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Characteristics of growth traits and their effects on body weight of G_1 individuals in the mud crab (*Scylla paramamosain*)

W. Jiang[1,2], H.Y. Ma[1], C.Y. Ma[1], S.J. Li[1], Y.X. Liu[1], Z.G. Qiao[1] and L.B. Ma[1]

[1]Key Laboratory of East China Sea and Oceanic Fishery Resources Exploitation, Ministry of Agriculture, East China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences, Shanghai, China
[2]College of Fisheries and Life Science, Shanghai Ocean University, Shanghai, China

Corresponding authors: H.Y. Ma / L.B. Ma
E-mail: mahongyuhome@163.com / malingbo@vip.sina.com

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ABSTRACT. The mud crab (*Scylla paramamosain*) is considered a potentially important marine crab species for selective breeding. Here, we first examined sex ratio and differences in 16 growth traits between females and males in a G_1 population of *S. paramamosain*, and we then analyzed the correlation between these growth traits and their effects on body weight (BW). Of these growth traits, nine were significantly different between sexes. In females, the correlation coefficients in all trait pairs ranged from 0.524 to 0.997. The traits carapace length (CL) and distance between lateral spine 2 (DLS2) significantly affected BW directly, with the path coefficients being 1.124 and -0.186, respectively. The determination coefficients of traits CL and DLS2 to BW were 1.263 and 0.035 with the total value being 0.951, indicating that the two traits were the key factors affecting BW. In males, the correlation coefficients in all trait pairs ranged from 0.881 to 0.999. The three traits body height (BH), fixed finger height of the claw (FFHC), and meropodite length of pereopod 2 (MLP2) significantly affected BW directly, with the path coefficients being 0.484, 0.300, and 0.225, respectively. The determination coefficients of traits BH, FFHC and MLP2 to BW were 0.234, 0.090 and 0.051, with the total value being 0.967, indicating that these three traits played a key role in affecting BW. Moreover, we constructed two best-fit linear regression equations, which were Y (BW) = 4.969 X_1 (CL) - 0.758 X_2 (DLS2) - 140.177 and Y (BW) = 3.806 X_1 (BH) + 2.371 X_2 (FFHC) + 1.725 X_3 (MLP2) - 123.559 in females and males, respectively.

Key words: *Scylla paramamosain*; Growth traits; Correlation analysis; Path analysis; Multiple regression equation

INTRODUCTION

The mud crab (*Scylla paramamosain*), a large marine crab species, is widely distributed along the southeastern coastal region of China. It is an important marine fishery resource and aquaculture species in China, because of its abundant fishing yields, fast growth rate, large culture scale, and significant commercial values. Records of *S. paramamosain* aquaculture can date back more than 100 years in China (Shen and Lai, 1994) and more than 30 years in other Asian countries (Keenan and Blackshaw, 1999). It is reported that the total culture area expanded more than 270 x 10^6 m^2, and the aquaculture outcome reached 110,000 tons in 2011 in China (Fishery Bureau of Ministry of Agriculture of China, 2012). However, this production scale could not meet the market demand.

An artificial selective breeding program is considered as an effective way to improve and enhance economic traits in aquaculture organisms. Many studies have been conducted on the phenotypic and genetic relationships of growth traits in aquaculture animals, such as pearl oyster (*Pinctada martensii*) (Deng et al., 2008), common carp (*Cyprinus carpio*) (Wang, 2009), small abalone (*Haliotis diversicolor*) (You et al., 2010), Japanese flounder (*Paralichthys olivaceus*) (Tian et al., 2011), and sea urchin (*Strongylocentrotus intermedius*) (Chang et al., 2012). Research on *S. paramamosain* has mainly focused on reproductive performance (Djunaidah et al., 2003; Zeng, 2007), culture biology (Nghia et al., 2007; Ut et al., 2007), functional genes (Rosa et al., 2008; Wang et al., 2012), population genetic diversity (Shu et al., 2011; Ma et al., 2011a, 2012), and molecular markers (Ma et al., 2011b,c). In addition, limited differences of morphological traits of individuals from different coasts of southeastern China were determined by morphological discriminant analysis (Li et al., 2004). A very significant correlation ($P < 0.01$) was found in each pair of 20 growth traits, of which two traits, carapace length and fixed finger height of the claw, were suggested to play an important role in affecting body weight ($P < 0.01$) (Ma et al., 2013). Beside the above, there is little information about the characteristics of morphological traits available in *S. paramamosain*.

The objective of this study was to first determine sex ratio and differences of 16 growth traits between females and males of a G_1 population in *S. paramamosain*, and then to analyze the correlation of these growth traits and their effects on body weight in females and males. This study should be helpful in better understanding the differences between sexes, relationships between growth traits and artificial selective breeding in this crab species and other closely related species.

MATERIAL AND METHODS

Crab sampling and sex identification

A first-generation (G_1) family was constructed and cultured in a pond on Hainan Island, China. Ninety-six full-sib individuals aged nearly 3 months were randomly collected in October 2012 (Table 1). The sex of individuals was identified based on the shape of the abdomen. The females have a wider and more globular abdomen, whereas the males have a narrow and straight abdomen (Ikhwanuddin et al., 2011).

Table 1. Differences of 16 growth traits between females and males in *Scylla paramamosain*.

Trait	Gender	No.	Minimum	Maximum	Mean ± SE	Standard deviation (SD)	Coefficient of variation (CV, %)	P
CL	Females	32	37.34	63.19	53.50 ± 0.90	5.12	9.57	0.008**
	Males	64	26.03	65.02	49.70 ± 1.07	8.58	17.26	
CW	Females	32	56.69	94.40	81.24 ± 1.40	7.92	9.75	0.007**
	Males	64	47.35	97.07	75.43 ± 1.57	12.59	16.69	
ICW	Females	32	54.57	89.52	77.03 ± 1.28	7.24	9.40	0.010*
	Males	64	45.61	93.35	71.86 ± 1.50	12.00	16.70	
CFW	Females	32	22.16	34.28	29.88 ± 0.43	2.42	8.10	0.023*
	Males	64	19.82	35.88	28.36 ± 0.50	3.99	14.07	
AW	Females	32	19.06	34.46	27.69 ± 0.57	3.23	11.66	0.000**
	Males	64	15.74	32.25	24.05 ± 0.48	3.86	16.05	
BH	Females	32	21.48	37.55	31.31 ± 0.56	3.19	10.19	0.015*
	Males	64	18.20	39.44	29.23 ± 0.62	5.00	17.11	
CWS8	Females	32	55.20	92.53	79.52 ± 1.33	7.54	9.48	0.008**
	Males	64	46.86	94.94	74.01 ± 1.55	12.43	16.80	
DLS1	Females	32	28.33	44.11	39.46 ± 0.55	3.09	7.83	0.015*
	Males	64	27.25	46.60	37.34 ± 0.66	5.30	14.19	
DLS2	Females	32	25.12	55.04	46.86 ± 0.95	5.33	11.37	0.189
	Males	64	30.68	56.33	45.19 ± 0.83	6.61	14.63	
FFLC	Females	32	34.87	55.70	48.45 ± 0.90	5.10	10.53	0.720
	Males	64	27.28	69.75	47.88 ± 1.30	10.36	21.64	
FFWC	Females	32	8.82	17.38	13.19 ± 0.35	1.97	14.94	0.775
	Males	64	7.05	21.25	13.34 ± 0.42	3.39	25.41	
FFHC	Females	32	12.14	22.44	18.70 ± 0.38	2.16	11.55	0.440
	Males	64	9.97	32.39	19.28 ± 0.65	5.20	26.97	
MLP1	Females	32	19.28	30.50	26.63 ± 0.49	2.79	10.48	0.722
	Males	64	15.92	35.68	26.35 ± 0.62	4.99	18.94	
MLP2	Females	32	21.29	32.14	28.29 ± 0.51	2.90	10.25	0.856
	Males	64	17.71	38.52	28.14 ± 0.65	5.16	18.34	
MLP3	Females	32	17.21	27.46	24.07 ± 0.45	2.55	10.59	0.631
	Males	64	12.29	31.51	23.74 ± 0.53	4.27	17.99	
BW (g)	Females	28	30.77	144.46	91.86 ± 4.38	23.16	25.21	0.044*
	Males	56	17.82	176.82	77.78 ± 5.30	39.64	50.96	

CL = carapace length; CW = carapace width; ICW = internal carapace width; CFW = carapace frontal width; AW = abdomen width; BH = body height; CWS8 = carapace width at spine 8; DLS1 = distance between lateral spine 1; DLS2 = distance between lateral spine 2; FFLC = fixed finger length of the claw; FFWC = fixed finger width of the claw; FFHC = fixed finger height of the claw; MLP1 = meropodite length of pereopod 1; MLP2 = meropodite length of pereopod 2; MLP3 = meropodite length of pereopod 3; BW = body weight. *$P < 0.05$; **$P < 0.01$.

Growth trait measurement

Sixteen growth traits were measured according to the methods of Keenan et al. (1998)

and Gao et al. (2008). These traits included carapace length (CL), carapace width (CW), internal carapace width (ICW), carapace frontal width (CFW), abdomen width (AW), body height (BH), carapace width at spine 8 (CWS8), distance between lateral spine 1 (DLS1), distance between lateral spine 2 (DLS2), fixed finger length of the claw (FFLC), fixed finger width of the claw (FFWC), fixed finger height of the claw (FFHC), meropodite length of pereopod 1 (MLP1), meropodite length of pereopod 2 (MLP2), meropodite length of pereopod 3 (MLP3), and body weight (BW). The former 15 morphological traits were measured to the nearest 0.01 mm with Vernier calipers. BW was measured to an accuracy of 0.01 g with a digital electronic balance.

Statistical analysis

The mean value and standard deviation of each trait was calculated using the SPSS version 11.5 software. The coefficient of variation (CV) of each trait was estimated using the following formula: CV = (standard deviation / mean) x 100%. The path analysis was conducted using the SPSS 11.5 software also as described by Du and Chen (2010). The correlation analysis and multiple regression analysis were also performed using SPSS 11.5. The multiple regression equation was constructed as follows: if the correlation variables Y, X_1, X_2, and X_3 exist in a linear equation, the regression equation is described as $Y = b_0 + b_1X_1 + b_2X_2 + b_3X_3$, where Y is the dependent variable, X_1, X_2, and X_3 are the independent variables, b_0 is the constant, and b_1, b_2, and b_3 are the partial regression coefficients for Y on X_1, X_2, and X_3.

The determination coefficient was calculated using the alternative formulas: 1) $d_i = P_i^2$; and 2) $d_{ij} = 2r_{ij} \times P_i \times P_j$, where d_i is the effect of a single trait i on BW, d_{ij} is the effect of traits i and j on BW, P_i is the path coefficient of the single trait i to BW, r_{ij} is the correlation coefficient between traits i and j, and P_j is the path coefficient of the single trait j to BW.

RESULTS

Sex ratio in G_1 population

Of the 96 individuals collected in this study, 32 were identified as females and 64 as males (Table 1). The sex ratio (female:male) was estimated to be 1:2. A significant difference was found in the ratio between females and males compared with the ideal ratio 1:1 ($P < 0.05$).

Differences in growth traits between sexes

The mean values, standard deviations, coefficients of variation of growth traits between sexes are listed in Table 1. Nine traits (CL, CW, ICW, CFW, AW, BH, CWS8, DLS1, and BW) exhibited significant differences between sexes, while the others (DLS2, FFLC, FFWC, FFHC, MLP1, MLP2, and MLP3) showed no significant differences. Of 16 traits, 14 were higher (mean value) in females than in males (exceptions, FFWC and FFHC). The CVs of BW were the largest among 16 cases in both females and males (25.21 and 50.96, respectively), whereas DLS1 was the lowest (7.83%) in females and CFW was the lowest (14.07%) in males. The standard deviations of BW were the largest among 16 cases in both females and males (23.16 and 39.64, respectively), whereas FFWC was the lowest in both females and males (1.97 and 3.39. respectively).

Correlation relationships between growth traits

The relationships between the 16 growth traits were estimated by correlation analysis and the results are shown in Tables 2 and 3. In females, a significant positive correlation was detected in all 120 trait pairs ($P < 0.01$). The correlation coefficients ranged from 0.524 (DLS2 and FFWC) to 0.997 (ICW and CWS8). A significant positive correlation ($P < 0.01$) was observed between BW and each of the other 15 morphological traits, with the correlation coefficients ranging from 0.654 (BW and FFWC) to 0.970 (BW and CL). In males, a significantly positive correlation was also detected in all 120 trait pairs ($P < 0.01$), where the correlation coefficients ranged from 0.881 (CFW and FFHC) to 0.999 (CW and ICW, CW and CWS8, ICW and CWS8). A significant positive correlation ($P < 0.01$) was found between BW and each of the other 15 morphological traits, with the correlation coefficients ranging from 0.923 (BW and MLP3) to 0.973 (BW and ICW).

Table 2. Correlation coefficients among 16 growth traits in females of *Scylla paramamosain*.

Trait	CL	CW	ICW	CFW	AW	BH	CWS8	DLS1	DLS2	FFLC	FFWC	FFHC	MLP1	MLP2	MLP3	BW
CL	1	0.990**	0.986**	0.935**	0.969**	0.954**	0.990**	0.968**	0.830**	0.797**	0.690**	0.674**	0.903**	0.874**	0.877**	0.970**
CW		1	0.994**	0.941**	0.969**	0.955**	0.996**	0.965**	0.831**	0.802**	0.685**	0.673**	0.902**	0.873**	0.869**	0.967**
ICW			1	0.944**	0.961**	0.955**	0.997**	0.971**	0.826**	0.808**	0.682**	0.683**	0.914**	0.878**	0.876**	0.968**
CFW				1	0.907**	0.910**	0.952**	0.932**	0.809**	0.738**	0.592**	0.618**	0.868**	0.807**	0.798**	0.914**
AW					1	0.918**	0.962**	0.919**	0.776**	0.763**	0.651**	0.643**	0.853**	0.838**	0.831**	0.961**
BH						1	0.955**	0.932**	0.833**	0.736**	0.620**	0.600**	0.851**	0.846**	0.826**	0.931**
CWS8							1	0.974**	0.837**	0.805**	0.676**	0.680**	0.912**	0.872**	0.877**	0.967**
DLS1								1	0.862**	0.807**	0.647**	0.692**	0.904**	0.873**	0.871**	0.936**
DLS2									1	0.670**	0.524**	0.532**	0.753**	0.695**	0.719**	0.747**
FFLC										1	0.891**	0.943**	0.879**	0.854**	0.821**	0.790**
FFWC											1	0.875**	0.751**	0.724**	0.701**	0.654**
FFHC												1	0.818**	0.771**	0.722**	0.710**
MLP1													1	0.929**	0.910**	0.893**
MLP2														1	0.933**	0.890**
MLP3															1	0.865**
BW																1

CL = carapace length; CW = carapace width; ICW = internal carapace width; CFW = carapace frontal width; AW = abdomen width; BH = body height; CWS8 = carapace width at spine 8; DLS1 = distance between lateral spine 1; DLS2 = distance between lateral spine 2; FFLC = fixed finger length of the claw; FFWC = fixed finger width of the claw; FFHC = fixed finger height of the claw; MLP1 = meropodite length of pereopod 1; MLP2 = meropodite length of pereopod 2; MLP3 = meropodite length of pereopod 3; BW = body weight. **Highly significant at the 0.01 level (two-tailed).

Path coefficients and determination coefficients

In females, two morphological traits (CL and DLS2) showed significant direct effects on BW ($P < 0.05$) (Table 4). Trait CL showed the largest direct effect ($P_i = 1.124$) on BW, whereas DLS2 showed a negative indirect effect ($P_i = -0.186$) on BW. The indirect effects of traits CL and DLS2 on BW were -0.154 and 0.993, respectively. The multiple correlation coefficient (R^2) was 0.951 (higher than 0.85), indicating that traits CL and DLS2 were the key growth traits affecting BW. The determination coefficient of CL was the largest (1.263), and the determination coefficient of DLS2 was the lowest (0.035), whereas the co-determination coefficient of CL and DLS2 was negative (-0.347) (Table 5). The total determination coefficient (*d* = 0.951) of morphological traits to BW was equal to the multiple correlation coefficient (R^2 = 0.951) of morphological traits to BW.

Table 3. Correlation coefficients among 16 growth traits in males of *Scylla paramamosain*.

Trait	CL	CW	ICW	CFW	AW	BH	CWS8	DLS1	DLS2	FFLC	FFWC	FFHC	MLP1	MLP2	MLP3	BW
CL	1	0.986**	0.986**	0.975**	0.974**	0.977**	0.985**	0.948**	0.984**	0.930**	0.890**	0.885**	0.964**	0.962**	0.924**	0.958**
CW		1	0.999**	0.986**	0.981**	0.985**	0.999**	0.961**	0.994**	0.946**	0.903**	0.905**	0.978**	0.976**	0.938**	0.971**
ICW			1	0.986**	0.983**	0.986**	0.999**	0.960**	0.994**	0.946**	0.903**	0.906**	0.979**	0.978**	0.938**	0.973**
CFW				1	0.972**	0.976**	0.987**	0.949**	0.983**	0.928**	0.884**	0.881**	0.968**	0.964**	0.923**	0.956**
AW					1	0.985**	0.981**	0.937**	0.974**	0.929**	0.889**	0.889**	0.966**	0.960**	0.925**	0.967**
BH						1	0.985**	0.943**	0.980**	0.938**	0.905**	0.895**	0.971**	0.961**	0.925**	0.974**
CWS8							1	0.960**	0.994**	0.947**	0.903**	0.906**	0.977**	0.976**	0.938**	0.971**
DLS1								1	0.959**	0.946**	0.906**	0.904**	0.935**	0.960**	0.901**	0.941**
DLS2									1	0.934**	0.892**	0.888**	0.970**	0.969**	0.930**	0.966**
FFLC										1	0.971**	0.983**	0.943**	0.948**	0.932**	0.964**
FFWC											1	0.967**	0.901**	0.906**	0.892**	0.934**
FFHC												1	0.904**	0.914**	0.891**	0.945**
MLP1													1	0.981**	0.940**	0.965**
MLP2														1	0.944**	0.970**
MLP3															1	0.923**
BW																1

CL = carapace length; CW = carapace width; ICW = internal carapace width; CFW = carapace frontal width; AW = abdomen width; BH = body height; CWS8 = carapace width at spine 8; DLS1 = distance between lateral spine 1; DLS2 = distance between lateral spine 2; FFLC = fixed finger length of the claw; FFWC = fixed finger width of the claw; FFHC = fixed finger height of the claw; MLP1 = meropodite length of pereopod 1; MLP2 = meropodite length of pereopod 2; MLP3 = meropodite length of pereopod 3; BW = body weight. **Highly significant at the 0.01 level (two-tailed).

Table 4. Direct and indirect effects of morphological traits on body weight in females of *Scylla paramamosain*.

Trait	Correlation coefficient (r_{ij})	Direct effect (P_i)	Total of indirect effect (Σ)	Indirect effect (r_{ij} x P_j)	
				CL	DLS2
CL	0.970	1.124	-0.154		-0.154
DLS2	0.747	-0.186	0.933	0.933	

CL = carapace length; DLS2 = distance between lateral spine 2.

Table 5. Determination coefficients of morphological traits to body weight in females of *Scylla paramamosain*.

Trait	CL	DLS2
CL	1.263	-0.347
DLS2	-	0.035

CL = carapace length; DLS2 = distance between lateral spine 2.

In males, three morphological traits (BH, FFHC, and MLP2) showed significant direct effects on BW (P < 0.05) (Table 6). Trait BH showed the largest direct effect (P_i = 0.484) on BW, FFHC showed a relatively lower direct effect (P_i = 0.300), and MLP2 showed the lowest effect (P_i = 0.225). The indirect effects of traits BH, FFHC, and DLS2 on BW were 0.485, 0.639, and 0.739, respectively. The multiple correlation coefficient (R^2) was 0.973 (higher than 0.85), indicating that traits BH, FFHC and MLP2 played an important role in affecting body weight. The co-determination coefficient of BH and FFHC was the highest (0.260), whereas the co-determination coefficient of MLP2 was the lowest (0.051) (Table 7). The total determination coefficient (*d* = 0.967) of morphological traits to BW was approximately equal to the multiple correlation coefficient (R^2 = 0.973) of morphological traits to BW.

Table 6. Direct and indirect effects of morphological traits on body weight in males of *Scylla paramamosain*.

Trait	Correlation coefficient (r_{ij})	Direct effect (P_i)	Total of indirect effect (Σ)	Indirect effect (r_{ij} x P_j)		
				BH	FFHC	MLP2
BH	0.974	0.484	0.485	-	0.269	0.216
FFHC	0.945	0.300	0.639	0.433	-	0.206
MLP2	0.970	0.225	0.739	0.465	0.274	-

BH = body height; FFHC = fixed finger height of the claw; MLP2 = meropodite length of pereopod 2.

Table 7. Determination coefficients of morphological traits to body weight in males of *Scylla paramamosain*.

Trait	BH	FFHC	MLP2
BH	0.234	0.260	0.209
FFHC	-	0.090	0.123
MLP2	-	-	0.051

BH = body height; FFHC = fixed finger height of the claw; MLP2 = meropodite length of pereopod 2.

Construction of multiple regression equation

The regression relationship between BW and other morphological traits was estimated by the following steps: first by testing the significance of partial regression coefficients of different traits and then by stepwise removal of non-significant morphological traits. The results indicated that in females, trait BW showed a significant regression relationship to two traits (CL and DLS2) (P < 0.01; Table 8). A best-fit linear multiple regression equation was constructed as follows: $Y = 4.969X_1 - 0.758X_2 - 140.177$ (Y = BW, X_1 = CL, X_2 = DLS2). While in males, trait BW showed a significant regression relationship to three traits (BH, FFHC and MLP2) (P < 0.01; Table 8). A best-fit linear multiple regression equation was constructed as follows: $Y = 3.806X_1 + 2.371X_2 + 1.725X_3 - 123.559$ (Y = BW, X_1 = BH, X_2 = FFHC, X_3 = MLP2). The constants and partial coefficients of regression equations were tested by the *t*-test, which suggested a significant effect on BW (P < 0.05; Table 9) in both females and males.

Table 8. Analysis of variance (ANOVA) of multiple regression equation in *Scylla paramamosain*.

Gender	Index	Sum of squares	d.f.	Mean square	F	P
Female	Regression analysis	13765.596	2	6882.798	241.803	0.000
	Residual	711.613	25	28.465		
	Total	14477.210	27			
	Multiple correlation	R = 0.975	R^2 = 0.951	Adjusted R^2 = 0.947	SE = 5.335	
Male	Regression analysis	84112.970	3	28037.657	634.735	0.000
	Residual	2296.956	52	44.172		
	Total	86409.926	55			
	Multiple correlation	R = 0.987	R^2 = 0.973	Adjusted R^2 = 0.972	SE = 6.646	

d.f. = degrees of freedom; SE = standard error.

Table 9. The *t*-test for constant and partial regression coefficients in multiple regression equation in *Scylla paramamosain*.

Gender	Index	Partial coefficient	Standard error	*t*-value	P
Female	Constant	-140.177	10.620	-13.199	0.000
	CL	4.969	0.351	14.146	0.000
	DLS2	-0.758	0.324	-2.337	0.028
Male	Constant	-123.559	6.057	-20.400	0.000
	BH	3.806	0.729	5.223	0.000
	FFHC	2.371	0.453	5.233	0.000
	MLP2	1.725	0.758	2.276	0.027

CL = carapace length; DLS2 = distance between lateral spine 2; BH = body height; FFHC = fixed finger height of the claw; MLP2 = meropodite length of pereopod 2.

DISCUSSION

This study investigated the sex ratio and differences of 16 growth traits between females and males of a G_1 population in the mud crab (*S. paramamosain*). In theory, the sex ratio is expected to be 1:1. However, among 96 individuals randomly collected from a G_1 family, 32 females and 64 males were identified, with the sex ratio (1:2) significantly deviating from 1:1 ($P < 0.05$). This was the first report about the sex ratio of a cultured population of *S. paramamosain*. The mechanism underlying this sex ratio deviation from 1:1 was not clearly determined so far, but it should not be related to sampling strategy and the limited numbers of individuals used in this study.

Females were significantly bigger than males in regard to nine growth traits (CL, CW, ICW, CFW, AW, BH, CWS8, DLS1, and BW; $P < 0.05$). Of 16 growth traits, the mean values of 14 cases were greater in females than in males. This result indicated that females grew significantly faster and bigger than males in *S. paramamosain*. The similar phenomena were found in half-smooth tongue sole (*Cynoglossus semilaevis*) (Chen et al., 2012) and spotted halibut (*Verasper variegatus*) (Dou, 1995). In contrast, males grew faster and bigger than females in tilapia (*Oreochromis niloticus*) (Mair et al., 1997).

All 16 growth traits showed abundant variation in the G_1 population of *S. paramamosain*. Trait BW had the largest variation (25.21 and 50.96% in females and males, respectively), as observed in our previous study in wild individuals of *S. paramamosain* (CV = 56.09%; Ma et al., 2013). Traits DLS1 and CFW exhibited the lowest variation in females (CV = 7.83%) and males (CV = 14.07%), while trait DLS1 had the lowest variation in the wild population. This high variation in growth traits can provide sufficient materials for economic performance selection. Furthermore, a high level of genetic diversity has been estimated by molecular markers, such as mitochondrial DNA, single nucleotide polymorphisms, and microsatellites (Ma et al., 2011a,b, 2012).

Morphological traits are ordinarily employed as a reference for selection in artificial breeding programs (Neira et al., 2006; Takeshita and Soyano, 2009). For *Pinctada martensii*, the traits shell length, shell width, shell height, and total weight were found to be significantly correlated with each other ($P < 0.05$) (Deng et al., 2008). For *Portunus trituberculatus*, five growth-related traits of carapace length, carapace width, internal carapace width, body height, and body weight were confirmed to be significantly correlated with one another ($P < 0.01$) (Liu et al., 2009). In this study, all 16 growth traits were found to be significantly correlated with one another ($P < 0.01$). This result means that it is feasible to select one targeting trait through one other or more traits in a breeding process. The high correlation between traits may result from pleiotropy in the determination of these traits (Falconer, 1981).

Path analysis is an effective method for multiple statistics that can separate the total effects of independent variables into direct and indirect effects on dependent variables (Rodrigueza et al., 2001). In this study, of 15 morphological traits, two (CL and DLS2) and three (BH, FFHC and MLP2) showed significant direct effects on BW ($P < 0.05$) in females and males, respectively. The multiple correlation coefficients between morphological traits and body weight was high (more than 0.85) in both females and males, and approximately equal to the determination coefficients; hence, the two traits (CL and DLS2) and the three traits (BH, FFHC and MLP2) could be considered as the key factors affecting BW in female and male individuals of *S. paramamosain*. In the previous study, two traits (CL and FFHC) were found to have significant direct effects on BW ($P < 0.05$) in both females and males (Ma et al., 2013). By using path analysis, the main factors affecting body weight have been found in other aquaculture animals, such as *Eriocheir sinensis* (Geng et al., 2007), *Pinctada martensii* (Deng et al., 2008), and *Portunus trituberculatus* (Liu et al., 2009). In contrast, the multiple correlation coefficient for edible tissue weight of 2- and 3-year-old *Ruditapes philippinarum* was found to be lower than 0.85, indicating that some other factors affecting edible tissue weight may be omitted (Huo et al., 2010).

CONCLUSION

In this study, we investigated the sex ratio and differences of growth traits between females and males, correlation between 16 growth traits, and direct and indirect effects of morphological traits on body weight in a G_1 population of the mud crab (*S. paramamosain*). We then constructed a multiple regression equation concerning body weight and morphological traits in females and males separately. The findings in this study will be helpful in better understanding the differences between sexes, relationships between growth traits and artificial selective breeding in this crab species and other closely related species.

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