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Estimation of genetic parameters for growth relevant traits in adult Pacific abalone (*Haliotis discus hannai*)

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Abstract

Pacific abalone (*Haliotis discus hannai*) is one of the most valuable aquaculture species in China. However, the rapid development of the aquaculture industry has caused problem of germplasm degeneration. It is important to carry out genetic improvement of economic traits for *H. discus hannai*. This study was conducted to estimate genetic parameters of growth traits in Pacific abalone to provide a database for selective breeding programs. Data of 10 growth-related traits—shell length (SL), shell width (SW), shell height (SH), shell weight (SWT), wet weight (WW), foot muscle weight (MW), soft tissue weight (STW), visceral mass weight (VW), foot muscle weight/wet weight ratio (MWR) and soft tissue weight/wet weight ratio (SWR)—were collected from 1059 adults sampled from 115 families. Significant growth differences existed between abalone under different culture modes. Abalone with red shell colour presented poorer growth performance than the normal shell colour group, and their hybrids displayed mid-parent heterosis. The heritability values of SL, SW, SH, SWT, WW, MW and STW were 0.65 ± 0.06, 0.63 ± 0.06, 0.51 ± 0.08, 0.59 ± 0.09, 0.54 ± 0.05, 0.43 ± 0.08 and 0.43 ± 0.08, respectively, indicating high heritability. The heritabilities of VW and MWR were moderate, with estimates of 0.36 ± 0.07 and 0.21 ± 0.06, respectively, and SWR had low heritability with value of 0.17 ± 0.06. Genetic and phenotypic correlations among the growth traits were positive, in the ranges 0.24–0.99 and 0.12–0.99 respectively. Genetic correlation coefficients among most of the growth traits were close to or higher than 0.9. The results of this study demonstrate the genetic improvement potential of Pacific abalone in selective breeding. Traits such as SL, SW, SH and WW could be selected and improved simultaneously.

KEYWORDS
genetic correlation, genetic parameter, growth trait, *Haliotis discus hannai*, heritability

Muzhi Zhou and Jiarui Chen contributed equally to this work.

 | **1**

1 | INTRODUCTION

The Pacific abalone (*Haliotis discus hannai*) is a marine mollusc distributed along the coastal waters of East Asia. It is one of the most valuable and popular aquaculture species, especially in China, Japan and Korea (Li et al., 2004; Sharker et al., 2019). In China, the large-scale farming of Pacific abalone began in the 1980s, and in the mid-to-late 1990s, crossing with abalone strains introduced from Japan rapidly increased production (Zhao, 2016). According to the data published by the Ministry of Agriculture and Rural Affairs of the People's Republic of China, the annual production of China's abalone farming industry reached 180,267 tons in 2019. However, with increasing culture scale and density, environmental deterioration in farmed marine areas has made disease outbreaks more frequent (Morash & Alter, 2016). Furthermore, the germplasm degradation caused by accumulated inbreeding practice has become increasingly serious (Di et al., 2015). These problems will eventually result in lower quality and production of abalone, thereby reducing the benefits to customers and farmers. Cultivation of new varieties of Pacific abalone with improved traits has thus become an urgent need for healthy development of the farming industry.

Selective breeding is an effective way to produce new varieties with desirable traits. Compared with other breeding methods, the genetic gain from a selection program can be heritable for offspring and can persist for generations (Lind et al., 2012). At present, selective breeding research has been carried out in many aquatic species, and positive results have been attained. De Melo et al. (2016) estimated genetic parameters and performed selection in the Pacific oyster (*Crassostrea gigas*) for five generations, and the genetic gains were 19% for production and 15% for survival. Huang et al. (2012) established a selected strain of Pacific white shrimp (*Litopenaeus vannamei*) with increased resistance to white spot syndrome virus (WSSV), and the strain also showed improved body weight (+32.51%) and yield (+82.14%) compared with common strains in pond culture experiments. Application of selective breeding in Pacific abalone has been suggested by many researchers due to the high level of genetic variation of the wild population (Kobayashi & Kijima, 2010). However, there are only a few reports concerning abalone selective breeding. For example, Park et al. (2012) reported improvements in growth rate of the shell and total weight in selected strains. Li, Wang, et al. (2018) observed higher shell growth rate and survival rate in the selected group compared with the wild population. It is thus necessary to carry out further research on selective breeding for multiple growth traits in Pacific abalone.

In selective breeding programs, estimation of genetic parameters is an essential prerequisite. Heritability represents the relative degree to which a trait is influenced by genetic effects, directly relating to selection response, and genetic correlations reflect the interrelationships among traits that can produce indirect selection. Many researchers have estimated genetic parameters in aquatic animals, especially in species such as the Pacific oyster (Azéma et al., 2017; Chi et al., 2021; Degremont et al., 2007), Pacific white shrimp (Sui et al., 2016; Tan et al., 2019; Zhang et al., 2017),

fishes such as Atlantic salmon (*Salmo salar*) (Powell et al., 2008; Quinton et al., 2005), Japanese flounder (*Paralichthys olivaceus*) (Liu et al., 2016; Li et al., 2018), and Nile tilapia (*Oreochromis niloticus*) (Bentsen et al., 2012; Thodesen et al., 2011). For Pacific abalone, several researchers have estimated genetic parameters of shell morphology and total weight. These growth traits can be measured easily and are related to customers' preferences and economic benefits of farmers. For example, Deng (2005) estimated the heritability of shell length and shell width in 10-, 20-, and 30-day-old abalone, where the values ranged from 0.20 to 0.49 and 0.14 to 0.43 for shell length and shell width, respectively, and highly positive genetic correlations among these traits were found. Choe et al. (2009) reported that their estimated heritability values for shell length, shell width and total weight were 0.29, 0.29 and 0.31, respectively, in 9-month-old *H. discus hannai*. Shi et al. (2019) estimated the heritability of shell width, shell length and total body weight of 2-year-old abalone as 0.39, 0.39 and 0.35, respectively, and the traits were highly positively correlated (0.98–0.99). Previous estimates illustrated the genetic improvement potential of growth traits in *H. discus hannai*. However, compared with other economically important aquaculture species, the number of reports is quite insufficient. Additionally, the previous studies have focused on the early growth stages of Pacific abalone, and the growth traits reported have been relatively limited. Notably, there is a lack of information concerning the heritability of anatomical characters; evaluation of such characters is important for abalone farming, since they directly affect the edible portions of the mollusc.

In this study, 10 growth-related traits were examined in 2.5-year-old Pacific abalone, including shell length (SL), shell width (SW), shell height (SH), shell weight (SWT), wet weight (WW), foot muscle weight (MW), soft tissue weight (STW), visceral mass weight (VW), foot muscle weight/wet weight ratio (MWR) and soft tissue weight/wet weight ratio (SWR). Potential influencing factors for these traits were analysed initially, and phenotypic correlations among the traits were calculated, and heritabilities and genetic correlations were estimated. The aim of this study was to provide an optimal reference for breeding strategies in genetic improvement for Pacific abalone, especially the preliminary data for genome selection.

2 | MATERIALS AND METHODS

2.1 | Broodstock and production of families

Broodstock candidates were from one northern population (Changdao) from Shandong Province and four southern populations (Yangxia, Jinjiang, Dongshan, and a red shell mutant population) from Fujian Province, China. All of the populations represented long-term undergoing domestication groups, except for the red shell samples, which were collected from a natural mutant group, since the special shell colour is preferred in Chinese markets. The candidates were cultured in Fuda Abalone Aquaculture Co. Ltd., Jinjiang,

Fujian Province, China. In October 2016, a nested design with one male mating to three females was applied among the candidates to produce 210 full-sib families.

2.2 | Reproduction and larvae rearing

Broodstock candidates with good vitality and fully developed gonads were selected to produce the experimental samples. Males and females collected were separately placed in baskets and then exposed to a cool and dry environment for about 1 hour and 1.5 hours, respectively to ensure the synchronization of spawning. After that, males and females were transferred to 10 L polypropylene buckets, among which the distance was kept above 0.5 m to avoid contamination. Seawater that was previously irradiated with ultraviolet light for about 8 hours was added to the buckets. The temperature of seawater was about 22°C; the salinity was 32 ppt, and the seawater was changed every hour until the broodstock abalone spawned. Eggs were first filtered through 80 mesh silk screens (180 μm opening width) to remove impurities, and then were collected by 500 mesh silk screens (25 μm opening width). After collection, sperm was added to the eggs at a density of about 10–20 sperm per egg. Fifteen minutes after fertilization, the original seawater in the buckets was changed to wash the eggs. This process was performed every 20 minutes and repeated three times to remove excess sperm. One hour after fertilization, eggs were observed to check the status of fertilization. The successfully fertilized eggs would begin to hatch after about 8 hours, and then at 12 hours after fertilization the hatched larvae from different families were separately moved to 960 L tanks for rearing. Temperature and salinity of tank water were kept at 22°C and 32 ppt respectively. Aeration was provided in the tanks, and running seawater was stopped. After 3 days, running seawater was provided, and membranes with diatoms were put into the tanks for settlement of larvae. After 45 days, juveniles were removed onto the bucket and fed with commercial feed daily. Aeration and running seawater were provided.

2.3 | Tagging and mixed culture

In January 2018, after 1 year of farming in separate families, growth traits including shell length (SL), shell width (SW) and wet weight (WW) were measured for the first time and recorded as initial SL, initial SW and initial WW. Then, 33,656 individuals from 136 families were randomly selected to be tagged. The method of tagging was to place plastic labels on the shells of the abalone using glue. The labels and glue were ordered from Qingdao Starfish Instrument Co., LTD. Lost rate of tags was about 10% for 1 year under this method. The labelled abalone were then randomly divided into nine pools (10 m long, 5 m width, 1.5 m depth) for mixed culture. The pools were cleaned every day, and fresh *Gracilariopsis lemaneiformis* was provided.

2.4 | Separated culture and data recording

Three months after preparation of the mixed culture, in April 2018, the labelled individuals were randomly divided into two groups. One group of about 14,000 individuals was moved to a sea-based farm in Dongshan and cultured at a density of 45 individuals per cage, and the other group (about 19,000 individuals) was continuously cultured at a land-based farm in Jinjiang. In June 2019, SL, SW and WW were measured again for 8787 tagged abalones from 136 families, of which the individual ID and pool number (No.) were recorded. Then 1059 individuals from 115 families were randomly selected to carry out dissection. For these samples, the sex was recorded during dissection and the shell colour was derived from their family information, recorded as normal, red and heterozygote which was sourced from crossing between normal shell and red shell abalone. Growth traits including shell height (SH), shell weight (SWT) and foot muscle weight (MW) were measured. All the size-related traits were measured by digital callipers (0.01 mm), and weight-related traits were measured by electronic scales (0.1 g). Based on the measured data, four new growth relevant traits were calculated: soft tissue weight (STW = WW – SWT), visceral mass weight (VW = STW – MW), foot muscle weight/wet weight ratio (MWR) and soft tissue weight/wet weight ratio (SWR).

2.5 | Data analysis

Outliers in the data were eliminated by the boxplot method. Values larger than the upper quartile plus 1.5 times the interquartile range (IQR) or smaller than the lower quartile minus 1.5 times the IQR were removed. Then, basic descriptive statistical analyses were conducted for all traits. Significance of fixed effects including culture mode, sex, pool No. and shell colour, and linear covariates including three growth traits measured in January 2018 (i.e., initial SL, initial SW, and initial WW) were tested by Wald test with ASReml-R 4.0 (Butler et al., 2017). The fixed effects and covariates that had significant effects on traits were included in the subsequent model except for shell colour, considering that the information provided by shell colour recording was partially consistent with pedigree information, and part of the genetic difference would be shielded if shell colour were added. After that, growth traits were compared between samples under different culture modes and with different shell colour, and the significance of differences was tested by one-way ANOVA in R. Phenotypic correlations among growth traits studied were calculated through Pearson correlation analysis using R and were consistent with the reported literature (Boxriker et al., 2018; Li et al., 2019). Genetic parameters were estimated using the mixed model in ASReml-R 4.0 via the REML algorithm. Heritability was estimated by univariate analysis, and genetic correlation was estimated by multivariate analysis. Additionally, common environment effect was not considered during estimation, since the variance components could not converge when this effect was added into model. The final model was as follows:

$$y = f + u + bx + e,$$

where y is the phenotypic observation; f is the fixed effect; u is the random additive genetic effect; b is regression coefficient; x is the linear covariate and e is the random residual.

Heritability (h^2) was calculated as follows:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2},$$

where σ_a^2 is the additive genetic variance, σ_e^2 is the residual variance, and their sum is equal to the phenotypic variance.

Genetic correlation coefficients (r_g) among traits were calculated as follows:

$$r_g = \frac{\sigma_{a12}}{\sqrt{\sigma_{a1}^2 * \sigma_{a2}^2}},$$

where σ_{a12} is the genetic covariance between trait 1 and 2; σ_{a1}^2 and σ_{a2}^2 are genetic variances of trait 1 and 2 respectively.

3 | RESULTS

3.1 | Descriptive statistics

Minimum values, maximum values, mean values, standard deviations (SD), and coefficients of variation (CV) of original records for 10 growth traits are listed in Table 1. The overall means of SL, SW and WW were 62.97 ± 9.40 mm, 42.64 ± 5.94 mm, and 33.04 ± 12.99 g respectively. There were different levels of phenotypic variation among the 10 growth traits. MW had the highest coefficient of variation (0.47), the range was 2.99–33.87 g, and the average value was 14.91 g. STW, WW, VW and SWT also had relatively high CVs with values of 0.44, 0.39, 0.42 and 0.39 respectively. The CVs of rest traits were comparatively lower with the range of 0.04–0.16, and SWR showed the smallest CV (0.04). MWR and SWR, which are the ratios between two common traits, had approximately normal distribution (Figure 1) with skewness and kurtosis of −0.02 and −0.40, −0.36 and −0.18 respectively.

3.2 | Effects of fixed factors and covariates

The significance of fixed factors and covariates is presented in Table 2. Culture modes and initial SL had highly significant effects on nearly all of the traits. Pool No. and shell colour had significant effects on the majority of the traits. Initial SW and initial WW had highly significant effects on SL, SW and WW. For sex, the effects were non-significant.

3.3 | Comparisons of growth traits

The mean value of each growth trait between different culture modes was compared (Table 3). Except for SWR, the means of all the growth traits of abalone in the sea-based farm were higher than those from the land-based farm, and the differences were highly significant in all of the traits.

Comparison was also made among samples with different shell colour (Table 4). Abalone with normal shell colour had the highest means of growth traits, followed by heterozygotes, and growth trait values of abalone with red shell colour were the lowest. The difference was highly significant in almost all of growth traits except MWR and SWR.

3.4 | Genetic parameters

The estimates of heritability and variance components of 10 growth traits are given in Table 5. Heritability can be roughly divided into three levels (Gjerde, 1986; Hannrup et al., 2004): heritability greater than 0.4 indicates high heritability; heritability between 0.2 and 0.4 is moderate, and heritability less than 0.2 is low. SL, SW, SH, SWT, WW, MW and STW had high heritabilities, with values of 0.65 ± 0.06, 0.63 ± 0.06, 0.51 ± 0.08, 0.59 ± 0.09, 0.54 ± 0.05, 0.43 ± 0.08 and 0.43 ± 0.08 respectively. VW and MWR had moderate heritabilities, with values of 0.36 ± 0.07 and 0.21 ± 0.06 respectively. Heritability of SWR was low, with value of 0.17 ± 0.06.

TABLE 1 Descriptive statistics of growth-related traits

Traits	Number	Min	Max	Mean	SD	CV
Shell length (SL, mm)	8701	37.34	88.38	62.97	9.40	0.15
Shell width (SW, mm)	8692	26.50	58.88	42.64	5.94	0.14
Shell height (SH, mm)	1032	10.37	23.11	16.16	2.43	0.16
Shell weight (SWT, g)	1036	2.74	19.82	9.59	3.72	0.39
Wet weight (WW, g)	8540	4.57	68.88	33.04	12.99	0.39
Foot muscle weight (MW, g)	996	2.99	33.87	14.91	7.00	0.47
Soft tissue weight (STW, g)	1026	1.73	63.08	27.91	12.39	0.44
Visceral mass weight (VW, g)	983	1.80	27.78	12.50	5.19	0.42
MW/WW (MWR)	979	0.26	0.52	0.40	0.05	0.12
STW/WW (SWR)	980	0.66	0.82	0.74	0.03	0.04

Abbreviations: CV, coefficient of variation; SD, standard deviation.

Genetic correlations (r_g) among 10 growth traits were all positive and in the range of 0.24–0.99 (Table 6). The two ratio traits (MWR and SWR) had relatively lower genetic correlations with other traits ($r_g = 0.24–0.84$ and $r_g = 0.67–0.90$ respectively), while the remaining growth traits were highly genetically correlated ($r_g = 0.93–0.99$).

4 | DISCUSSION

4.1 | Effects of culture models and shell colours on growth traits

Before analyses, outliers were removed from original data under the following considerations. Firstly, the outliers included wrong recordings and recordings with excessive deviation, which were lack of accuracy and credibility. Besides, the outliers only occupied a small part of the data while their existence could easily affect the normality which is the precondition for estimation process (Cavus et al., 2017; Searle, 1994). The final estimates may be inaccurate due to the outliers; hence, it was necessary to delete them.

Culture mode had highly significant effects on all growth traits studied, with better growth performance of abalone cultured in the sea-based farm compared with the land-based farm; this could be attributed to complex environmental factors such as temperature, dissolved oxygen (DO), pH, light intensity, and nutrition (Li et al., 2007). For example, the exchange amount of water in sea-based farms is of high quantity and is rich in plankton and materials for growth of abalone, while the water used in land-based farms has been filtered before being pumped into the pools. In addition, a higher water flow rate with more DO in the sea can improve the growth performance of abalone (Wu & Zhang, 2016). The pools used in the land-based farm were smaller, containing more individuals, and the culture system was comparatively closed. As a result, the high growth density could have negatively affected growth due to water deterioration in the pools, while in the open system of the sea-based farm, the water quality would be less influenced by culture density, and the levels of DO and ammonia could be kept within suitable ranges, thereby providing a more favourable environment for the abalone (Huchette et al., 2003; Wu, et al., 2009). It could be preliminarily concluded
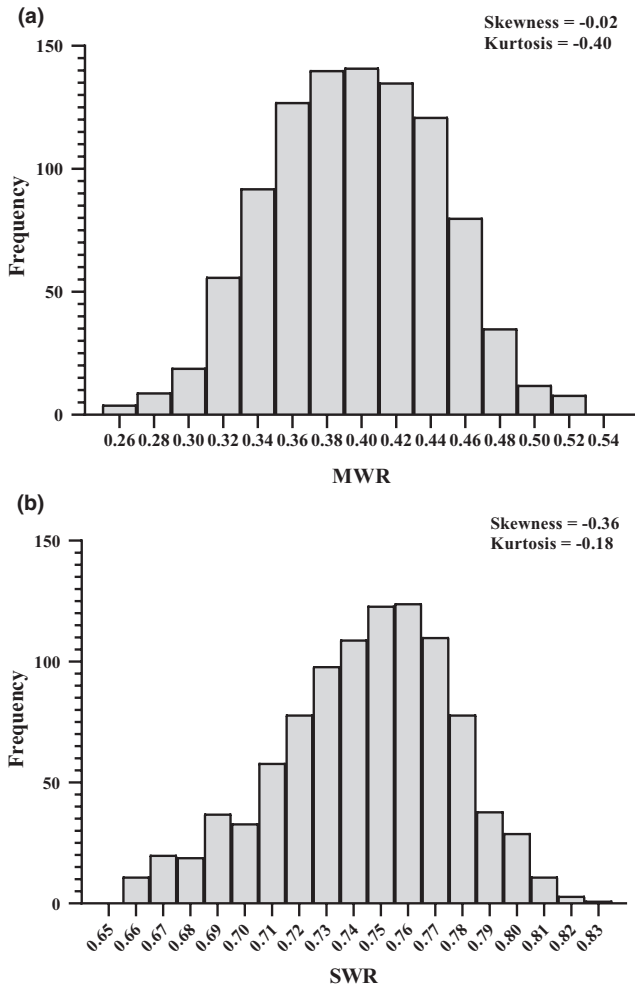

FIGURE 1 Histograms of MWR (a) and SWR (b)

TABLE 2 Significance analysis of fixed effects and covariates (*p*-value)

Traits	Culture modes	Pool no.	Sex	Shell colour	Initial SL	Initial SW	Initial WW
SL	<2e−16***	3.331e−16***	/	/	<2.2e−16***	2.93e−3***	6.00e−16***
SW	<2e−16***	<2.2e−16***	/	/	<2.2e−16***	5.55e−16***	2.74e−04***
SH	<2e−16***	0.49	0.56	0.02*	<2e−16***	0.74	0.15
SWT	<2e−16***	0.10	0.33	6.99e−03**	<2e−16***	0.26	0.05
WW	<2e−16***	2.01e−12***	/	/	<2.2e−16***	2.631e−09***	3.401e−06***
MW	<2e−16***	7.51e−04***	0.59	4.70e−03**	<2e−16***	0.02*	0.07
STW	<2e−16***	0.01*	0.24	2.03e−03**	<2e−16***	0.50	0.12
VW	1.08e−08***	0.45	0.44	5.52e−03**	<2e−16***	0.22	0.82
MWR	2.22e−16***	2.24e−10***	0.44	0.43	0.02*	0.36	0.02*
SWR	9.75e−11***	1.55e−06***	0.7	0.20	1.29e−04***	0.40	0.21

Note: /, There were no complete recordings of sex and shell colour for 8787 individuals.

***,**,* Refer to the significant levels of $p < 0.001$, $p < 0.01$ and $p < 0.05$ respectively.

that the sea-based farm provided more suitable conditions for the growth of Pacific abalone.

For the shell colour factor, abalone with normal shell colour grew better than heterozygotes and red shell abalone. Even though the sample size of red shell colour abalone was small in this study, where there were only 56 red shell colour types in a sample of 1059, the results matched expectations of experience accumulated from years of production practice. Generally, the shell colour of abalone can be influenced by many factors, including genetic control, feeding baits, physiological metabolism, and living environment (Hoang et al., 2017; Kobayashi et al., 2004). Different from common environmental controlled shell colour variations, the red shell variant observed here was mainly attributed to natural mutation of a gene. Mating experiment has verified that this trait presents Mendelian ratio, and belongs to recessive trait controlled by a single gene (result not shown), which is the same with the orange shell abalone

reported by Liu et al. (2009). However, the specific gene and detailed genetic mechanisms behind this trait are still under-researched. Natural mutation of a gene is normally harmful to the organism, hence it was reasonable to find that red shell individuals presented poor growth performance. Previous research also examined the relationships between shell colour and fitness-related traits, such as survival and growth rate (Winkler et al., 2001). In some shellfish, groups with lighter shell colour had lower fitness. For instance, in pearl oysters (*Pinctada martensii*), a dark shell colour group had better growth performance in shell length and shell height than lighter shell colour groups in different growth periods (Wang et al., 2008). The growth depression shown in red shell Pacific abalone could be explained by pleiotropy of genes controlling shell colour, or it could be caused by the mutation of loci that are closely linked to the shell colour mutation locus. For the latter situation, it would be possible to ameliorate the growth disadvantage through backcrossing with the normal shell colour population for several generations, since mid-parent heterosis was observed in the hybrid between normal and red shell abalone. However, the feasibility of this method needs to be investigated through more comparative experiments. In the wild, the red shell variant is not conducive to abalone research since it is scarce, and the possible reason is the inferior of red shell in predation avoidance (Liu et al., 2009). Shell colour is one of the elements that can affect the visibility of shellfish under water (Gimenez-Casalduero et al., 1999). Usually, light with long wavelength is absorbed quickly under clear water, such as the red light (Kinney et al., 1967), which makes red objects present dark in the deep water. However, Pacific abalone naturally live in shallow water areas (depth < 10 m) with rich phytoplankton and organic matter which can change light transmission (Gao et al., 2016); hence, red shells abalones may be obvious compared with natural colours of their habitat, making the red forms the target of predators. As a result, red shell individuals are rare in wild. In Chinese culture, red colour usually has positive implications and is in line with consumers' aesthetics; hence, it is meaningful and economically beneficial to study the inherited characteristics behind

TABLE 3 Comparison of mean ± SD of growth traits in *H. discus hannai* under different culture modes (land-based farm and sea-based farm)

Traits	Culture modes		
	Land-based	Sea-based	p-Value
SL	61.3 ± 8.42	71.89 ± 8.74	<2e−16[***]
SW	41.51 ± 5.36	48.13 ± 5.54	<2e−16[***]
SH	15.31 ± 1.95	18.2 ± 2.25	<2e−16[***]
SWT	8.33 ± 2.91	12.8 ± 3.62	<2e−16[***]
WW	31.40 ± 12.16	41.88 ± 13.76	<2e−16[***]
MW	13.18 ± 5.79	19.58 ± 7.80	<2e−16[***]
STW	25.26 ± 10.86	34.83 ± 13.44	<2e−16[***]
VW	12 ± 5.22	13.85 ± 4.88	6.66e−07[***]
MWR	0.4 ± 0.05	0.42 ± 0.05	6.15e−15[***]
SWR	0.75 ± 0.03	0.73 ± 0.03	5.38e−10[***]

[***]Refers to $p < 0.0001$ (Bonferroni-adjusted significant level).

TABLE 4 Comparison of means of growth traits in *H. discus hannai* with different shell colours (normal, heterozygote and red)

Traits	Shell colour			
	Normal	Heterozygote	Red	p-Value
SL	71.41 ± 10.39	68.19 ± 10.35[a]	62.98 ± 7.31[a]	5.87e−10[***]
SW	48.30 ± 6.52	45.95 ± 6.55[a]	42.63 ± 4.22[a]	8.34e−12[***]
SH	16.58 ± 2.44	16.07 ± 2.55[a]	14.78 ± 1.49[ab]	4.16e−07[***]
SWT	10.40 ± 3.78	9.58 ± 3.80[a]	7.51 ± 2.00[a]	6.06e−08[***]
WW	41.55 ± 16.51	37.17 ± 15.96[a]	29.01 ± 9.73[a]	1.25e−08[***]
MW	16.29 ± 7.08	15.10 ± 7.19[a]	11.42 ± 4.68[a]	4.84e−06[***]
STW	30.87 ± 12.89	27.16 ± 12.05[a]	21.49 ± 7.91[a]	1.35e−08[***]
VW	13.60 ± 5.32	12.27 ± 5.16[a]	9.93 ± 3.74[a]	5.43e−07[***]
MWR	0.40 ± 0.05	0.40 ± 0.05	0.39 ± 0.04	0.25
SWR	0.75 ± 0.03	0.74 ± 0.03	0.74 ± 0.03	1.8e−02

[a]Compared with normal colour, $p < 0.0002$ (Bonferroni-adjusted significant level).
[b]Compared with heterozygote, $p < 0.0002$ (Bonferroni-adjusted significant level).
[***]Refers to $p < 0.0001$ (Bonferroni-adjusted significant level).

this trait and then to develop stable red shell strains for future commercial production. In short, based on our results, the red shell group of Pacific abalone showed unfavourable growth performance, and thus this type needs further improvement for the creation of potential economic benefits.

4.2 | Genetic parameters

Heritability reflects the relative degree of additive genetic variation affecting phenotypic traits. As such, it plays a central role in prediction of selection responses. The heritability estimates of traits studied in this research ranged from 0.17 to 0.65, corresponding to a low to high degree, a result that conforms to the general range of the heritability in aquaculture animals ($h^2 = 0$–0.83) (Li et al., 2019) and matching the common result of estimated heritabilities of production traits in shellfish (Fang et al., 2021). Most of the growth traits in our study presented high heritability, which was basically consistent with previous research (Peng

et al., 2021), indicating that in Pacific abalone, clear hereditary progress may be observed after selective breeding for these growth traits. The heritabilities estimated for SL and SW were 0.64 and 0.63, respectively, which were higher than estimates for 10-day-old (0.49 and 0.43) and 20-day-old (0.44 and 0.34) abalone (Deng, 2005). Heritability of WW was 0.54, higher than the estimate for 2-year-old abalone (0.35) (Shi et al., 2019). A possible reason for the higher estimates is that sampled individuals used in our study were older than those of previous studies, and heritability of growth traits can fluctuate with age. The case in which heritability increases with age has been reported in many aquatic species, including Pacific white shrimp, giant freshwater prawns (*Macrobrachium rosenbergii*), sea cucumbers (*Apostichopus japonicus*), and masu salmon (*Oncorhynchus masou*) (Li et al., 2009; Ren et al., 2020; Zhang et al., 2013). Our results demonstrated that the selection can be made at later growth stages of Pacific abalone, consistent with a study in *C. gigas* (Chi et al., 2021). Apart from this, differences in experimental design and model selection can affect the results of estimates. Estimation in this study was based on full-sib group information, which generally can cause higher estimates of heritability (Li et al., 2009). Also, the sample size in each family was relatively small, causing lower phenotypic variance. Another possible reason is that the pedigree had only one generation, of which the depth was not enough, as a result, the genetic connection between individuals was weak, which made it difficult to effectively separate the common environmental effect from the additive effect, thereby increasing the heritability (Luan et al., 2015). For the remaining growth traits studied, there are no reports for *H. discus hannai* to the best of our knowledge; hence, the comparisons were made with other aquatic species. For SH, the heritability was 0.51, higher than the heritability of shell height of juvenile *C. gigas* (0.28) (Zhao et al., 2019). Heritability of SWT (0.59) was higher than the estimate of 0.46 reported for larval *C. gigas* (Lannan, 1972) and was much higher than the value for adult oysters (Wang et al., 2012). Heritability of STW (0.43) was much higher than the estimate

TABLE 5 Heritabilities (±SD) of 10 growth traits

Growth traits	Additive genetic variance	Residual variance	Heritability
SL	40.00	20.01	0.65±0.06
SW	16.30	9.35	0.63±0.06
SH	2.03	1.94	0.51±0.09
SWT	5.25	3.68	0.59±0.09
WW	77.22	65.05	0.54±0.05
MW	16.13	21.19	0.43±0.08
STW	53.43	70.80	0.43±0.08
VW	8.77	15.35	0.36±0.07
MWR	4.33e−04	1.65e−03	0.21±0.06
SWR	3.10e−04	1.54e−03	0.17±0.06

TABLE 6 Genetic and phenotypic correlations among growth traits

Traits	SL	SW	SH	SWT	WW	MW	STW	VW	MWR	SWR
SL		0.97	0.87	0.94	0.92	0.87	0.89	0.81	0.31	0.24
SW	0.99		0.87	0.95	0.93	0.89	0.91	0.82	0.34	0.25
SH	0.93	0.93		0.90	0.86	0.81	0.82	0.73	0.28	0.17
SWT	0.98	0.99	0.95		0.93	0.89	0.88	0.78	0.33	0.13
WW	0.99	0.96	0.95	0.99		0.96	0.99	0.91	0.39	0.42
MW	0.98	0.99	0.94	0.98	0.99		0.96	0.80	0.59	0.40
STW	0.99	0.99	0.95	0.98	0.99	0.99		0.93	0.41	0.50
VW	0.99	0.98	0.95	0.97	0.99	0.97	0.99		0.12	0.52
MWR	0.63	0.70	0.54	0.63	0.79	0.91	0.82	0.24		0.25
SWR	0.80	0.80	0.72	0.67	0.86	0.87	0.89	0.90	0.84	

Note: Genetic correlations are in the lower diagonal and phenotypic correlations are in the upper diagonal.

reported for green lip abalone (*Haliotis laevigata*) (0.10) (Kube et al., 2007). The estimate for MW was lower than the 0.74 heritability of weight of adductor muscle reported in 9-month-old Caribbean scallops (*Argopecten nucleus*) (Barros et al., 2018). Heritability of SWR estimated in this study was relatively low (0.17), consistent with the estimate reported in 360-day-old *C. gigas* (0.19) (Wang et al., 2012), and was higher than the estimate reported in 5-month-old *L. vannamei* (0.12) (Xu, 2014). The comparisons confirmed the reliability of our results and further indicated the ascendancy of growth traits of Pacific abalone for selective improvement. Except for the traits mentioned above, the heritability of VW and MWR have not been reported to the best of our knowledge, and these traits showed improvement potentials with moderate heritabilities in our study. MWR was directly related to the proportion of edible parts in abalone, a trait that is commercially significant, and VW can be further related to reproductive performance, a trait that plays an important role in artificial reproduction on which Pacific abalone culture industry largely depends. Thus, it is meaningful to study these traits for the economic benefit of abalone farming. Heritabilities of two ratio traits (MWR and SWR) were significantly lower than those of other traits; this could be attributed to the calculation method for such traits that eliminates variation caused by different sizes of abalone samples, resulting in lower estimates. Hence, improvement of these two traits should be performed through genomic selection rather than by common selection methods.

There were highly positive genetic correlations among most of the growth traits, with the correlation coefficients close to or greater than 0.9, and phenotypic correlations among traits were basically consistent with genetic correlations, similar to the results of previous studies (Choe et al., 2007; Deng et al., 2007; Shi et al., 2019). This suggests that the genes controlling these traits were identical or were linked, and selection of one trait can thus improve the others, indicating the feasibility of simultaneous selection of these traits. In selective breeding programs, the general principle is to select traits that have high heritability and can be measured easily to collectively conduct selection of traits with low heritability or complex measurement procedures (Fang & Li, 2020). In this study, the three size-related traits (SL, SW and SH) and WW were appropriate targets to be selected for the collective improvement of others, especially for SWR which displayed low heritability while had relatively high correlation coefficients with these four traits (>0.7).

5 | CONCLUSION

In conclusion, our results showed that sea-based farming may be more suitable for the growth of Pacific abalone. The red shell colour variant was accompanied by growth depression; this may be improved by proper breeding strategies. Traits studied in this report had different levels of estimated heritability. Heritabilities of

SL, SW, SH, SWT, WW, MW and STW were high, heritabilities of VW and MWR were moderate, and heritability of SWR was low. The genetic correlations among most traits were highly positive. Different selection strategies should be applied to these traits according to the heritability, and traits with high genetic correlations, such as SL, SW, SH and WW could be selected simultaneously. This report can be used to support the selective breeding work in *H. discus hannai*.

CONFLICT OF INTEREST

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the position presented in, or the review of, the manuscript entitled, 'Estimation of genetic parameters for growth relevant traits in adult Pacific abalone (*Haliotis discus hannai*)'.

AUTHOR CONTRIBUTIONS

Caihuan Ke, Weiwei You, Xuan Luo, Wenzhu Peng, Feng Yu, Junyu Liu, designed this study. Caihuan Ke involved in acquisition of fundings. Qingyang Xie provided animal materials. Wenzhu Peng, Feng Yu, Muzhi Zhou, Jiarui Chen and Weihong Lin conducted the study and analyzed the data. Xuan Luo, Wenzhu Peng, Feng Yu, Junyu Liu, Muzhi Zhou and Jiarui Chen involved in manuscript writing. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

All data included in this study are available upon request by contact with the corresponding author.

ETHICS APPROVAL STATEMENT

This study was conducted according to ethical policies of the journal, as noted on the journal's author guidelines page.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.