



# Correlation and Path Analysis of Shell Morphological and Body Mass Traits in Pacific Abalone (*Haliotis discus hannai*)

Qi Luo<sup>1</sup> · Xiaolong Gao<sup>2,3,5</sup> · Mo Zhang<sup>4</sup> · Huiyang Huang<sup>1</sup> · Miaoqin Huang<sup>1</sup> · Huoqing Huang<sup>1</sup> · Caihuan Ke<sup>1</sup>

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## Abstract

Body mass, the primary target in the selective breeding of aquatic mollusks, is less intuitive to assess than shell morphological traits. To improve breeding efficiency, this study used path analysis to examine the influence of shell morphological traits on body mass. Shell length ( $X_L$ ), width ( $X_W$ ), height ( $X_H$ ), perimeter ( $X_P$ ), and area ( $X_A$ ), along with total weight ( $Y_W$ ) and soft body weight ( $Y_S$ ), were measured in 2-year-old female and male Pacific abalone (*Haliotis discus hannai*). Correlation and path analysis were conducted with shell morphological traits ( $X_L$ ,  $X_W$ ,  $X_H$ ,  $X_P$ , and  $X_A$ ) as independent variables and body mass traits ( $Y_W$  and  $Y_S$ ) as dependent variables. Correlation analysis revealed significant relationships between body mass and shell morphological traits in both sexes ( $P < 0.05$ ). Path analysis revealed that in females, shell perimeter (0.500), height (0.451), and length (0.212) had the strongest direct effects on total weight, whereas in males, shell area (0.611), length (0.431), and width (-0.039) were most influential. For soft body weight, shell length had the highest coefficient of determination in females (0.504), while shell area had the highest in males (0.458), indicating sex-specific differences in traits affecting body mass. Importantly, shell length was identified as a key determinant of body mass across all four multiple regression equations. These findings suggest that shell length can be directly used for rapid breeding selection on farms to efficiently identify abalones with higher body weight, thereby providing a theoretical foundation for improved germplasm resource utilization and innovative breeding strategies.

**Keywords** Pacific abalone · Shell morphological traits · Body mass traits · Path analysis · Sex differences

## Introduction

Abalone (*Haliotis* spp.) is a widely distributed marine gastropod inhabiting subtropical and temperate waters worldwide and is one of the most valuable fishery products. However, due to environmental changes and overfishing, wild abalone populations have drastically declined, leading to the depletion of natural resources (The IUCN Red List of Threatened Species 2025). This decline has driven both market demand and price increases. Consequently, abalone aquaculture has expanded rapidly, now supplying more than 95% of the global market (Gao et al. 2023). In 2023, China's abalone production exceeded 245,000 tons (Wang and Gao 2024), accounting for over 80% of global output (Gao et al. 2023), making China the world's leading abalone producer. Pacific abalone (*H. discus hannai*), a temperate species, is naturally distributed in the Yellow and Bohai Seas of China, along the coast of Hokkaido, Japan, and around the Korean Peninsula (Gao et al. 2021). A breakthrough in artificial hybridization in the 1990s led to the successful breeding of

✉ Xiaolong Gao  
gaoxiaolong1@nbu.edu.cn

✉ Caihuan Ke  
chke@xmu.edu.cn

<sup>1</sup> State Key Laboratory of Mariculture Breeding, College of Ocean and Earth Sciences, Xiamen University, Xiamen, Fujian Province 116023, China

<sup>2</sup> National Engineering Research Center of Marine Biotechnology and Engineering, Ningbo University, Ningbo 315211, China

<sup>3</sup> Key Laboratory of Aquacultural Biotechnology, Ministry of Education Ningbo, Ningbo University, Zhejiang 315211, China

<sup>4</sup> College of Biosystems Engineering and Food Science, Zhejiang University, Hangzhou 310058, China

<sup>5</sup> The School of Marine Sciences, Ningbo University, Ningbo, Zhejiang Province 315832, China

the “Dalian No. 1” strain, which exhibited superior growth and heat tolerance. The survival rate of it was increased by 1.9-fold, while the growth rate was improved by over 20%. (Wu et al. 2020; Zhang et al. 2005). This advancement enabled the expansion of China’s abalone aquaculture from Liaoning and Shandong to the coasts of Fujian and Guangdong (Chen et al. 2017), markedly increasing its economic value.

Body mass, a critical determinant of abalone’s economic value, directly influences market grading and price differentiation. Common abalones (30–50 g) are typically priced at 80–150 CNY/kg, while premium large abalones (>200 g) can reach over 300 CNY/kg, representing a three- to four-fold price increase (Ke 2013). Despite its importance, body mass is a less intuitive breeding target compared to shell morphological traits such as length or height. This is because short-term environmental fluctuations (e.g., salinity, temperature, food supply) can rapidly alter body weight (Augley et al. 2008), reducing the accuracy of selective breeding. In contrast, shell morphological traits are relatively stable and less affected by environmental conditions. Therefore, clarifying the correlation between shell morphological traits and body mass is essential for optimizing artificial breeding (Kvingedal et al. 2010; Wang et al. 2011).

Based on Wright’s path analysis theory from the 1920s (Wright 1977), this study applies path analysis to examine the correlations and coefficients of determination between shell morphological traits (length, width, height, perimeter, area) and body mass traits (total and soft body weight), thereby enabling a direct assessment of abalone body mass through measurable shell traits. Path analysis has been widely applied in marine organisms, including fish (Mohamed et al. 2021; Xu et al. 2023), shrimp and crabs (Cui et al. 2021; Waqairatu et al. 2012), and mollusks (Luo et al. 2013; Zhao et al. 2014). In mollusks, studies have been conducted on species such as *Sinonovacula constricta* (Chen et al. 2021), *Meretrix meretrix* (Zhang et al. 2023), and *Pinctada fucata* (Deng et al. 2019). Previous research on abalone, including *H. discus hannai*, has consistently identified shell length as the most influential trait affecting body mass (Ding et al. 2014; Li et al. 2024). For example, Li et al. (2024) examined different strains of *H. discus hannai* and found that, in contrast to shell width, shell length was the key morphological trait determining the body mass of the “Huangxun No. 1” strain. However, these findings are not universally applicable, as the morphological traits influencing body mass vary with species, geographic population, and breeding objectives. For instance, in *H. discus hannai* ♀ × *H. gigantea* ♂ hybrids, shell height shows the strongest correlation with body weight, whereas in *H. gigantea* ♀ × *H. discus hannai* ♂ hybrids, shell width is the determining factor (Luo et al. 2013). Similarly, in male *Crassostrea*

*hongkongensis*, body height is the second most influential factor for body weight, while in females, body height has the strongest direct effect, followed by body length (Xiao et al. 2011). In *Chlamys farreri*, correlation and path analyses revealed that shell length, shell thickness, and shell height all have highly significant correlations with body weight (Liu et al. 2002). Moreover, Wang (2013) reported that sex differences also contribute to variations in the morphological traits affecting body weight. Taken together, these findings suggest that the shell morphological traits influencing body mass in *H. discus hannai* may differ between males and females. However, to our knowledge, this hypothesis has not been systematically investigated.

In abalone breeding, the demand for females far exceeds that for males, with 7–8 females typically paired with a single male for fertilization. Excessive use of males increases sperm concentration, requiring additional egg-washing cycles to improve hatching rates (Gao et al. 2024), thereby reducing efficiency. As a result, farmers often prefer to sell sorted males and retain females for breeding. Therefore, measuring the shell morphological traits of female and male abalones separately before conducting path analysis can facilitate the breeding of high-quality commercial abalones tailored to their specific sex, as well as market demands. This approach not only enhances breeding efficiency but also directly improves economic returns.

This study is the first to systematically explore the correlation between shell morphological traits (length, width, height, perimeter, area) and body mass traits (total weight and soft body weight) in male and female Pacific abalone. By applying path and multiple regression analyses to evaluate the direct and indirect effects of shell traits on body mass, the most influential morphological traits for each sex can be identified, thereby clarifying key sex-specific traits affecting body weight and filling an important gap in breeding research related to sexual differences in this species. The findings provide a theoretical foundation for innovative germplasm utilization and the development of standardized seedling production technologies.

## Materials and Methods

### Experiment Material

All abalones used in the experiment were obtained from the Jinjiang Fuda Abalone Farm in Quanzhou City, Fujian Province (118°60′ E, 24°53′ N). The aquaculture conditions were as follows: seawater was sourced from the natural sea area and treated by sedimentation and sand filtration before use, ensuring that dissolved oxygen (DO) levels consistently remained above 6.5 mg/L. The temperature was 20±0.5 °C,

salinity was  $30 \pm 1$ . Abalones were fed once daily at 17:00 with a formulated diet containing 31% crude protein and 5% crude fat, at a feeding rate equivalent to 3% of their wet body weight.

### Measurement Methods

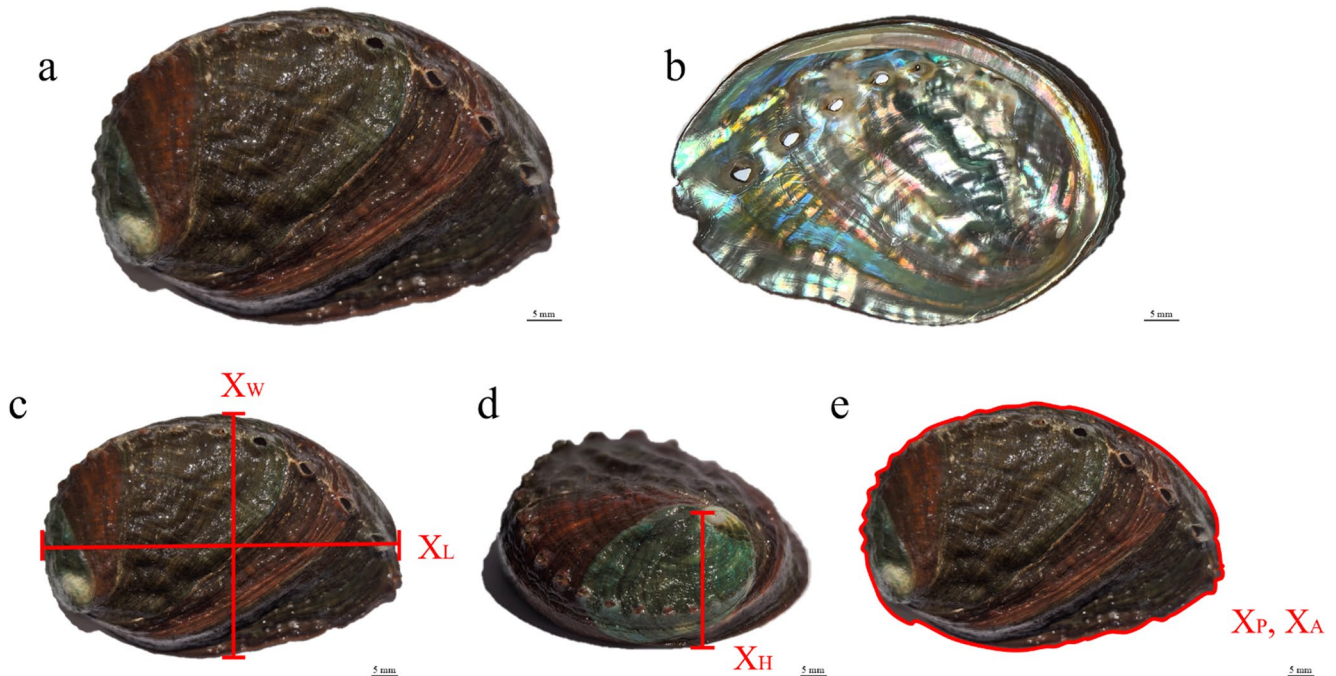
A total of 150 female abalones (Weight:  $33.301 \pm 5.964$ , Shell length:  $64.494 \pm 4.037$ ) and 150 male abalones (Weight:  $42.169 \pm 10.077$ , Shell length:  $67.630 \pm 5.396$ ) were randomly selected. Female and male abalones can be distinguished by visual inspection: the gonad is dark green in females, whereas it is milky white in males. Epibionts on the shell surface were carefully removed, and excess water from both the external and internal shell surfaces was absorbed using gauze. Shell length ( $X_L$ ), shell width ( $X_W$ ), and shell height ( $X_H$ ) were measured with a digital vernier caliper (accuracy  $\pm 0.01$  mm, DL91150, DELI). Total live body weight ( $Y_W$ ) and shell weight were recorded using an electronic balance (accuracy  $\pm 0.01$  g, CN-KT001, KTRUE). These measurements constituted the five main shell morphological traits (Fig. 1). Additionally, shell perimeter ( $X_P$ ) and shell area ( $X_A$ ) were obtained by photographing abalone shells with a digital camera (EOS R10, Canon). Images were analyzed in ImageJ (version 1.53k). Each abalone shell included a ruler and a corresponding identification number to facilitate scale calibration in ImageJ. Subsequently, the outline of each shell was manually traced, and the corresponding data were obtained by selecting Analyze

→ Measure → Results. All parameters were compiled in Microsoft Excel. Soft body weight ( $Y_S$ ) was then calculated using the following formula:

$$Y_S = Y_W - \text{Shell weight}$$

### Data Analysis

Firstly, a significant deviation of the direct genetic correlation between females and males from 1 indicates sexual dimorphism in the direct genetic effects of these traits, thereby supporting the feasibility of independent selection in the two sexes. Then, correlation and path analyses were performed using IBM SPSS Statistics v27.0.1. All data were first tested for normality using the Shapiro-Wilk test. Pearson correlation analysis was then conducted to assess relationships among traits. Path analysis was carried out using the stepwise regression method to establish optimal regression equations for estimating body mass traits based on shell morphological traits. For the linear regression analysis, shell morphological traits— $X_L$  (shell length),  $X_W$  (shell width),  $X_H$  (shell height),  $X_P$  (shell perimeter), and  $X_A$  (shell area)—were set as independent variables, while body mass traits— $Y_W$  (body weight) and  $Y_S$  (soft body weight)—were treated as dependent variables. The significance threshold was set at  $P < 0.05$ , with  $P < 0.01$  considered highly significant. In addition, justify the model choice using Bayesian Information Criterion (BIC). Figures were generated using GraphPad Prism 10.1.4 and Chiplot (<https://www.chiplot>).



**Fig. 1** Shell morphological traits of *Haliotis discus hannai*. (a) Dorsal view; (b) ventral view; (c) shell length ( $X_L$ ) and shell width ( $X_W$ ); (d) shell height ( $X_H$ ); (e) shell perimeter ( $X_P$ ) and shell area ( $X_A$ ), scar bar, 5 mm

online/) (Ji et al. 2022; Li et al. 2023). The linear model employed for the regression between body weight ( $Y_W$ ) and soft body weight ( $Y_S$ ) was:

$$Y = a + b_1X_1 + b_2X_2 + \dots + b_iX_i$$

where  $Y$  ( $Y_W$  or  $Y_S$ ) represents the dependent variable;  $a$  is the constant term;  $b_i$  is the partial regression coefficient for the  $i$ -th variable;  $X_i$  is the  $i$ -th independent variable. Path coefficients were then calculated from the partial regression coefficients using the following formula (Zhang et al. 2014):

$$P_{Y.X_i} = b_i \times \frac{S_{X_i}}{S_Y}$$

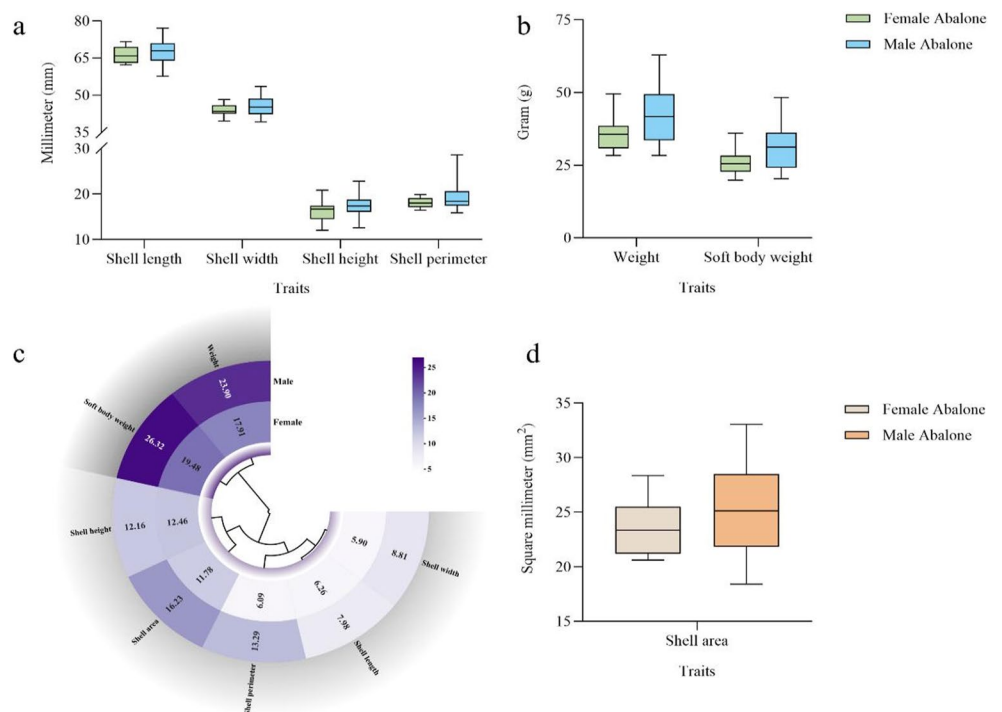
$$P_{X_iX_j} = r_{ij}P_{j,Y} (i \neq j)$$

In the equation,  $P_{Y.X_i}$  represents the direct path coefficient of  $X_i$  on  $Y$ ;  $S_{X_i}$  is the standard deviation of the independent variable  $X_i$ ;  $S_Y$  is the standard deviation of the dependent variable  $Y$ ;  $P_{X_iX_j}$  is the indirect path coefficient of  $X_i$  on  $Y$  through  $X_j$ ;  $r_{ij}$  is the correlation coefficient;  $P_{j,Y}$  is the path coefficient of  $X_j$  on  $Y$ . The following formulas were used to calculate the direct determination coefficients and indirect determination coefficients (Zhang et al. 2014):

$$d_i = P_{Y.X_i}^2$$

$$d_{ij} = 2r_{ij}P_{Y.X_i}P_{Y.X_j}$$

**Fig. 2** Statistical analysis of shell morphological (a) and body mass traits (b) in female and male *Haliotis discus hannai*, with coefficients of variation (c). Darker arcs indicate higher coefficients of variation



where  $d_i$  is the direct determination coefficient, and  $d_{ij}$  is the indirect determination coefficient.

## Results

### Statistical Analysis of Abalone Traits

Box plot analysis revealed that, for both female and male abalones, the distributions of shell morphological traits are relatively concentrated, whereas body mass traits show more dispersed distributions (Fig. 2a and b). In female abalones, the coefficients of variation for shell length, shell width, and shell perimeter are relatively small, while those for body weight and shell height are comparatively larger, with body weight and soft body weight exhibiting the highest variability (Fig. 2c). In male abalones, shell length and shell width also show relatively low variation, whereas shell height, shell perimeter, and shell area exhibit greater variation. Similarly, body weight and soft body weight have the highest coefficients of variation (Fig. 2c). The Shapiro-Wilk normality test indicates that, for both sexes, the  $P$ -values for all seven measured traits exceed 0.05 (Supplementary Table 1), confirming that the data conform to a normal distribution and are suitable for path analysis.

### Pearson Correlation Analysis of Abalone Traits

Pearson correlation analysis of the seven traits in female abalones revealed significant correlations ( $P < 0.05$ )

between body weight, soft body weight, shell length, and shell width with the other morphological traits. Shell perimeter and shell area exhibited highly significant correlations ( $P < 0.01$ ) with the other five traits, except for shell height, with which no significant correlation was observed. Among these, the correlation between shell perimeter and shell area was the strongest at 0.978 (Fig. 3a).

In male abalones, Pearson correlation analysis showed highly significant correlations ( $P < 0.01$ ) between body weight, soft body weight, shell length, shell width, and shell area with the other morphological traits, whereas shell perimeter displayed no significant correlation with shell height. The highest correlation was observed between body weight and soft body weight (0.989), while the lowest was between shell perimeter and shell height (0.201) (Fig. 3b).

### Path Analysis Model Screening

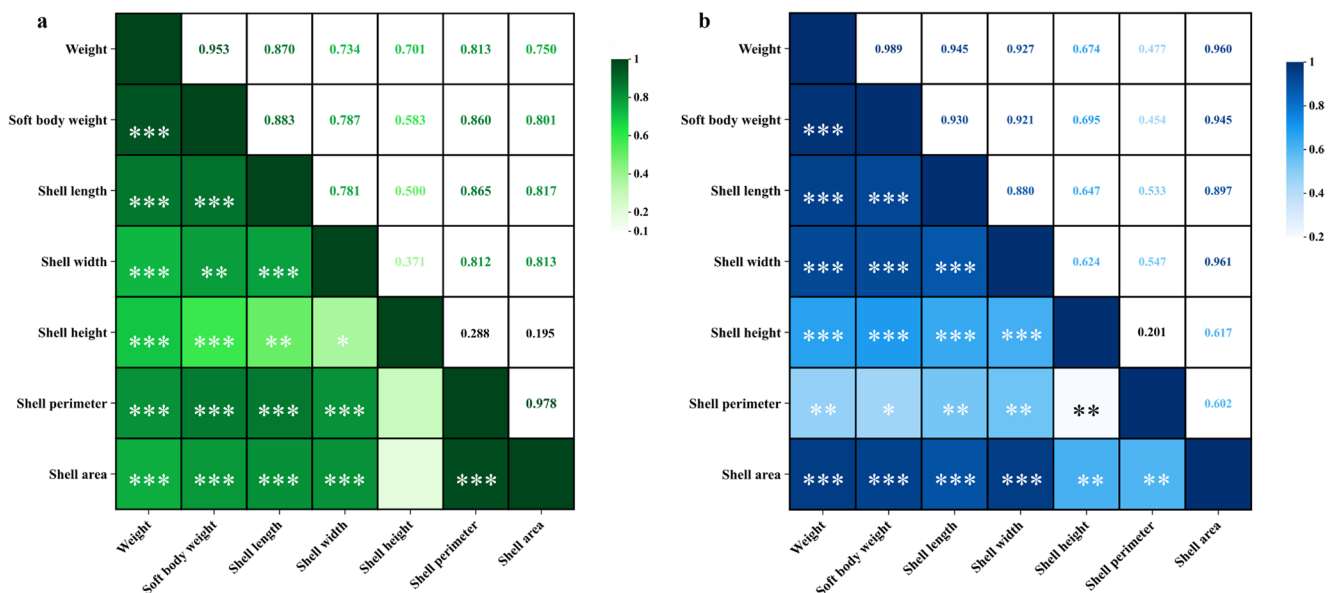
Using body weight as the dependent variable and the five shell morphological traits as independent variables, three models were evaluated for female abalones (Fig. 4). Model I included only shell length as the independent variable, excluding the other four traits. Model II included shell height, excluding the remaining three traits. Model III incorporated shell length, shell height, and shell perimeter, excluding shell width and shell area. As independent variables were progressively added, both the correlation coefficient ( $R$ ) and the coefficient of determination ( $R^2$ ) increased, and the model exhibited the lowest BIC values (Supplementary Table 2), indicating an enhanced effect of the additional variables on the dependent variable. Therefore, Model III ( $R^2 = 0.892$ ) was selected for subsequent analysis.

For male abalones, three models were similarly predicted (Fig. 4). Model I included only shell length. Model II included shell length and shell width. Model III included shell length, shell width, and shell area, excluding shell height and shell perimeter. Among these, Model III exhibited the highest  $R^2$  (0.951), with the lowest BIC values among all models (Supplementary Table 2), indicating the best fit, and was therefore selected for further analysis.

When using soft body weight as the dependent variable and the five shell morphological traits as independent variables, only two models were predicted for female abalones (Fig. 4). Model I included only shell length as the independent variable, while Model II included shell height, excluding the other three traits. Model II, with an  $R^2$  of 0.816, and the model exhibited the lowest BIC values (Supplementary Table 2), was selected for subsequent analysis. For male abalones, three models were evaluated (Fig. 4). Model I included only shell area. Model II included shell area and shell length. Model III included shell area, shell length, and shell perimeter, excluding shell width and shell height. Among these, Model III, with the highest  $R^2$  of 0.940, and the BIC values of the model were the lowest (Supplementary Table 2), was selected for subsequent analysis.

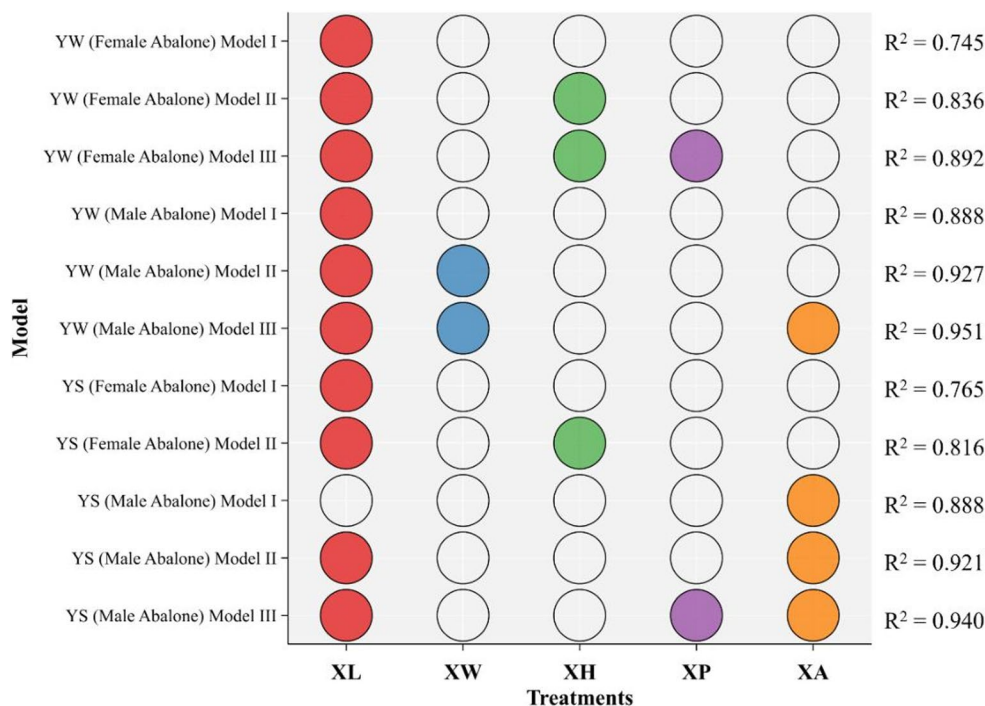
### Effects of Shell Morphological Traits on Body Weight Traits

For female abalones, the three shell morphological traits included in Model III and their correlation coefficients, as well as direct and indirect effects on body weight, are presented in Table 1. Among these traits, shell perimeter had the greatest direct effect on body weight (0.500,  $P < 0.01$ ),



**Fig. 3** Pearson correlation coefficients among traits in female (a) and male (b) *Haliotis discus hannai*. Asterisks indicate significance: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ; no asterisks indicate  $P > 0.05$

**Fig. 4** Overview of models selected via path analysis. Body weight and soft body weight of female and male abalones were dependent variables, with shell length, width, height, perimeter, and area as independent variables. Each row represents one model, with R<sup>2</sup> shown at the far right. Uncolored variables were excluded during model selection. Colors indicate traits: red=shell length, blue=shell width, green=shell height, purple=shell perimeter, orange=shell area



**Table 1** Effect of shell morphological traits on body weight in female abalone

Dependent variable	Independent variable	Correlation Coefficient	Direct effect	Indirect effect			Sum
				X <sub>L</sub>	X <sub>H</sub>	X <sub>P</sub>	
Y <sub>W</sub>	X <sub>L</sub>	0.870**	0.212	-	0.166	0.183	0.349
	X <sub>H</sub>	0.701**	0.451**	0.225	-	0.13	0.355
	X <sub>P</sub>	0.813**	0.500**	0.433	0.406	-	0.839

**Table 2** Effect of shell morphological traits on body weight in male abalone

Dependent variable	Independent variable	Correlation Coefficient	Direct effect	Indirect effect			Sum
				X <sub>L</sub>	X <sub>W</sub>	X <sub>A</sub>	
Y <sub>W</sub>	X <sub>L</sub>	0.945**	0.431**	-	0.379	0.387	0.766
	X <sub>W</sub>	0.927**	-0.039	-0.034	-	-0.038	-0.072
	X <sub>A</sub>	0.960**	0.611**	0.548	0.587	-	1.136

**Table 3** Effect of shell morphological traits on soft body weight in female abalone

Dependent variable	Independent variable	Correlation Coefficient	Direct effect	Indirect effect		Sum
				X <sub>L</sub>	X <sub>H</sub>	
Y <sub>S</sub>	X <sub>L</sub>	0.883**	0.710**	-	0.355	0.355
	X <sub>H</sub>	0.583**	0.297*	0.148	-	0.148

followed by shell height (0.451,  $P < 0.01$ ). Analysis of the indirect effects indicates that shell perimeter also has the largest overall effect on body weight (0.839).

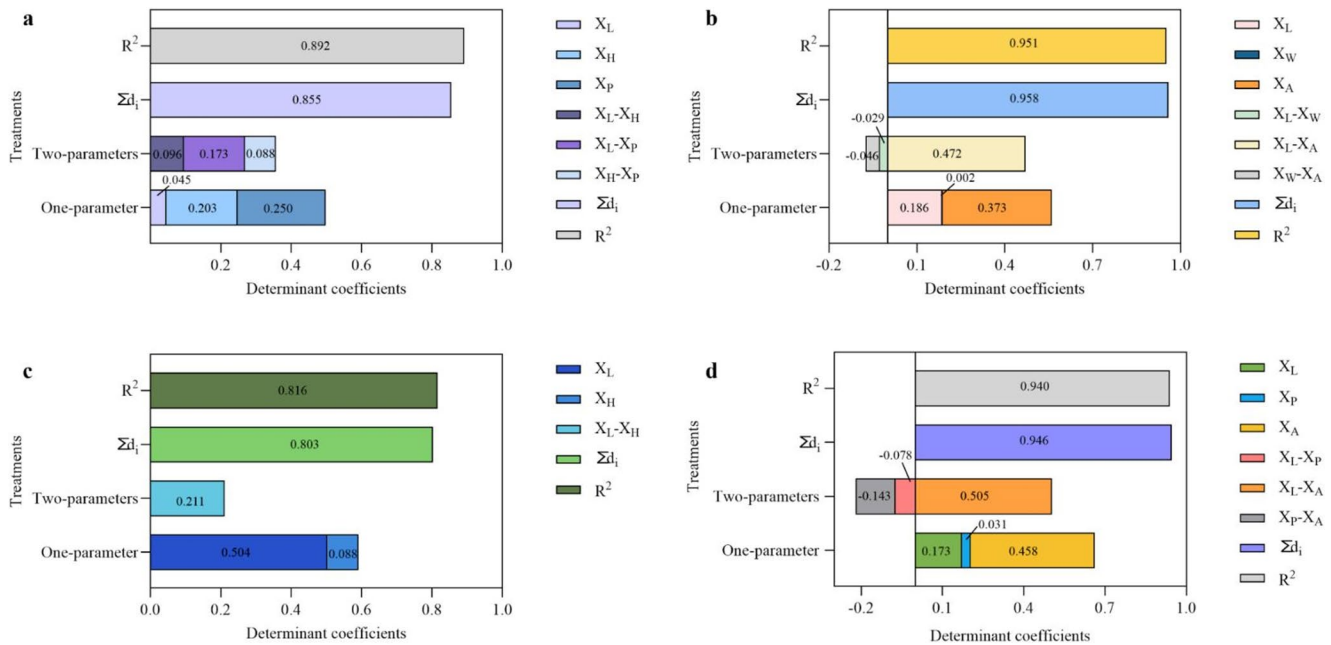
For male abalones, the three traits in Model III showed that shell area had the greatest direct effect on body weight (0.611,  $P < 0.01$ ), followed by shell length (0.431,  $P < 0.01$ ), while shell width had the smallest effect (-0.039,  $P > 0.05$ ). The indirect effects analysis revealed that shell area still exerted the largest overall effect on body weight (1.136) (Table 2).

Using Model II for female abalones, the direct and indirect effects of shell length and shell height on soft body weight are summarized in Table 3. Shell length had the strongest direct effect on soft body weight (0.710,  $P < 0.01$ ), followed by shell height (0.297,  $P < 0.05$ ). Indirect effects analysis revealed that shell length retained the largest overall influence on soft body weight (0.355).

For male abalones, the direct and indirect effects of shell length, shell perimeter, and shell area on soft body weight are shown in Table 4. Among the three traits, shell area had the greatest direct effect on soft body weight (0.677,

**Table 4** Effect of shell morphological traits on soft body weight in male abalone

Dependent variable	Independent variable	Correlation Coefficient	Direct effect	Indirect effect			Sum
				$X_A$	$X_L$	$X_P$	
$Y_S$	$X_A$	0.945**	0.677**	-	0.608	0.407	1.015
	$X_L$	0.930**	0.416*	0.373	-	0.222	0.595
	$X_P$	0.454*	-0.175*	-0.105	-0.093	-	-0.199



**Fig. 5** Coefficients of determination of shell morphological traits on body weight and soft body weight. (a) Body weight in female abalones; (b) body weight in male abalones; (c) soft body weight in female abalones; (d) soft body weight in male abalones. Analyses include

individual traits (one-parameter) and pairwise combinations (two-parameter).  $\sum d_i$  represents the sum of coefficients from both analyses;  $R^2$  denotes the adjusted coefficient of determination

$P < 0.01$ ), followed by shell length (0.431,  $P < 0.05$ ), with shell perimeter having the smallest effect ( $-0.175$ ,  $P < 0.05$ ). Analysis of the indirect effects demonstrated that shell area still exerted the largest overall effect on soft body weight (1.015).

### Shell Morphological Traits and their Influence on Body Mass Traits

The direct coefficients of determination of individual shell morphological traits (shell length, shell width, shell height, shell perimeter, and shell area) for body mass traits (body weight and soft body weight), as well as the direct coefficients of determination for pairwise shell morphological traits, are shown in Fig. 5. In female abalones, shell perimeter (0.250) and shell length (0.504) had the highest direct coefficients of determination for body weight and soft body weight, respectively. For pairwise traits, the highest direct coefficients of determination were observed for shell length–shell perimeter (0.173) on body weight and shell length–shell height (0.211) on soft body weight (Fig. 5a

and c). In male abalones, shell area had the highest direct coefficients of determination for body weight and soft body weight, at 0.373 and 0.458, respectively. Among pairwise traits, shell length–shell area exhibited the highest direct coefficients of determination for body weight and soft body weight, at 0.472 and 0.505, respectively (Fig. 5b and d). For both female and male abalones, the total sum of the coefficients of determination ( $\sum d_i$ ) of shell morphological traits on body mass traits was close to the respective correlation coefficients ( $R^2$ ), consistent with the results of the path and correlation analyses.

### Path Analysis Results and Multiple Regression Analysis

The path analysis results are summarized in Table 5. Standardized coefficients (Beta) represent the path coefficients, indicating the direct effect of each independent variable on the dependent variable, while unstandardized coefficients (Beta) correspond to the coefficients of the independent variables in the multiple regression equations. Based on

**Table 5** Multivariate regression analysis between shell morphological traits and body mass traits

Dependent variable	Sex	Model	Unstandardized Coefficients Beta	Std. Error	Standardized Coefficients Beta	t	Sig.
Y <sub>W</sub>	Female Abalone	Constant	-37.428	5.496	-	-6.810	0.000
		X <sub>L</sub>	0.245	0.189	0.212	1.296	0.210
		X <sub>H</sub>	1.051	0.200	0.451	5.268	0.000
		X <sub>P</sub>	2.142	0.634	0.500	3.379	0.003
	Male Abalone	Constant	-45.717	11.070	-	-4.130	0.000
Y <sub>S</sub>	Female Abalone	X <sub>L</sub>	0.805	0.193	0.431	4.178	0.000
		X <sub>W</sub>	-0.098	0.412	-0.039	-0.239	0.814
		X <sub>A</sub>	1.510	0.437	0.611	3.459	0.002
		Constant	-25.804	6.012	-	-4.292	0.001
	Male Abalone	X <sub>L</sub>	0.626	0.113	0.710	5.539	0.000
Y <sub>S</sub>	Female Abalone	X <sub>H</sub>	0.576	0.249	0.297	2.316	0.035
		Constant	-34.874	7.295	-	-4.781	0.000
		X <sub>A</sub>	1.356	0.241	0.677	5.621	0.000
		X <sub>L</sub>	0.630	0.172	0.416	3.660	0.001
	X <sub>P</sub>	-0.567	0.203	-0.175	-2.790	0.011	

the optimal models identified in Sect. 3.3, path analysis for female abalones was conducted with shell length (X<sub>L</sub>), shell height (X<sub>H</sub>), and shell perimeter (X<sub>P</sub>) as independent variables and body weight (Y<sub>W</sub>) as the dependent variable. The resulting multiple regression equation is:

$$Y_W = -37.428 + 0.245 * X_L + 1.051 * X_H + 2.142 * X_P (R^2 = 0.892)$$

For male abalones, path analysis was conducted with shell length (X<sub>L</sub>), shell width (X<sub>W</sub>), and shell area (X<sub>A</sub>) as independent variables and body weight (Y<sub>W</sub>) as the dependent variable. The resulting multiple regression equation is:

$$Y_W = -45.717 + 0.805 * X_L - 0.098 * X_W + 1.510 * X_A (R^2 = 0.951)$$

For the soft body weight (Y<sub>S</sub>) of female abalones, path analysis was conducted with shell length (X<sub>L</sub>) and shell height (X<sub>H</sub>) as independent variables. The resulting multiple regression equation is:

$$Y_S = -25.804 + 0.626 * X_L + 0.576 * X_H (R^2 = 0.816)$$

For male abalones, path analysis was conducted with shell area (X<sub>A</sub>), shell length (X<sub>L</sub>), and shell perimeter (X<sub>P</sub>) as independent variables and soft body weight (Y<sub>S</sub>) as the dependent variable. The resulting multiple regression equation is:

$$Y_S = -34.874 + 1.356 * X_A + 0.630 * X_L - 0.567 * X_P (R^2 = 0.940)$$

## Discussion

In selective aquaculture breeding, the phenotypic coefficient of variation (CV) is a key indicator for assessing the variability of growth traits. Traits with higher CV values typically exhibit greater potential for genetic improvement and are therefore prioritized in selection programs (Zhao et al. 2023). The breeding potential of shellfish, including the pearl oyster *Pinctada fucata* (Wang et al. 2018), the ark shell *Scapharca broughtonii* (Xin et al. 2021), and the veined rapa whelk *Rapana venosa* (He et al. 2021), has been shown to correlate positively with the CV of the traits. In this study, CV was used to quantify the variability of seven measured traits. Shell length and shell width consistently showed the lowest CV values in both female and male abalones, whereas body weight and soft body weight exhibited the highest CVs, indicating that body mass traits have the greatest breeding potential.

Although body weight is the most direct target in shellfish breeding, it is less readily measurable than shell morphological traits such as shell length, width, and height. Consequently, path analysis is necessary to elucidate the relationships between shell morphological traits and body mass traits and to determine the extent to which shell traits influence body mass (Chang et al. 2008). This approach enables the identification of key shell morphological traits that exert the strongest effects on body mass, allowing these traits to be used for the rapid selection of individuals with higher body weight and thereby improving the efficiency of abalone genetic breeding programs.

The correlation coefficient serves as a comprehensive indicator of the interrelationships among variables. Pearson correlation analysis of the seven traits in *H. discus hannai*

revealed significant correlations between the two body mass traits (body weight and soft body weight) and the five shell morphological traits in both female and male abalones. This indicates that all of the examined shell morphological traits significantly influence body mass, although the magnitude of their effects varies. Consequently, more precise characterization requires further analysis using path and multiple regression analyses. Path analysis, widely applied in animal and plant breeding (Bhatt 1973; Khalil et al. 2016), can distinguish direct and indirect effects among variables, thereby reflecting their true associations without interference from other factors (Liu et al. 2016). In this study, path analysis showed that shell length, shell height, and shell perimeter were the primary determinants of body weight in female abalones, whereas shell length, shell width, and shell area were the primary determinants in males. For soft body weight, shell length and shell height were the main determinants in females, while shell length, shell area, and shell perimeter were the primary determinants in males. These results indicate that the influence of shell morphological traits differs not only between sexes for the same body mass trait but also across different body mass traits within the same sex.

In regression analysis, an  $R^2 \geq 0.850$  indicates that the primary independent variables influencing the dependent variable have been successfully identified (Liu et al. 2002). In this study, path analysis for male abalones, using either body weight or soft body weight as the dependent variable, produced  $R^2$  values consistently exceeding 0.940. This demonstrates the reliability of the selected shell morphological traits and confirms that the key shell traits affecting body mass in males have largely been determined. In contrast, path analysis for female soft body weight yielded a model with  $R^2 < 0.850$ , suggesting that factors beyond the five measured shell morphological traits may have significant influence on female soft body weight. This phenomenon is commonly observed in shellfish research. For example, in the Pacific oyster (*Crassostrea gigas*), path analysis for soft body weight also resulted in  $R^2 < 0.850$ , leading authors to speculate that, in addition to shell height, length, and width, other factors may affect soft body weight (Han and Li 2017). Similarly, studies on the Japanese scallop (*Patinopecten yessoensis*) indicate that soft body weight may be related to features such as ridged and grooved shells, hinge development, shell surface area (Zhao et al. 2023), and environmental factors (light, temperature, bait, tide and sediment) (Liu et al., 2015). In addition, Huo et al. reported that the  $R^2$  values and coefficients of determination for the relationships between shell morphological traits and soft body weight in 2-year-old and 3-year-old *Ruditapes philippinarum* were below 0.850, suggesting that gonad weight may be an important factor influencing soft body weight (Huo et al., 2010). Similarly, in female abalones, ovarian development

during the reproductive season increases the proportion of gonad weight relative to total soft body weight, which may partly explain the residual variation not accounted for by shell morphology. Therefore, gonad weight should be incorporated into future studies to improve model performance. Taken together, future research on female abalones could expand the range of shell morphological traits investigated, including, but not limited to, the number and spacing of respiratory holes and overall shell volume. Additionally, environmental variables and gonad weight should be incorporated into the analysis to better explain variations in soft body weight.

The primary purpose of path analysis is to use readily observable shell morphological traits to directly identify individuals with greater body weight, thereby enhancing breeding efficiency or enabling the sale of larger abalones to increase economic returns. Based on the analyses above, shell length was identified as the most important trait for breeding programs targeting different sexes and body mass traits, followed by shell area. This indicates that future breeding efforts for *H. discus hannai* should prioritize these two traits. Furthermore, breeding programs should consider female and male abalones separately. While some shell traits influencing body weight are shared between sexes, significant differences exist. For example, shell height should also be incorporated into female breeding programs.

Research on morphological traits should not be limited to their relationship with body mass. Environmental factors such as salinity, temperature, and food supply not only influence body mass but also directly affect the physiology of aquatic organisms (Bromage et al. 2001; Pankhurst and Porter 2003). Stagnation in shell length or shell area growth may indicate that abalones are experiencing environmental stress or disease pressure, whereas larger shell length or shell area generally reflects higher growth efficiency and energy acquisition capacity, which may be associated with greater environmental tolerance. Morphological traits could therefore be correlated with physiological indicators, enabling direct assessment of environmental adaptability and health status based on phenotypic changes. In the era of big data, aquaculture is shifting from “experience-driven” to “data-driven” practices through artificial intelligence (AI). Moreover, computer vision technology facilitates the digitization of morphological traits, while deep learning bridges the gap between genotype and phenotype. Path analysis offers a novel perspective for AI development, particularly in species with complex morphologies such as fish, shrimp, and crabs, where computer vision capture and code implementation are challenging. By first identifying key morphological traits through path analysis, targeted computer vision modules can be developed, ultimately enhancing production efficiency.

In summary, the path analysis results indicate that the shell morphological traits influencing body weight differ between female and male abalones. For females, shell perimeter has the greatest direct and indirect influence on body weight, whereas for males, shell area plays the most significant role. Regardless of sex, shell length consistently shows a strong correlation with body mass traits. Accordingly, selective breeding programs for *H. discus hannai* can prioritize high-quality females with greater shell length and perimeter, and high-quality males with larger shell area, as broodstock. This strategy will enhance the efficiency of trait improvement in abalone. Overall, this study provides a scientific foundation for developing standardized breeding systems, including trait measurement, breeding techniques, and supporting equipment, thereby improving the precision and efficiency of abalone breeding programs.

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**Data Availability** All data generated or analyzed in this study are included in this published article and its Supplementary Information files.

## Declarations

**Ethics Approval** This study of animals was reviewed and approved by the Animal Welfare Committee of the College of Ocean & Earth Sciences, Xiamen University (permit no. SYXK 2023-0010).

**Competing interests** The authors declare no competing interests.

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