

Genetic Parameters of Body Length and Response to Selection for Growth Across Four Generations of *Artemia sinica*

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Abstract To investigate the genetic components of growth in the brine shrimp *Artemia sinica*, we estimated the genetic parameters of body length and the response to selection using a fully pedigreed population of *A. sinica*. The base population was generated from four wild founder populations. We tested 4160 offspring in 360 families over four generations for growth and survival performance. Across four generations, we produced full- and half-sib families with nested mating, where two dams were mated to the same sire. Individual body length was measured for each nauplius at day 20 post-hatching. Heritability of body length was estimated across four generations with the restricted maximum likelihood method. The heritability of body length in *A. sinica* was low (0.14 ± 0.05), and the common environmental effect was 0.14 ± 0.02 . We estimated the response to selection for body length by calculating the difference in the mean breeding values between different generations. The accumulated genetic gain in body length was 278.94 μm after three generations of selection. This low response to selection was probably caused by the low heritability of body length, small sample size, and the low selection intensity (50%). The results suggest that *A. sinica* selective breeding programs must be changed to generate any substantial, sustainable genetic increases in body length. We suggest that optimal genetic gains could be achieved by introducing wild strains into the nuclear breeding population to increase genetic variation, and by increasing the size of the breeding population to allow for increased selection intensity.

Key words *Artemia sinica*; body length; heritability; selection responses

1 Introduction

Brine shrimp (Artemiidae: *Artemia*) are a fundamental link in the aquatic food chain (Sorgeloos *et al.*, 2001). The biology, evolution, development, and ecology of brine shrimp have been well studied (Zhou *et al.*, 2008), as well as their resistance to unfavorable conditions, such as low temperature and high salinity (Jiang *et al.*, 2007; Zheng *et al.*, 2011). Brine shrimp are often used to evaluate aquatic resource management policies (Raikow *et al.*, 2006). In addition, brine shrimp are considered ideal models for genetic research because they are small, have short life cycles, form pairs easily, and are both parthenogenesis and amphigenesis (Barigozzi *et al.*, 1974; Briskia *et al.*, 2008).

Brine shrimp at various life cycle stages are an important food source for many economically important aquaculture species. However, if the brine shrimp is too small,

it will be difficult for the predator's mouth to adapt to the size, which restricts their uses as food resources. It is possible that selective breeding could solve this problem by increasing the size of brine shrimp (Shirdhankar *et al.*, 2003). Despite the wide range of literature on brine shrimp, studies of quantitative genetic characters are rare, and previous studies have tended to focus on *A. franciscana*. Browne *et al.* (1984) analyzed the genetic components of several traits in 12 strains of *A. franciscana*, while the heritability values of various traits related to growth and reproduction were studied by Shirdhankar *et al.* (2003) and Briska *et al.* (2008). Further studies have indicated that the heritability of nauplii length was moderate and that the heritability of nauplii width was high. It has been suggested that these traits could be exploited using selective breeding techniques (Leger *et al.*, 1986; Tackaert *et al.*, 1987; Shirdhankar *et al.*, 2003). However, to our knowledge, no information on the heritability of growth traits is available for *A. sinica*, which is an endemic brine shrimp species restricted to China.

Here, we provide a reliable estimate of the heritability

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of growth traits in *A. sinica*. We analyzed several generations of data using the restricted maximum likelihood method (REML). We then calculated the predicted response of *A. sinica* to selective breeding by performing four generations of selection. Finally, we discussed the sustainability of a breeding program with respect to genetic improvement or deterioration.

2 Methods

2.1 Origin of the Base Population

Our breeding experiments were performed at the National Marine Genetic Breeding Center (31°44'40.14''N, 118°54'29.53''E) in Qingdao City, Shandong, China. The base population (G_0 generation) was generated with a diallele cross in 2009. This diallele cross involved four wild founder populations. These populations were obtained as cysts from geographically isolated locations in China (Xiechi Salt Lake, Shanxi; Alashanzuoqi, Inner Mongolia; Badanjilin, Inner Mongolia; and Yikezhao-meng, Inner Mongolia) between 1991 and 2002.

2.2 Selection Procedure

The population used for selection was originated from the base population. The G_0 progeny was selected using a combined family and within-family selection strategy that was based on differences in body length and survival. The breeding values for body length and survival were calculated using the animal mixed model (Charo-Karisa *et al.*, 2006) to establish a selection index distribution for the base population and to determine the cut-off weights for selection. We used multi-trait index selection. The relative weight of body length in the selection index was 100% in the G_0 generation (Table 1). The relative weights were 70% for body length and 30% for survival in generations G_1 and G_2 (Table 1). The relative weights were 85% for body length and 15% for survival in generation G_3 (Table 1). The selected population was maintained by mating the top selected males to females with a selection index > 50%. To maintain an effective population size and to control the number of selected individuals from the same full-sib family, we imposed certain restrictions on the mating process to control inbreeding (*e.g.*, we did not allow full-sib, half-sib, or cousin mating). The inbreeding coefficient was not allowed to exceed 1.0%.

Table 1 Some parameters of *Artemia sinica* in each generation

Generation	Population	Family (full-sib)	Sires	Dams	Relative weight (%)	
					Body length	Survival
G_0	Base	88	64	95	100	0
G_1	Selected	69	51	69	70	30
G_2	Selected	155	133	155	70	30
G_3	Selected	48	48	48	85	15

2.3 Production and Rearing of Families

We randomly selected 64 sires and 95 dams from the founder stocks to produce the G_0 generation (Table 1).

The G_1 generation was produced by the G_0 individuals (Table 1). Similarly, the G_2 and G_3 populations were produced by the G_1 and G_2 generations, respectively (Table 1). The selection of subsequent generations (G_1 to G_3) was separated and discrete.

Full- and half-sib families were produced in the G_0 and G_1 generations with a nested mating design: each male candidate was mated with two female candidates. Half-sibs were produced by mating each sire to a second dam after the first mating.

Selected male-female pairs were kept in 50 mL plastic vials containing 30 mL seawater with a salinity of 70 until the dormant cysts were released. Dormant cysts produced by each pair were collected in a Petri dish, washed with the seawater with a salinity of 70, and allowed to dehydrate for at least 20 h. Dormant cysts were transferred to a glass desiccator for 2–3 days. To eliminate diapause, all dormant cysts were separated by full-sib family and frozen for 30 days at -20°C in 1.5 mL Eppendorf tubes.

Cysts of each full-sib family were hatched in 20 mL Petri dishes containing 15 mL seawater with a salinity of 30. The Petri dishes were incubated at 26°C in 400 L illumination incubators. The nauplii of each full-sib family were transferred separately to 500 mL plastic beakers containing the seawater with a salinity of 70 at 23.5°C . After five days, 10–20 nauplii from each full-sib family were selected randomly and transferred individually to transparent 50 mL plastic vials. Each vial containing one individual nauplius was tagged with a unique six digit ID. We recorded sire ID, dam ID, individual ID, cyst collection date, nauplii collection date, and tagging date for each nauplius.

2.4 Growth and Survival Test

We performed growth and survival tests in 14 layers using two 400 L illumination incubators. We placed equal numbers of nauplii from each full-sib family in each incubator layer, at a density of $330 \text{ nauplii m}^{-2}$. Nauplii were reared under the standard conditions reported by Shirdhankar *et al.* (2003) and fed *Dunaliella salina* and *Spirulina* powder (0.5 and 0.4 g, respectively) every other day. All feces and uneaten food were removed every other day during water renewal.

The body length of each individual was measured under a microscope at day 20 post-hatching. We calculated the survival rate of each family by counting the number of surviving individuals in each family. We also recorded the harvest date, individual ID, illumination incubator ID, layer ID, and sex for each individual.

2.5 Statistical Analysis

We designed our experiments that the generations were discrete, and sires and dams were mated only within generations. Therefore, the complete pedigrees of all brine shrimp from G_0 onwards were used in our analyses.

We used the average information REML method in ASReml (Gilmour *et al.*, 2009) to calculate the variance components and to estimate the heritability of body

length. The mixed model used in the matrix notation was as follows:

$$y_{ijklmn} = u + Gen_i + Sex_j + Tank_k + Gen_i * Sex_j + Gen_i * Tank_k + Sex_j * Tank_k + Gen_i * Sex_j * Tank_k + hour_m(Gen_i * Sex_j * Tank_k) + a_l + c_m + e_{ijklmn},$$

where y_{ijklmn} is a vector of observed body length of the l th individual at day 20 post-hatching, and u is the overall mean of the body length at day 20 post-hatching. Gen_i is the fixed effect of the i th generation (four generations); Sex_j is the fixed effect of the j th gender (male and female brine shrimps), and $Tank_k$ is the fixed effect of the k th tank. The mutual interactions of these variables ($Gen_i * Sex_j$, $Gen_i * Tank_k$, $Sex_j * Tank_k$, and $Gen_i * Sex_j * Tank_k$) were also fitted as fixed effects. The variable $hour_m(Gen_i * Sex_j * Tank_k)$ was a linear covariate nested within the interaction among Gen_i , Sex_j , and $Tank_k$. The additive genetic effect of the l th animal, a_l , was the additive genetic effect of the l th animal, a_l ($0, A\sigma_a^2$), where A was the additive genetic relationship matrix among all brine shrimp; c_m was a vector of random common full-sib effects of the m th family, c ($0, I\sigma_c^2$), where I is the common environmental effect relationship matrix among all

families of brine shrimp; and e_{ijklmn} was the random residual error of the n th individual, e ($0, I\sigma_e^2$), where I is the residual effect (co)variance matrix among all brine shrimp. Phenotypic variance was calculated as $\sigma_p^2 = \sigma_a^2 + \sigma_c^2 + \sigma_e^2$. Heritability (h^2) was calculated as $h^2 = \sigma_a^2 / \sigma_p^2$, and the common environmental effects (c^2) were calculated as $c^2 = \sigma_c^2 / \sigma_p^2$.

Least-squares means were the best linear unbiased estimates of the marginal means in our experimental design. We calculated the least-squares means for the base population (G_0) with a linear mixed model. The least-squares means of the G_0 population was a fixed quantity calculated using the percentage of nauplii responding to selection. The following linear mixed model was fit in AS-Reml (Gilmour *et al.*, 2009) to estimate the least-squares means of the G_0 populations:

$$y_{ijklmn} = u + Pop_i + Sex_j + Tank_k + Tank_k * Sex_j + hour_l(Sex_j * Tank_k) + Pop_i(Fam_m) + e_{ijklmn},$$

where (y_{ijklmn}) was observed body length of the n th individual at day 20 post-hatching each generation at harvest; u was the overall mean; Pop_i was the fixed effect of the i th population; Sex_j was the fixed effect of the j th gender (male and female *A. sinica*); $Tank_k$ was the fixed effect of the k th pond; $Tank_k * Sex_j$ was the fixed effect of the interaction of the j th sex and k th tank; $hour_l(Sex_j * Tank_k)$ was a linear covariate nested within the interaction between gender and tank; $Pop_i(Fam_m)$ was the random effect of the i th population nested within the m th family; and e_{ijklmn} was the random residual error associated with observation $ijklmn$.

The predicted genetic gains in body length per generation at day 20 post-hatching were estimated across all generations. The breeding value of body lengths at day 20 post-hatching for all *A. sinica* across the four generations was obtained based on best linear unbiased prediction in ASReml software. The predicted genetic gain for each generation was calculated as the difference in the mean breeding values between the current and previous generations. We used the z -score to indicate whether the least-squares means and the mean breeding values between generations were significantly different (Nguyen *et al.*, 2007).

The Z -score was calculated as follows:

$$Z = \frac{x_i - x_j}{\sqrt{(\sigma_i^2 + \sigma_j^2)}}$$

where x_i and x_j are the least-squares means or mean breeding values for different generations, and σ_i and σ_j are their respective standard errors. The resulting Z -score was

tested against a large normal distribution sample.

3 Results

3.1 Descriptive Statistics

We recorded data for 4160 *A. sinica* at day 20 post-hatching across the four generations (G_0 to G_3 ; Table 2). The mean harvest body lengths of all selected nauplii in all post- G_0 generations (G_1 , G_2 , and G_3) were greater than those of the G_0 population. Across the generations G_1 , G_2 , and G_3 , the lowest mean body length was observed in the G_2 population (2144 nauplii were measured; Table 2). G_2 comprised nearly twice as many nauplii as G_1 and three times as many as G_3 (Table 2). In addition, the G_2 population had the largest coefficient of variation across all generations. Thus, the difference in mean body length that we observed may have been due to the presence of many small brine shrimp in G_2 . The distribution of body length for each generation is shown by a box-plot (Fig.1). The coefficients of variation across all generations ranged from 14.5% to 19.6% (mean: 17%).

Table 2 Body lengths of nauplii *Artemia sinica* at harvest (at day 20 post-hatching) for each generation

Population	Generation	Sample size (n)	Body length (µm)			
			Mean	Min	Max	Cv (%)
Base	G_0	1679	9212.7	3229.8	17225.6	18.8
	G_1	1290	10018.7	4655.3	14644.3	14.5
	G_2	2144	9760.2	2687.5	16062.5	19.6
Selection	G_3	726	10957.3	4375.2	15400.0	16.9
	Overall	4160	10245.4	2687.5	14644.3	17.0

Note: Cv, coefficient of variation.

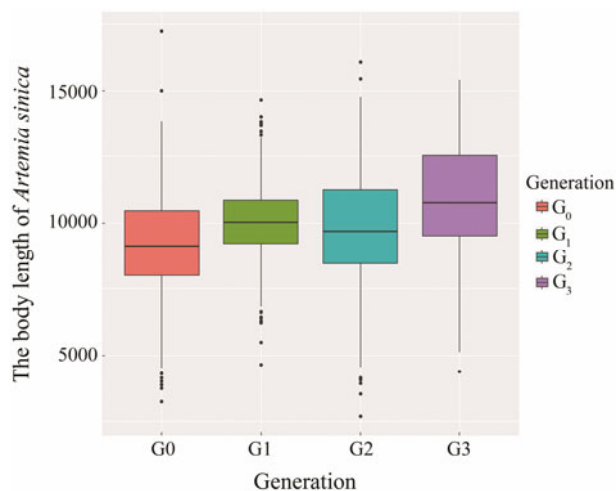


Fig.1 Body lengths (μm) of *Artemia sinica* at day 20 post-hatching for each generation.

3.2 Heritability and Common Environmental Effects

We used the Wald test to identify the fixed effects of the animal model with the average information REML method in ASReml (Table 3). All fixed effects and interactions were significant and were included in our models of variance components and heritability (Table 4). The estimates of heritability within generations were inaccurate, because we did not have complete pedigree information to utilize the phenotypic value of more individuals across generations (Maluwa *et al.*, 2007). Thus, we did not use the estimates of heritability within generations in our model. The heritability estimate for body length was moderate to low (0.14 ± 0.05), but significantly greater than zero ($P < 0.05$). The estimate of the common environmental effect on body length across generations was also moderate to low (0.14 ± 0.02), and was also significantly greater than zero ($P < 0.05$).

Table 3 Analysis of variance of body length in *Artemia sinica*: test of fixed effect using the average information REML method in ASReml

	Df	Sum of squares	F statistic	P>F
Intercept	1	2.9476e+10	32570	<2.2e-16*
Generation	3	1.4424e+08	159	<2.2e-16*
Sex	1	5.2344e+09	5784	<2.2e-16*
Tank	37	1.5095e+09	1668	<2.2e-16*
Generation: Sex	3	2.3459e+08	259	<2.2e-16*
Generation: Tank	3	3.5004e+08	387	<2.2e-16*
Sex: Tank	37	9.7599e+07	108	7.543e-09*
Generation: Sex: Tank	3	2.5771e+07	28	2.886e-06*
Generation: Sex: Tank: hours	88	4.0104e+08	443	<2.2e-16*
Residual (MS)		9.0501e+05		

Note: * ($P < 0.05$).

Table 4 Variance components of body length, heritability estimate, and estimate of common environmental effects across four generations of *Artemia sinica*

Variance components				Heritability	Common environmental effects
σ_a^2	σ_c^2	σ_e^2	σ_p^2	$h^2 \pm se$	$c^2 \pm se$
173185.05	177870.33	905012.52	1256067.84	$0.14 \pm 0.05^*$	$0.14 \pm 0.02^*$

Note: Estimate was significantly different from zero ($P < 0.05$).

3.3 Response to Selection

The least-squares mean of individual body length for the G_0 population was $9569.05 \mu\text{m}$. The mean breeding value increased between G_0 and G_3 : the mean breeding value of G_0 was -25.28 , the mean breeding value of G_1 was 140.79 , the mean breeding value of G_2 was 174.10 , and the mean breeding value of G_3 was 253.66 (Table 5). We

used the difference in mean breeding values between the current and previous generations to calculate the selection response of each generation. The predicted genetic gain was $166.07 \mu\text{m}$ in G_1 , $33.31 \mu\text{m}$ in G_2 , and $79.56 \mu\text{m}$ in G_3 (Table 5). That is, the largest gain in mean breeding value was between G_0 and G_1 , followed by the gain between G_2 and G_3 . The total predicted genetic gain between G_0 and G_3 , relative to the base population, was $278.94 \mu\text{m}$ (2.92%).

Table 5 Estimates of predicted genetic gain in body length for the selected strains of *Artemia sinica* calculated using the genetic parameters for each generation

Generation	Body length (μm)			
	Population	Mean breeding value	Genetic gain per generation	Percentage [†]
G_0	Control	-25.28	–	–
G_1	Selection	140.79	166.07	1.74
G_2	Selection	174.10	33.31	0.35
G_3	Selection	253.66	79.56	0.83
Cumulative			278.94	2.92

Note: [†] Percentage refers to actual units in relation to the least-squares means of body length of the G_0 population ($9569.05 \mu\text{m}$).

4 Discussion

4.1 Phenotypic Results

Brine shrimp body length is typically significantly correlated with body weight (Pérez-Rostro *et al.*, 2003) and is thought to be a key trait to assess growth performance. Here we found that the mean body length of *A. sinica* increased gradually across generations, except in G_2 (Table 2). In G_2 , mean body length was relatively low, but this generation also contained the longest brine shrimp in any generation (Table 2). Possibly the presence of large numbers of small brine shrimp in G_2 caused this discrepancy (Fig.1). Supporting this hypothesis, the coefficients of variation for G_1 and G_3 were lower than that of G_0 , but the coefficient of variation for G_2 was higher, suggesting the presence of many small brine shrimp. The reason might also be that smaller individuals died in G_1 and G_3 due to breeding management issues, causing the observed increase in minimum body length and in mean body length. Indeed, G_1 and G_3 had lower survival rates (data not shown).

4.2 Heritability and the Common Environmental Effect

Many factors can influence the accuracy of heritability estimates, including sample size, analytical model, strain, and pedigree structure (Falconer and Mackay, 1996). Here, we estimated the variance components of the brine shrimp model, including some fixed and random effects that the F test indicated were significant using REML. To improve the accuracy of our body length heritability estimate, we used the complete pedigree of each brine shrimp nauplius along with all of the descriptive data. The heritability of body length across all generations was moderate (0.14 ± 0.05), commensurate with the common environmental effect (0.14 ± 0.02 ; Table 4). These results were consistent with the heritability value of female *A. franciscana* for length at 3 days of age reported by Shirdhankar *et al.* (2003), but lower than the heritability values of female nauplius for length and males for length at 3 days of age. Our results are consistent with those of Elvingson *et al.* (1993), who showed that the heritability of rainbow trout body length at harvest is moderate (0.13–0.18).

Little is known about the genetic parameters affecting body length in *A. sinica*. However, the heritability estimates for total length and total weight in other shellfish vary widely. For example, heritability estimates for growth of whiteleg shrimp *Penaeus vannamei* range from 0.17 ± 0.04 to 0.44 ± 0.07 (Pérez-Rostro and Ibarra, 2003; Gitterle *et al.*, 2005a, b; Sui *et al.*, 2015, 2016; Tan *et al.*, 2016). However, heritability estimates are much higher in the giant tiger prawn, *P. monodon*, ranging from 0.45 ± 0.11 to 0.56 ± 0.04 (Kenway *et al.*, 2006). In the giant river prawn, *Macrobrachium rosenbergii*, the heritability estimate for growth was much lower than that of *P. vannamei* and *P. monodon* (0.056 ± 0.014 ; Luan *et al.*, 2012). The incongruence between our estimate of growth heritability and those previously published might be due to a variety of differences among experiments, including the analyti-

cal model (*i.e.*, not correcting for significant fixed effects), the population genetic background, the environmental conditions during growth, and the experimental design (*e.g.*, selection intensity or allowing half-sib and full-sib mating).

We found that the common environmental effect, particularly the maternal common environmental effect and the non-additive (dominant) genetic effect, were very large. Strong genetic ties between generations, generated by reuse of some sires and dams, improve the accuracy of heritability estimates (Vehviläinen *et al.*, 2008). More intense selection within families is recommended when the common environmental effect is large (Villanueva and Woolliams, 1997). Here, the standard errors of both the heritability estimates and the common environmental effect were small. The low standard errors may have been due to the relatively large number of full sibs per family or by the structure of our breeding design (*i.e.*, more generations and more families).

In general, the breeding population of *A. sinica* investigated here had considerable additive genetic variation with respect to body length; these results could help improve growth performance.

4.3 Selection Responses

Selection responses in a small population can be influenced by sampling errors, variable selection differentials, random genetic drift, environmental effects, and the intensity of selection (Falconer and Mackay, 1996). We used two separate methods to calculate selection responses. We calculated the realized genetic gain in body length with the least-squares mean method in the G_0 generation only. Then, we predicted the genetic gain in each subsequent generation by calculating the mean estimated breeding values (EBV) of each population. In general, the estimated genetic gain in body length based on the mean population EBV is more accurate due to use of the across-generation phenotypic dataset, which contains some full-sib and half-sib family information and eliminating deviations caused by common environmental effects.

We found a low response to selection for body length (0.35%–1.74% of the selected population) in *A. sinica*. This result is consistent with previous studies on arthropods: the average selection response in *Fenneropenaeus chinensis* was 1.28% per generation after five generations of multi-trait selection (Sui *et al.*, 2016), while the average selection response in *M. rosenbergii* was 2.25% per generation after five generations of multi-trait selection (Luan *et al.*, 2012). However, these selection responses are lower than those found in fish. Previous studies have recovered high responses to selection in Atlantic salmon (14%; Gjerde *et al.*, 1999), rainbow trout (13%; Gjerde *et al.*, 1986), channel catfish (13%; Dunham *et al.*, 2006), tilapia (23%; Eknath *et al.*, 1993), and abalone, *H. diversicolor* (9.2%; Liu *et al.*, 2015). According to Gjedrem (2016), the genetic gain for growth of shellfish is comparatively low, averaging 8.7% (eight estimates reported by Fjalestad *et al.*, 1997; Hetzel *et al.*, 2000; Goyard *et al.*, 2002; Preston *et al.*, 2004; Gitterle *et al.*, 2007; Andrian-

tahina *et al.*, 2012; Luan *et al.*, 2012; Hung *et al.*, 2013). The genetic gain is lower for the body length of some aquatic species (Tilapia, 2.3% per generation, Brzeski and Doyle, 1995; Atlantic salmon, 2.8%, Friars *et al.*, 1990, and Common carp, 4.7% per generation, Ninh *et al.*, 2013).

There are three primary explanations for this difference. First, although the four wild founder strains used in our study were geographically isolated, they lacked sufficient genetic variation. Thus additional wild strains must be introduced into the nuclear breeding population to achieve a greater rate of genetic gain. Second, because we selected parents to control inbreeding, we did not eliminate sires or dams with low EBVs. Some individuals with a smaller EBV were selected as parental candidates. Third, problems with breeding management late in the rearing period caused a substantial increase in mortality rate, and some of the potential breeding candidates died. Taking steps to ensure survival is critical to future selective breeding projects. Finally, as our population size was limited by our cultivation equipment, our selection intensity was correspondingly limited.

The genetic gain of body length between the two headmost generations G_0 and G_1 was greater than those between G_1 and G_2 , and between G_2 and G_3 . Indeed, previous reports have suggested that high selection responses are limited and decrease gradually with each subsequent generation. Phenotypic variation and heritability can decrease over long period of selection, resulting in lower rates of genetic change (Li *et al.*, 2006). In addition, negative genetic correlations may reduce long-term genetic gains (Falconer *et al.*, 1989). In *A. sinica*, a rapid response to selection was observed between G_0 and G_1 because the genetic variation of the population selected from G_0 had the highest genetic variation relative to the other generations. In addition, the relative weight of body length in the selection index was the largest in the G_0 generation (100%). Although the genetic gains in body length at day 20 post-hatching in *A. sinica* were lower than in other farmed species, they could be improved by increasing the size of the breeding population and the intensity of breeding. Such improvements can be easily achieved because *A. sinica* is highly fecund. Alternatively, long-term genetic gains could be improved by introducing wild individuals into the breeding population.

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