

# Genetic parameters of growth and survival in the Pacific oyster *Crassostrea gigas*

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## Funding information

Shandong Province, Grant/Award Number: 2017LZGC009; National Natural Science Foundation of China, Grant/Award Number: 31972789; Weihai City, Grant/Award Number: 2018NS01; Ocean University of China-Auburn University Joint Research Center for Aquaculture and Environmental Science

## Abstract

The Pacific oyster *Crassostrea gigas* is a representative bivalve mollusc that is widely cultured in the world and is the largest molluscan group cultured in China. In order to assess the feasibility of improving survival of *C. gigas* through genetic selection, the heritability and genetic correlations for growth and survival traits between different life stages were examined. Genetic parameters were estimated based on intraclass correlations of 49 full-sib families (29 half-sib families) in larvae (4 and 20 days after fertilization) and spat (140 days after fertilization) stages. The heritability for growth traits in larvae and spat was 0.30–0.86 and 0.53–0.59, respectively, and varied with ages. The heritability of survival was low in larvae ( $0.13 \pm 0.05$  and  $0.17 \pm 0.04$ , respectively for 4 and 20 days after fertilization) but medium ( $0.39 \pm 0.07$ ) in spat, suggesting that selection for increasing spat survival was feasible. The genetic correlation between growth traits within age was medium to high and positive (ranging from 0.47 to 0.96, respectively, between shell length (SL) and shell height (SH) at 20 days and between SL and SH at 140 days after fertilization), suggesting that selection to improve single growth trait will cause positive response in another growth traits in *C. gigas*. The genetic correlations between survival and growth traits at 140 days were low but positive (ranging from 0.23 to 0.27, respectively, between survival and SH and between survival and SL at 140 days after fertilization), suggesting that selection for survival may not have a negative response in growth. Overall, this study suggests that survival traits should be taken as improving target of next selection breeding programme in *C. gigas*.

## KEYWORDS

*Crassostrea gigas*, genetic correlation, growth, heritability, Pacific oyster, survival

## 1 | INTRODUCTION

The Pacific oyster (*Crassostrea gigas*) is one of the most important cultured species worldwide, naturally distributed in the northwest Pacific Ocean. It has been transport to so many countries due to its fast growth and strong adaptability to environment (Miossec et al., 2009). As with many farmed species, growth and survival are the most important economic traits of *C. gigas*, because they can directly affect yield and the profitability of production (Dégremont et al., 2005). Genetic improvement of important economic traits is

the most effective way to increase production because it can accumulate the best genes among individuals, which would be inherited in following generations (Gjedrem & Baranski, 2009).

The potential for genetic improvement through selective breeding is well documented for shellfish species due to the high fecundity, short generation interval and high genetic variability in wild population (Newkirk, 1983). Several studies have demonstrated that it is possible to improve the growth traits in Pacific oysters through selective breeding (De Melo et al., 2016; Dégremont et al., 2010; Gomes et al., 2018; Langdon et al., 2003). In Sydney rock oyster

(*Saccostrea commercialis*), a genetic gain for growth rate of 18% after two generations selection was observed (Nell et al., 1996). In *Ostrea chilensis*, an increase in size from 8% to 38% in selected lines was showed compared with control lines (Newkirk & Haley, 1982). In *Ostrea edulis*, selection in growth rate showed an increase of 9% to 12% after the first generation selection (Toro et al., 1996).

Large-scale oyster mortality events have been reported for many years in different parts of the world and the economic implications of these mortalities are often serious. The causes of this phenomenon are complex. Some of these cases are unknown origin, but numerous cases have been ascribed to epizootics caused by infections agents (Sindermann, 1976). Because the environment cannot be controlled, genetic improvement for survival or disease resistant is an attractive option to reduce their impact on the culture industry (Dégremont, Garcia, et al., 2015). Several countries have implemented some selective breeding programs focused on the improvement of survival or disease resistance of oysters (Ford & Haskin, 1987; Ragone-Calvo et al., 2003; Dégremont et al., 2007; Dégremont, Nourry, et al., 2015; Frank-Lawale et al., 2014).

Heritability estimates the proportion of phenotypic variation caused by gene additive effect and plays an important role in the prediction of selection response, comparison of selection methods and selective programme planning (Falconer & Mackay, 1996). Heritability estimates for traits such as weight, growth and survival in oyster have been widely reported. In USA, Langdon et al. (2003) observed heritability values for yield ranging from 0.22 to 0.77 for *C. gigas* cultured in different locations. Evans and Langdon (2006) reported a positive heritability of 0.37 for body weight at harvest in *C. gigas*. In France, Dégremont et al. (2007) found high narrow-sense estimates for survival, ranging from 0.47 to 1.08 for 6- to 8-month-old Pacific oysters planted at three sites. In China, Li et al. (2011) reported realized heritability was 0.15–0.40 for growth in three stocks of *C. gigas*. For different populations of the same species, these estimations are strongly affected by rearing conditions and the estimation method being applied (Gjedrem & Baranski, 2009; Langdon et al., 2003). Total phenotypic variation is the result of both genetic and environmental variation as well as interactions between them. Different genotypes may have a different performance response to environment changes (Falconer & Mackay, 1996), a phenomenon known as genotype-by-environment ( $G \times E$ ) interaction. For designing an efficient and practical selective breeding program, it is needed to obtain accurate estimations of heritability in local environment.

China is the top oyster-producing country worldwide with total oyster production reaching  $5.14 \times 10^6$  tons in 2018 (BOF [Bureau of Fisheries], 2019). The Pacific oyster is a major species for shellfish aquaculture in northern China, supporting the development of shellfish industry. To improve the increasing valuable Pacific oyster industry in China, selective breeding programs have been initiated to improve growth trait (Li et al., 2011). By using mass selection over six generations, two fast-growing lines have been established (Zhang, 2018) and are widely cultured in China. In recent years, Pacific oysters have suffered from numerous disease outbreaks in China, where episodes of mortality generally occurred in summer.

Mortality events were usually observed in the spat stage and often cause high mortality. Because the environment cannot be controlled, genetic improvement for survival performance has become an urgent demand for oyster production in China.

In this study, we produced 49 full-sib and half-sib families by using parents from the two fast-growing lines of *C. gigas* and estimated heritability for growth and survival traits and their correlations at different ages. These data can be used to design and optimize a selective breeding scheme for not only fast growth but high survival line of this species.

## 2 | MATERIALS AND METHOD

### 2.1 | Establishment of full-sib families

In May 2019, 300 two-year-old Pacific oysters were collected from two selected lines (HD1 and HD2) on which mass selection for faster growth was performed over ten and eight generations, respectively, and maintained in Laizhou breeding base, Shandong Province, China. The genetic diversity of this two selected lines had been assessed by microsatellites and single nucleotide polymorphism markers in previous studies (Wang et al., 2016; Zhong et al., 2016). For mating experiments, artificial fertilization was conducted following the standard procedure described by Li et al. (2011). On May 20, the sex of ripe broodstock animals was determined and 29 males and 87 females were chosen at random to produce 87 families following a nested mating design (each male was mated with three different females). For each parent, gametes were rinsed into separate buckets by stripping the gonad. Sperm from each sire were divided into three equal portions and fertilized with eggs according to the crossing design at a sperm: egg ratio of 50, respectively. In total, 87 full-sib and 29 half-sib families were successfully created.

### 2.2 | Larvae culture

The culture of larvae was done following the methods described by Wang et al. (2012), and the rearing conditions were maintained the same for each family. Briefly, each family was hatched in separate containers until 24 hr post fertilization. The D-larvae from each family were collected and separately transferred into 100-L plastic bucket. Seawater was filtered through sand filters and non-wovens polypropylene fabric. Water temperature of each family was maintained at 23–25°C, with salinity at 30 psu. Fresh air was continuously pumped into each bucket and filtered seawater was changed three times a week. Stocking densities were initially set to approximately  $10 \text{ larvae ml}^{-1}$ . Larvae were fed enough algae diet of *Isochrysis galbana* and *Nitzschia closterium* according to the larvae density. Slow-growing larvae were not culled during the culture period.

Before water renewal, the content of each tank was homogenized using aeration and three independent 30-ml samples were taken and fixed with a drop of Lugol's solution in a Petri dish. The

larvae were counted three times per family under a microscope with a  $4 \times 10$  magnification. The larvae survival was estimated on days 4 and 20 post fertilization as the proportion of live larvae in each bucket with respect to the initial number of D-larvae, respectively. Shell height (SH) and shell length (SL) were measured using a microscope equipped with an ocular micrometer in 30 larvae haphazardly chosen from each family at 4 and 20 days post fertilization.

### 2.3 | Spat culture

When 30% or more of the progeny reached eyed stage, strings of scallop shells were used to collect the spat metamorphosed from eyed larvae. This occurred about 4–7 days for all eyed larvae metamorphosed to spat. When the SH of spat reached 500–600  $\mu\text{m}$ , the collectors with attached spat from each FS family were marked with family number and transported to an outdoor nursery pond to adapt to the ocean environment. After 30 days temporary rearing, oysters from each family were split and transported to Rongcheng, Shandong province, China, (37.1°N, 122.5°E). Due to the differential mortality at the larvae and nursery oyster spat, 49 full-sib families were deployed in the field on August 8th (79 days after fertilization). Oysters were raised according to local practices, and they were placed on nylon ropes and cultured on suspended long lines. Each family was placed in 9-layer lantern nets with 100 individuals per layer. Because mortality and growth were usually very low in late autumn, survival and growth were recorded in October 2019 when the oysters were 140 days after fertilization. Survival rate was determined by counting live and dead oysters for each lantern nets. Thirty oysters per family were randomly sampled and the SH and SL were measured using an electronic Vernier caliper (0.01 mm accuracy).

### 2.4 | Genetic and statistical analysis

Preliminary statistical analyses of data for growth traits and survival were performed using SPSS22.0 software. Genetic analyses were performed using the animal model implemented by ASREML 3.0 in the R Programming Language (Gilmour et al., 2009). The variance components of SH and SL were calculated using restricted maximum-likelihood algorithm of a univariate animal model as follows:

$$Y_{jkl} = \mu + \alpha_{jkl} + f_k + e_{jkl}. \quad (1)$$

Observation  $Y$  from sire  $j$ , dam  $k$  and individual  $l$ , was predicted from variables on the right-hand side of the equation. The  $k$  is nested within  $j$ , and that  $l$  is nested within dam and sire. The  $\mu$  is the mean value of the trait,  $\alpha_{jkl}$  is the additive genetic effects for the  $jkl$ th animal and were assumed  $\sim N(0, A\sigma_a^2)$ , where  $A$  and  $\sigma_a^2$  are the additive genetic relationship matrix and additive genetic variance.  $f_k$  was the random effects common to each full-sib family (including maternal effect and common environment effect due to separate rearing of

the families in larvae).  $e_{jkl}$  was the residual error. The  $f_k$  was omitted in later analyses because its variance is very small and not significant ( $z$  ratio  $< 1.5$ , the constraint is boundary). Thus, the model was simplified as:

$$Y_{jkl} = \mu + \alpha_{jkl} + e_{jkl}. \quad (2)$$

The heritability of SH and SL is calculated with the following formula by using univariate animal model:

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

Heritability was calculated as the ratio of additive genetic variance to the total phenotype variance, where  $\sigma_a^2$  is additive genetic variance, and  $\sigma_e^2$  is the residual variance.

A sire-dam threshold model was used for genetic parameters of survival. The dead individuals were recorded '0', and survival individuals were recorded '1'. The model is as follows:

$$\Pr(y_{ijk} = 1) = \Pr(l_{ijk} > 0) = \Phi(\mu + S_i + d_j + e_{ijk}). \quad (3)$$

The  $y_{ijk}$  is survival of  $k$ th individuals at the end of testing period;  $l_{ijk}$  is a latent variable, if  $l_{ijk} > 0$ ,  $y_{ijk} = 1$ ; if  $l_{ijk} \leq 0$ ,  $y_{ijk} = 0$ ,  $\mu$  is total mean,  $S_i$  is additive genetic effect of the  $i$ th sire and  $d_j$  is additive genetic effect of the  $j$ th dam, Sire or Dam  $\sim N(0, A\sigma_{sd}^2)$ , where  $A$  is the additive genetic relationship matrix and  $\sigma_{sd}^2$  is the sire-dam additive genetic variance,  $e_{ijk}$  is the random residual error of the  $k$ th individual. The  $i$  is nested within  $j$ , and that  $k$  is nested within dam and sire.

The heritability of survival is calculated as follows:

$$h^2 = \frac{4\sigma_{sd}^2}{2\sigma_{sd}^2 + \sigma_e^2},$$

where  $\sigma_{sd}^2$  is the sire-dam additive genetic variance (mean of variance of sire and dam), and  $\sigma_e^2$  is the residual variance, with logistic distribution value = 3.289 (the residual error for a logit link).

The genetic correlation and phenotypic correlation between SH and SL were estimated by using a bivariate animal model.

The formula was as follows:

$$r = \frac{\sigma_{a(x,y)}}{\sqrt{\sigma_{a(x)}^2 \sigma_{a(y)}^2}},$$

where  $(x, y)$  is the estimated additive genetic covariance components of SH and SL,  $x$  and  $y$  are additive genetic variance components of SH and SL, respectively. Genetic correlations between growth traits and survival were expressed as Pearson correlation between breeding values predicted in three separate univariate model for these traits. The genetic and phenotypic correlations between growth traits and survival were calculated by Pearson correlation with SPSS 22.0. The  $t$  test was then used to test the significance level of heritability, genetic and phenotypic correlations.  $t = \frac{h^2}{\sigma_{h^2}}$  and  $t = \frac{R_A(x,y)}{\sigma_{R_A(x,y)}}$  were used to calculate  $t$  value (Liu et al., 2005).

### 3 | RESULTS

#### 3.1 | Descriptive statistics of growth and survival

The sample number, mean, maximum, minimum, standard deviation and coefficient variation for growth and survival traits of *C. gigas* are shown in Table 1. On day 4 after fertilization, the means of SH and SL and survival rate were 89.37  $\mu\text{m}$ , 90.84  $\mu\text{m}$  and 89.86%, respectively, with coefficient variation ranging from 6.68% to 8.21%. On day 20, the SH and SL and survival rate were 203.22  $\mu\text{m}$ , 167.35  $\mu\text{m}$  and 23.51%. On day 140, the SH and SL and survival rate were 25.23 mm, 19.16 mm and 62.27%, with coefficient variation ranging from 23.03% to 27.30%. The coefficient variation of survival is the greatest (27.30%), indicating that there was great variance in survival among families.

Shell height and survival rate among families in larvae are shown in Figure 1. On day 20, the full-sib families 29, 55, 49, 64, 62 and 53 showed high survival (37%–58%) compared to the other full-sib families. The full-sib families 75, 19, 78, 37, 84 and 52 showed low survival (3%–13%) compared to the other full-sib families (Figure 1a). The family mean SH among families ranged from 180.03 to 234.65  $\mu\text{m}$ , with a population average of 203.22  $\mu\text{m}$  (Figure 1b). Shell height and survival rate among families in spat are shown in Figure 2. On day 140, the full-sib families 58, 54, 87, 20, 52 and 2 had high survival (84%–90%) compared to the other half-sib families. Conversely, the full-sib families 83, 53, 9, 17, 37 and 75 showed low survival (25%–40%) compared to the other full-sib families (Figure 2a). The family mean SH among families ranged from 19.25 to 33.62 mm, with a population average of 25.23 mm (Figure 2b).

#### 3.2 | Genetic parameters

The variance components and heritability for growth traits and survival of *C. gigas* are presented in Table 2. The heritability estimate for SH and SL at different life stages was 0.30–0.77, and 0.39–0.86, respectively. The heritability of survival in larvae stage was low (0.13–0.17), but was medium in spat stage (0.39,  $p < .01$ ).

The genetic and phenotypic correlations between growth traits and survival of *C. gigas* were shown in Table 3. The genetic correlations (0.466–0.964,  $p < .01$ ) were higher than the phenotypic correlations (0.162–0.728,  $p < .01$ ) and were high and positive between SH and SL at different life stages. The genetic correlations between different life stages of SH (0.237–0.294,  $p < .01$ ), SL (0.151) and survival (–0.145 to 0.289) were all low except that there were medium but significant positive correlations of SL between 20 and 140 days (0.456,  $p < .01$ ) and SH between 4 and 20 days (0.437,  $p < .01$ ). Similarly, low phenotypic correlations were observed in SH (0.064–0.118), SL (0.050–0.130) and survival (–0.046 to 0.195) between different life stages.

The genetic correlations between growth traits and survival were low and non-significant negative in larvae (–0.043 to –0.210). On the contrary, low but non-significant positive correlation was obtained between growth traits and survival (0.231–0.273) in spat. In terms of the phenotypic correlations, there were low (–0.151 to 0.083) values between growth traits and survival in larvae, as well as low but significant positive values between growths traits and survival in spat (0.316–0.351,  $p < .05$ ).

### 4 | DISCUSSION

In oyster, survival is an important trait that affects profitability. High genetic variance in offspring survival is very pervasive in marine organisms (Hedgecock, 1994). Differential survival observed in this study was consistent with that seen in other studies (Boudry et al., 2002; Dégremont et al., 2007), which revealed a significant and strong genetic basis for survival in *C. gigas*. In this study, the culture management and field environment are the same to all full-sib families. The main factors responsible for survival variability in oysters are parent-related factors such as larval competitiveness quality of gametes, and viability. (Kong et al., 2015). The families with high survival will be selected for producing the next generation.

Hatchery and field mortality are the major problems affecting the production of *C. gigas* in China. Mortality events were usually

**TABLE 1** Description statistics of growth traits and survival in larvae and spat of *Crassostrea gigas*

Age	Traits	<i>n</i>	Replicate	Mean	Max	Min	SD	CV
4d	S (%)	49	3	89.86	98.00	75.00	6.00	6.68
4d	SH ( $\mu\text{m}$ )	49	30	89.37	108.95	72.03	7.34	8.21
4d	SL ( $\mu\text{m}$ )	49	30	90.84	112.39	71.81	7.38	8.12
20d	S (%)	49	3	23.51	58.00	3.00	11.15	47.42
20d	SH ( $\mu\text{m}$ )	49	30	203.22	269.48	137.36	22.93	11.28
20d	SL ( $\mu\text{m}$ )	49	30	167.35	246.52	120.04	26.54	15.86
140d	S (%)	49	3	62.27	90.00	25.00	17.00	27.30
140d	SH (mm)	49	30	25.23	43.62	13.35	5.81	23.03
140d	SL (mm)	49	30	19.16	34.94	10.15	4.71	24.58

Note: The *n* is the number of families. The Mean is the mean among families, and Max is the best individual across all families and Min is the worst individual across all families.

Abbreviations: d, day age; S, survival; SH, shell height; SL, shell length.

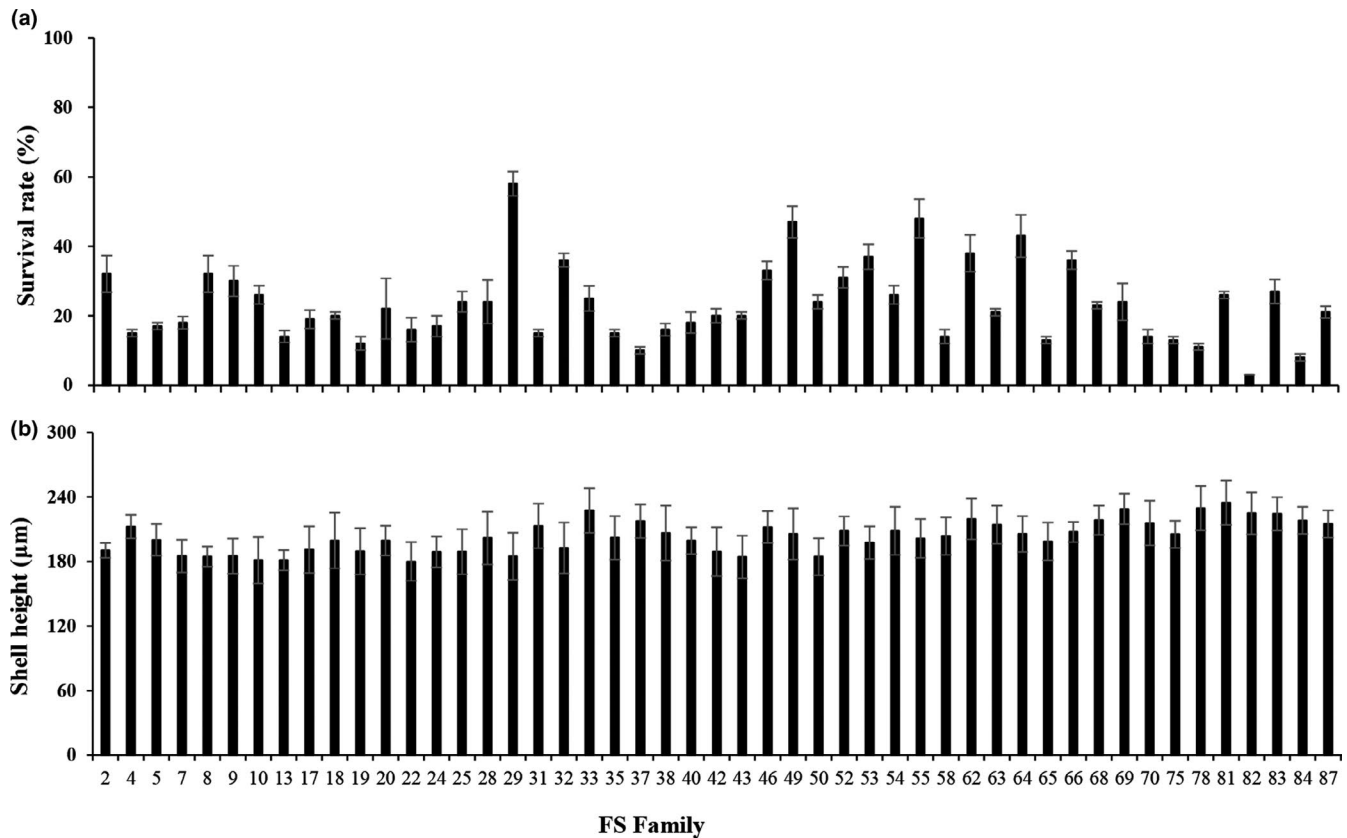


FIGURE 1 Survival rate (a) and shell height (b) of each full-sib family in larvae (20 days after fertilization) of *Crassostrea gigas*

observed in spat stage during summer and often causing high economic losses. Mortalities cannot be explained by a single factor but the results of the combination of environment and oyster (Dégremont et al., 2005). Considering environmental influences, high temperature is one of the importance factors associated with summer mortality, because spawning usually occurs during the summer, the seawater temperature favours the pathogens. Larvae stage has crucial importance for the production of commercial hatcheries in terms of the regularity of spat production throughout the whole year. Many pathogens induce larval mortality in *C. gigas*, such as *Vibrio coralliilyticus*, *V. tubiashii* or OsHV-1 (Dégremont et al., 2016; Richards et al., 2015). The causes of mass mortality in farms worldwide have been mainly attributed to a specific variant of the *Ostreid herpesvirus* in recent times (Divilov et al., 2019). Some major pathogens also reportedly induce mortality in pacific oysters of spat stage, such as OsHV-1 and *Vibrio aestuarianus* (Azéma et al., 2017).

#### 4.1 | Heritability for growth traits and survival

Heritability is an important genetic parameter for a selective program. It allows inferring the potential selection response for a specific trait in a population. Generally, it can be classified in to three levels: lower ( $h^2 \leq 0.30$ ), medium ( $0.30 < h^2 < 0.50$ ) and higher heritability ( $h^2 \geq 0.50$ ) (Falconer & Mackay, 1996). The heritability

estimates for growth trait were medium to high (0.30–0.86) in larvae and spat. These results indicated that the crosses between the two fast-growing lines still had the potential for genetic improvement by selection. Many previous studies have also found moderate-to-high estimates for growth traits in different mollusks species. In *C. gigas*, the heritability of individual average weight was 0.72–0.88 in two different locations (De Melo et al., 2019). In *C. virginica*, the heritability of growth traits was 0.51–0.60 in larvae stage (Newkirk et al., 1977). In *Mytilus edulis*, the heritability of growth was 0.2–0.8 in larvae and juvenile (Strömgen & Nielsen, 1989). In *Argopecten nucleus*, the heritability of SL was 0.31–0.69 in larvae and post-larvae (Barros et al., 2018). Some of the factors that can affect heritability estimations at different ages are the maternal effects and those of common environment (Gjedrem & Baranski, 2009). However, random effects common to each full-sib family (maternal effects and the common environment effects) included in this study were not significant. Therefore, the impact of maternal and common environment effects on the heritability estimations is negligible.

Survival is trait highly related to individual fitness, and such traits usually have low heritabilities than growth traits (Mousseau & Roff, 1987). Only a few studies provide estimates of heritability for survival in *C. gigas*. Dégremont et al. (2007) reported narrow-sense heritability, ranging from 0.47 to 1.08, for survival at 6–8 months in three different locations. Ernande et al. (2004) analysed the heritability for survival at 18-month-old was 0.16–0.43 tested in either controlled or field conditions. Evans and Langdon (2006) found the

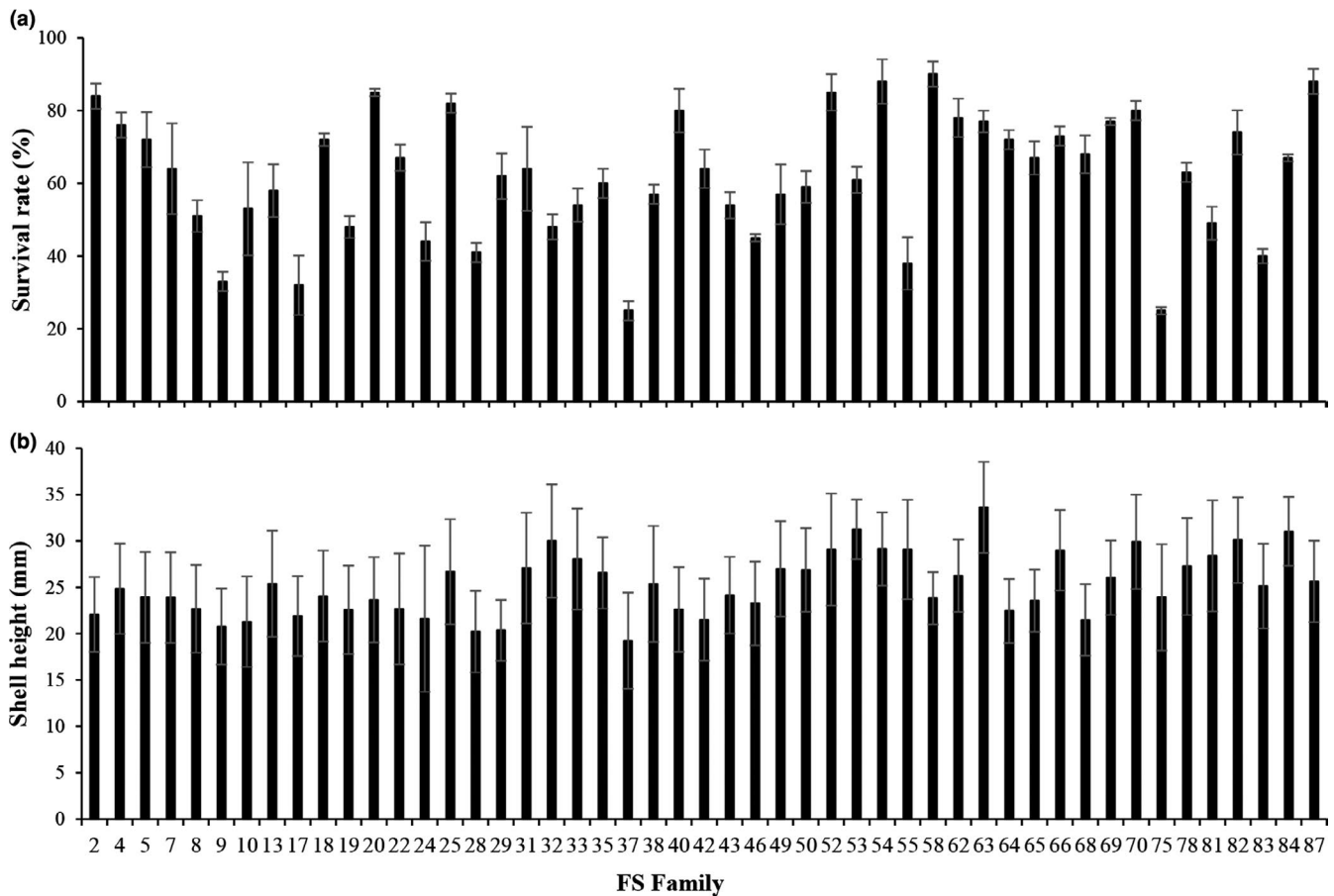


FIGURE 2 Survival rate (a) and shell height (b) of each full-sib family in Spat (140 days after fertilization) of *Crassostrea gigas*

TABLE 2 Variance components and heritability estimates for traits in larvae and spat of *Crassostrea gigas*

Age	Traits	Additive variance	Residual variance	Heritability
4d	S (%)	0.116	3.289	0.13 ± 0.05*
4d	SH (μm)	15.947	37.073	0.30 ± 0.06**
4d	SL (μm)	21.488	33.178	0.39 ± 0.08**
20d	S (%)	0.151	3.289	0.17 ± 0.04**
20d	SH (μm)	408.346	119.363	0.77 ± 0.10**
20d	SL (μm)	211.650	35.858	0.86 ± 0.11**
140d	S (%)	0.404	3.289	0.39 ± 0.07**
140d	SH (mm)	19.791	13.539	0.59 ± 0.10**
140d	SL (mm)	11.494	10.315	0.53 ± 0.09**

Note: Values after the plus/minus are standard errors.

Abbreviations: d, day age; S, survival; SH, shell height; SL, shell length.

Significance: \*  $p < .05$ , \*\*  $p < .01$ .

heritability of survival was 0.36–0.71 in 34 full-sib families. De Melo et al. (2018) found the heritability of survival was higher ( $0.45 \pm 0.02$ ) in intertidal than in subtidal environments ( $0.31 \pm 0.02$ ). In this study, we found that heritabilities for survival were low (0.13–0.17) in larvae, suggesting a low potential for improving survival in larvae by

direct selection. In addition, the heritability estimates for survival were medium (0.39) in spat, demonstrating quite a good potential for selection.

## 4.2 | Genetic and phenotypic correlations

Estimate of genetic correlations between two traits is a common method to select the target traits. The genetic correlations between growth traits have been widely reported. In *Pinctada fuctua*, Liu et al. (2017) reported that genetic correlation between shell width and body weight was positive and high (0.883). In *C. gigas*, Wang et al. (2012) identified positive and high (0.76) genetic correlation between SH and SL. In our study, the genetic and phenotypic correlations between SH and SL among different life stages were medium to high (0.466–0.964) and positive, which are consistent with previous reports. This result suggested that SH and SL may be controlled by the same set of genes, SL can be improved when selecting SH. The high genetic correlations estimated between traits allow inferring a high potential of correlated response to selection for productive traits in *C. gigas*.

It is important to understand the genetic correlation of important economic traits that would result from selecting at different ages in order to optimize the design of selection strategies in

**TABLE 3** Genetic correlations (below diagonal), phenotypic (above diagonal) correlations between growth traits and survival in larvae and spat of *Crassostrea gigas*

	SH <sub>4d</sub>	SL <sub>4d</sub>	SH <sub>20d</sub>	SL <sub>20d</sub>	SH <sub>140d</sub>	SL <sub>140d</sub>	S <sub>4d</sub>	S <sub>20d</sub>	S <sub>140d</sub>
SH <sub>4d</sub>	–	0.162**	0.118**	0.074	0.064	0.067	–0.021	0.084	–0.020
SL <sub>4d</sub>	0.742**	–	0.092	NE	0.048	0.050	–0.033	0.065	–0.099
SH <sub>20d</sub>	0.437**	0.275	–	0.205**	0.106*	0.125*	0.031	–0.151	0.142
SL <sub>20d</sub>	0.348**	NE	0.466**	–	0.146**	0.130**	0.010	0.083	0.255
SH <sub>140d</sub>	0.294*	0.103	0.342*	0.404**	–	0.728**	0.171	0.012	0.316*
SL <sub>140d</sub>	0.374*	0.151	0.407**	0.456**	0.964**	–	0.182	0.006	0.351*
S <sub>4d</sub>	–0.043	–0.057	–0.011	0.056	0.190	0.192	–	0.191	0.195
S <sub>20d</sub>	0.029	–0.029	–0.210	–0.145	–0.038	–0.049	0.194	–	–0.046
S <sub>140d</sub>	–0.090	–0.145	0.121	–0.029	0.231	0.273	0.289*	–0.145	–

Abbreviations: d, day age; NE, not estimate; S, survival; SH, shell height; SL, shell length.

Significance: \* $p < .05$ , \*\* $p < .01$ .

breeding programmes (Kenway et al., 2006). Genetic correlations of the same trait under different environmental conditions or different developmental stages maybe exist large difference. Some previous reports had discussed the genetic correlation of oysters between different growth stages. In *C. gigas*, Ernande et al. (2003) found significant correlations of SL between post-larvae and spat, but did not find significant genetic correlations between larvae and spat. In *O. edulis*, Newkirk and Haley (1982) reported a significant but negative genetic correlations of SL between larvae and spat. In the present study, the genetic correlations between growth traits at different growth stages were relatively low (0.151–0.456). In addition, the genetic correlations between survival traits at different growth stages were low (–0.145 to 0.289). This result suggests that selection to improve the growth and survival traits of *C. gigas* at the larval stage may not have large response in later growth-out stages. So we suggest that selection for growth and survival traits in *C. gigas* at an early age is not optimal and should not be undertaken until the later stages.

Survival and growth should be considered collectively in the breeding programme of oysters, and the genetic correlations between survival and growth traits were low in this study, indicating that genes controlling these two traits are most probably different and unlinked. The results essentially agreed with the Barros et al. (2018) and Dégremont et al. (2007), who studied genetic correlation between SH and survival of *A. nucleus* and genetic correlation between growth rate and survival of *C. gigas*, respectively. In this study, the genetic correlations between growth traits and survival at larvae were low and negative (–0.057 to –0.210). From a view of resource allocation theory point, the negative correlation between growth and survival would be expected, given that these are two competing resource-demanding mechanisms (Rauw et al., 1998). Negative correlations make it hard to improve both growth and survival traits through selection, which indicate that selection for survival in larvae stage is not the optimal selection strategy. On the contrary, the optimal stages to improve survival should be taken in spat stage, in which the genetic correlations are positive and the

heritability was medium. Selection for survival in spat is expected to have a positive effect in growth traits. Growth and survival can directly affect yield, and harvestable yield could therefore be improved by choosing survival as a primary character for selective breeding.

## 5 | CONCLUSION

Our study suggests that a broad genetic variance still remains in these selected lines and there is a potential for genetic improvement in growth-related traits through selective breeding. The presence of low to moderate heritabilities for survival indicates that selective breeding for these traits can be successfully applied in this species. It is feasible to improve the spat survival of *C. gigas* through genetic selection without affecting growth since the correlation between growth trait and survival was not antagonistic. This result provides supportive evidence for the continuity of the Pacific oyster selective breeding programme.

## ETHICS STATEMENT

The present study was performed according to the standard operation procedures (SOPs) of the Guide for the Use of Experimental Animals of the Ocean University of China. All animal care and use procedures were approved by the Institutional Animal Care and Use Committee of Ocean University of China.

## ACKNOWLEDGEMENTS

This work was supported by the grants from National Natural Science Foundation of China (31972789), Shandong Province (2017LZGC009), Weihai City (2018NS01), and the Ocean University of China-Auburn University Joint Research Center for Aquaculture and Environmental Science.

## CONFLICT OF INTEREST

None declared.

## AUTHOR CONTRIBUTION

Qi Li designed the study. Yong Chi, Lingfeng Kong and Shikai Liu performed the study. Yong Chi analysed the data and wrote the paper. All authors read and approved the final manuscript.

## DATA AVAILABILITY STATEMENT

The data used to support the findings of this study are available from the first author upon request.

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**How to cite this article:** Chi Y, Li Q, Liu S, Kong L. Genetic parameters of growth and survival in the Pacific oyster *Crassostrea gigas*. *Aquac Res* 2021;52:282–290. <https://doi.org/10.1111/are.14891>