 ± 0.119
	FER2	1.40E–02	7.69E–02	9.09E–02	0.15 ± 0.068
	FCR2	2.00E–02	4.69E–03	2.50E–02	0.19 ± 0.087
	RFI2	7.20E–06	3.66E–05	4.37E–05	0.16 ± 0.070
	ADG	1.07E–04	1.21E–04	2.28E–04	0.47 ± 0.129
	Days 1–56	SGR	1.33E–02	1.86E–02	3.18E–02
DFI		1.44E–05	1.70E–05	3.13E–05	0.46 ± 0.127
FER		1.19E–02	4.86E–02	6.05E–02	0.20 ± 0.077
FCR		3.35E–03	2.04E–02	2.38E–02	0.14 ± 0.064
RFI		2.63E–06	1.59E–05	1.86E–05	0.14 ± 0.064
SL/SW		1.49E–03	2.22E–03	3.71E–03	0.41 ± 0.118

RFI: residual feed intake; FER: feed efficiency ratio; FCR: feed conversion ratio; SGR: special growth rate; shell width growth; DFI: daily feed intake. ADG: average daily gain; SL: shell length; SW: shell width.

exhibited higher genetic correlations (SGR = 0.899 ± 0.123 , DFI = 0.984 ± 0.073 , and RFI = 0.824 ± 0.323 ; Table 4).

In addition, the FER differed significantly between the two periods, with an improvement in the second period compared to the first period

Table 3
Phenotypic and genetic correlations with the standard error (SE) between different traits.

Period	Correlation	Traits				
		RFI–DFI	RFI–SGR	FER–DFI	FER–SGR	DFI–SGR
1–28	Phenotypic	0.821 ± 0.015	–0.035 ± 0.047	0.081 ± 0.047	0.839 ± 0.014	0.507 ± 0.036
	Genetic	0.939 ± 0.110	0.698 ± 0.355	0.875 ± 0.225	0.913 ± 0.086	0.902 ± 0.098
29–56	Phenotypic	0.867 ± 0.012	–0.020 ± 0.053	–0.118 ± 0.056	0.762 ± 0.020	0.430 ± 0.047
	Genetic	0.926 ± 0.052	0.622 ± 0.223	0.628 ± 0.224	0.924 ± 0.062	0.869 ± 0.087
1–56	Phenotypic	0.774 ± 0.019	0.008 ± 0.054	0.148 ± 0.055	0.815 ± 0.016	0.598 ± 0.038
	Genetic	0.893 ± 0.076	0.626 ± 0.216	0.810 ± 0.141	0.983 ± 0.030	0.905 ± 0.059

RFI–DFI: correlation between the residual feed intake and the daily feed intake; RFI–SGR: correlation between the residual feed intake and the specific growth rate; FER–DFI: correlation between the feed efficiency ratio and the daily feed intake; FER–SGR: correlation between the feed efficiency ratio and the specific growth rate; DFI–FER: correlation between the daily feed intake and the specific growth rate.

($P < 0.01$), and significant fluctuations were observed in RFI values (Figs. 3 and 4).

3.4. Evaluation of different feeding modes

The basic statistics for the BW_0 , DFI, SGR, and FER under the two aquaculture modes are presented in Table 5. Of the 264 snails in the individual breeding experiment, 263 survived, while 391 of 393 snails in the group breeding mode survived. The survival rate ranged from 99 % to 100 %, with no significant difference between the two modes. The average BW_0 of snails selected for the two aquaculture modes was not significantly different. Individuals from the same family did not show significant differences in the two modes ($P > 0.05$) (Fig. 5a). After 56 days of evaluation, only one family displayed a significant difference in the average DFI between the two farming modes. Overall, the individual farming mode produced slightly higher DFI, but the difference was not significant ($P > 0.05$) (Fig. 5b). In terms of specific growth rates, there were no significant differences among families or in the overall data (Fig. 5c). Two of the 11 families displayed significantly higher FER values in the group farming mode compared to the individual farming mode. Overall, the FER under the group farming mode was higher than that under the individual farming mode, ($P = 0.061 > 0.05$). The difference was not significant, but close to the critical value. Spearman correlation analysis was conducted on the ranks of trait values for each family under the two farming modes. The correlations between the SGR and the FER under different farming modes were 0.855 and 0.773, respectively (Fig. 5 and Table 5).

4. Discussion

Although the feed efficiency of spotted Babylons is an economically

Table 4
Phenotypic and genetic correlations with standard errors (SE) of the same traits in the two breeding periods.

Correlation	Traits				
	SGR1–SGR2	DFI1–DFI2	FER1–FER2	FCR1–FCR2	RFI1–RFI2
Phenotypic	0.154 ± 0.053	0.339 ± 0.048	0.171 ± 0.045	0.177 ± 0.043	0.108 ± 0.045
Genetic	0.899 ± 0.123	0.984 ± 0.073	0.578 ± 0.277	0.675 ± 0.401	0.824 ± 0.323

SGR1–SGR2: correlation of the specific growth rate between periods; DFI1–DFI2: correlation of the daily feed intake between periods; FER1–FER2: correlation of the feed efficiency ratio between periods; FCR1–FCR2: correlation of the feed conversion ratio; RFI1–RFI2: correlation of the residual feed intake between periods.

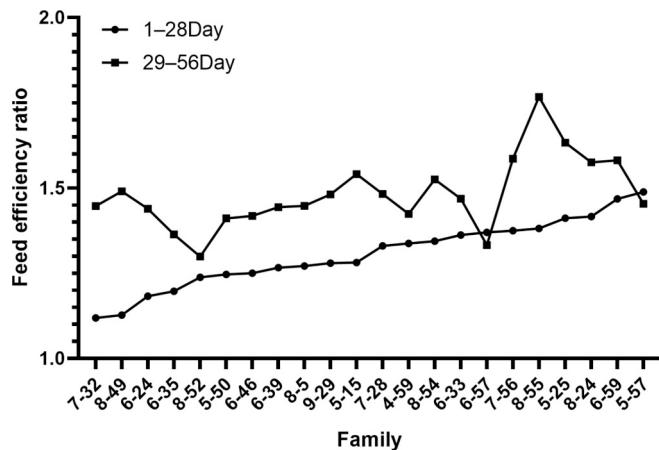


Fig. 3. Mean feed efficiency ratios (FERs) of 22 families during the first and second test periods.

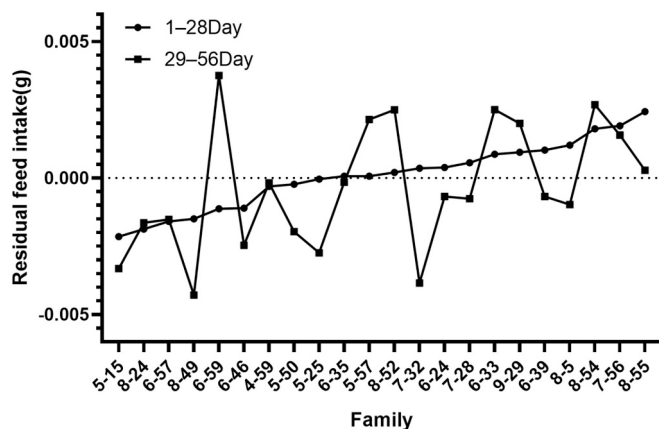


Fig. 4. Mean residual feed intake (RFI) of 22 families during the first and the second test periods.

Table 5
Descriptive statistics for the initial body weight (BW₀), daily feed intake (DFI), specific growth rate (SGR), and feed efficiency ratio (FER) in the individual feeding experiment and the group feeding experiment.

Trait	Individual feeding experiment		Group feeding experiment	
	N	Mean	N	Mean
BW ₀	264	4.76	393	4.85
DFI	263	0.049	391	0.047
SGR	263	1.10	391	1.07
FER	263	1.40	391	1.49

BW₀: initial body weight; DFI: daily feed intake; SGR: specific growth rate; FER: feed efficiency ratio; N: number; Mean: means of the trait estimates.

important trait, little research has been conducted on this subject to date (Sun et al., 2023; Sun et al., 2024). There are two main reasons for this. First, spotted Babylons have a habit of burrowing into sand, making it difficult to separate food and sand when mixed, which increases error and the workload required to obtain measurements. Sand-free cultivation not only does not conform to actual breeding practices but can also adversely affect the growth traits and survival rate (Chaitanawisuti and Kritsanapuntu, 1997). Second, spotted Babylons are prone to submerging sand during feeding, increasing evaluation errors and presenting difficulty in recovering residual feed. Therefore, this study used a feeding platform to reduce the probability of sand and residual feed being mixed. In this study, squid was utilized as the feed, and the firm texture of the meat minimized the problem of residual feed scattering. The spotted Babylons were fed every 2 days, with multiple operators working in shifts while checking the operation of the equipment daily to ensure normal operation. At the end of this experiment, the WGR of the spotted Babylons reached 84.3 %, nearly doubling, and the final absolute weight was 8.79 g, indicating that the spotted Babylons were close to sexual maturity and market weight. In addition, the spotted Babylons survival rate reached as high as 99.8 %, demonstrating the feasibility of this evaluation method.

Common indicators used to evaluate animal feed efficiency include the FER, FCR, and RFI. The FER and FCR are reciprocals, and thus they essentially measure the same trait. In this study, the FER and RFI values of the spotted Babylons were evaluated, and both displayed a normal distribution. The coefficient of variation of the FER was 18, and the difference between the maximum and minimum values had a ratio of five, indicating significant variation among individuals. The RFI value is essentially the residual term of the calculation model, and thus its mean and coefficient of variation cannot be calculated. However, the normal distribution trends of individual RFI values reflected significant differences in this trait among individuals. Previous studies of *H. discus hannai* (Yu et al., 2022), *L. vannamei* (Dai et al., 2017), *O. niloticus* (de Verdal et al., 2018), and *Salmo salar* (Thodesen et al., 2001) also reported significant genetic variation in the FER and RFI, and the findings provided a basis for selective breeding to improve feed efficiency traits.

The RFI, as a commonly used indicator for the evaluation of feed efficiency, is widely employed in research on terrestrial animals, shrimp, and other organisms. In this study, the heritability of RFI was low at 0.14 ± 0.064. This heritability was lower than those of species including *H. discus hannai* (Yu et al., 2022), *L. vannamei* (Dai et al., 2017), and *Oncorhynchus mykiss* (Grima et al., 2008). The FER is another important indicator of feed efficiency. The heritability of 0.2 ± 0.077 in this study indicated moderate heritability. This value was lower than values reported for animals including chickens (Aggrey et al., 2010), *H. discus hannai* (Yu et al., 2022), and *L. vannamei* (Dai et al., 2017). Differences between species (Mestav et al., 2018), the iterations of the pedigree (Cesarani et al., 2021), and genetic relationships between selected families (Pettersson et al., 2019) all have an impact on the assessment of heritability. Currently, among the animals that have been studied for the heritability of feed efficiency, the most closely related species to spotted Babylon is abalone (*H. discus hannai*), but this species belongs to a different order. Therefore, compared to other species, the spotted Babylon has many unique characteristics in terms of feed efficiency. Due to the special nature of fertilization within the body of the spotted Babylon, it is difficult and labor-intensive to construct a half-sibling family

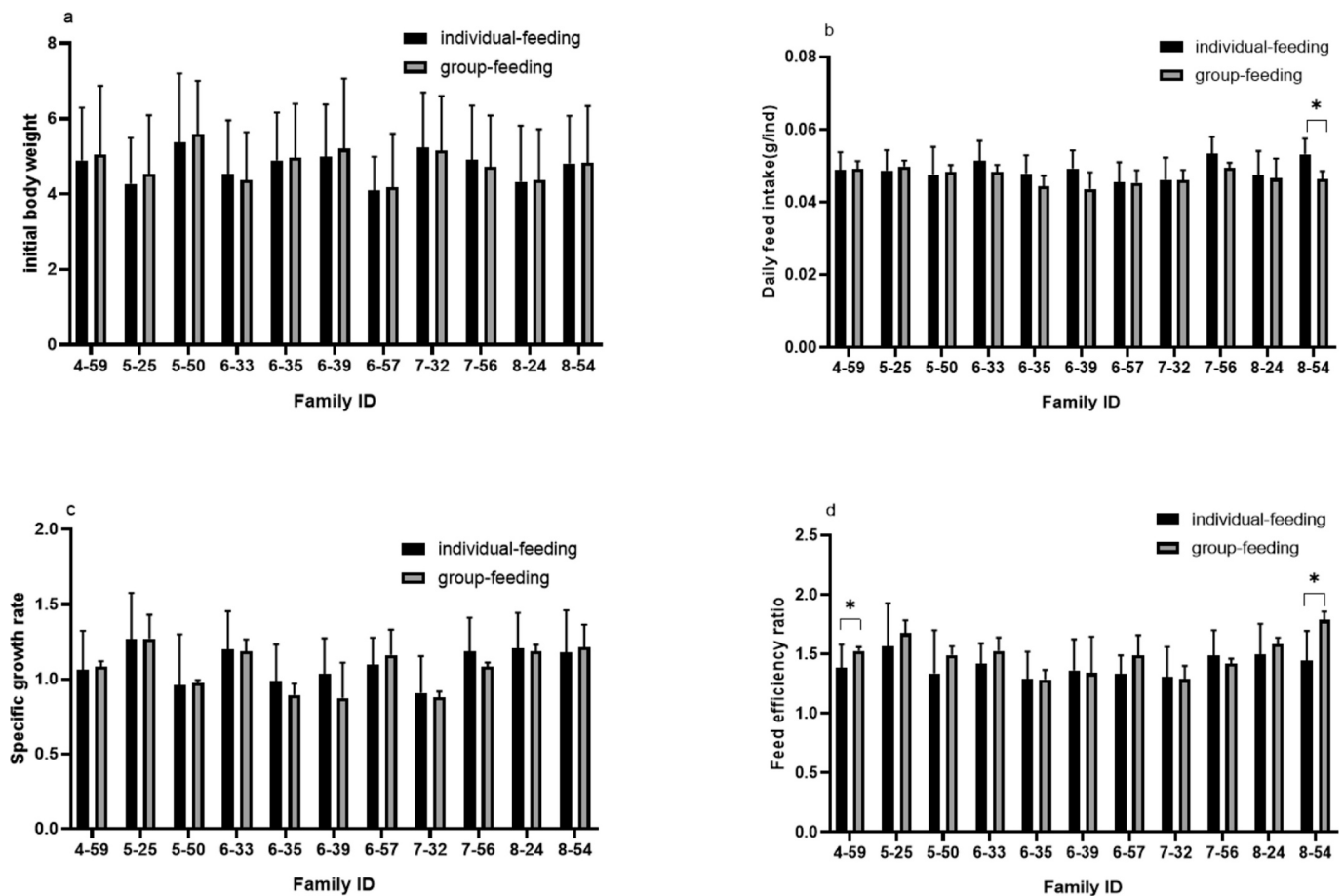


Fig. 5. Comparisons of the (a) average initial body weight (BW_0), (b) average daily feed intake (DFI), (c) average specific growth rate (SGR), and (d) feed efficiency ratio (FER) of 11 families in the individual feeding experiment and the group feeding experiment. * $P < 0.05$.

composed of one male and multiple females, and the success rate of such efforts is usually low. Moreover, there is currently no technology available to facilitate the construction of half-sibling families containing one female and multiple males. Therefore, the 22 families used in this study were all full-sibling families, and the influence of paternal and maternal effects on heritability could not be calculated. The 22 families used in this study were obtained through population breeding, and the genetic relationships among the families could not be traced.

This study detected strong genetic correlations between the FER, SGR, and DFI, which were primarily determined by their definitions. The high positive correlation between the FER and growth traits was similar to current research findings in most animals (Yu et al., 2022; Dai et al., 2017; Do et al., 2013). The RFI was also highly correlated with the SGR and DFI, but there was a weak phenotypic correlation with the SGR. This finding indicates that the correlation between the RFI and growth traits has certain limitations. Using this indicator for breeding can reduce spotted Babylon food intake while minimizing the impact on growth traits. Moreover, the strong positive correlation between the DFI and the RFI suggests that using the RFI for breeding can effectively decrease food intake. In most animal studies, it is generally assumed that there are no correlations or weak correlations between the RFI and growth traits (Dai et al., 2017; Do et al., 2013; de Verdal et al., 2018). However, previous research on *H. discus hammai* (Yu et al., 2023) revealed a moderate correlation between growth traits and RFI traits under certain environmental conditions. The differences between reported results may be related to differences between species and evaluation methods.

In the present study, the heritabilities of FER and RFI were not stable between the two periods, as the heritability in the second period was

higher than that in the first period. This phenomenon has been observed in previous studies on cattle (Archer et al., 1997) and *L. vannamei* (Dai et al., 2017), and it may be related to the gradual adaptation of animals to the environment and age-related changes during breeding experiments (Henryon et al., 2002). However, there were high genetic correlations between each trait in the two periods, demonstrating the rationality of this evaluation method. In addition, in subsequent evaluations, it may be necessary to shorten the evaluation cycle through extending the temporary breeding time. In the present study, the heritability of the FER was higher than that of the RFI. The high positive correlation between the FER and growth traits indicates that breeding based on the FER can simultaneously select for growth traits. However, the high genetic correlation between the SGR and the DFI also suggests that employing the FER when breeding for feed efficiency may have certain limitations, with each approach having its advantages and disadvantages. The specific selection of indicators should be based on the relevant indicator, and the differences between the two indicators under various factors need to be explored (Yu et al., 2023).

To accurately calculate the actual food intake of each snail, this study adopted a single individual evaluation model. However, group breeding is conducted in aquaculture. Therefore, to eliminate the impact of aquaculture modes on this study, a control experiment was designed for individual and group aquaculture modes. The experiment was conducted simultaneously using the same circulating water system, while ensuring consistent environmental conditions. Under the conditions of this experiment, there were no significant differences in growth traits within the same family and within the overall population of the spotted Babylon. The DFI and FER only displayed significant differences in a small number of families, and the overall effect was not significant.

However, the analysis of the FER produced a *P*-value of 0.061, very close to the significance threshold of 0.05, indicating that different breeding modes may have a weak impact on the feed efficiency of spotted Babylon snails. In a study of abalone, Yu et al. (2022) found that there was no significant difference in growth traits between the two modes, but the amount of feed consumed by abalone was significantly reduced in the group farming mode, leading to a significantly lower FER in the individual farming mode compared to the group farming mode. This may be related to competition between abalone and other social behaviors that lead to limited feeding in some individuals. The use of a snout tube for feeding the spotted Babylon ensures that multiple snails can feed simultaneously, greatly improving space utilization. Spotted Babylon snails feed rapidly, and feeding can usually be completed within 20 min. Therefore, even if some individuals did not eat immediately, they could continue to eat after other snails had finished. Thus, the unique feeding characteristics of spotted Babylon greatly reduce feeding competition, and both modes result in sufficient quantities being consumed, resulting in no significant differences in growth traits, feeding traits, or feed efficiency traits between the two modes. In studies on species including *L. vannamei* (Dai et al., 2018), *S. salar* (Metcalfe, 1999), and *O. niloticus* (Schreiber et al., 1998), farming patterns were found to affect feeding and feed efficiency traits, which was related to the social interactions of fish (Koebele, 1985) and shrimp (Luan et al., 2015). The spotted Babylon operates as a single individual in its natural state, and thus the effects of its social behaviors are relatively weak. However, the long-term domestication of high-density group breeding models may make snails more adaptable to group breeding models, which may have an impact on traits such as the feed efficiency. Because the statistical analysis showed that there was no significant difference between the two modes, the results indicate that it is feasible to use a single individual breeding model for evaluation and breeding. In addition, there are limited data available under the group farming mode, and RFI values estimated through regression analysis are not accurate. Therefore, the evaluation of the RFI for the spotted Babylon under the two farming modes is limited.

5. Conclusion

This study established an individual-based method for measuring the feed efficiency of spotted Babylons. The quantitative genetic parameters for the FER and RFI were measured, and the results showed that there was significant variation between the two characteristics. In addition, no significant differences were found in various traits between individual and group rearing modes, indicating the rationality of this method. Accordingly, this study provides a reliable trait evaluation method for breeding toward a high feed efficiency in spotted Babylons.

CRedit authorship contribution statement

Linwei Nie: Writing – review & editing, Writing – original draft, Resources, Methodology, Formal analysis, Data curation, Conceptualization. **Yijie Kong:** Resources, Methodology, Data curation. **Ziyi Ma:** Resources, Methodology, Data curation. **Jingqiang Fu:** Writing – review & editing, Software, Methodology, Funding acquisition. **Shengtai Liu:** Resources, Methodology, Data curation. **Xuan Luo:** Resources, Investigation. **Weiwei You:** Writing – review & editing, Validation, Investigation, Funding acquisition. **Caihuan Ke:** Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

References

- Aggrey, S.E., Karnuah, A.B., Sebastian, B., Anthony, N.B., 2010. Genetic properties of feed efficiency parameters in meat-type chickens. *Genet. Sel. Evol.* 42, 1–5. <https://doi.org/10.1186/1297-9686-42-25>.
- Archer, J., Arthur, P., Herd, R., Parnell, P., Pitchford, W., 1997. Optimum postweaning test for measurement of growth rate, feed intake, and feed efficiency in British breed cattle. *J. Anim. Sci.* 75, 2024–2032. <https://doi.org/10.2527/1997.7582024x>.
- Butler, D., Cullis, B., Gilmour, A., Gogel, B., 2009. ASReml-R reference manual.
- Byerly, T., 1941. Feed and Other Costs of Producing Market Eggs. Univ Maryland Agric ExpStn, College Park, MD, Bull (A1 (Technical).
- Cesarani, A., Garcia, A., Hidalgo, J., Degano, L., Vicario, D., Macciotta, N.P.P., Lourenco, D., 2021. Genomic information allows for more accurate breeding values for milkability in dual-purpose Italian Simmental cattle. *J. Dairy Sci.* 104 (5), 5719–5727. <https://doi.org/10.3168/jds.2020-19838>.
- Chaitanawisuti, N., Kritsanapuntu, A., 1997. Effects of stocking density and substrate presence on growth and survival of juvenile spotted babylon, *Babylonia areolata* link, 1807 (Neogastropoda: Buccinidae). *J. Shellfish Res.* 16 (2), 429–433.
- Chaitanawisuti, N., Kritsanapuntu, A., 1999. Effects of different feeding regimes on growth, survival and feed conversion of hatchery-reared juveniles of the gastropod mollusc spotted babylon *Babylonia areolata* (link 1807) in flowthrough culture systems. *Aquac. Res.* 30 (8), 589–593. <https://doi.org/10.1046/j.1365-2109.1999.00366.x>.
- Chaitanawisuti, N., Kritsanapuntu, A., Natsukari, Y., Kathinmai, S., 2001. Effects of feeding rates on the growth, survival and feed utilization of hatchery-reared juvenile spotted babylon *Babylonia areolata* link 1807 in a flowthrough seawater system. *Aquac. Res.* 32 (9), 689–692. <https://doi.org/10.1046/j.1365-2109.2001.00603.x>.
- Chaitanawisuti, N., Choeychom, C., Piyatiratitvorakul, S., 2011a. Effect of dietary supplementation of brewers yeast and nucleotide singularly on growth, survival and vibriosis resistance on juveniles of the gastropod spotted babylon (*Babylonia areolata*). *Aquac. Int.* 19 (3), 489–496. <https://doi.org/10.1007/s10499-010-9364-1>.
- Chaitanawisuti, N., Kritsanapuntu, S., Santaweek, W., 2011b. Effects of dietary protein and lipid levels and protein to energy ratios on growth performance and feed utilization of hatchery-reared juvenile spotted babylon (*Babylonia areolata*). *Aquac. Int.* 19 (1), 13–21. <https://doi.org/10.1007/s10499-010-9337-4>.
- Crampton, E., Bell, J., 1946. The effect of fineness of grinding on the utilization of oats by market hogs. *J. Anim. Sci.* 5 (2), 200–210. <https://doi.org/10.2527/jas1946.52200x>.
- Dai, P., Luan, S., Lu, X., Luo, K., Meng, X., Cao, B., Kong, J., 2017. Genetic assessment of residual feed intake as a feed efficiency trait in the Pacific white shrimp *Litopenaeus vannamei*. *Genet. Sel. Evol.* 49, 61. <https://doi.org/10.1186/s12711-017-0334-1>.
- Dai, P., Kong, J., Meng, X., Luo, K., Lu, X., Chen, B., Luan, S., 2018. Genotype by environment interaction for feed efficiency trait of the juvenile Pacific white shrimp *Litopenaeus vannamei* held in individuals vs. in groups. *Aquaculture* 500, 506–513. <https://doi.org/10.1016/j.aquaculture.2018.10.063>.
- de Verdal, H., Komen, H., Quillet, E., Chatain, B., Allal, F., Benzie, J., Vandeputte, M., 2017. Improving feed efficiency in fish using selective breeding: areview. *Rev. Aquac.* 1–19. <https://doi.org/10.1111/raq.12202>.
- de Verdal, H., Vandeputte, M., Mekkiaw, W., Chatain, Béatrice, Benzie, J.A.H., 2018. Quantifying the genetic parameters of feed efficiency in juvenile Nile tilapia *Oreochromis niloticus*. *BMC Genet.* 19. <https://doi.org/10.1186/s12863-018-0691-y>.
- Do, D., Strathe, A., Jensen, J., Mark, T., Kadarmideen, H., 2013. Genetic parameters for different measures of feed efficiency and related traits in boars of three pig breeds. *J. Anim. Sci.* 91 (9), 4069–4079. <https://doi.org/10.2527/jas.2012-6197>.
- Falconer, D.S., Mackay, T., 1990. Introduction to quantitative genetics. *Biometrics* 46, 1231.
- Fu, J., You, W., Luo, X., Ke, J., Ke, C., 2023. Advances in biology and genetic breeding of *Babylonia*. *J. Xiamen Univ. (Nat. Sci.)* 62 (3), 356–364.
- Grima, L., Quillet, E., Boujard, T., Robert-Granie, C., Chatain, B., Mambrini, M., 2008. Genetic variability in residual feed intake in rainbow trout clones and testing of indirect selection criteria (open access publication). *Genet. Sel. Evol.* 40, 607. <https://doi.org/10.1186/1297-9686-40-6-607>.
- Henryon, M., Jokumsen, A., Berg, P., Lund, I., Pedersen, P.B., Olesen, N.J., Slierendrecht, W.J., 2002. Genetic variation for growth rate, feed conversion

- efficiency, and disease resistance exists within a farmed population of rainbow trout. *Aquaculture* 209 (1–4), 59–76. [https://doi.org/10.1016/S0044-8486\(01\)00729-3](https://doi.org/10.1016/S0044-8486(01)00729-3).
- Jackson, L., Robinson, E.H., Li, M., Wolters, W.R., McKee, D.A., 2003. Restricted and satiate feeding of two genetically isolated strains of juvenile channel catfish *Ictalurus punctatus* reared on 28% and 32% protein diets. *J. World Aquacult. Soc.* 34 (4), 478–486. <https://doi.org/10.1111/j.1749-7345.2003.tb00086.x>.
- Kause, A., Tobin, D., Dobby, A., Houlihan, D., Martin, S., Mantysaari, E.A., Ruohonen, K., 2006. Recording strategies and selection potential of feed intake measured using the X-ray method in rainbow trout. *Genet. Sel. Evol.* 38, 389–409. <https://doi.org/10.1186/1297-9686-38-4-389>.
- Koch, R., Swiger, L., Chambers, D., Gregory, K., 1963. Efficiency of feed use in beef cattle. *J. Anim. Sci.* 22, 486–494. <https://doi.org/10.2527/jas1963.222486x>.
- Koebele, B., 1985. Growth and the size hierarchy effect: an experimental assessment of three proposed mechanisms; activity differences, disproportional food acquisition, physiological stress. *Environ. Biol. Fish* 12, 181–188. <https://doi.org/10.1007/BF00005149>.
- Kolstad, K., Grisdale-Helland, B., Gjerde, B., 2004. Family differences in feed efficiency in Atlantic salmon (*Salmo salar*). *Aquaculture* 241 (1–4), 169–177. <https://doi.org/10.1016/j.aquaculture.2004.09.001>.
- Luan, S., Luo, K., Chai, Z., Cao, B., Meng, X., Lu, X., Liu, N., Xu, S., Kong, J., 2015. An analysis of indirect genetic effects on adult body weight of the Pacific white shrimp *Litopenaeus vannamei* at low rearing density. *Genet Sel Evol* 47, 1–8.
- Maluwa, A., Gjerde, B., Ponzoni, R., 2006. Genetic parameters and genotype by environment interaction for body weight of *Oreochromis shiranus*. *Aquaculture* 259 (1–4), 47–55. <https://doi.org/10.1016/j.aquaculture.2006.06.033>.
- Martins, C., Schrama, J., Verreth, J.A., 2006. The relationship between individual differences in feed efficiency and stress response in African catfish *Clarias gariepinus*. *Aquaculture* 256 (1–4), 588–595. <https://doi.org/10.1016/j.aquaculture.2006.02.051>.
- Martins, C., Conceição, L., Schrama, J., 2011. Feeding behavior and stress response explain individual differences in feed efficiency in juveniles of Nile tilapia *Oreochromis niloticus*. *Aquaculture* 312 (1–4), 192–197. <https://doi.org/10.1016/j.aquaculture.2010.12.035>.
- Mestav, B., Tatlyer, A., Ba, S., 2018. Meta-analysis of heritability estimates for growth trait in different sheep breeds. In: *Proceedings of the 1st International Agricultural Science Congress*, pp. 1173–1180.
- Metcalfe, A., 1999. Costs of rapid growth: the risk of aggression is higher for fast-growing Salmon. *Funct. Ecol.* 13 (6), 793–800.
- Pettersson, E., Lichtenstein, P., Larsson, H., Song, J., Agrawal, A., Borglum, A.D., Polderman, T., et al., 2019. Genetic influences on eight psychiatric disorders based on family data of 4 408 646 full and half-siblings, and genetic data of 333 748 cases and controls. *Psychol. Med.* 49 (7), 1166–1173.
- Santana, M., Utsunomiya, Y., Neves, H., Gomes, R., Garcia, J., Fukumasu, H., Ferraz, J., et al., 2014. Genome-wide association analysis of feed intake and residual feed intake in Nellore cattle. *BMC Genet.* 15, 1–8. <https://doi.org/10.1186/1471-2156-15-21>.
- Schreiber, S., Focken, U., Becker, K., 1998. Individually reared female Nile tilapia (*Oreochromis niloticus*) can grow faster than males. *J. Appl. Ichthyol.* 14 (1–2), 43–47. <https://doi.org/10.1111/j.1439-0426.1998.tb00612.x>.
- Silverstein, J., 2006. Relationships among feed intake, feed efficiency, and growth in juvenile rainbow trout. *N. Am. J. Aquac.* 68 (2), 168–175. <https://doi.org/10.1577/A05-010.1>.
- Sun, Y., Du, X., Yang, Y., Wang, A., Gu, Z., Liu, C., 2023. Dietary taurine intake affects the growth performance, lipid composition, and antioxidant defense of juvenile ivory shell (*Babylonia areolata*). *Animals* 13, 2592. <https://doi.org/10.3390/ani13162592>.
- Sun, Y., Yang, W., Yang, Y., Yu, F., Liu, C., 2024. Effects of allixin supplementation on the growth performance, biochemical composition and immune responses of ivory shell (*Babylonia areolata*). *Aquac. Rep* 38. <https://doi.org/10.1016/j.aqrep.2024.102306>.
- Tamburi, N., Martín, P., 2009. Feeding rates and food conversion efficiencies in the apple snail *Pomacea canaliculata* (Caenogastropoda: Ampulariidae). *Malacologia* 51 (2), 221–232. <https://doi.org/10.4002/040.051.0201>.
- Thodesen, J., Gjerde, B., Grisdale-Helland, B., Storebakken, T., 2001. Genetic variation in feed intake, growth and feed utilization in Atlantic salmon (*Salmo salar*). *Aquaculture* 194 (3–4), 273–281. [https://doi.org/10.1016/S0044-8486\(00\)00527-5](https://doi.org/10.1016/S0044-8486(00)00527-5) Get rights and content.
- Xue, M., Ke, C., Wang, D., Wei, Y., 2010. Effects of starvation and recovery on growth, proximate composition and RNA/DNA ratio in juvenile spotted ivory shell (*Babylonia areolata*). *J. Fish. China* 34 (3), 481–488. <https://doi.org/10.3724/SP.J.1231.2010.06558>.
- Yu, W., Liu, J., Yu, F., Shen, Y., Gong, S., Lu, Y., Peng, W., Wang, Y., Gan, Y., Xiao, Q., Luo, X., You, W., Ke, C., 2022. Heritability and genetic correlation for residual feed intake of Pacific abalone *Haliotis discus hannai*. *Aquaculture* 553, 738060. <https://doi.org/10.1016/j.aquaculture.2022.738060>.
- Yu, W., Shen, Y., Liu, J., Zou, W., Huang, Z., Huang, M., Lu, Y., Ke, J., Luo, X., You, W., Ke, C., 2023. Genotype by environment interactions in feed efficiency of Pacific abalone (*Haliotis discus hannai*) reared at different water temperatures. *Aquaculture* 562, 738764. <https://doi.org/10.1016/j.aquaculture.2022.738764>.
- Zhang, Y., 2010. New direction in integrated researches on animal nutrition with genetics/breeding. *China Cattle Sci.* 36, 1–8.
- Zhang, L., Zhou, Q., Cheng, Y., 2009. Effect of dietary carbohydrate level on growth performance of juvenile spotted babylon (*babylonia areolata* link 1807). *Aquaculture* 295 (3–4), 238–242. <https://doi.org/10.1016/j.aquaculture.2009.06.045>.
- Zhong, M., Liu, X., Xu, R., Liu, X., Jiang, Q., Song, X., Lu, Y., Luo, X., Yue, C., Qin, S., Lü, W., 2023. Effects of light quality and intensity on the juvenile physiological metabolism of *Babylonia areolata*. *Aquac. Rep* 33, 101758. <https://doi.org/10.1016/j.aqrep.2023.101758>.